Purple martin (*Progne subis*) movement ecology during three stages of the annual cycle

Kristen Marianne Lalla

Department of Natural Resource Sciences

Agricultural and Environmental Sciences

McGill University, Montréal

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To my grandparents

TABLE OF CONTENTS

ABSTRACT

Avian aerial insectivores are experiencing drastic declines in Canada. While there are likely multiple contributing causes of decline, the main driver or whether there is a main driver is unknown. The purple martin (*Progne subis*) is North America's largest swallow, breeding in North America from southern Canada to Mexico and overwintering in South America, primarily in Brazil. The purple martin is a colonial species; it roosts in large numbers and breeds in colonies using mainly artificial nest boxes. My thesis seeks to study important periods in the annual cycle of the purple martin to better understand its decline, especially the disproportionately strong decline in the northeast. Chapter 1 examines foraging behaviour of both breeding and wintering purple martins using GPS biologgers. Foraging range is much larger for overwintering birds compared to breeding birds as breeding birds are constrained by the need to feed their nestlings, and, during both periods of the annual cycle, purple martins select water-based habitats. Chapter 2 studies the breeding success of purple martins in southern Quebec and juvenile dispersal using radio telemetry. Reproductive success in Quebec is comparable to other parts of North America, and departure of fledglings from the colony is predicted by lay date as well as habitat characteristics. Conservation efforts for the purple martin, in addition to current efforts managing nest boxes for the species, should be focused on preserving wetland and open water habitats for this species, especially during the post-fledging period.

RESUMÉ

Les insectivores aériens sont en déclin au Canada. Il existe plusieurs causes possibles, mais l'importance de ces facteurs ainsi que le facteur principal de ce déclin est encore inconnu. L'hirondelle noire (*Progne subis*) est l'espèce d'hirondelle la plus grande en Amérique du Nord. Elle niche en Amérique du Nord, du sud du Canada au Mexique et hiverne en Amérique du Sud, principalement au Brésil. L'hirondelle noire est une espèce coloniale. Elle niche en grand nombre et utilise principalement des nichoirs artificiels. Ma thèse a pour but d'étudier les deux périodes importantes dans le cycle annuel de l'hirondelle noire pour mieux comprendre le déclin de cette espèce. Le premier chapitre examine le comportement d'alimentation chez les hirondelles noires pendant la reproduction et l'hivernage en utilisant des émetteurs GPS. La taille des aires d'alimentation est plus grande chez les hirondelles hivernant que chez les hirondelles en reproduction, car les hirondelles qui nourrissent leurs oisillons ont besoin de retourner au nid fréquemment. Les hirondelles noires sélectionnent des zones humides et des cours d'eau pour s'alimenter durant les deux périodes étudiées. Le deuxième chapitre se concentre sur le succès reproducteur des hirondelles noires et la dispersion juvénile en utilisant la radio-télémétrie au sud du Québec et de l'Ontario. Le succès reproducteur est comparable à d'autres régions d'Amérique du Nord et le départ des jeunes est prédit par la date de ponte et des caractéristiques de l'habitat. Les efforts de conservation pour l'hirondelle noire, en plus des efforts actuels de gestion des nichoirs artificiels, devraient être axés sur la préservation des habitats incluant des zones humides et des cours d'eau.

LIST OF TABLES

LIST OF FIGURES

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CONTRIBUTION TO ORIGINAL KNOWLEDGE

This thesis aims to address some of the research gaps in purple martin (*Progne subis*) movement ecology. Juvenile dispersal is generally understudied in birds, and this thesis aims to understand how long fledglings remain near the colony after fledging, and if habitat composition affects their decision to leave the colony area. Foraging behaviour, including foraging range and habitat selection, is also not well-studied in songbirds across the annual cycle. Recent developments in biologging technology, notably the miniaturization of biologgers, now allow for songbird tracking, opening new areas of research. Part of this thesis aims to quantify foraging habitat requirements and foraging habitat selection in purple martins using biologging.

CONTRIBUTION OF AUTHORS

I conceptualized this project with Kyle Elliott, Kevin Fraser, and Barbara Frei with input from Jeff Cardille and Mario Cohn-Haft. I planned data collection with input from Kyle Elliott, Barbara Frei, and Kevin Fraser. I collected radio-tracking and GPS data with the help of field assistants in Quebec. Additional radio-tracking data were obtained from Ontario collected by Saeedeh Bani-Assadi, and additional GPS tracks were obtained from Jason Fischer (Florida), Joe Siegrist (Pennsylvania), and James Ray (Texas). I carried out radio-tracking data analysis advised by Kyle Elliott, Saeedeh Bani Assadi, and Kevin Fraser. With coding assistance from Barbara Frei, I carried out GPS data analysis advised by Kyle Elliott, Barbara Frei, and Kevin Fraser. I wrote the thesis with advice and edits primarily from Kyle Elliott and Kevin Fraser. All co-authors reviewed the data chapters and provided feedback.

INTRODUCTION

Aerial insectivores, or animals foraging on insects while in flight, are declining across North America (Berzins et al. 2020; Nebel et al. 2020; North American Bird Conservation Initiative Canada 2019; Rosenberg et al. 2019). There are several factors thought to contribute to the decline, including habitat loss, climate change, and agricultural intensification, particularly the increased use of pesticides (Berzins et al. 2020; Nebel et al. 2010; Rosenberg et al. 2019). Swallows (Family Hirundinidae) are a taxon of aerial insectivores that include several species declining in Canada, with two formerly common swallow species now federally listed (barn swallow *Hirundo rustica*: Special Concern; bank swallow *riparia riparia*: Threatened; Berzins et al. 2020). Most *Progne* martins are listed as Least Concern on the IUCN Red List; however, some species are in decline (BirdLife International 2016a; 2016b; 2016c; 2016d; 2020a; 2020e). For example, the Sinaloa martin (*Progne sinaloe*) is listed as vulnerable but little is known about the species (BirdLife International 2020d), the Peruvian martin (*P. murphyi*) is near threatened due to threats from native species, disease, and pollution from agriculture and forestry (BirdLife International 2020c), and the Galapagos martin (*P. modesta*) is endangered due to threats from invasive species, disease, and climate change-induced droughts (BirdLife International 2020b). The purple martin (*Progne subis*) is the largest swallow in North America. Purple martins breed in parts of Canada, the United States, and Mexico and overwinter in South America (Brown et al. 2013; Fraser et al. 2017; Fraser et al. 2013). Purple martins are colonial, nesting in groups primarily in artificial nest boxes and roosting communally (Brown et al. 2013). This species is declining in some areas, especially in the northeastern part of its range (Pardieck et al. 2020; Sauer et al. 2017). Traditional purple martin conservation involves erecting and maintaining artificial nest boxes to make up for the loss of natural cavities (Doughty and Fergus 2002); however, the main driver of the purple martin decline is unknown, and other factors in their decline, such as pesticides, habitat loss and climate change, can occur across different parts in their annual cycle (Nebel et al. 2010).

The goal of this thesis is to study purple martin behaviour using biologging to better understand movement ecology of the purple martin, and, ultimately, the cause of purple martin population declines. Purple martins are known to nest in artificial nest boxes in open habitats, frequently near water (Brown et al. 2013), and roost in island-type habitats during migration (Fournier et al. 2019) and the over-wintering period (Fraser et al. 2017). After purple martin nestlings fledge and leave the nest, their behaviour is largely unknown. They are thought to stay around the nest for a few days before departing (Brown et al. 2013). In my first chapter, I aim to quantify fledging and dispersal using Very High Frequency (VHF) radio telemetry (Taylor et al. 2017). I estimated fledging date and departure date of fledglings in southern Quebec and Ontario and tested whether departure date is linked to habitat composition around the nest site. Like fledgling dispersal, foraging habitat requirements of adult birds are understudied. Recent advances in GPS technology, primarily the miniaturization of biologgers, now allow researchers to GPS-track medium-sized passerines at a fine scale that was not previously possible (Fraser et al. 2017). In my second chapter, I studied home range size and habitat selection of purple martins breeding in Quebec, Canada, and Texas and Florida, USA, and overwintering individuals in South America, primarily in Brazil. Foraging behaviour in purple martins, and songbirds in general, is not well studied across the annual cycle, and I aim to address some of the knowledge gaps. Central place foraging theory suggest that breeding purple martins will have smaller foraging ranges than non-breeding purple martins because they must feed their chicks frequently, while non-breeding individuals must only return to a central place, a roost, once per day. Understanding foraging habitat selection will allow for a better understanding of habitat requirements and can identify important habitats for conservation. By studying the purple martin at several periods across the annual cycle, my thesis will not only improve understanding of the movement ecology of neotropical migrants across the full annual cycle but will also contribute to evidence-based conservation focused on the periods of the annual cycle where population declines are suspected to originate.

LITERATURE REVIEW

Aerial insectivores

Aerial insectivores are a rapidly declining avian guild (Hallmann et al. 2017). They are experiencing the largest declines of any avian guild in Canada, likely due to reduced food supply (North American Bird Conservation Initiative Canada 2019). Globally, many insect populations have declined (Forister et al. 2019; Hallmann et al. 2017; Janzen and Hallwachs 2019; Sánchez-Bayo and Wyckhuys 2019; van Grunsven et al. 2020; Wagner et al. 2021). Insect declines are linked to several causes, including pesticide use associated with agricultural intensification, climate change, pollution, habitat loss, invasive species, and artificial light at night (Nocera et al. 2012; van Grunsven et al. 2020; Wagner et al. 2021). In addition to a reduced food supply, aerial insectivores may also be affected by habitat loss, reducing critical habitats in various stages of the annual cycle (Nebel et al. 2010). For example, tree swallows (*Tachycineta bicolor*) breeding in intensive agriculture had lower return rates than grassland-breeding tree swallows, likely due to lower prey availability in areas of intensive agriculture (Stanton et al. 2017). Apart from habitat loss potentially leading to reduced food supply, habitat loss may also reduce protection from predators or loss of suitable roosts. Climate change can amplify any impact of reduced food supply by leading to a mismatch between insect peak abundance and insectivore peak requirements, potentially leading to reduced reproductive success or starvation (Nebel et al. 2010). Some species may be more affected by climate change than others; barn swallows and tree swallows in eastern Canada advanced their lay dates in response to warmer spring temperatures while bank swallows (*Riparia riparia*) have not advanced their lay dates and are declining more drastically, likely due to phenological mismatches (Imlay et al. 2018). Cavity nesters face increased competition for nest sites with invasive species (Nebel et al. 2010). Furthermore, exposure to artificial light at night can alter a bird's perceived photoperiod and therefore can change the timing of key life events in the annual cycle, such as migration, that can lead to phenological mismatches (Smith et al. 2021). Certain species of aerial insectivores that forage close to the ground are likely to be killed by cars and other road vehicles (Mead 1979). Aerial insectivore populations in northeastern North America are declining more drastically than in other parts of North America (Nebel et al. 2010). In addition, long-distance migrants are more affected than short-distance migrants, and different factors can affect their decline in different parts of their range (Nebel et al. 2010).

Conservation: Importance of studying the full annual cycle

Studying the full annual cycle is important in the conservation of declining species. A species may be impacted by different factors at different stages in the annual cycle, especially for migratory species that use a variety of habitats throughout the year. Carryover effects may result from stressors at a given point in the annual cycle that impact other points in the annual cycle (Imlay et al. 2019). Therefore, conservation strategies encompassing an entire species' year-round distribution are important and may require collaboration among different countries. Carryover effects are important to consider when studying various components of the annual cycle. Carryover effects occur when individuals experience stress during one part of the annual cycle, such as breeding, and effects are felt throughout other parts of the annual cycle, for example, post-breeding moult. One study found carryover effects in three species of swallows from the non-breeding period into the breeding period. For instance, overwintering habitat of male bank swallows was linked to nestling survival (Imlay et al. 2019). Breeding tree swallows had higher levels of oxidative stress in areas with lower insect biomass, which was correlated with lower interannual survival (Stanton et al. 2017). Most studies focus only on the breeding period, yet other periods of the annual cycle may be equally important. For example, juvenile dispersal is an often-understudied aspect of the life cycle of many species. Tree swallows are likely limited by juvenile survival and recruitment (Berzins et al. 2020; Cox et al. 2018; Taylor et al. 2018; Weegman et al. 2017). Barn swallow (*Hirundo rustica*) fledglings have lower survival and are more likely to use cropland habitat than older birds (Boynton et al. 2020). Thus, the post-fledging period might be a critical period in the annual cycle of swallows.

Understanding the requirements of species during different periods of the annual cycle is essential for effective conservation planning, such as the resources, habitats, and space needed to survive and reproduce during the different periods. Studying species distributions allows researchers to understand the space requirements for individuals of a given species, and how those range requirements may change in response to environmental changes (Wilson et al. 2019). For example, overwintering ovenbirds were found to have home ranges of 0.50 ± 0.15 hectares and used primarily cropland and natural mosaic habitat as well as forests (Hallworth and Marra 2015). Quantifying home range or foraging range throughout the annual cycle allows for researchers to better understand space requirements at different life stages. Resource selection functions compare habitats used, or selected, by an individual compared to available habitats. Understanding resource or habitat selection of declining species is useful to identify essential habitats to conserve or manage. For example, one study found that wetlands were important habitats for a wide variety of birds in the UK, but different assemblages of birds preferred different habitat compositions, suggesting that a variety of management practises are needed for conservating bird biodiversity (Fuller et al. 2005). Breeding European nightjars (*Caprimulgus europaeus*) selected oak scrub habitat, a habitat declining in the Alps, highlighting the need to preserve that habitat (Sierro et al. 2001). Habitat selection by eastern whip-poor-wills' (*Antrostomus vociferus*) differs throughout the annual cycle, selecting forests in winter and open habitats during breeding (Tonra et al. 2019). Therefore, understanding habitat selection in different parts of the annual cycle is important for understanding species' declines and planning conservation measures.

Movement ecology: Using biologging to study behaviour

For vertebrates, movement is an essential part of life, necessary for foraging, migration, predator evasion, and many other activities (Nathan et al. 2008). Wildlife tracking through the use of biologging allows for the study of animal behaviour, such as migration, habitat use, predator-prey interactions, and occurrence, and is especially useful for animals where it is difficult to make direct observations (Sampson and Delgiudice 2006; Wilmers et al. 2015). Biologging allows for quantification of movement using sensors (Nathan et al. 2008; Wilmers et al. 2015). Some biologgers collect environmental data in addition to location data, providing further context (Wilmers et al. 2015). Animal migration was not a widely understood phenomenon in some human societies until few hundred years ago; before then, people observed that birds disappeared at certain times of the year and came up with different explanations. Indeed, Aristotle believed that birds changed into different species because some disappeared for the winter while others appeared, such as redstarts changing into European robins. Some people believed that swallows hibernated in mud for the winter (The Royal Society for the Protection of Birds n.d.). Recently, biologging work has been done on the migration patterns of birds using geolocators (Jacobsen et al. 2017), foraging behaviour of black-legged kittiwakes (*Rissa tridactyla*) using GPS loggers (Kotzerka et al. 2010), using biologgers to quantify muscle condition (Lalla et al. 2020), determining kill sites of large mammals such as jaguars (*Panthera onca*) in South America using GPS collars (Gese et al. 2016), and measuring home ranges of American Oystercatchers (*Haematopus palliatus*) in their breeding grounds using satellite tags and radio telemetry (Loring et al. 2017). Therefore, biologging has a wide array of implications in wildlife research, and there are many types of units that can be used for different study objectives.

There are several types of biologgers. Global Positioning System (GPS) units are advantageous because of their high accuracy, typically 10 m; however, many types of GPS units require the animal to be recaptured to obtain the data, and lightweight units suitable for small animals have the disadvantage of a low number of possible fixes due to the smaller battery size (Bridge et al. 2011). Satellite or cellular-transmitting GPS tags can transmit the data to a server, and thus do not require recapture. However, they are larger and more expensive (Loring et al. 2017; Ponchon et al. 2013). Global light sensing units, or geolocators, use the timing of light levels to allow for the estimation of an animal's position, have the advantage of being low-cost, lightweight, and have a long battery life, but they require recapture and have low spatial accuracy, especially at high latitudes where it can be impossible to estimate location (Ponchon et al. 2013). Accelerometers measure acceleration in the x, y, and z axes and allow for the analysis of fine scale behaviour, and can be especially powerful when combined with other types of biologgers, such as GPS loggers (Collins et al. 2020; Collins et al. 2015; Collins et al. 2016; Elliott et al. 2013; Lalla et al. 2020; Patterson et al. 2019). However, they usually require recapture if raw data is recorded at high sampling frequency. Radio, or very high frequency (VHF) telemetry nanotags, have the advantage of being extremely small and lightweight and are thus suitable for small animals, and do not require recapture to obtain data. However, nanotags require receivers to detect tags, which can be costly, and detections can only occur where receivers are placed (Bridge et al. 2011). Receivers can be stationary or mobile and allow the user to obtain a signal strength and direction of the tagged animal whose location can be estimated using triangulation (Camacho et al. 2014; Taylor et al. 2017). Improvements have been made to biologgers in recent years. Smaller models with longer battery life, often using solar panel technology, allow researchers to study the behaviour of species that were previously too small to be outfitted with a biologgers (Fraser et al. 2017; Taylor et al. 2017). Though not a typical form of wildlife tracking, weather radar can be used to track bird migration or locate swallow roosts. Migrating birds can be picked up on weather radar and travel in the direction of migration (Gauthreaux 1996). Swallows tend to leave their roosts in coordinated movements in the early morning, approximately 30 minutes before sunrise, resulting in localized concentric circle patterns in weather radar (Bridge et al. 2016; Russell et al. 1998). Thus, there are many types of biologgers, as well as remote recording via weather radar, each with a set of tradeoffs, and the biologger type selected should reflect the needs of a given project (Ponchon et al. 2013).

Biologging has implications for conservation. Biologging studies identify migratory routes (Fournier et al. 2019; Stutchbury et al. 2016b), foraging behaviour (Elliott et al. 2009; Patterson et al. 2019), breeding behaviour (Collins et al. 2016), habitat preference (Sierro et al. 2001; Tonra et al. 2019), and more, providing data that are useful to assessing at-risk species. Multiple studies make links to conservation, intending their data to have conservation implications. Many species status reports (COSEWIC, IUCN Red List, etc.) and recovery plans make use of these studies, suggesting they do actually contribute to conservation (Fraser et al. 2018). For example, in British Columbia, individuals of the Haida Gwaii subspecies of the northern saw-whet owl (*Aegolius acadicus brooksi*) were tracked to determine home range and habitat use. The owls use four habitat types: open habitat and three forest types, but do not roost in open habitat (Waterhouse et al. 2017). This study was used in the 2017 Committee on the Status of Endangered Wildlife in Canada (COSEWIC) report on the *brooksi* subspecies, in part assisting in recommendation of the subspecies as Threatened (COSEWIC 2017).

Purple martin life history and previous research

The purple martin (*Progne subis*) is a colonial aerial insectivore ranging in its breeding grounds from southern Canada to Florida (USA) to Mexico. The eastern subspecies (*P. subis subis*) overwinters in South America (Brown et al. 2013). Three subspecies are known: eastern that breeds in mainly in artificial nest boxes and therefore is commonly found in developed areas, northwestern (*P. s. arboricola*) that breeds primarily in natural cavities, mainly in dead trees near intermediate successional habitat, and southwestern (*P. s. hesperia*) that breed in cavities in cacti (Baker et al. 2008; Bridge et al. 2016; Sherman and Hagar 2021). Purple martins are long-distance neotropical migrants, breeding in North America and wintering in Brazil (Fraser et al. 2013; Stutchbury et al. 2016a; Stutchbury et al. 2016b; Stutchbury et al. 2009b). Purple martins migrate northward in spring, typically from February to May (Arab et al. 2016). Males arrive at their breeding grounds earlier than females, and older males arrive earlier than younger males (Arab et al. 2016; Wagner et al. 1996). Males arrive early to obtain nest sites at colonies, and later pair with females. Interannual site fidelity is high (Stutchbury et al. 2016a). Birds breeding at the northern limit of their range spend 13% less time in their breeding grounds than southern-breeding individuals (Neufeld et al. 2021). Purple martins are socially monogamous, but extra-pair fertilizations, polygamy, and divorce are known (Brown 1975; Stutchbury et al. 2016a; Wagner et al. 1996). Both males and females defend multiple cavities (Stutchbury 1991). Females are usually responsible for nest-building (Brown 1975), and use mud, grass, and small sticks (Brown 1978). Purple martins are single-brooded, laying an average of 4 to 5 eggs in a clutch (Bent 1963; Brown et al. 2013). Incubation is typically 15 to 18 days and is carried out mainly by the female (Brown et al. 2013). The young are fed by both parents and fledge around 28 days old. After they fledge, they are guided to a location away from the colony and are fed by their parents for up to a week (Brown et al. 2013). Parents feed their chicks a variety of insects across a variety of orders, including Hymenoptera (ants, bees, wasps), Coleoptera (beetles), Diptera (true flies), Odonata (dragonflies and damselflies), Lepidoptera (butterflies and moths), Hemiptera (true bugs), and Ephemeroptera (mayflies) (Forsman et al. submitted; Helms et al. 2016; Sherman 2019).

After breeding, purple martins form post-breeding roosts that can comprise hundreds of birds. Many post-breeding roost sites in North America are found in cropland. While roosts are most common in cropland, purple martins prefer urban sites, suggested by their interannual persistence (Bridge et al. 2016). However, in a study of migratory roosts between North and South America, mainly in Central America, purple martins primarily use forest “islands” as roosts (Fournier et al. 2019). During fall migration, purple martins average 450 km/day for the first 2000 km, then slow down, with longer stopovers. The route that individuals take is determined by their breeding longitude. For instance, eastern breeding populations migrate south through Florida, then pass through Cuba as they cross the Gulf of Mexico for Central America (Fraser et al. 2013). Individuals breeding further north depart later for both spring and fall migration (Neufeld et al. 2021). Interestingly, and unlike previously thought, many migrating purple martins cross the Gulf of Mexico and the Caribbean Sea at night (Lavallée et al. 2021). Stopover duration is largely affected by breeding latitude, with more northern breeders having longer stopovers (Van Loon et al. 2017). In their wintering grounds in the Amazon, purple martins form roosts. These roosts are typically island-type habitats or actual islands rather than continuous forests, and are close to bodies of water (Fraser et al. 2017). Birds from a given breeding ground mix with birds from other breeding sites within roosts. In addition, individuals move across roosts within their wintering grounds, referred to as intratropical migration (Fraser et al. 2012; Stutchbury et al. 2016b).

Purple martins are relatively long-lived for swallows, and therefore may make migration decisions based on prioritizing subsequent survival over current reproduction. Generation time is approximately 3.3 years (Baker et al. 2008). Young birds have the lowest survival, estimated at 0.27 for males and females combined (Tarof et al. 2011). Except for 2-4-year-olds, males have higher survival than females (Table 1). This is likely due to higher reproductive costs in females, as well as higher reproductive risk, such as predation. In addition, birds older than five years have lower survival than their younger counterparts, likely demonstrating senescence (Stutchbury et al. 2009a).

Table 1. Survival of purple martins across age groups. Adapted from Stutchbury et al. 2009, Tarof et al. 2011.

Age	Female	Male
Hatch year	0.27*	
1 year	0.48	0.59
2-4 years	0.64	0.62
≥ 5 years	0.51	0.52

*Note: hatch-year sex can only be determined using DNA analysis

Purple martin trends and conservation

Purple martins have declined by 30% in North America and 60% in Canada from 1970 to 2014, but in Canada show a population stabilization in recent years. In the province of Quebec, Canada, specifically, the population has declined by 94% over the same period and does not show signs of stabilization (Bédard 2016, Sauer et al. 2017, Figure 1). As of 2021, the purple martin has not been assessed by the Committee on the Status of Endangered Wildlife (COSEWIC) to determine if the species should be listed as a species-at-risk in Canada (Bédard 2016).

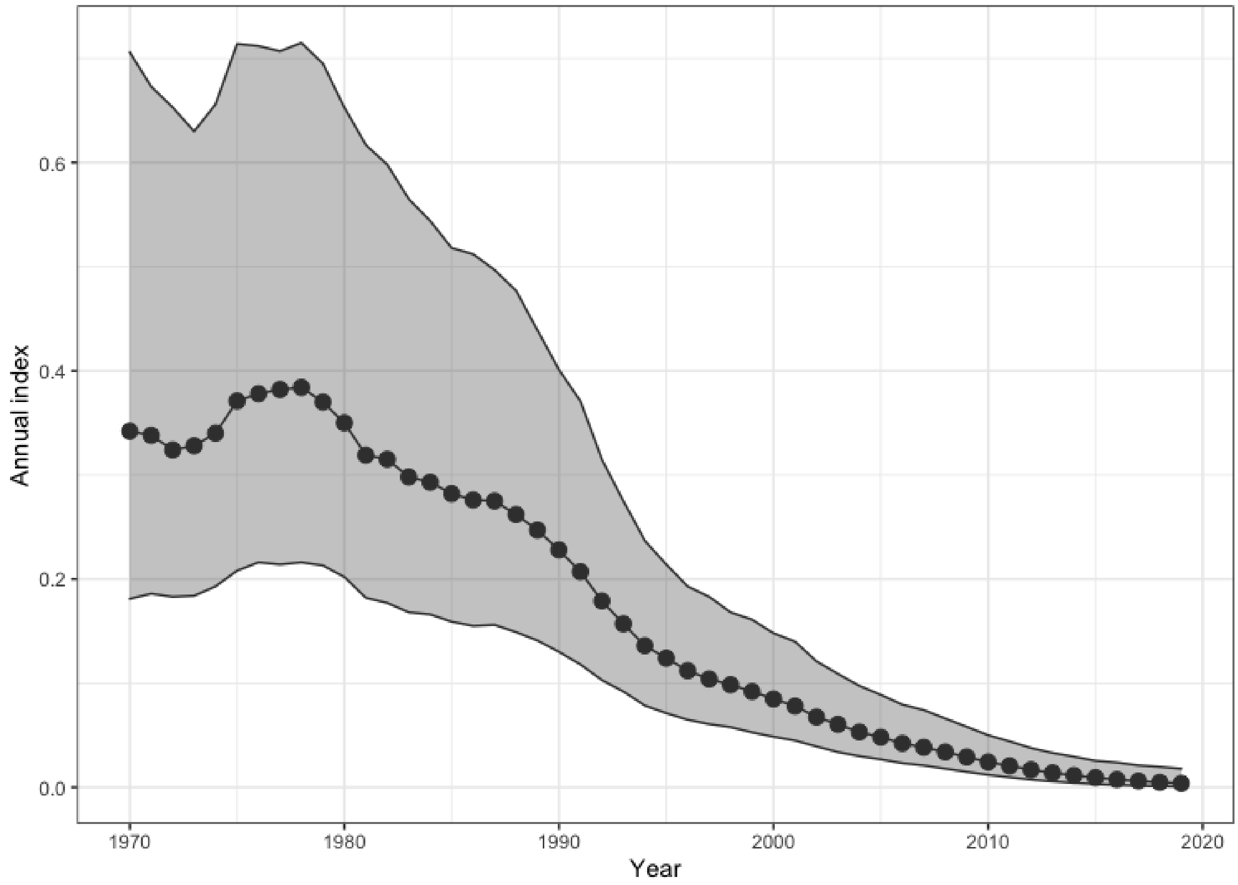

Figure 1. Purple martin population annual index of abundance in Quebec from 1970 to 2019 from the Breeding Bird Survey (Smith et al. 2020).

Initiatives to increase purple martin populations occurred before European settlement in North America. Indigenous peoples hollowed out gourds and placed them on poles to encourage purple martins to nest by their fields (Doughty and Fergus 2002). European colonizers recognized the willingness of purple martins to nest near humans, and many installed nest boxes to encourage this practise. The practise of installing and maintaining nest boxes for purple martins continues today (Doughty and Fergus 2002), and managed housing is important for their persistence due to the lack of natural cavities, especially for the eastern subspecies (Cousens and Lee 2012; Fraser et al. 1999; Raleigh et al. 2019). Some purple martin landlords have gone as far as to purchase live crickets to feed purple martins when the weather is unfavourable (Doughty and Fergus 2002).

Factors affecting survival

Like other aerial insectivores, the main cause of the purple martin's decline is uncertain and may be due to several contributing factors. Long-distance migrants such as the purple martin are declining more strongly than many short-distance migrants (Nebel et al. 2010). A reduction in insect populations via the use of pesticides may be a contributing factor in the purple martin's decline (Nocera et al. 2012; Wagner et al. 2021). Like other aerial insectivores, purple martin populations in northeastern North America are declining more drastically than in other parts of their range. Nest box competition is another potential factor. Purple martins compete with European starlings (*Sternus vulgaris*) and house sparrows (*Passer domesticus*) for breeding compartments (Bédard 2016). Furthermore, many artificial nest boxes are not maintained and become unsuitable for breeding (pers. obs.). Purple martins can also be affected by blood parasites, for example, *Haemoproteus prognei*, a haematozoan, and filarial nematodes (phylum Nematoda). Individuals can persist with one type of blood parasite, but individuals possessing two types of blood parasites are likely to die (Davidar and Morton 2006). Younger birds are less robust to parasites, and are more likely to die than older individuals (Davidar and Morton 2006). In their wintering grounds in Brazil, habitat loss due to land conversion, especially at key roosting sites, may negatively impact purple martins (Fraser et al. 2017; Stutchbury et al. 2016b). Since purple martins are panmictic in winter, changing roost sites regularly, one breeding population is likely not affected more than another by habitat loss in Brazil (Fraser et al. 2017; Stutchbury et al. 2016b).

Climate change has been proposed as a threat to purple martins, creating a phenological mismatch. Purple martins do not appear to alter their timing of migration in response to winter temperature or the North Atlantic Oscillation (Arab et al. 2016). Purple martins likely respond to insect abundances once they arrive in North America, tracking insect abundances north (Arab et al. 2016). Thus, though climate change may advance the peak in insect abundance, martins are unlikely to be aware of these changes or able to quickly respond to such advances, potentially causing a mismatch in phenology (Arab et al. 2016).

The northeastern breeding population of purple martins is declining more rapidly than southern and western populations. One hypothesis that has been posed to explain this pattern is a higher prevalence of acid rain in the northeastern areas of the range that affects insect populations (Fraser et al. 2012; Nebel et al. 2010). In addition, purple martins can die of starvation in cold periods because of reduced insect availability, or even die from hypothermia, making northern breeding populations more at risk of decline due to weather fluctuations (Mayfield 1969). Northern birds spend less time at their breeding sites than southern ones, suggesting that birds could be more strongly affected by phenological mismatches (Neufeld et al. 2021). Studying purple martins in the northeastern portion of their range is therefore important to better understand their drastic decline.

In sum, purple martins are a declining aerial insectivore that nests in artificial nest boxes, making them an ideal species to study (Raleigh et al. 2019). While causes of decline have been identified, namely agricultural intensification, habitat loss, and climate change, the main driver is unknown (Nocera et al. 2012). A knowledge gap exists in juvenile dispersal and foraging behaviour in purple martins, and new technologies have opened new possibilities for research. Studying purple martins in an area of strong decline such as Quebec can help in identifying areas in the annual cycle of concern and identifying important habitats for this species.

NOTE ON CHAPTER 1

This chapter corresponds to a manuscript with the same title in which I am first author. This manuscript will be submitted to *Biology Letters*. Mario Cohn-Haft (Instituto Nacional de Pesquisas da Amazonia), Kyle Elliott (McGill University), Jason Fischer (Disney Animals, Science and Environment), Kevin Fraser (University of Manitoba), Barbara Frei (Canadian Wildlife Service), James Ray (Consolidated Nuclear Security, LLC, U.S. Department of Energy-National Nuclear Security Administration Pantex Plant), and Joe Siegrist (Purple Martin Conservation Association) are co-authors. J.F., J.R., and J.S. provided data outside of Quebec. This chapter uses GPS data to quantify foraging range and habitat selection in chick-rearing and overwintering purple martins.

A female purple martin with a GPS biologger

CHAPTER 1: Central place foraging poses variable constraints year-round in a neotropical migrant

Kristen M. Lalla[1]
Kevin C. Fraser[2]
Barbara Frei[3,4]
Jason D. Fischer[5]
Joe Siegrist[6]
James D. Ray[7]
Mario Cohn-Haft[8]
Kyle H. Elliott[1]

[1] Department of Natural Resource Sciences, McGill University, Canada
[2] Department of Biological Sciences, University of Manitoba, Canada
[3] Canadian Wildlife Service, Environment and Climate Change Canada, Canada
[4] Migration Research Foundation, Inc., Canada
[5] Disney Animals, Science and Environment, USA
[6] Purple Martin Conservation Association, USA
[7] Consolidated Nuclear Security, LLC, U.S. Department of Energy-National Nuclear Security Administration Pantex Plant, Amarillo, TX 79120, USA
[8] Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil

Abstract

Central-place foragers are constrained in their habitat selection and foraging range by the frequency that they need to return to a central place. For example, chick-rearing songbirds that must feed their offspring hourly might be expected to have smaller foraging ranges and be less selective of habitat compared to non-breeding songbirds that return nightly to a roost. To test this idea, we used GPS units to compare the foraging behaviour of an aerial insectivore bird, the purple martin (*Progne subis*), during the breeding season in three regions across North America, as well as the non-breeding season in South America. Foraging range (14.0 ± 39.2 km^2) during breeding did not vary among regions and was far smaller than during the nonbreeding period (8840 ± 8150 km^2). Purple martins strongly preferred aquatic habitats to other available habitats year-round and commuted from night roosts in low productivity black water with lower predation risk to purple martins to daytime foraging sites in productive white water in the Amazon. Understanding foraging constraints and habitat of aerial insectivores may help plan conservation throughout their annual cycle.

Keywords

Aerial insectivore, biologging, foraging, habitat selection, home range, songbird

Introduction

Many animals return to a central place when foraging, such as a roost, nest or perch (Orians and Pearson 1979). For central-place foragers, foraging time includes transit time to and from the central place in addition to searching and handling time, and 'optimal' foragers are expected to select nearby foraging patches and travel along the most direct path to and from the central place (Orians and Pearson 1979; Ydenberg et al. 1994). Distant foraging patches will be used only if net energy gain is higher than at nearby patches (Houston and McNamara 1985; Kacelnik and Cuthill 1990; Waite and Ydenberg 1996; Weimerskirch et al. 2003). The frequency at which the central place is visited will determine the average foraging range and, consequently, habitat selectivity necessary to optimize energy gain (Kacelnik 1984). Within a species, individuals that must return frequently to a nest would be expected to have smaller foraging ranges and be less selective than individuals that only need to return to a roost at night.

Foraging behaviour of migratory birds varies throughout the year as they use different environments during different parts of their annual cycle: breeding, migratory stopovers, and wintering. Northern saw-whet owl (*Aegolius acadius*) males have larger home ranges in winter compared to spring and overlap with other individuals only during winter (Waterhouse et al. 2017). Eastern whip-poor-wills' (*Antrostomus vociferus*) habitat selection differs throughout the annual cycle; they select forests in winter and open habitats during breeding (Tonra et al. 2019). Other aerial insectivores, such as swallows that often roost in large congregations, must be able to adjust their foraging behaviour to environmental variation throughout the annual cycle, including variation in the central place. Many aerial insectivores nest in small colonies during the breeding season and roost in large groups during winter, creating the potential for both intraspecific competition and central place foraging (Brown et al. 2013; Saldanha 2016; Saldanha et al. 2019).

As swallows must feed their offspring many times per day but only return to a roost once per day outside of breeding, foraging range may be much larger during the non-breeding than breeding season and, consequently, swallows can be more selective of habitat during the non-breeding season. Recent miniaturization of GPS biologgers allows researchers to track large swallows year-round to answer these questions (Fournier et al. 2019; Fraser et al. 2017).

We used the purple martin (*Progne subis*) as a model species for colonial aerial insectivores, as they are one of the largest swallows and can therefore be tracked year-round. Purple martins breed in North America and winter in in South America, where individuals from many breeding sites mix with birds from other breeding sites in enormous roosts, some with over ten thousand purple martins (Fraser et al. 2017; Fraser et al. 2013; Hill 1993; Stutchbury et al. 2016b). Similar to other aerial insectivores, purple martins have declined by 30% in North America over the last 5 decades (Sauer et al. 2017). Purple martins feed on flying insects, some of which are commonly observed near water, such as dragonflies (Helms et al. 2016). Purple martins roost colonially during the non-breeding season (Fournier et al. 2019; Fraser et al. 2017) in island-type habitats close to bodies of water and, in the Amazon basin, in flooded forest near streams, rivers, and other wetlands (Barbosa in prep.; Fraser et al. 2017). While roosting and nesting habitat in purple martins is well described, foraging habitat has not been well studied.

We deployed GPS units on adult purple martins to collect data during chick-rearing and the over-wintering period to examine habitat selection and foraging range, providing the first year-round, fine-scale information on the foraging behaviour of a small neotropical migrant. We hypothesized purple martins would be constrained year-round by central place foraging and predicted that (1) foraging range will be smaller and habitat selectivity weaker in chick-rearing than overwintering birds and (2) purple martins select resources in water-based habitats because they are associated with wetlands and open water for breeding and roosting, with breeding birds showing weaker selection because they are more constrained and forage more locally than non-breeding birds that may select productive waters, such as ‘white water’ that has a high sediment content (Laranjeiras et al. 2021). This would hold true even if these sites are further away from night roosts. Our study is the first fine-scale biologging study testing central place foraging theory comparing breeding and wintering foraging behaviour of a long-distance migratory songbird. Given that aerial insectivores, including purple martins, are a rapidly declining avian guild (Hallmann et al. 2017; North American Bird Conservation Initiative Canada 2019; Rosenberg et al. 2019), and there is no consensus on the main cause of decline (Berzins et al. 2020; Mayfield 1969; Nebel et al. 2010). Understanding year-round habitat requirements is critical for developing management practices that would contribute to conservation (Fuller et al. 2005; Wilson et al. 2019).

Methodology

We carried out fieldwork for this study across four regions in the breeding range from 2016 to 2020: Quebec (Canada), Pennsylvania (USA), Florida (USA), and Texas (USA). We captured 101 chick-rearing purple martins (Table 1) and outfitted them with GPS tracking units (Lotek PinPoint10 or Pathtrack nanoFix GEO-MINI, ~1g) using a leg-loop backpack harness made of Teflon ribbon (Rappole and Tipton 1991). Tags were programmed either to collect data during chick-rearing (one or ten-minute intervals) for 24 hours or during the non-breeding period (two to four points per 24 h; see supplementary methods). Chick-rearing GPS birds were recaptured a few days after deployment to recover the tags and data, while non-breeding GPS individuals were recaptured when they returned to their breeding sites the following breeding season. For each GPS track, we identified the central place, either a nest or roost(s), and calculated distance to the central place from each GPS point. Points during the day and away from the central place were labelled as foraging. We used the ctmm package in R (Calabrese et al. 2016) to estimate foraging area for each individual at a given central place, then analysed predictors of foraging range area with linear mixed models using lme4 and lmerTest packages, with latitude, breeding status and their interaction as fixed effects and individual as a random effect. We analysed habitat selection in four regions: Quebec, Florida, Amazon, and Dry Diagonal (Figure 2). Based on the distance distribution of GPS data, we generated two sets of random points to examine local (1x distance distribution) and broad (2x distance distribution) scale selection. For each point, we generated a set of buffer sizes and extracted land cover for each buffer. We calculated edge habitat metrics for wetland and open water. We assessed correlation between land cover types, removing one or more land cover types if they were highly correlated with another. We used logistic regression to examine resource selection in purple martins comparing used versus random points using land cover and year, if applicable, as fixed effects and colony (breeding) or ID (non-breeding) as random effects. We used the “glmer” function in the lme4 package in R. Optimal buffer size was selected based on AIC ranking. Then, different models (full, null, water-based, natural, and open habitat) were compared, again using AIC selection. See supplementary materials for more detailed methods.

Results

Chick-rearing purple martins averaged a maximum foraging distance across individuals of 2.94 km ± 2.26 km from the colony whereas non-breeding birds travelled much farther from their roost, averaging 78.4 km ± 37.9 km per roost (Table 2, t_{100}=5.61, $p < 0.01$). There was no evidence of variation in foraging area among breeding regions controlling for the effect of year and colony ($F_{2,81}$=2.99, p=0.06). Non-breeding birds also had much larger home ranges than chick-rearing birds (t_8=5.62, $p<0.01$) and latitude did not predict foraging range size (t_2=-1.85, p=0.25) when controlling for the random effect of year (Table 2, Figure 2, Supplementary Figure 1).

Table 2. Foraging range area (± SD) and maximum foraging range by region for purple martins.

			Foraging area (km^2)			Maximum foraging distance (km)		
	Region	N	Mean	Min.	Max.	Mean	Min.	Max.
Breeding	Quebec	17	7.19 ± 14.6	0.44	63.1	2.68 ± 3.04	0.66	14.0
	Texas	2	11.1± 9.05	4.73	17.5	4.18 ± 2.94	2.10	6.26
	Florida	73	15.7± 43.3	0.33	362	2.97 ± 2.05	0.51	10.7
Non-breeding	Amazon	6	9980 ± 9970	669	26 400	78.0 ± 39.9	30.3	148
	Dry diagonal	5	7470 ± 6130	209	14 900	77.7 ± 39.9	11.9	117

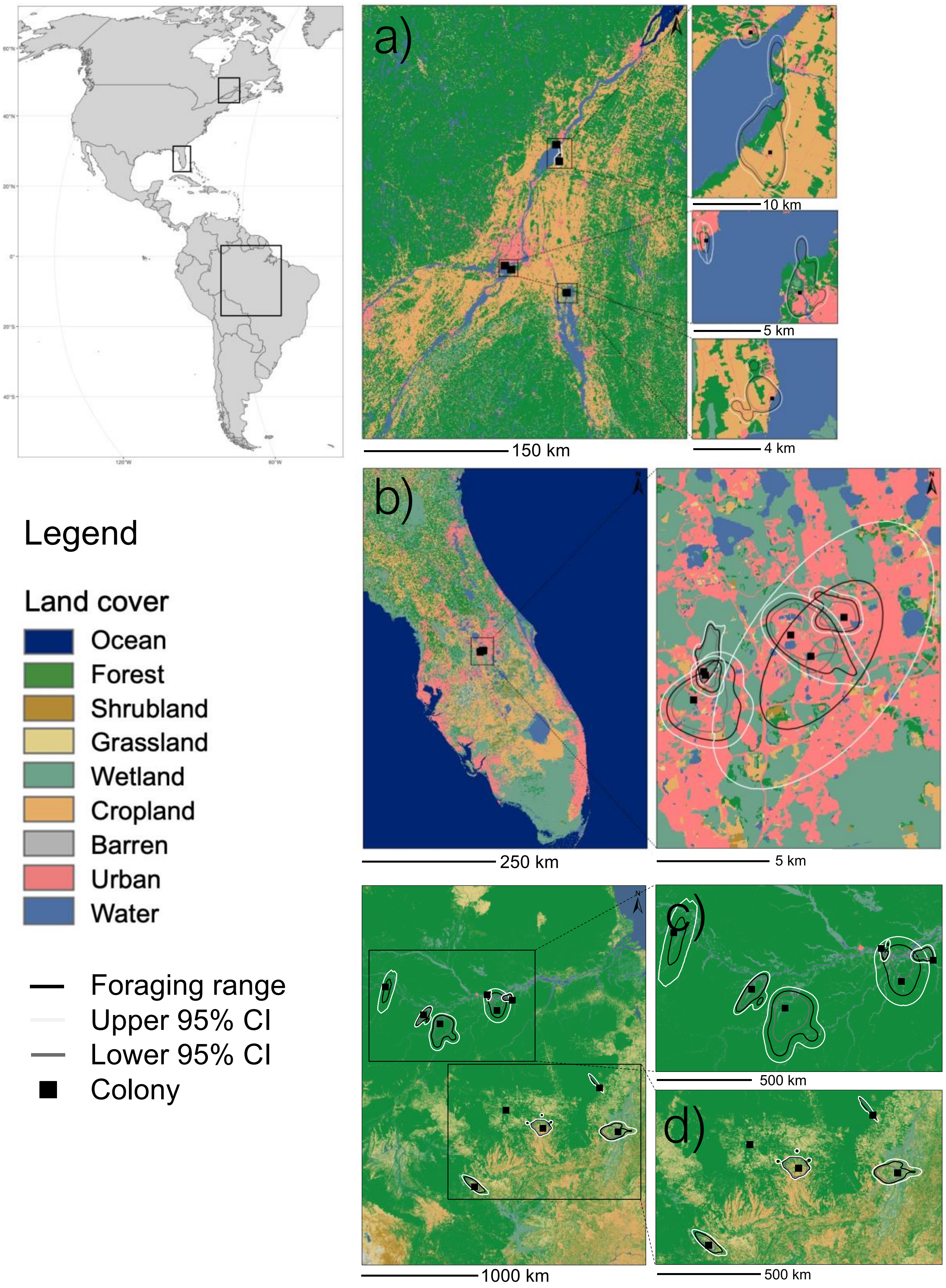
60°N
40°N
20°N
0°
20°S
40°S
120°W
60°W
a)
10 km
5 km
150 km
4 km
b)
250 km
5 km
c)
d)
1000 km
500 km
500 km
Legend
Land cover
Ocean
Forest
Shrubland
Grassland
Wetland
Cropland
Barren
Urban
Water
Foraging range
Upper 95% CI
Lower 95% CI
Colony

Figure 2. Representative foraging range estimates for each colony or roost with confidence intervals showing habitat types for a) Quebec, b) Florida, c) the Amazon, and d) Dry Diagonal.

In Quebec, purple martins selected water edge at a local scale and open water at a broader scale while avoiding wetland edge at both scales (Supplementary Tables 4, 5). In Florida, purple martins selected wetlands and avoided forested habitat at both scales (Supplementary Tables 6, 7). In the Amazon, martins selected wetland and habitats near high-sediment water and avoided open water at both scales (Supplementary Tables 8, 9). In the Dry Diagonal, martins selected open water habitats only at the local scale and avoided grassland, shrubland, and cropland as well as barren and developed habitat at both scales (Supplementary Tables 10, 11). Selectivity was higher at the broader scale for all habitats except the Amazon and was higher for the Amazon than all other habitats using pseudo-R^2 measures of selectivity at the local scale (Supplementary Table 3).

Discussion

As expected, the frequency of return to the central place (nest or roost) is important in predicting foraging range size, with foraging area roughly 100 times larger during the non-breeding period. Thus, the movement of adult birds while chick-rearing is constrained by the need to feed their chicks frequently. In contrast, non-breeding purple martins that return to the roost only once per day and are not territorial during the non-breeding period, foraged up to 117 km from the roost. Breeding birds could be taking advantage of seasonal resource pulses associated with higher latitudes which may reduce foraging range size; however, we did not find evidence for a latitudinal gradient in foraging range size. This first test of central foraging theory across the range of a long-distance migratory songbird shows the importance of this constraint during foraging year-round.

The importance of central place foraging is also shown in comparison to birds that do not roost in winter, and so are not constrained by central place foraging then. For example, territorial migratory songbirds such as ovenbirds (*Seiurus aurocapilla*) and black-and-white warblers (*Mniotilta varia*) show similar territory sizes during breeding and non-breeding (Cooper et al. 2021; Hallworth and Marra 2015; James and Neal 1986; Mattsson and Niemi 2008; Stewart et al. 1958; Westworth and Telfer 1993). As many other swallows also roost in large numbers during winter, our results are likely applicable to many aerial insectivores. Our foraging range sizes during breeding are the first we are aware of that have been documented for purple martins and are similar or larger than those measured for other aerial insectivores. For example, chick-rearing bank swallows (*Riparia riparia*) had foraging ranges that were less than 2 km (Saldanha 2016); chick-rearing tree swallows (*Tachycineta bicolor*) "a few hundred metres" (McCarty and Winkler 1999); overwintering eastern whip-poor-wills (*Antrostomus vociferus*) 0.0524km^2 ± 0.0054km^2 (Tonra et al. 2019); and breeding European nightjars (*Caprimulgus europaeus*) 0.24-0.40km^2 (Sierro et al. 2001).

Purple martins in our study selected wetland habitat, open water, and water edge habitats. Purple martins in the Amazon tended to roost near water with low sediment, which is black or clear water (Bogotá-Gregory et al. 2020), but foraged over or near high-sediment water, also referred to as white water. Low-sediment water is associated with lower species richness and abundance and therefore has fewer predators compared to high-sediment white water that has higher insect prey abundance (Bogotá-Gregory et al. 2020; Emmons 1984; Kay et al. 1997). Non-breeding purple martins are less constrained than breeding individuals in terms of foraging range size (2.94km for breeding vs. 78.4km for overwintering), only returning to a central place once per day, and therefore can move from nutrient-poor to nutrient-rich habitats to meet their needs during different times of the day. In their non-breeding habitat in South America and especially in the Amazon, forest cover was the dominant land cover type yet was not selected; relatively unconstrained purple martins were easily able to forage over their preferred habitats.

For Quebec, Florida, and the dry diagonal, habitat selection strengthened as the scale of the random points increased. The Amazon had the strongest local-scale selection, likely because of large differences in prey abundance among high and low-sediment waters. Low habitat selection at the local scale might suggest, within the distance from colony travelled by breeding birds, they are not strongly selective in habitats close to the colony, possibly because they are selecting for nest locations and roosts in good quality habitats. The large increase in R^2 observed in Quebec (R^2 = 10% to 46%) was stronger than the other regions and could indicate that there are limited areas where habitat is suitable for breeding in Quebec, a region where purple martins are declining strongly (Sauer et al. 2017). Many of the colonies in Quebec had a high proportion of agricultural lands or urban areas, which were not selected foraging habitats, and may not be suitable foraging habitat for purple martins.

As purple martins forage on flying insects above ground or water, they are likely less constrained by fine-scale habitat type than ground- or tree-foraging species, especially in winter when they can travel large distances during the day. Foraging purple martins fly higher on average (mean 119m) while foraging compared to tree swallows (mean 69m) and barn swallows (mean 34m) (Dreelin et al. 2018). Since purple martins are foraging above habitats rather than within them, there may be a spillover effect of insects with larval stages in aquatic habitats to other habitats as purple martins frequently eat insect prey with aquatic stages (Dunoyer 2021; Forsman et al. submitted; Helms et al. 2016). Birds in our study tended to nest near bodies of water or wetland and non-breeding birds spent a lot of their time within a few kilometers of rivers or wetland. Water-type habitats are therefore important in their annual cycle, and future conservation planning should protect water-based habitats, especially wetlands, including preserving or improving water quality. Other migratory swallows might show similar trends in foraging range across the annual cycle and may also require large amounts of land for overwintering.

Future studies could examine repeatability in foraging range and habitat selection within individuals. We assumed that points during away from the central place during the day represented foraging points; however, some of these points may represent perching or commuting rather than foraging. If technology advances sufficiently, GPS-accelerometers and GPS-altimeters could be deployed on purple martins to identify bouts of active foraging in three dimensions and narrow habitat selection analysis to these periods. Future studies could also examine foraging range and habitat selection of incubating, post-breeding, and migratory birds and assess the potential effects of climate and weather.

Our study is the first to quantify purple martin foraging range and foraging habitat selection and test central place foraging theory across two points in the annual cycle. Purple martins have larger foraging ranges during the overwintering period compared to breeding, likely because chick-rearing birds are constrained by the need to return to the central place more frequently than non-breeding birds that return to a roost once per day, and they select water-type habitats across their range. Purple martins can forage hundreds of meters in altitude, and awareness of the importance of these aerial habitats year-round to aerial insectivores highlights the need for conservation practices that incorporate airspaces above and surrounding important land and water habitats (Davy et al. 2017; Helms et al. 2016; Kelly et al. 2013).

Permits

This work was carried out with banding permits from the Bird Banding Office (Canada) and US Geological Survey (United States) and Animal Use Protocols under McGill University and the University of Manitoba.

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References

Barbosa P. in prep. Holidays in the amazon? Use and selection of the habitat of a migratory bird, the purple martin (*progne subis*, hirundinidae), during the winter period in the brazilian amazon. [Brazil].

Barron DG, Brawn JD, Weatherhead PJ. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods in Ecology and Evolution. 1(2):180-187.

Berzins L, Clark R, Kardynal K, Krebs E, Mahony N, Morrissey C. 2020. Research, conservation and outreach priorities for conserving aerial insectivore populations in canada: Report from march 2020 aerial insectivore workshop in saskatoon, sk. Canada: Environment and Climate Change Canada & University of Saskatchewan.

Bogotá-Gregory JD, Lima FCT, Correa SB, Silva-Oliveira C, Jenkins DG, Ribeiro FR, Lovejoy NR, Reis RE, Crampton WGR. 2020. Biogeochemical water type influences community composition, species richness, and biomass in megadiverse amazonian fish assemblages. Scientific Reports. 10(1):15349.

Brown CR, Tarof SA, Poole AF. 2013. Purple martin (*progne subis*), version 2.0. The Birds of North America. Ithaca, NY: Cornell Lab of Ornithology.

Calabrese JM, Fleming CH, Gurarie E. 2016. Ctmm: An r package for analyzing animal relocation data as a continuous-time stochastic process. Methods in Ecology and Evolution. 7(9):1124-1132.

Cooper NW, Thomas MA, Marra PP. 2021. Vertical sexual habitat segregation in a wintering migratory songbird. Ornithology. 138(1).

Davy CM, Ford AT, Fraser KC. 2017. Aeroconservation for the fragmented skies. Conservation Letters. 10(6):773-780.

Dreelin RA, Shipley JR, Winkler DW. 2018. Flight behavior of individual aerial insectivores revealed by novel altitudinal dataloggers. Frontiers in Ecology and Evolution. 6(182).

Dunoyer J. 2021. Analyzing purple martin habitat, foraging range, and diet composition through biologging and DNA barcoding. [Sainte-Anne-de-Bellevue, Canada]: McGill University.

Emmons LH. 1984. Geographic variation in densities and diversities of non-flying mammals in amazonia. Biotropica. 16(3):210-222.

Fassoni-Andrade AC, Paiva RCDd. 2019. Mapping spatial-temporal sediment dynamics of river-floodplains in the amazon. Remote Sensing of Environment. 221:94-107.

Forsman AM, Hoenig BD, Gaspar SA, Fischer JD, Siegrist J, Fraser K. submitted. Evaluating the impacts of metabarcoding primer selection on DNA characterization of diet in an aerial insectivore, the purple martin. Submitted to Ornithology.

Fournier AMV, Shave A, Fischer J, Siegrist J, Ray J, Cheskey E, MacIntosh M, Ritchie A, Pearman M, Applegate K et al. 2019. Precise direct tracking and remote sensing reveal the use of forest islands as roost sites by purple martins during migration. Journal of Field Ornithology. 90(3):258-265.

Fraser KC, Shave A, Savage A, Ritchie A, Bell K, Siegrist J, Ray JD, Applegate K, Pearman M. 2017. Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new gps technology. Journal of Avian Biology. 48(3):339-345.

Fraser KC, Stutchbury BJM, Kramer P, Silverio C, Barrow J, Newstead D, Mickle N, Shaheen T, Mammenga P, Applegate K et al. 2013. Consistent range-wide pattern in fall migration strategy of purple martin (*progne subis*), despite different migration routes at the gulf of mexico. The Auk. 130(2):291-296.

Fuller RM, Devereux BJ, Gillings S, Amable GS. 2005. Indices of bird-habitat preference from field surveys of birds and remote sensing of land cover: A study of south-eastern england with wider implications for conservation and biodiversity assessment. Global Ecology and Biogeography. 14(3):223-239.

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T et al. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PloS one. 12(10):e0185809-e0185809.

Hallworth MT, Marra PP. 2015. Miniaturized gps tags identify non-breeding territories of a small breeding migratory songbird. Scientific Reports. 5(1):11069.

Helms JA, Godfrey AP, Ames T, Bridge ES. 2016. Predator foraging altitudes reveal the structure of aerial insect communities. Scientific Reports. 6:28670.

Hill JRI. 1993. A giant martin roost on the amazon river. Purple Martin Update. 4:5-7.

Houston AI, McNamara JM. 1985. A general theory of central place foraging for single-prey loaders. Theoretical Population Biology. 28(3):233-262.

James DA, Neal JC. 1986. Arkansas birds : Their distribution and abundance. Fayetteville: University of Arkansas Press.

Kacelnik A. 1984. Central place foraging in starlings (sturnus vulgaris). I. Patch residence time. Journal of Animal Ecology. 53(1):283-299.

Kacelnik A, Cuthill I. 1990. Central place foraging in starlings (sturnus vulgaris). Ii. Food allocation to chicks. Journal of Animal Ecology. 59(2):655-674.

Kay RF, Madden RH, Van Schaik C, Higdon D. 1997. Primate species richness is determined by plant productivity: Implications for conservation. Proceedings of the National Academy of Sciences. 94(24):13023.

Kelly JF, Bridge ES, Frick WF, Chilson PB. 2013. Ecological energetics of an abundant aerial insectivore, the purple martin. PLoS ONE. 8(9):e76616.

Laranjeiras TO, Naka LN, Leite GA, Cohn-Haft M. 2021. Effects of a major amazonian river confluence on the distribution of floodplain forest avifauna. Journal of Biogeography. 48(4):847-860.

Mattsson BJ, Niemi GJ. 2008. Causes and consequences of distribution patterns in a migratory songbird across its geographic range. Canadian Journal of Zoology. 86(4):314-328.

Mayfield HF. 1969. Purple martin population changes over fifteen years. The Auk. 86(3):522-528.

McCarty JP, Winkler DW. 1999. Foraging ecology and diet selectivity of tree swallows feeding nestlings. The Condor. 101(2):246-254.

Nebel S, Mills A, McCracken JD, Taylor PD. 2010. Declines of aerial insectivores in north america follow a geographic gradient. Avian Conservation and Ecology. 5(2):1.

North American Bird Conservation Initiative Canada. 2019. The state of canada’s birds, 2019. Ottawa, Canada: Environment and Climate Change Canada.

Orians GH, Pearson NE. 1979. On the theory of central place foraging. In: Horn DJ, Mitchell R, Stair GR, editors. Analysis of ecological systems. Columbus: Ohio State University Press. p. 155-177.

Rappole JH, Tipton AR. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology. 62(3):335-337.

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, Stanton JC, Panjabi A, Helft L, Parr M et al. 2019. Decline of the north american avifauna. Science. 366(6461):120.

Saldanha S. 2016. Foraging and roosting habitat use of nesting bank swallows in sackville, nb. [Halifax]: Dalhousie University.

Saldanha S, Taylor PD, Imlay TL, Leonard ML. 2019. Biological and environmental factors related to communal roosting behavior of breeding bank swallow (riparia riparia). Avian Conservation and Ecology. 14(2).

Sauer JR, Niven DK, Hines JE, Jr DJZ, Pardieck KL, Fallon JE, Link. WA. 2017. The north american breeding bird survey, results and analysis 1966 - 2015. Laurel, MD: USGS Patuxent Wildlife Research Center.

Sierro A, Arlettaz R, Naef-Daenzer B, Strebel S, Zbinden N. 2001. Habitat use and foraging ecology of the nightjar (*caprimulgus europaeus*) in the swiss alps: Towards a conservation scheme. Biological Conservation. 98(3):325-331.

Stewart RE, Robbins CS, Fish US, Wildlife S, United States. Department of the I. 1958. Birds of maryland and the district of columbia. Washington D.C.: U.S. Dept. of the Interior, Fish and Wildlife Service.

Stutchbury BJM, Kramer PM, Barrow J, Mickle N, Mammenga P, Applegate K. Forthcoming 2013. Purple martin geolocator capture methods: Advice & lessons learned from experienced landlords.

Stutchbury BJM, Siddiqui R, Applegate K, Hvenegaard GT, Mammenga P, Mickle N, Pearman M, Ray JD, Savage A, Shaheen T et al. 2016. Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. The American Naturalist. 188(S1):S28-S40.

Tonra CM, Wright JR, Matthews SN. 2019. Remote estimation of overwintering home ranges in an elusive, migratory nocturnal bird. Ecology and Evolution. 9(22):12586-12599.

Waite TA, Ydenberg RC. 1996. Foraging currencies and the load-size decision of scatter-hoarding grey jays. Animal Behaviour. 51(4):903-916.

Waterhouse FL, Doyle FI, Turney L, Wijdeven B, Todd M, Bergman C, Vennesland RG. 2017. Spring and winter home ranges of the haida gwaii northern saw-whet owl (aegolius acadicus brooksi). Journal of Raptor Research. 51(2):153-164.

Weimerskirch H, Ancel A, Caloin M, Zahariev A, Spagiari J, Kersten M, Chastel O. 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. Journal of Animal Ecology. 72(3):500-508.

Westworth DA, Telfer ES. 1993. Summer and winter bird populations associated with five age-classes of aspen forest in alberta. Canadian Journal of Forest Research. 23(9):1830-1836.

Wilson KS, Pond BA, Brown GS, Schaefer JA. 2019. The biogeography of home range size of woodland caribou rangifer tarandus caribou. Diversity and Distributions. 25(2):205-216.

Ydenberg RC, Welham CVJ, Schmid-Hempel R, Schmid-Hempel P, Beauchamp G. 1994. Time and energy constraints and the relationships between currencies in foraging theory. Behavioral Ecology. 5(1):28-34.

CONNECTING STATEMENT

Chapter 1 examined foraging behaviour of purple martins in two points of the annual cycle (chick-rearing and overwintering) and found that breeding individuals had smaller foraging ranges than overwintering individuals and found that purple martins select water-based habitats such as lakes, rivers, and wetlands for foraging. Chapter 2 examines different points in the annual cycle, specifically, breeding and the early post-fledging period, to estimate breeding success and determine predictors of fledging and departure behaviour of juvenile purple martins.

A purple martin colony in southern Quebec

NOTE ON CHAPTER 2

This chapter corresponds to a manuscript with the same title in which I am first author. This chapter will be submitted to *Avian Conservation and Ecology*. Saeedeh Bani Assadi (University of Manitoba), Barbara Frei, Kevin Fraser, and Kyle Elliott are co-authors. S.B.A. contributed data from Ontario. Chapter 2 focuses on reproductive success and predictors of fledging and colony departure of juvenile birds with the goal of examining the disproportionate decline of northeastern purple martins.

CHAPTER 2: Habitat predictors of fledgling dispersal in a declining aerial insectivore

Kristen M. Lalla[1]
Saeedeh Bani Assadi[2]
Kyle H. Elliott[1]
Barbara Frei[3,4]
Kevin C. Fraser[2]

[1] Department of Natural Resource Sciences, McGill University, 21 111 Lakeshore, Sainte-Anne-de-Bellevue, Quebec, Canada, H9X 3V9
[2] Department of Biological Sciences, University of Manitoba, 50 Sifton Road, Winnipeg, Manitoba, Canada, R3T 2N2
[3] Canadian Wildlife Service, Environment and Climate Change Canada, Gatineau, Quebec, Canada
[4] Migration Research Foundation, Inc., Montreal, Canada

Abstract

Aerial insectivores have declined drastically in northeastern North America due to multiple threats such as agricultural intensification, climate change, and habitat loss. It is possible that low subadult survival drives population declines in some species, yet little is known about the post-fledging period. Purple martins (*Progne subis*) no longer breed in New Brunswick as of 2010, have declined by 94% since 1970 in Quebec where they are now largely restricted to areas adjacent to large bodies of water (e.g., Saint-Lawrence River, Lake Champlain), and have declined by 37% in Ontario. Here, we study the post-fledging movements of purple martins in Quebec and Ontario using an automated radio-telemetry system and compare reproductive success to other regions. Breeding efforts among individuals in 2019 and 2020 were largely successful and comparable to other regions with positive population trends. Radio-tagged juveniles fledged at 27.2 ± 2.0 days and departed the colony for the first time at 33.4 ± 5.9 days old. Among the colonies in Quebec, individuals that were hatched in a colony close to a wetland roosted in the wetland, whereas individuals in colonies that did not have wetland available to them roosted in the nest box until near departure or departed the colony very soon after fledging. Among six colonies in southern

Quebec and Ontario, individuals that departed at a younger age were hatched later and were from colonies with a higher proportion of wetland and open water habitat. We conclude that wetlands and open water may be important habitats for nestling development, and that post-fledging survival and migration may be a critical factor in the declining population trends of purple martins in eastern Canada.

Introduction

The post-fledging period is understudied in birds but can play an important role in population dynamics, especially as many species of birds show low survival rates during this period (Boynton et al. 2020; Evans et al. 2020; Maness and Anderson 2013; Stutchbury et al. 2009a; Tarof et al. 2011; Taylor et al. 2018; Weegman et al. 2017). Thus, understanding if juvenile mortality drives population declines and understanding causes of variation in post-fledging survival can be important to avian conservation (Saracco et al. 2010). Nonetheless, there are mixed results regarding the predictors of juvenile survival despite a broad consensus that juvenile survival is low (Boynton et al. 2020; Evans et al. 2020; Maness and Anderson 2013; Stutchbury et al. 2009a; Tarof et al. 2011; Taylor et al. 2018; Weegman et al. 2017). Fledglings with greater energy reserves at fledging typically have higher survival because reserves can provide a buffer for the time it takes young birds to learn to forage (Maness and Anderson 2013). Young birds that are hatched earlier also typically have higher survival after fledging because resources may be more abundant, they have a longer period of time to learn to care for themselves before migration, and they can build up more reserves for migration (Maness and Anderson 2013).

Avian aerial insectivores, or birds preying on insects while in flight, are a rapidly declining avian guild (Nebel et al. 2010). Given that juvenile survival is low among many species of aerial insectivore (Boynton et al. 2020; Evans et al. 2020; Stutchbury et al. 2009a; Tarof et al. 2011; Taylor et al. 2018; Weegman et al. 2017), the post-fledging period may contribute to declines in these species. Although there are many potential causes of decline (Nebel et al. 2020; Nebel et al. 2010), juvenile dispersal is an often-understudied aspect of the life cycle of many aerial insectivores, and juveniles may be especially vulnerable to threats. For example, tree swallows (*Tachycineta bicolor*) are likely limited by juvenile survival and recruitment (Berzins et al. 2020; Cox et al. 2018; Taylor et al. 2018; Weegman et al. 2017). Body condition is positively associated with juvenile survival in barn swallows (Evans et al. 2020). Barn swallow (*Hirundo rustica*) fledglings have lower survival and are more likely to use cropland habitat than older birds (Boynton et al. 2020), but, in another study, the presence of intensive agriculture positively impacts fledging success and body condition (Kusack et al. 2020). Thus, the post-fledging period might be a critical time period in the annual cycle of swallows, and carryover effects from the nestling period may impact subsequent survival (Imlay et al. 2021). Nonetheless, in swallows, the post-fledging period is relatively understudied and more work is needed to understand post-fledging behaviour and causes of mortality (Berzins et al. 2020). Because there may be multiple factors contributing their decline, it is especially important to understand the dispersal of fledgling swallows and their movements during the post-breeding period to provide additional information that may be useful for their conservation.

The purple martin (*Progne subis*) is an aerial insectivore that breeds across much of North America and overwinters in South America (Brown et al. 2013; Fraser et al. 2017). It is declining more steeply in the northeastern part of its range (Bédard 2016; Brown et al. 2013). In Quebec, purple martins have declined by over 90% since 1970 (Bédard 2016), and, in Ontario, have declined by 37% over the same period (Figure 3, Smith et al. 2020). Their range has contracted to the large water bodies in southern Quebec (Figure 4) according to the Quebec Breeding Bird Atlas (Quebec Breeding Bird Atlas 1984-1989, 2010-2014). Adult purple martins are frequently associated with water-based habitats for breeding (Brown et al. 2013), roosting (Fournier et al. 2019; Fraser et al. 2017), and foraging (Chapter 1), but little is known about habitat use during the post-fledging period. Breeding phenology in purple martins varies across latitude impacting the timing of post-fledging; individuals breeding in the southern parts of the purple martin's range begin breeding much sooner (typically March) than birds in the northern part of their range (typically June, Brown et al. 2013), and breeding phenology is more variable in the southern part of their range compared to the northern limit of their range (Neufeld et al. 2021). Pairs typically fledge 3-4 young (Raleigh et al. 2019) that are cared for by their parents for 7-10 days after fledging (Tarof et al. 2011). After departing the colony, purple martins gather in pre-migratory roosts (Brown et al. 2013; Tarof et al. 2011). During this period, juvenile survival is high, but it decreases drastically during migration and the overwintering period (Tarof et al. 2011). Purple martins are panmictic on wintering grounds (Fraser et al. 2017; Fraser et al. 2012; Stutchbury et al. 2016b) and because parts of the population are declining more than others despite shared wintering grounds and migration routes (Bédard 2016; Nebel et al. 2010), causes of population declines likely occurs outside this period. Therefore, it is important to study breeding success and post-fledging behaviour.

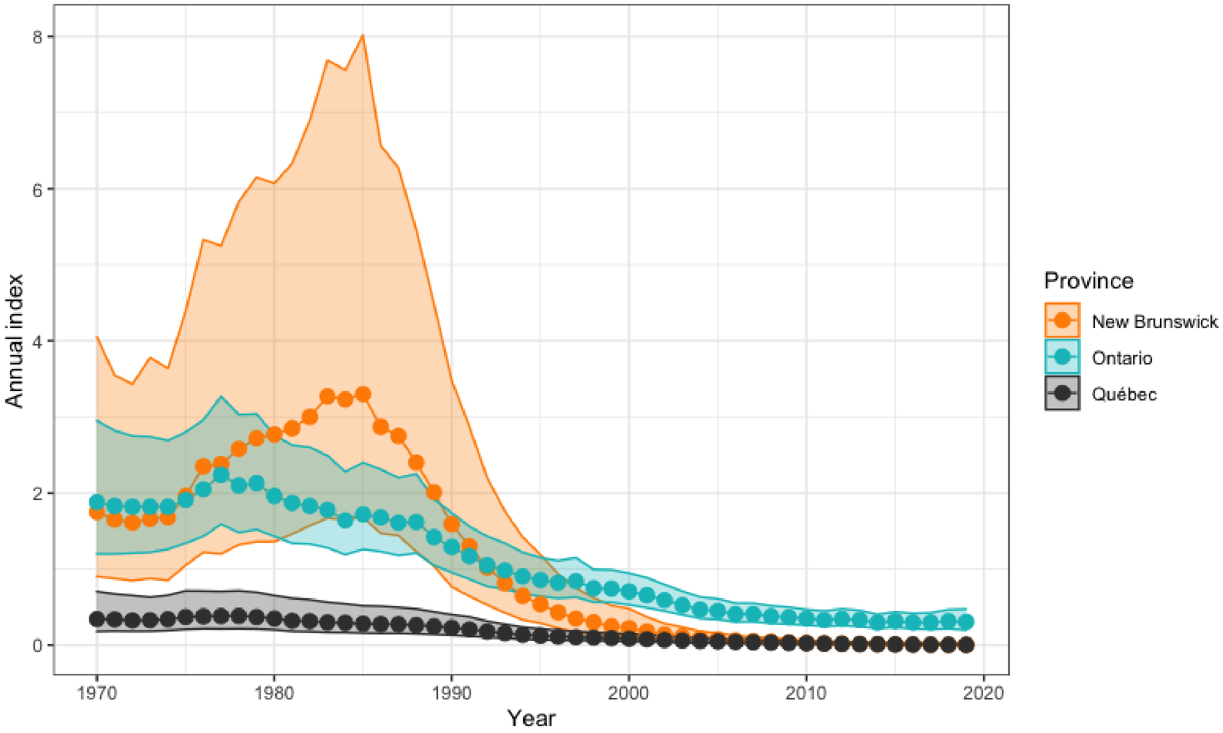

Figure 3. Purple martin population annual indices with upper and lower limits from 1970 to 2019 for three provinces: Quebec (grey), Ontario (blue), and New Brunswick (orange). All three provinces show declines. Adapted from Canadian Breeding Bird Survey data (Smith et al. 2020).

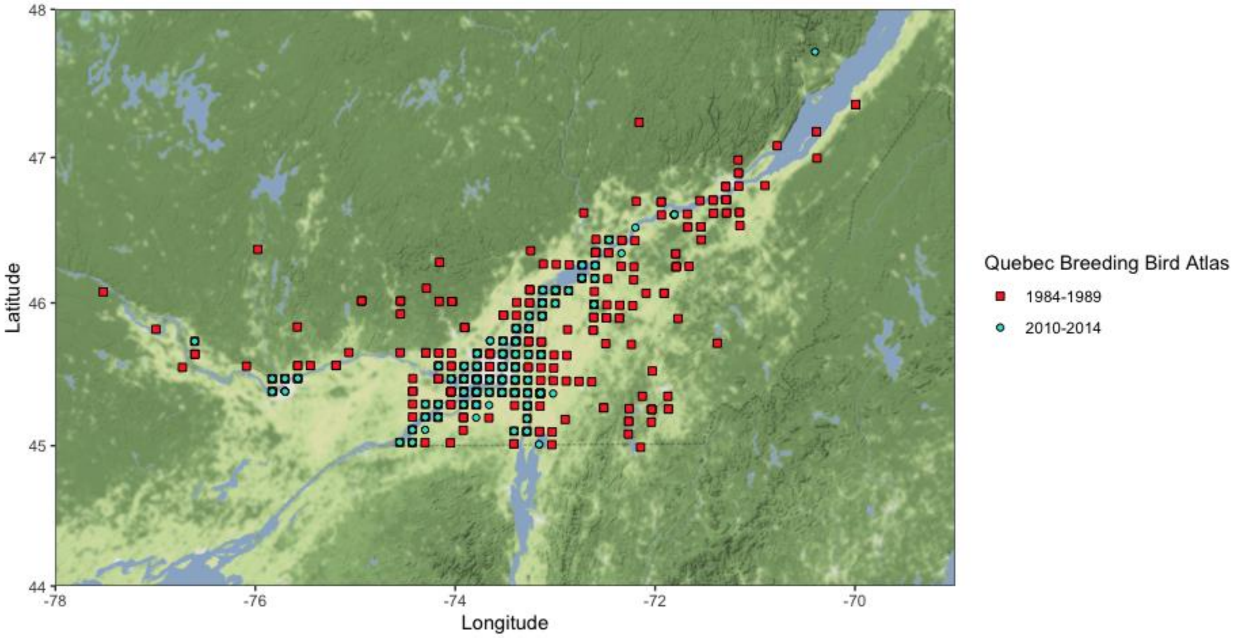

Figure 4. Quebec Breeding Bird Atlas breeding locations between the first (1984-1989, red squares) and second (2010-2014, green circles) atlases (Quebec Breeding Bird Atlas 1984-1989, 2010-2014). Many of the breeding locations in the first edition that are far from major water bodies are absent in the second, and there are few locations present in the second edition not present in the first. Map tiles are from Stamen Maps.

We studied breeding success and post-fledging behaviour of purple martins where the population has experienced some of the steepest declines to better understand the stages of the annual cycle where purple martins are vulnerable. We recorded breeding success in Quebec and compared values to areas where martin populations are stable. Using an automated radio-telemetry system, specifically the Motus Wildlife Tracking System (Taylor et al. 2017), we recorded post-fledging behaviour, and predicted that juveniles hatched earlier in the breeding season will fledge and depart the colony at a younger age, likely because later birds have missed peak food abundance. Furthermore, we expected that local habitat composition will influence departure dates due to differences in habitat quality, and we predicted that fledglings with a higher proportion of wetland and open water will depart the colony at a later date because those habitats provide good foraging and roosting habitat (Berzins et al. 2020; Ghilain and Bélisle 2008; Michelson et al. 2018; Twining et al. 2016; Twining et al. 2018).

Methods

Breeding success & nest box occupancy

Nests at six colonies were monitored twice per week (Figure 5). Nest progress, number of eggs, number of nestlings, lay date, and hatch date were recorded for each nest compartment. If we were unsure when nestlings hatched, we used a photo identification nestling growth chart available from the Purple Martin Conservation Association to estimate their age. We assumed that number of nestlings at banding was comparable to the number of nestlings that fledged as we did not observe nestlings dead in the nest between banding and fledging. We monitored purple martin nest boxes along the southern shoreline of Montreal, Quebec, approximately every two weeks in 2019 and twice in 2020 to estimate occupancy by purple martins. We considered a nest box occupied if it was used by one or more pairs of purple martins.

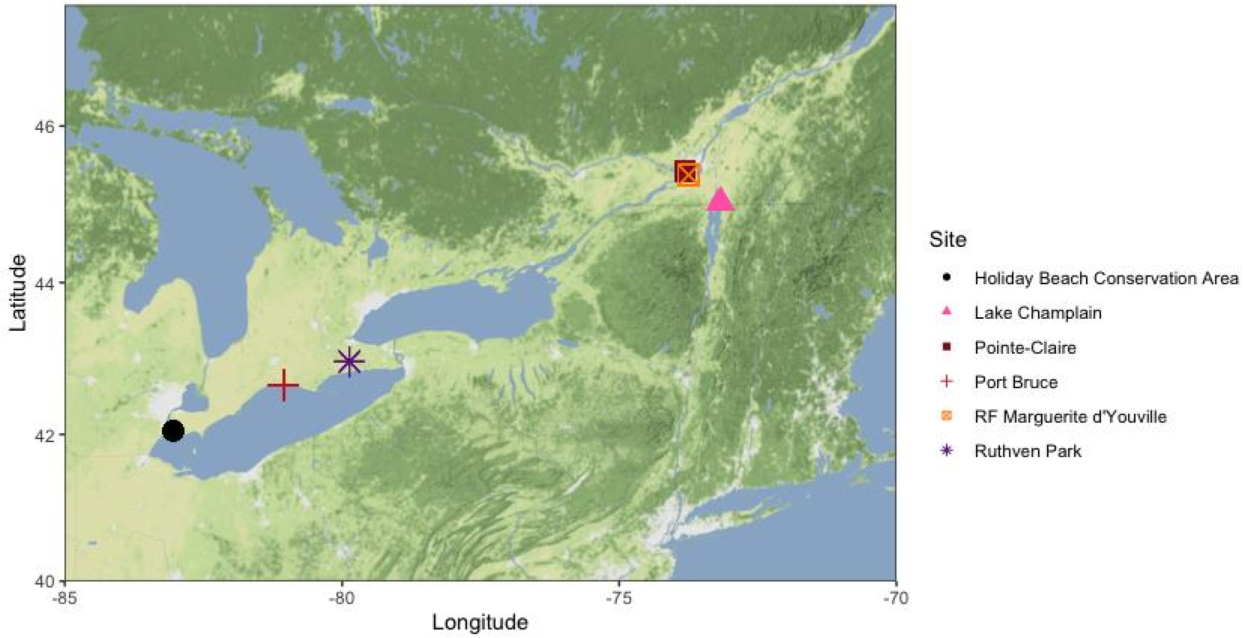

Figure 5. Six purple martin colonies used in our study: Holiday Beach Conservation Area (2017-2018, 42.05, -83.04), Lake Champlain (2019-2020, 45.03, -73.18), Pointe-Claire (2019-2020, 45.43, -73.82), Port Bruce (2017-2018, 42.66, -81.06), Reserve faunique Marguerite d'Youville (2019-2020, 45.38, -73.75), and Ruthven Park (2019, 42.97, -79.87). We used Stamen maps from the ggmap package in R.

Radio-tagged fledglings

The Motus Wildlife Tracking System is a radio telemetry system that uses individually coded nanotags all operating at the same frequency that can be detected by a network of stationary receivers, which are currently most numerous in parts of our study area in eastern Canada (Taylor et al. 2017). Radio telemetry is a suitable technique to study small passerines as radio tags are typically small (< 1g) and do not require recapture (Bridge et al. 2011; Taylor et al. 2017). 30 nestlings at three colonies in Quebec and 74 nestlings at three colonies in Ontario were radio-tagged with Motus radio tags (Lotek NTQB2-3-2 nanotag, 0.6g). We attached radio tags to the lower back of individuals using leg-loop harnesses (Rappole and Tipton 1991) using stretchy string (Bead Landing 1mm elastic cord, Texas, USA) in Quebec and a polypropylene thread in Ontario. Nestlings were tagged at 16-26 days old so that they had reached or exceeded their asymptotic size (Brown et al. 2013), but were young enough to prevent forcing early fledging. Motus-tagged nestlings at five of the six colonies were monitored with stationary Motus receivers. Data were uploaded to Motus and were analysed in R to produce detection graphs allowing us to estimate fledging, departure from the colony (first departure from the range of the Motus stationary receiver), and departure from the colony area (departure from the range of the Motus stationary receiver if the individual returned after its first departure) dates. In Southern Quebec, we used handheld tracking at least twice per week (and at least 3 times per week at the Pointe-Claire colony where we did not have a stationary Motus receiver) to monitor fledglings and estimate roosting locations using a 3-element Yagi antenna (range <300m) paired with a Lotek receiver (SRX 800 M-1). We used the sigloc package in R to estimate locations.

To determine if presence of wetland or water habitat near the colony influence fledging and departure age, we extracted proportion of land cover for wetland and water habitat within a 1km range of the colony using 30m land cover data from the Commission for Environmental Cooperation (Land Cover 30m, 2015, Landsat) in R. We created a linear model to determine predictors of departure age. We used first egg date (day of year), latitude, interaction between first egg date and latitude, brood size (number of nestlings), proportion of wetland, proportion of water, and year as fixed effects. We scaled numeric variables (all except year, which we treated as a factor) to achieve normality in the residuals.

Results

Along the shoreline of Montreal, Quebec, nest box occupancy by purple martins was low; nest box occupancy was estimated at 10% (10/100) in 2019 and 16% (16/100) in 2020 (Figure 6).

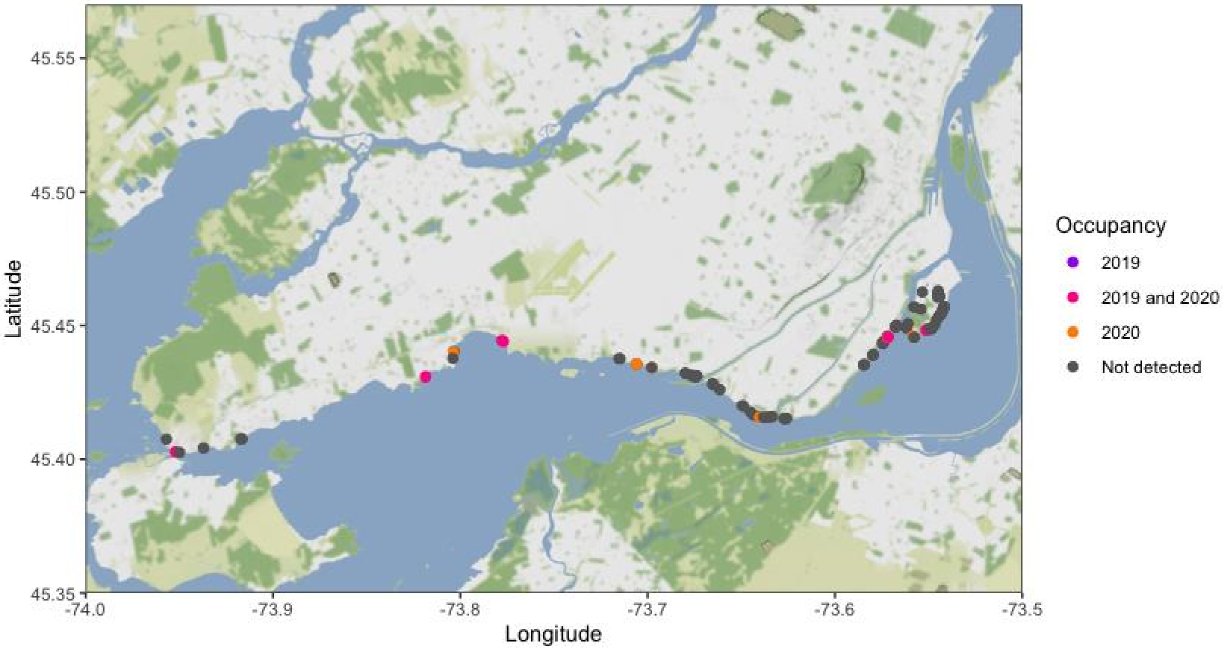

Figure 6. Nest box occupancy of 100 purple martin nest boxes along the southern shoreline on the island of Montreal, Quebec.

Breeding success in Quebec is comparable to Canada and the continental average (Table 3, Raleigh et al. 2019). Between 2019 and 2020, two of the three colonies (Pointe-Claire and Reserve faunique Marguerite d'Youville) in Quebec doubled in number of nests while one colony (Lake Champlain) did poorly in 2020 compared to 2019. In 2021, the same two colonies continued to grow while the third declined slightly. Fledglings at Reserve faunique Marguerite d'Youville colony primarily roosted in the wetland, whereas fledglings at the other 2 colonies in Quebec roosted either in the nest box or at an unknown location.

Table 3. Breeding success of purple martins at 3 colonies in Southern Quebec, Canada (± standard deviation) compared to Canada and North America. Sample size (number of nests) in parentheses.

Year	**Eggs laid/nest**	**Eggs hatched**	**Nestlings at banding** (Quebec) **or number of fledglings** (Raleigh et al. 2019)
Quebec 2019	4.74 ± 0.86 (26)	4.37 ± 1.15 (26)	4.04 ± 1.24 (25)
Quebec 2020	4.77 ± 0.76 (31)	4.43 ± 1.28 (28)	3.70 ± 1.70 (30)
Canada (*P. subis subis* across 19 years, Purple Martin Conservation Association data in Raleigh et al. 2019)	4.96 ± 0.04 (864)	NA	3.74 ± 0.06 (864)
North America (*P. subis subis* across 19 years, Purple Martin Conservation Association data in Raleigh et al. 2019)	4.9 ± 0.02 (69 714)	NA	3.6 ± 0.02 (69 714)

28/30 Motus-tagged nestlings in Quebec likely departed the colony area; we observed 2 fledglings dead in the nest after fledging.

Individuals in our study fledged at an average of 27.2 ± 2.0 days old and departed the colony for the first time at 33.4 ± 5.9 days old (Table 4).

Table 4. Age at fledging and age at departure by colony with standard deviation.

Colony	**Age at fledging (days)**	**Age at departure (days)**
Holiday Beach Conservation Area	28.2 ± 2.3	36.0 ± 6.1
Lake Champlain	27.0 ± 2.0	29.5 ± 2.7
Pointe-Claire	27.0 ± 2.0	42.0 ± 2.6
Port Bruce	26.5 ± 1.5	29.7 ± 3.8
RF Marguerite d'Youville	29.0 ± 0	39.3 ± 3.7
Ruthven Park	26.8 ± 1.0	32.0 ± 2.5

Age at fledging was not influenced by proportion of open water (t_{76}=-1.36, p=0.18) or wetland (t_{76}=0.20, p=0.84) habitat within 1km, first egg date (t_{76}=-0.72, p=0.47), latitude (t_{76}=0.74, p=0.46), brood size (t_{76}=-0.31, p=0.76) or the interaction between first egg and latitude (t_{76}=1.80, p=0.08). Year was significant; however, pairwise differences were not significant when accounting for the number of pairwise comparisons (post-hoc Tukey test, $p_{2017-2018}$=0.47, $p_{2017-2019}$=0.91, $p_{2018-2019}$=0.73).

Age at departure was predicted by first egg date (t_{71}=-2.37, p<0.0001), latitude (t_{71}=4.10, p=0.0001), proportion of open water (t_{71}=-4.39, p<0.0001) and wetland (t_{71}=-2.44, p=0.02) habitats, but not the interaction term of first egg date and latitude ($t_{1,72}$=-1.51, p=0.14) or brood size (t_{71}=-0.98, p=0.33), and post-hoc pairwise comparisons of year were not significant (Tukey, $p_{2017-2018}$=0.80, $p_{2017-2019}$=0.99, $p_{2018-2019}$=0.64). Age at departure was negatively correlated with first egg date, proportion of each open water and wetland, and positively with latitude (Figure 7).

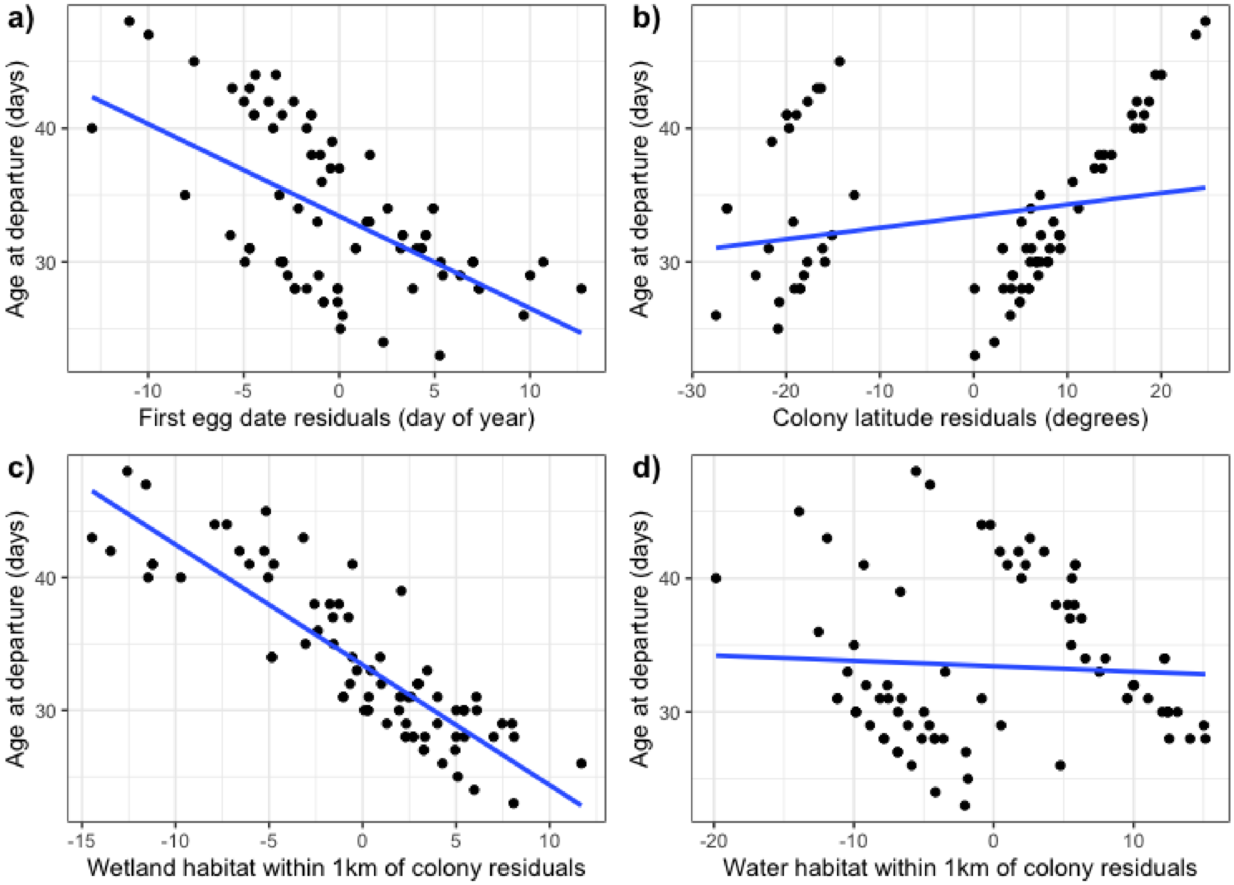

Figure 7. Age of departure residual plots for a) first egg date, b) colony latitude, c) wetland within 1km, and d) open water within 1km for Motus-tagged fledglings in Quebec and Ontario.

Fledglings in Pointe-Claire, a colony near water but not wetland, used their nest box to roost before departing to an unknown roosting location, while individuals hatched in a wetland environment at RF Marguerite d'Youville roosted in the wetland for approximately two weeks after hatching (Figure 8). In southern Quebec, GPS data from adult birds in 2020 and 2021 showed 2 roosts: one (44.98N, 73.16W) 5 km from the Lake Champlain colony and the other (45.36N, 73.83W) 6 km from RF Marguerite d'Youville in the Saint-Lawrence River (Lac St-Louis) that we suspected birds from Pointe-Claire also used (8 km), as birds from a separate colony in 2021 in Beauharnois, Quebec, also used this same roost (6 km). In 2019, we observed the roost near the Lake Champlain colony but did not detect any fledgling birds using this roost, although it is possible that they used a different roost closer to the colony that we were unable to detect. We did not visit the Saint-Lawrence River roost in 2019 as we were only aware of its presence the following year when we were no longer radio-tagging purple martins.

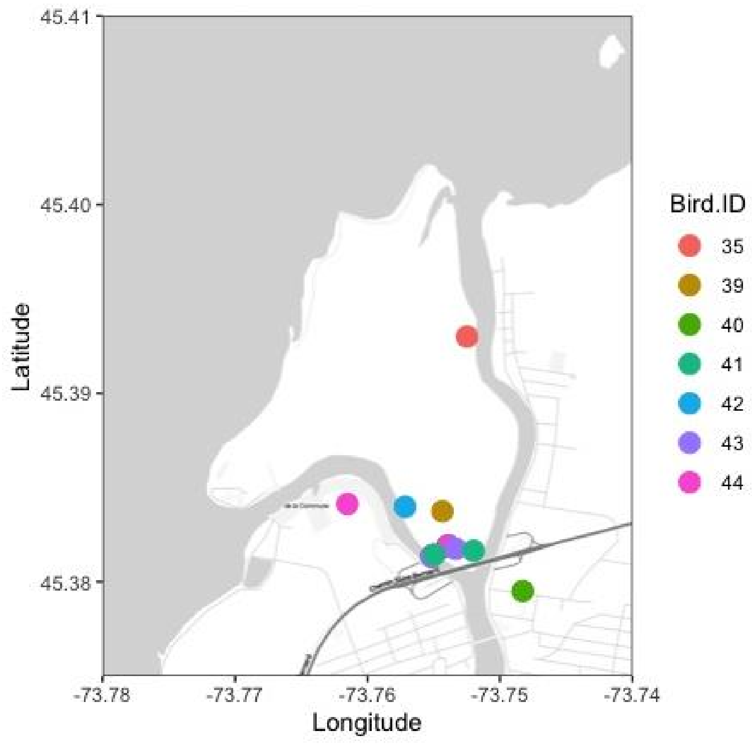

Figure 8. Roosting locations of fledglings estimated from handheld tracking triangulation at Reserve faunique Marguerite d'Youville.

Discussion

Our research aims to contextualize the stronger decline in the northeastern range of the purple martin as compared to other parts of its range and examine predictors of juvenile behaviour. Contrary to our prediction, breeding success was high in 2019 and 2020 in southern Quebec, suggesting that the cause of decline occurs outside of the breeding period; the proportion of occupied nest boxes was low in our study area. The number of eggs per nest at our Quebec colonies was slightly lower than the Canadian average reported by Purple Martin Conservation Association community science participants, but the number of fledglings per nest in Quebec was comparable to numbers in Canada and the North American average (Raleigh et al. 2019). We examined predictors of fledging and juvenile departure from the natal colony. Juvenile departure age from the colony was positively associated with latitude and negatively associated with wetland and open water habitats as well as first egg date; however, we did not find fledging age to be significantly associated with any of the variables in our model.

Although reproductive success was not exceptionally low in southern Quebec (Raleigh et al. 2019), increased weather variability with climate change could influence when purple martins initiate breeding, especially in southern Quebec and Ontario where winters are colder than other parts of their breeding range (Nebel et al. 2010). Starvation due to poor weather conditions (cold, rain) can occur in spring as birds arrive at their breeding grounds, and populations at the northern part of purple martins' range may be more susceptible as they are more constrained in the timing of breeding and must migrate greater distances than southern breeders (Neufeld et al. 2021). The erection and maintenance of purple martin nest boxes is an important aspect of purple martin conservation, and nest boxes maintenance is needed to improve their use by purple martins (Raleigh et al. 2019). However, the provision and maintenance of nest boxes may not be sufficient to stabilize population declines as there are many empty nest boxes in southern Quebec.

We predicted that fledglings in colonies with a higher proportion of wetland and water habitats would depart at a later age because wetlands and water offer good-quality foraging and roosting habitats (Berzins et al. 2020). Wetland is likely the most suitable and safe roosting habitat for fledglings, possibly because of lower predation risk (Fournier et al. 2019; Natusch et al. 2017), and we expected the fledglings to stay longer at colonies where wetland habitat was more abundant; however, we observed the opposite effect. Perhaps, fledglings in those areas departed at a younger age because their parents were able to feed them more frequently and those fledglings were in better condition (Evans et al. 2020; Imlay et al. 2021). However, we noted that fledglings at RF Marguerite d'Youville tended to roost in wetland near the colony for several days after fledging but individuals at the Pointe-Claire colony used their nest box as a roosting location for several days, suggesting that the use of nest boxes as roost locations removes the need for other safe roosting spaces before fledglings depart the colony. We also found that purple martins hatched at earlier dates departed at an older age. Individuals hatched earlier are less constrained and likely have more time to increase reserves before departing (Tarof et al. 2011). Later individuals are more constrained and might depart at a younger age to increase departure synchrony within the colony and, later, migration synchrony (Grüebler and Naef-Daenzer 2010; Tarof et al. 2011). Departure synchrony could be driven by photoperiod or social cues (Bani Assadi and Fraser in review; Both 2010). We did not find an effect of brood size on departure seen in Bani Assadi and Fraser (in review). We also found that colonies at higher latitude had fledglings that departed at an older age, independent of first egg date. At more northern latitudes in the summer, day length is longer and photoperiod could influence timing of departure (Both 2010). We did not find these relationships with fledge age; possibly, fledging is more constrained than departure and could be genetically determined (Bani Assadi and Fraser in review).

We found that breeding success of purple martins and apparent post-fledging survival of juveniles in the area were high; 85% of juveniles in Ontario were detected in the post-fledging period where Motus tower density is high (Bani Assadi and Fraser in review) and 93% in Quebec were detected outside the nest after fledging or presumed fledging (day 28) if we were unable to determine an exact fledge date; however, Motus tower coverage density in southern Quebec is low and we were unable to follow many of the fledglings after they departed from their natal colony. Our Motus-tagged juveniles stayed around the colony up to a few weeks after fledging; however, we had difficulty locating roosts if they were not close to the colony. One of the caveats of radio telemetry is we could not confirm if the fledglings truly departed the area or if they died outside of the range of Motus towers. An enhanced network with additional receivers in southern Quebec and the northeastern US would be needed to evaluate survival of these fledglings after they departed the colony, and future work could study juvenile behaviour after fledglings depart the colony. One study examining the post-fledging period found that the post-fledging pre-migratory period is associated with high survival in purple martins (0.73-0.87, Tarof et al. 2011), but post-fledging survival is low in the first year of life; first-year juvenile purple martin survival is reported at 0.27 with late fledglings having higher rates of mortality possibly associated with carryover effects (Imlay et al. 2021; Stutchbury et al. 2009a; Tarof et al. 2011). It is possible that low post-fledging survival after colony departure is contributing to population declines. In juvenile barn swallows, survival declined after parents stopped caring for their young (Grüebler and Naef-Daenzer 2010). Because purple martins are panmictic in winter (Stutchbury et al. 2016b), winter location is unlikely to cause variation in population trends and juvenile mortality is a likely candidate for population declines in Quebec and Ontario (Tarof et al. 2011). Post-fledging survival during the pre-migration period was found to be relatively high in purple martins (0.73-0.87), and migration and the overwintering period together are associated with higher mortality (Tarof et al. 2011); therefore, migration might be attributed to high mortality in the northeastern population that must migrate a greater distance to reach overwintering areas. The pace of migration is influenced by body condition, stopover habitat quality, and weather, with late swallows migrating at a faster pace (Imlay et al. 2021). Therefore, carryover effects from the nestling and post-fledging pre-migratory periods, especially in individuals hatched later, may influence juvenile survival (Imlay et al. 2021; Tarof et al. 2011). Further work on juvenile purple martins should aim to quantify juvenile survival during the migration and overwintering periods to disentangle those two potential areas of mortality and determine the factors contributing to mortality in those periods, including carryover effects (Imlay et al. 2021; Tarof et al. 2011).

In our study, we aimed to examine possible causes of decline of northeastern purple martins. We demonstrate that purple martins in southern Quebec have breeding success comparable to other regions (Raleigh et al. 2019) and departure age is influenced by habitat composition, first egg date, and latitude. We suspect that the disproportionate decline in northeastern purple martins may be in part due to low juvenile survival, possibly driven by the greater migration distance of these individuals, greater seasonal constraints, and carryover effects resulting from these constraints (Imlay et al. 2021; Neufeld et al. 2021; Tarof et al. 2011). Perhaps wetland and open water habitat quality throughout their range is important for purple martins given their influence on fledgling departure from the colony.

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Permits

Animal Care Protocol: McGill University and University of Manitoba

Bird banding permits were issued by the Bird Banding Office of Canada and held by Simon Duval (Quebec) and Kevin Fraser (Ontario)

References

Bani Assadi S, Fraser KC. in review. Does hatch date set the clock? Timing of post-fledge movements for families of a colonially breeding, long-distance migratory songbird. Journal of Avian Biology.

Bédard S. 2016. Portrait de situation de l’hirondelle noire au québec. Montreal, Quebec: Regroupement QuébecOiseaux.

Berzins L, Clark R, Kardynal K, Krebs E, Mahony N, Morrissey C. 2020. Research, conservation and outreach priorities for conserving aerial insectivore populations in canada: Report from march 2020 aerial insectivore workshop in saskatoon, sk. Canada: Environment and Climate Change Canada & University of Saskatchewan.

Both C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. Current Biology. 20(3):243-248.

Boynton CK, Mahony NA, Williams TD. 2020. Barn swallow (hirundo rustica) fledglings use crop habitat more frequently in relation to its availability than pasture and other habitat types. The Condor. 122(2).

Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW, Hartl P, Kays R, Kelly JF, Robinson WD et al. 2011. Technology on the move: Recent and forthcoming innovations for tracking migratory birds. BioScience. 61(9):689-698.

Brown CR, Tarof SA, Poole AF. 2013. Purple martin (*progne subis*), version 2.0. The Birds of North America. Ithaca, NY: Cornell Lab of Ornithology.

Cox AR, Robertson RJ, Fedy BC, Rendell WB, Bonier F. 2018. Demographic drivers of local population decline in tree swallows (tachycineta bicolor) in ontario, canada. The Condor. 120(4):842-851.

Evans DR, Hobson KA, Kusack JW, Cadman MD, Falconer CM, Mitchell GW. 2020. Individual condition, but not fledging phenology, carries over to affect post-fledging survival in a neotropical migratory songbird. Ibis. 162(2):331-344.

Fournier AMV, Shave A, Fischer J, Siegrist J, Ray J, Cheskey E, MacIntosh M, Ritchie A, Pearman M, Applegate K et al. 2019. Precise direct tracking and remote sensing reveal the use of forest islands as roost sites by purple martins during migration. Journal of Field Ornithology. 90(3):258-265.

Fraser KC, Shave A, Savage A, Ritchie A, Bell K, Siegrist J, Ray JD, Applegate K, Pearman M. 2017. Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new gps technology. Journal of Avian Biology. 48(3):339-345.

Fraser KC, Stutchbury B, Silverio C, Kramer P, Barrow J, Newstead D, Mickle N, Cousens BF, Charlene Lee J, M Morrison D et al. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore.

Ghilain A, Bélisle M. 2008. Breeding success of tree swallows along a gradient of agricultural intensification. Ecological Applications. 18(5):1140-1154.

Grüebler MU, Naef-Daenzer B. 2010. Survival benefits of post-fledging care: Experimental approach to a critical part of avian reproductive strategies. Journal of Animal Ecology. 79(2):334-341.

Imlay TL, Mann HAR, Taylor PD. 2021. Autumn migratory timing and pace are driven by breeding season carryover effects. Animal Behaviour. 177:207-214.

Kusack JW, Mitchell GW, Evans DR, Cadman MD, Hobson KA. 2020. Effects of agricultural intensification on nestling condition and number of young fledged of barn swallows (hirundo rustica). Science of The Total Environment. 709:136195.

Maness TJ, Anderson DJ. 2013. Predictors of juvenile survival in birds. Ornithological Monographs. 78(1):1-55.

Michelson CI, Clark RG, Morrissey CA. 2018. Agricultural land cover does not affect the diet of tree swallows in wetland-dominated habitats. The Condor. 120(4):751-764.

Natusch DJD, Lyons JA, Shine R. 2017. Safety first: Terrestrial predators drive selection of highly specific nesting sites in colonial-breeding birds. Journal of Avian Biology. 48(8):1104-1113.

Nebel S, Casey J, Cyr M-A, Kardynal KJ, Krebs EA, Purves EF, BÈlisle M, Brigham RM, Knight EC, Morrissey C et al. 2020. Falling through the policy cracks: Implementing a roadmap to conserve aerial insectivores in north america. Avian Conservation and Ecology. 15(1).

Nebel S, Mills A, McCracken JD, Taylor PD. 2010. Declines of aerial insectivores in north america follow a geographic gradient. Avian Conservation and Ecology. 5(2):1.

Neufeld LR, Muthukumarana S, Fischer JD, Ray JD, Siegrist J, Fraser KC. 2021. Breeding latitude is associated with the timing of nesting and migration around the annual calendar among purple martin (progne subis) populations. Journal of Ornithology.

Quebec Breeding Bird Atlas. 1984-1989, 2010-2014. Quebec breeding bird atlas data. NatureCounts, a node of the Avian Knowledge Network, Birds Canada.

Raleigh D, Ray JD, Grisham BA, Siegrist J, Greene DU. 2019. Nest survival data confirm managed housing is an important component to the conservation of the eastern purple martin. Wildlife Society Bulletin. 43(1):93-101.

Rappole JH, Tipton AR. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology. 62(3):335-337.

Saracco JF, Royle JA, DeSante DF, Gardner B. 2010. Modeling spatial variation in avian survival and residency probabilities. Ecology. 91(7):1885-1891.

Smith AC, Hudson M-AR, Aponte VI, Francis CM. 2020. North american breeding bird survey - canadian trends website, data-version 2019. Gatineau, Quebec, K1A 0H3: Environment and Climate Change Canada.

Stutchbury BJM, Hill Iii JR, Kramer PM, Rush SA, Tarof SA. 2009. Sex and age-specific annual survival in a neotropical migratory songbird, the purple martin (*progne subis*). The Auk. 126(2):278-287.

Stutchbury BJM, Siddiqui R, Applegate K, Hvenegaard GT, Mammenga P, Mickle N, Pearman M, Ray JD, Savage A, Shaheen T et al. 2016. Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. The American Naturalist. 188(S1):S28-S40.

Tarof SA, Kramer PM, Hill JR, Tautin J, Stutchbury BJM. 2011. Brood size and late breeding are negatively related to juvenile survival in a neotropical migratory songbird. The Auk. 128(4):716-725.

Taylor LU, Woodworth BK, Sandercock BK, Wheelwright NT. 2018. Demographic drivers of collapse in an island population of tree swallows. The Condor. 120(4):828-841.

Taylor PD, Crewe TL, Mackenzie SA, Lepage D, Aubry Y, Crysler Z, Finney G, Francis CM, Guglielmo CG, Hamilton DJ et al. 2017. The motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology. 12(1).

Twining CW, Brenna JT, Lawrence P, Shipley JR, Tollefson TN, Winkler DW. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. Proceedings of the National Academy of Sciences. 113(39):10920.

Twining CW, Shipley JR, Winkler DW. 2018. Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. Ecology Letters. 21(12):1812-1820.

Weegman MD, Arnold TW, Dawson RD, Winkler DW, Clark RG. 2017. Integrated population models reveal local weather conditions are the key drivers of population dynamics in an aerial insectivore. Oecologia. 185(1):119-130.

GENERAL DISCUSSION

This thesis aims to address knowledge gaps in the purple martin's annual cycle to better pinpoint causes of decline. Previous purple martin research relating to habitat selection mainly studied roosting habitat (Bridge et al. 2016; Fournier et al. 2019; Fraser et al. 2017), and this thesis adds additional insight to the habitat requirements of breeding and overwintering adults as well as departure decisions in juvenile birds related to habitat (Figure 9).

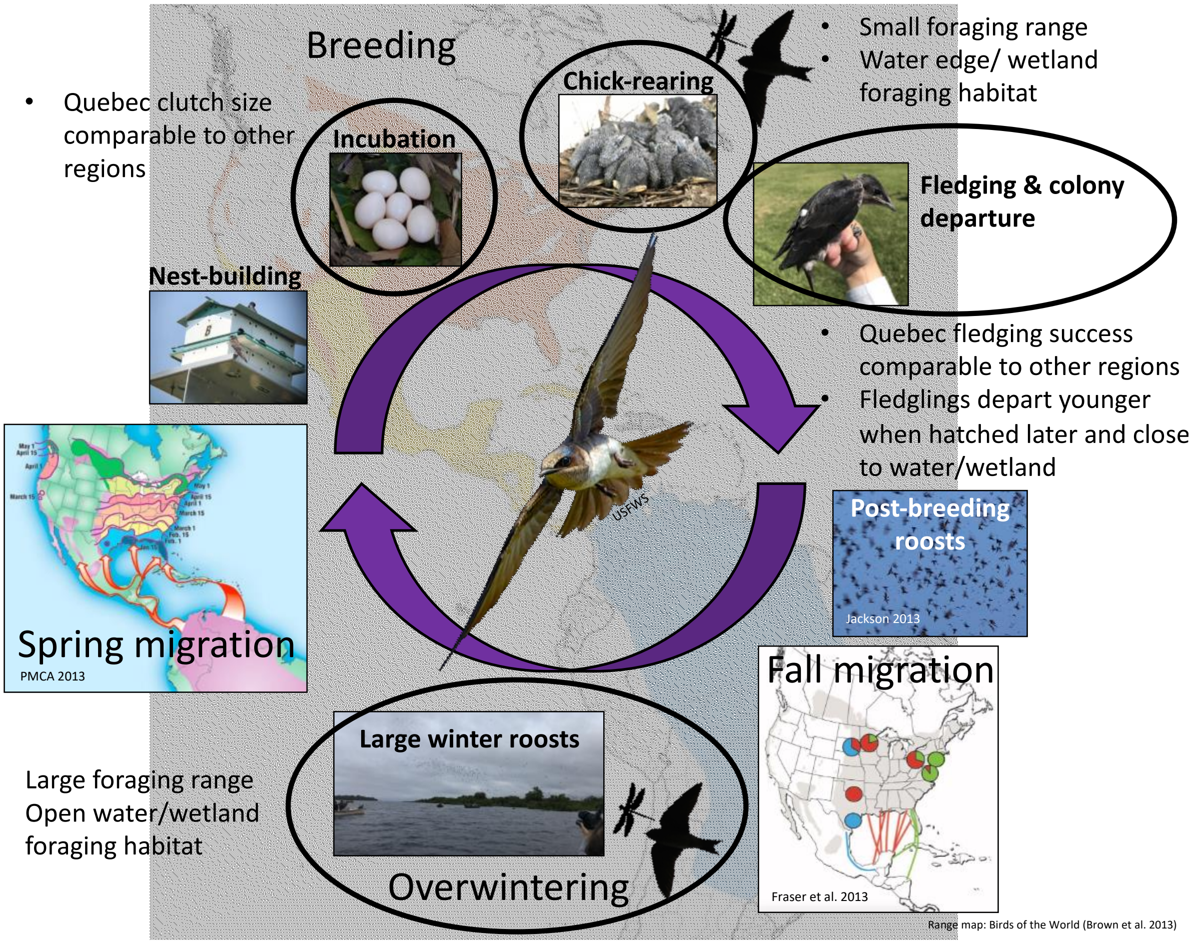


Figure 9. The annual cycle of purple martins with the main findings of my thesis.

Chapter 1 examined the foraging behaviour of adult purple martins and found that purple martins are constrained in foraging range size as predicted by the frequency of return to the central place. As predicted, breeding purple martins had smaller foraging ranges than non-breeding individuals. During chick-rearing, purple martins returned to the nest several times per hour, while non-breeding birds returned to a roost once per day. This suggests that quality habitat is needed close to the central place during breeding to fulfil the needs of adults and their nestlings, whereas, during the overwintering period, purple martins are less constrained and can travel farther to find suitable foraging habitat. Purple martins roosting in nutrient-poor black water in the Brazilian Amazon traveled to more productive white waters during the day to forage. Across breeding and non-breeding birds, purple martins preferred water-based habitats, suggesting the need to preserve these habitats.

Chapter 2 aimed to examine reproductive success in adult purple martins and fledgling behaviour in young birds. I predicted that reproductive success in Quebec would be poor compared to other regions, and fledglings would depart the colony at a younger age if they were hatched later and would stay at the colony longer if there was a greater presence of water-type habitats. However, reproductive success of southern Quebec purple martins in 2019-2020 was comparable to other locations in North America (Raleigh et al. 2019). Therefore, the cause of the decline should be elsewhere in the annual cycle, although reproduction poses constraints in adult foraging behaviour and may result in carryover effects into other stages in the annual cycle (Imlay et al. 2021). Younger birds departed colonies at a younger age where there is a higher proportion of available wetland and open water, suggesting that those birds were fed better by their parents and that water and wetland are therefore quality habitats for purple martins. Furthermore, fledglings hatching earlier departed at a later age, likely because they were not as constrained by food availability. The post-fledging period in young birds is relatively understudied, and future research should work to address that knowledge gap in purple martins and other aerial insectivores (Tarof et al. 2011). Future research should examine the post-fledging period in more detail to examine if it is a contributor to purple martin declines, breaking up the pre-migration post-fledging period, migration, and overwintering, and determine if there are carryover effects leading to mortality or future reproduction from the nestling and early fledging stages on future stages in the annual cycle of juvenile birds.

Both chapters suggest that water-based habitats are important for purple martins. This thesis shows that wetland and open water are important foraging habitats for adults and juveniles departed the colony earlier in the presence of these habitats. Current conservation practises for purple martins and other cavity-nesting aerial insectivores involve providing and maintaining nest boxes (Cox et al. 2018; Raleigh et al. 2019); however, conservation efforts should also focus on preserving water-based habitats to prevent habitat loss and degradation. In Quebec, purple martins are largely restricted to large water bodies, further highlighting the need for habitat conservation (Quebec Breeding Bird Atlas 1984-1989, 2010-2014). Conservation decisions should also consider airspace use by purple martins as they are a species that forages on flying insects up to several hundred metres in altitude (Dreelin et al. 2018). Globally, insects are declining (Forister et al. 2019; Nebel et al. 2020; Sánchez-Bayo and Wyckhuys 2019), and conservation efforts should act on the abundant knowledge surrounding insect declines (Forister et al. 2019) to implement conservation measures to ensure a continued food supply to this declining aerial insectivore.

GENERAL CONCLUSION AND SUMMARY

My research aimed to examine gaps in the annual cycle of the purple martin to better understand their decline. Adult purple martins selected wetland and open water habitats for foraging during the chick-rearing and over-wintering periods. Breeding purple martins returning to the nest several times per hour were more constrained in foraging range size than over-wintering individuals that returned to a roost once per day. Departure from the colony of young fledgling birds was predicted by the presence of open water and wetland such that water-based habitats were associated with earlier departure, suggesting that those habitats have more food available and therefore those fledglings were able to depart at a younger age. Water-based habitats were therefore important during multiple stages in the life cycle of the purple martin. Future research should address knowledge gaps in the survival and causes of mortality juvenile purple martins and work to better understand how the airspace, where purple martins forage, is linked to the habitats below. Current conservation efforts focus on providing and maintaining artificial nest box structures (Raleigh et al. 2019), but conservation efforts should also focus on preserving wetland and open water habitats where purple martins forage, especially in southern Quebec where purple martins have declined more strongly than in many other regions. Perhaps, these results can also be useful when considering conservation measures for other swallows with similar life history traits.

SUPPLEMENTARY MATERIALS for Chapter 1

Extended methodology and results

Data collection

Fieldwork for this study was carried out from 2016 to 2020 across 4 regions: Quebec (Canada), Pennsylvania (USA), Florida (USA), and Texas (USA). Nests were monitored approximately twice per week to follow breeding success. Chick-rearing adult purple martins were captured in their nest boxes using either (1) a trap door on the outside of the compartment that could be manually lowered when the individual went in its nest compartment, (2) a lightweight trap door propped up by a stick inside the nest compartment, or (3) a paint roller attached to a long pole. We used targeted trapping to avoid causing unnecessary stress to non-target individuals (Stutchbury et al. 2013). GPS units (Lotek PinPoint10 or Pathtrack, ~1g) were deployed on 101 individuals between 2016 and 2020. We attached GPS units using leg-loop harnesses (Rappole and Tipton 1991). The combination of GPS and harness weighed no more than 3% of an individual's body mass (Barron et al. 2010). Each individual was banded and we took standard measurements (age, sex, fat score, mass, and wing chord). In Quebec, breeding GPSs were programmed to take points every 10 minutes beginning approximately 30 minutes before sunrise. In Orlando, Florida, 73 GPS units (Lotek PinPoint10, ~1g), were deployed on chick-rearing birds in 2016, 2017, and 2018 across 7 colonies. GPS units were programmed to take points beginning 30 minutes before sunrise for either 1-minute or 10-minute intervals. In Texas, 8 GPS units (Lotek PinPoint10, ~1g), were deployed on chick-rearing individuals with 4 points recorded per day, 3 during the day and 1 at night, and two units were retrieved. Non-breeding tracks from 8 individuals (Pathtrack nanoFix GEO-MINI or Lotek PinPoint10, ~1g, 2018-2020) were deployed in the breeding season prior to migration and recaptured on return to southern Quebec (Canada), Orlando (Florida, USA), Erie (Pennsylvania, USA), or Amarillo (Texas, USA) the following year. Non-breeding tags were programmed to take points two to four times per day, typically with one point at night to confirm roost location.

Foraging range

We analysed foraging range of every GPS track, using colony or roost as a central place. Distance from the colony or roost was calculated for every point, and then points labeled as foraging (>100m from the colony to remove points where birds were presumably carrying food to and from their nests for breeding birds, and points during the day for non-breeding birds) were selected. Foraging range was conducted for each individual using the ctmm package (Calabrese et al. 2016) in R. This package accounts for autocorrelation among points, sampling frequency, and number of points, though we discarded any individual foraging points with fewer than 10 points. To examine predictors of breeding bird foraging area, we constructed a linear mixed model with foraging range as the dependent variable and breeding status (chick-rearing or non-breeding), latitude, and the interaction between latitude and breeding status as fixed effects and year as a random effect using the R packages lme4 and lmerTest.

Habitat selection analysis

We analysed habitat selection in four regions: Quebec, Florida, the Amazon, and dry diagonal (central South America). For habitat selection analysis, we generated two sets of random points: one based on the distance distribution (exponential) of each individual's GPS data to examine local-scale selection and another based on twice the distance distribution to examine selection at a broader scale. We used 30m Landsat and RapidEye raster land cover data for North America from the Commission for Environmental Cooperation (2015) and 100m land cover data derived from Copernicus Global Land Operations (2020) for South America. We simplified land cover data; for example, we aggregated forest types into a single category. Wetland is defined as land cover where vegetation is adapted to live in soils saturated by water throughout the year or at least seasonally, including marshes, swamps, bogs, and, particularly in the Amazon, seasonally flooded forest. We define open water as water land cover consisting of freshwater bodies including rivers and lakes, as purple martins did not use salt water in our study. We extracted nearest water sediment value for purple martins in the Amazon using a raster of river sediment values for the Amazon basin (Fassoni-Andrade and Paiva 2019; Laranjeiras et al. 2021). For both GPS points and randomly generated locations, we created 100m, 200m, and 500m buffers around each point for breeding birds and 250m, 500m, 1000m for non-breeding birds and generated habitat selection models for each Quebec (breeding), Florida (breeding), Amazon (non-breeding), and dry diagonal (non-breeding) comparing used vs random habitats. For each wetland and open water, we calculated the length of edge between each of those habitat types and adjacent habitat types within the buffers surrounding points and refer to each those as "wetland edge" and "water edge", respectively. In our resource selection models, we used colony as a random effect for breeding birds and ID for non-breeding birds. We added year as a fixed effect for regions that had more than one year; all had 3 years or less. We carried out logistic regression using the "glmer" function in the R package lme4 and selected buffer size using AIC selection. We created correlation matrices for each Florida and Quebec. For each region, we removed strongly correlated habitat types from the models to reduce multicollinearity. In Florida, wetland and developed habitats were strongly correlated ($R^2 = -0.90$ 1x, $R^2 = -0.86$ 2x model); thus, developed habitat was removed from the habitat selection analysis as we believed it to be less biologically relevant. Furthermore, for both the Amazon and dry diagonal, forest was strongly correlated with other habitat types and was removed (Amazon: forest and water $R^2 = -0.83$ 1x, $R^2 = -0.77$ 2x; dry diagonal: forest and grassland, shrubland, cropland $R^2 = -0.90$ 1x, $R^2 = -0.92$ 2x), and wetland and wetland edge (Amazon: $R^2 = 0.74$ 1x, $R^2 = 0.73$ 2x; dry diagonal: $R^2 = 0.82$ 1x, $R^2 = 0.89$ 2x) and open water and water's edge (Amazon: $R^2 = 0.42$ 1x, $R^2 = 0.46$ 2x; dry diagonal: $R^2 = 0.74$ 1x, $R^2 = 0.77$ 2x) were strongly correlated, and we removed the edge habitats from the model. For Quebec, the 50m buffer size ranked best while the 200m buffer size ranked best for Florida based on AIC. The 1000m buffer Amazon model ranked the best and we chose the 1000m buffer size for the dry diagonal as the 500m and 1000m models were within AIC=0.2 of each other to allow us to better compare the non-breeding models (see Supplementary Table 1).

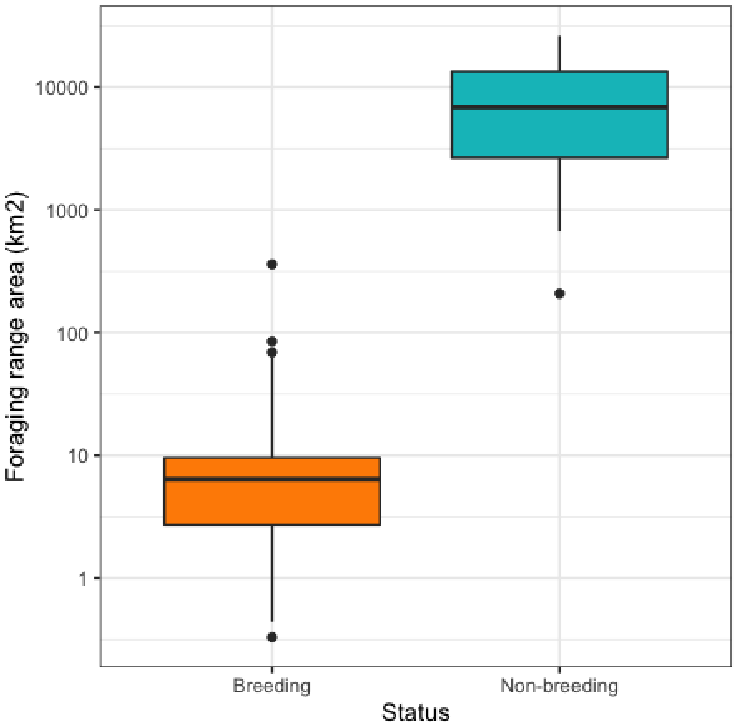
Supplementary Table 1. AIC rankings of models with different buffer sizes. Bolded AIC values represent selected models.

Breeding									Non-breeding								
	Quebec				Florida					Amazon				Dry diagonal			
	1x distance		2x distance		1x distance		2x distance			1x distance		2x distance		1x distance		2x distance	
Buffer (m)	df	AIC	df	AIC	df	AIC	df	AIC	Buffer (m)	df	AIC	df	AIC	df	AIC	df	AIC
50	10	**2826**	10	**2782**	11	14839	11	14663	250	10	674	10	682	8	914	8	924
100	10	2841	10	2792	11	14814	11	14628	500	10	664	10	675	8	908	8	919
200	10	2844	10	2784	11	**14807**	11	**14628**	1000	10	**657**	10	**667**	8	**908**	8	**916**

After selecting the optimal buffer size for each region, we compared different model types: full, water-based, natural, open, and null models. For all regions, the full model ranked best based on AIC (see Supplementary Table 2).

Supplementary Table 2. AIC rankings of different habitat type models. Bolded AIC values represent selected model.

	Breeding								Non-breeding							
	Quebec 50m				Florida 200m				Amazon 1000m				Dry diagonal 1000m			
	1x distance		2x distance		1x distance		2x distance		1x distance		2x distance		1x distance		2x distance	
Model	df	AIC	df	AIC	df	AIC	df	AIC	df	AIC	df	AIC	df	AIC	df	AIC
Full	10	**2826**	10	**2782**	11	**14807**	11	**14628**	10	**657**	10	**667**	8	**908**	8	**916**
Water-based	7	2831	7	2795	9	14815	9	14639	8	657	8	668	6	915	6	921
Natural	5	2875	5	2851	7	14892	7	14745	6	730	6	741	5	917	5	920
Open	4	2868	4	2845	6	14859	6	14701	7	738	7	745	6	911	6	917
Null	3	2874	3	2850	5	14932	5	14794	5	736	5	745	4	922	4	921



Supplementary Figure 1. Log-scaled foraging area among breeding and non-breeding birds ($t_{7.88}$=5.62, p<0.01)

Resource selection function results

Supplementary Table 3. R^2 for selected models

	Quebec		Florida		Amazon		Dry diagonal	
	1x	2x	1x	2x	1x	2x	1x	2x
R^2	0.10	0.46	0.03	0.06	0.26	0.20	0.07	0.08
Nagelkerke's R^2	0.03	0.04	0.01	0.02	0.17	0.17	0.04	0.02
McFadden's R^2	0.02	0.03	0.01	0.01	0.12	0.12	0.02	0.01
Cox and Snell R^2	0.02	0.03	0.01	0.01	0.10	0.10	0.02	0.01

Supplementary Table 4. Model output for Quebec habitat selection (R^2 = 10%) with a 50m buffer.

	Estimate	Std. error	z value	p value
(Intercept)	-3.03	0.281	**-10.8**	**< 0.001**
Barren, developed	12.9	22.2	0.582	0.6
Grassland, shrubland, cropland	12.4	22.2	0.559	0.6

Forest	12.9	22.2	0.58	0.6
Wetland	13.6	22.2	0.61	0.5
Open water	11.5	22.2	0.518	0.6
Wetland edge	-0.00621	0.00242	**-2.57**	**0.01**
Water edge	0.00741	0.00131	**5.66**	**< 0.001**
log(Distance to colony)	0.236	0.0429	**5.51**	**< 0.001**

Supplementary Table 5. Model output for Quebec 2x habitat selection ($R^2 = 46\%$) with a 50m buffer.

	Estimate	Std. error	z value	p value
(Intercept)	-0.788	0.345	**-2.29**	**0.02**
Barren, developed	15.3	21.3	0.716	0.5
Grassland, shrubland, cropland	14.8	21.3	0.692	0.5
Forest	15.2	21.3	0.713	0.5
Wetland	15.8	21.3	0.739	0.5
Open water	13.7	21.3	0.641	0.5
Wetland edge	-0.00568	0.00243	**-2.33**	**0.02**
Water edge	0.00760	0.00129	**5.91**	**< 0.001**
log(Distance to colony)	-0.156	0.0372	**-4.19**	**< 0.001**

Supplementary Table 6. Florida best model output ($R^2 = 3\%$) with a 200m buffer. Models exclude urban because of its high (negative) correlation with wetland.

	Estimate	Std. error	z value	p value
(Intercept)	-2.41	0.134	**-18.0**	**<0.001**
Grassland, shrubland, cropland	-0.386	0.210	-1.84	0.07
Forest	-1.364	0.512	**-2.67**	**0.008**
Wetland	0.650	0.0727	**8.96**	**<0.001**
Open water	-0.477	0.447	-1.07	0.29
Wetland edge	0.000313	0.000580	0.540	0.59
Water edge	0.00169	0.00170	0.992	0.32

log(Distance to colony)	0.128	0.0190	**6.71**	**< 0.001**
Year2017	-0.0188	0.0685	-0.274	0.78
Year2018	-0.0462	0.0633	-0.731	0.46

Supplementary Table 7. Florida best model output (R^2 = 6%) with a 200 m buffer and 2x distance distribution. Models exclude urban because of its high (negative) correlation with wetland (200m buffer).

	Estimate	Std. error	z value	p value
(Intercept)	-0.0191	0.122	-0.157	0.88
Grassland, shrubland, cropland	-0.458	0.203	**-2.26**	**0.024**
Forest	-1.44	0.500	**-2.88**	**0.0040**
Wetland	0.723	0.0692	**10.4**	**<0.001**
Open water	-0.384	0.393	-0.978	0.33
Wetland edge	0.000876	0.000590	1.49	0.14
Water edge	0.000381	0.00164	0.232	0.82
log(Distance to colony)	-0.237	0.0171	**-13.8**	**<0.001**
Year2017	-0.0467	0.0530	-0.882	0.38
Year2018	0.0594	0.0559	1.06	0.3

Supplementary Table 8. Model output for the Amazon (R^2 = 26%) removing forest, wetland edge, and water edge with 1000m buffer.

	Estimate	Std. error	z value	p value
(Intercept)	-3.47	0.997	**-3.44**	**< 0.001**
Grassland, shrubland, cropland	-3.34	2.54	-1.32	0.2
Barren, developed	1.96	1.31	1.49	0.1
Open water	-2.38	0.688	**-3.46**	**< 0.001**
Wetland	4.03	0.525	**7.68**	**< 0.001**
Nearest water sediment	0.0184	0.00733	**2.51**	**0.01**
log(Distance to roost)	0.161	0.100	1.61	0.1
Year2019	-0.115	0.274	-0.418	0.7

Year2020	0.131	0.375	0.350	0.7

Supplementary Table 9. Model output for the Amazon (R^2 = 20%) removing forest, wetland edge, and water edge with 1000m buffer at a 2x distance distribution.

	Estimate	Std. error	z value	p value
(Intercept)	1.40	0.850	1.65	0.1
Grassland, shrubland, cropland	-3.88	2.38	-1.63	0.1
Barren, developed	1.93	1.58	1.23	0.2
Open water	-2.19	0.632	**-3.45**	**< 0.001**
Wetland	3.22	0.452	**7.12**	**< 0.001**
Nearest water sediment	0.0333	0.00789	**4.23**	**< 0.001**
log(Distance to roost)	-0.318	0.0830	**-3.83**	**< 0.001**
Year2019	0.0889	0.265	0.335	0.7
Year2020	0.338	0.375	0.900	0.4

Supplementary Table 10. Model output for the dry diagonal (R^2 = 7%) removing forest, wetland edge, and water edge with 1000m buffer.

	Estimate	Std. error	z value	p value
(Intercept)	-4.74	0.700	**-6.77**	**< 0.001**
Grassland, shrubland, cropland	-0.775	0.236	**-3.28**	**0.001**
Barren, developed	-2.65	5.11	**-0.519**	**< 0.001**
Open water	1.71	0.666	**2.56**	**0.01**
Wetland	0.700	0.999	0.697	0.5
log(Distance to roost)	0.332	0.0722	**4.60**	**< 0.001**
Year2020	-0.292	0.183	-1.60	0.1

Supplementary Table 11. Model output for the dry diagonal (R^2 = 8%) removing forest, wetland edge, and water edge with 1000m buffer at a 2x distance distribution.

	Estimate	Std. error	z value	p value
(Intercept)	-0.209	0.634	-0.329	0.7

Grassland, shrubland, cropland	-0.490	0.233	**-2.10**	**0.04**
Barren, developed	-10.0	6.29	-1.59	0.1
Open water	1.28	0.772	1.66	0.10
Wetland	1.028	1.25	0.822	0.4
log(Distance to roost)	-0.144	0.0637	**-2.27**	**0.02**
Year2020	0.0396	0.177	0.223	0.8

REFERENCES

Arab A, Courter JR, Zelt J. 2016. A spatio-temporal comparison of avian migration phenology using citizen science data. Spatial Statistics. 18:234-245.

Baker AJ, Greenslade AD, Darling LM, Finlay JC. 2008. High genetic diversity in the blue-listed british columbia population of the purple martin maintained by multiple sources of immigrants. Conservation Genetics. 9(3):495-505.

Bani Assadi S, Fraser KC. in review. Does hatch date set the clock? Timing of post-fledge movements for families of a colonially breeding, long-distance migratory songbird. Journal of Avian Biology.

Barbosa P. in prep. Holidays in the amazon? Use and selection of the habitat of a migratory bird, the purple martin (*progne subis*, hirundinidae), during the winter period in the brazilian amazon. [Brazil].

Barron DG, Brawn JD, Weatherhead PJ. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods in Ecology and Evolution. 1(2):180-187.

Bédard S. 2016. Portrait de situation de l'hirondelle noire au québec. Montreal, Quebec: Regroupement QuébecOiseaux.

Bédard S. 2016. Portrait de situation de l'hirondelle noire au québec. Regroupement QuebecOiseaux.

Bent AC. 1963. Life histories of north american flycatchers, larks, swallows, and their allies. New York: Dover Publications.

Berzins L, Clark R, Kardynal K, Krebs E, Mahony N, Morrissey C. 2020. Research, conservation and outreach priorities for conserving aerial insectivore populations in canada: Report from march 2020 aerial insectivore workshop in saskatoon, sk. Canada: Environment and Climate Change Canada & University of Saskatchewan.

Progne cryptoleuca. 2016a. The IUCN Red List of Threatened Species 2016: e.T22712101A94319636; [accessed 2021 July 30].

Progne dominicensis. 2016b. The IUCN Red List of Threatened Species 2016: e.T22712104A94319815; [accessed 2021 July 30].

Progne elegans. 2016c. The IUCN Red List of Threatened Species 2016: e.T22731723A95037131; [accessed 2021 July 30].

Progne subis. 2016d. The IUCN Red List of Threatened Species 2016: e.T22712098A94319217; [accessed 2021 July 30].

Progne chalybea. 2020a. The IUCN Red List of Threatened Species 2020: e.T22712110A137689287; [accessed 2021 July 30].

Progne modesta. 2020b. [accessed 2021 July 30].

Progne murphyi. 2020c. The IUCN Red List of Threatened Species 2020: e.T22731728A180918515; [accessed 2021 July 30].

Progne sinaloae. 2020d. The IUCN Red List of Threatened Species 2020: e.T22712107A179699060; [accessed 2021 July 30].

Progne tapera. 2020e. The IUCN Red List of Threatened Species 2020: e.T22712092A137688210.; [accessed 2021 July 30].

Bogotá-Gregory JD, Lima FCT, Correa SB, Silva-Oliveira C, Jenkins DG, Ribeiro FR, Lovejoy NR, Reis RE, Crampton WGR. 2020. Biogeochemical water type influences community composition, species richness, and biomass in megadiverse amazonian fish assemblages. Scientific Reports. 10(1):15349.

Both C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. Current Biology. 20(3):243-248.

Boynton CK, Mahony NA, Williams TD. 2020. Barn swallow (*hirundo rustica*) fledglings use crop habitat more frequently in relation to its availability than pasture and other habitat types. The Condor. 122(2).

Bridge ES, Pletschet SM, Fagin T, Chilson PB, Horton KG, Broadfoot KR, Kelly JF. 2016. Persistence and habitat associations of purple martin roosts quantified via weather surveillance radar. Landscape Ecology. 31(1):43-53.

Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW, Hartl P, Kays R, Kelly JF, Robinson WD et al. 2011. Technology on the move: Recent and forthcoming innovations for tracking migratory birds. BioScience. 61(9):689-698.

Brown CR. 1975. Polygamy in the purple martin. The Auk. 92(3):602-604.

Brown CR. 1978. Inadequacies in the design of purple martin houses. Bird-Banding. 49(4):321-325.

Brown CR, Tarof SA, Poole AF. 2013. Purple martin (*progne subis*), version 2.0. The Birds of North America. Ithaca, NY: Cornell Lab of Ornithology.

Calabrese JM, Fleming CH, Gurarie E. 2016. Ctmm: An r package for analyzing animal relocation data as a continuous-time stochastic process. Methods in Ecology and Evolution. 7(9):1124-1132.

Camacho C, Palacios S, Sáez P, Sánchez S, Potti J. 2014. Human-induced changes in landscape configuration influence individual movement routines: Lessons from a versatile, highly mobile species. PLoS One. 9(8):e104974.

Collins PM, Green JA, Elliott KH, Shaw PJA, Chivers L, Hatch SA, Halsey LG. 2020. Coping with the commute: Behavioural responses to wind conditions in a foraging seabird. Journal of Avian Biology. 51(4):1-11.

Collins PM, Green JA, Warwick-Evans V, Dodd S, Shaw PJA, Arnould JPY, Halsey LG. 2015. Interpreting behaviors from accelerometry: A method combining simplicity and objectivity. Ecology and Evolution. 5(20):4642-4654.

Collins PM, Halsey LG, Arnould JPY, Shaw PJA, Dodd S, Green JA. 2016. Energetic consequences of time-activity budgets for a breeding seabird. Journal of Zoology. 300(3):153-162.

Cooper NW, Thomas MA, Marra PP. 2021. Vertical sexual habitat segregation in a wintering migratory songbird. Ornithology. 138(1).

COSEWIC. 2017. Cosewic assessment and status report on the northern saw-whet owl brooksi subspecies *aegolius acadicus brooksi* in canada. In: Wildlife CotSoE, Canada i, editors. Ottawa: Committee on the Status of Endangered Wildlife in Canada. p. xi + 34.

Cousens NBF, Lee JC. 2012. Status report on the western purple martin [*progne subis arboricola*] in british columbia. Victoria, B.C., Canada: Prepared for the British Columbia Ministry of Environment.

Cox AR, Robertson RJ, Fedy BC, Rendell WB, Bonier F. 2018. Demographic drivers of local population decline in tree swallows (*tachycineta bicolor*) in ontario, canada. The Condor. 120(4):842-851.

Davidar P, Morton ES. 2006. Are multiple infections more severe for purple martins (*progne subis*) than single infections? The Auk. 123(1):141-147.

Davy CM, Ford AT, Fraser KC. 2017. Aeroconservation for the fragmented skies. Conservation Letters. 10(6):773-780.

Doughty RW, Fergus R. 2002. The purple martin. Austin: University of Texas Press.

Dreelin RA, Shipley JR, Winkler DW. 2018. Flight behavior of individual aerial insectivores revealed by novel altitudinal dataloggers. Frontiers in Ecology and Evolution. 6(182).

Dunoyer J. 2021. Analyzing purple martin habitat, foraging range, and diet composition through biologging and DNA barcoding. [Sainte-Anne-de-Bellevue, Canada]: McGill University.

Elliott KH, Bull RD, Gaston AJ, Davoren GK. 2009. Underwater and above-water search patterns of an arctic seabird: Reduced searching at small spatiotemporal scales. Behav Ecol Sociobiol. 63.

Elliott KH, Le Vaillant M, Kato A, Speakman JR, Ropert-Coudert Y. 2013. Accelerometry predicts daily energy expenditure in a bird with high activity levels. Biol Lett. 9.

Emmons LH. 1984. Geographic variation in densities and diversities of non-flying mammals in amazonia. Biotropica. 16(3):210-222.

Evans DR, Hobson KA, Kusack JW, Cadman MD, Falconer CM, Mitchell GW. 2020. Individual condition, but not fledging phenology, carries over to affect post-fledging survival in a neotropical migratory songbird. Ibis. 162(2):331-344.

Fassoni-Andrade AC, Paiva RCDd. 2019. Mapping spatial-temporal sediment dynamics of river-floodplains in the amazon. Remote Sensing of Environment. 221:94-107.

Forister ML, Pelton EM, Black SH. 2019. Declines in insect abundance and diversity: We know enough to act now. Conservation Science and Practice. 1(8):e80.

Forsman AM, Hoenig BD, Gaspar SA, Fischer JD, Siegrist J, Fraser K. submitted. Evaluating the impacts of metabarcoding primer selection on DNA characterization of diet in an aerial insectivore, the purple martin. Submitted to Ornithology.

Fournier AMV, Shave A, Fischer J, Siegrist J, Ray J, Cheskey E, MacIntosh M, Ritchie A, Pearman M, Applegate K et al. 2019. Precise direct tracking and remote sensing reveal the use of forest islands as roost sites by purple martins during migration. Journal of Field Ornithology. 90(3):258-265.

Fraser DF, Copely D, Finlay JC. 1999. The return of the purple martin in british columbia. In: Biodiversity BCE, editor. Proc. Conference Biology & Management of Species and Habitats at Risk. p. 279-282.

Fraser KC, Davies KTA, Davy CM, Ford AT, Flockhart DTT, Martins EG. 2018. Tracking the conservation promise of movement ecology. Frontiers in Ecology and Evolution. 6:150.

Fraser KC, Shave A, Savage A, Ritchie A, Bell K, Siegrist J, Ray JD, Applegate K, Pearman M. 2017. Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new gps technology. Journal of Avian Biology. 48(3):339-345.

Fraser KC, Stutchbury B, Silverio C, Kramer P, Barrow J, Newstead D, Mickle N, Cousens BF, Charlene Lee J, M Morrison D et al. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore.

Fraser KC, Stutchbury BJM, Kramer P, Silverio C, Barrow J, Newstead D, Mickle N, Shaheen T, Mammenga P, Applegate K et al. 2013. Consistent range-wide pattern in fall migration strategy of purple martin (*progne subis*), despite different migration routes at the gulf of mexico. The Auk. 130(2):291-296.

Fuller RM, Devereux BJ, Gillings S, Amable GS. 2005. Indices of bird-habitat preference from field surveys of birds and remote sensing of land cover: A study of south-eastern england with wider implications for conservation and biodiversity assessment. Global Ecology and Biogeography. 14(3):223-239.

Gauthreaux SA, Jr. 1996. Bird migration: Methodologies and major research trajectories (1945-1995). The Condor. 98(2):442-453.

Gese EM, Terletzky PA, Cavalcanti SMC. 2016. Identification of kill sites from gps clusters for jaguars *panthera onca* in the southern pantanal, brazil. Wildlife Research. 43(2):130-139.

Ghilain A, Bélisle M. 2008. Breeding success of tree swallows along a gradient of agricultural intensification. Ecological Applications. 18(5):1140-1154.

Grüebler MU, Naef-Daenzer B. 2010. Survival benefits of post-fledging care: Experimental approach to a critical part of avian reproductive strategies. Journal of Animal Ecology. 79(2):334-341.

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T et al. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PloS one. 12(10):e0185809-e0185809.

Hallworth MT, Marra PP. 2015. Miniaturized gps tags identify non-breeding territories of a small breeding migratory songbird. Scientific Reports. 5(1):11069.

Helms JA, Godfrey AP, Ames T, Bridge ES. 2016. Predator foraging altitudes reveal the structure of aerial insect communities. Scientific Reports. 6:28670.

Hill JRI. 1993. A giant martin roost on the amazon river. Purple Martin Update. 4:5-7.

Houston AI, McNamara JM. 1985. A general theory of central place foraging for single-prey loaders. Theoretical Population Biology. 28(3):233-262.

Imlay TL, Angelier F, Hobson KA, Mastromonaco G, Saldanha S, Leonard ML. 2019. Multiple intrinsic markers identify carry-over effects from wintering to breeding sites for three nearctic–neotropical migrant swallows. The Auk. 136(4).

Imlay TL, Mann HAR, Taylor PD. 2021. Autumn migratory timing and pace are driven by breeding season carryover effects. Animal Behaviour. 177:207-214.

Imlay TL, Mills Flemming J, Saldanha S, Wheelwright NT, Leonard ML. 2018. Breeding phenology and performance for four swallows over 57 years: Relationships with temperature and precipitation. Ecosphere. 9(4):e02166.

Jacobsen LB, Jensen NO, Willemoes M, Hansen L, Desholm M, Fox AD, Tøttrup AP, Thorup K. 2017. Annual spatiotemporal migration schedules in three larger insectivorous birds: European nightjar, common swift and common cuckoo. Animal Biotelemetry. 5(1):4.

James DA, Neal JC. 1986. Arkansas birds : Their distribution and abundance. Fayetteville: University of Arkansas Press.

Janzen DH, Hallwachs W. 2019. Perspective: Where might be many tropical insects? Biological Conservation. 233:102-108.

Kacelnik A. 1984. Central place foraging in starlings (*sturnus vulgaris*). I. Patch residence time. Journal of Animal Ecology. 53(1):283-299.

Kacelnik A, Cuthill I. 1990. Central place foraging in starlings (*sturnus vulgaris*). Ii. Food allocation to chicks. Journal of Animal Ecology. 59(2):655-674.

Kay RF, Madden RH, Van Schaik C, Higdon D. 1997. Primate species richness is determined by plant productivity: Implications for conservation. Proceedings of the National Academy of Sciences. 94(24):13023.

Kelly JF, Bridge ES, Frick WF, Chilson PB. 2013. Ecological energetics of an abundant aerial insectivore, the purple martin. PLoS ONE. 8(9):e76616.

Kotzerka J, Garthe S, Hatch SA. 2010. Gps tracking devices reveal foraging strategies of black-legged kittiwakes. Journal of Ornithology. 151(2):459-467.

Kusack JW, Mitchell GW, Evans DR, Cadman MD, Hobson KA. 2020. Effects of agricultural intensification on nestling condition and number of young fledged of barn swallows (*hirundo rustica*). Science of The Total Environment. 709:136195.

Lalla KM, Whelan S, Brown K, Patterson A, Jimenez AG, Hatch SA, Elliott KH. 2020. Accelerometry predicts muscle ultrastructure and flight capabilities in a wild bird. The Journal of Experimental Biology. 223(22):jeb234104.

Laranjeiras TO, Naka LN, Leite GA, Cohn-Haft M. 2021. Effects of a major amazonian river confluence on the distribution of floodplain forest avifauna. Journal of Biogeography. 48(4):847-860.

Lavallée CD, Bani Assadi S, Korpach AM, Ray JD, Fischer JD, Siegrist J, Fraser KC. 2021. The use of nocturnal flights for barrier crossing in a diurnally migrating songbird. Movement Ecology. 9(21):11.

Loring PH, Griffin CR, Sievert PR, Spiegel CS. 2017. Comparing satellite and digital radio telemetry to estimate space and habitat use of american oystercatchers (*haematopus palliatus*) in massachusetts, USA. Waterbirds. 40(sp1):19-31.

Maness TJ, Anderson DJ. 2013. Predictors of juvenile survival in birds. Ornithological Monographs. 78(1):1-55.

Mattsson BJ, Niemi GJ. 2008. Causes and consequences of distribution patterns in a migratory songbird across its geographic range. Canadian Journal of Zoology. 86(4):314-328.

Mayfield HF. 1969. Purple martin population changes over fifteen years. The Auk. 86(3):522-528.

McCarty JP, Winkler DW. 1999. Foraging ecology and diet selectivity of tree swallows feeding nestlings. The Condor. 101(2):246-254.

Mead CJ. 1979. Mortality and causes of death in british sand martins. Bird Study. 26(2):107-112.

Michelson CI, Clark RG, Morrissey CA. 2018. Agricultural land cover does not affect the diet of tree swallows in wetland-dominated habitats. The Condor. 120(4):751-764.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America. 105(49):19052-19059.

Natusch DJD, Lyons JA, Shine R. 2017. Safety first: Terrestrial predators drive selection of highly specific nesting sites in colonial-breeding birds. Journal of Avian Biology. 48(8):1104-1113.

Nebel S, Casey J, Cyr M-A, Kardynal KJ, Krebs EA, Purves EF, Bélisle M, Brigham RM, Knight EC, Morrissey C et al. 2020. Falling through the policy cracks: Implementing a roadmap to conserve aerial insectivores in north america. Avian Conservation and Ecology. 15(1).

Nebel S, Mills A, McCracken JD, Taylor PD. 2010. Declines of aerial insectivores in north america follow a geographic gradient. Avian Conservation and Ecology. 5(2):1.

Neufeld LR, Muthukumarana S, Fischer JD, Ray JD, Siegrist J, Fraser KC. 2021. Breeding latitude is associated with the timing of nesting and migration around the annual calendar among purple martin (*progne subis*) populations. Journal of Ornithology.

Nocera JJ, Blais JM, Beresford DV, Finity LK, Grooms C, Kimpe LE, Kyser K, Michelutti N, Reudink MW, Smol JP. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous chimney swifts. Proceedings of the Royal Society B: Biological Sciences. 279(1740):3114.

North American Bird Conservation Initiative Canada. 2019. The state of canada's birds, 2019. Ottawa, Canada: Environment and Climate Change Canada.

Orians GH, Pearson NE. 1979. On the theory of central place foraging. In: Horn DJ, Mitchell R, Stair GR, editors. Analysis of ecological systems. Columbus: Ohio State University Press. p. 155-177.

Pardieck KL, Ziolkowski Jr. DJ, Lutmerding M, Aponte VI, Hudson M-AR. 2020. North american breeding bird survey dataset 1966 - 2019: U.S. Geological survey data release.

Patterson A, Gilchrist HG, Chivers L, Hatch S, Elliott K. 2019. A comparison of techniques for classifying behavior from accelerometers for two species of seabird. Ecology and Evolution. 9(6):3030-3045.

Ponchon A, Grémillet D, Doligez B, Chambert T, Tveraa T, González-Solís J, Boulinier T. 2013. Tracking prospecting movements involved in breeding habitat selection: Insights, pitfalls and perspectives. Methods in Ecology and Evolution. 4(2):143-150.

Quebec Breeding Bird Atlas. 1984-1989, 2010-2014. Quebec breeding bird atlas data. NatureCounts, a node of the Avian Knowledge Network, Birds Canada.

Raleigh D, Ray JD, Grisham BA, Siegrist J, Greene DU. 2019. Nest survival data confirm managed housing is an important component to the conservation of the eastern purple martin. Wildlife Society Bulletin. 43(1):93-101.

Rappole JH, Tipton AR. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology. 62(3):335-337.

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, Stanton JC, Panjabi A, Helft L, Parr M et al. 2019. Decline of the north american avifauna. Science. 366(6461):120.

Russell KR, David SM, Gauthreaux SA. 1998. Large-scale mapping of purple martin premigratory roosts using wsr-88d weather surveillance radar. Journal of Field Ornithology. 69(2):316-325.

Saldanha S. 2016. Foraging and roosting habitat use of nesting bank swallows in sackville, nb. [Halifax]: Dalhousie University.

Saldanha S, Taylor PD, Imlay TL, Leonard ML. 2019. Biological and environmental factors related to communal roosting behavior of breeding bank swallow (*riparia riparia*). Avian Conservation and Ecology. 14(2).

Sampson BA, Delgiudice GD. 2006. Tracking the rapid pace of gis-related capabilities and their accessibility. Wildlife Society Bulletin (1973-2006). 34(5):1446-1454.

Sánchez-Bayo F, Wyckhuys KAG. 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation. 232:8-27.

Saracco JF, Royle JA, DeSante DF, Gardner B. 2010. Modeling spatial variation in avian survival and residency probabilities. Ecology. 91(7):1885-1891.

Sauer JR, Niven DK, Hines JE, Jr DJZ, Pardieck KL, Fallon JE, Link. WA. 2017. The north american breeding bird survey, results and analysis 1966 - 2015. Laurel, MD: USGS Patuxent Wildlife Research Center.

Sherman L. 2019. Habitat associations and diet composition of western purple martins in western oregon. [Corvallis, Oregon]: Oregon State University.

Sherman L, Hagar J. 2021. The snag's the limit: Habitat selection modeling for the western purple martin in a managed forest landscape. Forest Ecology and Management. 480:118689.

Sierro A, Arlettaz R, Naef-Daenzer B, Strebel S, Zbinden N. 2001. Habitat use and foraging ecology of the nightjar (*caprimulgus europaeus*) in the swiss alps: Towards a conservation scheme. Biological Conservation. 98(3):325-331.

Smith AC, Hudson M-AR, Aponte VI, Francis CM. 2020. North american breeding bird survey - canadian trends website, data-version 2019. Gatineau, Quebec, K1A 0H3: Environment and Climate Change Canada.

Smith RA, Gagné M, Fraser KC. 2021. Pre-migration artificial light at night advances the spring migration timing of a trans-hemispheric migratory songbird. Environmental Pollution. 269:116136.

Stanton R, Clark RG, Morrissey CA. 2017. Intensive agriculture and insect prey availability influence oxidative status and return rates of an aerial insectivore. Ecosphere. 8(3):e01746.

Stewart RE, Robbins CS, Fish US, Wildlife S, United States. Department of the I. 1958. Birds of maryland and the district of columbia. Washington D.C.: U.S. Dept. of the Interior, Fish and Wildlife Service.

Stutchbury BJ. 1991. Floater behaviour and territory acquisition in male purple martins. Animal Behaviour. 42(3):435-443.

Stutchbury BJM, Fraser KC, Silverio C, Kramer P, Aeppli B, Mickle N, Pearman M, Savage A, Mejeur J. 2016a. Tracking mated pairs in a long-distance migratory songbird: Migration schedules are not synchronized within pairs. Animal Behaviour. 114:63-68.

Stutchbury BJM, Hill Iii JR, Kramer PM, Rush SA, Tarof SA. 2009a. Sex and age-specific annual survival in a neotropical migratory songbird, the purple martin (*progne subis*). The Auk. 126(2):278-287.

Stutchbury BJM, Kramer PM, Barrow J, Mickle N, Mammenga P, Applegate K. Forthcoming 2013. Purple martin geolocator capture methods: Advice & lessons learned from experienced landlords.

Stutchbury BJM, Siddiqui R, Applegate K, Hvenegaard GT, Mammenga P, Mickle N, Pearman M, Ray JD, Savage A, Shaheen T et al. 2016b. Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. The American Naturalist. 188(S1):S28-S40.

Stutchbury BJM, Tarof SA, Done T, Gow E, Kramer PM, Tautin J, Fox JW, Afanasyev V. 2009b. Tracking longdistance songbird migration by using geolocators. Science. 323.

Tarof SA, Kramer PM, Hill JR, Tautin J, Stutchbury BJM. 2011. Brood size and late breeding are negatively related to juvenile survival in a neotropical migratory songbird. The Auk. 128(4):716-725.

Taylor LU, Woodworth BK, Sandercock BK, Wheelwright NT. 2018. Demographic drivers of collapse in an island population of tree swallows. The Condor. 120(4):828-841.

Taylor PD, Crewe TL, Mackenzie SA, Lepage D, Aubry Y, Crysler Z, Finney G, Francis CM, Guglielmo CG, Hamilton DJ et al. 2017. The motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology. 12(1).

Understanding migration. n.d. United Kingdom: The Royal Society for the Protection of Birds; [accessed 2021 May 6].

Tonra CM, Wright JR, Matthews SN. 2019. Remote estimation of overwintering home ranges in an elusive, migratory nocturnal bird. Ecology and Evolution. 9(22):12586-12599.

Twining CW, Brenna JT, Lawrence P, Shipley JR, Tollefson TN, Winkler DW. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. Proceedings of the National Academy of Sciences. 113(39):10920.

Twining CW, Shipley JR, Winkler DW. 2018. Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. Ecology Letters. 21(12):1812-1820.

van Grunsven RHA, van Deijk JR, Donners M, Berendse F, Visser ME, Veenendaal E, Spoelstra K. 2020. Experimental light at night has a negative long-term impact on macro-moth populations. Current Biology. 30(12):R694-R695.

Van Loon A, Ray JD, Savage A, Mejeur J, Moscar L, Pearson M, Pearman M, Hvenegaard GT, Mickle N, Applegate K et al. 2017. Migratory stopover timing is predicted by breeding latitude, not habitat quality, in a long-distance migratory songbird. Journal of Ornithology. 158(3):745-752.

Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D. 2021. Insect decline in the anthropocene: Death by a thousand cuts. Proceedings of the National Academy of Sciences. 118(2):e2023989118.

Wagner RH, Schug MD, Morton ES. 1996. Condition-dependent control of paternity by female purple martins: Implications for coloniality. Behavioral Ecology and Sociobiology. 38(6):379-389.

Waite TA, Ydenberg RC. 1996. Foraging currencies and the load-size decision of scatter-hoarding grey jays. Animal Behaviour. 51(4):903-916.

Waterhouse FL, Doyle FI, Turney L, Wijdeven B, Todd M, Bergman C, Vennesland RG. 2017. Spring and winter home ranges of the haida gwaii northern saw-whet owl (aegolius acadicus brooksi). Journal of Raptor Research. 51(2):153-164.

Weegman MD, Arnold TW, Dawson RD, Winkler DW, Clark RG. 2017. Integrated population models reveal local weather conditions are the key drivers of population dynamics in an aerial insectivore. Oecologia. 185(1):119-130.

Weimerskirch H, Ancel A, Caloin M, Zahariev A, Spagiari J, Kersten M, Chastel O. 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. Journal of Animal Ecology. 72(3):500-508.

Westworth DA, Telfer ES. 1993. Summer and winter bird populations associated with five age-classes of aspen forest in alberta. Canadian Journal of Forest Research. 23(9):1830-1836.

Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. 2015. The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. Ecology. 96(7):1741-1753.

Wilson KS, Pond BA, Brown GS, Schaefer JA. 2019. The biogeography of home range size of woodland caribou rangifer tarandus caribou. Diversity and Distributions. 25(2):205-216.

Ydenberg RC, Welham CVJ, Schmid-Hempel R, Schmid-Hempel P, Beauchamp G. 1994. Time and energy constraints and the relationships between currencies in foraging theory. Behavioral Ecology. 5(1):28-34.