THE FALL MIGRATION ECOLOGY OF A DECLINING AERIAL INSECTIVORE, THE BANK SWALLOW (*RIPARIA RIPARIA*)

by

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Abstract

Migratory animals are experiencing population declines worldwide. Knowledge of a species' movements, habitat use and geographic linkages throughout the annual cycle is an important first step to understand the drivers of population declines. I used the Motus Wildlife Tracking System to track the fall migration of 610 Bank Swallows (*Riparia riparia*) from breeding sites across North America. Bank Swallows appeared to follow three migration routes (Western, Central, and Eastern), two of which were previously undocumented for the species. Swallows that followed the Central route departed later than Eastern birds in 2022 and had faster migration pace and ground speeds than Eastern and Western birds in both years. These results highlight that Bank Swallows from different breeding regions in North America may be exposed to different threats as they migrate and suggest that the appropriate scale of management is that of the migration route rather than province/territory/state.

Dedication

This thesis is dedicated with love to my Oma and Opa, Corinne and Frank Endenburg, who loved birds and supported the pursuit of higher education for all their children and grandchildren.

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Acknowledgements

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1 CHAPTER 1 - General Introduction

1.1 Migratory Species

Every year, billions of animals migrate hundreds to thousands of kilometers between the habitats they use at different parts of the annual cycle (Bauer and Hoye 2014). Migration is seen across many taxa (Chapman et al. 2014), and avian migrants show an incredibly diverse range of migration patterns (Newton 2023), including some of the longest documented migration routes of any animal (Egevang et al. 2010). Globally, an estimated 17% of bird species are migratory (Bird Life International 2024), but this number is much higher in some areas. For example, an estimated 86% of bird species found in Canada are migratory (Bird Life International 2024).

The spatial and temporal patterns of avian migrants throughout their annual cycles have implications for biodiversity and ecosystem functioning (Bauer and Hoye 2014), and for conservation of species at risk. Migration is energetically expensive (Wikelski et al. 2003) and exposes individuals to threats in multiple, often novel, geographic locations and time periods throughout the annual cycle, including inclement weather (Newton 2006, 2007), insufficient food availability (Baker et al. 2004), increased predation while migrating (Hebblewhite and Merrill 2007; Béguer-Pon et al. 2012), and collisions with anthropogenic structures (Machtans et al. 2013; Calvert et al. 2013; Loss et al. 2015). When such threats are severe, they can limit population growth. Migratory periods are estimated to have higher mortality rates than the more stationary breeding and wintering periods (Sillett and Holmes 2002), and the effects of conditions experienced during migration can also “carry over” to impact fitness and survival during other periods of the annual cycle (Norris et al. 2004; Imlay et al. 2021).

1.2 Migratory Connectivity

One way to understand how exposure to threats during migration differs among populations is through migratory connectivity analyses. In landscape ecology, “connectivity” refers to “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). Landscape connectivity can be considered in a structural sense, which focuses on the amount and configuration of habitat, or a functional one, which also incorporates a species’ response to the landscape that impacts the ease with which an organism can move between patches (Taylor et al. 2006). High landscape connectivity occurs when organisms can easily move between different habitat patches, while low landscape connectivity occurs when organisms in different habitat patches are functionally segregated from one another due to an inability to move easily between patches. Similarly, population connectivity is often used to describe the ease with which individuals or genes can move between populations, with high population connectivity representing a high degree of inter-population movement (Kozakiewicz et al. 2019; Cramer et al. 2023). In contrast, the language of migratory connectivity focuses on the degree of segregation of breeding populations throughout the annual cycle (Marra et al. 2011). Migratory connectivity is considered high when individuals from separate breeding populations remain segregated from one another during migration and on the wintering grounds (Marra et al. 2011)(Figure 1.2.1). In other words, “high migratory connectivity” is used to describe strong associations between individuals from a given breeding population during migration and on the wintering grounds. When individuals from different breeding populations mix in space and time as they migrate and overwinter, the “connection” between a given breeding site and a given overwintering location is reduced, and migratory connectivity is considered low (Marra et al. 2011).

Migratory connectivity is often quantified using Mantel tests to analyze the degree to which individuals overlap in space and time (Ambrosini et al. 2009; Cormier et al. 2013; Finch et al. 2015; Stanley et al. 2015; Bégin-Marchand et al. 2020, 2021; Walker et al. In review). The Mantel test produces R Mantel values, with a high R Mantel (close to one) representing a strong correlation between the distribution of individuals on the breeding grounds and at a given point during migration, which is considered high migratory connectivity. In contrast, a low R Mantel (close to zero) indicates a lack of correlation between the distribution of individuals on the breeding grounds and at a given point on migration, which is considered low migratory connectivity. Migratory connectivity can include both spatial and temporal components – spatial migratory connectivity is the degree to which individuals from different breeding populations remain spatially separated during migration, whereas temporal migratory connectivity is the degree to which individuals from different breeding populations remain separated in time (i.e., whether they are passing through the same areas at the same or different times).

While I think that migratory connectivity is an important ecological concept and a useful analytical tool, I find this use of the term "connectivity" to be counter-intuitive and confusing, particularly to those with a background in landscape ecology or population genetics. To avoid confusion, in my thesis, I will instead use the terminology of spatial and temporal overlap of individuals from different breeding sites. As such, a high R Mantel value represents a low degree of spatial or temporal overlap of individuals from different breeding sites during migration (i.e., high migratory connectivity), whereas a low R Mantel represents a high degree of spatial or temporal overlap (i.e., low migratory connectivity; Figure 1.2.1). For my analyses, I use the terminology of “breeding sites” as opposed to “breeding populations”, where breeding sites refer to the colonies where we tagged and banded Bank Swallows (*Riparia riparia*). The population structure of the Bank Swallow in North America is unknown (COSEWIC 2013), and I did not want to assume that individuals from geographically distant breeding sites represent distinct populations. Nonetheless, the concepts of spatial and temporal overlap and the associated conservation implications still apply – individuals from breeding sites that follow the same migration routes, and that share migration timing, may be impacted by similar threats during migration.

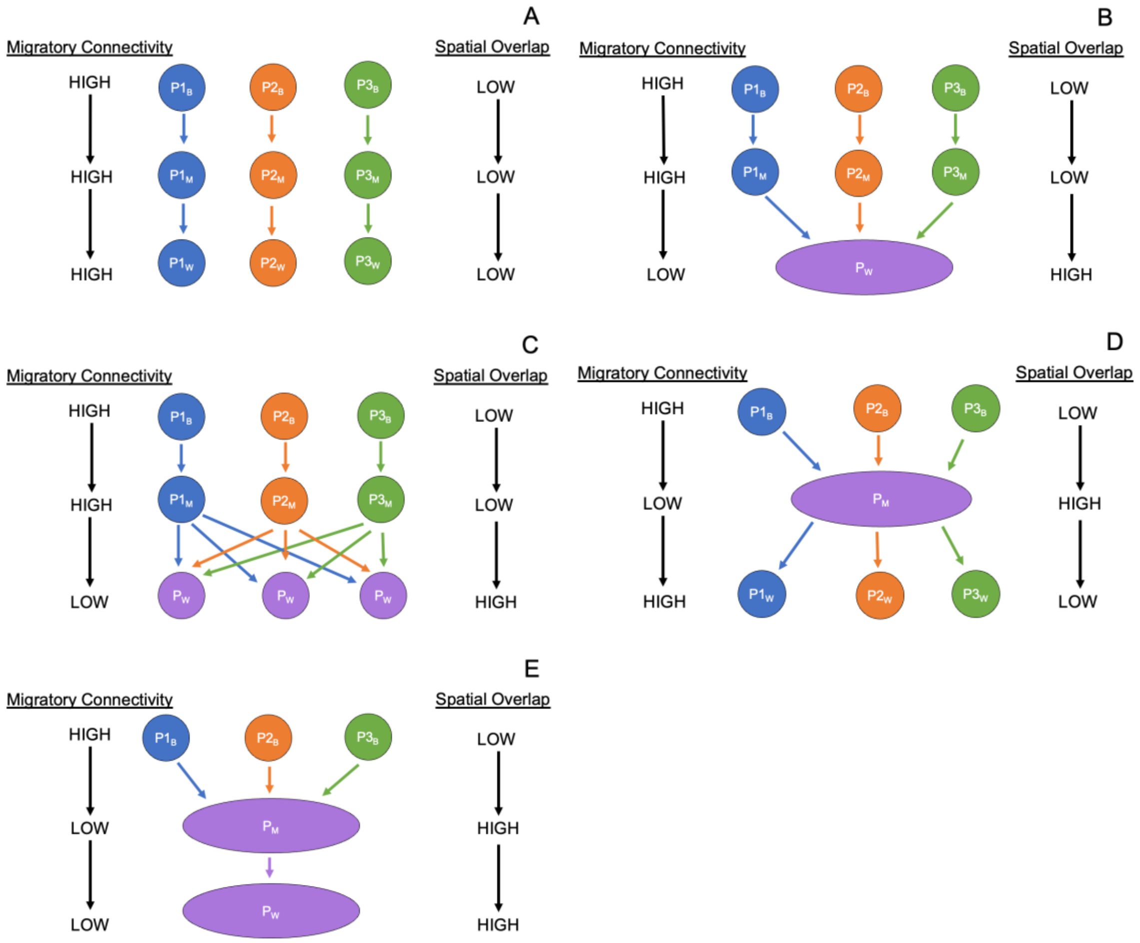


Figure 1.2.1: Five scenarios of spatial migratory connectivity. Circles and ovals represent three hypothetical populations (P) on the breeding grounds (subscript "B"), throughout migration (subscript "M"), and on the overwintering grounds (subscript "W").

1.3 Motus Wildlife Tracking System

The data for my analyses were collected using the Motus Wildlife Tracking System (hereafter, Motus). Developed in 2013, Motus has made it possible to track long-distance migratory movements of species that are too small to carry larger, heavier GPS tags and geolocators, including many songbirds (Bridge et al. 2011; Taylor et al. 2017). Motus consists of a network of radio telemetry receivers deployed by collaborators across North America, Central and South America (Figure 1.3.1), with more recent additions on other continents. Receivers can detect any Motus-compatible tag that is within detection range, including "nano-tags" that are light-weight enough

(~0.3g) for most small birds (Lotek Wireless Inc. 2024). Typical maximum detection ranges are 500 m for omnidirectional antennas and 15 km for Yagi 9-element directional antennas, although actual detection distances often vary based on factors including local topography and vegetation (Mills et al. 2011; Taylor et al. 2017; Elizondo, unpublished data). Detection data are archived by the receivers, eliminating the need to recapture animals to retrieve the data. The data are uploaded to the Motus database automatically, for network-connected receivers, or manually by receiver operators. The spatial accuracy of Motus detections is higher than with geolocators (~15 km compared to 100s of km), and animals can be tracked over large distances.

As with any other tracking technology, the Motus system has limitations. First, tagged animals can only be detected where there are receivers, which can be an issue in locations where receiver distribution is sparse (Figure 1.3.1). This can also result in temporally discontinuous detections, whereas other tracking technologies like geolocators or GPS tags tend to acquire position data at semi-regular intervals, regardless of where the animal is in space. Second, the Motus system relies on radio frequency signals emitted by tags and detected by receivers, which makes it a powerful tool for the study of long-distance migration patterns, but also means that ambient noise and other issues with tag signals can result in false detections that must be screened out prior to analysis (see section 2.2, Radio Telemetry Data Analysis, for more information). Furthermore, it can be difficult to determine the reasons underlying a lack of detections, which can include tag loss or malfunction, receiver malfunction, mortality of tagged individuals, or simply that tagged animals did not pass within range of active receivers. There is also a trade-off between tag weight, battery life, and burst interval (the amount of time between tag signal pulses). A larger battery and long burst interval extend the life of the tag but come at the expense of a heavier tag and likely fewer detections. Nonetheless, this technology has allowed researchers to uncover previously unknown migration behaviour for many passerines that cannot be tracked with GPS tags or geolocators.

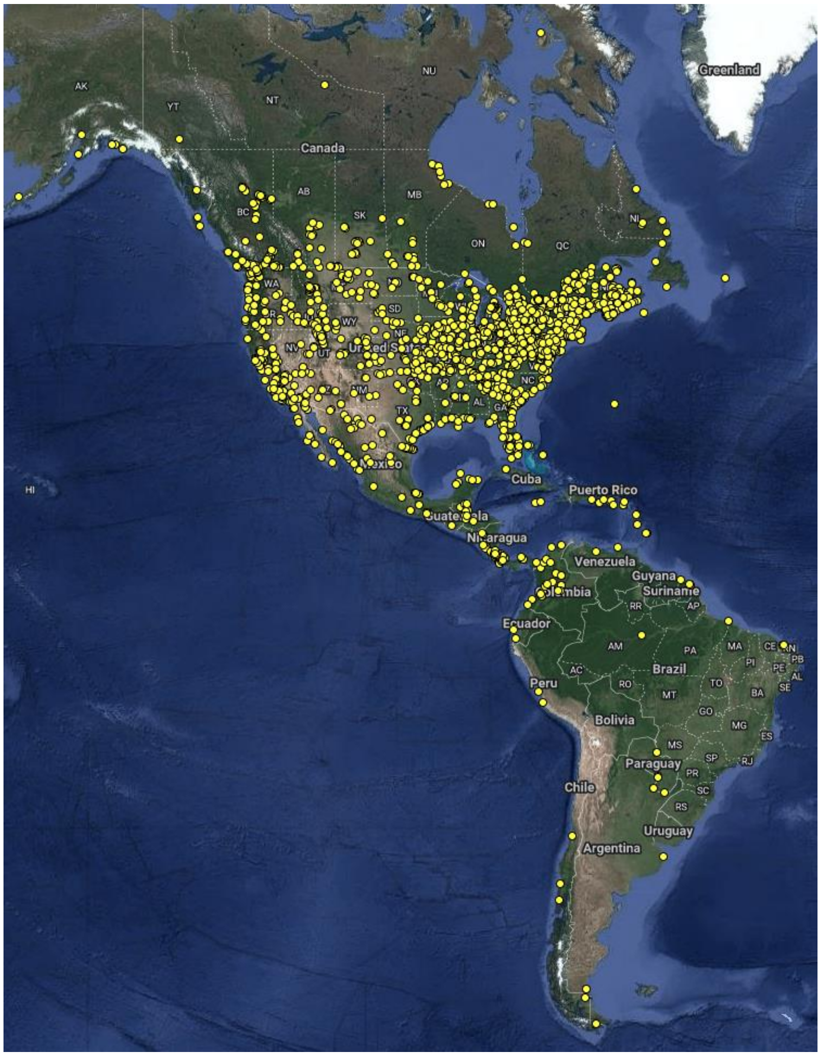


Figure 1.3.1: Motus receiver distribution in the Americas, as of September 2024. From www.motus.org.

1.4 Identifying Migration Routes

Quantitative approaches have been used to identify broad-scale migration routes that are used by individuals from different breeding populations to travel between their breeding and wintering habitats (Palm et al. 2015; Buhnerkempe et al. 2016; Knight et al. 2018), which are often referred to as migratory “flyways” (Lincoln 1935; Kirby et al. 2008). However, these approaches are not well suited for automated radio-telemetry detections because they require more continuous spatial and temporal data from across the entirety of a species’ annual cycle, which are not always available with automated radio telemetry. In my thesis, I apply migratory connectivity analyses with Mantel tests to automated radio-telemetry detections to support the visual identification of broad-scale migration routes used by Bank Swallows (*Riparia riparia*) from across their North American breeding range. I show that Mantel tests can be used to support the identification of shared migration routes, even when data are discontinuous and/or incomplete across the annual cycle. The identification of migration routes for migratory species can provide a spatial framework for research and international conservation efforts (Myers et al. 1987; Kirby et al. 2008; Klaassen et al. 2008; Eren et al. 2024).

1.5 Thesis Overview

In Chapter 2, I use Motus automated radio telemetry data to describe the fall migration ecology of Bank Swallows (*Riparia riparia*) from breeding sites across Canada and in Alaska. My thesis provides a solid foundation for future research into the threats driving Bank Swallow population declines by documenting migration routes and the timing of migratory movements for birds from breeding sites across North America. This research also directly responds to knowledge gaps identified in the 2022 Bank Swallow Recovery Strategy (Environment and Climate Change Canada 2022). In Chapter 3, I speculate further on my results and provide suggestions for future research.

2 CHAPTER 2 – Fall migration routes and timing of Bank Swallows (*Riparia riparia*) from breeding sites across North America

2.1 Introduction

Migratory species are experiencing population declines worldwide (Sanderson et al. 2006; Bolger et al. 2008; Kirby et al. 2008; Berger et al. 2008; Nebel et al. 2010). It is often challenging to determine the drivers of decline for migratory species or populations because they encounter different threats in multiple, geographically dispersed habitats that they rely on throughout their annual cycle. Population trends of migratory species can be impacted by factors acting on the breeding grounds, the wintering grounds or during migration, either directly through mortality during these periods (Diehl et al. 2014; Klaassen et al. 2014), or indirectly through sub-lethal effects that carry-over to reduce survival and fitness during other periods of the annual cycle (Smith and Moore 2003; Norris et al. 2004; Gow et al. 2019b; Imlay et al. 2019). When assessing threats for a species at risk, focusing on one period of the annual cycle at the expense of the others may result in overlooking key threats and potentially also the opportunity to target conservation actions where they will have the greatest benefit (Martin et al. 2007).

The migration routes used and the timing of migratory movements determine the exact threats that individuals will face because factors that can limit the populations of migratory species vary in space and time (Szep 1995; Mduma et al. 1999; Hebblewhite and Merrill 2007; McKinnon et al. 2010, 2015; González-Prieto and Hobson 2013; Iwamura et al. 2013; Hope et al. 2014; Womersley et al. 2022). Individuals passing through the same area will likely face similar threats, whereas individuals that pass through different areas during migration may experience different or fewer threats. For example, Whale Sharks (*Rhincodon typus*) that migrated through areas with high marine vessel activity were more likely to be involved in a collision than sharks that migrated through areas with lower vessel activity (Womersley et al. 2022). Differences in migration timing, which can result from variation in departure timing and/or variation in the pace of migration (Gow et al. 2019a; González et al. 2020; Morbey and Hedenström 2020; Dossman et al. 2023), can also expose individuals following the same routes to different threats. For example, late-migrating Western Sandpipers (*Calidris mauri*) passing through the Fraser River Delta experienced higher predation pressure from Peregrine Falcons (*Falco peregrinus*) than early-migrating sandpipers moving through the same area (Hope et al. 2014). Therefore, the first step to understanding potential threats to migratory animals is knowing where animals are in space and time throughout their annual cycle (Allen and Singh 2016; Fraser et al. 2018; Katzner and Arlettaz 2020).

Once a migratory species' annual movements are characterized, we can identify threats experienced during migration and the locations and times where those threats may be most likely to occur. We can then estimate the relative impacts of threats on migratory populations and species to identify the key drivers of population decline. For example, Wellicome et al. (2014) used knowledge of Burrowing Owl (*Athene cunicularia*) migration routes and timing to show that apparent survival was negatively related to the occurrence of storms during migration. Similarly, Fossette et al. (2014) identified areas where Leatherback Turtle (*Dermochelys coriacea*) migration routes overlapped with longline fishery activity, suggesting that turtles in these areas are at higher risk of being caught as bycatch. Mora Alvarez et al. (2019) calculated the mortality of Monarch butterflies (*Danaus plexippus*) due to automobile collisions at two “hotspots” where migration routes intersected large highways in Mexico.

In an age where conservation resources are limited and the number of species at risk continues to climb (Environment and Climate Change Canada 2010, 2024), it is important to make cost-effective, targeted conservation and management decisions. When individuals from multiple breeding populations overlap in space and time during migration, mitigating threats encountered during these overlaps can benefit multiple populations. For example, Iwamura et al. (2013) predicted that a 35% loss of intertidal habitat along the East Asian-Australasian flyway could result in a 60% reduction in the number of shorebirds migrating through those regions, because individuals from multiple breeding populations funnel through a relatively narrow region during migration. Conversely, if different breeding populations do not overlap in space and time during migration, threats acting during migration may result in population declines for only specific breeding regions.

In addition to helping to identify key threats and priority areas for conservation, understanding where migratory animals are in space and time allows conservation practitioners to communicate, plan, and coordinate actions across geo-political boundaries (Wilcove and Wikelski 2008; Fraser et al. 2018; Mason et al. 2020). Migrating animals often cross jurisdictional borders (Thirgood et al. 2004; Shillinger et al. 2008; Fraser et al. 2012, 2013; Stanley et al. 2015; Mason et al. 2020), whereas conservation resources are typically managed on a jurisdictional basis. For example, habitat for species at risk in Canada is protected within Canada, but if a threatened individual moves across the border it enters unprotected habitat unless the neighbouring country also has habitat protection policies in place. This mismatch between the scale of conservation actions and the scale at which migratory animals use the landscape limits the protection of migratory species at risk (Thirgood et al. 2004; Martin et al. 2007; Berger et al. 2008; Runge et al. 2015; Santini et al. 2016). Improved knowledge of where migratory animals are throughout the year is essential to coordinate conservation and management.

An estimated 40% of migratory bird species have declining population trends, and 16% are considered globally Near Threatened, Vulnerable, Endangered or Critically Endangered by the International Union for the Conservation of Nature (IUCN;(Bird Life International 2024)), but the migration ecology of most migratory bird species is poorly understood. This is particularly true for small songbirds, for whom tracking technologies have only recently become small enough for safe deployment (Bridge et al. 2011). For example, the Motus Wildlife Tracking System (Taylor et al. 2017), hereafter Motus, is an international automated radio telemetry array that scans on a single radio frequency to detect birds fitted with small digitally encoded VHF tags. While still expanding in geographic coverage, Motus provides an opportunity to fill key knowledge gaps with respect to the migration ecology of small migratory birds, such as migration routes and timing.

The Bank Swallow (*Riparia riparia*) is a small aerial insectivore in the family Hirundinidae with a near-worldwide distribution (Garrison and Turner 2020a). Bank Swallows nest in burrows dug into sand banks along lake shores, rivers, and within sand and gravel pits, forming colonies ranging in size from ten to thousands of breeding pairs (Garrison and Turner 2020b, c, d). While breeding, Bank Swallows preferentially forage in open areas above and around wetlands, lakes, rivers and ocean coasts (Garrison and Turner 2020e, c). Individuals that breed in North America primarily overwinter in Central and South America (Imlay et al. 2018; Garrison and Turner 2020a; Hobson and Kardynal 2023), although studies on Bank Swallow wintering locations have only been carried out for a small number of possible breeding regions. Bank Swallows are diurnal, fly-and-forage migrants and may travel slowly or stopover during migration to forage en route (Winkler 2006; Imlay et al. 2020). At night, migrating Bank Swallows typically roost in large numbers, often with other swallow species in tall, vertical vegetation (Winkler 2006; Garrison and Turner 2020f).

The Bank Swallow is listed as Least Concern by the International Union for the Conservation of Nature (IUCN) because of its large range and large global population size, although populations are declining globally (BirdLife International 2016). Regional population trends of Bank Swallows vary across North America (COSEWIC 2013), but populations have declined precipitously in some regions, including declines of 95% in Canada between 1970-2022 (Smith et al. 2024). Bank Swallows are listed as Threatened in Canada under the Species at Risk Act (COSEWIC 2013; Environment and Climate Change Canada 2022), and the species is classified as being at risk in several US states (Garrison and Turner 2020g). Importantly, uncertainty about Bank Swallow migration routes and timing and the connectivity of individuals from breeding sites across North America limits our ability to assess threats for the species. These knowledge gaps were identified as urgent research needs in the 2022 Bank Swallow

Recovery Strategy (Environment and Climate Change Canada 2022), and by the Aerial Insectivore Working Group (Berzins et al. 2020).

My main research objective was to identify migration routes of Bank Swallows from breeding sites in Alaska and across Canada, and to determine the extent to which birds from different breeding regions overlapped spatially during migration. To meet this objective, I used Motus to qualitatively describe migration routes and orientation, and to describe the extent to which migration routes for different breeding sites spatially overlapped. My second objective was to determine the extent to which migration timing and the rate of migration varied or overlapped within and across migration routes. To meet this objective, I again used Motus to assess variation in departure timing across migration routes; temporal overlap, or the extent to which birds were migrating across similar latitudes at the same time within migration routes; and variation in migration pace (the average number of kilometers traveled per day, in km/day) and ground speed (the rate of travel between consecutive, same-day detections, in m/s) to further quantify variation in migration timing. By meeting these objectives, I lay the foundation for future research testing the mechanisms behind this variation and provide critical information for conservation planning for Bank Swallows.

2.2 Methods

Field Methods

I supported the development of a network of collaborators to help tag Bank Swallows at breeding sites (colonies) across North America (Figure 2.2.1; see Acknowledgements for a list of collaborators). Bank Swallows were captured using mist nets and tube traps between June 6 – July 16, 2022, and June 19 – July 21, 2023. Netting took place by either carrying the mist net up to the bottom of the colonies or dropping it from the top of the colonies. All breeding sites in this study were found along riverbanks, lakeshores, or coastal bluffs, except for one site in Québec (QC) that was in an artificial nesting structure, one site in Alaska (AK) that was in a human-made soil pit, and one site in southern British Columbia (BC) that was in an abandoned quarry. Birds were fitted with a uniquely numbered aluminum leg band from either the Canadian Wildlife Service (Canadian sites) or the U.S. Geological Survey (AK) and a 0.32g Lotek NTQB-2-2 VHF nanotag using a leg-loop harness made from elastic cord (Rappole and Tipton 1991). The combined weight of the tag and harness was less than 3% of the body weight of 99.8% of the tagged birds and was therefore not expected to impact survival or fitness of tagged individuals, although tags may have affected behaviour in unknown ways (Anich et al. 2009; Gow et al. 2011; Fairhurst et al. 2015; Matyjasiak et al. 2016). Burst intervals (the amount of time between consecutive tag signal emissions; Figure 2.2.2) ranged from 26.3s to 34.9s in 2022 and from 15.1s to 34.9s in 2023. Both the tag battery life and the harness material were estimated to last at least 100 days (Streby et al. 2015), which was anticipated to span the length of the fall migration period (Imlay et al. 2020). All captured individuals were weighed using digital or Pesola scales (in grams), and wing chord (the distance between the wrist joint and the tip of the longest primary, measured on a bent wing) was measured using a wing chord ruler (in millimeters). Sex of adult birds was determined by the presence/absence of a brood patch or cloacal protuberance.

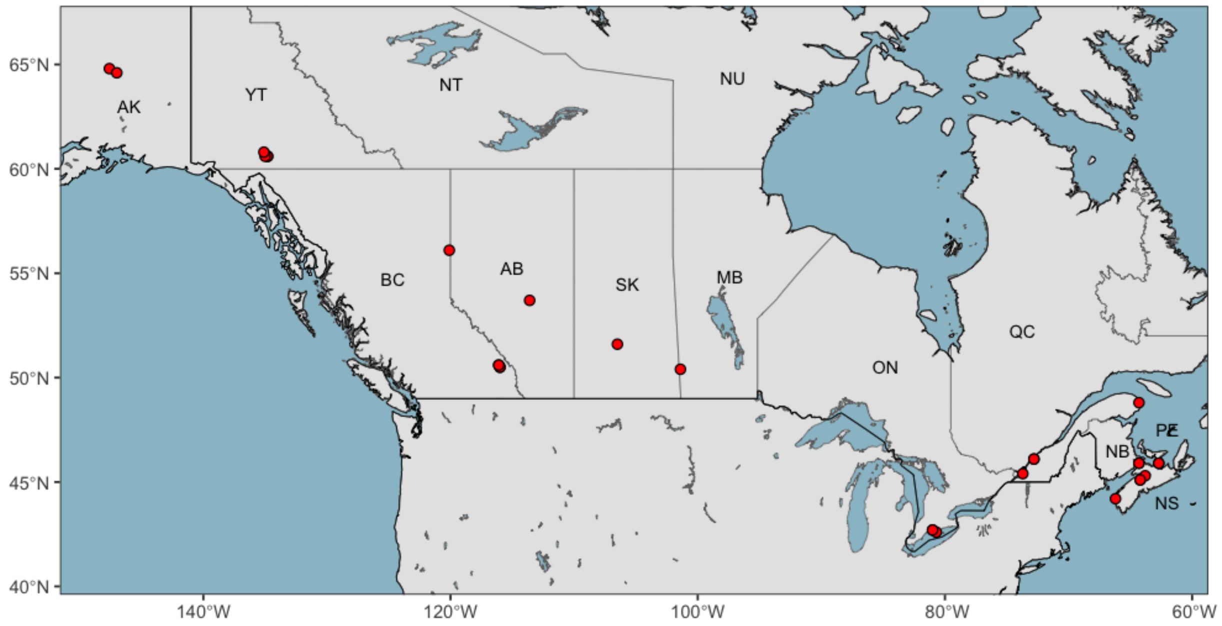


Figure 2.2.1: Bank Swallow (*Riparia riparia*) tag deployment sites for 2022 and 2023.

Ethics

Animal care permitting for all sites in 2022 was obtained through Environment and Climate Change Canada (22GM01). In 2023, animal care permitting was obtained for northern BC from Environment and Climate Change Canada (20TI02), from the Bird Banding Laboratory for AK (125-2024-038), and from Carleton University (119102) for all other sites. In Canada, Bank Swallows were banded and tagged under the following permits issued by Environment and Climate Change Canada: 10911, 10613, 10365 DZ, 10761G, 10973, 10973A, 10743T, 10169 CL, 10365 EB, 10801, 10473B, 10365EE and 10407 V. In AK, Bank Swallows were banded and tagged under banding permit MB22395 from the US Geological Survey Bird Banding Laboratory, and Institutional Animal Care and Use Committee Protocol 125-2024-038. No injuries or mortalities were observed.

Automated Radio Telemetry Array

Bank Swallows were tracked using the automated Motus Wildlife Tracking System (Taylor et al. 2017). The number of Motus receivers in North, Central and South America that were active at some point between June 1 and December 31 (which spans the expected lifespan of our tags) was 839 in 2022 and 820 in 2023. Motus receiver stations (omnidirectional and/or 9-element Yagi antenna) were set up at any breeding site that did not already have a Motus station within 15 km. The typical maximum detection radius for omnidirectional antennas is approximately 500 m, and the typical maximum detection range for 9-element Yagi antennas is approximately 15 km in the direction it is pointing (Taylor et al. 2017). However, actual antenna detection ranges can vary due to factors such as local topography and vegetation (Mills et al. 2011; Taylor et al. 2017; Elizondo, unpublished data). Most receivers with Yagi antennas have at least three antennas pointing in different directions (Figure 2.2.2).

Radio Telemetry Data Analysis

Motus detection data were downloaded on April 17, 2024, from the Motus website. I also manually processed and added data from three receivers in Québec that had malfunctioning GPS units and for which the data was not available through the Motus website.

The Motus system is a network of automated radio receivers that can detect and decode signals emitted by radio tags in specific patterns of pulses and bursts, referred to as digital coding (Figure 2.2.2). The “raw” detected signals are archived by receivers and then uploaded to the Motus system where they are combined with an archive of active tag and receiver metadata to assign the detections to specific tags. This approach is powerful in that it allows any Motus-compatible tag to be detected on any receiver and does not require the receiver to switch between multiple radio frequencies which can result in missing signal detections while running through a scan cycle of different frequencies. However, it can also result in false, ambiguous, incorrectly attributed or duplicated detections (Birds Canada et al. 2024). For example, false detections can occur when ambient noise is interpreted as tag signals, which are assigned to whatever tag code matches the specifics of the detections. Ambiguous detections can also occur when two tags emit signals that appear indistinguishable from one another. Two tags may have the same signal emission pattern due to limitations on the number of unique tag codes that can be manufactured, and the system may not be able to tell which tag was actually present at the time of detection. Incorrectly attributed detections can occur when two or more tags are within detection range of a receiver and their signals overlap to give the appearance of another tag that was not actually there or their signals overlap in a way that makes it impossible to determine the actual digital codes (referred to as aliasing). Aliasing may be more common when large numbers of tags are deployed close to one another (Motus 2022), such as for Bank Swallows tagged at breeding colonies. Last, duplicated detections can occur due to an error in the system when receiver data is re-processed or when receiver deployments are mistakenly duplicated in the system by users.

When setting up new receivers to collect detections, receiver operators must create “deployments” for receiver antennas in the Motus system, including latitude and longitude and the timing of deployment, so that detections can be assigned to the correct location. Missing or incorrect deployments for receivers or antennas that have been deployed multiple times can result in detections being assigned to incorrect locations by the data processing system, or in missing data due to a lack of receiver metadata.

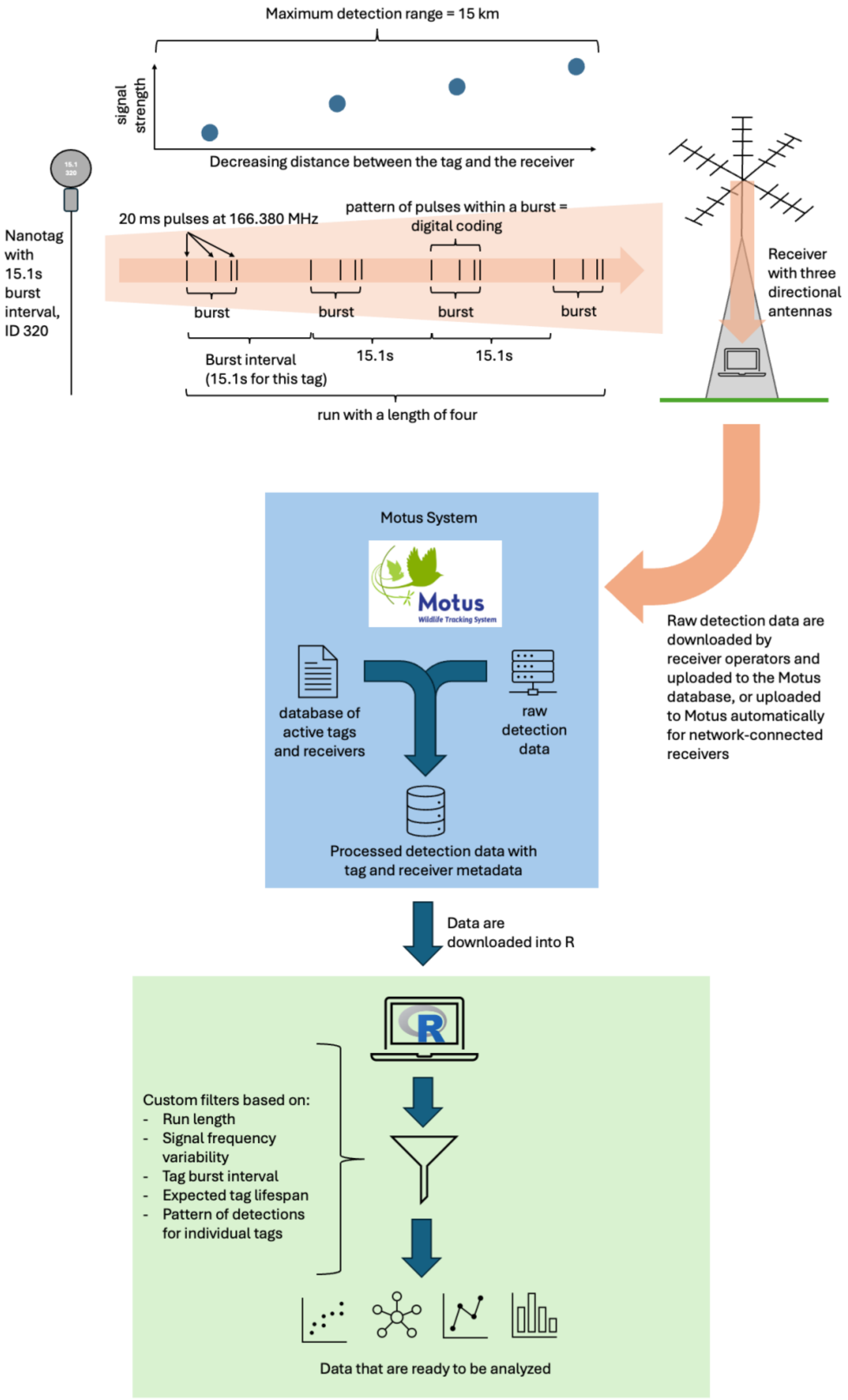

Maximum detection range = 15 km
signal strength
Decreasing distance between the tag and the receiver
15.1 320
Nanotag with 15.1s burst interval, ID 320
20 ms pulses at 166.380 MHz
pattern of pulses within a burst = digital coding
burst
burst
burst
burst
Burst interval (15.1s for this tag)
15.1s
15.1s
run with a length of four
Receiver with three directional antennas
Raw detection data are downloaded by receiver operators and uploaded to the Motus database, or uploaded to Motus automatically for network-connected receivers
Motus System
Motus
Wildlife Tracking System
database of active tags and receivers
raw detection data
Processed detection data with tag and receiver metadata
Data are downloaded into R
R
Custom filters based on:
- Run length
- Signal frequency variability
- Tag burst interval
- Expected tag lifespan
- Pattern of detections for individual tags
Data that are ready to be analyzed

Figure 2.2.2. Diagram of how Motus automated radio telemetry works, including nanotag signal emission, receiver detection, data download and processing. The receiver in this figure has three Yagi antennas with a typical maximum detection range of 15km for a bird in flight. Receivers with an omnidirectional antenna would have a typical maximum detection range of 500m. Individual nanotags are identified by the Motus system based on the pattern (amount of time) between sections of a burst, referred to as digital coding. False detections can be the result of ambient noise that the receiver interprets as tag emissions; signals from two tags that overlap and give the appearance that a third tag is present; or two tags with duplicate digital coding (also called ambiguous detections).

It is therefore important to separate out "real" detections from "false" detections and to remove duplicate detections before performing analyses, to avoid producing misleading results. I devised a filtering system to identify and remove detections with a high likelihood of being false based on run length (i.e., the number of sequential signal bursts from a tag), frequency standard deviation (i.e., the variability in tag signal frequency), the timing of detections relative to the tag burst interval (e.g., the time elapsed between sequential detections should be equal to or a multiple of the tag burst interval), other detections for that individual, and expected broad-scale movement patterns for birds from each breeding location (e.g., if a single tag deployed in Atlantic Canada was detected on a single receiver in BC, it would be filtered out). Full details of my filtering methodology can be found in Appendix 1. I chose only to use and present data that I was highly confident were real detections. Nonetheless, it is very possible that my filtering process removed some real detections, and an absence of detections does not necessarily indicate that Bank Swallows did not pass through that area. A lack of data can also be due to inconsistent receiver coverage, operational receiver issues, data not being uploaded in a timely manner, issues during data processing by the Motus system, or tag loss. Therefore, I focus the interpretation of my results to detections as opposed to interpreting absences of detections.

Following my filtering process, I removed all detections for individual tags that had constant signal detections with little variability in signal strength at the breeding site where the tag was deployed (n = 10); such detections suggest that a bird either died/was killed or a tag was dropped. I removed all detections for 113 tags with less than 24 hours between release and the bird's last detection, as this was an indication that the tag likely stopped working shortly after deployment. It is also possible that tagged birds with less than 24 hours of detections were vagrants that were tagged while visiting the colony, rather than breeding there, or that they died or were killed shortly after being tagged but out of range of a Motus receiver. Mortality at the colony is unlikely to affect such a high proportion (113/890 or 13%) of tagged birds (G. Mitchell, pers. comm.). Nevertheless, the available data did not permit me to distinguish between these possible explanations and further work will be required to do so.

I removed detections at a single receiver for two tags that were replaced two days post-deployment because their signals were not detected on a Lotek receiver when the birds were recaptured, suggesting tag failure. I also removed four hatch-year birds and seven birds of unknown age because the sex of juvenile birds cannot be determined in the same way as for adults, migration behaviour can differ between juveniles and adults (Mitchell et al. 2015), and I did not have a large enough sample size of hatch-year birds to test for these differences.

Bank Swallows tagged in Ontario were not detected outside of Ontario in either 2022 or 2023, therefore I excluded these individuals from all statistical analyses because I do not know if this lack of detections was due to mortality, tag loss, or technical issues with the Motus system. However, some Ontario birds did have post-departure detections within Ontario, so I included those birds on Figure 2.3.1.

After this process, I retained 7 479 336 detections for 610 birds on 235 receivers. Final tag numbers by jurisdiction and analysis sample sizes following the removal of likely false positive detections and noisy data can be found in Tables 2.3.1 and 2.3.2.

Data Summaries, Visualizations and Statistical Analyses

Departure Bearings

I calculated migratory departure bearings as the bearing between an individual's departure location and the first receiver on which it was detected post-departure, similar to Imlay et al. (2020). I excluded any detections <50 km from the departure location to avoid erroneous bearings due to overlapping receiver detection ranges that can result in simultaneous or near simultaneous detections on receivers within 30-50km of one another (Appendix 1: Figures S10 & S11). This is likely conservative given typical maximum detection range of ~15 km for Motus stations with Yagi antennae. I only determined departure bearings for individuals that had valid departure dates (see Departure Timing below).

Spatial and Temporal Overlap

I followed the methodology of Bégin-Marchand et al. (2020, 2021) and Walker et al. (In review) to use Mantel tests to quantify the degree of spatial and temporal overlap of individuals from my different breeding sites throughout migration. I included all birds with valid departure dates, including two individuals with missing wing chord values that were not included in my final departure date model (see Departure Timing, below). I use the terminology of "breeding sites", which are the colonies where we banded and tagged swallows, as opposed to “breeding populations” because the population structure of Bank Swallows in North America is unknown (COSEWIC 2013).

First, I aggregated post-departure detections into latitude-longitude grid cells of 1x1 degree and recorded the presence or absence of individuals in each cell (Appendix 1: Figure S2). I then calculated Bray-Curtis dissimilarity values to determine if individuals were detected in exactly the same cells (Bray-Curtis dissimilarity = 0) or entirely different cells (Bray-Curtis dissimilarity = 1) (Goslee 2010), generating a migratory detection dissimilarity matrix. Individual birds could be detected in multiple grid cells and dissimilarity values were calculated using all grid cells for detected individuals, where Bray-Curtis values could range anywhere between the minimum of 0 and maximum of 1 depending on the degree to which individuals differed in the cells where they were detected. Similarly, I generated a breeding site dissimilarity matrix for all individuals, where Bray-Curtis dissimilarity values of 1 indicated that individuals were tagged at different breeding sites and Bray-Curtis dissimilarity values of 0 indicated that individuals were tagged at the same breeding site (i.e., there were no intermediate values between 0 and 1 in this matrix; Appendix 1: Figure S4). I used partial Mantel tests with 10 000 permutations to test the correlation between the migratory detection and breeding site dissimilarity matrices, while also controlling for any differences between the two study years due to different receiver distributions (Lichstein 2007; Legendre and Legendre 2012). This generated R Mantel values between -1 and 1, as well as 95% confidence intervals for R Mantel using 100 bootstrap samples. R Mantel values close to 1 represent a high correlation between the breeding site and migratory detection dissimilarity matrices, indicating that individuals are migrating only with other individuals from the same breeding site and there is low spatial overlap of individuals from different breeding sites. An R Mantel closer to 0 indicates that there is a low correlation between the breeding site and migratory detection dissimilarity matrices, meaning that there is a high degree of spatial overlap between individuals from different breeding sites as they migrate. An R Mantel between 0 and -1 would indicate that individuals from different breeding sites are more separate during migration than they were on the breeding grounds. I repeated my analysis of spatial overlap over n = 19 5°-latitude windows between 60°N and 35°N, shifting by 1° latitude each time (e.g., 60-55°N, 59-54°N …40-35°N) to assess whether the degree of overlap changed as Bank Swallows moved along their migration routes. In other words, I repeated the Mantel test for every latitude window, generating 19 R Mantel values (one per 5°-latitude window). The number of grid cells varied between latitude windows depending on the number of receivers with detections within that latitude range, therefore the detection and dissimilarity matrices varied in size between latitudes (Appendix 1: Tables S2-S4 and Figure S2). I chose 5°-latitude windows because there were gaps in my detection data at some latitudes, so using a latitude window of this size allowed me to expand the range of latitudes over which I could calculate spatial overlap. The northern limit of 60°N corresponds roughly to the latitude of the YT breeding sites where we tagged, and I chose this northern limit because detections north of that point were only for AK-tagged Bank Swallows. The southern limit of 35°N was simply the point south of which there were insufficient detections to perform the Mantel test.

I used the same methodology to assess the degree of temporal overlap during migration, except that I used the week of detection within each 5-degree latitude window for the detection matrix, rather than the latitude-longitude of the detection (Appendix 1: Figure S3). My analysis of temporal overlap assessed the degree to which individuals were detected within each latitude window at the same or different times, at the scale of one week.

My initial analysis of spatial and temporal overlap, which used detections for Bank Swallows from all breeding sites, appeared to be heavily impacted by the latitudes at which I had detections for birds from different breeding sites. For example, Bank Swallows from breeding sites in AK, Yukon (YT), northern BC, Alberta (AB), Saskatchewan (SK) and Manitoba (MB) were primarily detected at more northern latitudes than Bank Swallows from breeding sites in Eastern Canada or southern BC. As such, I repeated my spatial and temporal overlap analyses three more times with detections grouped based on visual assessment of migration routes and departure orientations: 1) Bank Swallows from breeding sites in AK, YT, northern BC, AB, SK, and MB; 2) Bank Swallows from the southern BC breeding site; and 3) Bank Swallows from breeding sites in Eastern Canada, which included Québec (QC), New Brunswick (NB), Nova Scotia (NS), and Prince Edward Island (PEI). Despite appearing to follow a unique migration route, I was unable to analyze the southern BC birds alone because my overlap analysis required the inclusion of at least two breeding sites. I expected that spatial overlap among birds from different breeding sites would increase within a migration route if birds were converging spatially as they migrated south. Alternatively, I expected that spatial overlap would be lower if birds from different breeding sites followed different migration routes.

To visually illustrate the temporal overlap of birds from different breeding sites during migration, I plotted detections of the different migration routes on maps, grouped into one-week intervals. I grouped detections into one-week intervals because Motus detections are temporally discontinuous and selecting shorter time-intervals resulted in many maps with few detections on each one, which were not informative.

To test if the resolution of the latitude-longitude grid cells affected my results, I repeated all three analyses of spatial and temporal overlap using 0.1x0.1 and 0.01x0.01-degree grid cells. There were some differences in R Mantel values between the analyses using 1x1 and 0.1x0.1 grid cells; however, the overall trends remained consistent, so I arbitrarily decided to present the results using grid cells of 0.1x0.1 degrees for analyses (results for the 1x1 and 0.01x0.01 resolutions can be found in Appendix 1).

Departure Timing

I used each individual's last detection within 50 km of the breeding site as a proxy for the timing of migratory departure. This generated similar results to using the last detection at the closest receiver to the colony (per the methodology of Imlay et al., 2020), while accounting for the possibility that individuals may make regional scale movements prior to actually departing on migration (Brown and Taylor 2015) and may therefore be detected on multiple receivers around the colony. When individuals were only detected at a colony, the last detection could reflect tag loss or mortality rather than a migratory departure because there were no further detections to verify whether the individual was still alive and migrating. To minimize conflating these scenarios, I determined earliest departures for birds with migratory tracks, defined as detections that occurred after my estimated departure dates and at least 50 km away from the breeding location, for each of the unique migration routes that I defined using the spatial overlap analysis above. I removed departure dates for birds without migratory tracks that occurred before these “cutoffs”. I used a linear mixed effects model (R package lme4)(Bates et al. 2024) to analyze the effects of migration route on departure timing while accounting for any potential impacts of sex (Imlay et al. 2020), wing chord (Bennett et al. 2019), body mass (Mitchell et al. 2012; Cooper et al. 2015; Eng et al. 2019; Anderson et al. 2021), and year (Imlay et al. 2020). Body mass is considered an index of body condition when wing chord is included in the same model and is considered a better index than the ratio of mass to wing chord (Schamber et al. 2009; Labocha and Hayes 2012). I also included a random intercept for each breeding site to account for spatial autocorrelation, and an interaction term for migration route and year to assess potential differences in departure timing between migration routes across years.

Migration Pace and Ground Speed

I calculated migration pace (km/day) for Bank Swallows with detections at a minimum of three different receivers post-departure that were at least 30 km apart from one another, to avoid artificially inflating pace calculations due to overlapping receiver detection ranges that can result in near-simultaneous detections (Appendix 1: Figures S10 & S11). Using 30 km instead of 50 km, as I did for my departure timing analyses, increased my sample size for analysis but still reduced the risk of artificially inflating migration pace calculations due to overlapping receiver detection ranges. I also only used detections that were at least 24 hours apart so that I was using different detections from my ground speed analysis (described below) and to ensure that my migration pace estimates were more representative of each individual’s overall migration pace, rather than during a short segment of migration. Like Imlay et al. (2021), I regressed the Vincenty ellipsoid distance from the departure location by the amount of time elapsed since departure for the highest signal strength detection, which represents the point at which the individual was closest to each receiver with detections (Figure 2.2.3). I used the slope of that relationship (in km/day) as the pace of migration. I then used a linear mixed effect model to examine differences in migration pace across migration routes, and to control for potential effects of sex (Imlay et al. 2020), body mass (Schamber et al. 2009; Labocha and Hayes 2012; Gómez et al. 2017), wing chord, departure date (González et al. 2020; Imlay et al. 2021) and year on migration pace. I included a random intercept for each breeding site to control for spatial autocorrelation and used a log transformation on the response variable to improve model fit as visually assessed by the model residuals. I was not able to include an interaction between year and migration route in my migration pace model because my sample size was too small.

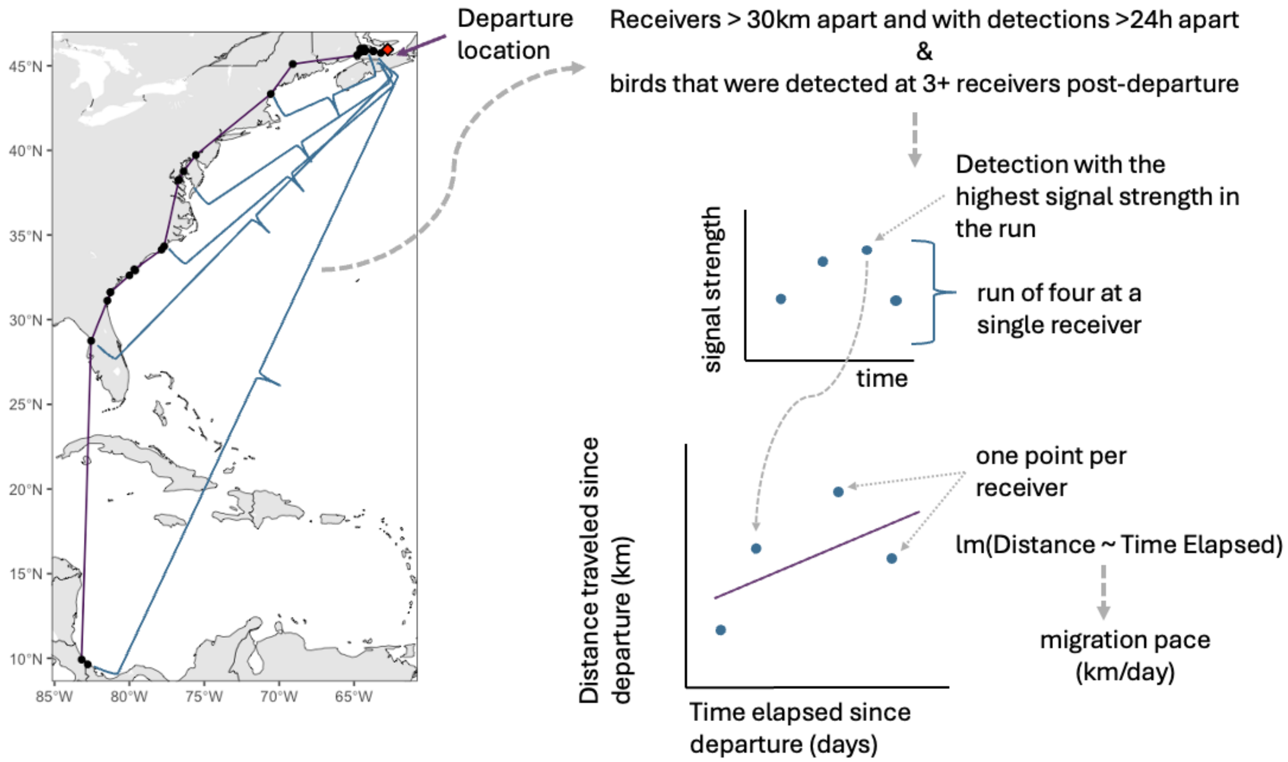


Figure 2.2.3. Methodology for the estimation of Bank Swallow (*Riparia riparia*) migration pace from migratory Motus detections. Eliminating detections from receivers <30km apart reduced the risk of artificially inflating migration pace calculations due to near-simultaneous detections at receivers with overlapping detection ranges. Selecting detections that were at least 24h apart and using a regression of distance and time, rather than simply dividing the furthest distance by the time since departure, ensured that migration pace estimates reflected the overall rate of migration rather than being driven by certain portions of migration. I used the detection with the highest signal strength at each receiver, representing the point at which the individual was closest to the receiver.

Also following the methodology of Imlay et al. (2020), I estimated ground speed as the Vincenty ellipsoid distance between consecutive, same-day post-departure runs at receivers at least 50 km apart (to avoid near-simultaneous detections due to overlapping receiver detection ranges; Appendix 1: Figures S10 & S11) divided by the time elapsed between the detections with the highest signal strength in each run (which represents the point at which the individual was closest to the receiver; Figure 2.2.4). I used a linear mixed effects model to examine variation in ground speed across migration routes while accounting for potential effects of sex (Imlay et al. 2020), body mass (Schamber et al. 2009; Labocha and Hayes 2012; Gómez et al. 2017), wing chord, departure date (Imlay et al. 2021) and year on ground speed. I included nested random intercepts for breeding site and individual to control for spatial autocorrelation and because multiple ground speeds were estimated for some individuals. I also included an interaction term for migration route and year to account for differences in the breeding sites where we tagged between years.

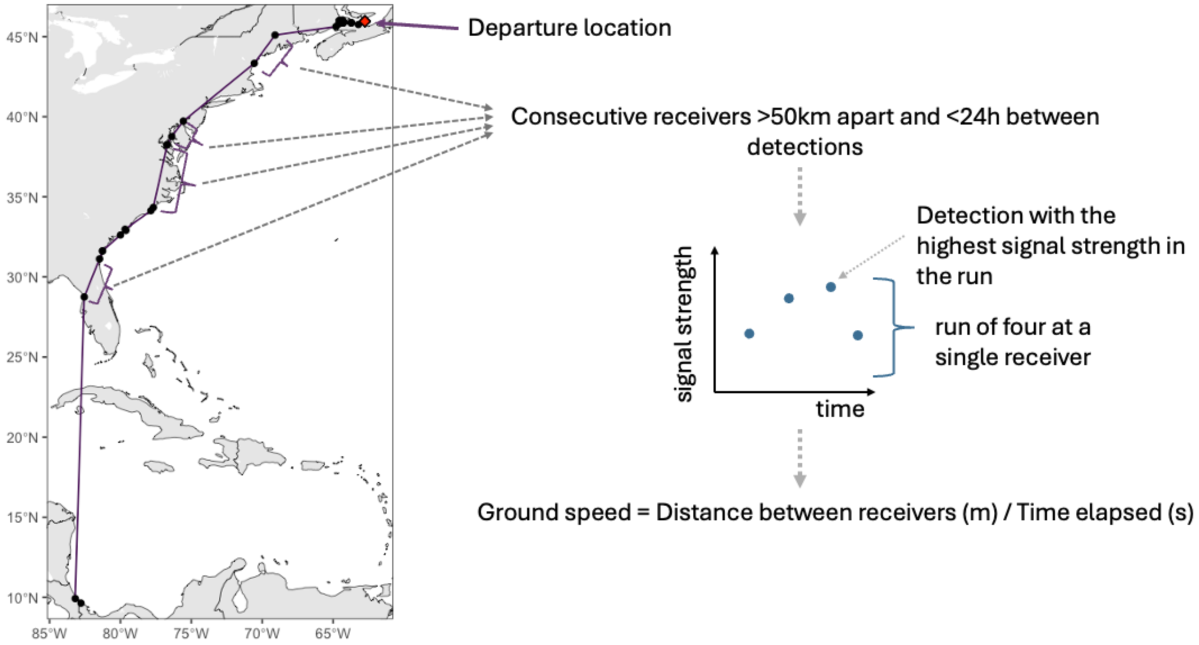


Figure 2.2.4. Methodology for the estimation of Bank Swallow (*Riparia riparia*) ground speed from migratory Motus detections. Eliminating detections from receivers <50km apart reduced the risk of artificially inflating ground speed calculations due to near-simultaneous detections at receivers with overlapping detection ranges. I used consecutive detections with <24h between them to minimize the risk of capturing stationary periods such as stopovers or overnight roosting. I used the detection with the highest signal strength at each receiver, representing the point at which the individual was closest to the receiver.

Statistical Analyses

For my departure date, migration pace and flight speed analyses, I used a single global model that contains all my predictor variables for each analysis instead of using model selection. My reasons for taking this approach are as follows: First, my predictor variables are biologically informed and I have no a priori reason to remove any of them from the model; Second, performing model selection with AIC would have a high likelihood of producing a Type I error because of the number of possible models required to test every predictor combination, and AIC model selection often retains variables with high p-values (Arnold 2010; Sutherland et al. 2023); Third, correlations between my predictors were low to moderate (0.05 – 0.3) and did not appear to have a substantial effect on model parameter estimates or p-values when I re-ran models without correlated predictors; and fourth, I am not using my models predictively, but rather to understand which, if any, of my predictors affect Bank Swallow migration behaviour.

The first time I ran each model, I only included individuals with complete data for all predictor variables, thereby excluding individuals with missing or unknown sex, mass or wing chord (n = 35). In cases where a predictor variable did not appear to have a significant impact on the response, and when I had individuals with missing data for that predictor, I re-ran the model without the predictor(s) in question and included the individuals with missing data. My models only fit data for individuals with complete data for all predictors, so this approach allowed me to maximize my sample size for each analysis. I used model residuals to visually assess model fit for each model. For situations with significant factor level comparisons, I carried out post-hoc Tukey's tests to further examine these relationships.

All analyses and figures were performed using R version 4.3.2. I used the motus R package (Brzustowski et al. 2024) to download Motus detection data, and I used the tidyverse (Wickham et al. 2019) and lubridate (Grolemund and Wickham 2011) packages for data cleaning, manipulation, and plots. I used the Rnaturalearth (Massicotte and South 2024), ggplot2 (Wickham 2016) and ggforce (Pedersen 2024) packages for mapping and data visualization, and the geosphere (Hijmans et al. 2022) package to calculate Vincenty ellipsoid distances and departure bearings. I also used the circular package to calculate circular means and dispersion (Lund et al. 2023) and the lme4 (Bates et al. 2024), lmerTest (Kuznetsova et al. 2020), glmmTMB (Brooks et al. 2024) and DHARMa (Hartig and Lohse 2022) packages for model building and testing. Last, I used the vegan (Oksanen et al. 2022) and ecodist packages (Goslee and Urban 2023) for Bray-Curtis dissimilarity calculations and partial Mantel tests.

2.3 Results

General Results

Between 2022 and 2023, 890 nanotags were deployed on Bank Swallows at the breeding sites shown in Figure 2.2.1. Of those, 610 (68.5%) were detected by the Motus network and had usable data that passed my filters, and 245 adult birds (27.5%) were detected post departure from breeding sites (Table 2.3.1). Visual inspection of flight paths (Figure 2.3.1; see also the Spatial and Temporal Overlap analysis below) suggested that tagged birds were migrating along three broad-scale migration routes during the initial phase of their fall migration. Specifically, Bank Swallows tagged in southern BC followed what I refer to as the Western migration route; swallows tagged in AK, YT, northern BC, and SK followed what I refer to as the Central migration route; and swallows tagged in QC, NB, NS, and PEI followed what I refer to as the Eastern migration route.

Bank Swallows tagged in southern BC headed in a south-southeast direction with a mean bearing of 164 ± 11 degrees (Figures 2.3.1 & 2.3.2). Many southern BC birds were detected migrating through Montana and Idaho (n = 51/100). In 2023, two of 50 tagged individuals appeared to head further east towards Govenlock, Alberta and Bowdoin National Wildlife Refuge in Montana. After being detected in Montana and Idaho, one of the 50 tagged birds was next detected in Costa Rica from October 30 to December 16, 2022. The route this bird used to travel between the northwestern US and Costa Rica is unknown as it was not detected in between.

Bank Swallows tagged in AK, YT, northern BC, and SK generally flew in a southeastern direction with a mean bearing of 109 ± 13 degrees (Figures 2.3.1 & 2.3.2). Many of these birds (n = 60/284) were detected in Manitoba just north of the Canada-US border, between July 17 – August 8, 2022, and July 19 – August 7, 2023. One of 35 birds tagged in northern BC was detected traveling through Iowa and Missouri, with a final detection in Texas on August 29, 2023. One of 50 individuals tagged in SK was detected in Iowa in July 2023 before appearing in Nicaragua on September 18, 2023. One of 50 SK birds was detected in Texas in late August 2023 before appearing in Costa Rica on September 14, 2023. One of 50 SK birds was also detected in Missouri on August 22, 2023, and then appeared in Costa Rica on September 29, 2023. Two of 50 SK birds were also detected in Colombia: one on November 9 and one on December 4, 2023.

Only one of the 31 Bank Swallows that were tagged in Alberta (AB) was detected by the Motus network. It flew in a southeastern direction through SK and into Manitoba (MB), appearing to follow the Central migration route described above. Similarly, one of the seven Bank Swallows that were tagged in MB was detected heading southeast towards the MB-US border, while the rest (6/7) of the MB-tagged birds were only detected at the colony.

Bank Swallows tagged in QC, NB, NS and PEI generally flew in a southwestern direction with a mean bearing of 239 ± 49 degrees (Figures 2.3.1 & 2.3.2). Birds tagged in PEI, NB and NS appeared to stay within about 200-300 km of the Atlantic coast of North America as they migrated south. Sixteen of the 128 birds tagged in QC were first detected heading further inland towards the southern shore of Lake Ontario near Syracuse, New York, before heading further out towards the Atlantic coast as they made their way south. One of the 128 QC birds and one of the 94 PEI birds were detected in Costa Rica on September 29 and October 12, 2022, respectively. The southernmost detections for birds from these breeding sites include one of 128 QC birds detected in Texas on September 29, 2023; two of 128 QC birds detected in Costa Rica on September 15 and 21 2023, respectively, and one of 64 NB birds was detected in Panama on October 28, 2023.

For sites where we tagged Bank Swallows in both study years (southern BC, YT, QC, NS, NB and PEI), migration routes did not appear to differ substantially between years and migration tracks for both years are shown together on Figure 2.3.1.

Table 2.3.1: Number of tags deployed, with usable data, and detected post-departure, by jurisdiction. Usable data means that tags were detected by the Motus network, and the detections passed my filters. I considered post-departure detections to be anything that occurred after the departure date, which I defined as the last detection within 50 km of the breeding location.

Jurisdiction	Year	Number of tags deployed	Number of tags with usable data (% in parentheses)	Number of tags with post-departure detections (% in parentheses)
AK	2023	99	95 (96%)	50 (50.5%)
AB	2022	3	0 (0%)	0 (0%)
	2023	28	1 (3.6%)	1 (3.6%)
BC	2022	50	47 (94%)	26 (52%)
	2023	85	78 (92%)	48 (56%)
SK	2023	50	42 (84%)	7 (14%)
MB	2022	7	7 (100%)	1 (14%)
NS	2022	36	18 (50%)	3 (8.3%)
	2023	44	25 (57%)	0 (0%)
ON	2022	50	3 (6%)	3 (6%)
	2023	50	3 (6%)	3 (6%)
PE	2022	44	22 (50%)	7 (32%)
	2023	50	22 (44%)	0 (0%)
QC	2022	39	27 (69%)	11 (28%)
	2023	89	76 (85%)	28 (31%)
YT	2022	50	44 (88%)	18 (36%)
	2023	50	42 (84%)	16 (32%)
NB	2022	23	19 (83%)	8 (35%)
	2023	41	39 (95%)	16 (39%)
Total		**890**	**610 (68.5%)**	**245 (27.5%)**

Table 2.3.2: Number of tagged Bank Swallows (*Riparia riparia*) used for each analysis. Of the 106 individuals included in the ground speed analysis, 40 had multiple ground speed values, for a total of 162 ground speed measurements.

Analysis	2022	2023	Total
Departure orientation	77	164	241
Departure date	179	410	589
Migration pace	9	49	58
Ground speed	44	62	106
Spatial and temporal overlap	154	341	495

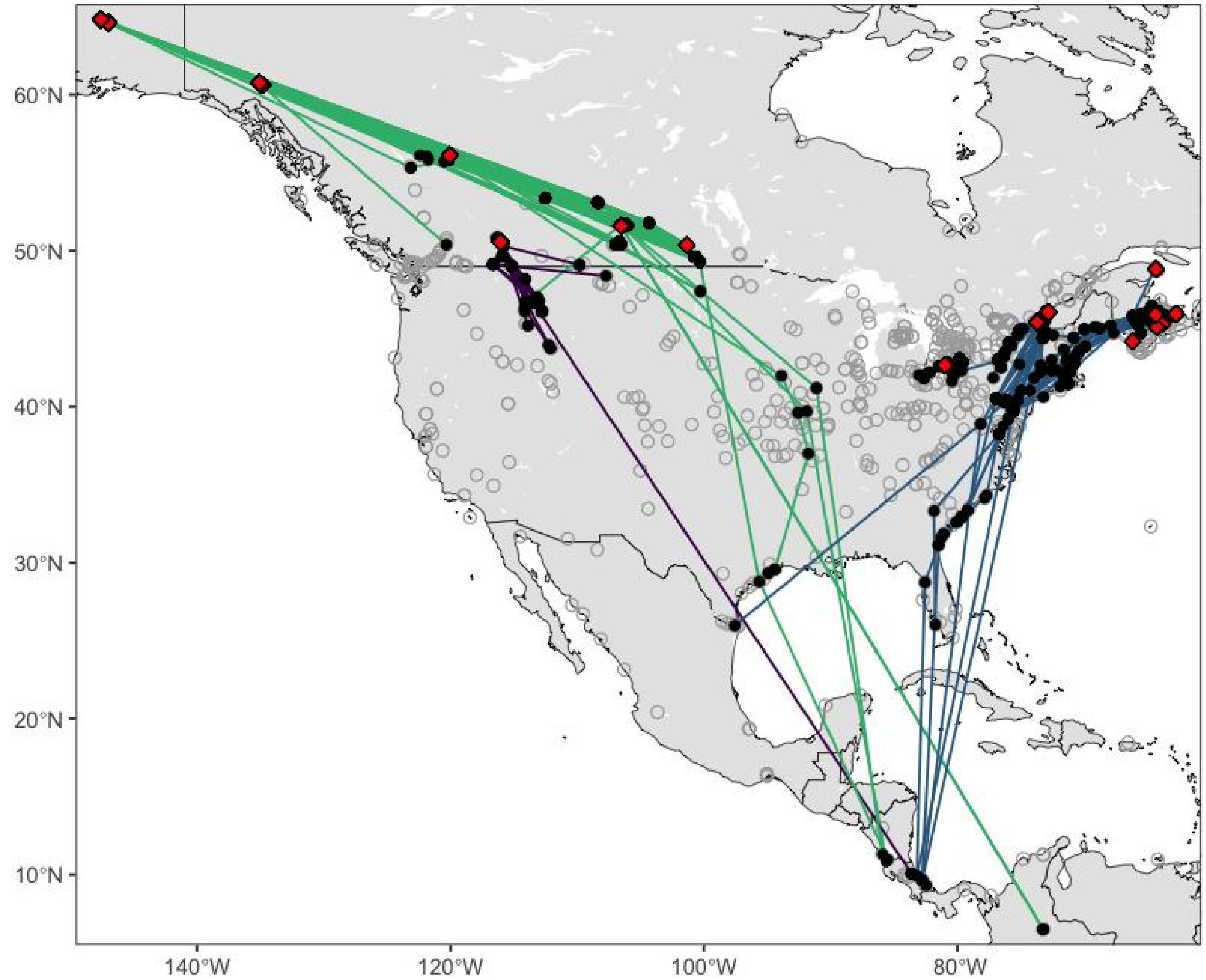


Figure 2.3.1: Post-departure migration tracks for adult Bank Swallows (*Riparia riparia*) tagged in 2022 and 2023 (n = 245). Red diamonds represent breeding locations, black filled circles represent receivers with detections, and grey open circles represent active receivers without detections. The lines join consecutive detections for an individual but do not necessarily represent the route the individual would have travelled. The lines are colour-coded by migration route: green = Central, purple = Western, and blue = Eastern.

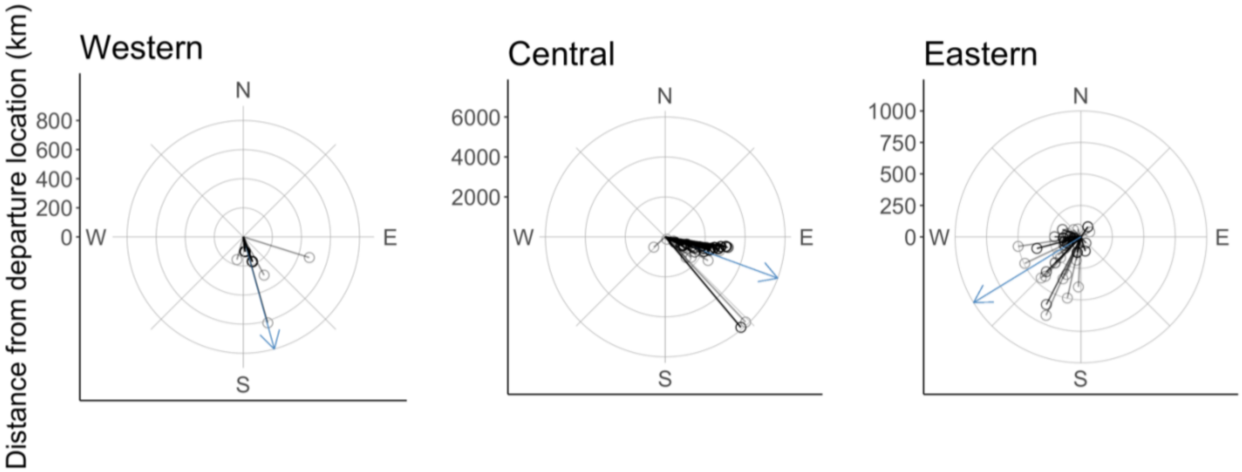


Figure 2.3.2: Departure bearings for Bank Swallows (*Riparia riparia*) that followed the Western (n = 54), Central (n = 110), and Eastern (n = 77) migration routes. Line lengths represent the distance from the departure location (the last detection within 50 km of the breeding site) to the next detection that was a minimum of 50 km away (the detection used to calculate departure bearing). Arrows represent mean departure bearings for each migration route, but the length of the arrow does not represent distance.

Spatial and Temporal Overlap

The results of my spatial overlap analyses supported my visual assignment of migration routes based on observed flight paths (Figure 2.3.1). When all tagged birds were included in the analysis, spatial overlap started out moderately low (i.e., R Mantel values were high, indicating that birds from different tagging sites were not mixing) (Figure 2.3.3). Spatial overlap increased briefly in the early stages of migration but then decreased again between 53°N-44°N. Spatial overlap rapidly increased south of 44°N (i.e., R Mantel decreased), indicating greater spatial overlap among individuals from different tagging sites, especially between 37-39°N (Appendix 1: Table S3). Temporal overlap was overall higher than spatial overlap and followed a similar latitudinal pattern – it started out moderate, increased between 54°N-50N, decreased between 49°N-43°N, and then increased again south of 43°N.

When I restricted my analysis only to include birds that followed the Western and Central migration routes, spatial overlap started out low, increased towards 54°N but then decreased again around 53°N and remained moderate with decreasing latitude (Figure 2.3.4A). R Mantel values were statistically significant at all latitudes, indicating that there was a significant correlation between the detection and breeding site matrices (Appendix 1: Table S6).

When southern BC was removed from the analysis (leaving only birds that I visually assigned to the Central migration route), spatial overlap consistently increased with decreasing latitude, suggesting a high degree of spatial mixing of the birds from AK, YT, northern BC, and SK (Figure 2.3.4B). R Mantel values were statistically significant above 48°N, indicating that there was a significant correlation between breeding site and detection matrices at higher latitudes (Appendix 1: Table S9).

Temporal overlap was consistently high across all latitudes both with and without southern BC when considering the Western and Central migration routes (Figure 2.3.4 A & B, Figure 2.3.5), and all R Mantel values for temporal overlap were statistically significant (Appendix 1: Tables S6 & S9). Together, these two analyses support the visual assignment of Bank Swallows to the Western and Central migration routes.

For Bank Swallows from eastern Canada, spatial overlap started out low but increased starting around 42°N until R Mantel reached almost zero (Figure 2.3.4C). Temporal overlap was high throughout (Figure 2.3.6). R Mantel values were not statistically significant below 40°N for spatial overlap and below 38°N for temporal overlap, indicating that there was no correlation between the breeding site and detection matrices at these latitudes (Appendix 1: Table S12). This analysis supports my visual assignment of birds from QC, NB, NS, and PEI to the Eastern migration route.

I did not plot detections for the Western migration route as it consisted of a single breeding site. I was also only able to plot 2023 detections for the Central migration route (Figure 2.3.5) because in 2022 there was only one breeding site (YT) that followed this route, and departure dates differed between years so I could not combine years on a single plot. For consistency, I also show 2023 detections for the Eastern route (Figure 2.3.6), although 2022 detections for the Eastern route can be seen in Appendix 1 (Figure S9).

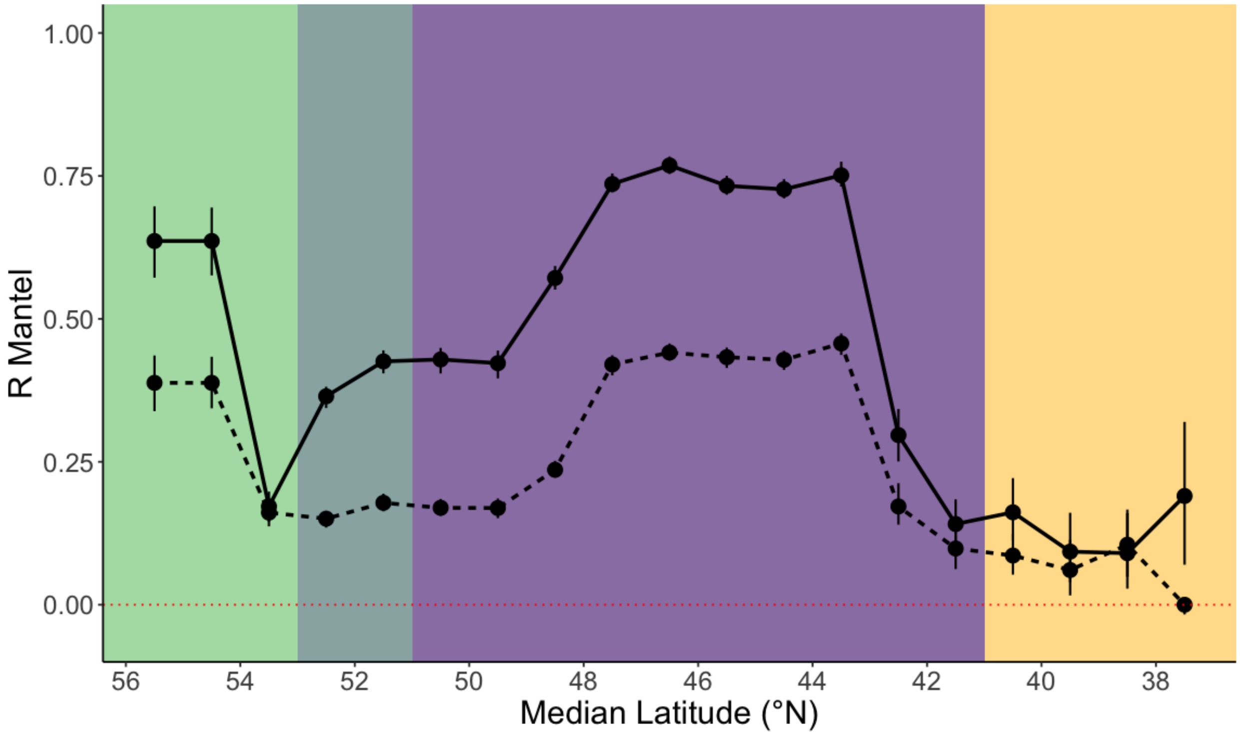


Figure 2.3.3. Spatial (solid line) and temporal (dashed line) overlap of migrating Bank Swallows (*Riparia riparia*) from breeding sites across North America (n = 495). Coloured backgrounds illustrate what birds were detected in each latitudinal window: Green = Central route only; Blue = Central & Western routes; Purple = Central, Western and Eastern routes; and Yellow = Central and Eastern routes. The latitudes on

the x-axis are the median latitude for each 5°-latitude window in my analysis (e.g., a median latitude of 57.5°N means that the window extended from 60°N to 55°N). The red dotted line marks an R Mantel value of zero, which represents complete overlap of birds from different breeding sites during migration. All analyses were performed using 0.1x0.1 latitude-longitude grid cells, results for analyses using 1x1 and 0.01x0.01 grid cells can be found in Appendix 1 (Figures S5 & S6).

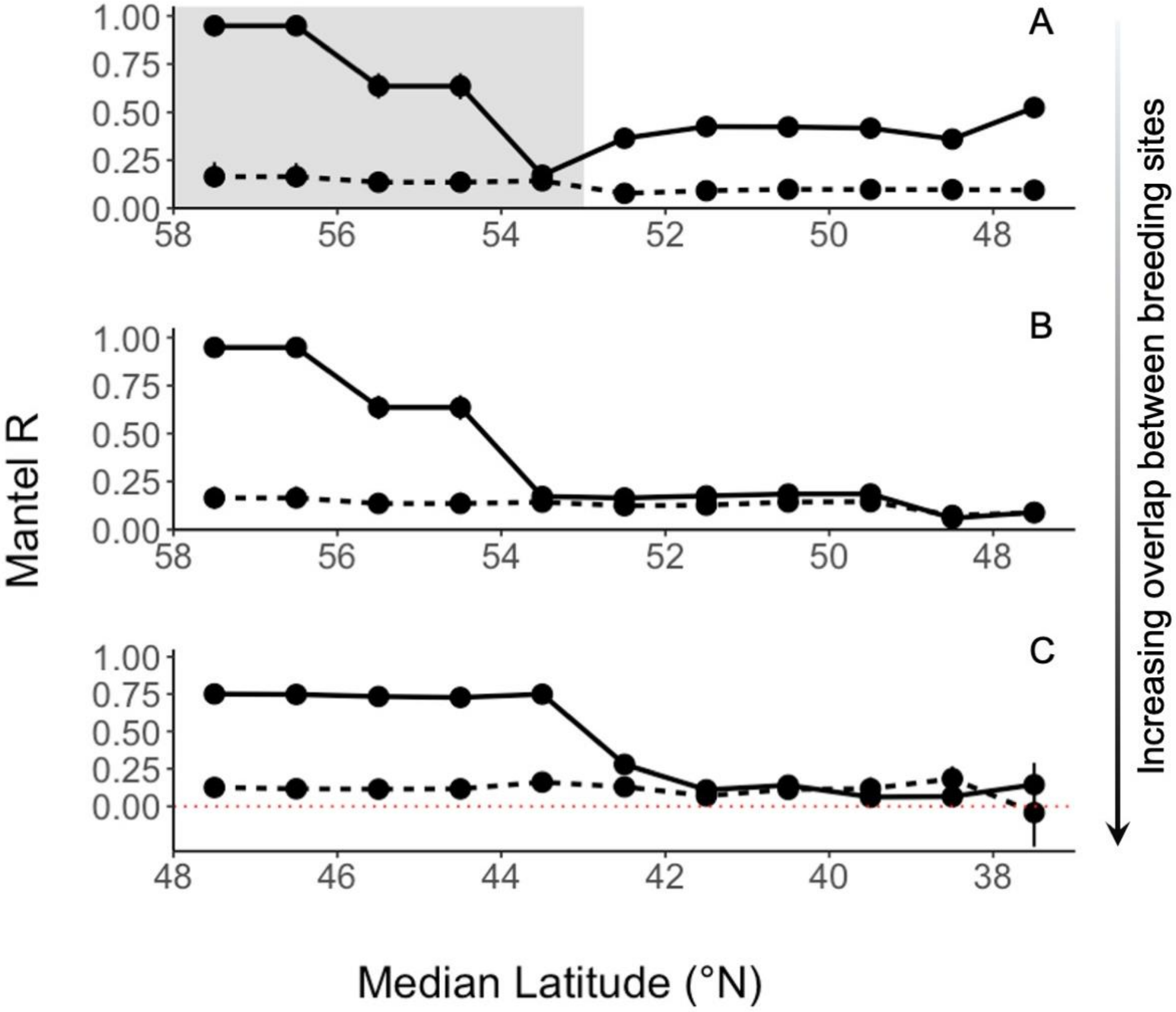
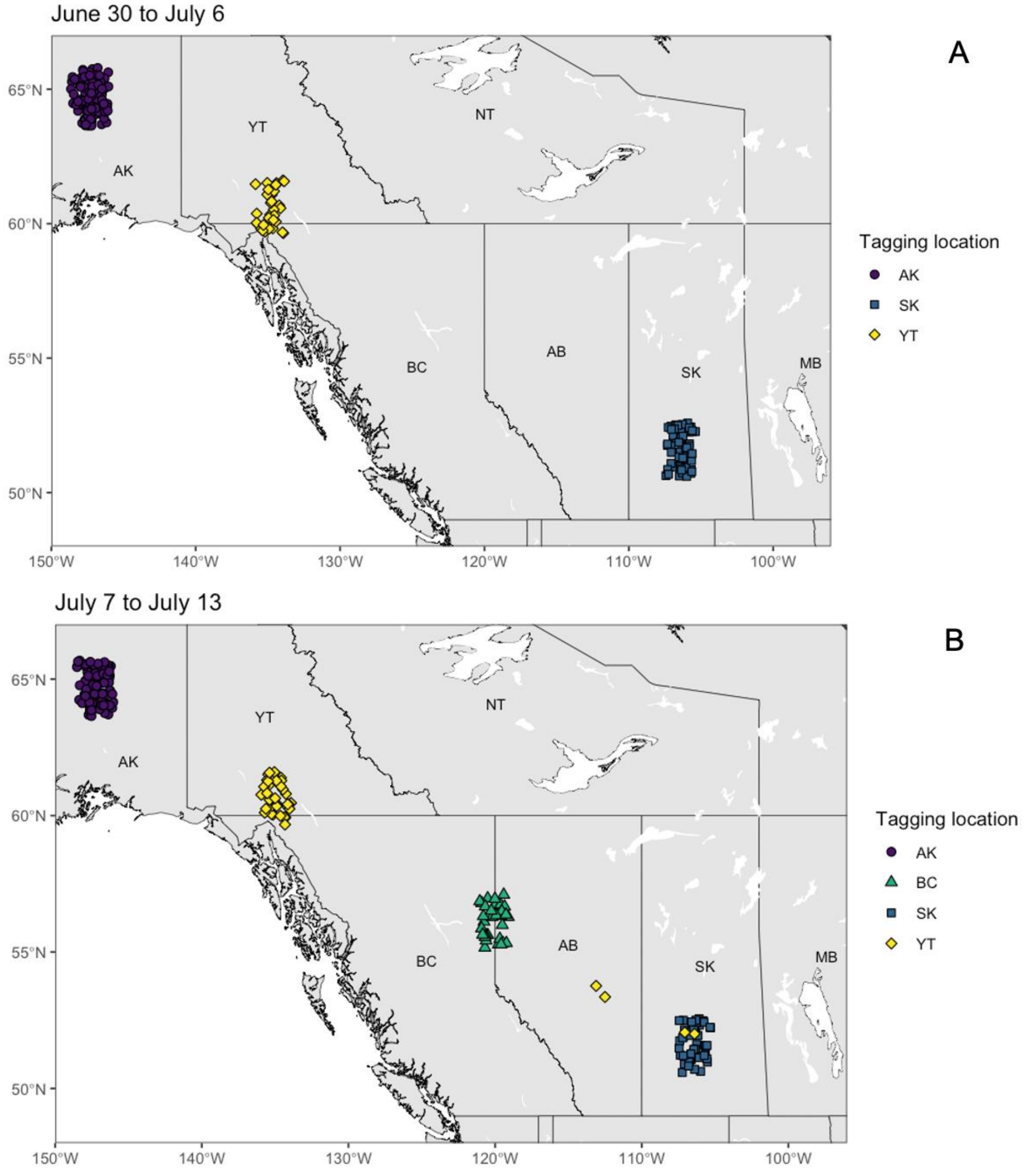
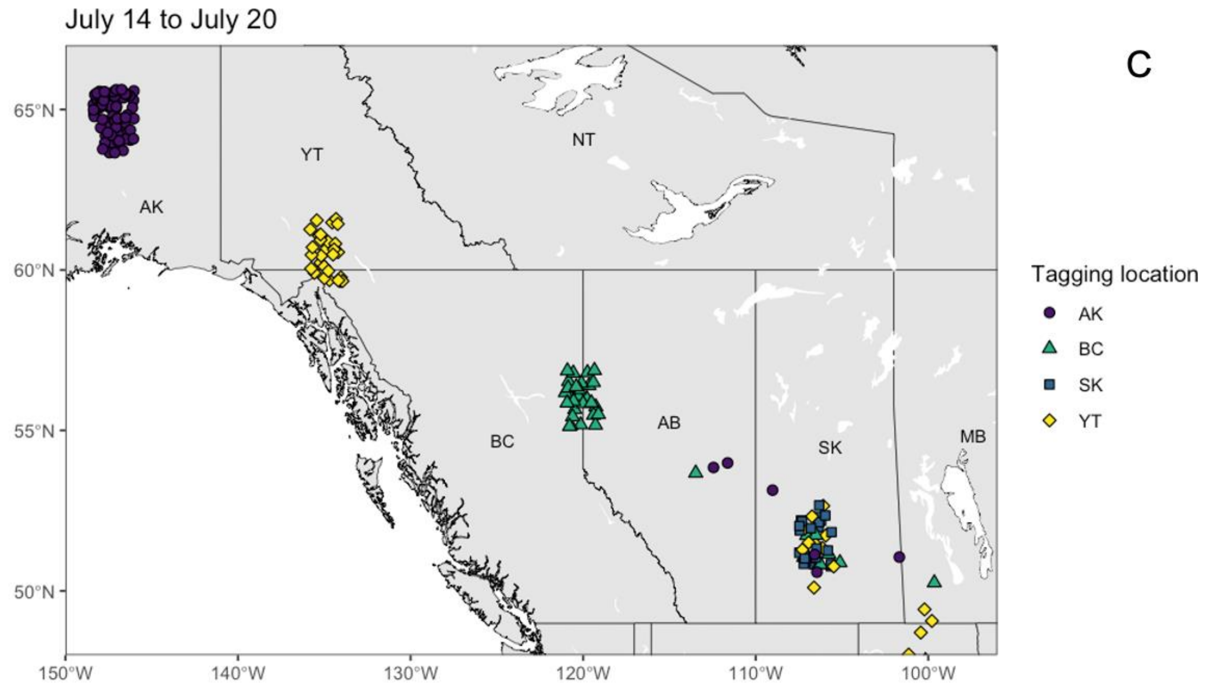
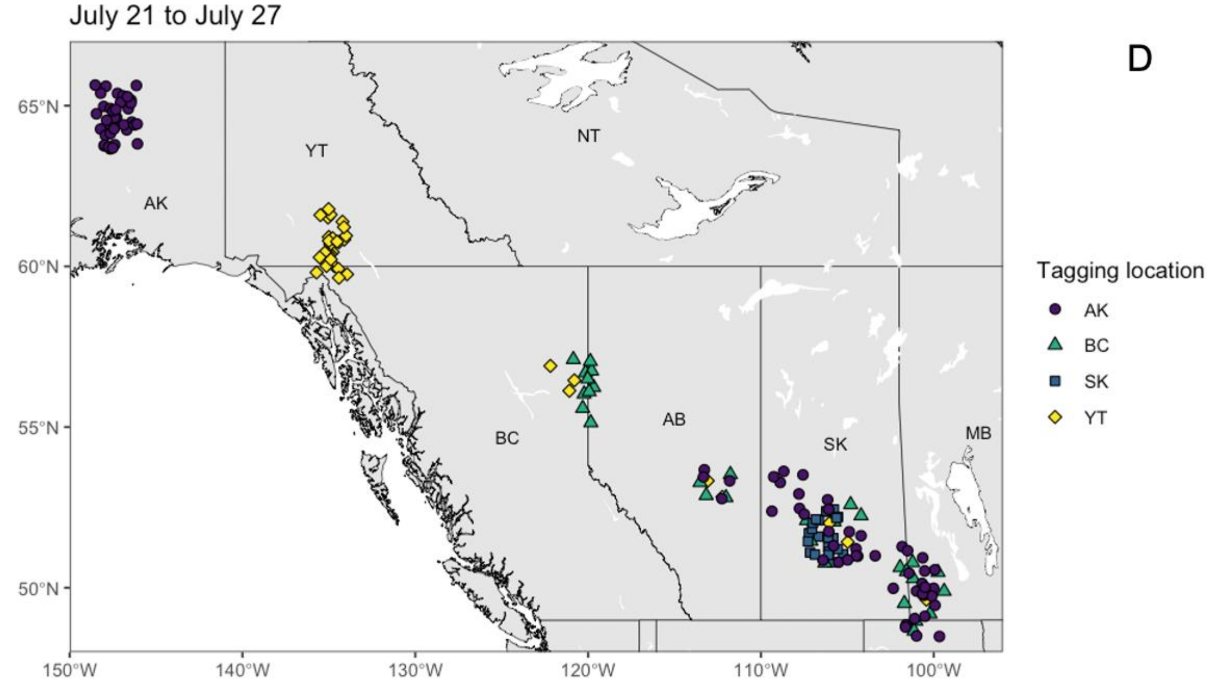


Figure 2.3.4: Spatial (solid line) and temporal (dashed line) overlap for Bank Swallows (*Riparia riparia*) that followed the Western and Central migration routes (Figure A, n = 255); the Central migration route alone (Figure B, n = 162); and the Eastern migration route (Figure C, n = 240). The latitudes on the x-axis are the median latitude for each 5°-latitude window in my analysis (e.g., a median latitude of 57.5°N means that the window extended from 60°N to 55°N). Vertical lines are 95% confidence intervals. A higher R Mantel (closer to one) indicates that individuals from different breeding sites remained spatially and/or temporally segregated from one another, whereas a lower R Mantel (closer to zero) indicates that there was a high degree of spatial or temporal overlap of individuals from different breeding sites. Red

dotted line represents zero on panel C. Grey shading on panel A shows latitudes where only Central route birds were detected; latitudes with no shading had detections for both Central and Western route birds. Results are shown for the latitude ranges at which there were sufficient data to calculate Mantel R. All analyses were performed using 0.1x0.1 latitude-longitude grid cells, results for analyses using 1x1 and 0.01x0.01 grid cells can be found in Appendix 1 (Figures S7 & S8).




July 14 to July 20


July 21 to July 27

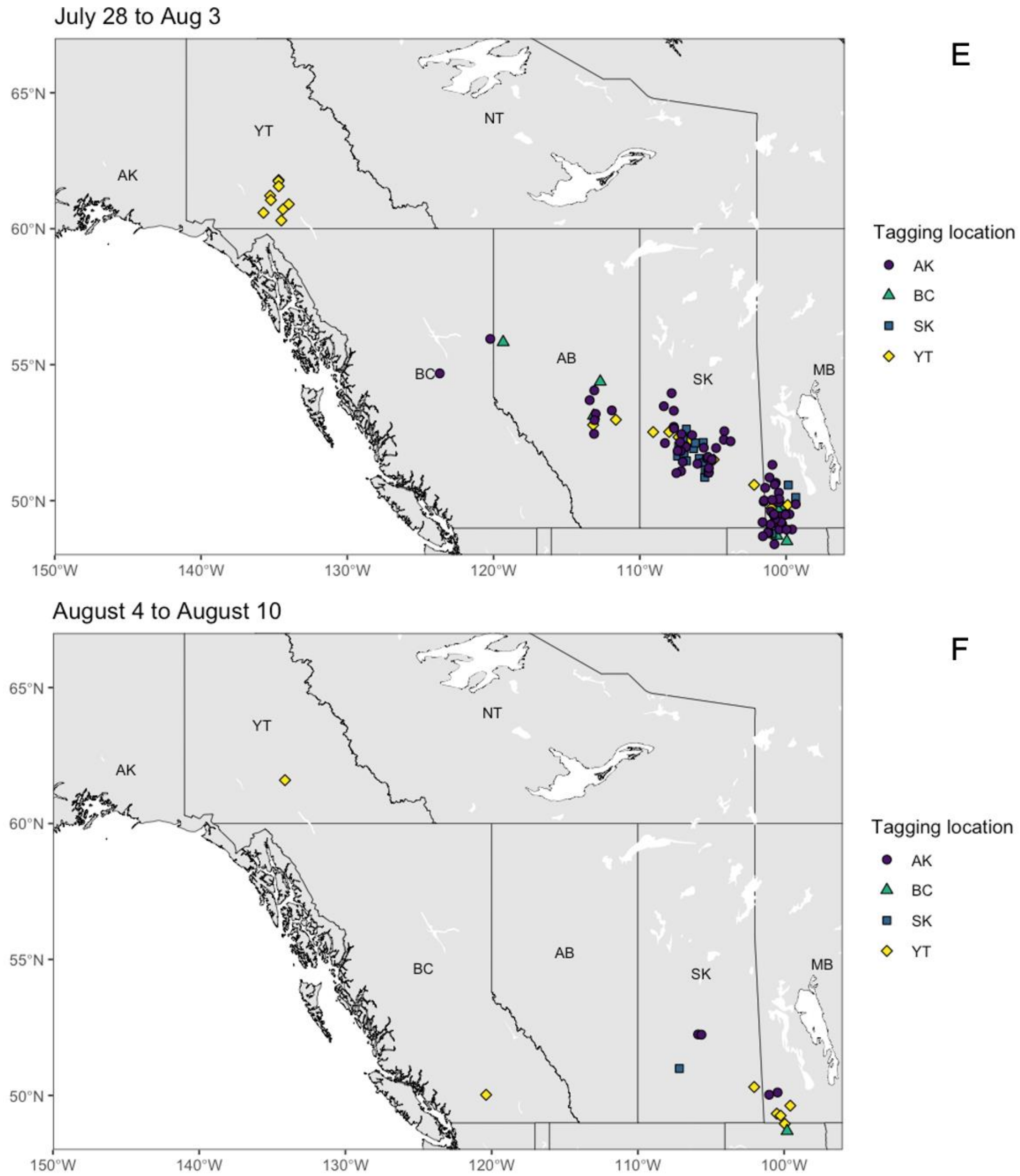
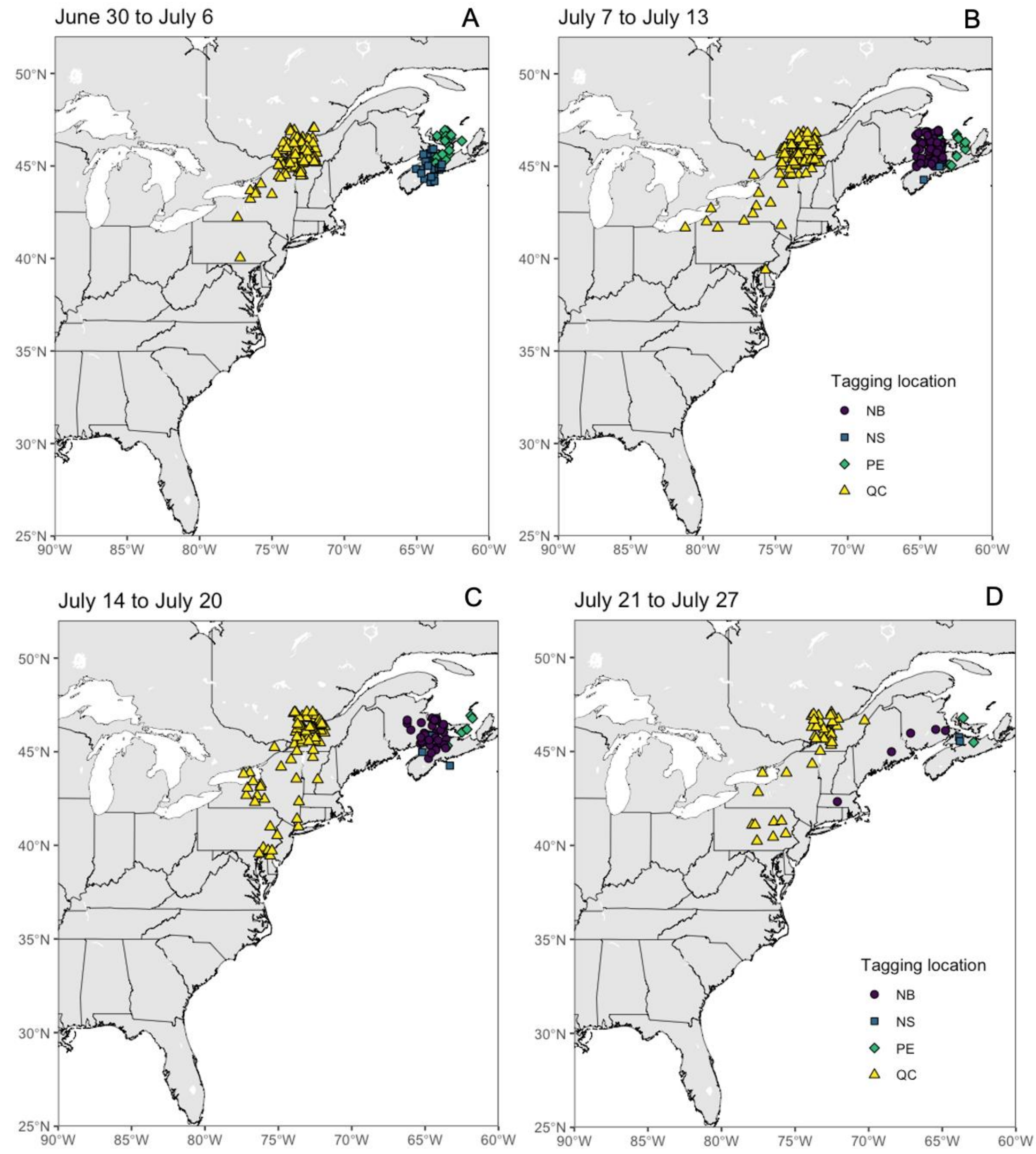


Figure 2.3.5: Temporal overlap of Bank Swallows (*Riparia riparia*) that followed the Central migration route in 2023, with detections grouped into one-week intervals. Points are jittered to reduce overlap so locations are not exact, and there may be multiple points per individual on each map due to the one-week grouping. Departure dates differed between 2022 and 2023, so I was unable to plot both years together. I chose to focus on 2023 because we only had one tag site that followed the Central route in 2022 (YT). A: June 30 to July 6; B: July 7-13; C: July 14-20; D: July 21-27; E: July 28 – August 3; F: August 4-10.


June 30 to July 6
A
July 7 to July 13
B
July 14 to July 20
C
July 21 to July 27
D
50°N
45°N
40°N
35°N
30°N
25°N
90°W
85°W
80°W
75°W
70°W
65°W
60°W
Tagging location
● NB
■ NS
◆ PE
▲ QC

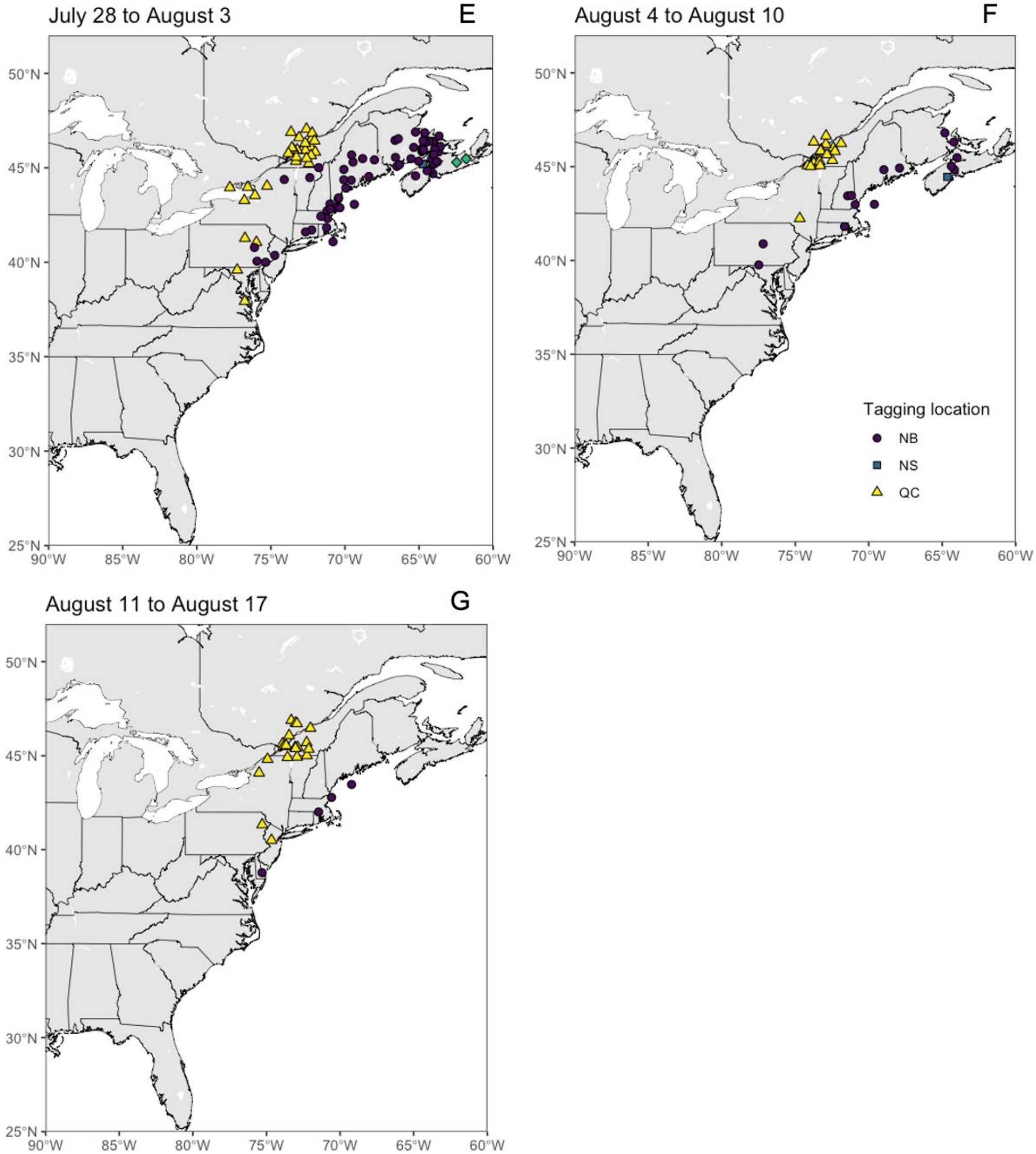


Figure 2.3.6: Temporal overlap of Bank Swallows (*Riparia riparia*) that followed the Eastern migration route in 2023, with detections grouped into one-week intervals. Points are jittered to reduce overlap so locations are not exact, and there may be multiple points per individual on each map due to the one-week grouping. Departure dates differed between 2022 and 2023, so I was unable to plot both years on together. I chose to focus on 2023 for easier comparison with the Central route (Figure 2.3.5), but maps for the Eastern route in 2022 can be found in Appendix 1 (Figure S4).

A: June 30 – July 6; B: July 7-13; C: July 14-20; D: July 21-27; E: July 28 – August 3; F: August 4-10; G: August 11-17.

Departure Timing

Breeding ground departure dates ranged from June 28 to August 11 in 2022, and from June 26 to September 2 in 2023, with 91.5% (539/589) of birds departing in July (Figure 2.3.6). My initial model did not predict significant effects of mass or sex on departure dates (Table S11), so here I present results from my second model that excluded these variables and included individuals for which these data were missing (n = 33; Table 2.3.3).

Bank Swallow departure timing differed between migration routes, but the degree to which it differed depended on the year. In 2022, Bank Swallows that followed the Central migration route departed an average of 12.04 ± 3.49 days later than Bank Swallows that followed the Eastern migration route, but there was no significant difference in departure timing between the Central and Western or Eastern and Western routes (Table 2.3.3, Table 2.3.4 & Figure 2.3.6). In 2023, there was no significant difference in departure timing between any of the three migration routes. On average, Bank Swallow departures were 10.23 ± 2.24 days later in 2022 than in 2023. Mean annual departure dates were July 24, 2022, and July 17, 2023, for the Central migration route; July 16, 2022, and July 15, 2023, for the Western migration route; and July 16, 2022, and July 14, 2023, for the Eastern migration route.

Table 2.3.3: Model-predicted effects of migration route, wing chord, and year on Bank Swallow (*Riparia riparia*) departure dates (n = 589). Breeding site was included as a random effect (σ = 5.355), all other effects are fixed. This model includes individuals with missing mass or sex (n = 33) but excludes individuals with missing wing chord values (n = 2).

Term	Estimate	Std.error	df	t value	p-value
(Intercept)	230.6893	15.4134	580.9420	14.967	< 2e-16 ***
Route$_{\text{Eastern}}$	-12.0439	3.4681	20.3220	-3.473	0.00236 **
Route$_{\text{Western}}$	-10.1349	6.0912	10.6259	-1.664	0.12531
Wing chord	-0.2252	0.1523	579.3667	-1.479	0.13969
Year$_{2023}$	-10.2341	2.2393	292.0504	-4.570	0.0000072 ***
Route$_{\text{Eastern}}$ * Year$_{2023}$	7.9587	2.6071	363.8832	3.053	0.00243 **
Route$_{\text{Western}}$ * Year$_{2023}$	8.2717	2.9326	450.8344	2.821	0.500

Table 2.3.4: Results of Tukey's post-hoc test of the model in Table 2.3.3 to compare pairwise differences in Bank Swallow (*Riparia riparia*) departure timing (m/s) between the Western, Central and Eastern migration routes in interaction with study year (n = 589).

	Comparison	Estimate	Std.error	df	t.ratio	p-value
2022	Central-Eastern	12.04	3.49	25.5	3.453	0.0053
	Central-Western	10.13	6.10	13.4	1.661	0.2555
	Eastern-Western	-1.91	5.91	12.1	-0.323	0.9444
2023	Central-Eastern	4.09	3.03	14.9	1.350	0.3907
	Central-Western	1.86	5.82	11.4	0.320	0.9454
	Eastern-Western	-2.22	5.88	11.7	-0.378	0.9249

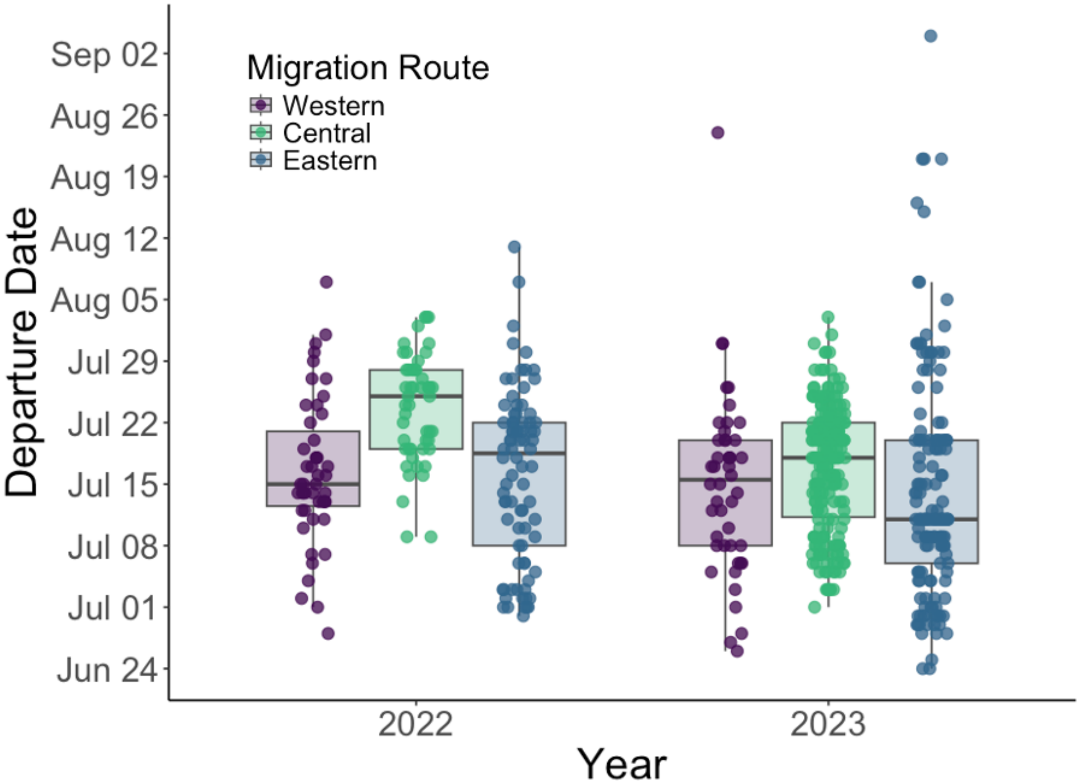


Figure 2.3.7: Bank Swallow (*Riparia riparia*) departure dates (n = 589) grouped by year and migration route. $n_{Western}$ = 93, $n_{Central}$ = 257, $n_{Eastern}$ = 239 (one departure date per individual). The horizontal lines in each box represent the first quartile (Q1), median (Q2) and third quartile (Q3). The vertical lines on the top and bottom of each box plot represent Q1 - 1.5*(Q3-Q1) and Q3 + 1.5*(Q3-Q1).

Migration Pace and Ground Speed

The migration pace of Bank Swallows ranged from 14 km/day to 479 km/day. My initial model did not predict significant effects of wing chord or sex on migration pace (Table S18), so I re-ran my model without those predictors and including individuals for which I was missing wing chord or sex (n = 4). On average, Bank Swallows that followed the Central migration route migrated faster than individuals that followed the Eastern migration route (Table 2.3.5 & Figure 2.3.8). I was only able to calculate migration pace for one bird that followed the Western migration route, which was 44 km/day. The average migration pace for birds that followed the Central migration route (n = 33) was 325 ± 108 km/day, while the average migration pace for birds that followed the Eastern migration route (n = 26) was 77 ± 59 km/day. After accounting for differences between migration routes, later departing birds migrated faster, with an estimated difference in migration pace of 1km/day for every day later an individual departed. Migration pace values were 2 km/day faster, on average, in 2023 than in 2022. There was no evidence that mass had any effect on migration pace.

Ground speeds for Bank Swallows ranged from 2 m/s to 22 m/s. My initial model did not find a significant effect of sex on Bank Swallow ground speeds and there were no significant interactions between route and year (Table S19), so here I present the results from my second model that included individuals for which sex was unknown (n = 5) and did not include interaction terms. On average, ground speeds were higher for birds that followed the Central migration route (mean = 11 ± 4 m/s) than for birds that followed the Western (mean = 7 ± 3 m/s) or Eastern (mean = 7 ± 4 m/s) migration routes (Table 2.3.6 & Figure 2.3.8). There was no significant difference in ground speed between the Eastern and Western routes (Table 2.3.7). My model predicted a positive effect of mass on ground speeds based on effect sizes, with an estimated difference of 6 m/s between the lightest (11g) and heaviest (16.5g) tagged Bank Swallows. Ground speeds did not differ between the two study years, and there was no evidence for the effect of wing chord or departure date on ground speeds.

Table 2.3.5: Model predicted effects of migration route, mass, departure date, and year on Bank Swallow (*Riparia riparia*) migration pace (km/day; n = 58). Breeding site was included as a random effect (σ = 0.5559), all other effects are fixed. This model includes individuals with unknown or missing sex or wing chord (n = 4). The reference level for migration route and year was the Central route and 2022, respectively. The response (migration pace) was log-transformed to improve model fit as assessed using residuals. There was only one bird with a migration pace from the Western route, so it was not included in this analysis.

Term	Estimate	Std.error	df	t value	p-value

(Intercept)	2.170950	1.399638	45.510094	1.551	0.12781
Route$_{\text{Eastern}}$	-1.318114	0.368532	9.057892	-3.577	0.00590 **
Mass	-0.042043	0.064101	44.598035	-0.656	0.51526
Departure date	0.016459	0.005571	43.373096	2.954	0.00505 **
Year$_{2023}$	0.777756	0.264615	49.762608	2.939	0.00498 **

Table 2.3.6: Model predicted effects of migration route, mass, wing chord, departure date, and year on Bank Swallow (*Riparia riparia*) ground speed (m/s; n = 162 for 106 individuals). Individuals nested within breeding sites were included as random effects (σ = 0.2255 and σ = 0.0770, respectively), all other effects are fixed. This model includes individuals with unknown sex (n = 3). Reference levels for migration route and year are the Central route and 2023, respectively. The response (ground speed) was log-transformed to improve model fit as assessed using residuals.

Term	Estimate	Std.error	z value	p-value
(Intercept)	-1.369920	1.883365	-0.727	0.46699
Route$_{\text{Eastern}}$	-0.409129	0.150415	-2.720	0.00653 **
Route$_{\text{Western}}$	-0.450157	0.158049	-2.848	0.00440 **
Mass	0.076753	0.041293	1.859	0.06306
Wing chord	0.011256	0.015011	0.750	0.45335
Departure date	0.007226	0.004549	1.588	0.11221
Year$_{2022}$	0.109996	0.091098	1.208	0.22726

Table 2.3.7: Results of Tukey's post-hoc test of the model in Table 2.3.6 to compare pairwise differences in Bank Swallow (*Riparia riparia*) ground speed (m/s) between the Western, Central and Eastern migration routes (n = 162 for 106 individuals). Results are averaged over two years (2022 and 2023).

Comparison	Estimate	Std.error	df	t ratio	p-value
Central-Eastern	0.3912	0.152	159	2.569	0.0298
Central-Western	0.4488	0.163	159	2.760	0.0176
Eastern-Western	0.0576	0.138	159	0.418	0.9083

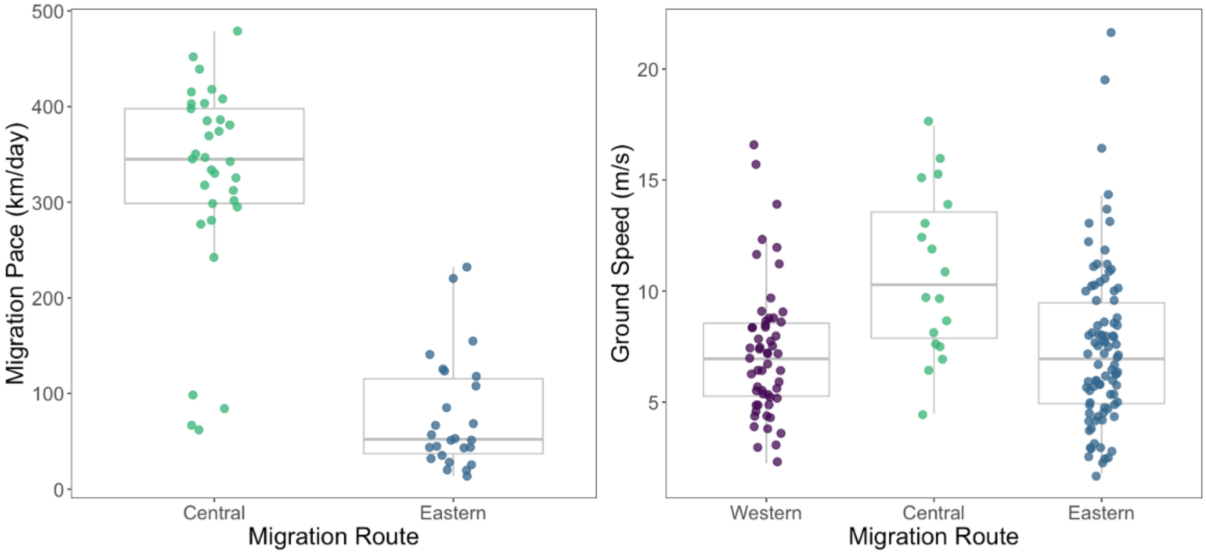


Figure 2.3.8: Box and whisker plots of migration pace (n = 58) and ground speed (n = 162, 106 individuals) for Bank Swallows (*Riparia riparia*) that followed the Western, Central and Eastern migration routes in 2022 and 2023. Migration pace values ranged from 13.5 km/day to 479 km/day. Ground speeds ranged from 1.55 m/s to 21.7 m/s. The horizontal lines in each box represent the first quartile (Q1), median (Q2) and third quartile (Q3). The vertical lines on the top and bottom of each box plot represent Q1 - 1.5*(Q3-Q1) and Q3 + 1.5*(Q3-Q1).

2.4 Discussion

Prior to this study, the migration routes of Bank Swallows from across North America were unknown. My research shows the use of three different migration routes by Bank Swallows breeding from Alaska to the Maritimes during the initial phase of their fall migration. The use of the Eastern migration route had been previously documented for Bank Swallows breeding in New Brunswick (Imlay et al. 2020), and my research shows that birds breeding in Nova Scotia, Prince Edward Island and Québec share this migration route as well. I identified previously undocumented Bank Swallow migration routes that mirrors the broad-scale migration routes used by other aerial insectivores including Tree Swallows (*Tachycineta bicolor*) and Barn Swallows (*Hirundo rustica*) (Hobson et al. 2015; Knight et al. 2018). Visually, the Central route appears to be a more circuitous route to overwintering locations in Central and South America than the

Western and Eastern routes, which appear to head more directly south while following the Rocky Mountains or the Atlantic coast, respectively. However, I propose a few reasons why Bank Swallows from Alaska, Northern BC, and the Yukon that used the Central migration route may have done so. First, they may have been avoiding a risky and energetically expensive crossing of the Rocky Mountains (Aurbach et al. 2018). Second, they may have been targeting foraging and roosting locations in the wetlands and rivers throughout the grasslands east of the Rocky Mountains, and eventually the Mississippi river (Lincoln 1935; Buler et al. 2007; Fraser et al. 2017). Third, the use of the Central route may be a legacy of historical geographic isolation during glacial periods (Boulet et al. 2006; Ruegg 2007). Fourth, the Central route may offer favourable environmental conditions, such as prevailing winds, that reduce the energetic costs of migration (La Sorte et al. 2014).

Characterizing Bank Swallow migration routes at the continental scale lays the foundation for important future research to assess threats that may be driving population declines. A first step could be to compare rates of population decline for Bank Swallows from different breeding regions to determine if these are associated with migration routes. Similar rates of decline for Bank Swallows from breeding regions that followed the same route could suggest that their population declines are impacted by shared threats experienced during migration (García-Pérez and Hobson 2014; Studds et al. 2017; Kramer et al. 2018). Future research could explicitly assess the various threats birds following each migration route might encounter. For example, Horton et al. (2019) used radar detections to show that nocturnal migrants following routes through the Central USA experience higher artificial light exposure than nocturnal migrants following more Western routes.

For diurnally migrating Bank Swallows, I suspect that an important threat is the loss of wetland habitat along migration routes. Wetlands provide important foraging habitat for Bank Swallows and other aerial insectivores (Saldanha 2016; Twining et al. 2016, 2018; Saldanha et al. 2019; Berzins et al. 2022), and Bank Swallows also roost in wetlands such as cattail (*Typha*) marshes (Falconer et al. 2016; Saldanha 2016; Fensore 2024). Several of the swallows in this study were detected around wetlands during migration, including Lake Manitoba and Whitewater Lake in southern Manitoba, and the southern shore of Lake Ontario in New York state and Pennsylvania (Figure 2.3.1). Bank Swallows that followed the Central migration route came from geographically distant breeding sites in AK, YT, northern BC and the Canadian prairies, yet all of these individuals seemed to funnel through the Prairie Pothole region during migration. Other aerial insectivores such as Tree Swallows (*Tachycineta bicolor*) have also been documented migrating through the Prairie Pothole region (Knight et al. 2018). I speculate that maintaining and restoring wetlands in this area could benefit aerial insectivores from multiple breeding regions, and may help to offset negative impacts of intensive agriculture in the prairies (Berzins et al. 2022).

Weather conditions during migration such as cold weather and heavy precipitation have also been linked to decreased survival in swallow species including Bank Swallows (Cowley and Siriwardena 2005; Hess et al. 2008; Møller 2011; Clark et al. 2018; Imlay and Leonard 2019). More detailed data on individual movements, habitat associations and weather conditions along the three migration routes could help better delineate various risks and benefits associated with each migration route.

The Bank Swallow migration route and timing information that I documented in this thesis may also contribute to the identification of new Key Biodiversity Areas (KBAs). KBAs are defined by the IUCN as “sites contributing significantly to the global persistence of biodiversity” (IUCN 2016), and the identification of KBAs can be used to guide protected area designation. KBAs are selected using a series of standardized criteria, some of which apply to large aggregations of a single species, including flocks of migratory birds. For example, criterion A1d applies to areas that contain “≥0.2% of the global population size and ≥10 reproductive units of a species listed as [vulnerable] due only to population size reduction in the past or present” (IUCN 2016), which could apply to Bank Swallows. In 2022, Whitewater Lake, in southern Manitoba, was designated a Canadian KBA because of the large aggregations of migratory birds, some of which are Species at Risk, during the spring and fall migratory periods (KBA Canada 2022).

Importantly, my results highlight how birds from a single geo-political jurisdiction can use different migration routes. For example, birds from northern BC followed the Central migration route while birds from southern BC followed the Western migration route, which means birds from the two BC breeding sites could be facing different threats during migration (Iwamura et al. 2013; Klaassen et al. 2014; Studds et al. 2017; Horton et al. 2019; Buchan et al. 2022, 2023). This suggests that human jurisdictional boundaries are not necessarily the optimal unit or scale of management for Bank Swallows. Previous research has shown that conservation and management actions need to match the scale and patterning of animal movement to be effective (Thirgood et al. 2004; Martin et al. 2007; Berger et al. 2008; Runge et al. 2015; Santini et al. 2016). For Bank Swallows and other migratory species, this may mean managing at the level of the migration route rather than adopting national or provincial and territorial management plans (Klaassen et al. 2008; Iwamura et al. 2014).

Differences in migratory departure timing, migration pace and ground speed for Bank Swallows following different migration routes translated into a moderate degree of temporal overlap when I included all birds in my analysis. Despite these differences, temporal overlap was higher than spatial overlap, indicating that the timing of migration was more similar than the migration routes used by Bank Swallows from different breeding sites across North America. Temporal overlap within individual migration routes was also high, suggesting that birds following the same migration routes are migrating at the same time. The faster migration pace of later-departing individuals may have compensated for initial differences in departure timing (González et al. 2020), although the effect size of departure date on migration pace was fairly small, suggesting minimal biological impact. It is possible that later-departing individuals experienced more favourable migration conditions that allowed for faster migration (e.g., more favourable winds, (Åkesson and Hedenström 2000; Mitchell et al. 2015)). Conversely, there may be selective pressure for late-departing individuals to migrate faster to avoid poor conditions en route as the season progresses (Hope et al. 2014; Acácio et al. 2022). Regardless of the exact reason, high temporal overlap for birds following the same migration route suggests that these individuals will be similarly affected by factors that vary in time, such as seasonal variation in insect abundance (Paquette et al. 2013;

Dunn et al. 2023) or weather conditions (Newton 2007; Wellicome et al. 2014). This could be beneficial if all, or most, individuals that follow a given migration route are able to time their migration to align with optimal conditions (Renfrew et al. 2013; Kölzsch et al. 2015; Pedersen et al. 2020). Conversely, high temporal overlap could contribute to population declines if there is a mismatch between when most individuals are migrating and the timing of optimal conditions along the migration route (Both et al. 2006; Møller et al. 2008; Clausen and Clausen 2013). For example, sub-optimal weather conditions during migration, such as storms, can cause mass-mortality of migrating birds (Newton 2007).

My analysis of spatial and temporal overlap was focused on latitudes north of 38°N due to a lack of detections south of 38°N that I suspect is largely due to low Motus receiver densities in those regions. It is possible that I may have observed increased spatial overlap at lower latitudes if birds from all three migration routes converged around the Gulf of Mexico, similar to patterns seen in Common Nighthawks (*Chordeiles minor*) and Eastern Whip-poor-wills (*Antrostomus vociferus*) (Knight et al. 2021; Korpach et al. 2022). Alternatively, spatial overlap may have remained low if birds from the three migration routes used divergent strategies around the Gulf of Mexico, which has been seen in Barn Swallows (*Hirundo rustica*) and Tree Swallows (*Tachycineta bicolor*) (Hobson et al. 2015; Knight et al. 2018). Answering this question will require either increased Motus receiver density at lower latitudes or the advent of smaller GPS tracking technologies.

Ideally, I would have liked to perform Mantel tests on pairwise combinations of breeding sites to quantitatively identify sites that used common migration routes along which spatial overlap reached a minimum. I was unable to do this because my detections were not at the same latitudes for all sites (i.e. the Central sites had detections at higher latitudes than the Eastern and Western sites), and individual sites did not always have enough spatially continuous detections due to inconsistent latitudinal representation of Motus receivers. Therefore, I grouped my breeding sites based on visual assessment of migration tracks and used the Mantel tests to provide statistical support for my visual groupings.

The similarity of migration routes across years at breeding sites with repeated tagging suggests that there is repeatability in fall migration routes for Bank Swallows from a given breeding region. However, we did not tag any individual birds in both 2022 and 2023, so it is possible that while the observed site-level migration routes remained relatively consistent between years, individual birds may have changed their migration routes from one year to the next, which has been observed in Wood Thrush (*Hylocichla mustelina*) (Stanley et al. 2012) and Osprey (*Pandion haliaetus*) (Alerstam et al. 2006). Nonetheless, the similarity in migration routes between years could reflect a lack of flexibility in migration routes that prevents migrating Bank Swallows from adapting to environmental changes en route (Alerstam et al. 2006; Stanley et al. 2012; Vardanis et al. 2016).

The later 2022 departure timing for birds that followed the Central migration route may be at least partly driven by the higher breeding latitude of the YT Bank Swallows (the only Central route site that I had in 2022) compared to the lower breeding latitudes of birds that followed the Western and Eastern migration routes. The onset of spring is generally later at higher latitudes compared to lower latitudes (Briedis et al. 2020), which can result in a later breeding season and subsequently later migratory departures (Gow et al. 2019a; Briedis et al. 2020; Imlay et al. 2021). Indeed, when I re-ran my departure date model without the AK, YT and northern BC sites, leaving only my lower latitude Central migration route breeding sites in SK and MB, there was no longer a significant difference in departure timing between the Eastern and Central migration routes (Table S9). Later migratory departures at higher breeding latitudes have also been observed in Common Swifts (*Apus apus*) (Åkesson et al. 2020), Purple Martins (*Progne Subis*) (Neufeld et al. 2021) and Tree Swallows (*Tachycineta bicolor*) (Gow et al. 2019a).

However, the patterns in departure timing that I documented in my research cannot entirely be explained by breeding latitude. First, there were no differences in departure timing between any of the three migration routes in 2023. The year by route interaction in departure timing does not appear to be driven by differences in breeding locations between years, because when I re-ran my model only including sites where we tagged in both years, there still was no difference in departure timing between the three routes in 2023 (Table S13, Figure S5). Second, even in 2022, southern BC Bank Swallows did not depart significantly earlier than the Central route swallows, despite breeding at a latitude comparable to many of my Eastern sites. The parameter estimate for the Western route suggested that Bank Swallows from southern BC departed an average of 10 days earlier than swallows that followed the Central route, compared to a difference of 12 days between the Eastern and Central routes. However, the difference between the Western and Central routes was not significant.

Alternatively, I suspect that other environmental factors that I was unable to quantify may have impacted the departure timing of Bank Swallows in my study. For example, it is possible that smoke or habitat loss due to wildfires may have altered breeding and migratory behaviour of Bank Swallows (Overton et al. 2022; Nemes et al. 2023). Birds may also delay migratory departures during periods of warmer weather (Brisson-Curadeau et al. 2020), so differences in weather patterns between western and eastern North America, and between 2022 and 2023, may also have contributed to the interacting effects of migration route and year on departure timing. Flexibility in migration timing could allow Bank Swallows to respond to changing environmental conditions and select favourable conditions for migratory departure (Mitchell et al. 2015; Horton et al. 2023). This contrasts with the results of Fraser et al. (2013), who found that Purple Martins (*Progne subis*) did not change their spring migratory departure timing in years with warmer springs. The timing of fall migration may be under less selective pressure than the timing of spring migration, possibly because of the association between the timing of arrival on the breeding grounds and reproductive success (Norris et al. 2004; Alves et al. 2013). Indeed, Stanley et al. (2012) found that the timing of Wood Thrush (*Hylocichla mustelina*) spring migration was more repeatable than the timing of autumn migration. Alternatively, the later fall departures in 2022 may be a function of constraints associated with the timing of breeding (Mitchell et al. 2012; Gow et al. 2019a; Imlay et al. 2021). Further research into the factors that influence fall migration timing in Bank Swallows could help to understand how individuals respond to different environmental conditions.

The fall migration departure dates that I documented in this study could be useful in providing a timeline during which Bank Swallow breeding colonies should not be disturbed. I would suggest restricting activity around colonies between April, when Bank Swallows typically start to arrive on the breeding grounds (Garrison and Turner 2020d), and the end of July, by which point most of my tagged birds had departed from the colony. Keeping dogs on leash and reducing outdoor cat activity around colonies during those times could also help to reduce nest predation (Burke et al. 2019). Assuming that the timing of breeding in our study colonies is similar to that of colonies nesting in anthropogenic habitat such as sand and gravel pits, which are readily inhabited by Bank Swallows (Burke et al. 2019), sand harvesting should not occur until August to avoid disrupting breeding.

Bank Swallows that followed the Central migration route had higher migration pace than birds that followed the Eastern route, as well as higher ground speeds than birds that followed either the Eastern or Western routes. In the context of later departures for the Central route birds in 2022, this suggests Bank Swallows from those breeding sites may be under pressure to catch up with earlier-departing birds that bred in other regions, perhaps to avoid unfavourable weather conditions (Newton 2007; Acácio et al. 2022) or to reach the wintering grounds before food resources en route are diminished (Baker et al. 2004). Alternatively, faster ground speeds and migration paces for the Central migration route birds may reflect a lack of suitable roosting and foraging habitat at more northern latitudes due to unfavourable land cover (e.g. forest) or low aerial insect availability. Bank Swallows are fly-and-forage migrants (Imlay et al. 2020) and spending less time foraging would likely result in an increased rate of travel compared to areas with more abundant foraging resources where the rate of travel would be slower due to increased foraging (Hadjikyriakou et al. 2020). The four individuals from the Central migration route that had low migration pace values (Figure 2.3.7) all had very long migration tracks that extended down into Central America, which is further evidence that my migration pace values might be influenced by the latitudes at which I have detections. Nonetheless, my migration pace and ground speed estimates were on par with other studies of aerial insectivores (Fraser et al. 2013; Imlay et al. 2020, 2021).

Differences in migration pace, but not ground speed, across years could be explained by several factors. It is possible that migrating Bank Swallows had fewer stopovers, or that stopovers were shorter in duration, in 2023 than in 2022, both of which would increase the overall pace of migration even in the absence of increased ground speeds (Duijns et al. 2017; Schmaljohann and Both 2017; Schmaljohann 2018; Bennett et al. 2019). However, I suspect that the difference in migration pace between 2022 and 2023 may also have been impacted by differences in breeding sites between the two study years. We had more Central route sites in 2023 with the addition of AK, northern BC and SK. The Central route birds tended to have higher migration pace values, so I think that may have resulted in overall faster migration paces in 2023 than in 2022. However, I was unable to test for an interaction between migration route and year in my migration pace model due to limitations in my sample size.

It is important to note that my results may have been impacted by limitations of the Motus system or my filtering and analysis methodologies. For example, I was unable to assess Bank Swallow migration routes and timing through the southern portions of their migration. The lack of detections in these regions may be due to low receiver densities, or they may reflect delays in data uploads or technological issues/limitations with tags or receivers that can result in missing or incorrect data, or they may be due to tag loss/mortality. For example, tag batteries weaken with increasing time since deployment, which may have resulted in weaker signals as birds migrated through lower latitudes. This may have shown up as shorter run lengths if weak signals went undetected by receivers, which may have resulted in detections being filtered out. My filtering process may also have removed some legitimate detections, potentially more so at southern latitudes because many of the receivers were noisy and run lengths were often short. The Motus system tends to produce a high number of false and ambiguous detections that must be scrutinized and/or filtered out - I chose only to present data that I have a high degree of confidence in, meaning that I removed some ambiguous but potentially real data.

I am also unable to determine the reasons underlying a lack of detections for certain tags. A total of 280 of the 890 tags that we deployed were never detected at all, an issue that I suspect is largely due to technological issues with the tags because all tags were deployed within detection distance of a receiver. There were also 365 Bank Swallows that were detected at their breeding sites but were not detected post migratory departure, including 35 of the 38 ON tags that had detections (three ON tags had post-departure detections within ON). The lack of migratory departure for Ontario-tagged birds is especially surprising considering the high density of receivers immediately south of Ontario. One possible explanation is that Bank Swallows that were not detected post-departure followed different migration routes from birds that had migratory detections, specifically routes that did not pass close enough to receivers to be detected. Alternatively, tags may have fallen off or these birds may have died soon after departing from their breeding sites. I find it unlikely that the tags resulted in high levels of mortality for only the birds from Ontario given similar capture and tagging methods relative to other sites. Therefore, if there was a high level of mortality for Ontario Bank Swallows, I suspect that it would be related to anthropogenic stressors such as collisions with towers or wind turbines. Another explanation that I am currently investigating is whether technological issues with receivers and the Motus data processing system resulted in detections being screened out erroneously. Unfortunately, I cannot currently differentiate between all of these possible explanations.

I am also unable to say where untagged Bank Swallows migrated. While my results show that many birds do follow the Central, Western and Eastern migration routes, there may be other important Bank Swallow migration routes that went undetected because they were taken by untagged individuals such as juveniles (Hope et al. 2014; McKinnon et al. 2014; Verhoeven et al. 2022). Nonetheless, the repeatability of migration routes between years and similarities between the migration routes that I documented here and those that have been documented in other swallows, namely Tree Swallows (Knight et al. 2018) and Barn Swallows (Hobson et al. 2015), suggests that I was still able to capture important migration routes. The results of this study also illustrate the amount of tagging effort required to collect range-wide migration data for a broadly distributed species.

My results also suggest that an important future research avenue could be an assessment of potential genetic population structure amongst the migration routes (Calderón et al. 2016; Kimble et al. 2020). Migratory divides can create or maintain genetic differentiation between populations (Ruegg and Smith 2002; Irwin and Irwin 2005; Ruegg 2007), which could provide further evidence that Bank Swallows following the three migration routes that I documented in this study require separate conservation strategies (Ruegg et al. 2021).

While I have suggested avenues for important future research, it is my hope that the information on Bank Swallow fall migration that I have documented in this thesis will support conservation practitioners in initiating cross-boundary conservation actions. For example, knowledge of Monarch Butterfly (*Danaus plexippus*) migration routes has allowed for the creation of tri-national conservation initiatives involving Canada, the USA and México, the three countries that span the entirety of the Monarch's annual cycle in North America (Diffendorfer et al. 2023). Although my Motus migration tracks did not extend to likely wintering locations for most individuals in my study, future research into the overwintering locations of Bank Swallows from across the North American breeding range would help to identify countries in Central and South America that could be partners in conservation with Canada and the USA.

3 CHAPTER 3 - General Discussion

In this study, I documented for the first time the migration routes and timing of Bank Swallows from geographically distant sites across their North American breeding range. This study was observational and exploratory in nature, but that does not detract from its conservation value. My research is a necessary first step towards future conservation research and actions and provides fundamental information about where North American breeding Bank Swallows are in space and time throughout their annual cycle.

It is important to note that our understanding Bank Swallow movements and habitat use throughout the non-breeding season does not detract from the potential importance of population limiting factors acting on the breeding grounds. Potential stressors occurring on the breeding grounds include wetland loss (Clark et al. 2018; Penfound and Vaz 2022; Birch et al. 2022), declines in insect abundance (Benton et al. 2002; Paquette et al. 2013; Morrissey et al. 2015; Pisa et al. 2015), and shoreline hardening (COSEWIC 2013; Environment and Climate Change Canada 2022). Nonetheless, for a migratory species like the Bank Swallow, it is important to take a full annual cycle approach to conservation because there are strong linkages between all periods of the annual cycle (McKinnon et al. 2015; Gow et al. 2019a, b; Imlay et al. 2021), and focusing on one period at the expense of another may result in a failure to identify the key drivers of decline (Martin et al. 2007).

Although I successfully documented novel migration routes for Bank Swallows from across the species' northern breeding range, there were still some areas where I did not get the detections that I had expected. Despite a high density of receivers in Southern Ontario and northeastern USA, I unfortunately did not have any migratory detections for

Ontario-tagged Bank Swallows in either 2022 or 2023. I am currently investigating whether technical issues with receivers in the area or errors in the data processing pipeline may have contributed to the lack of detections for Ontario birds. Alternatively, Ontario Bank Swallows may have followed a migration route that did not pass within detection range of any Motus receivers. For example, I think it is possible that at least some of the birds may have migrated southwest into Ohio and then followed the Mississippi River basin. Given the current distribution of towers and the lack of detections of any birds in that region, any birds that were closely associated with the Mississippi River may have avoided detection on the Motus array. Had they followed the Eastern migration route, I would have expected at least some migratory detections due to the high density of towers along that route. Another possible explanation is that Bank Swallows tagged in Ontario experienced extremely high levels of mortality after leaving Ontario. I find this explanation unlikely due to the high densities of Bank Swallows that nest along the north shore of Lake Erie every year, and the moderate to high breeding site fidelity that has been documented in Bank Swallows in other areas (Szabó and Szép 2010; Garrison and Turner 2020f), but it is a possibility that cannot be ruled out without migratory detection data.

There were also very few detections for AB-tagged Bank Swallows, which was especially surprising in 2023 when 28 birds were tagged but only one was detected, compared with 2022 when three birds were tagged, and none were detected. In 2023, the receiver near the breeding colony may have been installed too late to detect tagged birds prior to departure. Specifically, the receiver was installed on July 24, 2023, and given departures dates at adjacent breeding sites, it is possible that early departures were missed. The AB breeding site was also close to the Canada-US border, and very few birds that followed the Central migration route were detected past that point, likely owing to low receiver densities in Central and Western USA.

I also lacked detections for most birds below about 38°N, which limited my ability to determine what routes Bank Swallows may have followed in the southern portion of their migration. Tree swallows (*Tachycineta bicolor*) and Barn Swallows (*Hirundo rustica*) that followed routes similar to the Western route I documented in Bank Swallows traveled south through western USA down to Mexico (Hobson et al. 2015; Knight et al. 2018), which may be how Bank Swallows from my southern BC site are also migrating. Both Tree Swallows and Barn Swallows that took a Central migration route showed divergent strategies around the Gulf of Mexico, with some individuals crossing the Gulf of Mexico while others appeared to go around via Texas and Mexico (Hobson et al. 2015; Knight et al. 2018). I had a handful of detections for the Central route Bank Swallows in Texas, but those birds were not detected any further south, so I cannot be sure if they then proceeded to cross the gulf or if they instead followed the coast of Mexico. Most of the Barn Swallows that followed an Eastern migration route appeared to cross the gulf from Florida to the Caribbean Islands before entering South America via Venezuela and Colombia (Hobson et al. 2015), which may be how Bank Swallows using this route migrate as well. Previous studies with geolocators and stable isotopes indicate that Bank Swallows overwinter in Central and South America (Imlay et al. 2018; Hobson and Kardynal 2023), so I am confident that the lack of detections is due to study limitations rather than a true lack of presence in those locations.

Despite finding significant differences in departure timing within migration routes and across years, there was still substantial within route variability. It is possible that differences in the timing of arrival to the breeding grounds may have carried over to affect the timing of breeding (Norris et al. 2004; Gow et al. 2019a) and subsequently the timing of fall migratory departures (Gow et al. 2019a; Imlay et al. 2021). In other avian migrants, individuals that overwintered in high quality habitats arrived earlier to the breeding grounds than individuals that overwintered in poor quality habitats (Norris et al. 2004; McKinnon et al. 2015; Imlay et al. 2019). Previous studies using stable isotopes found weak migratory connectivity between breeding and wintering sites (Imlay et al. 2018; Hobson and Kardynal 2023), which could mean that individuals that breed together do not necessarily overwinter together and may therefore occupy habitats of differing quality outside of the breeding season. Previous stable isotope studies of Bank Swallow overwintering locations were limited in their sampling distribution so this requires further investigation, but there could be important conservation implications if differences in overwintering locations result in differential timing of annual events for individuals that breed close together. I suggest that an important next step would be to identify potential overwintering areas for Bank Swallows using stable isotope analysis of feathers collected on the breeding grounds.

Motus has greatly enhanced our ability to track the movements of small animals across large spatial extents, but as with any tracking technology, there are limitations. Detections can be very difficult to verify, particularly for short runs on isolated receivers where there are no other receivers nearby on which an animal might be detected. Most false detections have indicators such as high frequency standard deviation or spuriously high ground speeds between receivers that an individual was detected on. However, other detections may occur in novel but plausible locations with plausible timelines, and without physically being in that location and seeing the tagged bird, it is impossible for me to truly know if the detections are real or not. Legitimate detections may be assigned to the wrong tag or receiver if metadata are incorrect, and tag aliasing is fairly common when multiple tags are deployed within a small distance of one another (which is common when tagging colonial species like Bank Swallows). It is often not possible to connect receivers to the network for automatic uploads, which means that data must be downloaded and uploaded manually, which introduces a time delay. Receivers can also experience a range of technological issues that can go unnoticed until data are downloaded. For example, incorrect GPS timestamps due to malfunctioning GPS units can result in data being automatically filtered out by the Motus system, an issue that is apparent only in the lack of data from locations where receivers were deployed and tagged animals were known to have been nearby based on manual tracking.

Nonetheless, the Bank Swallow migration routes and timing that I documented in this thesis were previously unknown and lay the foundation for future research and conservation actions for the species. My thesis adds to a growing body of movement ecology research that aims to support the conservation of Species at Risk (Allen and Singh 2016; Fraser et al. 2018; Katzner and Arlettaz 2020). The conservation of broadly distributed migratory species can be challenging for many reasons, including differences in behaviour and conservation requirements for spatially disparate populations (Hauser et al. 2014; Rushing et al. 2016; Kramer et al. 2017) and the logistical complexity of coordinating large-scale research and conservation (Mason et al.

2020). With this project, we created a network of collaborators from across Canada and in the US to help tag Bank Swallows from sites across their North American breeding range. To my knowledge, movement ecology studies that cover such a large spatial extent are relatively rare, and I hope that my thesis research can serve as a template for future studies of other Species at Risk.

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APPENDIX 1. SUPPLEMENTARY MATERIAL

Table S1. Glossary of key terms and their working definitions, as used in this thesis.

Term	Working definition
Spatial overlap	The degree to which individuals from different breeding sites use the same or different migration routes. High spatial overlap means that individuals from different breeding sites mix as they migrate along shared routes. Low spatial overlap means that individuals from different breeding site are migrating along different routes and remain spatially isolated as they migrate.
Temporal overlap	The degree to which individuals from different breeding sites pass through shared areas on migration at the same or different times. High temporal overlap means that individuals from different sites are migrating with similar timing, while low temporal overlap means that the timing of migration is different for individuals from different breeding sites.
Migration Pace	The overall rate of travel, in km/day, for individual Bank Swallows. Calculated using only detections from different days, this metric is impacted by stopovers and periods of foraging as well as ground speed (defined below). Each individual has just one migration pace value.
Ground speed	The rate of travel, in m/s, between consecutive detections at different receivers on the same day. This metric is intended to exclude extended stopovers. Individuals could have multiple ground speed values from different portions of the migration route, as long as the detections met my criteria for this analysis.
Departure date	The last detection within 50 km of the breeding site. I calculated one departure date per individual.
Departure bearing	The direction of travel between the departure location (the location of the last detection within 50 km of the breeding site, above) and the next detection that was a minimum of 50 km away to reduce errors due to overlapping antenna ranges. I calculated one departure bearing per individual.

Filtering methodology

The raw data that I downloaded from Motus in April 2024 consisted of 9 444 977 detections. I also manually processed and added data from three receivers in Québec that had malfunctioning GPS units and for which the data was not available through Motus (n = 282 224), for a total of 9 727 201 detections on 807 receivers.

I identified duplicate detections as those in which the timestamp, receiver ID, tag ID and signal strength were identical to one another, and removed all but one copy of each duplicated detection (n = 1 618 removed). I then applied several filters to remove detections that had a high likelihood of being false positives or were ambiguous (Figure S1).

First, I removed runs, which are series of consecutive detections for an individual at a given receiver, of less than three detections and any detections for which the receiver location was not available (n = 631 094 detections). Noisy towers tend to generate shorter runs than more reliable towers and runs of only two detections are difficult to verify visually based on the pattern of detections and signal strength.

Second, I calculated the proportion of "noisy" detections by calculating the proportion of detections, per individual bird, per receiver station, per day, that had a frequency standard deviation greater than 0.1, which is an indication that the detection is likely to be false. When the proportion of noisy detections exceeded 0.25, I removed all detections for that individual for the station and day in question (n = 106 431 detections). A proportion of 0.25 was chosen by visually inspecting plots for individual receivers showing the proportion of noisy detections. In comparing these plots to one another, I found that most of the detections that occurred in plausible locations at realistic times (such as at the colony immediately post tag deployment) had a proportion of noisy hits under 0.25. In contrast, most detections in improbable locations (like a PEI bird detected in BC) and/or at unlikely times (like in Canada in January) tended to have a proportion of noisy hits greater than 0.25.

Third, I removed all runs with detections that were closer together than the burst interval of the tag (e.g., detections that were 7s apart but assigned to a tag with a 35s burst interval, a signal that can occur via random radio noise, ambiguous tags, tag aliasing, or duplicated receiver deployments; n = 156 detections).

Fourth, I flagged overlapping runs for individual birds at receivers > 30 km apart, because overlapping runs at receivers > 30 km apart, on average, suggest false detections on one of the receivers given the detection range for Yagi antennas is ~15 km. I used these flags to help identify noisy tower, described in more detail below.

Fifth, I calculated the minimum ground speed required for post-departure movements between receivers that were more than 50 km apart (to avoid flagging near-simultaneous detections; Appendix 1: Figures S10 & S11) and flagged any movements with apparent ground speeds > 40 m/s (Imlay et al. 2021) for further investigation in later stages of filtering.

Sixth, I removed all detections for specific “noisy” towers that looked suspicious when visually inspecting the detections (n = 5 359 detections and 48 receivers). The criteria that I used to identify “noisy” receivers were: little to no variability in signal strength and/or frequency; run lengths that were predominantly short (3-4); detections of tags that were inconsistent with the migration route for the majority of tags from the same breeding site; frequent detections in North America in the fall and winter; detections of individual tags that spanned many months at locations other than the breeding colony or potential wintering sites; and frequent detections that resulted in overlapping runs at receivers >30 km apart (see step four) or spuriously high minimum ground speeds (> 100 m/s) between receivers > 50 km apart (see step five). When comparing two towers with overlapping runs or detections that resulted in spuriously high ground speeds, I decided which tower was “noisy” based on the biological feasibility of the detection histories at the two towers in question. For example, if a tag was deployed close to a station and the bird was consistently detected there, and then momentarily “detected” at a tower 100 km away, the detections 100 km away were classified as false.

Seventh, I removed all detections for individual tags that appeared to have been dropped near the breeding colony or the tagged individual died/was killed, which showed up as continuous detections spanning months and often extending well past the expected fall migration departure dates for Bank Swallows (Imlay et al. 2020)*,* with little variability in signal strength (n = 1 196 341 detections, n = 10 tags). I also removed detections for two tags that were replaced two days post-deployment because their signals were not detected on a Lotek receiver when the birds were recaptured, suggesting tag failure (n = 235 detections).

Eighth, I removed individual detections at otherwise reliable receivers that occurred outside of the known seasonal distribution for Bank Swallows (for example, detections in Canada in December or in Mexico in July); detections that were inconsistent with the expected movement pattern of individual birds (such as detections on a single receiver in British Columbia for a bird that was tagged at a colony in Prince Edward Island); and detections that resulted in spuriously high flight speeds as calculated in step five (n = 69 detections). When comparing detections for an individual tag, I used multiple lines of evidence to decide whether to keep or remove detections because migratory behaviour can vary between individuals from the same breeding site (Stanley et al. 2012; Fraser et al. 2013). For example, I considered the detection histories at each receiver (e.g., in some instances the tag was detected in South America before being detected at the colony); whether the individual was detected on multiple receivers in a novel area or just one; whether any other individuals from the same colony were detected in the novel area; the run length of the detections (longer runs are typically more reliable); whether the apparent rate of migration for the individual to travel between receivers was biologically feasible; and whether the tag had been detected at the colony or only other, noisy receivers.

Ninth, I removed tags with < 24 hours between release and the birds last detection, as this was an indication that the tag likely fell off or stopped working shortly after deployment (n = 17 323 detections and n = 113 individual birds).

Last, I removed detections that occurred past the expected tag lifespan for that tag’s burst interval (eg. an NTQB-2-2 tag with a 27.1 second burst interval is anticipated to last roughly 184 days; Lotek Wireless Inc. 2024b, M. Vandentillaart, personal communication) (n = 33).

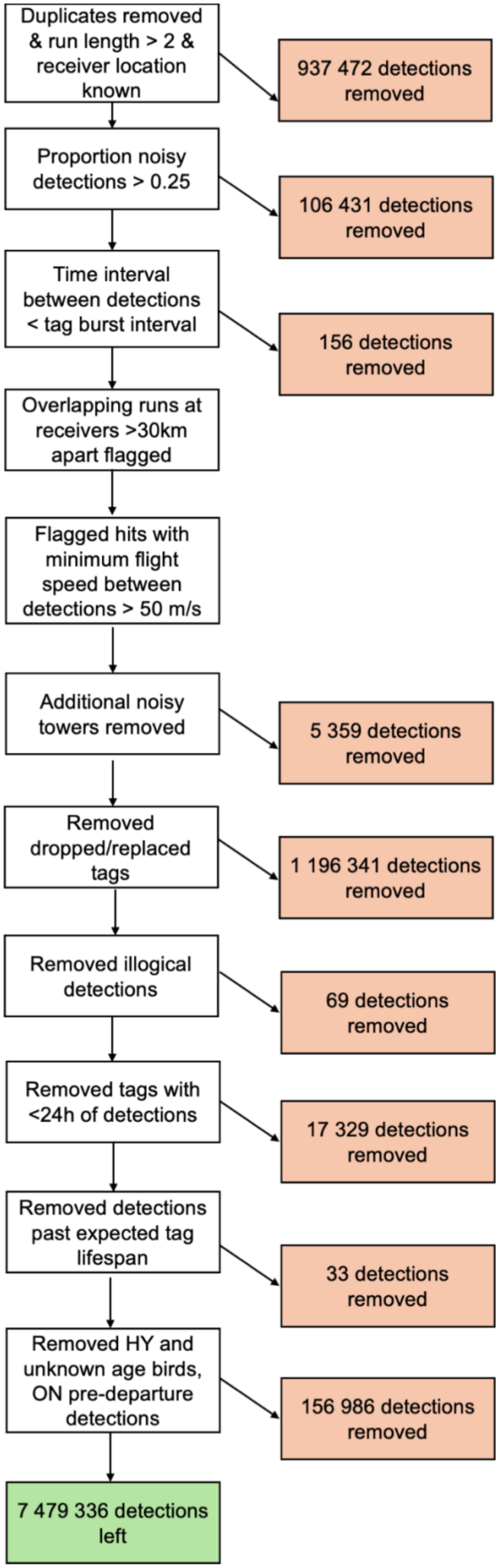
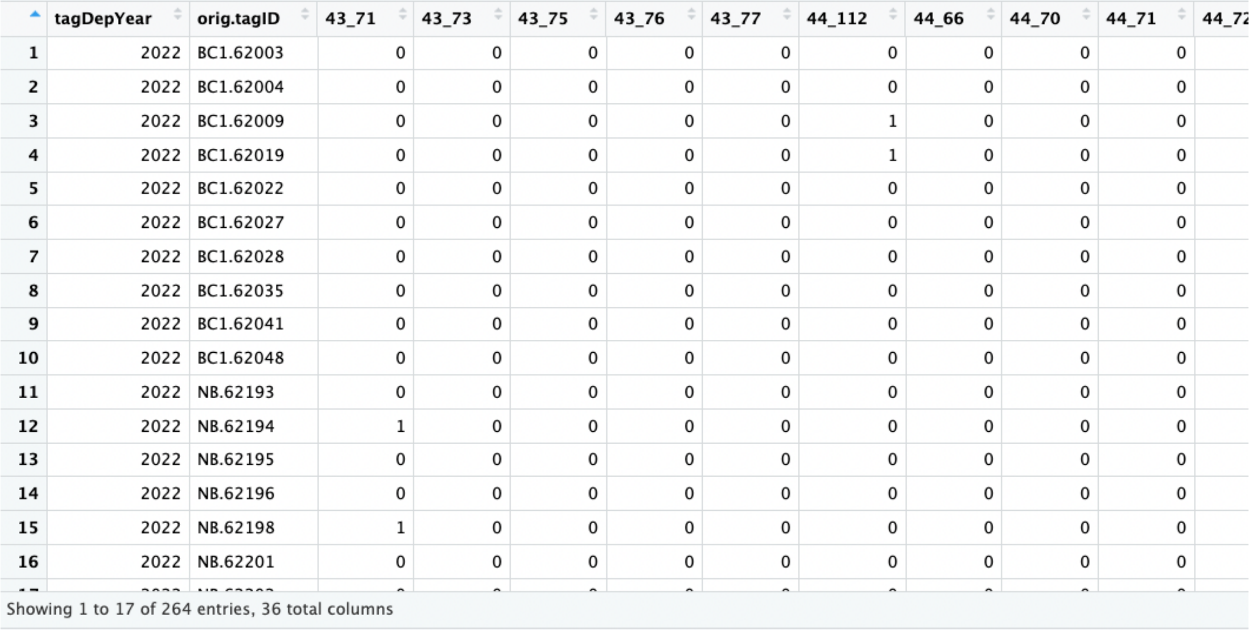

Duplicates removed & run length > 2 & receiver location known
937 472 detections removed
Proportion noisy detections > 0.25
106 431 detections removed
Time interval between detections < tag burst interval
156 detections removed
Overlapping runs at receivers >30km apart flagged
Flagged hits with minimum flight speed between detections > 50 m/s
Additional noisy towers removed
5 359 detections removed
Removed dropped/replaced tags
1 196 341 detections removed
Removed illogical detections
69 detections removed
Removed tags with <24h of detections
17 329 detections removed
Removed detections past expected tag lifespan
33 detections removed
Removed HY and unknown age birds, ON pre-departure detections
156 986 detections removed
7 479 336 detections left

Figure S1. Motus data filtering pipeline to remove detections with a high likelihood of being false. The "proportion of noisy detections" is the proportion of detections, per individual, per day, per receiver, with a frequency standard deviation greater than 0.1. "Noisy" towers met one or more of the following criteria: low variability in signal strength and/or frequency; short run lengths (3-4); detections of multiple tags that were inconsistent with the migration route for the majority of tags from the same breeding site; frequent detections in North America in the fall and winter; recurring detections spanning many months at locations other than the breeding colony or potential wintering sites; and frequent detections that resulted in overlapping runs at receivers >30 km apart or spuriously high minimum ground speeds (> 100 m/s) between receivers > 50 km apart. "Illogical" detections met one or more of the following criteria: occurred outside of the known seasonal distribution for Bank Swallows (*Riparia riparia*); detections that were inconsistent with the expected movement pattern.

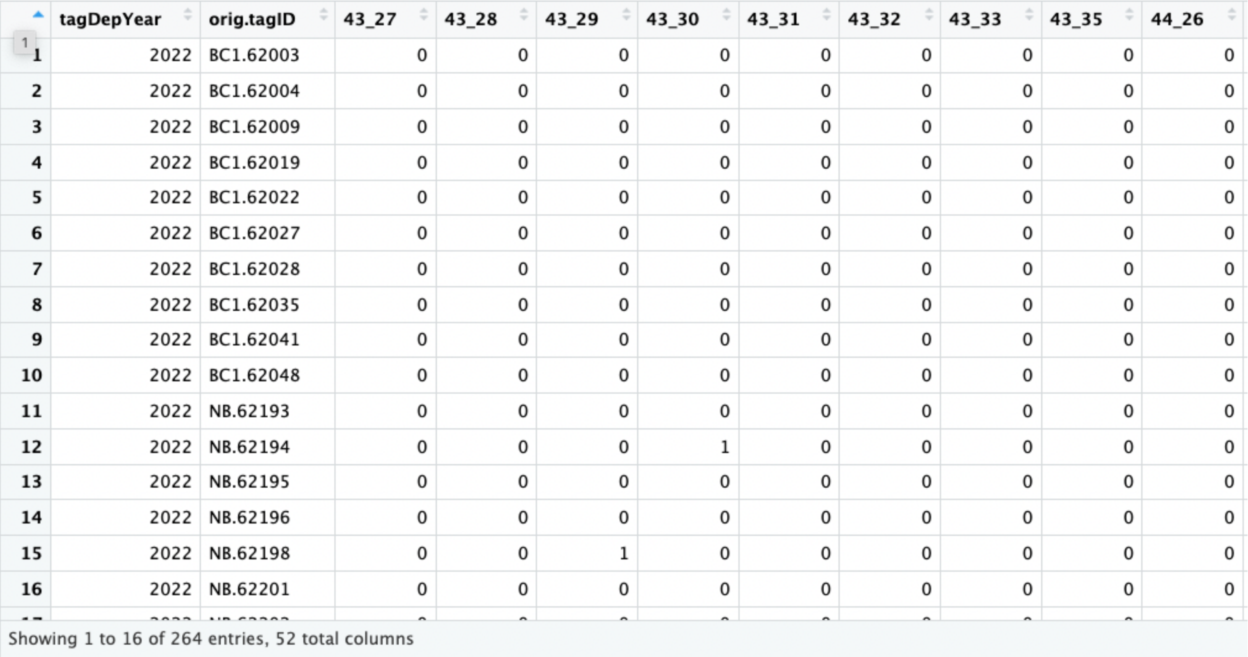
Spatial and Temporal Overlap



	tagDepYear	orig.tagID	43_71	43_73	43_75	43_76	43_77	44_112	44_66	44_70	44_71	44_7
1	2022	BC1.62003	0	0	0	0	0	0	0	0	0	
2	2022	BC1.62004	0	0	0	0	0	0	0	0	0	
3	2022	BC1.62009	0	0	0	0	0	1	0	0	0	
4	2022	BC1.62019	0	0	0	0	0	1	0	0	0	
5	2022	BC1.62022	0	0	0	0	0	0	0	0	0	
6	2022	BC1.62027	0	0	0	0	0	0	0	0	0	
7	2022	BC1.62028	0	0	0	0	0	0	0	0	0	
8	2022	BC1.62035	0	0	0	0	0	0	0	0	0	
9	2022	BC1.62041	0	0	0	0	0	0	0	0	0	
10	2022	BC1.62048	0	0	0	0	0	0	0	0	0	
11	2022	NB.62193	0	0	0	0	0	0	0	0	0	
12	2022	NB.62194	1	0	0	0	0	0	0	0	0	
13	2022	NB.62195	0	0	0	0	0	0	0	0	0	
14	2022	NB.62196	0	0	0	0	0	0	0	0	0	
15	2022	NB.62198	1	0	0	0	0	0	0	0	0	
16	2022	NB.62201	0	0	0	0	0	0	0	0	0	

Showing 1 to 17 of 264 entries, 36 total columns

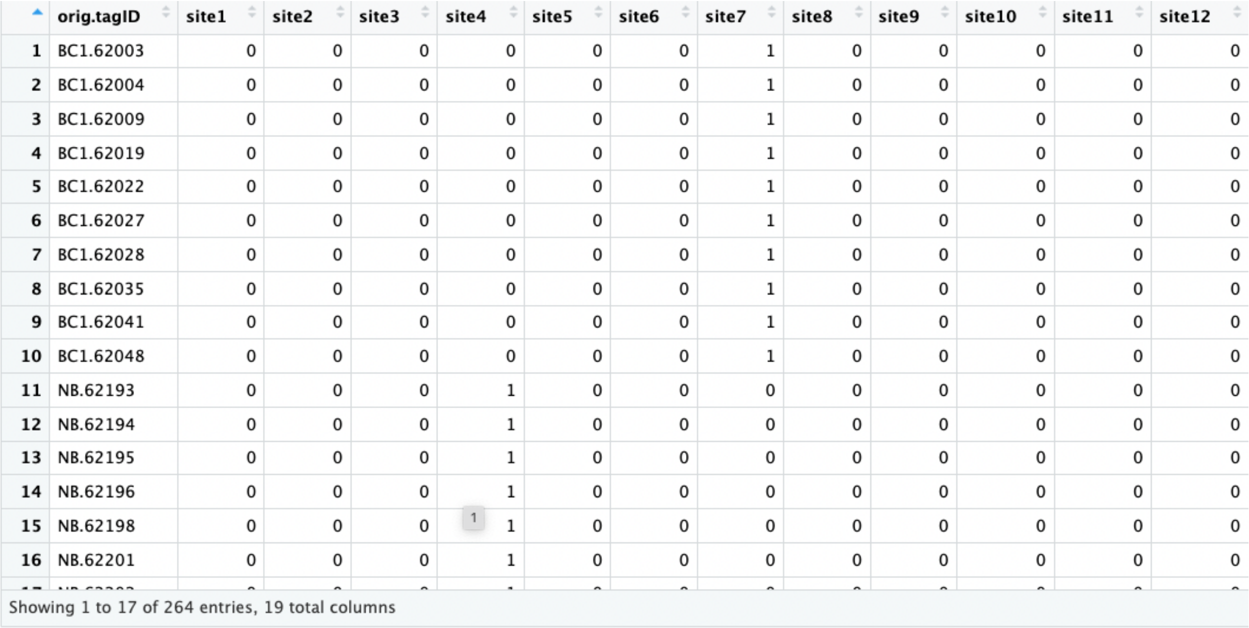
Figure S2. Screenshot of the first 16 rows and 11 columns of the detection matrix used to calculate detection Bray-Curtis dissimilarity values in my spatial overlap analysis. This matrix is for the latitude window from 43-48°N and with detections aggregated/rounded into latitude-longitude grid cells of 1x1 degree. TagDepYear is the year of tag deployment (2022 or 2023); orig.tagID is a unique identifier for each tag that is composed of a tag site code and the tag's Motus ID. The rest of the column headings (43_71, 43_73, etc.) are the latitude and longitude of the grid cell (i.e., 43_71 = latitude of 43°N and longitude of 71°W). A cell value of 0 indicates that the orig.tagID in that row was not detected in that grid cell, whereas a cell value of 1 indicates that the orig.tagID in that row was detected in that cell.



	tagDepYear	orig.tagID	43_27	43_28	43_29	43_30	43_31	43_32	43_33	43_35	44_26
1	2022	BC1.62003	0	0	0	0	0	0	0	0	0
2	2022	BC1.62004	0	0	0	0	0	0	0	0	0
3	2022	BC1.62009	0	0	0	0	0	0	0	0	0
4	2022	BC1.62019	0	0	0	0	0	0	0	0	0
5	2022	BC1.62022	0	0	0	0	0	0	0	0	0
6	2022	BC1.62027	0	0	0	0	0	0	0	0	0
7	2022	BC1.62028	0	0	0	0	0	0	0	0	0
8	2022	BC1.62035	0	0	0	0	0	0	0	0	0
9	2022	BC1.62041	0	0	0	0	0	0	0	0	0
10	2022	BC1.62048	0	0	0	0	0	0	0	0	0
11	2022	NB.62193	0	0	0	0	0	0	0	0	0
12	2022	NB.62194	0	0	0	1	0	0	0	0	0
13	2022	NB.62195	0	0	0	0	0	0	0	0	0
14	2022	NB.62196	0	0	0	0	0	0	0	0	0
15	2022	NB.62198	0	0	1	0	0	0	0	0	0
16	2022	NB.62201	0	0	0	0	0	0	0	0	0

Showing 1 to 16 of 264 entries, 52 total columns

Figure S3. Screenshot of the first 16 rows and 11 columns of the detection matrix used to calculate detection Bray-Curtis dissimilarity values in my temporal overlap analysis. This matrix is for the latitude window from 43-48°N and with detections aggregated/rounded into latitude-week grid cells of 1 degree latitude x 1 week. TagDepYear is the year of tag deployment (2022 or 2023); orig.tagID is a unique identifier for each tag that is composed of a tag site code and the tag's Motus ID. The rest of the column headings (43_27, 43_28, etc.) are the latitude and week of the detection (i.e., 43_27 = latitude of 43°N and week 27). A cell value of 0 indicates that the orig.tagID in that row was not detected in that grid cell, whereas a cell value of 1 indicates that the orig.tagID in that row was detected in that cell.



	orig.tagID	site1	site2	site3	site4	site5	site6	site7	site8	site9	site10	site11	site12
1	BC1.62003	0	0	0	0	0	0	1	0	0	0	0	0
2	BC1.62004	0	0	0	0	0	0	1	0	0	0	0	0
3	BC1.62009	0	0	0	0	0	0	1	0	0	0	0	0
4	BC1.62019	0	0	0	0	0	0	1	0	0	0	0	0
5	BC1.62022	0	0	0	0	0	0	1	0	0	0	0	0
6	BC1.62027	0	0	0	0	0	0	1	0	0	0	0	0
7	BC1.62028	0	0	0	0	0	0	1	0	0	0	0	0
8	BC1.62035	0	0	0	0	0	0	1	0	0	0	0	0
9	BC1.62041	0	0	0	0	0	0	1	0	0	0	0	0
10	BC1.62048	0	0	0	0	0	0	1	0	0	0	0	0
11	NB.62193	0	0	0	1	0	0	0	0	0	0	0	0
12	NB.62194	0	0	0	1	0	0	0	0	0	0	0	0
13	NB.62195	0	0	0	1	0	0	0	0	0	0	0	0
14	NB.62196	0	0	0	1	0	0	0	0	0	0	0	0
15	NB.62198	0	0	0	1	0	0	0	0	0	0	0	0
16	NB.62201	0	0	0	1	0	0	0	0	0	0	0	0

Showing 1 to 17 of 264 entries, 19 total columns

Figure S4. Screenshot of the first 16 rows and 12 columns of the tag site matrix used to calculate tag site Bray-Curtis dissimilarity values. orig.tagID is a unique identifier for each tag that is composed of a tag site code and the tag's Motus ID. The rest of the column headings (site1, site2, etc.) represent each of the breeding sites where we deployed tags (tag sites). A cell value of 1 means that the orig.tagID in that row was tagged at the site indicated in that column heading, whereas a cell value of 0 means that orig.tagID was not tagged at that particular site.

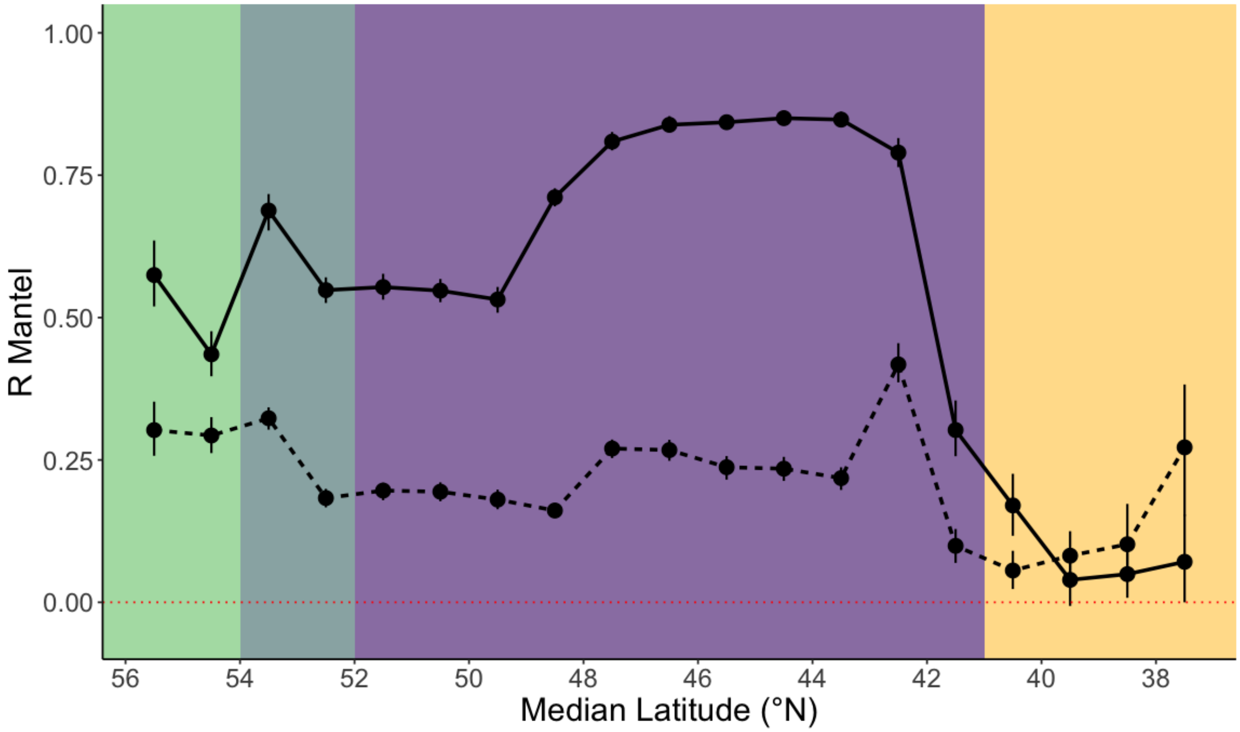


Figure S5. Spatial (solid line) and temporal (dashed line) overlap of migrating Bank Swallows (*Riparia riparia*) from breeding sites across North America (n = 495). Coloured backgrounds illustrate what birds were detected in each latitudinal window: Green = Central route only; Blue = Central & Western routes; Purple = Central, Western and Eastern routes; and Yellow = Central and Eastern routes. The latitudes on the x-axis are the median latitude for each 5°-latitude window in my analysis (e.g., a median latitude of 57.5°N means that the window extended from 60°N to 55°N). The red dotted line marks an R Mantel value of zero, which represents complete overlap of birds from different breeding sites during migration. All analyses were performed using 1x1 latitude-longitude grid cells.

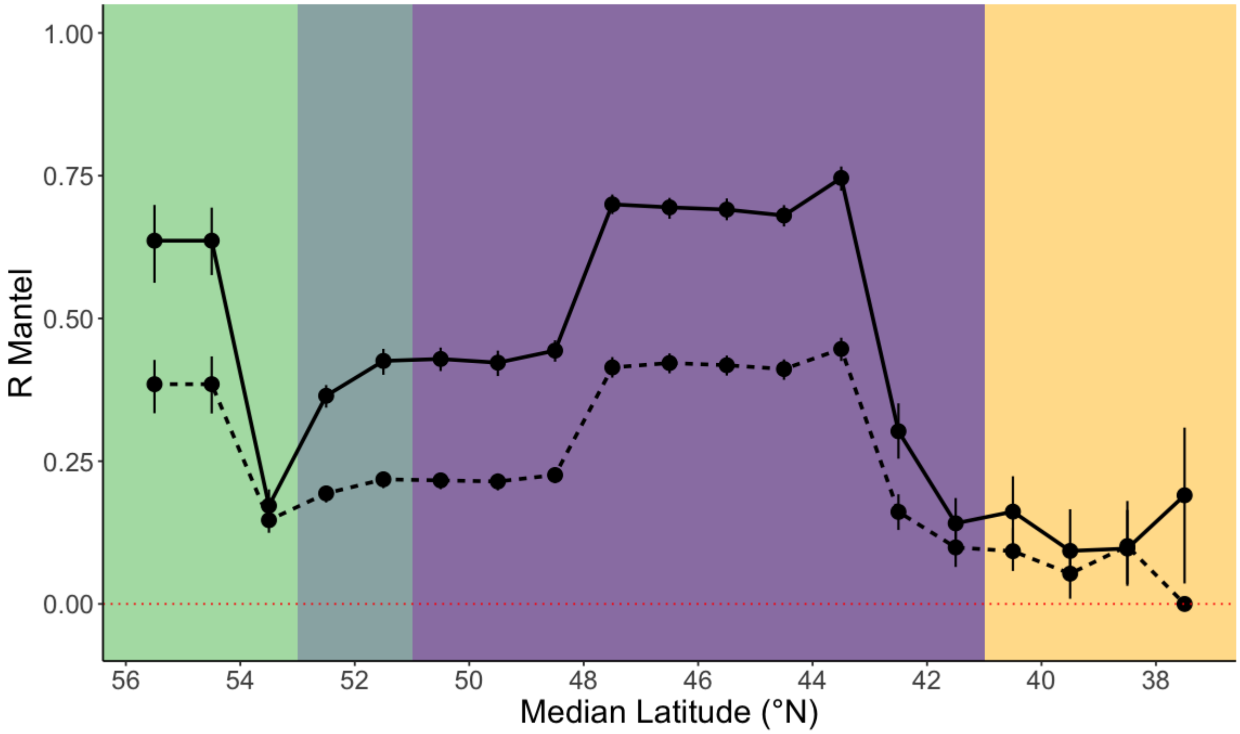


Figure S6. Spatial (solid line) and temporal (dashed line) overlap of migrating Bank Swallows (*Riparia riparia*) from breeding sites across North America (n = 495). Coloured backgrounds illustrate what birds were detected in each latitudinal window: Green = Central route only; Blue = Central & Western routes; Purple = Central, Western and Eastern routes; and Yellow = Central and Eastern routes. The latitudes on the x-axis are the median latitude for each 5°-latitude window in my analysis (e.g., a median latitude of 57.5°N means that the window extended from 60°N to 55°N). The red dotted line marks an R Mantel value of zero, which represents complete overlap of birds from different breeding sites during migration. All analyses were performed using 0.01x0.01 latitude-longitude grid cells.

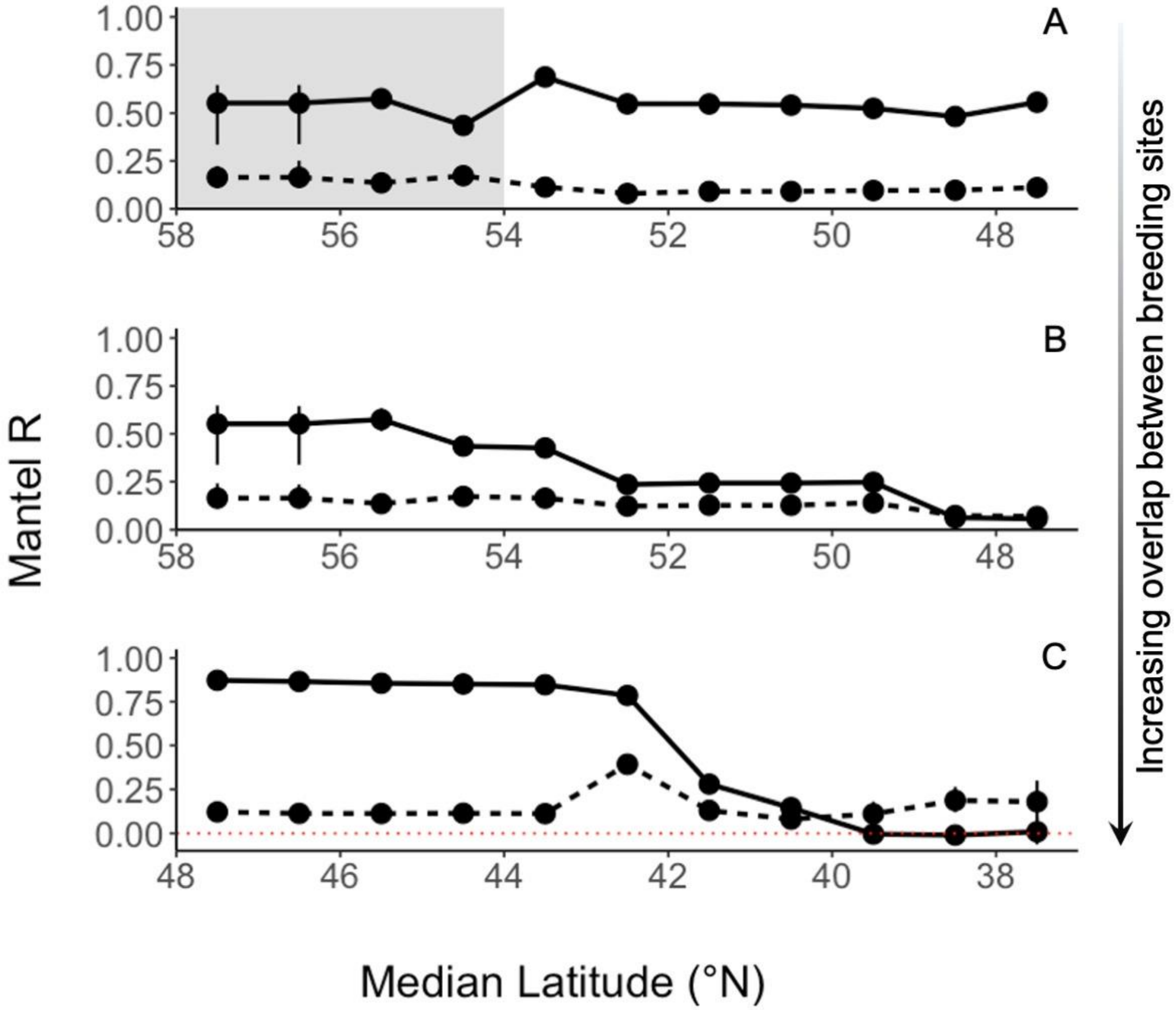


Figure S7. Spatial (solid line) and temporal (dashed line) overlap for Bank Swallows (*Riparia riparia*) that followed the Western and Central migration routes (Figure A, n = 255); the Central migration route alone (Figure B, n = 162); and the Eastern migration route (Figure C, n = 235). Vertical lines are 95% confidence intervals. A higher R Mantel (closer to one) indicates that individuals from different breeding sites remained spatially and/or temporally segregated from one another, whereas a lower R Mantel (closer to zero) indicates that there was a high degree of spatial or temporal overlap of individuals from different breeding sites. Red dotted line represents zero on panel C. Grey shading on panel A shows latitudes where only Central route birds were detected; latitudes with no shading had detections for both Central and Western route birds. Results are shown for the latitude ranges at which there were sufficient data to calculate Mantel R. All analyses were performed using 1x1 latitude-longitude grid cells.

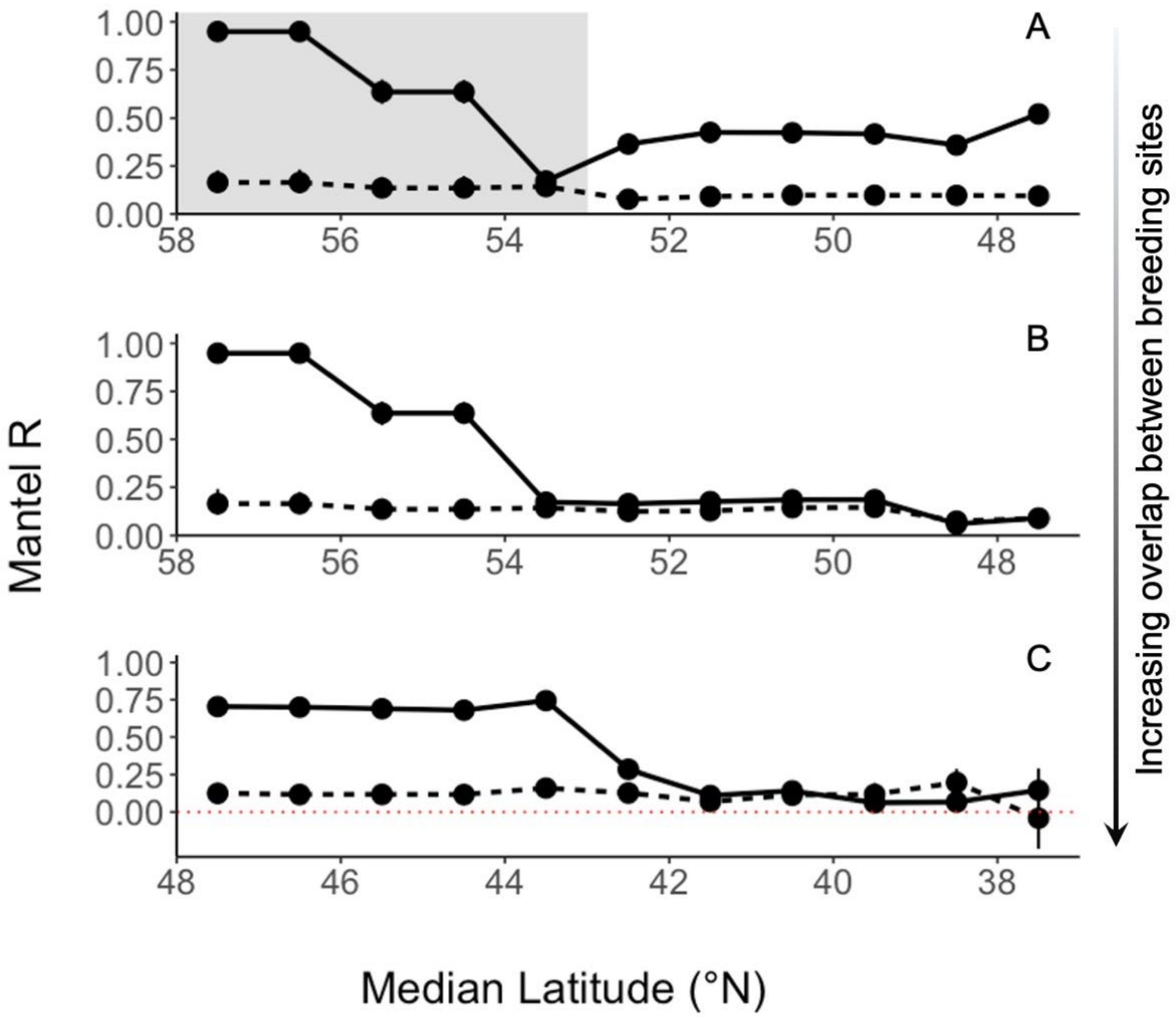
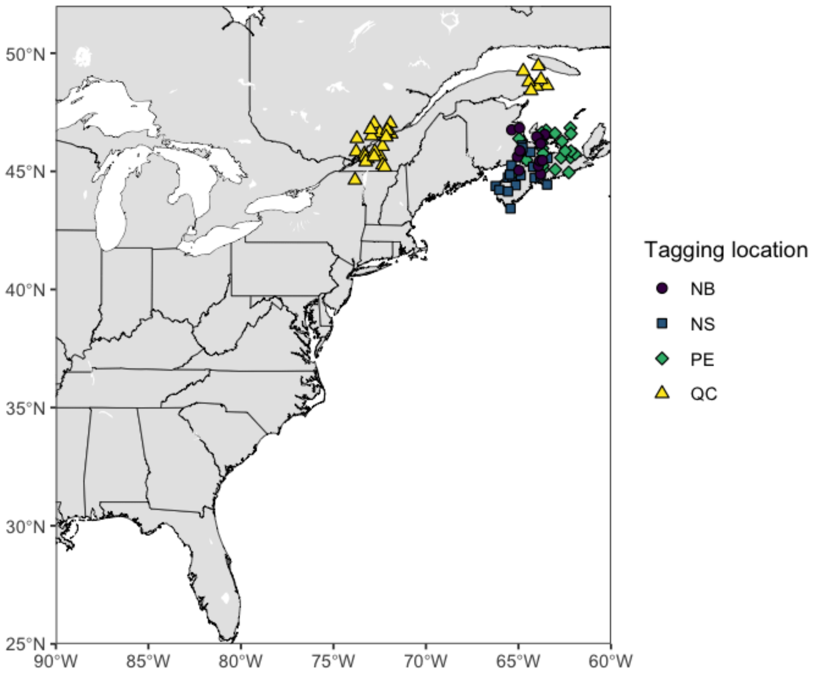
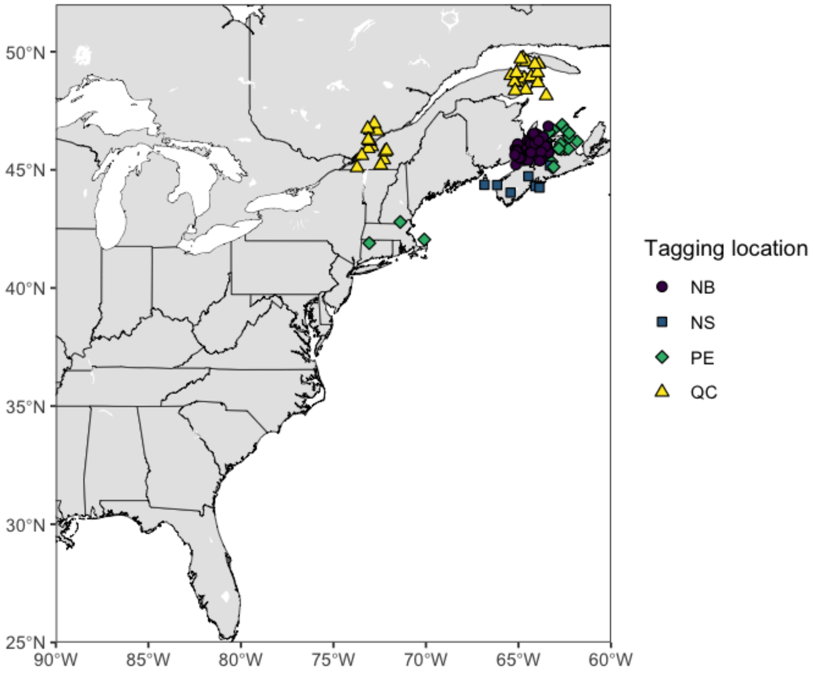
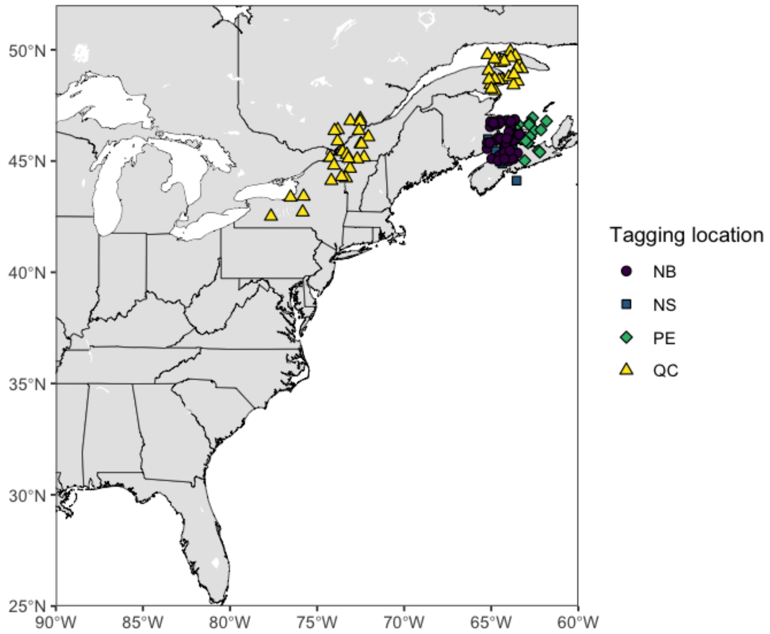


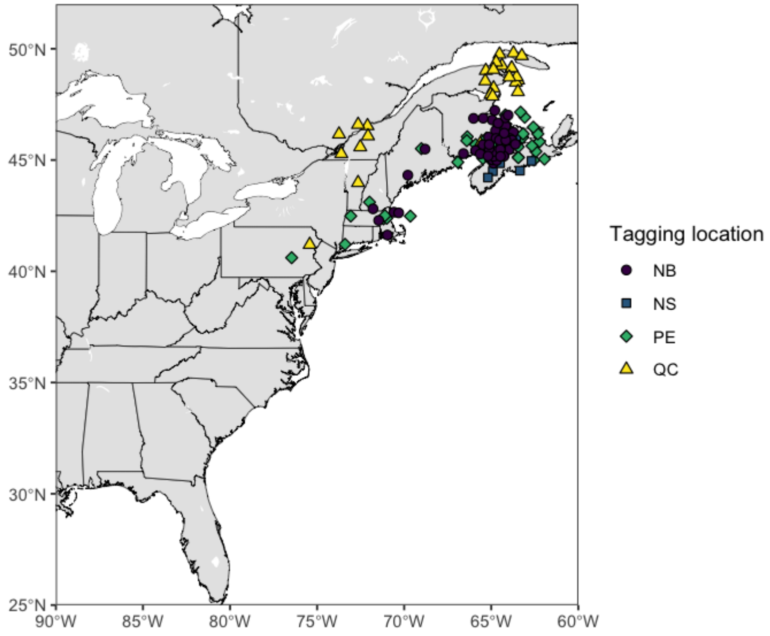
Figure S8. Spatial (solid line) and temporal (dashed line) overlap for Bank Swallows (*Riparia riparia*) that followed the Western and Central migration routes (Figure A, n = 255); the Central migration route alone (Figure B, n = 162); and the Eastern migration route (Figure C, n = 235). Vertical lines are 95% confidence intervals. A higher R Mantel (closer to one) indicates that individuals from different breeding sites remained spatially and/or temporally segregated from one another, whereas a lower R Mantel (closer to zero) indicates that there was a high degree of spatial or temporal overlap of individuals from different breeding sites. Red dotted line represents zero on panel C. Grey shading on panel A shows latitudes where only Central route birds were detected; latitudes with no shading had detections for both Central and Western route birds. Results are shown for the latitude ranges at which there were sufficient data to calculate Mantel R. All analyses were performed using 0.01x0.01 latitude-longitude grid cells.


June 30 to July 6


July 7 to July 13

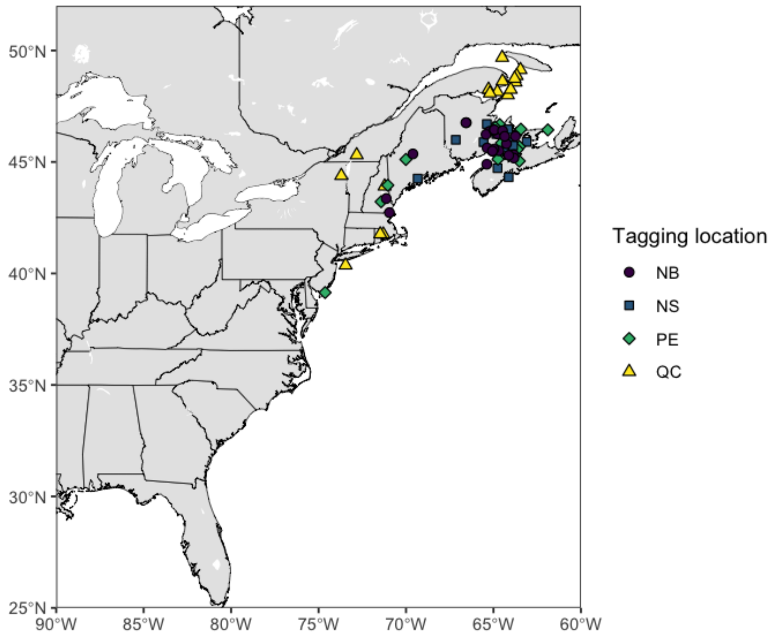


July 14 to July 20



July 21 to July 27

July 28 to August 3



August 4 to August 10

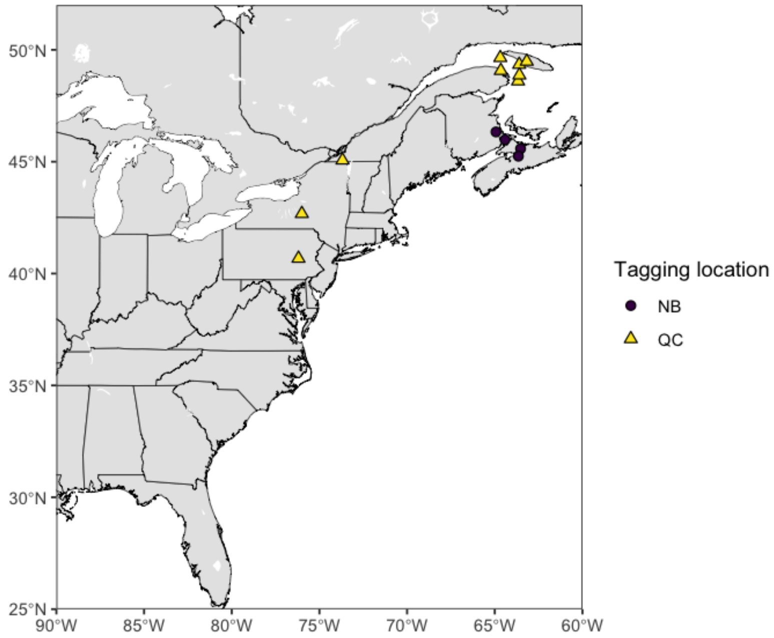


Figure S9. Temporal overlap of Bank Swallows (*Riparia riparia*) that followed the Eastern migration route in 2022, with detections grouped into one-week intervals. Points are jittered to reduce overlap so locations are not exact, and there may be multiple points per individual on each map due to the one-week grouping. Departure dates differed between 2022 and 2023, so I was unable to plot both years together.

Table S2. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) (n = 495) from breeding sites across North America at 19 latitude intervals, using 1x1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	37.5	40 to 35	19	8	0.0711	0.1771	0.8230	0.3605	0.0000	0.1543
	38.5	41 to 36	30	15	0.0495	0.1506	0.8495	0.3003	0.0079	0.1052
	39.5	42 to 37	36	22	0.0394	0.1589	0.8412	0.3349	-0.0064	0.0845
	40.5	43 to 38	50	26	0.1701	0.0001	1.0000	0.0001	0.1168	0.2257
	41.5	44 to 39	68	32	0.3025	0.0001	1.0000	0.0001	0.2566	0.3544
	42.5	45 to 40	128	40	0.7896	0.0001	1.0000	0.0001	0.7643	0.8152
	43.5	46 to 41	244	43	0.8476	0.0001	1.0000	0.0001	0.8352	0.8615
	44.5	47 to 42	258	39	0.8502	0.0001	1.0000	0.0001	0.8378	0.8637
	45.5	48 to 43	264	34	0.8430	0.0001	1.0000	0.0001	0.8322	0.8552
	46.5	49 to 44	321	34	0.8385	0.0001	1.0000	0.0001	0.8260	0.8537
	47.5	50 to 45	363	31	0.8089	0.0001	1.0000	0.0001	0.7937	0.8259
	48.5	51 to 46	327	23	0.7113	0.0001	1.0000	0.0001	0.6952	0.7269
	49.5	52 to 47	228	19	0.5317	0.0001	1.0000	0.0001	0.5086	0.5537
	50.5	53 to 48	245	18	0.5472	0.0001	1.0000	0.0001	0.5270	0.5678
	51.5	54 to 49	245	16	0.5535	0.0001	1.0000	0.0001	0.5315	0.5769
	52.5	55 to 50	237	12	0.5482	0.0001	1.0000	0.0001	0.5256	0.5706
	53.5	56 to 51	187	10	0.6879	0.0001	1.0000	0.0001	0.6530	0.7169
	54.5	57 to 52	132	8	0.4354	0.0001	1.0000	0.0001	0.3970	0.4760
	55.5	58 to 53	70	5	0.5747	0.0001	1.0000	0.0001	0.5196	0.6353
Temporal	37.5	40 to 35	19	17	0.2721	0.0032	0.9969	0.0032	0.1514	0.3825
	38.5	41 to 36	30	23	0.1019	0.0361	0.9640	0.0400	0.0441	0.1728
	39.5	42 to 37	36	30	0.0818	0.0354	0.9647	0.0457	0.0302	0.1248
	40.5	43 to 38	50	37	0.0558	0.0435	0.9566	0.0624	0.0234	0.0905
	41.5	44 to 39	68	44	0.0991	0.0001	1.0000	0.0001	0.0692	0.1287

42.5	45 to 40	128	50	0.4177	0.0001	1.0000	0.0001	0.3863	0.4550
43.5	46 to 41	244	52	0.2181	0.0001	1.0000	0.0001	0.1973	0.2370
44.5	47 to 42	258	53	0.2346	0.0001	1.0000	0.0001	0.2132	0.2554
45.5	48 to 43	264	50	0.2372	0.0001	1.0000	0.0001	0.2155	0.2568
46.5	49 to 44	321	49	0.2673	0.0001	1.0000	0.0001	0.2485	0.2854
47.5	50 to 45	363	47	0.2700	0.0001	1.0000	0.0001	0.2533	0.2857
48.5	51 to 46	327	43	0.1612	0.0001	1.0000	0.0001	0.1529	0.1704
49.5	52 to 47	228	41	0.1803	0.0001	1.0000	0.0001	0.1635	0.1979
50.5	53 to 48	245	39	0.1942	0.0001	1.0000	0.0001	0.1774	0.2106
51.5	54 to 49	245	35	0.1962	0.0001	1.0000	0.0001	0.1793	0.2100
52.5	55 to 50	237	29	0.1831	0.0001	1.0000	0.0001	0.1667	0.1992
53.5	56 to 51	187	26	0.3232	0.0001	1.0000	0.0001	0.3032	0.3424
54.5	57 to 52	132	20	0.2929	0.0001	1.0000	0.0001	0.2620	0.3251
55.5	58 to 53	70	11	0.3024	0.0001	1.0000	0.0001	0.2573	0.3523

Table S3. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) (n = 495) from breeding sites across North America at 19 latitude intervals, using 0.1x0.1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	37.5	40 to 35	12	9	0.1903	0.0721	0.9280	0.1027	0.0700	0.3198
	38.5	41 to 36	28	19	0.0902	0.0598	0.9403	0.0775	0.0282	0.1601
	39.5	42 to 37	35	28	0.0929	0.0288	0.9713	0.0323	0.0393	0.1609
	40.5	43 to 38	47	43	0.1617	0.0004	0.9997	0.0004	0.1130	0.2215
	41.5	44 to 39	56	51	0.1412	0.0003	0.9998	0.0003	0.1074	0.1843
	42.5	45 to 40	71	60	0.2967	0.0001	1.0000	0.0001	0.2507	0.3424
	43.5	46 to 41	202	82	0.7511	0.0001	1.0000	0.0001	0.7313	0.7749
	44.5	47 to 42	256	90	0.7266	0.0001	1.0000	0.0001	0.7108	0.7444
	45.5	48 to 43	257	76	0.7328	0.0001	1.0000	0.0001	0.7172	0.7502
	46.5	49 to 44	293	69	0.7685	0.0001	1.0000	0.0001	0.7534	0.7838
	47.5	50 to 45	328	65	0.7359	0.0001	1.0000	0.0001	0.7211	0.7542
	48.5	51 to 46	274	46	0.5715	0.0001	1.0000	0.0001	0.5513	0.5924
	49.5	52 to 47	228	33	0.4225	0.0001	1.0000	0.0001	0.3960	0.4446
	50.5	53 to 48	227	31	0.4290	0.0001	1.0000	0.0001	0.4046	0.4492
	51.5	54 to 49	239	29	0.4256	0.0001	1.0000	0.0001	0.4047	0.4449
	52.5	55 to 50	232	22	0.3646	0.0001	1.0000	0.0001	0.3441	0.3813
	53.5	56 to 51	113	14	0.1720	0.0001	1.0000	0.0001	0.1452	0.1979
	54.5	57 to 52	70	10	0.6362	0.0001	1.0000	0.0001	0.5760	0.6947
	55.5	58 to 53	70	10	0.6362	0.0001	1.0000	0.0001	0.5721	0.6967
Temporal	37.5	40 to 35	12	19	0.0000	0.2833	0.7168	0.7731	-0.0170	0.0085
	38.5	41 to 36	28	37	0.1050	0.0390	0.9611	0.0423	0.0490	0.1665
	39.5	42 to 37	35	48	0.0607	0.0822	0.9179	0.1322	0.0163	0.1135
	40.5	43 to 38	47	69	0.0861	0.0096	0.9905	0.0101	0.0527	0.1238
	41.5	44 to 39	56	91	0.0984	0.0012	0.9989	0.0012	0.0625	0.1324

42.5	45 to 40	71	108	0.1720	0.0001	1.0000	0.0001	0.1402	0.2126
43.5	46 to 41	202	137	0.4571	0.0001	1.0000	0.0001	0.4369	0.4745
44.5	47 to 42	256	160	0.4285	0.0001	1.0000	0.0001	0.4107	0.4441
45.5	48 to 43	257	143	0.4330	0.0001	1.0000	0.0001	0.4142	0.4498
46.5	49 to 44	293	127	0.4411	0.0001	1.0000	0.0001	0.4271	0.4568
47.5	50 to 45	328	121	0.4203	0.0001	1.0000	0.0001	0.4012	0.4363
48.5	51 to 46	274	100	0.2360	0.0001	1.0000	0.0001	0.2223	0.2516
49.5	52 to 47	228	86	0.1692	0.0001	1.0000	0.0001	0.1514	0.1858
50.5	53 to 48	227	78	0.1695	0.0001	1.0000	0.0001	0.1555	0.1850
51.5	54 to 49	239	76	0.1782	0.0001	1.0000	0.0001	0.1635	0.1942
52.5	55 to 50	232	55	0.1505	0.0001	1.0000	0.0001	0.1350	0.1643
53.5	56 to 51	113	32	0.1612	0.0001	1.0000	0.0001	0.1371	0.1835
54.5	57 to 52	70	18	0.3881	0.0001	1.0000	0.0001	0.3436	0.4337
55.5	58 to 53	70	18	0.3881	0.0001	1.0000	0.0001	0.3386	0.4359

Table S4. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) (n = 495) from breeding sites across North America at 19 latitude intervals, using 0.01x0.01 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	37.5	40 to 35	12	9	0.1903	0.0712	0.9290	0.1023	0.0359	0.3088
	38.5	41 to 36	26	17	0.0970	0.0615	0.9386	0.0781	0.0317	0.1803
	39.5	42 to 37	35	27	0.0929	0.0297	0.9704	0.0319	0.0489	0.1658
	40.5	43 to 38	47	43	0.1617	0.0003	0.9998	0.0003	0.1112	0.2236
	41.5	44 to 39	56	51	0.1412	0.0003	0.9998	0.0003	0.1043	0.1854
	42.5	45 to 40	70	58	0.3024	0.0001	1.0000	0.0001	0.2544	0.3513
	43.5	46 to 41	201	87	0.7460	0.0001	1.0000	0.0001	0.7237	0.7660
	44.5	47 to 42	252	98	0.6803	0.0001	1.0000	0.0001	0.6611	0.6984
	45.5	48 to 43	257	84	0.6906	0.0001	1.0000	0.0001	0.6720	0.7101
	46.5	49 to 44	268	78	0.6945	0.0001	1.0000	0.0001	0.6745	0.7112
	47.5	50 to 45	328	73	0.6998	0.0001	1.0000	0.0001	0.6828	0.7169
	48.5	51 to 46	235	48	0.4437	0.0001	1.0000	0.0001	0.4243	0.4618
	49.5	52 to 47	228	33	0.4225	0.0001	1.0000	0.0001	0.3991	0.4436
	50.5	53 to 48	227	31	0.4290	0.0001	1.0000	0.0001	0.4079	0.4489
	51.5	54 to 49	239	29	0.4256	0.0001	1.0000	0.0001	0.4013	0.4467
	52.5	55 to 50	232	22	0.3646	0.0001	1.0000	0.0001	0.3438	0.3833
	53.5	56 to 51	113	14	0.1720	0.0001	1.0000	0.0001	0.1466	0.2006
	54.5	57 to 52	70	10	0.6362	0.0001	1.0000	0.0001	0.5760	0.6940
	55.5	58 to 53	70	10	0.6362	0.0001	1.0000	0.0001	0.5624	0.6987
Temporal	37.5	40 to 35	12	19	0.0000	0.2771	0.7230	0.7736	-0.0085	0.0085
	38.5	41 to 36	26	37	0.1014	0.0517	0.9484	0.0604	0.0350	0.1646
	39.5	42 to 37	35	51	0.0530	0.1058	0.8943	0.1817	0.0091	0.0974
	40.5	43 to 38	47	74	0.0924	0.0053	0.9948	0.0053	0.0578	0.1329
	41.5	44 to 39	56	96	0.0990	0.0011	0.9990	0.0011	0.0648	0.1383

42.5	45 to 40	70	114	0.1612	0.0001	1.0000	0.0001	0.1295	0.1921
43.5	46 to 41	201	169	0.4466	0.0001	1.0000	0.0001	0.4254	0.4663
44.5	47 to 42	252	203	0.4114	0.0001	1.0000	0.0001	0.3926	0.4283
45.5	48 to 43	257	188	0.4181	0.0001	1.0000	0.0001	0.4000	0.4350
46.5	49 to 44	268	170	0.4220	0.0001	1.0000	0.0001	0.4039	0.4388
47.5	50 to 45	328	167	0.4142	0.0001	1.0000	0.0001	0.3964	0.4323
48.5	51 to 46	235	132	0.2257	0.0001	1.0000	0.0001	0.2114	0.2390
49.5	52 to 47	228	114	0.2145	0.0001	1.0000	0.0001	0.1989	0.2287
50.5	53 to 48	227	106	0.2164	0.0001	1.0000	0.0001	0.2010	0.2302
51.5	54 to 49	239	107	0.2182	0.0001	1.0000	0.0001	0.2028	0.2321
52.5	55 to 50	232	80	0.1936	0.0001	1.0000	0.0001	0.1777	0.2071
53.5	56 to 51	113	48	0.1467	0.0001	1.0000	0.0001	0.1246	0.1693
54.5	57 to 52	70	24	0.3848	0.0001	1.0000	0.0001	0.3336	0.4335
55.5	58 to 53	70	24	0.3848	0.0001	1.0000	0.0001	0.3339	0.4273

Table S5. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) from Western breeding sites (AK, YT, BC, AB, SK, MB) at 11 latitude intervals, using 1x1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	57.5	60 to 55	40	3	0.5520	0.0020	0.9981	0.0020	0.3391	0.6579
	56.5	59 to 54	40	3	0.5520	0.0025	0.9976	0.0025	0.3350	0.6551
	55.5	58 to 53	70	5	0.5747	0.0001	1.0000	0.0001	0.5094	0.6353
	54.5	57 to 52	132	8	0.4354	0.0001	1.0000	0.0001	0.3944	0.4778
	53.5	56 to 51	187	10	0.6879	0.0001	1.0000	0.0001	0.6534	0.7217
	52.5	55 to 50	237	12	0.5482	0.0001	1.0000	0.0001	0.5245	0.5687
	51.5	54 to 49	239	15	0.5478	0.0001	1.0000	0.0001	0.5244	0.5710
	50.5	53 to 48	239	17	0.5414	0.0001	1.0000	0.0001	0.5199	0.5610
	49.5	52 to 47	222	18	0.5246	0.0001	1.0000	0.0001	0.5003	0.5442
	48.5	51 to 46	163	17	0.4821	0.0001	1.0000	0.0001	0.4567	0.5088
	47.5	50 to 45	130	16	0.5565	0.0001	1.0000	0.0001	0.5179	0.5967
Temporal	57.5	60 to 55	40	5	0.1643	0.0159	0.9842	0.0159	0.1090	0.2270
	56.5	59 to 54	40	5	0.1643	0.0177	0.9824	0.0177	0.1128	0.2466
	55.5	58 to 53	70	6	0.1356	0.0004	0.9997	0.0004	0.0895	0.1820
	54.5	57 to 52	132	9	0.1729	0.0001	1.0000	0.0001	0.1421	0.2094
	53.5	56 to 51	187	9	0.1133	0.0001	1.0000	0.0001	0.0943	0.1331
	52.5	55 to 50	237	10	0.0801	0.0001	1.0000	0.0001	0.0686	0.0953
	51.5	54 to 49	239	10	0.0910	0.0001	1.0000	0.0001	0.0771	0.1062
	50.5	53 to 48	239	10	0.0910	0.0001	1.0000	0.0001	0.0761	0.1072
	49.5	52 to 47	222	10	0.0958	0.0001	1.0000	0.0001	0.0800	0.1141
	48.5	51 to 46	163	8	0.0968	0.0001	1.0000	0.0001	0.0740	0.1189
	47.5	50 to 45	130	8	0.1112	0.0001	1.0000	0.0001	0.0871	0.1407

Table S6. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) from Western breeding sites (AK, YT, BC, AB, SK, MB) at 11 latitude intervals, using 0.1x0.1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	57.5	60 to 55	40	7	0.9487	0.0001	1.0000	0.0001	0.8949	0.9787
	56.5	59 to 54	40	7	0.9487	0.0001	1.0000	0.0001	0.9169	0.9833
	55.5	58 to 53	70	10	0.6362	0.0001	1.0000	0.0001	0.5714	0.7021
	54.5	57 to 52	70	10	0.6362	0.0001	1.0000	0.0001	0.5678	0.7018
	53.5	56 to 51	113	14	0.1720	0.0001	1.0000	0.0001	0.1457	0.1992
	52.5	55 to 50	232	22	0.3646	0.0001	1.0000	0.0001	0.3448	0.3825
	51.5	54 to 49	239	29	0.4256	0.0001	1.0000	0.0001	0.4031	0.4466
	50.5	53 to 48	221	28	0.4238	0.0001	1.0000	0.0001	0.4017	0.4431
	49.5	52 to 47	222	30	0.4173	0.0001	1.0000	0.0001	0.3967	0.4404
	48.5	51 to 46	163	34	0.3603	0.0001	1.0000	0.0001	0.3354	0.3857
	47.5	50 to 45	95	23	0.5248	0.0001	1.0000	0.0001	0.4798	0.5676
Temporal	57.5	60 to 55	40	5	0.1643	0.0167	0.9834	0.0167	0.1090	0.2409
	56.5	59 to 54	40	5	0.1643	0.0180	0.9821	0.0180	0.1074	0.2354
	55.5	58 to 53	70	6	0.1356	0.0006	0.9995	0.0006	0.0938	0.1889
	54.5	57 to 52	70	6	0.1356	0.0004	0.9997	0.0004	0.0907	0.1910
	53.5	56 to 51	113	9	0.1427	0.0001	1.0000	0.0001	0.1094	0.1801
	52.5	55 to 50	232	10	0.0775	0.0001	1.0000	0.0001	0.0647	0.0916
	51.5	54 to 49	239	10	0.0910	0.0001	1.0000	0.0001	0.0775	0.1056
	50.5	53 to 48	221	10	0.0983	0.0001	1.0000	0.0001	0.0841	0.1152
	49.5	52 to 47	222	10	0.0977	0.0001	1.0000	0.0001	0.0828	0.1142
	48.5	51 to 46	163	8	0.0968	0.0001	1.0000	0.0001	0.0757	0.1213
	47.5	50 to 45	95	7	0.0943	0.0004	0.9997	0.0004	0.0648	0.1289

Table S7. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) from Western breeding sites (AK, YT, BC, AB, SK, MB) at 11 latitude intervals, using 0.01x0.01 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	57.5	60 to 55	40	7	0.9487	0.0001	1.0000	0.0001	0.8979	0.9852
	56.5	59 to 54	40	7	0.9487	0.0001	1.0000	0.0001	0.9167	0.9826
	55.5	58 to 53	70	10	0.6362	0.0001	1.0000	0.0001	0.5734	0.6999
	54.5	57 to 52	70	10	0.6362	0.0001	1.0000	0.0001	0.5756	0.6976
	53.5	56 to 51	113	14	0.1720	0.0001	1.0000	0.0001	0.1474	0.1992
	52.5	55 to 50	232	22	0.3646	0.0001	1.0000	0.0001	0.3442	0.3837
	51.5	54 to 49	239	29	0.4256	0.0001	1.0000	0.0001	0.4029	0.4461
	50.5	53 to 48	221	28	0.4238	0.0001	1.0000	0.0001	0.3994	0.4436
	49.5	52 to 47	222	30	0.4173	0.0001	1.0000	0.0001	0.3941	0.4386
	48.5	51 to 46	163	37	0.3590	0.0001	1.0000	0.0001	0.3335	0.3830
	47.5	50 to 45	95	26	0.5216	0.0001	1.0000	0.0001	0.4754	0.5673
Temporal	57.5	60 to 55	40	5	0.1643	0.0175	0.9826	0.0175	0.1194	0.2275
	56.5	59 to 54	40	5	0.1643	0.0173	0.9828	0.0173	0.1102	0.2317
	55.5	58 to 53	70	6	0.1356	0.0005	0.9996	0.0005	0.0883	0.1938
	54.5	57 to 52	70	6	0.1356	0.0001	1.0000	0.0001	0.0911	0.1986
	53.5	56 to 51	113	9	0.1427	0.0001	1.0000	0.0001	0.1098	0.1773
	52.5	55 to 50	232	10	0.0775	0.0001	1.0000	0.0001	0.0637	0.0928
	51.5	54 to 49	239	10	0.0910	0.0001	1.0000	0.0001	0.0774	0.1059
	50.5	53 to 48	221	10	0.0983	0.0001	1.0000	0.0001	0.0824	0.1149
	49.5	52 to 47	222	10	0.0977	0.0001	1.0000	0.0001	0.0822	0.1138
	48.5	51 to 46	163	8	0.0968	0.0001	1.0000	0.0001	0.0751	0.1220
	47.5	50 to 45	95	7	0.0943	0.0001	1.0000	0.0001	0.0633	0.1323

Table S8. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) that followed the Central migration route (AK, YT, northern BC, AB, SK, MB) at 11 latitude intervals, using 1x1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	57.5	60 to 55	40	3	0.5520	0.0021	0.9980	0.0021	0.3363	0.6516
	56.5	59 to 54	40	3	0.5520	0.0028	0.9973	0.0028	0.3363	0.6496
	55.5	58 to 53	70	5	0.5747	0.0001	1.0000	0.0001	0.5204	0.6393
	54.5	57 to 52	132	8	0.4354	0.0001	1.0000	0.0001	0.3975	0.4810
	53.5	56 to 51	134	9	0.4260	0.0001	1.0000	0.0001	0.3905	0.4636
	52.5	55 to 50	144	10	0.2353	0.0001	1.0000	0.0001	0.1982	0.2688
	51.5	54 to 49	146	10	0.2428	0.0001	1.0000	0.0001	0.2094	0.2764
	50.5	53 to 48	146	10	0.2428	0.0001	1.0000	0.0001	0.2083	0.2739
	49.5	52 to 47	129	10	0.2469	0.0001	1.0000	0.0001	0.2106	0.2826
	48.5	51 to 46	70	7	0.0621	0.0964	0.9037	0.1731	0.0292	0.1003
	47.5	50 to 45	69	6	0.0565	0.1170	0.8831	0.2217	0.0225	0.0934
Temporal	57.5	60 to 55	40	5	0.1643	0.0199	0.9802	0.0199	0.1077	0.2428
	56.5	59 to 54	40	5	0.1643	0.0160	0.9841	0.0160	0.1107	0.2397
	55.5	58 to 53	70	6	0.1356	0.0002	0.9999	0.0002	0.0955	0.1911
	54.5	57 to 52	132	9	0.1729	0.0001	1.0000	0.0001	0.1429	0.2066
	53.5	56 to 51	134	9	0.1639	0.0001	1.0000	0.0001	0.1364	0.1942
	52.5	55 to 50	144	9	0.1225	0.0001	1.0000	0.0001	0.0992	0.1463
	51.5	54 to 49	146	9	0.1270	0.0001	1.0000	0.0001	0.1057	0.1508
	50.5	53 to 48	146	9	0.1270	0.0001	1.0000	0.0001	0.1048	0.1540
	49.5	52 to 47	129	9	0.1402	0.0001	1.0000	0.0001	0.1164	0.1707
	48.5	51 to 46	70	5	0.0736	0.0094	0.9907	0.0095	0.0531	0.1016
	47.5	50 to 45	69	5	0.0688	0.0202	0.9799	0.0209	0.0444	0.0944

Table S9. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) that followed the Central migration route (AK, YT, northern BC, AB, SK, MB) at 11 latitude intervals, using 0.1x0.1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	57.5	60 to 55	40	7	0.9487	0.0001	1.0000	0.0001	0.9134	0.9809
	56.5	59 to 54	40	7	0.9487	0.0001	1.0000	0.0001	0.9184	0.9812
	55.5	58 to 53	70	10	0.6362	0.0001	1.0000	0.0001	0.5746	0.6980
	54.5	57 to 52	70	10	0.6362	0.0001	1.0000	0.0001	0.5708	0.6999
	53.5	56 to 51	113	14	0.1720	0.0001	1.0000	0.0001	0.1464	0.1992
	52.5	55 to 50	139	17	0.1641	0.0001	1.0000	0.0001	0.1410	0.1858
	51.5	54 to 49	146	20	0.1750	0.0001	1.0000	0.0001	0.1542	0.1974
	50.5	53 to 48	128	17	0.1846	0.0001	1.0000	0.0001	0.1642	0.2095
	49.5	52 to 47	129	18	0.1852	0.0001	1.0000	0.0001	0.1599	0.2103
	48.5	51 to 46	70	12	0.0591	0.0358	0.9643	0.0534	0.0288	0.0860
	47.5	50 to 45	41	5	0.0893	0.0690	0.9311	0.1129	0.0428	0.1383
Temporal	57.5	60 to 55	40	5	0.1643	0.0179	0.9822	0.0179	0.1077	0.2243
	56.5	59 to 54	40	5	0.1643	0.0172	0.9829	0.0172	0.1128	0.2249
	55.5	58 to 53	70	6	0.1356	0.0007	0.9994	0.0007	0.0919	0.1907
	54.5	57 to 52	70	6	0.1356	0.0004	0.9997	0.0004	0.0902	0.1927
	53.5	56 to 51	113	9	0.1427	0.0001	1.0000	0.0001	0.1105	0.1798
	52.5	55 to 50	139	9	0.1241	0.0001	1.0000	0.0001	0.1017	0.1507
	51.5	54 to 49	146	9	0.1270	0.0001	1.0000	0.0001	0.1034	0.1521
	50.5	53 to 48	128	9	0.1433	0.0001	1.0000	0.0001	0.1202	0.1730
	49.5	52 to 47	129	9	0.1448	0.0001	1.0000	0.0001	0.1199	0.1712
	48.5	51 to 46	70	5	0.0736	0.0132	0.9869	0.0132	0.0524	0.0988
	47.5	50 to 45	41	5	0.0880	0.0385	0.9616	0.0478	0.0528	0.1225

Table S10. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) that followed the Central migration route (AK, YT, northern BC, AB, SK, MB) at 11 latitude intervals, using 0.01x0.01 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	57.5	60 to 55	40	7	0.9487	0.0001	1.0000	0.0001	0.9036	0.9812
	56.5	59 to 54	40	7	0.9487	0.0001	1.0000	0.0001	0.9169	0.9811
	55.5	58 to 53	70	10	0.6362	0.0001	1.0000	0.0001	0.5728	0.6974
	54.5	57 to 52	70	10	0.6362	0.0001	1.0000	0.0001	0.5796	0.6942
	53.5	56 to 51	113	14	0.1720	0.0001	1.0000	0.0001	0.1462	0.1989
	52.5	55 to 50	139	17	0.1641	0.0001	1.0000	0.0001	0.1408	0.1871
	51.5	54 to 49	146	20	0.1750	0.0001	1.0000	0.0001	0.1517	0.1981
	50.5	53 to 48	128	17	0.1846	0.0001	1.0000	0.0001	0.1617	0.2087
	49.5	52 to 47	129	18	0.1852	0.0001	1.0000	0.0001	0.1611	0.2056
	48.5	51 to 46	70	12	0.0591	0.0388	0.9613	0.0555	0.0314	0.0863
	47.5	50 to 45	41	5	0.0893	0.0704	0.9297	0.1127	0.0458	0.1364
Temporal	57.5	60 to 55	40	5	0.1643	0.0160	0.9841	0.0160	0.1070	0.2404
	56.5	59 to 54	40	5	0.1643	0.0148	0.9853	0.0148	0.1111	0.2256
	55.5	58 to 53	70	6	0.1356	0.0007	0.9994	0.0007	0.0911	0.1917
	54.5	57 to 52	70	6	0.1356	0.0006	0.9995	0.0006	0.0945	0.1867
	53.5	56 to 51	113	9	0.1427	0.0001	1.0000	0.0001	0.1106	0.1773
	52.5	55 to 50	139	9	0.1241	0.0001	1.0000	0.0001	0.1034	0.1519
	51.5	54 to 49	146	9	0.1270	0.0001	1.0000	0.0001	0.1035	0.1513
	50.5	53 to 48	128	9	0.1433	0.0001	1.0000	0.0001	0.1200	0.1749
	49.5	52 to 47	129	9	0.1448	0.0001	1.0000	0.0001	0.1203	0.1733
	48.5	51 to 46	70	5	0.0736	0.0104	0.9897	0.0104	0.0499	0.1010
	47.5	50 to 45	41	5	0.0880	0.0365	0.9636	0.0454	0.0562	0.1232

Table S11. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) that followed the Eastern migration route (QC, NB, NS, PEI) at 11 latitude intervals, using 1x1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	47.5	50 to 45	233	15	0.8722	0.0001	1.0000	0.0001	0.8605	0.8914
	46.5	49 to 44	240	21	0.8653	0.0001	1.0000	0.0001	0.8540	0.8800
	45.5	48 to 43	235	25	0.8554	0.0001	1.0000	0.0001	0.8435	0.8700
	44.5	47 to 42	235	31	0.8510	0.0001	1.0000	0.0001	0.8390	0.8649
	43.5	46 to 41	235	37	0.8468	0.0001	1.0000	0.0001	0.8356	0.8624
	42.5	45 to 40	123	35	0.7854	0.0001	1.0000	0.0001	0.7586	0.8111
	41.5	44 to 39	64	28	0.2799	0.0001	1.0000	0.0001	0.2310	0.3230
	40.5	43 to 38	48	23	0.1453	0.0003	0.9998	0.0003	0.0915	0.2028
	39.5	42 to 37	34	18	-0.0043	0.4863	0.5138	0.9142	-0.0491	0.0405
	38.5	41 to 36	28	12	-0.0103	0.5185	0.4816	0.8333	-0.0513	0.0307
	37.5	40 to 35	18	6	0.0085	0.4066	0.5935	0.9034	-0.0685	0.0927
Temporal	47.5	50 to 45	233	11	0.1217	0.0001	1.0000	0.0001	0.1052	0.1393
	46.5	49 to 44	240	12	0.1135	0.0001	1.0000	0.0001	0.0960	0.1302
	45.5	48 to 43	235	12	0.1127	0.0001	1.0000	0.0001	0.0975	0.1285
	44.5	47 to 42	235	12	0.1144	0.0001	1.0000	0.0001	0.0981	0.1311
	43.5	46 to 41	235	12	0.1120	0.0001	1.0000	0.0001	0.0946	0.1277
	42.5	45 to 40	123	12	0.3929	0.0001	1.0000	0.0001	0.3592	0.4363
	41.5	44 to 39	64	12	0.1299	0.0001	1.0000	0.0001	0.0985	0.1707
	40.5	43 to 38	48	11	0.0803	0.0161	0.9840	0.0165	0.0345	0.1249
	39.5	42 to 37	34	11	0.1109	0.0153	0.9848	0.0154	0.0596	0.1803
	38.5	41 to 36	28	10	0.1869	0.0042	0.9959	0.0042	0.1198	0.2563
	37.5	40 to 35	18	9	0.1796	0.0285	0.9716	0.0299	0.0714	0.2901

Table S12. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) that followed the Eastern migration route (QC, NB, NS, PEI) at 11 latitude intervals, using 0.1x0.1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	47.5	50 to 45	233	42	0.7508	0.0001	1.0000	0.0001	0.7331	0.7713
	46.5	49 to 44	240	51	0.7475	0.0001	1.0000	0.0001	0.7309	0.7650
	45.5	48 to 43	235	60	0.7335	0.0001	1.0000	0.0001	0.7147	0.7521
	44.5	47 to 42	235	74	0.7272	0.0001	1.0000	0.0001	0.7118	0.7449
	43.5	46 to 41	197	77	0.7491	0.0001	1.0000	0.0001	0.7289	0.7740
	42.5	45 to 40	67	56	0.2794	0.0001	1.0000	0.0001	0.2301	0.3277
	41.5	44 to 39	52	46	0.1097	0.0014	0.9987	0.0014	0.0705	0.1606
	40.5	43 to 38	45	40	0.1408	0.0012	0.9989	0.0012	0.0928	0.2034
	39.5	42 to 37	33	24	0.0615	0.0834	0.9167	0.1331	0.0117	0.1269
	38.5	41 to 36	27	17	0.0649	0.1125	0.8876	0.1999	0.0025	0.1369
	37.5	40 to 35	11	7	0.1448	0.1448	0.8553	0.2612	-0.0119	0.2901
Temporal	47.5	50 to 45	233	11	0.1254	0.0001	1.0000	0.0001	0.1086	0.1441
	46.5	49 to 44	240	11	0.1169	0.0001	1.0000	0.0001	0.1009	0.1322
	45.5	48 to 43	235	12	0.1144	0.0001	1.0000	0.0001	0.0989	0.1302
	44.5	47 to 42	235	12	0.1163	0.0001	1.0000	0.0001	0.1016	0.1338
	43.5	46 to 41	197	11	0.1612	0.0001	1.0000	0.0001	0.1419	0.1827
	42.5	45 to 40	67	12	0.1298	0.0001	1.0000	0.0001	0.0988	0.1689
	41.5	44 to 39	52	11	0.0698	0.0211	0.9790	0.0222	0.0297	0.1119
	40.5	43 to 38	45	11	0.1128	0.0065	0.9936	0.0065	0.0641	0.1676
	39.5	42 to 37	33	10	0.1175	0.0156	0.9845	0.0156	0.0650	0.1941
	38.5	41 to 36	27	10	0.1841	0.0043	0.9958	0.0043	0.1107	0.2664
	37.5	40 to 35	11	9	-0.0416	0.5810	0.4191	0.7471	-0.2708	0.1262

Table S13. Number of birds, number of grid cells, Mantel R, p-values and 95% confidence intervals for spatial and temporal overlap analyses of Bank Swallows (*Riparia riparia*) that followed the Eastern migration route (QC, NB, NS, PEI) at 11 latitude intervals, using 0.1x0.1 latitude-longitude grid cells.

	Median latitude	Latitude range	# birds	# grid cells	Mantel R	p Mantel R <= 0	p Mantel R >= 0	p Mantel R = 0	95% CI lower limit	95% CI upper limit
Spatial	47.5	50 to 45	233	47	0.7043	0.0001	1.0000	0.0001	0.6840	0.7262
	46.5	49 to 44	240	59	0.7001	0.0001	1.0000	0.0001	0.6775	0.7207
	45.5	48 to 43	235	65	0.6897	0.0001	1.0000	0.0001	0.6694	0.7112
	44.5	47 to 42	235	81	0.6799	0.0001	1.0000	0.0001	0.6606	0.7004
	43.5	46 to 41	196	82	0.7440	0.0001	1.0000	0.0001	0.7224	0.7698
	42.5	45 to 40	66	54	0.2844	0.0001	1.0000	0.0001	0.2395	0.3318
	41.5	44 to 39	52	46	0.1097	0.0020	0.9981	0.0020	0.0710	0.1593
	40.5	43 to 38	45	40	0.1408	0.0008	0.9993	0.0008	0.0908	0.1963
	39.5	42 to 37	33	24	0.0615	0.0855	0.9146	0.1304	0.0065	0.1118
	38.5	41 to 36	25	15	0.0664	0.1316	0.8685	0.2265	0.0063	0.1523
	37.5	40 to 35	11	7	0.1448	0.1370	0.8631	0.2458	-0.0309	0.2901
Temporal	47.5	50 to 45	233	11	0.1247	0.0001	1.0000	0.0001	0.1075	0.1442
	46.5	49 to 44	240	11	0.1169	0.0001	1.0000	0.0001	0.1013	0.1363
	45.5	48 to 43	235	12	0.1177	0.0001	1.0000	0.0001	0.1001	0.1354
	44.5	47 to 42	235	12	0.1163	0.0001	1.0000	0.0001	0.0995	0.1335
	43.5	46 to 41	196	11	0.1592	0.0001	1.0000	0.0001	0.1409	0.1832
	42.5	45 to 40	66	12	0.1268	0.0002	0.9999	0.0002	0.0937	0.1668
	41.5	44 to 39	52	11	0.0698	0.0197	0.9804	0.0209	0.0248	0.1150
	40.5	43 to 38	45	11	0.1128	0.0082	0.9919	0.0082	0.0720	0.1708
	39.5	42 to 37	33	10	0.1175	0.0154	0.9847	0.0154	0.0633	0.1941
	38.5	41 to 36	25	9	0.1966	0.0047	0.9954	0.0047	0.1164	0.2871
	37.5	40 to 35	11	9	-0.0416	0.5798	0.4203	0.7543	-0.2462	0.1662

Departure Timing, Migration Pace and Ground Speed

Table S14. Model-predicted effects of migration route, mass, wing chord, year, age and sex on Bank Swallow (*Riparia riparia*) departure dates (n = 557). Breeding site was included as a random effect (σ = 4.911), all other effects are fixed. This model excluded individuals with missing mass, wing chord, or sex (n = 30). There was a correlation of 0.095 between mass and wing chord. The reference level for migration route and year was the Central route and 2022, respectively.

Term	Estimate	Std.error	df	t value	p-value
(Intercept)	233.4027	16.6361	547.9856	14.030	< 2e-16 ***
Route$_{\text{Eastern}}$	-9.7690	3.5102	21.6188	-2.783	0.01096 *
Route$_{\text{Western}}$	-8.0315	5.8153	10.3328	-1.381	0.19639
Mass	0.3150	0.4033	547.5894	0.781	0.43519
Wing chord	-0.3096	0.1571	547.1279	-1.971	0.04928 *
Sex$_{\text{M}}$	-1.0946	0.7996	543.2130	-1.369	0.17159
Year$_{2023}$	-8.4549	2.6010	129.9552	-3.251	0.00147 **
Route$_{\text{Eastern}}$ * Year$_{2023}$	6.0657	2.9520	171.7344	2.055	0.04141 *
Route$_{\text{Western}}$ * Year$_{2023}$	6.6622	3.2299	237.5973	2.063	0.04023 *

Table S15. Model-predicted effects of migration route, mass, wing chord, year, age and sex on Bank Swallow (*Riparia riparia*) departure dates (n = 378), excluding high-latitude breeding sites in YT, AK and northern BC (n = 207). Breeding site was included as a random effect (σ = 6.012), all other effects are fixed. The reference level for migration route and year was the Central route and 2022, respectively.

Term	Estimate	Std.error	df	t value	p-value
(Intercept)	231.6909	22.9502	282.6586	10.095	< 2e-16 ***
Route$_{\text{Eastern}}$	-2.7762	7.5889	8.5148	-0.366	0.723
Route$_{\text{Western}}$	-0.3764	9.4363	6.5005	-0.040	0.969
Wing chord	-0.3298	0.2136	368.6446	-1.544	0.123
Year$_{2023}$	-3.2940	9.4590	6.5634	-0.348	0.739
Route$_{\text{Eastern}}$ * Year$_{2023}$	1.0456	9.5827	6.8969	0.109	0.916
Route$_{\text{Western}}$ * Year$_{2023}$	1.1130	9.6941	7.2410	0.115	0.912

Table S16. Model-predicted effects of migration route, mass, wing chord, year, age and sex on Bank Swallow (*Riparia riparia*) departure dates (n = 424), excluding sites where we only tagged in 2023 (AK, SK, northern BC; n = 165). Breeding site was included as a random effect (σ = 6.605), all other effects are fixed. The reference level for migration route and year was the Central route and 2022, respectively.

Term	Estimate	Std.error	df	t value	p-value
(Intercept)	224.6694	19.8398	410.4172	11.324	< 2e-16 ***
$\text{Route}_{\text{Eastern}}$	-12.0467	4.6786	10.4310	-2.575	0.02682 *
$\text{Route}_{\text{Western}}$	-10.4875	7.7828	7.4368	-1.348	0.21742
Wing chord	-0.1633	0.1942	412.8071	-0.841	0.40082
Year_{2023}	-10.7046	2.5041	341.5210	-4.275	2.49e-05 ***
$\text{Route}_{\text{Eastern}}$ * Year_{2023}	8.4006	2.8854	364.5203	2.911	0.00382 **
$\text{Route}_{\text{Western}}$ * Year_{2023}	8.8717	3.2439	395.5259	2.735	0.00652 **

Table S17. Results of Tukey's post-hoc test of the model in Table S13 to compare pairwise differences in Bank Swallow (*Riparia riparia*) departure dates between the Western, Central and Eastern migration routes in interaction with study year (n = 424).

	Comparison	Estimate	Std.error	df	t.ratio	p-value
2022	Central-Eastern	12.05	4.70	12.30	2.566	0.0590
	Central-Western	10.49	7.79	8.78	1.346	0.4077
	Eastern-Western	-1.56	7.31	8.41	-0.213	0.9753
2023	Central-Eastern	3.65	4.62	11.31	0.789	0.7170
	Central-Western	1.62	7.71	8.47	0.210	0.9762
	Eastern-Western	-2.03	7.27	8.18	- 0.279	0.9581

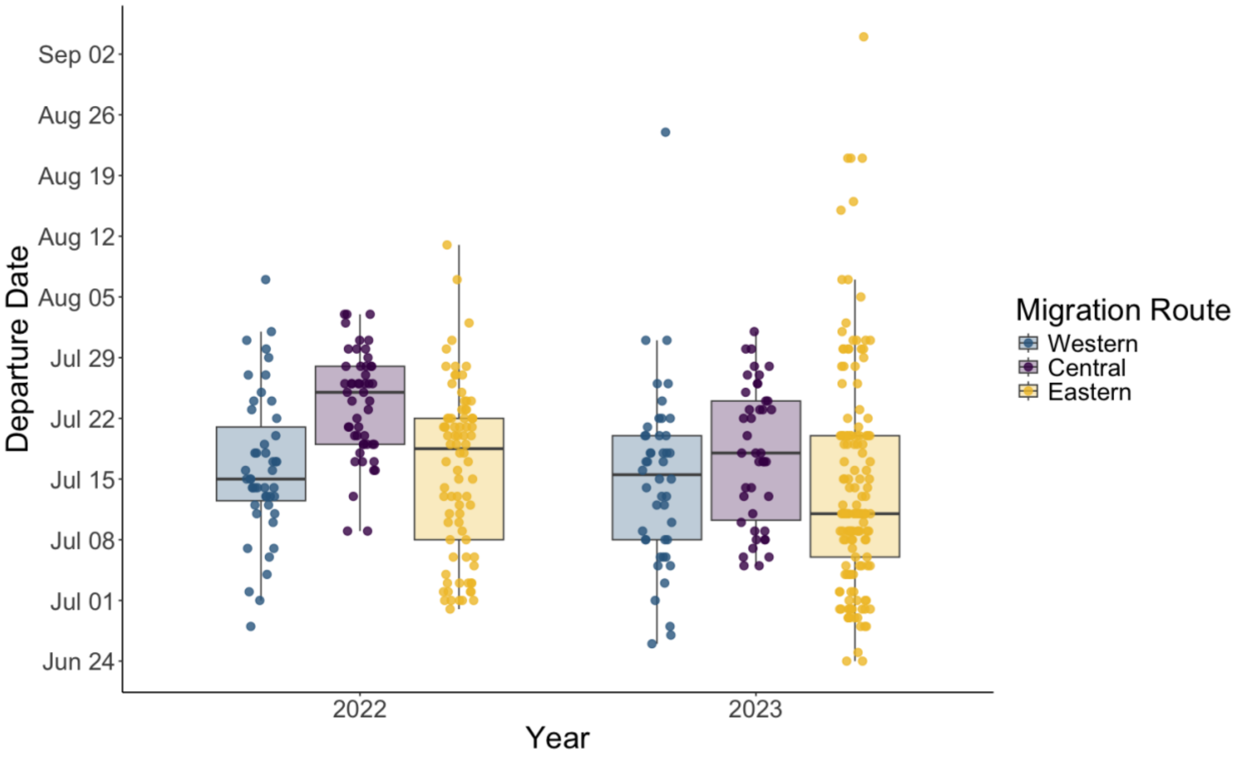


Figure S7. Bank Swallow (*Riparia riparia*) departure dates (n = 424) grouped by year and migration route. $n_{Western}$ = 93, $n_{Central}$ = 92, $n_{Eastern}$ = 237 (one departure date per individual). This plot only includes data for sites where we tagged in both 2022 and 2023, thereby excluding AK, SK and northern BC which were only tagged in 2023. The vertical lines in each box represent the first quartile (Q1), median (Q2) and third quartile (Q3). The horizontal lines on either side of each box plot represent Q1 - 1.5*(Q3-Q1) and Q3 + 1.5*(Q3-Q1).

Table S18. Model predicted effects of migration route, mass, wing chord, departure date, sex and year on Bank Swallow (*Riparia riparia*) migration pace (km/day; n = 53). Breeding site was included as a random effect (σ = 0.6347), all other effects are fixed. This model excludes individuals that had unknown sex or wing chord (n = 5). There was a correlation of 0.17 between mass and wing chord, 0.0004 between departure date and mass, and -0.15 between departure date and wing chord. The reference level for migration route and year was the Central route and 2022, respectively.

Term	Estimate	Std.error	df	t value	p-value
(Intercept)	4.248905	3.820563	43.032807	1.112	0.27226
$Route_{Eastern}$	-1.322394	0.425096	5.963755	-3.111	0.02099 *
Mass	-0.045998	0.067717	34.293322	-0.679	0.50153
Wing chord	-0.013047	0.033987	44.079463	-0.384	0.70291
Departure date	0.012534	0.006201	35.238848	2.021	0.05091
Sex_M	-0.185648	0.155907	37.576765	-1.191	0.24122

Year$_{2023}$	0.977833	0.336699	27.691693	2.904	0.00715 **

Table S19. Model predicted effects of migration route, mass, wing chord, departure date, sex and year on Bank Swallow (*Riparia riparia*) ground speed (m/s; n = 159 for 104 individuals). This model excludes individuals of unknown sex (n = 3). Individuals nested within breeding sites were included as random effects (σ = 0.22618 and σ = 0.08863, respectively), all other effects are fixed. Reference levels for the migration route and year are the Central route and 2023, respectively. This model includes interaction terms for Route * Year.

Term	Estimate	Std.error	z value	p-value
(Intercept)	-1.177621	2.066127	-0.570	0.5687
Route$_{\text{Eastern}}$	-0.418052	0.175971	-2.376	0.0175 *
Route$_{\text{Western}}$	-0.433865	0.183800	-2.360	0.0182 *
Mass	0.074457	0.042271	1.761	0.0782
Wing chord	0.011387	0.016330	0.697	0.4856
Departure date	0.006568	0.004718	1.392	0.1639
Sex$_{\text{M}}$	-0.093622	0.082849	-1.130	0.2585
Year$_{2022}$	0.139894	0.349813	0.400	0.6892
Route$_{\text{Eastern}}$ * Year$_{2022}$	-0.026480	0.371926	-0.071	0.9432
Route$_{\text{Western}}$ * Year$_{2022}$	-0.036197	0.374463	-0.097	0.9230

Table S20. Model predicted effects of migration route, mass, wing chord, departure date, and year on Bank Swallow (*Riparia riparia*) ground speed (m/s; n = 162 for 106 individuals). Individuals nested within breeding sites were included as random effects (σ = 0.22911 and σ = 0.08695, respectively), all other effects are fixed. This model includes individuals with unknown sex (n = 3). Reference levels for migration route and year are the Central route and 2023, respectively.

Term	Estimate	Std.error	z value	p-value
(Intercept)	-1.459994	2.032281	-0.718	0.4725
Route$_{\text{Eastern}}$	-0.390298	0.174326	-2.239	0.0252 *
Route$_{\text{Western}}$	-0.431116	0.181939	-2.370	0.0178 *
Mass	0.077813	0.041730	1.865	0.0622
Wing chord	0.011602	0.016220	0.715	0.4744
Departure date	0.007368	0.004615	1.596	0.1104
Year$_{2022}$	0.191776	0.343852	0.558	0.5770
Route$_{\text{Eastern}}$ * Year$_{2022}$	-0.086313	0.366680	-0.235	0.8139

Route$_{\text{Western}}$ * Year$_{2022}$	-0.094675	0.367953	-0.257	0.7969

Additional Analyses

Table S21. Negative binomial model summary for the relationship between the number of receivers individual Bank Swallows (*Riparia riparia*) were detected on post-departure and Motus tag burst interval, tag deployment longitude, mass at the time of tagging, and tag deployment year (n = 239). Breeding site was included as a random effect. All numeric fixed effects have been scaled. The reference level for Year was 2022.

Term	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.78871	0.18640	4.231	2.32e-05 ***
Longitude	0.22105	0.10227	2.161	0.0307 *
Longitude^2	0.18442	0.12105	1.524	0.1276
Burst interval	-0.17270	0.09592	-1.801	0.0718
Mass	0.06154	0.04828	1.275	0.2024
Year$_{2023}$	-0.02261	0.12623	-0.179	0.8579

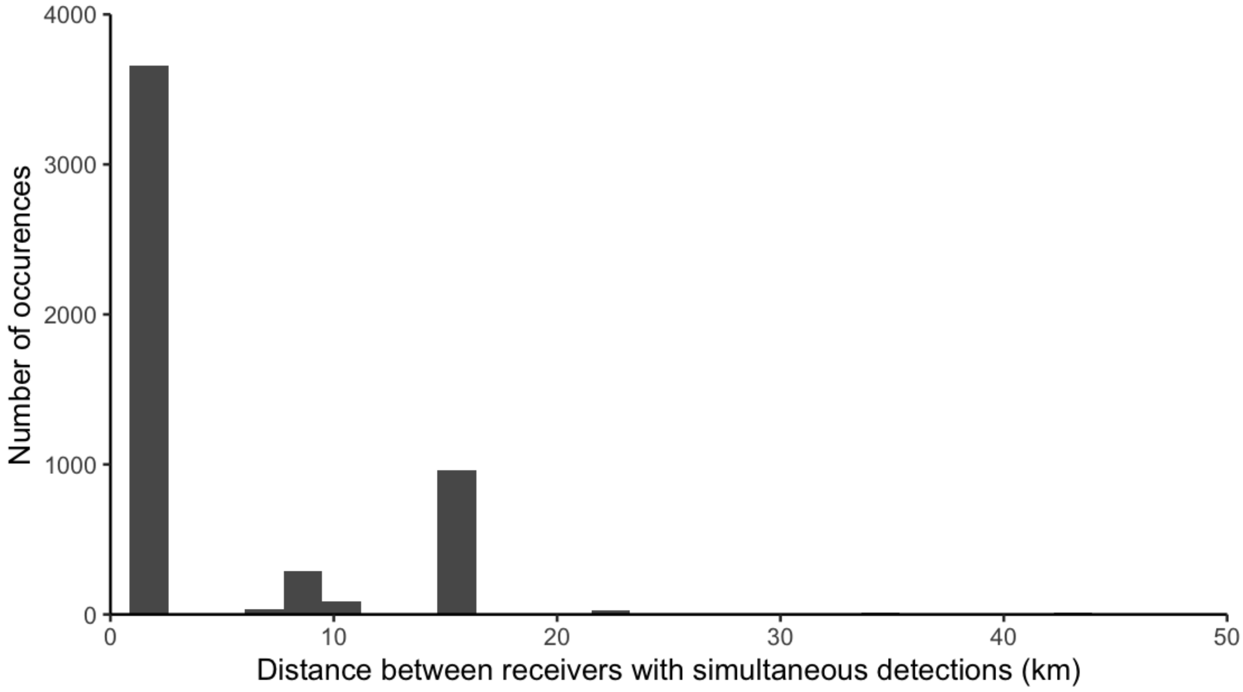


Figure S10. Distance between receivers (in km) that had simultaneous detections for tagged Bank Swallows (*Riparia riparia*), showing the number of runs at receivers <50km apart (see Figure S11 below for runs at receivers > 50km apart). I considered simultaneous detections to be runs of three or more consecutive tag emissions that overlapped in time with a run at another receiver. The total number of simultaneous detections was 5 104 out of a total of 966 873 unfiltered runs, and 5 101 of those simultaneous detections occurred at receivers <50km apart.

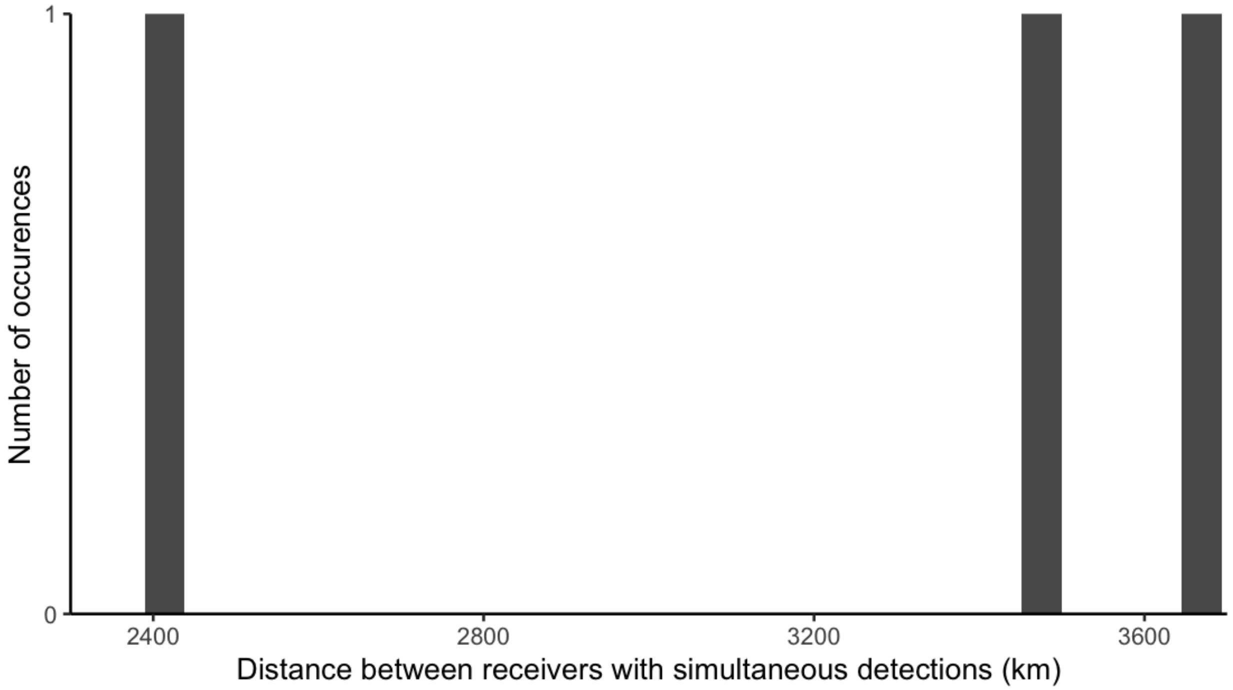


Figure S11. Distance between receivers (in km) that had simultaneous detections of tagged Bank Swallows (*Riparia riparia*), showing the number of occurrences at receivers >50km apart (see Figure S10 above for occurrences at receivers < 50km apart). I considered simultaneous detections to be runs of three or more consecutive tag emissions that overlapped in time with a run at another receiver. The total number of simultaneous detections was 5 104 out of a total of 966 873 unfiltered runs, and only 3 of those simultaneous runs occurred at receivers >50km apart.

Data and Code

Data for my models and most of my R code can be found on my OSF repository using the link below.

https://osf.io/9rypu/?view_only=0dac07601e3a40c0b37d9ae43355bfd7

Breeding latitude and longitude have been removed from data files for data confidentiality reasons. To access the raw data through Motus.org, please contact me to request access to the Motus project.