Fall Migratory Behaviour and Cross-seasonal Interactions in Semipalmated Plovers (*Charadrius semipalmatus)* Breeding in the Hudson Bay Lowlands, Canada

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Abstract

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I used the Motus Wildlife Tracking System to monitor the fall migration behaviour and assess the underlying drivers of migration strategy in a small shorebird, the Semipalmated Plover *(Charadrius semipalmatus),* breeding at two subarctic sites: Churchill, Manitoba and Burntpoint Creek, Ontario, Canada. Semipalmated Plovers from both sites departed breeding areas between mid-July and early August, with females preceding males and failed breeders preceding successful breeders. Migrants showed between and within-population variation in migration behaviour, though birds from both sites tended to follow interior or coastal routes and congregated in three major stopover regions along the mid-Atlantic coast of North America. I found that later-departing birds had initial flight tracks oriented more toward the south, faster overall ground speeds, were less likely to stopover in North America, and stopped at lower latitudes, suggesting that later-departing individuals use aspects of a time-minimizing strategy on fall migration. My findings emphasize the importance of the mid-Atlantic coast for Semipalmated Plovers and establish connectivity between sites used during breeding and migration.

Keywords: shorebird, Semipalmated Plover, *Charadrius*, migration behaviour, migration strategies, stopover ecology, cross-seasonal interactions, Motus, radio-telemetry, nest success, departure decisions.

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Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction

Background

Animal migration is one of the most extraordinary phenomena found in nature. Migratory species occur in all major taxonomic groups and across aquatic, terrestrial, and aerial environments (Shaw 2016). For most migratory species, migration consists of return-trip movement between two spatially discrete areas, one in which reproduction occurs (breeding site) and another in which individuals maintain or improve body condition to reproduce in the future (non-breeding site; Salewski and Bruderer 2007, Griswold et al. 2010). Migration confers a selective advantage by allowing individuals to exploit seasonal resource peaks in one portion of their range, while escaping seasonal depressions in another (Alerstam and Bäckman 2018, Robinson et al. 2020). Migratory distance varies greatly by species and population, with some travelling relatively short distances between seasonal ranges (e.g., 10-50 km; Sawyer et al. 2016, Hsiung et al. 2018) and others travelling vast distances (e.g., > 5,000 km; Luschi et al. 2003, Egevang et al. 2010, Stevick et al. 2011, Battley et al. 2012). The geographic separation of habitats used throughout the annual cycle makes the study of migration systems inherently complex, especially for long-distance migrants that travel across jurisdictional or continental boundaries.

Birds have an exceptionally widespread and conspicuous migration system that involves billions of individuals travelling between breeding and non-breeding areas annually, often at hemispheric scales (Cox 1985, Dokter et al. 2018). In addition to breeding and non-breeding areas, migrants temporarily occupy one or more ‘stopover sites’ along their migration route to rest and refuel, creating a network of interconnected habitats throughout a species’ range (Cox 1985, Warnock 2010). Globally, nearly one in five bird species are migratory (Kirby et al. 2008). Thus, bird migration is an ecologically important process that connects distant habitats through transport of biomass, nutrients, and energy (Bauer 2014, Alerstam and Bäckman 2018, Dokter et al. 2018). Considering the fundamental role that migratory birds play in ecosystem structure and processes, it is alarming that many migratory bird species are experiencing drastic and rapid population declines worldwide (Both et al. 2006, Kirby et al. 2008, Rosenberg et al. 2019). Threats including habitat loss (Iwamura et al. 2013, Perkin et al. 2015, Xu et al. 2019), climate change (Both et al. 2006, Newson et al. 2009), and overharvesting (Wilcove and Wikelski 2008, Kamp et al. 2015) are broadly considered the main drivers, though the impacts and specific causes of declines are often poorly understood. Although population loss can occur at any point throughout the annual cycle, for some species the largest source of mortality is migration (Sillett and Holmes 2002, Newton 2006, Klaassen et al. 2014). Mortality may be higher during migration because of the large time and energy costs associated with travelling often vast distances on strict annual schedules (Newton 2006). To identify potential drivers of population loss that occur during migration and proactively prevent declines, it is first necessary to characterize spatiotemporal patterns in migration behaviour and understand the mechanisms driving these patterns.

Drivers of Migration Behaviour

In birds, migration behaviour is characterized by the timing, speed, and direction of migratory flights, and the location, duration, and frequency of stopovers (Alerstam et al. 2003). Although there has been considerable effort to assess general migration patterns (i.e., when and where birds migrate), much less is known about the processes underlying these patterns (McKinnon and Love 2018). Early studies suggested that migration behaviour is under strict endogenous control (Berthold 1984, Berthold and Helbig 1992). Though there is evidence for an innate migration program (Wiltschko and Wiltschko 2015), a suite of modern studies have indicated that migration behaviour is also influenced by intrinsic factors such as sex (e.g., Briedis et al. 2019), age (e.g., Crysler et al. 2016), and morphology (e.g., Arizaga et al. 2006). These factors drive individual differences in body condition, experience, and life history constraints such as moult schedules and breeding system structure, which ultimately determine individual time and energy constraints experienced during migration (Cadahía et al. 2017, Bennett et al. 2019). In turn, these constraints influence migration behaviour. For instance, the need to acquire a breeding territory often results in males facing stricter time constraints than females during spring migration, leading to earlier departure from non-breeding sites and fewer, shorter stopovers *en route* (Dierschke et al. 2005, Briedis et al. 2019, Bell et al. 2021). Migration behaviour is also influenced by extrinsic factors such as weather (Erni et al. 2002). For instance, the timing of migratory flights is influenced by wind speed and direction, precipitation, and atmospheric pressure, with birds more likely to depart under wind conditions that support their direction of travel (Conklin and Battley 2011, Grönroos et al. 2012, Bozó et al. 2018). Wind speed and direction can also affect choice of migration route, flight height, and ground speed (Bruderer et al. 1995, Thorup et al. 2003, Anderson et al. 2019).

Events and processes occurring in preceding seasons may also affect migration behaviour. For instance, birds using lower-quality habitats during the non-breeding season are often in lower energetic state than conspecifics in higher-quality habitats, and consequently may delay departure for spring migration and/or spend more time refuelling *en route* (Cooper et al. 2015, Paxton and Moore 2015, McKinnon and Love 2018). These 'cross-seasonal interactions' often result from individuals transitioning seasons with altered time and/or energy constraints, which migrants compensate for by adjusting migration behaviour (Harrison et al. 2011). Although most studied in spring migrants (e.g., Norris et al. 2004, Zhou et al. 2016), cross-seasonal interactions may also affect fall migration behaviour. Specifically, time and energy costs imposed during the breeding season may carry over to influence departure decisions from the breeding site and subsequent migration behaviour (Conklin et al. 2010, Bogdanova et al. 2011, Mitchell et al. 2012). Breeding costs are primarily modulated by factors influencing individual parental effort (Williams 1966), including nest success (i.e., whether young were reared to fledging) and breeding system structure (e.g., uniparental versus biparental care). Individuals with nest success invest more time and energy into breeding than those with nest failure (Weiser et al. 2018), and therefore may depart later and transition into the migratory period in a lower energetic state and/or with stricter time constraints (Bogdanova et al. 2011, Hooijmeijer et al. 2014).

Similarly, in instances of uniparental care or unequal parental effort, the sex investing more into parental care typically departs later and may face stricter constraints during migration (Butler and Kaiser 1995, Ydenberg et al. 2005, Meissner and Krupa 2017, Weithman et al. 2017). Breeding costs may also be modulated by temporal factors such as the timing of clutch initiation. Individuals initiating clutches early in the season may have ample time to prepare for migration after breeding, whereas individuals initiating clutches later may face stricter time constraints and in turn, be forced to migrate later and/or in a lower energetic state (Mitchell et al. 2012). Thus, the time and energy costs of breeding are modulated by several factors and vary among individuals, which may lead to variable fall migration behaviour within a population. Cross-seasonal interactions between breeding and fall migration, however, remain understudied.

Optimal migration theory provides a framework for understanding how migrating birds optimize competing time and energy constraints during migration (Alerstam 2011). It postulates that individuals migrate using one of two main strategies: time-minimization or energy-minimization (Alerstam and Hedenstrom 1998). Under time-minimization, individuals reduce migration time by acquiring large fuel loads during long stopovers at few sites and by undertaking longer, faster, and more direct flights toward the migratory goal (Hedenström and Alerstam 1997, Alerstam and Hedenstrom 1998). These migrants often make larger ‘jumps’ across geographic barriers or areas of unsuitable habitat that act as barriers (Piersma 1987, Alerstam and Hedenstrom 1998), such as oceans or deserts (Gill et al. 2005, Battley et al. 2012). Conversely, under energy-minimization, individuals reduce energy expenditure by carrying lower fuel loads between a higher number of stopover sites used for shorter periods (Hedenström and Alerstam 1997). These migrants undertake shorter, slower flights (‘hops’) and may use less direct migration routes (Hedenström and Alerstam 1997). Additionally, energy-minimizers often avoid flying in weather conditions that increase energy expenditure, such as unsupportive winds (Delingat et al. 2008, Anderson et al. 2019). Though often discussed separately, these two strategies likely exist along a continuum, such that migrants use characteristics of each strategy depending on individual time and energy constraints that vary within and between migration periods (Miller et al. 2016, Imlay et al. 2020).

Migratory decisions expose individuals to variable weather conditions (Stanley et al. 2012), prey availability (Placyk and Harrington 2004), inter- and intraspecific competition (Moore and Yong 1991), and predation risk (Lank et al. 2003, Ydenberg et al. 2004) along migratory routes, which in turn can affect individual survival and overall population structure (Thomas et al. 2006). For instance, analysis of population trends in North American shorebirds found that compared to coastal migrants, shorebirds following continental routes were at a higher risk of population decline due to habitat loss and alteration of stopover sites (Thomas et al. 2006). Understanding the degree of individual variation in migration behaviour within and between populations can help to determine the underlying drivers of migration strategy, including variation in routes, which in turn can be used to identify pressures limiting populations.

Tracking Technologies for Migratory Birds

Due to the logistical challenges of tracking individuals across broad geographic ranges, studies of migratory birds have traditionally been restricted to one portion of the range (e.g., breeding sites; Bowlin et al. 2010, Bridge et al. 2011). However, recent advances in tracking technologies have significantly improved our ability to monitor birds within and between habitats throughout their range (Bridge et al. 2011, López-López 2016). Modern telemetry devices include data loggers (e.g., light-level geolocators, GPS loggers), which record information until it is retrieved from the tagged animal, and data transmitters (e.g., satellite and cellular transmitting devices, VHF radio transmitters), which transmit information and do not require recapturing the tagged animal (Bridge et al. 2011, McKinnon and Love 2018). Such devices have begun to revolutionize our understanding of avian migration systems and have revealed unprecedented migratory feats across numerous taxa (Bridge et al. 2011, López-López 2016). For instance, light-level geolocators deployed on Arctic Terns (*Sterna paradisaea*) uncovered annual migrations of up to 80,000 km, setting the record for the longest migration of any animal (Egevang et al. 2010). Similarly, satellite transmitters (PTTs) on Bar-tailed Godwits (*Limosa lapponica baaueri)* led to the discovery of birds making non-stop, trans-Pacific flights of more than 10,000 km in nine days from Alaska to New Zealand (Gill et al. 2005, Battley et al. 2012). In addition to providing information on the extent of migratory ranges and long-distance flights, such devices can identify important habitats used throughout the annual cycle (Bridge et al. 2011). For example, satellite transmitters deployed on globally Endangered Great Knots

(*Calidris tenuirostris*) led to the discovery of 42 previously unknown stopover locations in the East Asian-Australian Flyway (Chan et al. 2019). Similarly, satellite transmitters on Ivory Gulls (*Pagophila eburnea)* revealed previously unknown non-breeding areas in the Davis Strait and Labrador Sea (Spencer et al. 2014, 2016).

Most avian tracking studies have focused on larger-bodied birds due to the current weight restrictions of fine-scale tracking devices (e.g., satellite transmitters), leading to a substantial bias in the literature (Taylor et al. 2017). Other devices, such as light-level geolocators, can be deployed on smaller-bodied birds and have greatly facilitated the study of small bird migration (Robinson et al. 2010, López-López 2016, McKinnon and Love 2018). However, geolocators must be retrieved to recover data and have relatively large error margins in equatorial regions, thereby limiting their usage to specific applications (McKinnon and Love 2018). Radio telemetry is a well-established technology for tracking small birds (Millspaugh and Marzluff 2001), though traditional methods of radio telemetry involve labour-intensive manual tracking and are restricted to monitoring of local (i.e., non-migratory) movements (Taylor et al. 2017).

The recently developed Motus Wildlife Tracking System (‘Motus’) presents a viable solution to issues presented by other tracking modalities, as it is capable of monitoring large-scale movement patterns of animals as small as 10 g without the need for tag retrieval (Taylor et al. 2017). Motus is a collaborative, automated radio telemetry network that pairs lightweight (~0.2 to 2.6 g) digitally coded radio transmitters (‘tags’) with a static array of receiving stations distributed widely across

North America, and to a lesser extent, outside of North America (Taylor et al. 2017). Tags affixed to wildlife can be detected by any of the over 500 receiving stations in the network (www.motus.org), allowing for some species to be monitored throughout large portions of their range. The highest concentration of Motus receiving stations is along the Atlantic Flyway of North America, particularly along the mid-Atlantic coast from Nova Scotia, Canada, to Virginia, United States of America (USA). Since its inception in 2012, studies using Motus have provided valuable insights into migratory connectivity (Bégin-Marchand et al. 2021), migration schedules (Loring et al. 2017, Covino et al. 2020), and stopover behaviour (Morbey et al. 2018) across a wide range of species.

Shorebird Ecology and Knowledge Gaps

Shorebirds are a diverse group of wading birds in the order Charadriiformes. Most shorebirds are typically associated with coastal habitats, however some species prefer upland pastures, fields, or forests (O’Brien et al. 2006). Diets of most species are comprised of invertebrates such as worms, crustaceans, arthropods, and molluscs (O’Brien et al. 2006). Though some species travel short distances between breeding and non-breeding areas (e.g., American Oystercatcher [*Haematopus palliatus*]), most shorebirds are highly migratory (O’Brien et al. 2006, Conklin 2019). Shorebirds that breed in the Arctic undertake long migrations, with many species travelling tens of thousands of kilometers annually from breeding sites in the north to non-breeding sites in equatorial regions or the southern hemisphere. Arctic-breeding shorebirds spend a significant portion of the annual cycle on migration, yet for many species there is a paucity of information on spatiotemporal patterns of migration behaviour at an individual or population level.

To fuel such long migrations, Arctic breeding shorebirds rely on one or more stopover sites along their migration route to replenish energy reserves. Access to high-quality stopover sites is critical for migrants to improve body condition (Duijns et al. 2017), cross geographic barriers (Gill et al. 2005), and complete migration (Anderson et al. 2019). Though numerous studies have described stopover ecology, including habitat selection (Chan et al. 2019), length-of-stay (Henkel and Taylor 2015, Anderson et al. 2019), refuelling rates (Turcotte et al. 2013, Bianchini and Morrissey 2018), and departure decisions (Conklin and Battley 2011, Tan et al. 2018), most studies are restricted to a single stopover location within the larger migratory landscape. Moreover, few studies have investigated how stopover ecology is influenced by preceding events and processes, such as those occurring at breeding or non-breeding sites.

North American shorebird populations have experienced widespread and precipitous declines in recent years, with an average decline of 40% across all species since 1970 (North American Bird Conservation Institute Canada 2019). Population declines are most notable among Arctic breeding species (North American Bird Conservation Institute Canada 2019, Smith et al. 2020). Of the 91 Arctic breeding shorebird taxa with estimated trends, 51% are currently in decline (Smith et al. 2020).

Although Arctic breeders may be vulnerable during all stages of their annual cycle, the migration period may be especially limiting (Baker et al. 2004, Newton 2006). Arctic breeders may have increased vulnerability during migration because this phase of the annual cycle imposes strict time and energy constraints on individuals. For instance, during fall migration some species must balance high energetic requirements with the need to migrate quickly to avoid overlap with predator migration (Lank et al. 2003, Duijns et al. 2017), avoid deteriorating weather conditions and associated food shortages (Schneider and Harrington 1981), and acquire high-quality non-breeding territories (Colwell 2000).

Study Species

The Semipalmated Plover (*Charadrius semipalmatus)* is a small (~45 g) migratory shorebird that breeds in the Arctic, subarctic, and to a lesser extent, Atlantic Canada and temperate northwest (e.g., Haidi Gwai; Nol and Blanken 2014). This species nests in a variety of microhabitats including gravel ridges and flats, rocky outcrops, sand and cobble beaches, coastal mudflats, and tundra (Flynn et al. 1999, Nguyen et al. 2003). Males arrive at breeding territories earlier than females in spring (Flynn et al. 1999). In the subarctic, egg laying typically occurs in early June and most young have fledged by early August. A single clutch is typically laid during the short breeding season, though pairs may renest if nest failure occurs during early incubation (Flynn et al. 1999, Lishman et al. 2010). Chicks are precocial and begin foraging at nearby mudflats or beaches approximately 24 hours after hatch. Semipalmated Plovers exhibit biparental care, with both sexes engaging in duties including incubation, brooding of chicks, predator warning, and leading chicks to suitable foraging areas (Nol and Blanken 2014). However, females desert their brood and mate approximately two weeks after hatch, leaving males to remain with the brood for an additional week until fledging (Nol and Blanken 2014). After breeding, it remains unclear whether individuals migrate promptly or move to foraging areas prior to true departure.

During the non-breeding period, Semipalmated Plovers are found in coastal regions extending from southern North America to southern South America (Smith and Nol 2000, Rose and Nol 2010, Nol and Blanken 2014). Based on analysis of trace elements in feathers, this species has moderate migratory connectivity between breeding and non-breeding areas (Storm-Suke 2012). Specifically, Semipalmated Plovers breeding in Churchill, Manitoba and Akimiski Island, Nunavut match trace element signatures from French Guiana, whereas individuals from Egg Island, Alaska match signatures from both South Carolina and French Guiana, suggesting the latter population has a broader non-breeding range (Storm-Suke 2012). During migration, they have a wide distribution across coastal and inland North America, though densities are generally higher at the coast (O'Brien et al. 2006, Nol and Blanken 2014). Semipalmated Plovers most commonly occur in small, single-species flocks during migration, but do associate with other species at stopover sites (e.g., Sanderling [*Calidris alba*]; Nol and Blanken 2014, Cestari et al. 2020). It is believed that they are intermediate to long-distance migrants that exhibit a 'hop' strategy (Skagen et al. 1999, Nol and Blanken 2014, Henkel and Taylor 2015). However, migration strategies and connectivity between breeding, migration, and non-breeding habitats have not been described at an individual level, as tracking of this species has thus far been limited.

Study Areas

I studied two populations of Semipalmated Plovers breeding in the Churchill region of northern Manitoba, Canada (58.7°N, 94.1°W) and the Burntpoint Creek region of northern Ontario, Canada (55.2°N, 84.3°W). Both sites are in the Hudson Bay Lowlands region, which extends from the southern tip of James Bay in northern Ontario to northeastern Manitoba. The region consists of lowland plains that extend 100-150 km inward from the tidal flats of James Bay and Hudson Bay (Dredge and Dyke 2020). The Hudson Bay Lowlands are strongly influenced by the hydrological and atmospheric processes of Hudson Bay (Smith et al. 1998). As such, the region is characterized by a subarctic climate with long, harsh winters and short, cool summers. The Hudson Bay Lowlands comprise the largest wetland complex in North America and the second largest peatland in the world (Abraham and Keddy 2005). The region provides essential ecosystem services including water filtration and carbon storage and sequestration (Abraham and Keddy 2005). The Hudson Bay Lowlands also provide important nesting habitat for shorebirds, waterfowl, and to a lesser extent, passerines (Cadman et al. 2007, McKellar et al. 2015, Brook et al. 2021). Snowmelt often extends into late-May or early-June, resulting in short breeding seasons from early-June to mid-August (Hanis et al. 2013, Henkel and Taylor 2015). The region includes numerous areas designated by BirdLife International and partners as significant habitats for the conservation of birds and biodiversity, known as Important Bird Areas (IBAs; Wells et al. 2005). Though the area is a known area of importance for nesting birds, it remains understudied due to its remoteness and associated logistical challenges (McKellar et al. 2015, Brook et al. 2021).

Churchill, my focal study site, is on the west coast of Hudson Bay at the mouth of the Churchill River Estuary. It exists at the ecological junction between the Arctic Ocean, boreal forest, and Arctic tundra. Consequently, Churchill has unique habitat features including continuous subsurface permafrost, tundra ponds, mud flats, and extensive fens interspersed with open-canopy spruce-lichen woodlands (Dyke and Sladen 2010, Macrae et al. 2014, Dredge and Dyke 2020). Burntpoint Creek, my secondary study site, is located along the southern coast of Hudson Bay in Polar Bear Provincial Park, Ontario. The region predominantly consists of low-lying tundra, with boreal forest and fen complexes occurring inland and rocky outcrops, beaches, and mud flats occurring at the coast (Beresford 2011, Brown 2021). At both sites, Semipalmated Plovers nest in a variety of microhabitats including gravel ridges mixed with *Dryas integrifolia*, sand/gravel beaches dominated by *Sesuvium portulacastrum*, transitional gravel/mudflat, and mudflats with or without vegetative cover.

Thesis Objectives

My thesis broadly aims to describe Semipalmated Plover migration behaviour and identify its underlying processes. Specifically, my objectives were to: 1) describe fall migration behaviour of Semipalmated Plovers breeding near Churchill, MB, including departure timing, direction of initial flight track, migration route, ground speed, and stopover probability, latitude, and length-of-stay; 2) assess the effect of cross-seasonal interactions on migration strategy; and 3) qualitatively assess differences in migration behaviour between birds breeding at two locations in the Hudson Bay Lowlands.

After breeding, individual birds may enter the migratory period with varying time and energy constraints, which could influence migration strategy. Therefore, for objective 2 I hypothesized that time and energy constraints imposed during breeding (‘breeding constraints’) carry over to influence spatiotemporal aspects of migration, including departure timing, direction of initial flight track, route, ground speed, and stopover location, duration, and length-of-stay. I predicted that individuals would adopt varying migration strategies based on preceding breeding investment and departure timing from the breeding site. Specifically, since the decision of when to migrate is constrained by the need to provide care to young, I predicted that departure timing would be later for individuals investing more time into breeding (i.e., males and successful breeders) and earlier for those investing less (i.e., females and failed breeders). Similarly, I predicted that individuals initiating clutches early and/or completing breeding activities early would depart earlier than those with later clutch initiation and breeding completion dates. I also predicted that males, successful breeders, and later-departing individuals would compensate for stricter time constraints by adopting a time-minimizing migration strategy after departure, characterized by 1) a less variable, more direct migration route south; 2) faster ground speeds; and 3) longer and fewer stopovers at lower latitudes.

My findings will be the first to describe post-breeding migration routes, timing, and stopover ecology of this species, providing critical baseline data to inform future studies. Furthermore, although Semipalmated Plover populations are currently not threatened, proactive characterization of migration patterns can help prevent, rather than remedy, future population declines. These findings could also have relevance to a broader range of shorebirds with similar behavioural strategies and constraints, including Species at Risk (SAR).

Chapter 2: Methods

Model Species

Shorebirds are ideal species for Motus applications in North America, as many species are small (< 100 g), migratory, and known to use coastal regions where the density of receiving stations is high (i.e., Eastern USA and Canada). Additionally, shorebirds tend to fly through open habitats during migration, which makes them much more likely to be detected by Motus receiving stations compared to species that migrate through forested habitats (Taylor et al. 2017). The Semipalmated Plover was selected as a model shorebird species for this study because of its widespread breeding and migratory distribution, knowledge gaps surrounding its migration and stopover ecology, and its small size that cannot support most available tracking devices (e.g., GPS transmitters).

Study Areas

From 2015-2019, I studied two populations of Semipalmated Plovers breeding near Churchill and Burntpoint Creek in the Hudson Bay Lowlands (Figure 2.1). At Churchill, my focal site, the study area included inland and coastal sites along approximately 22 km of Hudson Bay shoreline east of Churchill and approximately 10 km of estuarine shoreline at the mouth of Churchill River (Figure 2.2). At Burntpoint, my secondary site, the study area included predominantly coastal sites located along approximately 8 km of Hudson Bay shoreline (Figure 2.3).

Nest Monitoring

Our field team located nests using knowledge of former territories, systematic walking surveys, and behavioural cues of nesting pairs (e.g., flushing adults from the nest, distraction displays, excessive calling and/or head-bobbing; Supplemental Methods). For nests found during incubation (80%), I estimated clutch initiation date using the egg floatation method (described in Liebezeit et al. 2007). I defined clutch initiation date as the date upon which the first egg was laid. To determine nest fates, we monitored nests approximately every 3-5 days (d) during incubation and every 24 hours (hr) after signs of hatching (i.e., starring or pipping on eggs) had begun. After hatch, we monitored adults and chicks until fledging (approximately 21 d post-hatch) or until we could not locate the chicks on two successive visits. In the latter case, chicks were assumed depredated or otherwise deceased. I classified nests as pre-hatch failure if no eggs hatched, post-hatch failure if ≥ 1 egg hatched but no chicks survived to fledging, and fledging success if ≥ 1 chick survived to fledging. I considered chicks to have fledged successfully if they were observed within 3 d of their estimated fledge date (i.e., ≥18 d from the date of hatching, as fledging occurs at approximately 21 d). I defined breeding completion date as the midpoint between the last date an individual was observed performing parental duties (i.e., incubating eggs [birds with pre-hatch failure] or observed with chicks [birds with post-hatch failure and fledging success]) and the date of our subsequent visit. The average period between nest visits was 4.3 ± 3.2 d (median ± SD).

Capture and Transmitter Deployment

From mid-June to early-July, our field team captured adult Semipalmated Plovers during mid-late incubation using bow nets at the nest. We did not capture birds during rain or when predators were observed nearby. In Churchill, we attached a total of 169 Lotek NTQB-3-2 or NTQB2-3-2 VHF transmitters (Lotek Wireless, Newmarket, Ontario, Canada; 'tags') to 147 birds from 2015-2019 (Table 2.1). We tagged 17 individuals in multiple years, though no bird was tagged more than twice. Additionally, we recaptured five birds 1-2 weeks (wk) after tag loss and affixed each with a replacement tag. At Burntpoint, we attached a total of 24 tags to 24 birds from 2016-2019 (Table 2.2). Tags were glued to trimmed feathers and skin above the uropygial gland (Warnock and Warnock 1993) using cyanoacrylate gel adhesive (Loctite® UltraGel™), which minimized risk by allowing tags to fall off naturally during definitive pre-basic molt (August-November; Nol and Blanken 2014). Negative effects of this attachment method include localized plumage damage at the attachment site and potentially heightened predation risk immediately after tagging (Mong and Sandercock 2007). However, several studies have found no effects of tag attachment on survival and/or return rates in other species (e.g., Johnson et al. 2001, Stantial et al. 2019).

The tags transmitted unique, identifiable bursts every 4.7 to 15.1 seconds (sec) for an estimated 67 to 224 d depending on model and burst rate. New captures were banded with a uniquely numbered Canadian Wildlife Service aluminum band and combination of 3-4 plastic color bands for re-identification from a distance. We sexed birds primarily by plumage, as males generally exhibit less distinct or absent supercilium stripes, more orange on the bill, and more black feathers in the crown and breast band (Teather and Nol 1997, Nol et al. 2013). We confirmed sex for ambiguous birds through comparison with mate's plumage.

The tags weighed 0.67 grams (g) and birds ranged in weight from 40.9 g to 55.7 g. Therefore, tags represented between 1.6% and 1.2% of an individual's mass, which is below the recommended upper weight limit of 3-5% (Barron et al. 2010). We released all birds immediately after processing and tagging (average total handling time was 11 minutes [min]). All procedures were conducted with permission from the Animal Care Committee at Trent University and banding permits issued by the Canadian Bird Banding Office (CBBO permit no: 10515).

Automated Radio Telemetry

To assess departure timing from the breeding site, our field team deployed four Motus receiving stations (hereafter 'breeding array') at five locations within our Churchill study area from June-August of 2015-2019 (Figure 2.2; Supplemental Methods). In 2017, the westernmost station was relocated an additional 5.5 km west because it had few detections in 2016. To improve departure estimates, we deployed an additional station from June-September 2018-2019 outside the breeding array at Nester 1 Research Station ('Nester 1'), located approximately 58 km east of Churchill in Wapusk National Park, Manitoba. Our field team also deployed a single Motus receiving station at Burntpoint Creek from June-August of 2016-2019 (Figure 2.3). All stations were equipped with SensorGnome (https://compudata.ca/sensorgnome/) receivers and an array of 2-3 nine-element Yagi antennas oriented toward major nesting sites.

After departure, many birds were detected at Motus receiving stations distributed throughout North America and to a lesser extent, Central and South America (hereafter 'southern array'). Because there were no instances of birds returning to the breeding array after detection at Nester 1, I classified Nester 1 as part of the southern array. Motus receiving stations were equipped with either Lotek SRX/DX (Lotek Wireless, Newmarket, Ontario) or SensorGnome (https://compudata.ca/sensorgnome/) receivers and an antenna array consisting of single-pole omnidirectional and/or directional (typically 3-6 five or nine-element Yagi) antennas (Taylor et al. 2017). Each station operates at a single frequency (166.380 MHz) and either searches for tags on all antennas simultaneously and continuously (sensorgnome receivers and some Lotek receviers) or by cycling between antennas continuously, with only one antenna active at any given time (some Lotek receivers). Under ideal conditions, tagged birds are detected in flight up to 50 km from a receiving station (Anderson et al. 2019). However, detection range is often much lower (5-15 km) due to adverse weather, orientation and model of antennas, obstruction by vegetation and changes in elevation (Taylor et al. 2017). When a tagged bird is in range, receivers automatically record the unique transmitter ID, date, time (hh:mm:ss; UTC), and antenna port and signal strength (nonlinear scale: 20-255 for lotek units; dBm for SensorGnomes). The spatial extent of the network increased over the duration of this study, from 615 active stations in 2015 to 971 in 2019 (Figure 2.4). My data were downloaded from the Motus repository on or before January 15, 2021.

Data Processing

I conducted all analyses and data processing using R version 3.6.2 (R Core Team 2020). I processed automated telemetry data following procedures described in Taylor et al. (2017) and Crewe et al. (2018). In summary, I filtered data to eliminate false positive detections caused by local radio-frequency interference. Specifically, I removed detections with <4 consecutive bursts at intervals of a tag's burst rate (Duijns et al. 2017, Anderson et al. 2019) and detections in months before deployment or beyond the expected lifetime of a tag based on projected battery life (here, excluding November-June), which eliminated most false detections. Filtering the remaining false detections involved removing detections from receivers that were particularly prone to interference, which were often receivers located near urban centers. These receivers systematically recorded false detections of tags (e.g., detections with <10 consecutive bursts hundreds of kilometers away from a bird's last known location and within an unreasonable time frame). I identified and removed these detections by examining plots of detections by latitude and time and through observation of recurrent detection patterns (low consecutive bursts and/or unlikely timing of detections) from specific 'noisy' receivers each year.

My sample of birds breeding at Burntpoint Creek was relatively small in comparison to Churchill (Table 2.1, 2.2), with many fewer birds detected at and beyond the breeding array. Additionally, nest fates were unknown for most birds from Burntpoint Creek. Therefore, my quantitative analyses of drivers of migration behaviour focus exclusively on birds breeding at Churchill. However, I present general departure, migration, and stopover patterns of birds from Burntpoint and qualitatively discuss these patterns in the context of breeding latitude.

Departure from Breeding Sites

I used filtered detection data to estimate departure dates of individuals from the breeding sites. I confirmed departure dates by visually examining plots of signal strength by time during the final hour of detection by the breeding array and/or assessing the length of time between the last detection at the breeding array and first detection by the southern array (Supplemental Methods). To assess the impact of breeding constraints on departure date, I fit a general linear model with Julian departure date as the response variable and sex, nest fate, and Julian clutch initiation date as predictor variables. I also included an interaction term between sex and nest fate because I predicted that, compared to females, males with breeding failure would remain in breeding areas longer to exploit re-nesting opportunities and/or to prospect future nesting sites (Eadie and Gauthier 1985, Doligez et al. 2004, Ponchon et al. 2015). However, this term was not statistically significant ($P > 0.05$) and was therefore removed from the final model for parsimony. Since many species experience seasonal declines in breeding performance (Weiser et al. 2018), Semipalmated Plovers that initiate nests earlier may be more likely to have fledging success than those initiating later. In turn, successful breeders may depart the breeding site within a similar timeframe to those that experience breeding failure, which could explain lower than expected differences in departure dates among nest fate categories. Therefore, I ran an *a posteriori* Type-II Sum of Squares two-way ANOVA to assess how initiation date varied by nest fate while controlling for potential year effects. I was also interested in assessing whether birds with varying nest fates varied in the amount of time spent preparing for migration, i.e., between breeding completion and departure date. Therefore, I fit a second general linear model to explore the specific interaction of nest fate and Julian breeding completion date on Julian departure date. I compared the fit of the two departure models using AICc (Bedrick and Tsai 1994).

I centred breeding completion dates to improve interpretation of main effects and interactions (Schielzeth 2010). Although there were departure dates of five individuals tagged in two different years, I did not include bird ID as a random effect in either model because it introduced singularities. Similarly, I did not include year as a random effect because likelihood-ratio tests (LRT) indicated that including year did not significantly improve model fit for the first model including sex, nest fate, and clutch initiation date as predictors (LRT: $\chi^2 = 2.8$, $P = 0.09$) or the second including the interaction of breeding completion date and nest fate as the predictor (LRT: $\chi^2 = 1.5$, P = 0.22; Morrell 1998). I did not include birds with ‘unknown’ departure detection patterns in these analyses because departure date may be biased earlier for these birds due to tag loss and nesting and/or departing from an area outside the spatial range of the breeding array (Anderson et al. 2019).

Route Mapping and Direction of Initial Flight Track

For each bird, I separated migration flights into distinct spatiotemporal segments (‘tracks’) representing the great circle trajectories and elapsed time between receiving station detections (Anderson et al. 2019). I then produced maps of each migrant’s sequential tracks to delineate general migration routes. To aid in interpretation and discussion of tracking data, I defined several broad geographic regions used by tagged birds within their migratory range. These regions included: 1) Canada – Southwestern Hudson Bay; 2) Canada – James Bay; 3) Canada – St. Lawrence River and Estuary; 3) Canada/USA – Great Lakes; 4) Canada – Maritimes; 5) USA – Coastal Maine; 6) Canada/USA – Northeast Interior; 7) USA – Cape Cod/Long Island; 8) USA – Delmarva Peninsula/Jersey Shore; 9) USA – South Atlantic Coast; 10) Caribbean; 11) Southern Central America; 12) Northern South America (Figure 2.5).

I assessed the direction of a bird’s initial flight track by calculating the bearing between the departure receiver (i.e., last receiver with detections in the breeding array) and the subsequent receiver (i.e., first receiver with detections in the southern array). The median distance between the two receivers used for bearing calculations (i.e., first track distance) was 1892 ± 130 km (median ± SE, *n* = 61, range = 36-5652). The tower with the most easterly possible bearing from Churchill in the southern array was Nester 1 in Polar Bear Provincial Park, Manitoba, whereas the tower with most westerly possible bearing was ‘Alaksen’ in Vancouver, British Columbia. Therefore, the maximum possible range of bearings was 90°-240°. To ensure I only used bearings of true departures, I removed birds with unknown departure detection patterns. Additionally, I removed two individuals with unknown nest fates. To assess the effects of breeding constraints and departure timing on initial migration direction, I fit a general linear model with bearing (degrees) as the response variable and sex, nest fate, and departure date as the predictor variables. I did not use circular statistics to assess track direction because the range of bearings was small, with all bearings oriented to the east and southeast (range = 90°-162°). A significant effect of departure date on initial flight direction may be explained by temporal changes in predominant wind direction throughout the breeding season, since wind drift can affect the flight paths of migratory birds (Wege and Raveling 1984, McLaren et al. 2012). Therefore, to assess temporal changes in wind direction at Churchill, I ran *a posteriori* circular-linear regression with daily direction of maximum wind gust as the circular response variable and Julian day of year as the linear predictor variable. I obtained daily wind data for the 'Churchill Climate' (58.7°N, 94.1°W) meteorological station from Environment and Climate Change Canada's historical weather database (ECCC 2021). I subset the wind data to exclude dates outside the range of departures present in the five-year dataset, which resulted in the inclusion of wind data from June 28 (earliest departure date) to August 21 (latest departure date) for each year.

Ground Speed

I estimated groundspeed (i.e., the speed of the bird relative to the ground) of each flight track by calculating the time between sequential receiving station detections divided by the track distance (Crewe et al. 2018). I considered ground speeds between 9 and 42 ms^{-1} to be representative of shorebird migratory flight and excluded tracks outside this range (Grönroos et al. 2012; Anderson et al. 2019). Low ground speeds (<9 ms^{-1}) may not represent true migratory flights, but rather undetected stops *en route* or a less direct route between receiving stations. High ground speeds (>42 ms^{-1}) often represent detections at two or more nearby receiving stations, some of which have overlapping ranges and may detect a single bird simultaneously (Crewe et al. 2018, Anderson et al. 2019).

To assess the effects of breeding constraints and departure timing on initial ground speeds during migration, I fit a general linear model with the ground speed of the initial flight track as the response variable and sex, nest fate, and departure date as predictors. I then fit a linear mixed-effects model assessing ground speeds of all recorded flight tracks to determine if the same predictors influenced all ground speeds. I included bird ID as a random factor to account for multiple tracks per individual. Each individual had 3 ± 0.2 tracks (median ± SE; *n* individuals = 72, *n* tracks = 367, range = 1-12).

Stopover Behaviour

I used summarized Motus detection data to determine the occurrence, location, and duration of stopovers in the southern array. For every bird detected at a given receiving station, I initially calculated length-of-stay as the time elapsed between the first detection and the last (i.e., time elapsed between sequential flight tracks).

However, most birds were detected simultaneously and/or making back and forth movements at two or more receiving stations with overlapping detection ranges, which resulted in short length-of-stays that were not biologically accurate. Back and forth detections may indicate a stopover, as birds often move between foraging and roosting sites within the greater stopover landscape (Placyk and Harrington 2004, Peters and Otis 2006). Therefore, to improve accuracy of lengths-of-stay estimates, I collapsed simultaneous and back and forth detections into single length-of-stay observations for groups of receiving stations with overlapping detection ranges. Two stations were considered to have overlapping detection ranges if the distance between them was ≤122.8 km (where both have SensorGnome receivers) or ≤184.4 km (where at least one has a Lotek receiver), as these are the maximum distances at which birds can be detected on two stations simultaneously (Anderson et al. 2019). For birds with simultaneous and/or back and forth detections, I classified birds as having made a stop if the length-of-stay was greater than the time it would take for a bird to fly across the maximum overlapping detection range of two receiving stations at a ground speed of 9 ms^{-1} (Anderson et al. 2019). Therefore, the stopover threshold was conservatively 4 h for stations with SensorGnome receivers and 9 h for stations with at least one Lotek receiver (see Anderson et al. 2019). For birds detected at a single receiving station, I classified birds as having made a stop if the length-of-stay was greater than the time it would take for a bird to fly across the maximum detection range of a single station. I defined the maximum detection distance of a single receiving station as 50% of the overlapping detection distance between two stations (Anderson et al. 2019), which equates to 61.4 km for SensorGnome receivers and 92.2 km for Lotek receivers. Therefore, the stopover threshold for these birds was 2 h for SensorGnome receivers and 4.5 h for Lotek receivers.

I assessed the effects of breeding constraints and departure timing on three aspects of stopover behaviour: whether an individual made a stop in the southern array ('stopover probability'), the location of the stopover, and the length-of-stay. I did not assess the number of stopovers per individual, as most migrants with stopovers were only detected making one stop (37/40; 93%). For all models, I included sex, nest fate and departure date as predictors. First, I investigated stopover probability using a generalized linear model with a binomial response variable (an individual stopped or did not stop). Second, I investigated stopover duration using a general linear model with length-of-stay as the response variable. I also performed *a posteriori* one-way ANOVA to examine whether stopover-length-of-stay varied among the three major stopover regions identified in this study. Third, I investigated stopover location using a general linear model with stopover latitude as the response variable. Latitude was selected as a proxy for stopover location because stopovers tended to be distributed latitudinally rather than longitudinally.

Statistical Analyses

I conducted mapping and statistical analyses using R 3.6.2 (R Core Team 2020). I ran models using the *aov* and *lm* function in the *stats* package (R Core Team 2020), *lmer* function in the *lme4* package (Bates et al. 2015), and *lm.circular* function in the *circular* package (Agostinelli and Lund 2017). I created figures using the *ggplot2* package (Wickham 2016) and created maps using the *ggmap* package (Kahle and Wickham 2013). For all models, reference levels for the sex and nest fate categories were female and pre-hatch failure, respectively. With the exception of the second departure model, I ran final models without interaction terms to preserve degrees of freedom given the small sample sizes and inclusion of multi-level categorical variables (Schielzeth 2010). With the exception of my model assessing the effect of sex, nest fate, and departure date on groundspeeds of all recorded flight tracks, I did not include a random effect of individual in my models. Similarly, I did not include a random effect of year in any model. Significance of parameter estimates were evaluated at $\alpha = 0.05$ (Bolker et al. 2009). I assessed model fit (normality and homoscedasticity of errors) using residual plots, and multicollinearity using the *vif* function in the *DAAG* package (Maindonald and Braun 2020). Summary statistics are reported as median ± SE unless otherwise noted.

Table 2.1. Sample sizes (*n*) of Semipalmated Plovers (*Charadrius semipalmatus)* fitted with VHF transmitters at a breeding site in Churchill, Manitoba, Canada, 2015-2019. Tagged (*n*) indicates the total number of tags deployed including those that were re-deployed after tag loss. Confirmed departure *(n)*, detected in southern array *(n),* and total stopovers *(n)* indicate the sample sizes used in subsequent analyses. Detected on stopover *(n)* indicates the number of birds recorded stopping in the southern array.

Year	Tags deployed (*n*)	Confirmed departure (*n*)	Detected in southern array (*n*)	Detected on stopover (*n*)	Total stopovers (*n*)
2015	15	7	7	5	6[1]
2016	29	9	8	3	4[1]
2017	31	12	12	8	8
2018	38	19	21	10	10
2019	56	25	36	14	15[1]
TOTAL	**169**	**72**	**84**	**40**	**43[1]**

[1] A total of three birds were detected making two stopovers.

Table 2.2. Sample sizes (*n*) of Semipalmated Plovers (*Charadrius semipalmatus)* fitted with VHF transmitters at a breeding site in Burntpoint Creek, Ontario, 2016-2019. Tagged (*n*) indicates the total number of tags deployed. Confirmed departure *(n)*, detected in southern array *(n),* and total stopovers *(n)* indicate the sample sizes used in subsequent analyses. Detected on stopover *(n)* indicates the number of birds recorded stopping in the southern array.

Year	Tags deployed *(n)*	Confirmed departure *(n)*	Detected in southern array *(n)*	Detected on stopover (*n*)	Total stopovers *(n)*
2015	0	0	0	0	0
2016	8	5	5	2	2
2017	2	0	0	0	0
2018	4	1	1	1	2[1]
2019	10	0	1	0	0
TOTAL	**24**	**6**	**7**	**3**	**4[1]**

[1] One bird was detected making two stopovers.

Figure 2.1. Map of the physiographic regions of Canada, including the Hudson Bay Lowlands region (yellow; center). Study sites are indicated by stars, with Churchill, Manitoba, Canada in blue and Burntpoint Creek, Ontario, Canada in orange. Map modified from (Acton et al. 2015; https://www.thecanadianencyclopedia.ca/en/article/physiographic-regions).

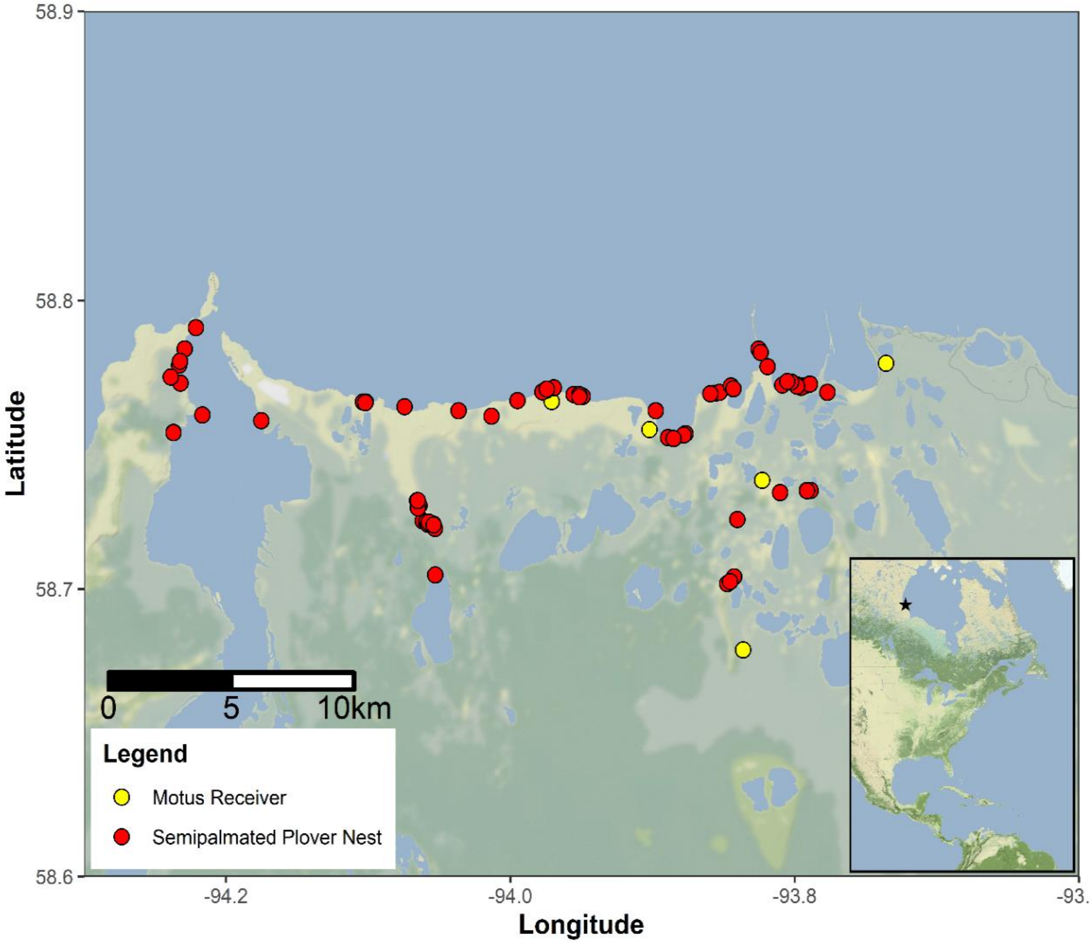

Figure 2.2. Map of the study area near Churchill, Manitoba, Canada. Yellow points indicate locations of Motus receiving stations and red points indicate locations of Semipalmated Plover *(Charadrius Semipalmatus)* nests and tagging locations, 2015-2019.

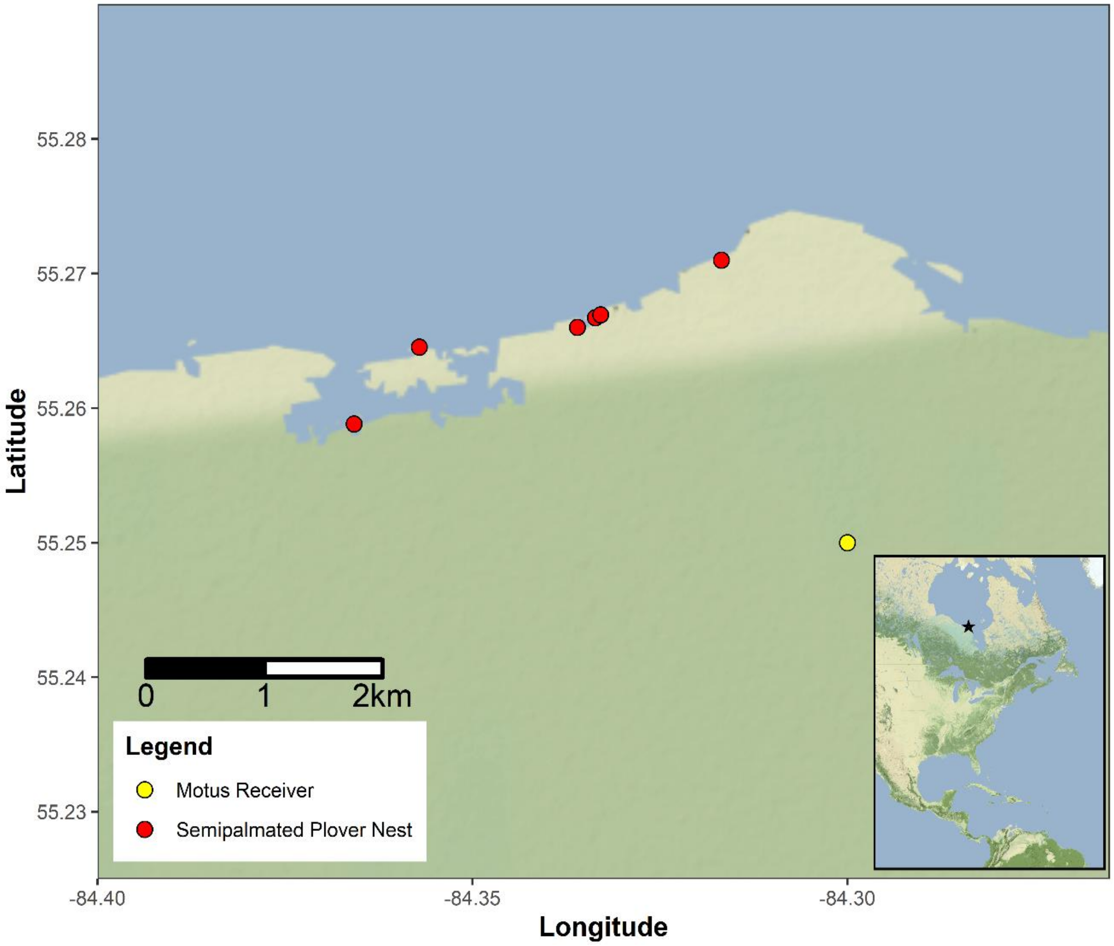

Figure 2.3. Map of the study area near Burntpoint Creek, Ontario, Canada. Yellow points indicate location of Motus receiving station and red points indicate locations of Semipalmated Plover *(Charadrius semipalmatus)* nests and tagging locations, 2016-2019.

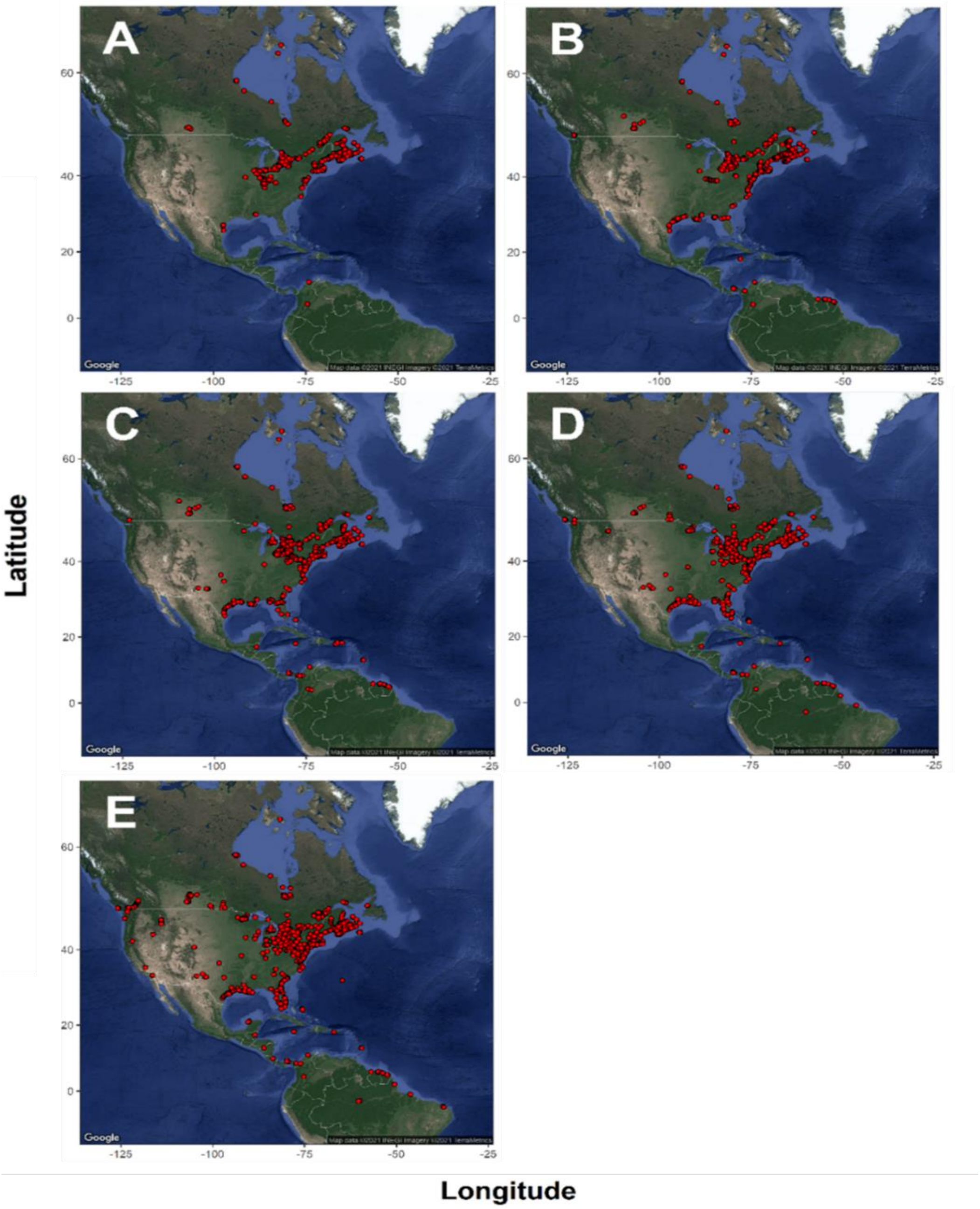

Figure 2.4 Extent of the Motus Wildlife Tracking System (www.motus.org) in North America, Central America, and northern South America **(A)** 2015 (*n* = 615); **(B)** 2016 (*n* = 717); **(C)** 2017 (*n* = 782); **(D)** 2018 (*n* = 742); **(E)** 2019 (*n* = 971). Red points indicate locations of receiving stations.

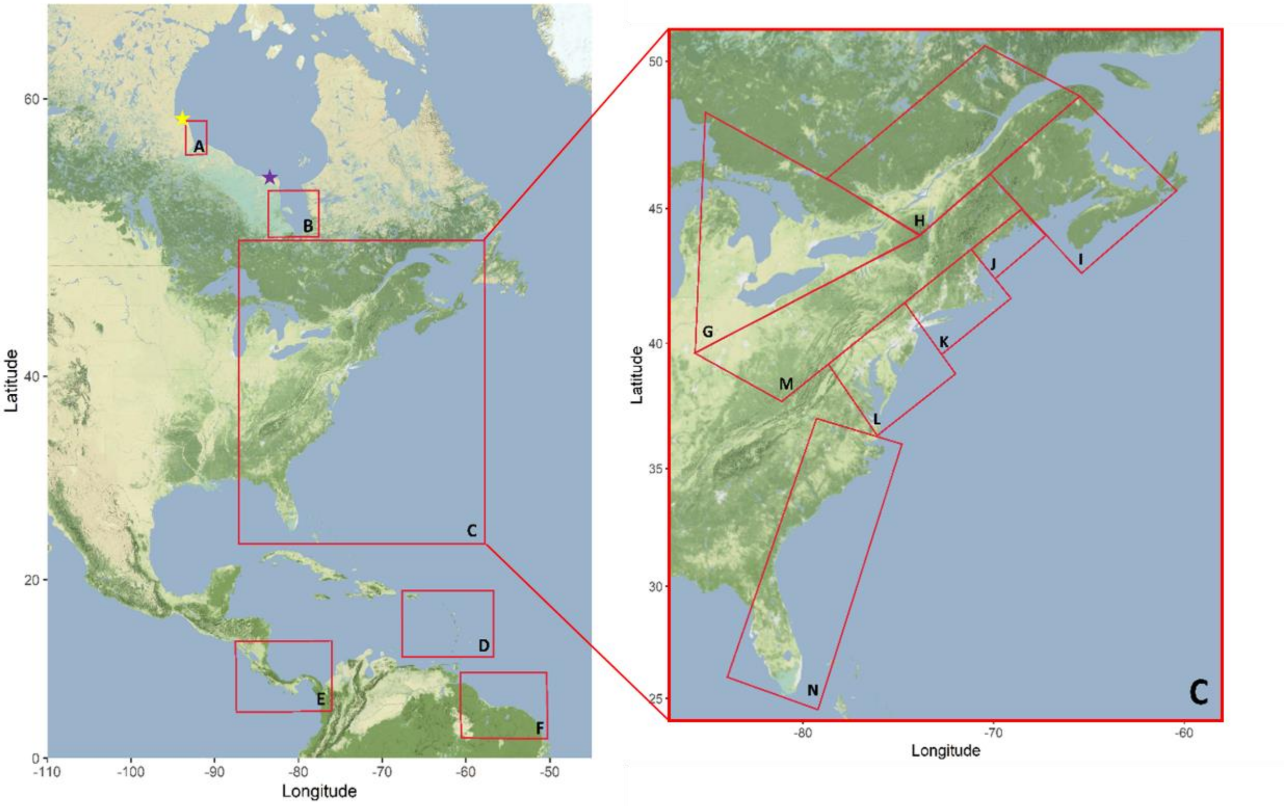

Figure 2.5. Delineations of general regions used by VHF-tagged Semipalmated Plovers on fall migration. Regions include **(A)** Canada – Southwestern Hudson Bay; **(B)** Canada – James Bay; **(C)** Eastern Canada and USA (includes regions G-N); **(D)** Caribbean; **(E)** Southern Central America; **(F)** northern South America; **(G)** Canada/USA – Great Lakes; **(H)** Canada – St. Lawrence River and Estuary**; (I)** Canada – Maritimes; **(J)** USA – Coastal Maine; **(K)** USA – Cape Cod/Long Island; **(L)** USA – Delmarva Peninsula/Jersey Shore; **(M)** Canada/USA – Northeast Interior **(N)** USA – South Atlantic Coast. Coloured stars indicate breeding site locations (yellow = Churchill, Manitoba; purple = Burntpoint, Ontario).

Chapter 3: Results

Departure from Breeding Site

Of the 169 tags deployed at Churchill, a total of 70 (41%) were detected departing the breeding array. Departure dates of Semipalmated Plovers from Churchill ranged from June 28-August 21, with a median date of July 26 ± 1.0 d (*n* = 70; Table 3.1, 3.2). Of the 24 tags deployed at Burntpoint Creek, a total of 6 (25%) were detected departing the breeding array. Departures from Burntpoint ranged from July 19-August 8, with a median date of July 26 ± 2.7 d (*n* = 6). My model examining the effects of sex, nest fate, and clutch initiation date on departure date found that all predictors were significant (Supplemental Table S1; general linear model, *F* = 10.6, *df* = 4 and 65, *P* <0.001). Females departed 8.5 d earlier than males (Figure 3.1; general linear model, males: β = 8.5, SE = 1.7, *t* = 5.1, *P* <0.001). Birds with pre-hatch failure departed 4.6 d earlier than birds with post-hatch failure and 6.7 d earlier than birds with fledging success (Figure 3.1; general linear model, post-hatch failure: β = 4.6, SE = 2.2, t = 2.1, *P* = <0.001; fledging success: β = 6.7, SE = 2.2, t = 3.0, *P* = <0.001). For each one-day increase in clutch initiation date, departure date was 0.4 d later (Figure 3.2; general linear model, β = 0.4, SE = 0.2, *t* = 2.7, *P* <0.01). My *a posteriori* model examining the effects of nest fate and year on clutch initiation date found that clutch initiation dates were not significantly different among years or birds of varying nest fates (Type-II Sum of Squares Two-way ANOVA, year: $F_{(4, 63)}$ = 1.4, *P* = 0.2; nest fate: $F_{(2, 63)}$ = 3.1, *P* = 0.06).

My model examining the interaction of breeding completion date and nest fate on departure date identified a significant interaction (Supplemental Table S2; general linear model, *F* = 16.2, *df* = 5 and 64, *P* < 0.001). The parameters for the interaction effect indicated a stronger influence of breeding completion date for birds with post-hatch failure (general linear model, post-hatch failure*breeding completion date: β = 0.9, SE = 0.2, *t* = 4.0, *P* <0.01) and fledging success (general linear model, fledging success*breeding completion date: β = 1.1, SE = 0.2, *t* = 5.2, *P* <0.01) than for those with pre-hatch failure (the reference category; Figure 3.3).

In summary, I found that sex, nest fate, and clutch initiation date significantly affected departure timing (Figure 3.1, 3.2; Supplemental Table S1). Among birds of varying nest fates, I observed relatively small, but significant differences in departure dates (Table 3.2) and no significant differences in clutch initiation dates. The relationship between breeding completion date and departure date was stronger for birds with post-hatch failure and fledging success than birds with pre-hatch failure (Figure 3.3; Supplemental Table S2).

Migration Routes

Of the 169 tags deployed at Churchill, a total of 84 (50%) were detected by at least one receiving station in the southern array. Of the birds with recorded departures (*n* = 70), 63 (90%) were subsequently detected in the southern array and seven (10%) had no detections after departure. After departure, all migrants detected in the southern array travelled southeast (Figure 3.4). Generally, birds either travelled along interior routes through the Canada/USA – Great Lakes region (‘Great Lakes’; 33/84; 39%), or coastal routes through the Canada – James Bay region (‘James Bay’; 11/84; 13%) and the Canada – St. Lawrence River and Estuary region (‘St. Lawrence Estuary’; 15/84; 18%). Although birds showed individual variability in migration route, most (71/84; 85%) were ultimately detected in three general locations along the mid-Atlantic coast of North America: 1) Canada – Maritimes (‘Maritimes’; 14/84; 16%); 2) USA – Cape Cod/Long Island region (‘Cape Cod’; 30/84; 36%); 3) USA – Delmarva Peninsula/Jersey Shore (‘Delmarva’; 39/84; 46%; Supplemental Table S3). Of the individuals using coastal routes, those travelling through the St. Lawrence Estuary were most often subsequently detected in the Maritimes (9/15; 60%), whereas those travelling through James Bay were most often detected in Cape Cod (7/11; 64%; Figure 3.4.). Individuals using interior routes were most often detected further south in Delmarva (24/39; 64%; Figure 3.4). Over half of birds detected in Cape Cod (16/30; 53%) were not detected anywhere between Manitoba and Cape Cod. Therefore, it is not clear whether these individuals took coastal or interior routes. Similarly, one male (ID: 33695) departed Churchill on an unknown date and was not subsequently detected until arriving near Jacksonville, Florida, USA on August 21, 2019.

Ten individuals were tracked beyond North America, including one male detected in Central America; one male detected in the Caribbean; and four females and four males detected in northern South America (Figure 3.5; Supplemental Table S3). The individual (ID: 24557) in Central America departed Churchill on August 4, 2017, and remained undetected until August 24, when it was detected in Panama for approximately 3 hr. The individual (ID: 24501) in the Caribbean departed Churchill on July 29, 2018, travelled through the Great Lakes to Delmarva, where it had an approximately 2-d stopover (August 3-4), and was subsequently detected in Barbados on August 28. The individuals in northern South America were detected on the coasts of Suriname and French Guyana (Figure 3.5). Prior to South America, four of these individuals were last detected in Delmarva and Cape Cod, and three were last detected in the Great Lakes and USA/Canada – Northeast Interior (‘Northeast Interior’). Only one bird (ID: 29275) was detected for longer than 1 hr in South America; this individual was detected for approximately 6 d. The median arrival date to South America was August 31 ± 3.9 d (*n* = 8, range = August 10-September 12).

Of the 24 tags deployed at Burntpoint Creek, a total of seven (29%) were detected by at least one receiving station in the southern array. After departure from the breeding area, all migrants travelled southeast (Figure 3.6). Individuals travelled to the mid-Atlantic coast (two females and three males), Northeast Interior (one male), and Maritimes (one male; Supplemental Table S4). All five birds that travelled to the mid-Atlantic coast were detected in Cape Cod. Of these, two were subsequently detected in the Delmarva Peninsula. No individuals from Burntpoint Creek were detected in the Great Lakes or James Bay regions. Additionally, none were tracked beyond North America.

Direction of Initial Flight Track

Bearings of initial flight tracks from Churchill ranged from 90°-162° (median = 140°, SE = 1.84°) where the maximum possible range was 90°-240°. My model examining the effects of sex, nest fate, and departure date on the direction of initial flight track found that later-departing individuals had bearings oriented in more southerly directions (Figure 3.7). For each one-day increase in departure date, there was a 0.6° increase in bearing of initial flight track (general linear model, $\beta = 0.6$, SE = 0.3, $t = 2.2$, $P < 0.05$). Bearing did not differ by sex (Figure 3.8) or nest fate (Supplemental Table S5). Daily maximum wind gust direction at Churchill did not change significantly over the course of the breeding season (circular-linear regression, $\beta = 1.1$, SE = 0.9, t = 1.2, $P = 0.12$).

Ground Speed

Fifty-one percent of initial flight tracks (41/81) and 24% of all flight tracks (88/367) had ground speeds <9 ms^{-1} and were excluded from analyses. Two percent of initial flight tracks (2/81) and 11% of all flight tracks (88/367) had ground speeds >42 ms^{-1} and were also excluded. With the exclusion of these tracks, the median ground speed of initial migratory flights from Churchill was 18.1 ± 1.0 m s^{-1} (range = 9.6-31.5, $n = 38$). My model examining the effects of sex, nest fate, and departure date on the ground speed of initial flight track found that none of the predictors in the model explained initial ground speed (Supplemental Table S6; general linear model, $F = 0.2$, df = 5 and 33, $P = 0.9$). The median ground speed of all migratory flights from Churchill was 17.3 ± 0.5 ms^{-1} (range = 9.4-41.9). My model examining the effects of sex, nest fate, and departure date on the ground speed of all migratory flights found that ground speed was faster for birds departing breeding sites later (linear-mixed effects model, $\beta = 0.2$, SE = 0.1, $P < 0.05$). None of the other predictors explained ground speed (Supplemental Table S7). While ground speeds varied widely across the dataset, after accounting for effects of departure date, this variation was not attributable to consistent differences among individuals, as Bird ID accounted for only 2% of the variation in ground speed (linear mixed-effects model, Bird ID: variance = 1.38, SD = 1.2; Residual: variance = 52.1, SD = 7.2).

Most (7/8; 88%) birds detected in northern South America had low ground speeds (< 9 ms^{-1}) between their last detection in North America and their first in South America (all South American migrants: $n = 8$, median = 2, range = 1.2-10.2). One individual (ID: 24537), however, appeared to undertake a non-stop migratory flight from Cape Cod to South America at a ground speed of 10.2 ms^{-1}. The flight occurred immediately following a 20-d stopover in Cape Cod (Supplemental Table S3, S8).

Stopover Behaviour

Of migrants from Churchill, forty-eight percent (40/84) of birds detected in the southern array stopped in North America at least once (Figure 3.9; Supplemental Table S8). Of these, three stopped twice. The majority (38/43; 88%) of stopovers occurred on the mid-Atlantic coast between the Bay of Fundy and Chesapeake Bay. Stopovers were concentrated in three general regions: the Maritimes ($n = 6$), Cape Cod ($n = 12$), and

Delmarva (*n* = 20; Figure 3.9; Supplemental Table S8). The median stopover length-of-stay was 11.7 ± 1.2 d in the Maritimes (range = 1.6-18.6), 10.2 ± 1.6 d in Cape Cod (range = 0.4-25.4), 11.8 ± 1.3 d in Delmarva (range = 0.2-21.4). Stopover length-of-stay did not vary significantly among these three regions (one-way ANOVA, $F_{2,35} = 0.0$, $P = 0.97$). In the Maritimes, five birds stopped in the interior Bay of Fundy, and one stopped in southwestern Nova Scotia (Figure 3.9). In the Cape Cod region, stopovers included two birds detected near Plum Island, Massachusetts; three birds near Great Bay Estuary, Massachusetts; one in Cape Cod, Massachusetts; three in coastal Rhode Island; and three on Long Island, New York (Figure 3.9). In the Delmarva Peninsula region, stopovers included three birds detected near Long Beach Island, New Jersey; four near Cape May, New Jersey; five near Delaware Bay, New Jersey and Delaware; three near Assateague Island, Maryland; and five near the mouth of Chesapeake Bay at Cape Charles, Virginia (Figure 3.9).

An additional five stopovers were recorded in North America, including four northwest of the Bay of Fundy, and one southwest of Chesapeake Bay. Two birds (IDs: 33713 and 34739), both females with early departure dates from the Churchill region, stopped in Wapusk National Park, Manitoba immediately after departure (i.e., same day). The first female left the breeding area on July 6, 2019, and stopped for 10.9 d, whereas the second left on July 9, 2019, and stopped for 0.4 d. The other stopovers included a 0.5 d stop by a female in James Bay (ID: 24552); a 0.4 d stop by a female (ID: 29286) in the St. Lawrence Estuary; and a 19.7 d stop in northeastern Florida, USA.

The most southern stopover was a male (ID: 29275) detected making a 6.2 d stop in northern South America. This individual departed the breeding area on August 2, 2019, was detected briefly in Cape Cod on August 8, and arrived in French Guiana on September 9. Due to the significant temporal gap (32 d) between departure from North America and arrival to South America, it is likely this individual stopped before arrival to French Guiana. Therefore, this observation represented a statistical outlier and was removed from models evaluating drivers of stopover latitude and length-of-stay.

Three individuals were observed making multiple stopovers. A female (ID: 33713) made a 10.8 d stop at Wapusk National Park immediately after leaving the breeding area on July 6, 2019, then arrived in Delmarva for 8.3 d beginning on July 24. A male (ID: 14648) with an unknown departure date made two stopovers in the Cape Cod region, including a 1.7 d stop near Plum Island, Massachusetts on August 3, 2015, followed by a 21.5-d stop near Aquidneck Island, Rhode Island beginning on August 5. Another male (ID: 20823) with an unknown departure date made a 1.0 d stop in Cape Cod beginning on August 6, 2016, followed by a 12.3 d stop in Delmarva on August 9.

Of migrants from Burntpoint Creek, a total of four stopovers were recorded from three males (Supplemental Table S9). Two birds (IDs: 19126 and 19127) stopped once in Cape Cod and one (ID: 28834) stopped twice in Delmarva. The birds in Cape Cod stopped 2.9 d and 1.4 d after departure from Burntpoint Creek on August 1 and July 26, 2016, respectively. The first stopover in Delmarva commenced 2 d after the bird’s departure on August 6. Stopover length ranged from 11-19 d (*n* = 4, median = 16.7, SE = 1.5).

Birds with unknown nest fates were omitted from analyses, including three individuals from the stopover probability model and a single individual from the stopover length-of-stay and latitude models. My model examining the effects of sex, nest fate, and departure date on stopover probability found that individuals departing Churchill later were less likely to make a stop than those departing earlier (Figure 3.10; general linear model, β = -0.1, $z = -2.2$, SE = 0.0, $P < 0.05$). For every one unit increase in departure date, there was an 10% decrease in the odds that an individual made a stop (odds ratio [OR] = 0.9, 95% confidence interval [CI] = 0.8-0.98). Neither nest fate nor sex influenced stopover probability (Supplemental Table S10). My model examining the effects of sex, nest fate, and departure date on stopover length found that males stopped for 8.9 d longer than females (Figure 3.11; general linear model, males: β = 8.9, SE = 3.6, t = 2.5, $p < 0.05$). Median stopover length was 16.9 ± 1.9 d for males (range: 0.2-25.4, *n* = 22) and 2.5 ± 1.64 d for females (range: 0.2-21.3, *n* = 22). Neither nest fate nor departure date influenced stopover length (Supplemental Table S11). My model examining the effects of sex, nest fate, and departure date on stopover latitude found that individuals departing later stopped at lower latitudes; for every one-day increase in departure date, stopover latitude decreased by 0.5 ° (general linear model, β =-0.5, SE = 0.2, t = -3.08, $P < 0.01$; Figure 3.12). Neither nest fate nor sex influenced stopover latitude (Supplemental Table S12).

Table 3.1. Summary statistics of migratory departure dates for female and male Semipalmated Plovers (*Charadrius semipalmatus*) breeding near Churchill, Manitoba, Canada, 2015-2019. *n* = number of individuals. Standard error (SE) and range shown in d. Data are combined across nest fate categories (pre-hatch failure, post-hatch failure, and fledging success).

Sex	*n*	Median ± SE	Minimum	Maximum	Range
Female	40	July 23 ± 1.2 d	June 28	August 6	39 d
Male	30	August 1 ± 1.3 d	July 21	August 21	31 d

Table 3.2. Summary statistics of migratory departure dates by nest fate of Semipalmated Plovers (*Charadrius semipalmatus)* breeding near Churchill, Manitoba, Canada, 2015-2019. *n* = number of individuals. Standard error (SE) and range shown in d. Data are combined across sexes.

Nest fate	*n*	Median ± SE	Minimum	Maximum	Range
Pre-hatch failure	16	July 22 ± 2.5	June 28	August 6	39
Post-hatch failure	25	July 26 ± 1.2	July 10	August 21	42
Fledging success	29	July 30 ± 1.8	July 16	August 8	23

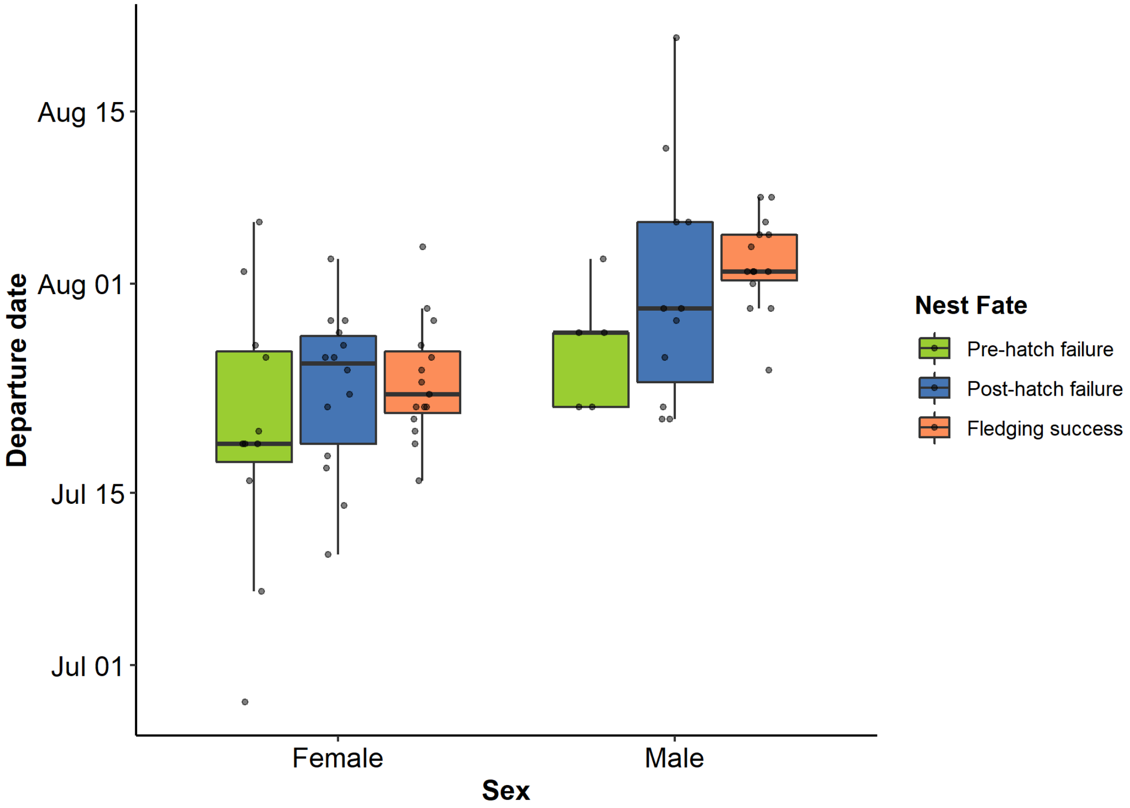

Figure 3.1. Sex and nest fate influence estimated departure dates of Semipalmated Plovers *(Charadrius semipalmatus)* breeding near Churchill, Manitoba, Canada, 2015-2019 (*n* = 70). Data are separated by sex and nest fate (pre-hatch failure = green; post-hatch failure = blue, fledging success = orange). Raw data were used to construct boxplot and are indicated by black points. Boxes indicate 50% CI, whiskers indicate 95% CI, and central lines indicate medians.

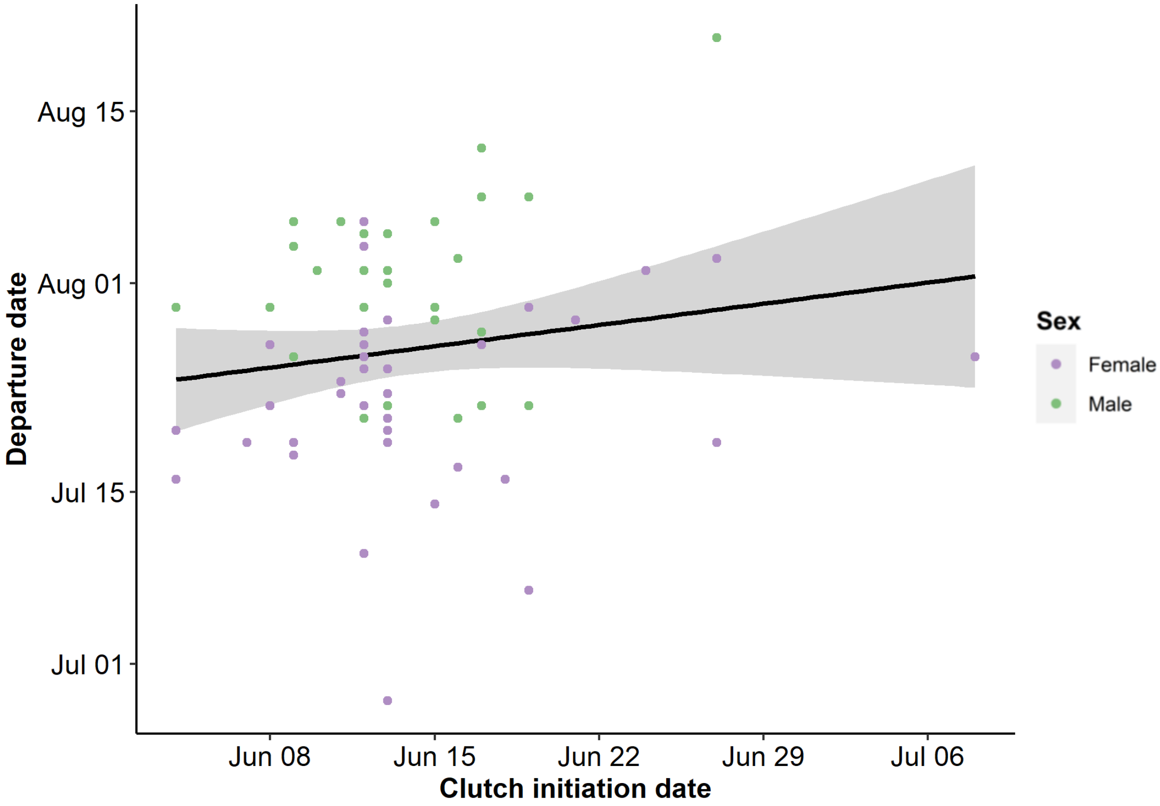

Figure 3.2. The timing of clutch initiation affects departure timing from the breeding site. Relationship between clutch initiation dates and estimated departure dates of Semipalmated Plovers *(Charadrius semipalmatus)* breeding near Churchill, Manitoba, Canada, 2015-2019 (*n* = 70). Raw data are plotted as points (females = purple; males = green). Model predicted slope and 95% confidence interval are indicated by black line and shaded area, respectively.

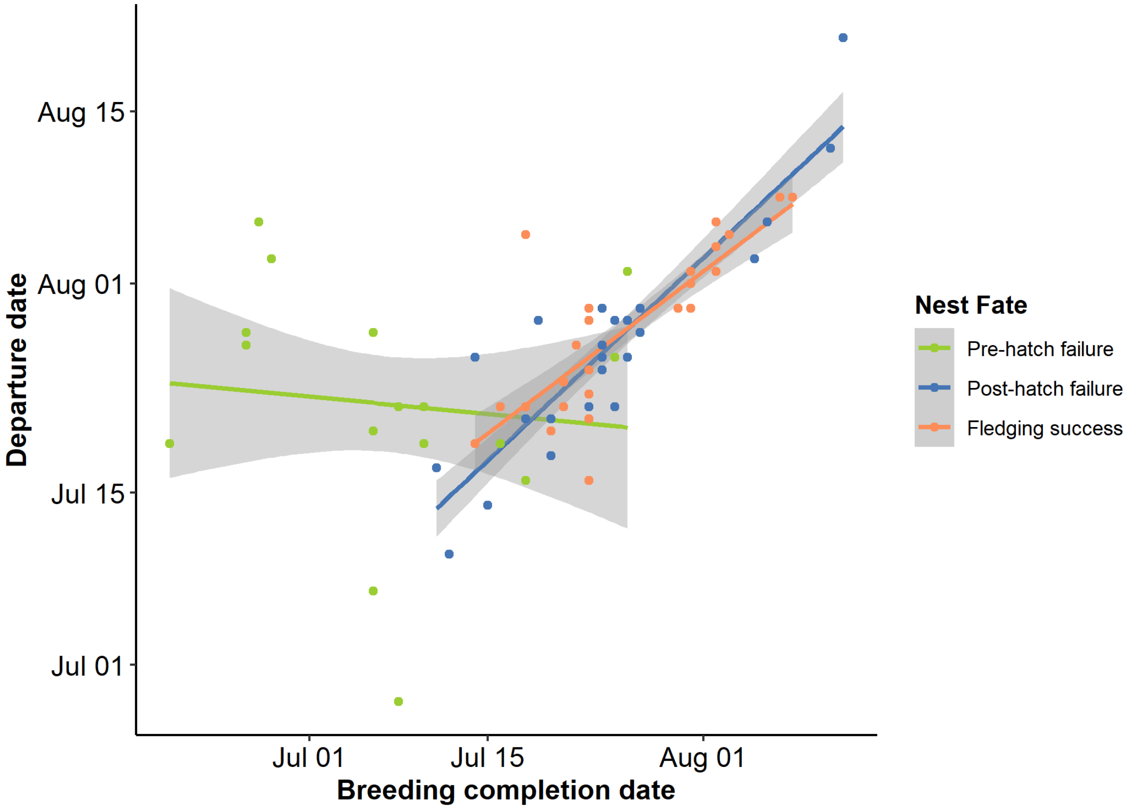

Figure 3.3. The effects of estimated breeding completion date on estimated departure dates are dependent on nest fate. Interaction of estimated breeding completion date and nest fate on estimated departure dates of Semipalmated Plovers *(Charadrius semipalmatus)* breeding near Churchill, Manitoba, Canada, 2015-2019 (*n* = 70). Raw data are indicated by points (pre-hatch failure =green; post-hatch failure = blue, fledging success = orange). Model predicted slopes and 95% confidence intervals are indicated as coloured lines and shaded areas, respectively.

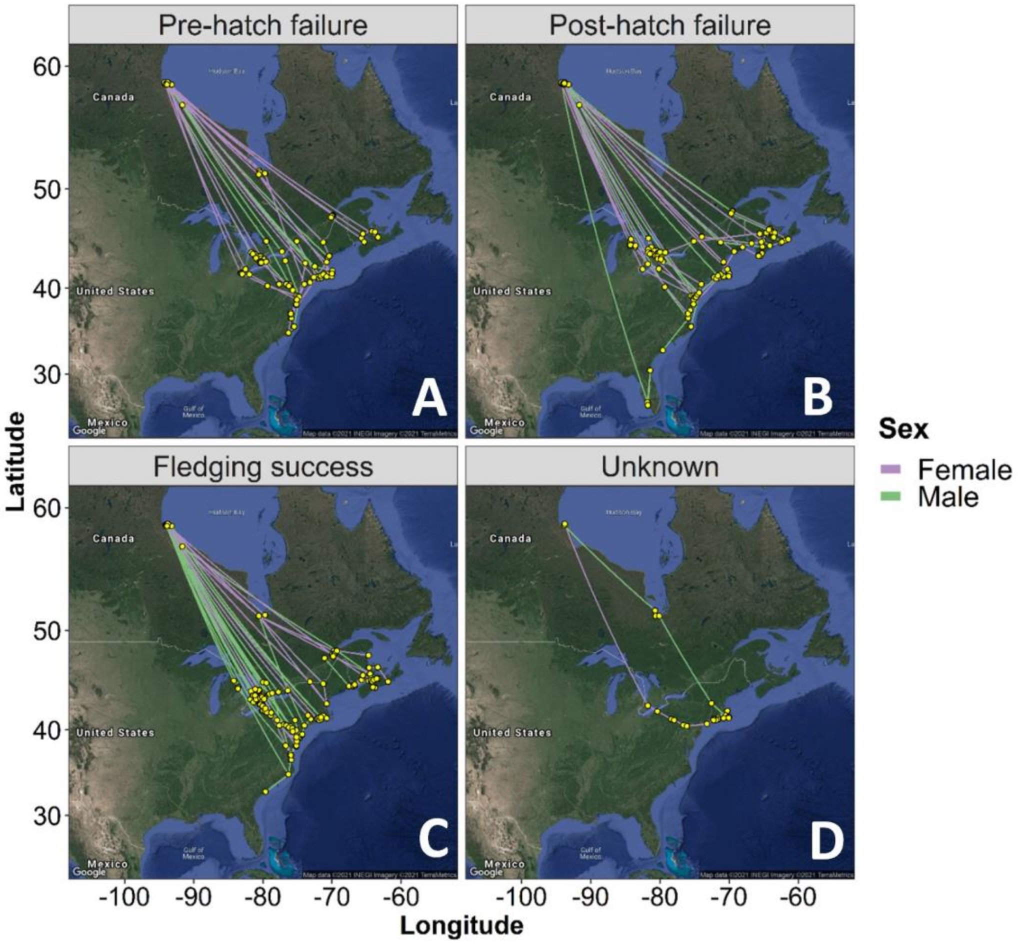

Figure 3.4. Estimated migration routes of Semipalmated Plovers *(Charadrius semipalmatus)* departing from Churchill, Manitoba, Canada, 2015-2019 (*n* = 74). **(A)** Birds with pre-hatch failure (*n* = 20); **(B)** Birds with post-hatch failure (*n* = 23); **(C)** Birds with fledging success (*n* = 29); **(D)** Birds with unknown nest fates (*n* = 2). Data obtained via the Motus Wildlife Tracking System (www.motus.org). Birds tracked beyond North America are omitted from figure (see Figure 3.5). Lines represent the great circle routes between receving stations (females = purple; males = green). Yellow points indicate locations of Motus receiving stations where migrants were detected. Motus stations without detections not shown (see Figure 2.4 for all station locations).

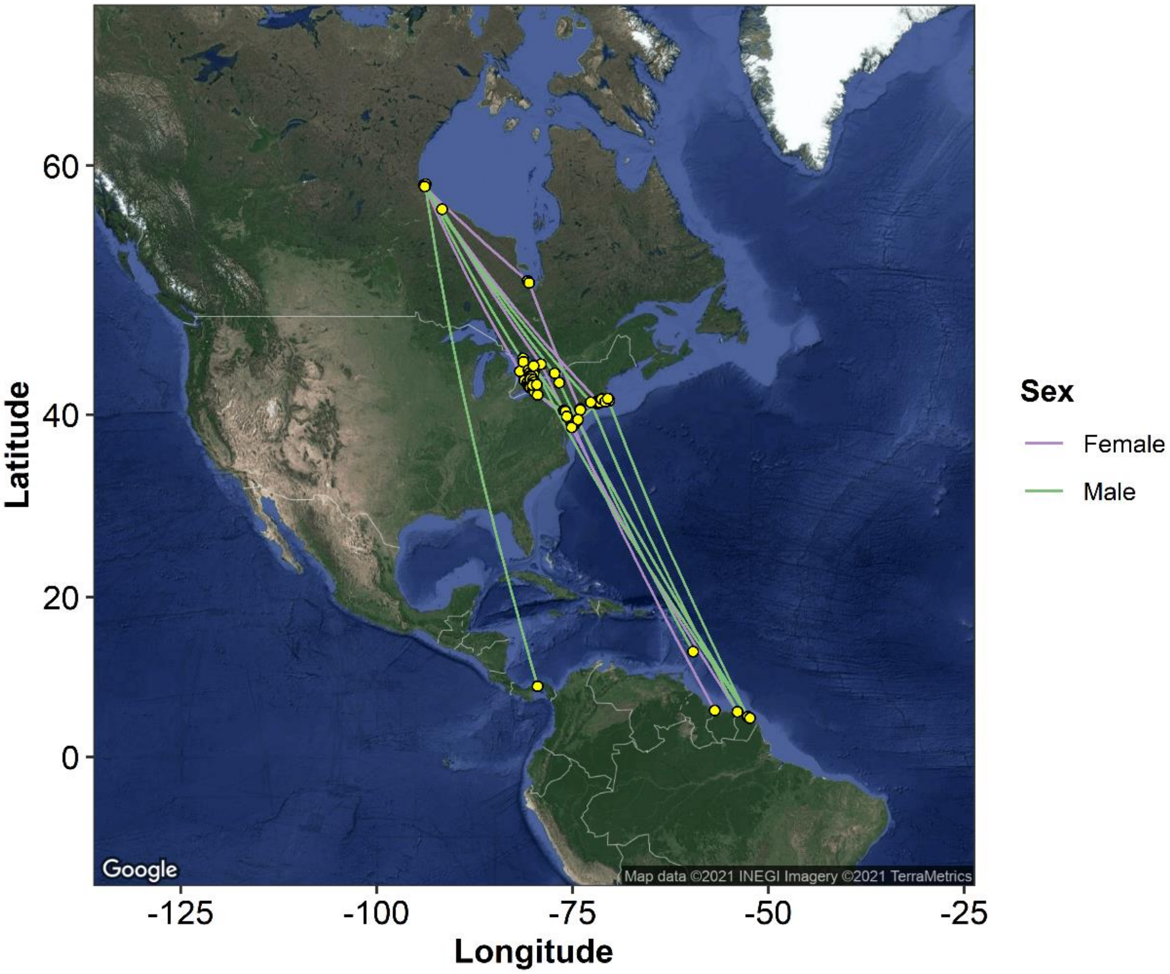

Figure 3.5. Estimated migration routes of Semipalmated Plovers *(Charadrius semipalmatus)* tracked beyond North America and departing from Churchill, Manitoba, Canada, 2015-2019 (*n* = 10). Data obtained via the Motus Wildlife Tracking System (www.motus.org). Lines represent the great circle routes between receving stations (females = purple; males = green). Yellow points indicate locations of Motus receiving stations where migrants were detected. Motus stations without detections not shown (see Figure 2.4 for all station locations).

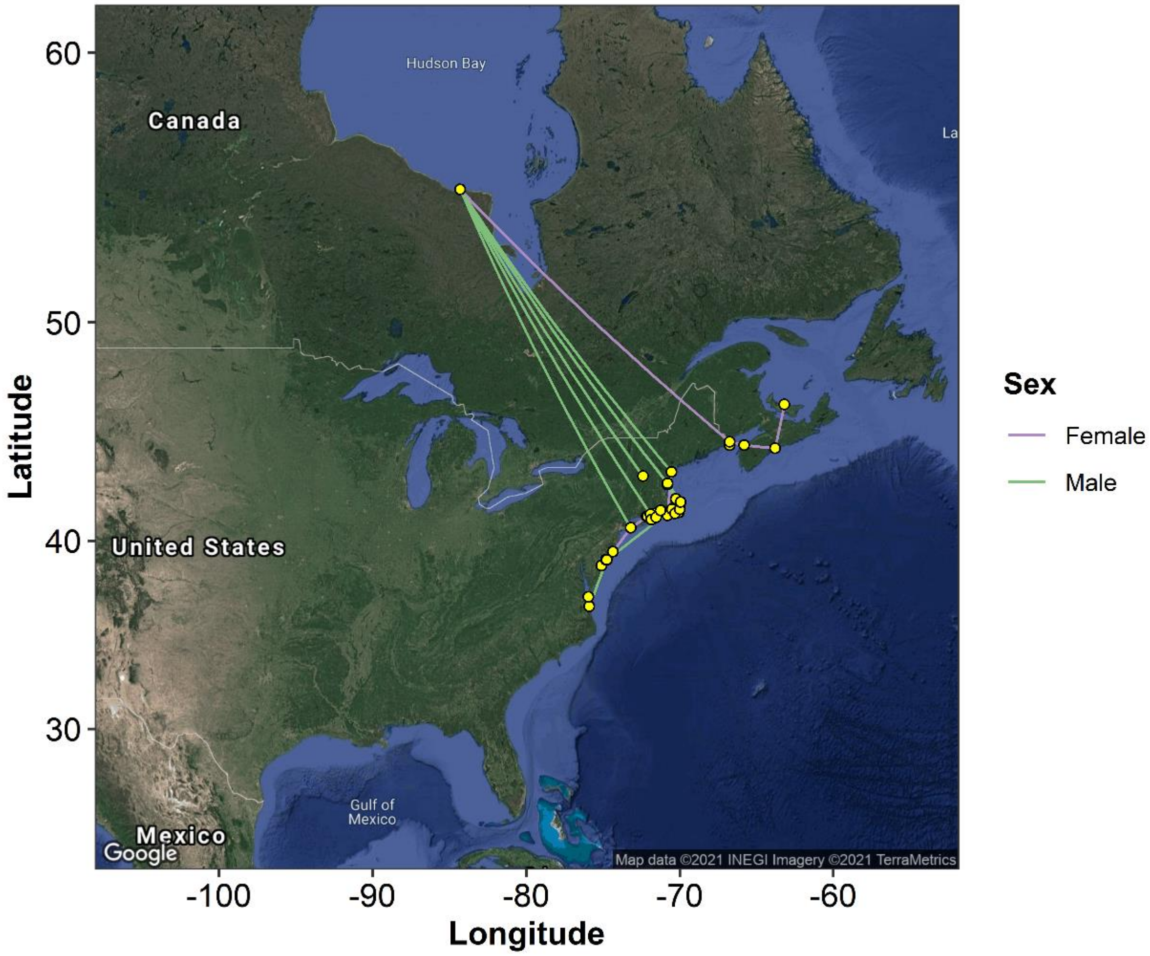

Figure 3.6. Estimated migration routes of Semipalmated Plovers *(Charadrius semipalmatus)* departing from Burntpoint Creek, Ontario, Canada, 2016-2019 (*n* = 7). Data obtained via the Motus Wildlife Tracking System (www.motus.org). Lines represent the great circle routes between receving stations (females = purple; males = green). Yellow points indicate locations of Motus receiving stations where migrants were detected. Motus stations without detections not shown (see Figure 2.4 for all station locations).

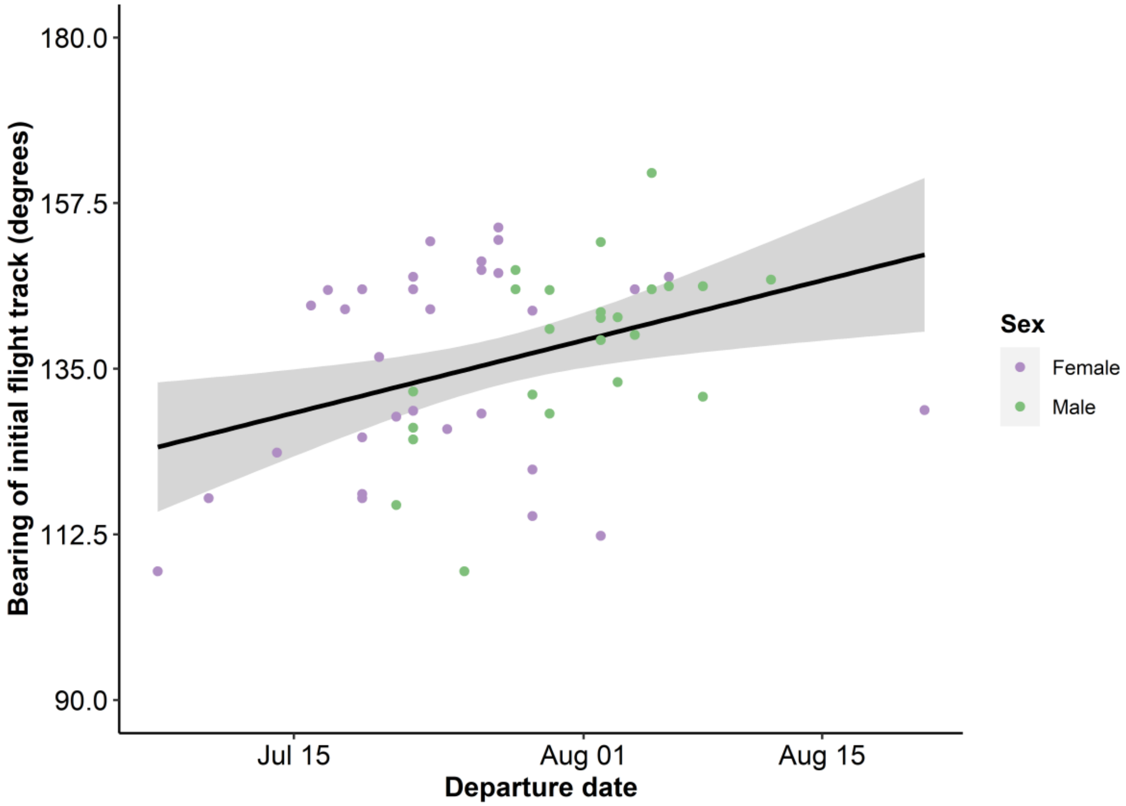

Figure 3.7. Migrants with later estimated departure dates have bearings oriented in more southernly directions. Relationship between estimated departure dates (Julian day of year) and bearing of initial flight track (degrees) of Semipalmated Plovers *(Charadrius semipalmatus)* departing from Churchill, Manitoba, Canada, 2015-2019 (*n* = 61). Raw data are indicated as points (females = purple, males = green). Y-axis ranges from easterly (bearing = 90.0°) to southernly (bearing = 180°) directions. Model predicted slope and 95% confidence interval are indicated by black line and shaded area, respectively.

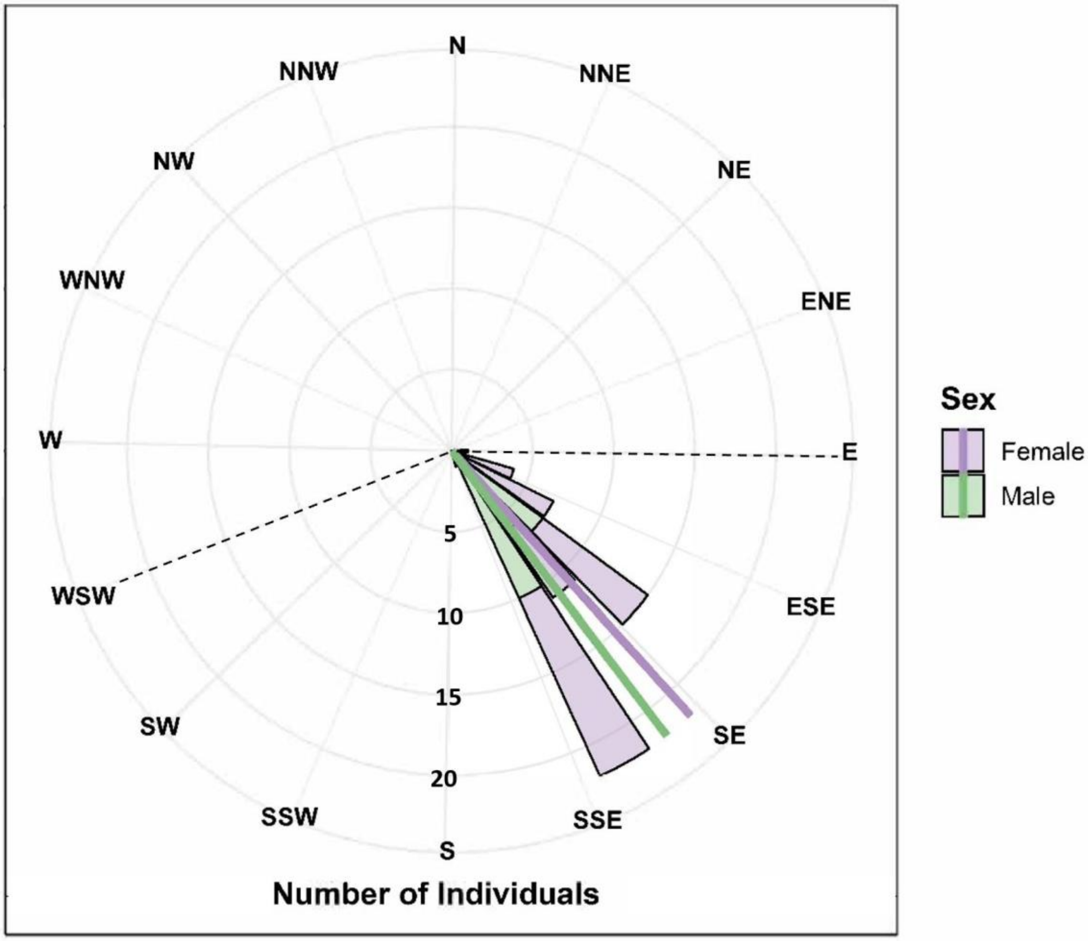

Figure 3.8. Males and females do not differ in initial migratory direction. Estimated cardinal bearings of first flight track of Semipalmated Plovers *(Charadrius semipalmatus)* departing from Churchill, Manitoba, 2015-2019 (*n* = 61). Concentric circles indicate the number of individuals travelling in each direction. Data are coloured by sex (females = purple; males = green). Median bearings for each sex are indicated as coloured lines. Dashed line indicates the potential range of cardinal bearings based on Motus receiving station locations (potential range = E-WSW).

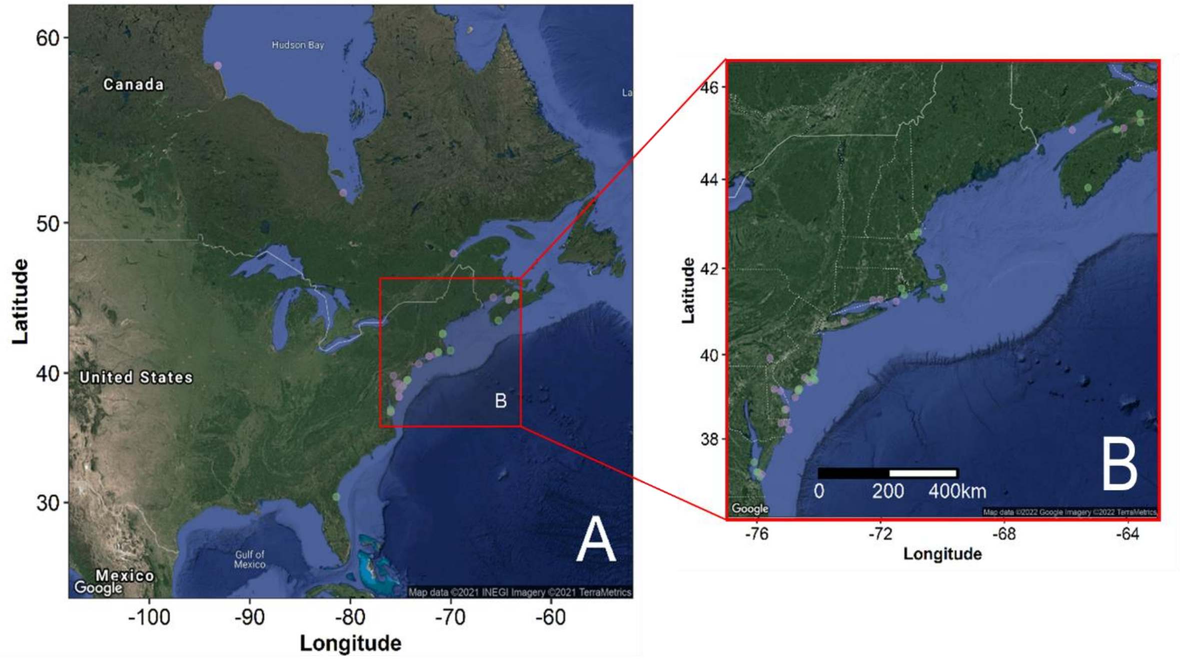

Figure 3.9. Fall stopover locations of Semipalmated Plovers *(Charadrius semipalmatus)* originating from Churchill, Manitoba, Canada, 2015-2019 (*n* = 43). Sex is indicated by circle colour (females = purple, *n* = 22; males = green, *n* = 21). **(A)** All stopover locations in North America; **(B)** Cluster of stopover locations on the mid-Atlantic coast of Canada and United States of America.

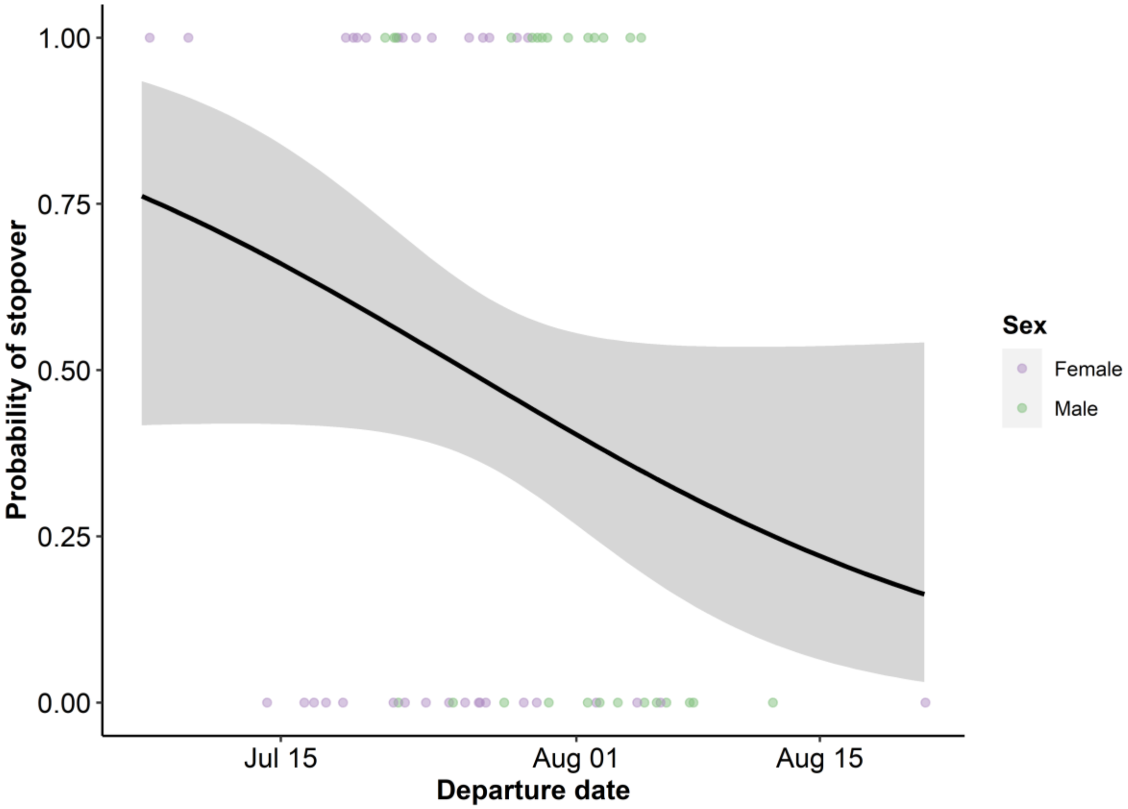

Figure 3.10. Migrants with later departure dates are less likely to stopover on fall migration. Model predicted fall stopover probability and departure dates of Semipalmated Plovers *(Charadrius semipalmatus)* originating from Churchill, Manitoba, Canada, 2015-2019 (*n* = 61). Raw data are indicated as points (females = purple; males = green). Shaded areas indicate 95% CI.

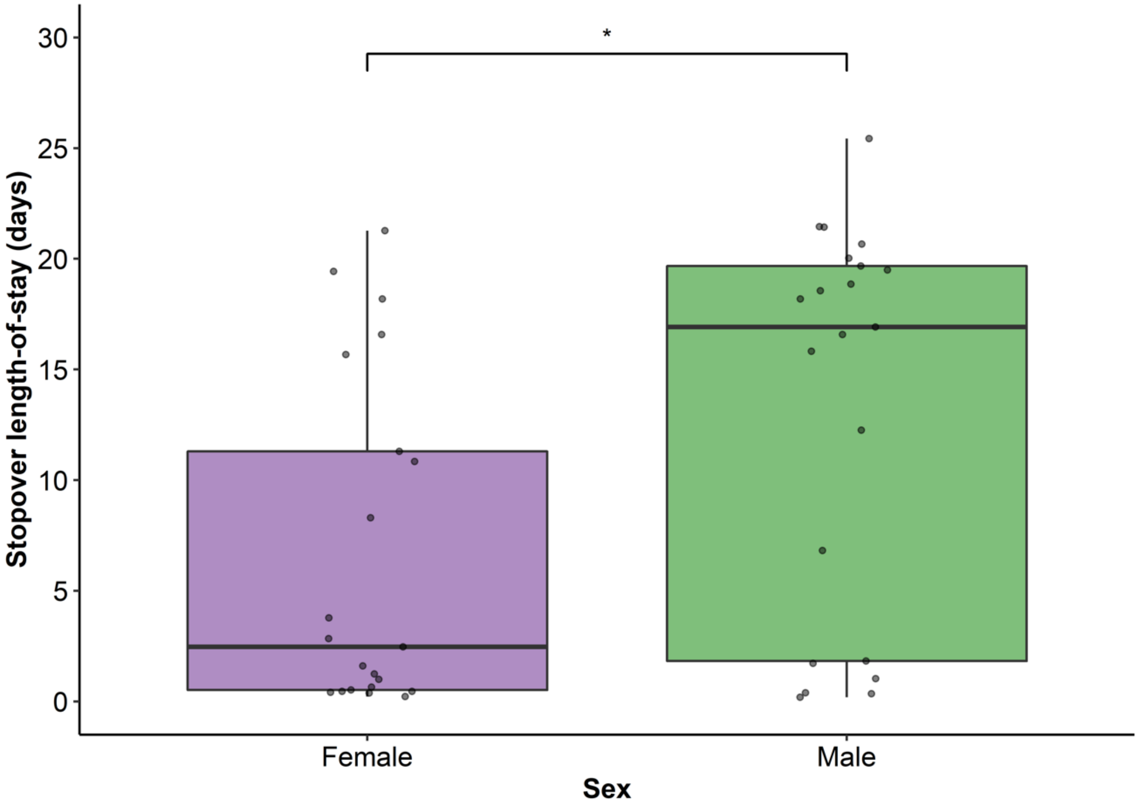

Figure 3.11. Males had longer stopovers than females. Stopover length-of-stay (LOS; d) of male (green) and female (purple) Semipalmated Plovers *(Charadrius semipalmatus)* during fall migration, 2015-2019 (*n* = 43). Raw data were used to construct boxplots. Boxes indicate 50% CI, whiskers indicate 95% CI, and central lines indicate medians. Significant difference is indicated with * ($\alpha = 0.05$).

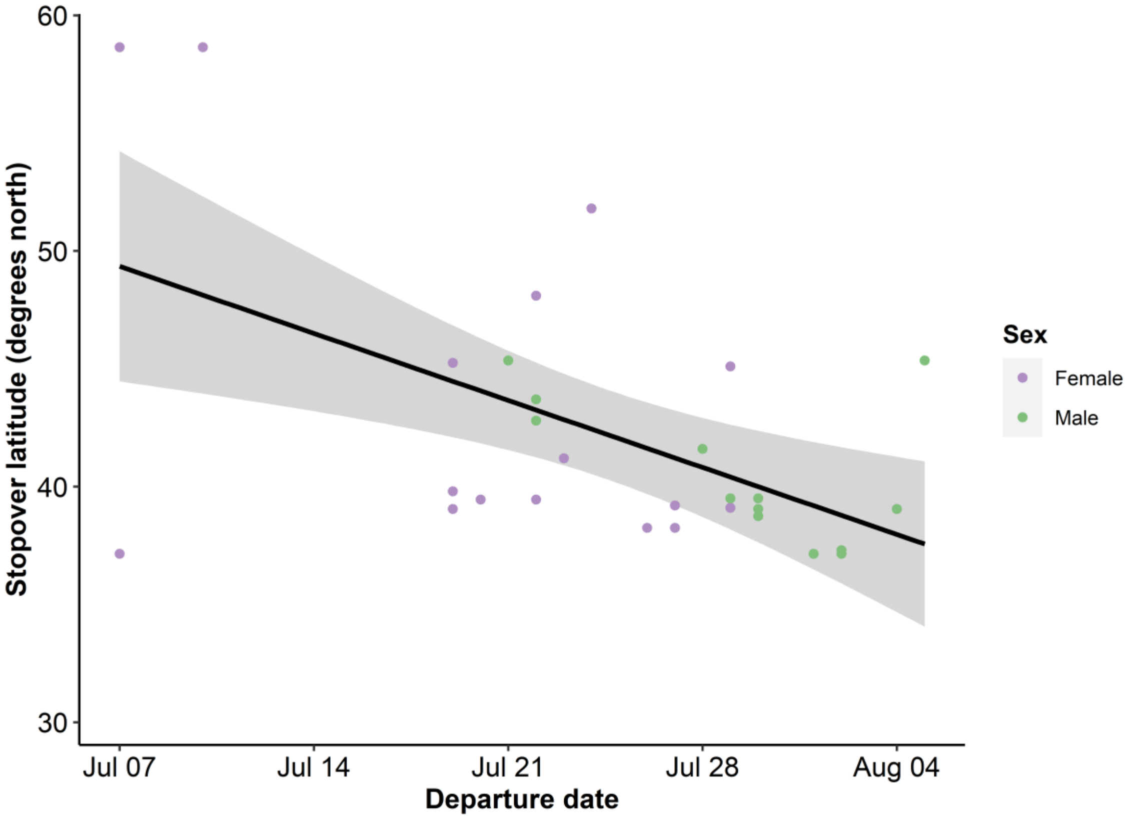

Figure 3.12. Migrants with later departure dates stopover at lower latitudes. Stopover latitude (degrees north) and estimated departure dates of Semipalmated Plovers *(Charadrius semipalmatus)* departing from Churchill, Manitoba, Canada, 2015-2019 (*n* = 29). Raw data are coloured by sex (females = purple; males = green). Model predicted slope and 95% CI (both sexes) are indicated as black line and shaded area, respectively.

Chapter 4: Discussion

My study is one of the first to track the fall migration of a small shorebird from subarctic breeding sites using the Motus Wildlife Tracking System. Semipalmated Plovers showed inter- and intrapopulation variation in migration behaviour, with individuals travelling on varying schedules and using diffuse migration routes and stopover locations within their migratory range. Birds followed both interior and coastal routes and congregated in three major stopover regions along the mid-Atlantic coast of North America. My results demonstrate that breeding constraints (nest success, clutch initiation date, and sex which determines level of parental care) influence departure timing from the breeding site, but do not affect most subsequent aspects of migration behaviour. I found that later-departing birds had initial flight tracks oriented more towards the south, faster overall ground speeds, were less likely to stopover in North America, and stopped at lower latitudes. These results suggest that later-departing individuals use aspects of a time-minimizing strategy on fall migration. However, departure date did not influence initial ground speed or stopover length-of-stay. My findings emphasize the importance of the mid-Atlantic coast for Semipalmated Plovers and the need for broad-scale conservation initiatives that consider inter- and intrapopulation variation in migration behaviour.

Departure Timing

I successfully monitored the departure of 70 Semipalmated Plovers breeding near Churchill and six near Burntpoint Creek. Individuals from both populations departed predominantly between mid-July and early-August, with little variation among years. As predicted, my results suggest that parental constraints are a major driver of departure timing for fall migration. Birds that initiated clutches earlier departed earlier, suggesting that the timing of breeding activities has downstream effects on the timing of fall migration. Although several studies have investigated the relationship between arrival timing to the breeding site and clutch initiation (Babcock et al. 2002, Meltofte et al. 2007, Smith et al. 2010, Grabowski et al. 2013), my study is one of the first to directly link clutch initiation to departure timing (but see Thorup et al. 2007). There are several environmental conditions that limit the timing of clutch initiation at subarctic breeding sites, including timing of snow melt (Babcock et al. 2002, Grabowski et al. 2013), presence of predators (Smith et al. 2010), and availability of invertebrates (Meltofte et al. 2007). Though not directly assessed in this study, my results suggest that environmental conditions upon arrival to the breeding site may have an indirect influence on departure dates through effects on clutch initiation timing. Interactions between early environmental conditions at breeding sites and subsequent migratory behaviour is an interesting avenue for future research.

My results also indicate that departure timing is sex-specific, with females departing earlier than males. Autumn protogyny, the earlier migration of females (Mills 2005), has been described for several shorebird species with male-biased parental investment in brood rearing, though the mechanisms underlying this pattern are unclear (Butler and Kaiser 1995, Ydenberg et al. 2005, Meissner and Krupa 2017, Weithman et al. 2017). In addition to undertaking chick defense in the absence of females, males may remain with the brood longer to defend breeding territories, thereby increasing the probability of territory retention in the subsequent breeding season (Ydenberg et al. 2005, Bai and Schmidt 2012). Alternatively, females may be in a lower post-breeding state than males, and therefore must abandon the brood early to ensure they have adequate time to prepare for migration. However, our observed difference in departure dates between sexes does not support this explanation. Females departed breeding areas ~8 d before males, which is approximately equal to the number of days males typically remain with chicks following brood abandonment by females (~7 d; Nol and Blanken 2014). Though not directly tested, this suggests that both sexes have pre-migration periods of similar duration, and therefore may be in similar post-breeding energetic states. It is possible that within the breeding season, the cost of extended brood rearing and territory defense in males is approximately equal to the cost of egg production in females, such that overall energy costs are approximately equal between sexes. However, empirical data on the relative costs of egg formation, territory defence, and parental care by shorebirds is necessary to test this hypothesis. Regardless of the mechanism, my study confirms that sex is a major driver of departure timing in this population.

Lastly, my results indicate that nest success is a predictor of departure date, with birds experiencing pre-hatch failure departing earliest, post-hatch failure departing at intermediate dates, and fledging success departing latest. Though statistically significant, the median difference in departure dates among birds with pre-hatch failure and fledging success was only 8 d, despite the latter being constrained by parental duties (i.e., chick rearing) for at least 18 d longer than the former. The small differences in departure dates among birds with varying nest fates could be explained by differences in clutch initiation dates, if birds who successfully fledged young initiated nests earlier than birds with pre- or post-hatch failure. For instance, a male that initiates its nest earlier and rears young for at least 18 d may only depart a few days later than another male that initiates later and does not rear chicks to 18 d (i.e., has breeding failure). However, my model assessing differences in clutch initiation dates among birds of varying nest fates does not fully support this explanation. Although birds with fledging success did initiate nests earlier than those with pre- or post-hatch failure, the difference was small (~4 d) and not significant. However, the *P* value for differences in nest initiation between birds with fledging success and pre-hatch failure was approaching significance ($P = 0.06$), suggesting that variation in clutch initiation date may have some small effect on nest fate and in turn, departure timing. Further study with a higher sample size would aid in understanding the relationship between clutch initiation date, nest fate, and departure timing.

An alternative explanation for these small differences in departure dates among nest fates is that birds with pre-hatch failure stayed at the breeding site after nest failure rather than promptly migrating. Indeed, my model examining the interaction between nest fate and breeding completion date on departure date showed that birds with fledging success and post-hatch failure tended to migrate promptly after breeding completion, whereas birds with pre-hatch failure delayed migration for up to 40 d after failure. This delay could be explained by three non-mutually exclusive processes. First, birds with pre-hatch failure may remain at breeding sites to prospect future breeding territories (Eadie and Gauthier 1985, Ponchon et al. 2015). Although anecdotal, Semipalmated Plovers in Churchill were commonly observed in suitable nesting habitat > 1 km from their territory after pre-hatch failure, suggesting these individuals may be searching for higher quality breeding territories to secure in future years. Second, birds may delay departure to take advantage of potential renesting opportunities at the breeding site. Semipalmated Plovers are known to renest if nest failure occurs in early to mid-incubation, however renesting after this period is rare (Flynn et al. 1999). Arctic-breeding shorebirds that renest late in the season have high rates of nest abandonment, as parents opt to maximize their own survival over reproductive output (Gates et al. 2013, Weiser et al. 2018). Therefore, while birds with pre-hatch failure may prioritize renesting, those with post-hatch failure and fledging success may prioritize migration over a low-benefit and risky second breeding attempt. Third, remaining in breeding areas after nest failure may be a strategy to optimize departure timing for migration. Although early departure from the breeding site may allow for acquisition of higher quality territories on non-breeding grounds (Kokko 1999) and reduce overlap with predator migration (Lank and Ydenberg 2003, Lank et al. 2003, Duijns et al. 2019), migrants may incur significant costs if they encounter a phenological mismatch between their early arrival to stopover and/or non-breeding sites and critical peaks in food abundance (Schneider and Harrington 1981, Wood and Kellermann 2015). Thus, delaying migration until some departure threshold may have several fitness benefits. An alternate explanation for this result, however, is that birds with pre-hatch failure locally emigrated to renest outside the study area, where nests were not detected by field personnel. Though possible, this explanation is unlikely for most birds given the low rate of renesting in this population and the large study area that I monitored, encompassing most suitable breeding habitat in the region (Flynn et al. 1999). Additionally, if birds with pre-hatch failure renested, these individuals should have some of the latest departure dates, which was not the case.

Though I did identify several drivers of departure timing, factors not assessed in this study may also influence departure from the breeding site. For instance, birds in higher post-breeding body condition may require less time to prepare for migration and in turn, depart breeding sites earlier than those in poor condition. I did not assess the effect of body condition on departure timing because the time between capture and departure varied significantly among individuals, with many individuals departing 30 or more days after condition metrics (i.e., mass and fat score) were assessed. Although this variation could be corrected for in theory, there are no data available on within-season changes in body condition for Semipalmated Plovers or similar species because of the difficulty of recapturing the birds during incubation and the potential disturbance that this might entail. Additionally, post-breeding body condition is likely influenced by individual variation in reproductive effort, microhabitat quality near the nest site, and predation pressure, all of which may vary between capture and departure (Neubauer et al. 2017). Therefore, body condition at departure could not be reliably estimated. Weather variables including wind speed and direction, atmospheric pressure, and precipitation have also been shown to influence departure timing of migratory flights (Conklin and Battley 2011, Grönroos et al. 2012, Bozó et al. 2018), but these variables were not assessed here. Future studies should investigate possible interactions between energetics, weather conditions, and departure decisions in this population.

Post-breeding Migration Behaviour

I successfully tracked the southward migration of 84 Semipalmated Plovers after departure from breeding sites in Churchill and of these, 40 were detected during stopover events. I also tracked seven migrants from breeding sites in Burntpoint Creek and detected three during stopover. Birds using interior routes generally travelled through the Great Lakes to the mid-Atlantic coast, arriving predominantly in the Delmarva region. Conversely, those using coastal routes generally travelled through James Bay and the St. Lawrence Estuary to the upper Atlantic coast, arriving predominantly to the Maritimes and to a lesser extent, Cape Cod. Despite these spatial patterns, I observed a high degree of individual variation in overall migration route, ground speed, and stopover behaviour.

Drivers of Post-breeding Migration Behaviour

Qualitatively, neither sex nor nest fate appeared to influence choice of migration route. Similarly, my quantitative analysis of direction of initial flight track found no sex- or nest fate-effects, which was contrary to my prediction. I did, however, find that birds departing later had greater flight track bearings, indicating they were more oriented toward the south. To determine if temporal shifts in predominant wind direction could explain this finding, I conducted *a posteriori* analysis of wind direction throughout the breeding season. I found no evidence of temporal shifts; therefore, my prediction of time-minimization in later-departing migrants is supported. This finding suggests an adoption of more direct initial flight tracks toward the mid-Atlantic in later departing birds compared to earlier birds. Those departing later may choose to orient themselves toward a more southern, inland route through the Great Lakes to arrive faster at high-quality stopover sites in the mid-Atlantic, rather than along more northern, coastal routes where prey sources may be depleting (Schneider and Harrington 1981).

Other factors that may explain my observed variation in migration routes and flight track direction are experience of migrants and environmental conditions at departure and *en route*. Semipalmated Plovers show annual fidelity to stopover sites (Smith and Houghton 1984), and therefore likely have some degree of route fidelity that may be driven by migratory experience. Adult birds often follow migration routes used successfully as juveniles, which themselves are often stochastic due to weather and wind conditions experienced *en route* (Thorup et al. 2003, Cresswell 2014). Stochastic deviations from the endogenous flight paths of juveniles can accrue with migration distance, leading to significant inter-individual variation in overall migration route (Cresswell 2014). Therefore, birds in my study may have experienced variable environmental conditions during juvenile migration, leading to variable routes used again as adults. Although environmental conditions may have a greater influence on juvenile migration routes, wind and weather conditions at departure and *en route* can also significantly affect the flight trajectories of adults (Agostini et al. 2005, Mellone et al. 2011). For instance, though I assessed temporal wind regimes at departure and found no change over time, temporal shifts in wind direction along the migration route may have affected trajectories through drift (Liechti 2006). Future studies should employ multi-year tracking to investigate inter- and intra-individual relationships between juvenile migration routes, environmental conditions, and route fidelity as adults.

Contrary to my prediction, I found that initial ground speeds of migratory flights did not vary greatly among birds of different sexes, nest fates, or departure dates. My prediction was partially supported for the overall ground speed model, as I found that departure date influenced ground speeds, but sex and nest fate did not. Birds with later departures had faster ground speeds, which could indicate that these individuals are time-stressed compared to individuals departing earlier. Interestingly, 51% of initial flights from Churchill and 24% of all flights had groundspeeds < 9 ms^{-1} and were omitted from analyses. These low groundspeeds are likely an effect of spatial gaps in the Motus array, whereby birds undertake circuitous migration routes and/or stopovers *en route* without being detected. It is unsurprising that initial flights had a higher incidence of low groundspeeds than all flights, as the Motus network has substantially lower coverage between Churchill and receiving stations to the south than amongst most stations in the southern array. My median ground speeds within the migratory flight range (9-42 ms^{-1}) for initial flights (18.1 ± 1.0 ms^{-1}) and all flights (17.3 ± 0.5 ms^{-1}) are very similar to mean ground speeds observed in Semipalmated Plovers migrating from stopover sites in James Bay, Ontario to the mid-Atlantic Coast (18.4 ± 1.2 m s^{-1}; Anderson et al. 2019).

Given my small sample size, particularly for the initial ground speed model (*n* = 38), it is possible that my models did not have the statistical power to adequately assess my predictors. Alternatively, initial ground speeds of birds from Churchill may be better explained by other predictors such as wind assistance along the migration route, which has been shown to impact ground speed (Butler et al. 1997, Grönroos et al. 2012, Duijns et al. 2017, Anderson et al. 2019). I did not assess the effects of wind assistance on ground speed because the distance between receiving stations in the breeding and southern arrays was often large (i.e., > 1000 km) and consequently, wind conditions would be highly variable along those routes. Additionally, my sample size was small and the time and distance between departure from the breeding array and arrival to the southern array varied greatly among individuals. Therefore, assistance *en route* could not be reliably estimated. Higher sample sizes and expansion of the Motus network into more northern areas (e.g., Hudson Bay Lowlands, Ontario boreal forest) may provide the ability to assess the impacts of wind assistance on ground speeds in future studies.

My predictions of stopover probability and latitude were partially supported. I found no effects of sex or nest fate in either model, but birds departing later were less likely to be detected making a stopover than those departing earlier. Additionally, when stopovers were recorded from later-departing individuals, they tended to occur at lower latitudes. These findings, coupled with my findings of more southern initial flight tracks and higher overall ground speeds in later-departing birds, suggest that later-departing migrants use several characteristics of a time-minimizing strategy on fall migration. Several processes could explain these findings. First, later migrants may adopt this strategy in response to reduced foraging opportunities at the breeding site and more northern stopover sites, which could occur due to a latitudinal gradient of diminishing food supplies caused by decreasing temperatures and/or increased competition from higher shorebird densities (Schneider and Harrington 1981, Novcic 2018). Second, since shorebirds tend to migrate before avian predators in fall (Duijns et al. 2019), later-departing individuals may use time-minimization to reduce overlap with predator migration (Lank and Ydenberg 2003). Finally, since Semipalmated Plovers are sometimes territorial at non-breeding sites (Colwell 2000, Nol and Blanken 2014, Nol 2019), time-minimization may allow for these individuals to acquire high-quality non-breeding territories despite later onset of migration.

I interpret my finding of lower stopover probability in later-departing birds with caution, as it may be confounded by other factors such as tag loss. The time and distance between tagging and potential arrival at stopover sites is greater for later-departing migrants than earlier-departing migrants, as the former were at the breeding site for longer and tended to stop at lower latitudes. Therefore, there is a higher likelihood of these tags falling off prior to stopover and in turn, migrants may have stopped in North America undetected. Additionally, since most stops occurred in known stopover areas with a high density of receiving stations, it is possible that later-departing migrants took undetected stopovers at less known stopover sites outside the Motus array. Considering that 51% of initial flights from Churchill and 24% of all flights had groundspeeds < 9 ms^{-1}, it is highly possible that some birds undertook undetected stopovers *en route*, particularly between the breeding array and southern array. Few studies have investigated factors underlying a bird's decision to make a stopover (but see Anderson et al. 2019), particularly within a single population. Considering the crucial role of stopovers in migratory systems, further study on intra- and interpopulation differences on stopover latitude and probability is warranted.

Though there were no sex-based differences in stopover probability or latitude, stopover length-of-stay was longer for males than females. Sex differences in stopover length-of-stay have been reported for several other shorebird species (Figuerola and Bertolero 1998, Farmer and Wiens 1999, Henkel and Taylor 2015), though studies are biased toward spring migration. In fall, male Semipalmated Plovers depart later and consequently, may opt to minimize time spent migrating by undertaking longer stopovers that would allow for longer and faster flights between stops (Alerstam and Hedenstrom 1998, Alerstam 2011). However, since stopovers represented the last point of detection for most individuals in my study, it remains unclear whether post-stopover flights were indeed longer and faster in males. Additionally, since stopover latitude and ground speed were not sex-based, my findings do not fully support adoption of a time-minimizing strategy in males. An alternative explanation is that the energy costs of extended parental care carry through into migration, requiring males to stop for longer to replenish energy reserves. Interestingly, such costs do not appear to affect departure date, possibly because time constraints favour prompt departure after breeding rather than refuelling at the breeding site. Thus, males may use a mixed strategy that is time-minimizing early in migration (i.e., at departure), and energy-minimizing later (i.e., at stopover).

I observed stopover lengths-of-stay ranging from 0.2-25.4 d across all Churchill migrants, which is similar to the range reported for juvenile Semipalmated Plovers stopping at the St. Lawrence Estuary, Quebec, Canada (range = 2-28 d; mean = 23, SD = 3.4; Turcotte et al. 2013). Although the breeding locations of migrants stopping at the St. Lawrence Estuary are not known, these results suggest that Semipalmated Plover adults and juveniles have similar refuelling requirements in fall but show significant inter-individual variation in stopover duration.

My prediction of time-minimization in later-departing birds was not supported regarding stopover length-of-stay; migrants that departed later did not have longer stopovers than those departing earlier. It is possible that our relatively small sample size (*n* = 44) was not sufficient to detect departure date effects. Alternatively, later migrants may not use all aspects of a time-minimizing strategy. Rather, the time-minimizing behaviours I observed in later departing birds (i.e., more southern initial flight tracks, faster groundspeeds, lower probability of stopover) may be sufficient to allow migrants to maintain an appropriate migration schedule without extended stopover.

Key Areas During Fall Migration

Almost half of migrants from Churchill and approximately one third of migrants from Burntpoint Creek were detected in the Delmarva region, which includes the coasts of Delaware Bay and Chesapeake Bay; the eastern coast of the Delmarva Peninsula; and the Atlantic shore of New Jersey. The region is highly productive, consisting of an extensive network of tidal and non-tidal marshes, beaches, and mudflats that constitute critical stopover habitat for thousands of migrant shorebirds in spring and fall (Clark et al. 1993, Burger et al. 1997, Gillings et al. 2009). Semipalmated Plovers are commonly observed in Delmarva during migration, roosting in various habitats and foraging predominantly on polychaete worms at low tide (Burger et al. 1997, Tsipoura and Burger 1999). However, my study is the first to provide quantitative evidence of this species using the area for extended stopover. Stopovers ranged from a few hours to 21 d, suggesting that the area is used for both short stops and longer periods of staging. My observed stopover lengths-of-stay are similar to those reported for radio-tagged Whimbrel (*Numenius phaeopus*) who also stopped in Delmarva after breeding near Churchill, Manitoba and Burntpoint Creek, Ontario (Mackellar 2020). Dunlin (*Calidris alpina hudsonia*) breeding in Churchill also rely on Delmarva for stopover, though the region is more frequented during spring migration than fall (Wright 2019). Thus, Delmarva constitutes important stopover habitat for multiple species breeding in the Hudson Bay Lowlands.

The importance of the Delmarva region is underscored by my finding that despite most birds travelling to Delmarva via the Great Lakes, there were no recorded stopovers in the Great Lakes region. Rather, most birds departed Churchill, travelled rapidly through the Great Lakes, and arrived in Delmarva within a few days of departure, indicating that few or no stops were made *en route*. Interestingly, Semipalmated Plovers are regular visitors to the Great Lakes during fall migration, albeit in relatively low numbers compared to other species (Kenyon Ross et al. 2012). Therefore, my results indicate that Semipalmated Plovers from Churchill choose to bypass the Great Lakes in favour of stopover sites in the mid-Atlantic, whereas individuals from other populations choose or are energetically required to visit stopover sites in the Great Lakes. It is possible that birds from Churchill made short stopovers in the Great Lakes without being detected by the Motus array, however the high density of receiving stations in the Great Lakes region make this explanation unlikely. Thus, rather than making smaller 'hops' through the interior of North America, many individuals from this population may 'jump' directly to the mid-Atlantic coast (Warnock 2010).

Another important destination for Semipalmated Plovers from both sites was the Cape Cod region, which includes the eastern coast of Massachusetts; Cape Cod, Massachusetts; coastal Rhode Island and Connecticut; and Long Island, New York. Cape Cod contains numerous barrier beaches, salt marshes, intertidal mudflats and estuarine habitats that are used extensively by migrant shorebirds (Placyk and Harrington 2004, Koch and Paton 2014). Thirty individuals from Churchill were detected in this region and approximately half of these made stopovers ranging from a few hours to 25 d. Similarly, five individuals from Burntpoint Creek were detected in Cape Cod along with two stopovers. Migrants arriving to Cape Cod used a variety of interior and coastal routes, however over half of birds arriving in the region were not detected between Manitoba and Cape Cod. These birds may have used an interior route through eastern Canada and USA, where Motus coverage was relatively lower than the Great Lakes and Maritimes. Despite many migrants stopping in Cape Cod, several birds opted to travel further south to Delmarva prior to making a stopover. It is possible that migrants favour Delmarva because it is of better quality due to lower competition, fewer predators, and/or higher food availability. However, testing these hypotheses would require comparative studies assessing Semipalmated Plover behaviour, invertebrate abundance, and predator presence in the two regions.

Although comparatively fewer birds travelled to the Maritimes, which includes the Bay of Fundy; coastal Nova Scotia; the Acadian Peninsula of New Brunswick; Prince Edward Island; and the Northumberland Strait, the region was an important area for some individuals on stopover. Of the 14 birds from Churchill detected in the region, six were detected making a stopover. Most stopovers occurred in the upper Bay of Fundy, which is a Western Hemisphere Shorebird Reserve Network (WHSRN) site of Hemispheric Importance to migrant shorebirds (McKellar et al. 2020). In fall, many hundred thousand shorebirds travel to the Bay of Fundy to take advantage of its wide intertidal mud flats that support a high-density, low diversity assemblage of invertebrates dominated by the amphipod *Corophium volutator* (Hicklin and Smith

1979, Hamilton et al. 2003). Semipalmated Sandpipers constitute the largest proportion of shorebirds present in fall, with peak counts of over 350,000 individuals in early August (Hicklin and Chardine 2004). Semipalmated Plovers are also known to use the region in fall, albeit in lower numbers (Hicklin 1987). Though no recent estimates are available, historical data indicate peak counts of approximately 8,400 Semipalmated Plovers in mid- to late August (Hicklin 1987). This peak corresponds to my observed stopover range of July 28-August 29 and the period of maximum invertebrate abundance in the region (Hicklin 1987, Wilson 1989, Gerwing et al. 2015). Thus, Semipalmated Plovers from Churchill likely time their arrival to the Bay of Fundy to exploit peaks in food resources.

Despite extensive Motus coverage, none of the Semipalmated Plovers that stopped in the Maritimes were detected elsewhere along the eastern seaboard. I cautiously interpret the lack of subsequent detections as possible evidence for transoceanic flights over the Atlantic after departure from the Maritimes. Although there is no direct evidence of such flights in Semipalmated Plovers thus far, several shorebird species are known to fly non-stop to wintering sites in northern South America after doubling their mass at the Bay of Fundy (Richardson 1979, Hicklin 1987). Confirmation of transoceanic flights would require tracking birds using another method (e.g., geolocators) or subsequent detection of birds in Central or South America with flight speeds indicative of a true, non-stop flights (i.e., > 9 ms^{-1}). An alternative explanation may be that birds lost their tags prior to departing the region, preventing the detection of birds travelling along coastal routes.

The three regions in which Semipalmated Plovers were most observed in this study include numerous Important Bird Areas (IBAs) and three WHSRN sites. As such, these regions represent known areas of importance for migrant shorebirds in the Atlantic Flyway of North America. Despite these designations, however, habitat quality and predictability of these regions for migrant shorebirds may be under threat (Rattner and Ackerson 2008). In the Delmarva and Cape Cod regions, threats include anthropogenic disturbance (Koch and Paton 2014), human development (Culbertson et al. 2009), environmental contaminants (Rattner and Ackerson 2008), and climate change (e.g., sea level rise, storm surges; Sims et al. 2013, Dohner 2016). In the Maritimes, sea level rise is expected to reduce available habitat and increase tidal range and frequency of extreme tidal events (Greenberg et al. 2012), all of which can increase energy expenditure and reduce foraging efficiency of shorebirds on stopover (Mann et al. 2017). Moreover, other threats including eutrophication (Bucci et al. 2020) and bait worm harvest (Shepherd and Boates 1999) may degrade currently available habitat. My observations of Semipalmated Plovers using these regions on migration, including numerous stopovers two to three weeks in duration, provide further evidence that effective management and conservation of these areas is critical to ensure the viability of Arctic breeding shorebird populations using the Atlantic Flyway of North America (Clark et al. 1993, Burger et al. 1997, 2007).

Migrants Tracked Beyond North America

A recent study tracking Semipalmated Plovers from stopover sites in James Bay, Ontario found similar dispersal patterns to Delmarva, Cape Cod, and the Maritimes as reported here (Anderson et al. 2019). However, my study is the first to directly track migrant Semipalmated Plovers from breeding sites to potential non-breeding sites beyond North America. I tracked 10 individuals from Churchill to Central America (i.e., Panama), the Caribbean (i.e., Barbados), and northern South America (i.e., French Guiana and Suriname). Notably, one male (ID: 24537) travelled at a ground speed of 10.2 ms^{-1} from Cape Cod to Kourou, French Guiana, suggesting this individual may have undertaken a non-stop flight over the Atlantic (Grönroos et al. 2012). If the individual did fly non-stop, it travelled an average of 800 km d^{-1} over 5 d. In total, the individual would have traveled 4,400 km, which is the longest non-stop flight recorded for this species. However, a higher sample size and/or tracking of birds at finer spatiotemporal resolution is necessary to corroborate these findings.

The other seven birds detected in South America travelled at ground speeds < 9 ms^{-1}, indicating they stopped at one or more stopover sites *en route* (Anderson et al. 2019). Of these, five birds were previously detected in either Delmarva or Cape Cod, suggesting these individuals either undertook transoceanic flights to regions of the Caribbean or northern South America without Motus coverage, or travelled along non-direct routes along the coast prior to crossing the Atlantic at a lower latitude (e.g., southern tip of Florida). Although the extent of the Motus array along coastal USA does decline with latitude, it is unlikely that birds travelling along a coastal route would evade detection. Therefore, I cautiously suggest that these migrants made transoceanic flights from the mid-Atlantic, but likely stopped in the Caribbean and/or other regions of northern South America prior to detection in French Guiana or Suriname. Interestingly, two individuals arrived in South America after last being detected in the Great Lakes region and one individual arrived in Panama 23 d after departure from Churchill, with no detections in between. The likely explanation for these data gaps is migrants' use of interior routes through USA, where Motus coverage is sparse.

Of the birds that travelled to South and Central America, one (ID: 29275) was detected for six days and the remainder were detected for a few hours or less. Since French Guiana represented the southernmost limit of the Motus array during the study period (Figure 2.4), these detections may have represented flybys and/or short stopovers prior to migrants continuing to non-breeding sites further south. Alternatively, these migrants may have overwintered nearby but outside the range of the few receiving stations present in the region. In addition to having few receiving stations, coastal regions of Suriname and French Guiana have wide, extensive mudflats that may allow birds to forage far from the existing stations and therefore, have lower detection probability. This explanation seems plausible, as another study found evidence of Semipalmated Plovers from Churchill overwintering in the region (Storm-Suke 2012). Specifically, trace element signatures from feathers were used to match Semipalmated Plovers breeding in Churchill to those overwintering in French Guiana. Additionally, a plover banded in Churchill during the breeding season was subsequently resighted in French Guiana during the early non-breeding period (Storm-Suke 2012), as was observed here. Regardless of exact overwintering location, my study demonstrates that some Semipalmated Plovers from this population spend the non-breeding period at least as far south as northern South America. The southward expansion of the Motus network is a necessary precursor to determine precise connectivity between breeding, stopover, and non-breeding sites of Semipalmated Plovers and other small Arctic breeding shorebirds.

Qualitative Site Comparison

Final sample sizes of birds originating from Burntpoint Creek were small, which precluded quantitative comparison of migratory behaviour between my two study sites. Therefore, I compare migrants from Burntpoint Creek and Churchill from a purely qualitative perspective. Interestingly, the median departure date was the same at both sites (July 26). The range of departures was larger in Churchill, which is likely explained by the higher sample size in Churchill and thus, higher likelihood of outliers in the data. Since snowmelt is expected to occur earlier at lower latitudes (Liebezeit et al. 2014), I would expect birds at Burntpoint Creek to initiate nests earlier and in turn, depart breeding sites sooner than conspecifics in Churchill. It is possible that, like migrants with pre-hatch failure from Churchill, migrants from Burntpoint Creek remain in breeding areas after breeding completion to optimize arrival timing at stopover sites (Mackellar 2020). However, as I did not have sufficient nest monitoring data to determine breeding completion dates for these individuals, this hypothesis remains untested.

Migrants from both sites used similar migration routes, though the spatial range of migration routes was broader in the Churchill population, probably again due to the larger sample size from Churchill. Migrants from each site travelled toward the mid-Atlantic coast and were ultimately detected in the three major stopover regions identified for the Churchill migrants. Birds from both populations had substantial overlap in the range of stopover sites, length-of-stay, and timing of stopover. These findings provide evidence that Semipalmated Plovers from two distinct breeding populations intermix during migration and stopover, and therefore likely experience similar conditions and pressures during fall migration.

Some individuals undertook apparently non-stop flights from their respective breeding sites to the mid-Atlantic coast. This implies that rather than undertaking shorter ‘hops’ along their migration route, as was expected for this species, individuals from both sites took larger ‘jumps’ of over 2,000 km to presumably arrive faster to the mid-Atlantic coast (Warnock 2010). These findings may suggest there is comparatively lower availability of food resources between the breeding site and the mid-Atlantic, which drives most individuals to travel directly to areas where food is potentially more predictable and abundant (e.g., Delmarva). However, since Semipalmated Plovers are commonly observed along the coasts of the Great Lakes during fall migration (Kenyon Ross et al. 2012), this may not be the only explanation. Another, non-mutually exclusive explanation is that these migrants depart the breeding site with adequate fuel reserves, and consequently there is no energetic requirement to stop between the breeding site and the mid-Atlantic. This would explain why the Great Lakes are used for stopover by some Semipalmated Plovers, but none from Churchill. For instance, migrants breeding further north (e.g., Southhampton Island, Nunavut) may need to stop in the Great Lakes to replenish diminishing fuel reserves, whereas migrants from Churchill have sufficient stores to last until arrival to the mid-Atlantic. Comparative studies of migration behaviour between Semipalmated Plovers breeding in the Hudson Bay Lowlands and portions of their breeding range closer to the mid-Atlantic (e.g., Nova Scotia, Canada) may provide valuable insights into the drivers of migration strategy in this species. For instance, if Semipalmated Plovers breeding in Nova Scotia make similar ‘jumps’ of 2,000 km or more after breeding site departure, it could provide evidence that migrants undertake long flights because they have adequate fuel reserves upon departure. Conversely, if migrants from the Nova Scotia population make several shorter ‘hops’ (i.e., flights of a few hundred kilometers or less; Piersma 1987, Warnock 2010) down the mid-Atlantic coast, it could indicate that migrants breeding in the Hudson Bay Lowlands use the ‘jump’ strategy to bypass lower quality stopover sites between the breeding site and the mid-Atlantic.

Interestingly, a lower proportion of birds tagged at the Burntpoint Creek site (29%) were subsequently detected in the southern array compared to the Churchill site (50%). This suggests that more birds from Burntpoint Creek used a route without receiving stations or were generally more likely to lose their tags compared to birds from Churchill. Differences in rate of tag loss between sites seems unlikely because the same tagging techniques were used at each site. It is possible that some birds from Burntpoint use migration routes much further to the east and use Canadian stopover areas without Motus coverage, such as Newfoundland and Labrador, the outer Gulf of St. Lawrence, or the northern coast of New Brunswick. Alternatively, though less likely, these birds may have used migration routes further to the west.

Overall, there was qualitatively higher variability in migration behaviour within each of the Churchill and Burntpoint populations than between populations. This may suggest that breeding latitude is not a major determinant of migration behaviour; however, before this can be determined with certainty, a quantitative comparison of migrants from various sites using greater sample sizes is necessary. This could be achieved in future studies by tagging and monitoring individuals from several breeding populations along a latitudinal gradient.

Limitations

Though the capabilities of Motus continue to improve, the technology is not without limitations. Despite an increasing number of receiving stations deployed annually, a major limiting factor is the spatial extent of the array (Taylor et al. 2017). Receiving stations are distributed non-randomly across the landscape, which led to missing and potentially biased data in my study. First, some birds nested outside the expected range of the breeding array, which may have led to fewer birds being detected departing the breeding area. Second, after departure many tagged birds ‘disappeared’ for days to weeks at a time, during which I was unable to monitor their whereabouts or behaviour. These data gaps occurred most often between the breeding sites and mid-Atlantic coast or Great Lakes, and likely occurred because birds used areas with low to minimal Motus coverage (e.g., the large expanse of boreal forest between the Hudson Bay Lowlands and the mid-Atlantic coast or Great Lakes). Third, the low density of receiving stations in South and Central America may have limited my ability to identify non-breeding sites. Finally, since the highest concentration of receiving stations was along the mid-Atlantic coasts of USA and Canada, my detection data may have been biased toward those locations. Expansion of the Motus network will significantly enhance our ability to monitor small birds at hemispheric scales. In the interest of shorebird-specific research, I recommend further expansion in the Hudson Bay Lowlands, boreal forest of Ontario and Quebec, interior North America, and coastal Central and South America.

Although Motus detection data have relatively higher spatial resolution than other tracking technologies suitable for small birds (i.e., geolocators), it is not currently possible to reliably estimate the detection range of a given receiving station or determine the precise location of tagged birds within the receiving station’s range (Taylor et al. 2017). The spatial range of each receiving station varies greatly by receiver type (i.e., SensorGnome versus Lotek; Anderson et al. 2019), local topography, and the number, quality, and orientation of the station’s antennas (Taylor et al. 2017). The detectability and strength of a tag’s signal as it arrives to a receiving station also varies based on current weather conditions and the flight altitude of the tagged bird.

Therefore, a tag's signal strength cannot be used to estimate the distance of a tagged bird from a receiving station. Moreover, though the receivers record which antenna detected the incoming signal, which provides a coarse estimate of the bird's orientation in relation to the station, it is challenging to determine the precise direction from which the signal originated. Consequently, though I identified general stopover regions (e.g., Delmarva), I was unable to determine precise stopover sites and habitats used within those sites (e.g., specific beaches or mudflats). I was also unable to reliably characterize specific behaviours or movement patterns during stopover events, such as diel movements from foraging to roost sites.

Despite tracking a significant number of birds, my final sample sizes were lower than expected. Of the 169 tags deployed in Churchill, only 41% were detected departing the breeding area and 50% were detected in the southern array. Similarly, only 29% of tags deployed in Burntpoint provided viable data. Birds that were tagged but not subsequently detected either took alternate migration routes outside the Motus array, were undetected departing the breeding area, or experienced tag loss prior to departure or *en route*. It is unlikely that many birds used alternate migration routes (e.g., through the Canadian Prairies) because 90% of birds with departures were subsequently detected in the southern array to the southeast. It is likely, however, that many birds experienced tag loss prior to or following departure. Birds can lose their tags due to skin/feathers sloughing off or removal of the tag by birds during preening, both of which were observed in Churchill. Although studies show that tag attachment using glue typically lasts at least 40 d in other species (e.g., Upland Sandpiper, *Bartramia longicauda*; Mong and Sandercock 2007), Semipalmated Plovers have strong, small, multipurpose bills that may increase their ability to remove tags compared to larger-billed species.

Conclusions

My study fills a critical knowledge gap on the migration behaviour of the Semipalmated Plover, an understudied Arctic breeding shorebird. I used Motus to identify previously unknown fall migration routes, describe stopover ecology in three major regions along the mid-Atlantic coast, and provide additional evidence of migratory connectivity between a subarctic breeding site and potential non-breeding sites in South America. I also identified several drivers of departure timing from the breeding site and found that departure timing influences subsequent migration strategy. Though I was unable to quantitatively assess differences in migration behaviour between birds from Churchill and Burntpoint Creek, I observed many qualitative similarities between these populations that warrant further study.

Semipalmated Plovers breeding in the Hudson Bay Lowlands showed a wide range of fall migration behaviours that varied greatly within, and to a lesser extent, between populations. Species with higher within-population variation in migration behaviour may be more resilient to environmental change (Gilroy et al. 2016, Lisovski et al. 2021), as the effects of site-specific threats (e.g., contamination at a stopover site) affect some, but not all, individuals in a population. This could explain why Semipalmated Plover populations are considered stable compared to Arctic breeding shorebirds with reliance on small numbers of stopover sites on migration, such as the *rufa* Red Knot (Baker et al. 2004, Gillings et al. 2009).

I identified three major stopover regions along the mid-Atlantic and found evidence that some individuals may make non-stop, transoceanic flights following stopover. Considering the critical importance of these regions to Semipalmated Plovers and other Arctic breeding shorebirds, it is alarming that all three are currently undergoing drastic changes from human-induced climate change (Greenberg et al. 2012, Sims et al. 2013, Dohner 2016), coastal development and disturbance (Shepherd and Boates 1999, Culbertson et al. 2009, Koch and Paton 2014), and environmental contamination (Rattner and Ackerson 2008, Bucci et al. 2020). Although my study provided general information on stopover ecology, further studies are necessary to assess whether Semipalmated Plover populations could face future pressures due to changes in stopover habitat quality and availability. Additional multi-season tracking studies will continue to improve our ability to identify potential population bottlenecks across a species' range. My study underscores the importance of the mid-Atlantic coast to migrant shorebirds and emphasizes the need for effective, broad-scale conservation initiatives that consider connectivity between habitats used throughout the annual cycle.

Chapter 5: Summary and Conclusions

My research is the first to characterize the post-breeding fall migration behaviour of Semipalmated Plovers from two subarctic sites. I found a high degree of intrapopulation variation in behavioural metrics including departure timing, direction of initial flight track, migration route, ground speed, and stopover probability, latitude, and length-of-stay. In general, however, migrants departed between mid-July and early August, travelled to the southeast along coastal or interior routes, and were subsequently detected in three major regions along the mid-Atlantic coast including the Maritimes, Delmarva, and Cape Cod. Many individuals used these regions for stopovers ranging from short (< 1 d) to long (> 20 d) durations. Within each larger stopover region, Semipalmated Plovers used a variety of stopover sites. Though typically considered a 'hop' migrant (Nol and Blanken 2014), I found evidence for significant 'jumps' over interior North America to the mid-Atlantic coast, suggesting that birds are in high body condition at departure or the cost of longer flights is outweighed by the benefit of arriving quickly to high-quality stopover sites. My findings provide further support for the protection and strategic management of vulnerable habitats along the mid-Atlantic, including the barrier beaches, tidal mud flats, salt marshes, and estuarine habitats relied on by thousands of shorebirds transiting to and from the Arctic.

Some individuals from Churchill were subsequently detected in South America, indicating that these migrants travel distances of at least 6,700 km (one-way) between breeding and non-breeding sites. Moreover, I found evidence of one individual making a possible transoceanic flight from a stopover site in Cape Cod to French Guiana, equating to a non-stop journey of over 4,440 km. To further understand transoceanic flights and critical links between breeding, non-breeding, and stopover sites used by Semipalmated Plovers and other small shorebirds, I recommend expansion of the Motus network in South America, Central America, and northern North America. Future tracking studies targeting Semipalmated Plovers may also consider use of geolocators, which have been used to assess the year-round movement behaviour of species with similar life history traits (e.g., Brown et al. 2017).

I assessed the effects of cross-seasonal interactions on migration strategy and found that breeding constraints affect departure timing from the breeding site, but not subsequent migration strategy. Clutch initiation date predicted breeding site departure date, males migrated earlier than females, and parents with nest and chick failure migrated earlier than parents with fledging success. After departure, the most important driver of migration strategy was departure date; individuals leaving the breeding site later had initial flight tracks oriented more toward the south, faster overall ground speeds, reduced probability of stopover, and stopped at lower latitudes. This suggests that later departure may lead to migrants using some, but not all, aspects of a time-minimizing strategy on fall migration. Though my study provides preliminary information on the drivers of migration strategy, I did not assess the relative impacts of body condition, weather experienced *en route*, and stopover habitat quality on migratory decisions. Since migration systems are dynamic, numerous processes likely operate in tandem to modulate migratory strategies. Therefore, I recommend that future studies build upon this work to assess other drivers of migration strategy in both spring and fall migrants.

I qualitatively assessed differences in departure timing, migration route, and stopover latitude and length-of-stay between birds from Churchill and Burntpoint Creek. I found higher variability in migration behaviour within than between breeding populations. The median departure date at both sites was July 26 and migrants used similar migration routes after departure. However, migrants from Burntpoint Creek did not use routes through James Bay or the Great Lakes and a lower percentage of tagged birds were subsequently detected in the southern array. Both populations used the same stopover regions for similar durations and timeframes. Thus, my results indicate that individuals from two Hudson Bay Lowlands populations intermix during migration and consequently may experience similar pressures along their migratory routes. I could not determine if these spatiotemporal similarities extended into regions further south, as I was unable to track any individuals from Burntpoint Creek beyond North America. However, I propose that assessments of range-wide migratory connectivity should be a research priority moving forward. Our capacity for assessing migratory connectivity and understanding pressures limiting migratory bird populations will continue to evolve alongside advancements in tracking technologies.

Supplemental Material

Supplemental Methods

Additional Details on Nest Monitoring

At Churchill, our field team conducted nest searches at least three times in June. Searches consisted of 2-3 researchers walking 50-75-m apart through suitable nesting habitat. When we observed Semipalmated Plovers and suspected nest presence, we hid 20-75 m away to watch adults return to their nest. We recorded nest locations with a Global Positioning System (GPS) in NAD83 UTM coordinates and marked nests at a distance (approximately 10 m) using small rock cairns. To minimize disturbance during nest visits, we usually confirmed nests were active by observing incubating adults from a distance using spotting scopes. When approaching a nest was necessary (e.g., to float eggs to determine clutch initiation date) we typically spent < 2 min within 5 m of the nest cup. We did not approach nests when predators were observed nearby. We assumed depredation for clutches that disappeared between visits unless another cause of failure was apparent (e.g., washed out by tides, destroyed by motor vehicles, or stepped on by humans/wildlife).

Details of Motus Breeding Array in Churchill, Manitoba

The breeding array in Churchill included four receivers. Of these, three had 10 m telescoping tripod poles towers (‘Four Mile Beach’, ‘Fen’ and ‘Gordon Point’), and one (‘CNSC’) was mounted an existing structure. Two receivers (CNSC and Gordon Point) had two antennas and two (Four Mile Beach and Fen) had three antennas.

Sensorgnome receivers used either RaspberryPi or BeagleBone hardware. The SensorGnomes were plugged into external AC power sources or powered by a 65 W solar panel connected to a 12 V DC sealed lead acid battery. In 2017, Four Mile Beach (previously named 'Bird Cove') was relocated because it recorded few detections at its location in 2016. We confirmed functionality and downloaded data from receivers at least three times per breeding season.

In 2018-2019, we supplemented detection data from receiving stations in Churchill by detecting tags opportunistically using a mobile SRX600 receiver (Lotek Wireless, Newmarket, Ontario) and a hand-held three-element Yagi antenna. Some pairs nested outside or bordering the estimated range of the breeding array (~5 km); therefore, the purpose of ground-tracking was to prevent exclusion of these birds from analyses by reducing potential gaps in receiver coverage. However, all birds were last detected by the breeding array rather than the mobile receiver.

Classification of Departures

I confirmed departure dates visually using plots of time and signal strength. As a bird flies through the beam of an antenna, signal strength of the tag shows a distinct upside-down 'U' shape over time (i.e., increases as the bird approaches and decreases after passing by; Mitchell et al. 2012, Anderson et al. 2019). I classified departures as 'confirmed' if they presented a u-shaped pattern (Churchill: n = 64; Burntpoint: n = 6) and 'unknown' if they presented no clear pattern (Churchill: n = 36; Burntpoint: n = 1). However, I classified six birds (male: n = 3, female: n = 3) with unknown departure patterns in Churchill as ‘confirmed’ because these individuals were detected by receiving stations in the southern array within 36 hr of the last detection by the breeding array. Since I was coarsely interested in departure date (i.e., Julian day of year), rather than date and time of day, the 36-hr threshold was sufficient to allow for an estimation of departure date to an appropriate temporal resolution with a small margin of error (~1.5 d). Moreover, the groundspeeds of most (66%) of these individuals were indicative of non-stop migratory flights (i.e., > 9 ms^{-1}) from the breeding array to the southern array.

Supplemental Tables

Table S1. Results of a general linear model on variables explaining departure date (Julian day of year) of Semipalmated Plovers *(Charadrius semipalmatus)* breeding near Churchill, Manitoba, Canada, 2015-2019 (*n* = 70). Model included sex, nest fate, and clutch initiation date (Julian day of year) as predictors. Significant coefficients at α = 0.05 are indicated in bold. Adjusted r^2 = 0.36.

Variables	Estimate	SE	*t*	*P*
(Intercept)	**130.6**	**25.8**	**5.1**	**<0.001**
Sex (male)	**8.5**	**1.7**	**5.1**	**<0.001**
Clutch initiation date	**0.4**	**0.2**	**2.7**	**<0.01**
Nest fate (post-hatch failure)	**4.6**	**2.2**	**2.1**	**<0.01**
Nest fate (fledged)	**6.7**	**2.2**	**3.0**	**<0.05**

Table S2. Results of a general linear model on variables explaining departure date (Julian day of year) of Semipalmated Plovers *(Charadrius semipalmatus)* breeding near Churchill, Manitoba, Canada, 2015-2019 (*n* = 70). Model included the interaction of nest fate and breeding completion date (Julian day of year) as predictors. Significant coefficients at α = 0.05 are indicated in bold. Adjusted $r^2 = 0.52$.

Variables	Estimate	SE	*t*	*P*
(Intercept)	**200.76**	**3.3**	**78.8**	**<0.001**
Nest fate (fledged)	4.1	2.9	1.4	0.2
Nest fate (post-hatch failure)	3.1	2.8	1.1	0.3
Breeding completion date	-0.1	0.1	-0.7	0.49
Nest fate (fledged): Breeding completion date	**0.9**	**0.2**	**4.0**	**<0.001**
Nest fate (post-hatch failure): Breeding completion date	**1.1**	**0.2**	**5.2**	**<0.001**

Table S3. Timing and general locations of Semipalmated Plovers *(Charadrius semipalmatus)* tracked during fall migration using VHF transmitters and the Motus Wildlife Tracking System (www.motus.org). Migrants were radio-tagged at breeding sites near Churchill, Manitoba, Canada, 2015-2019 (*n* = 84). General locations are defined in Figure 2.5.

Year	Tag ID	Sex	Departure Date	General Location	Detection Dates	Length-of-Stay (Days)
2015	14648	Male	-	USA - Cape Cod/Long Island	Aug 3-Aug 26	23.18
	14656	Female	Jul 17	Canada - Southwestern Hudson Bay	Jul 18	0.02
				USA - Cape Cod/Long Island	Jul 20	0.11
				USA - Delmarva Peninsula/Jersey Shore	Jul 21	0
	14661	Female	Jul 22	Canada - Southwestern Hudson Bay	Jul 23	0.02
				USA - Cape Cod/Long Island	Jul 27-Jul 28	1
	14662	Male	-	Canada - St. Lawrence River and Estuary	Jul 31	0
				Canada - Maritimes	Aug 6-Aug 24	18.23
	14664	Female	Jul 28	Canada - Southwestern Hudson Bay	Jul 28	0.03
				USA - Delmarva Peninsula/Jersey Shore	Aug 1	0.23
	14666	Female	Jul 13	USA - Maine Coast	Jul 26	0
				USA - Cape Cod/Long Island	Jul 28	0.11
	14670	Female	-	Canada/USA - Great Lakes	Jul 30	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 21-Sep 11	21.27
2016	20823	Male	-	USA - Cape Cod/Long Island	Aug 6	0
				USA - Delmarva Peninsula/Jersey Shore	Aug 6-Aug 19	13.28
	20828	Female	Jul 28	Canada - Maritimes	Aug 11	0.01
	20835	Female	Jul 25	Canada/USA - Great Lakes	Aug 4	0
				USA - Delmarva Peninsula/Jersey Shore	Aug 5-Aug 7	2.89
	20836	Male	Aug 5	Canada/USA - Great Lakes	Aug 5	0.09
				USA - South Atlantic Coast	Aug 5	0.02

Year	Tag ID	Sex	Departure Date	General Location	Detection Dates	Length-of-Stay (Days)
	20837	Male	Aug 11	Canada/USA - Northeast Interior	Aug 12	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 16	0.06
				USA - South Atlantic Coast	Aug 18	0.06
	20838	Female	Jul 16	Canada/USA - Great Lakes	Jul 23	0.01
	20840	Male	Aug 7	USA - South Atlantic Coast	Aug 20	0.01
	20841	Female	-	Canada - St. Lawrence River and Estuary	Jul 31	0.01
				USA - Cape Cod/Long Island	Aug 3-Aug 22	19.43
2017	24508	Female	Jul 26	Canada/USA - Great Lakes	Jul 27	0.01
				Canada/USA - Northeast Interior	Jul 28	0
				USA - Delmarva Peninsula/Jersey Shore	Jul 28	0.46
	24526	Female	Jul 21	Canada/USA - Great Lakes	Jul 25	0.04
				USA - Delmarva Peninsula/Jersey Shore	Jul 25-Jul 28	3.79
				Northern South America	Aug 24	0
	24531	Male	Jul 29	USA - Delmarva Peninsula/Jersey Shore	Jul 31-Aug 15	15.86
	24537	Male	-	Canada/USA - Great Lakes	Jul 27	0
				Canada/USA - Northeast Interior	Jul 27	0.01
				USA - Delmarva Peninsula/Jersey Shore	Jul 27	0.02
				USA - Cape Cod/Long Island	Jul 27-Aug 16	20.07
				Northern South America	Aug 21	0.02
	24548	Male	-	Canada - James Bay	Aug 23	0.01
				Canada/USA - Northeast Interior	Aug 24	0
				USA - Cape Cod/Long Island	Aug 24	0.05
	24550	Female	Jul 26	Canada/USA - Great Lakes	Jul 27	0.04
				USA - Delmarva Peninsula/Jersey Shore	Jul 28	0.01
	24552	Female	Jul 23	Canada - James Bay	Jul 27	0.52
				USA - Cape Cod/Long Island	Jul 29	0.23
				USA - Delmarva Peninsula/Jersey Shore	Jul 29	0.02
				Northern South America	Sep 6	0.04
	24554	Female	Jul 19	USA - Cape Cod/Long Island	Jul 27	0.04
				USA - Delmarva Peninsula/Jersey Shore	Aug 3-Aug 19	16.83

Year	Tag ID	Sex	Departure Date	General Location	Detection Dates	Length-of-Stay (Days)
				Northern South America	Sep 4	0.02
	24555	Male	Jul 29	Canada - James Bay	Jul 30	0.01
				Canada/USA - Great Lakes	Jul 30	0
				USA - Cape Cod/Long Island	Jul 31	0.37
				USA - Delmarva Peninsula/Jersey Shore	Jul 31-Aug 18	18.86
	24556	Male	Aug 3	USA - Delmarva Peninsula/Jersey Shore	Aug 6-Aug 25	19.49
	24557	Male	Aug 4	Southern Central America	Aug 27	0.13
	24563	Female	Aug 1	Canada - Maritimes	Sep 1	0.01
2018	24500	Male	Jul 27	Canada - Southwestern Hudson Bay	Jul 28	0.01
				USA - Cape Cod/Long Island	Aug 23-Sep 17	25.44
	24501	Male	Jul 29	Canada/USA - Great Lakes	Jul 30	0.11
				USA - Delmarva Peninsula/Jersey Shore	Aug 3-Aug 4	1.83
				Caribbean	Aug 28	0.3
	24507	Female	Jul 25	Canada/USA - Great Lakes	Jul 27	0.01
				Canada/USA - Northeast Interior	Jul 27	0.02
				USA - Cape Cod/Long Island	Jul 27-Aug 18	22.52
	24521	Female	Jul 18	Canada - Southwestern Hudson Bay	Jul 18	0
				Canada/USA - Great Lakes	Jul 19	0
				USA - Delmarva Peninsula/Jersey Shore	Jul 20-Aug 4	15.7
				Northern South America	Aug 10	0.01
	29250	Female	Jul 22	Canada/USA - Great Lakes	Jul 27	0
				USA - Delmarva Peninsula/Jersey Shore	Jul 27	0.02
	29255	Female	Aug 20	Canada - St. Lawrence River and Estuary	Aug 22	0
				Canada - Maritimes	Aug 23	0.03
	29257	Female	18 Jul	Canada - St. Lawrence River and Estuary	Jul 27	0.01
				Canada - Maritimes	Jul 28-Jul 29	1.61
	29261	Female	-	Canada - James Bay	Jul 14	0
				USA - Cape Cod/Long Island	Jul 18	0.02

Year	Tag ID	Sex	Departure Date	General Location	Detection Dates	Length-of-Stay (Days)
				USA - Delmarva Peninsula/Jersey Shore	Jul 18	0.1
	29270	Male	Jul 27	Canada/USA - Great Lakes	Jul 28	0.03
				Canada/USA - Northeast Interior	Jul 29	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 14	0.02
	29272	Female	Jul 26	Canada/USA - Great Lakes	Jul 27	0.05
				Canada/USA - Northeast Interior	Jul 28	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 8-Aug 19	11.32
	29275	Male	Aug 2	USA - Cape Cod/Long Island	Aug 5	0.01
				Northern South America	Sep 6-Sep 12	6.22
	29281	Male	-	Canada/USA - Great Lakes	Aug 6	0.01
				Northern South America	Sep 13	0
	29284	Female	Jul 25	Canada - St. Lawrence River and Estuary	Jul 27	0
				Canada/USA - Great Lakes	Jul	0.02
				Canada - Maritimes	Jul 27	0.03
	29285	Female	-	USA - Cape Cod/Long Island	Jul 20	0.46
				USA - Delmarva Peninsula/Jersey Shore	Jul 21	0.04
	29286	Female	Jul 21	Canada - Southwestern Hudson Bay	Jul 22	0.01
				Canada - James Bay	Jul 24	0.01
				Canada - St. Lawrence River and Estuary	Jul 26	0.42
	29287	Male	Jul 21	USA - Maine Coast	Jul 28	0.01
				USA - Cape Cod/Long Island	Jul 29	0.35
	29289	Male	Jul 21	USA - Cape Cod/Long Island	Jul 26	0
	29290	Male	Aug 4	Canada - Southwestern Hudson Bay	Aug 4	0
				Canada - St. Lawrence River and Estuary	Aug 12	0.14
				Canada - Maritimes	Aug 13-Aug 29	16.57
	29291	Female	Jul 18	Canada - James Bay	Jul 22	0.16
				Canada - St. Lawrence River and Estuary	Jul 27	0.02
				Canada - Maritimes	Sep 4	0.23

Year	Tag ID	Sex	Departure Date	General Location	Detection Dates	Length-of-Stay (Days)
	29292	Male	Aug 2	Canada - Southwestern Hudson Bay	Aug 2	0
				Canada/USA - Great Lakes	Aug 4	0
				USA - Delmarva Peninsula/Jersey Shore	Aug 4	0.02
				USA - South Atlantic Coast	Aug 5	0.02
	29296	Male	Aug 2	Canada/USA - Great Lakes	Aug 4	0
				Northern South America	Aug 26	0
	29296	Male	Aug 2	Canada - Southwestern Hudson Bay	Aug 02	0
2019	33689	Male	-	Canada/USA - Great Lakes	Jul 29	0.01
				Canada/USA - Northeast Interior	Jul 29	0.02
	33695	Male	-	USA - South Atlantic Coast	Aug 21-Sep 9	19.68
	33702	Female	-	Canada - St. Lawrence River and Estuary	Jul 29	0.01
				Canada - Maritimes	Jul 29	0
	33705	Female	Aug 5	Canada/USA - Great Lakes	Aug 6	0.01
				Canada/USA - Northeast Interior	Aug 7	0.01
	33707	Male	Aug 7	USA - Cape Cod/Long Island	Aug 9	0.01
	33709	Male	Jul 31	Canada - Northern Manitoba	Jul 31	0.01
				Canada/USA - Great Lakes	Aug 3	0.04
				Canada/USA - Northeast Interior	Aug 4	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 4-Aug 25	21.43
	33710	Male	Aug 1	Canada/USA - Great Lakes	Aug 2	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 5-Aug 21	16.91
	33711	Female	Jul 28	Canada - Maritimes	Jul 31-Aug 2	2.86
	33713	Female	Jul 6	Canada - Northern Manitoba	Jul 6-Jul 16	10.85
				USA - Cape Cod/Long Island	Jul 20	0.01
				USA - Delmarva Peninsula/Jersey Shore	Jul 24-Aug 1	8.3
				USA - South Atlantic Coast	Aug 6	0
	34734	Female	Jul 15	Canada/USA - Northeast Interior	Jul 18	0.02
				USA - Delmarva Peninsula/Jersey Shore	Jul 19	0.16
	34737	Male	-	Canada/USA - Great Lakes	Jul 30	0.03
				Canada/USA - Northeast Interior	Jul 31	0.02

Year	Tag ID	Sex	Departure Date	General Location	Detection Dates	Length-of-Stay (Days)
				USA - Delmarva Peninsula/Jersey Shore	Aug 10	0.41
	34739	Female	Jul 9	Canada - Northern Manitoba	Jul 9	0.38
				USA - Cape Cod/Long Island	Jul 21	0
	34744	Female	-	Canada - James Bay	Jul 20	0.01
				USA - Cape Cod/Long Island	Jul 21	0
	34745	Female	Jul 25	Canada - James Bay	Jul 26	0.01
				Canada - St. Lawrence River and Estuary	Jul 27	0.01
				USA - Cape Cod/Long Island	Jul 28	0.02
	34746	Male	Aug 1	Canada/USA - Great Lakes	Aug 3	0
				USA - Delmarva Peninsula/Jersey Shore	Aug 4	0
	34747	Male	Jul 20	Canada - St. Lawrence River and Estuary	Jul 29	0.01
				Canada - Maritimes	Aug 23-Aug 29	6.83
	34748	Male	Aug 1	Canada/USA - Great Lakes	Aug 3	0
				Canada/USA - Northeast Interior	Aug 3	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 3	0.02
	34749	Female	Jul 21	Canada - James Bay	Jul 29	0.01
				Canada - St. Lawrence River and Estuary	Jul 29	0.01
	34750	Male	Aug 1	Canada/USA - Great Lakes	Aug 2	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 3	0.21
	34751	Female	Jul 18	Canada - Northern Manitoba	Jul 18	0.02
				USA - Cape Cod/Long Island	Jul 20	0
				USA - Delmarva Peninsula/Jersey Shore	Jul 21-Aug 8	18.18
	34755	Female	Jul 20	Canada - St. Lawrence River and Estuary	Jul 28	0.01
				USA - Cape Cod/Long Island	Jul 28	0.02
	34756	Female	-	Canada - Maritimes	Jul 21	0.01
	34757	Female	Jul 24	Canada - Northern Manitoba	Jul 24	0.04
				Canada/USA - Great Lakes	Aug 2	0.03
				USA - Delmarva Peninsula/Jersey Shore	Aug 4	0

Year	Tag ID	Sex	Departure Date	General Location	Detection Dates	Length-of-Stay (Days)
	34758	Female	Aug 3	Canada/USA - Great Lakes	Aug 4	0.02
				Canada/USA - Northeast Interior	Aug 4	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 4	0.01
	34759	Male	Jul 24	Canada - Northern Manitoba	Jul 24	0.01
				USA - Cape Cod/Long Island	Aug 3	0.01
	34760	Female	Jul 25	Canada - James Bay	Jul 26	0
				Canada - St. Lawrence River and Estuary	Jul 27	0.02
				USA - Maine Coast	Jul 28	0
				USA - Cape Cod/Long Island	Jul 28	0.05
	34761	Male	Aug 5	Canada/USA - Great Lakes	Aug 6	0.08
				Canada/USA - Northeast Interior	Aug 7	0.02
	34763	Male	Jul 28	USA - Cape Cod/Long Island	Jul 30	0.02
				USA - Delmarva Peninsula/Jersey Shore	Jul 31-Aug 20	20.66
	34764	Male	Jul 29	Canada/USA - Great Lakes	Jul 31	0.01
				Canada/USA - Northeast Interior	Jul 31	0.02
				USA - Delmarva Peninsula/Jersey Shore	Aug 10	0.02
				USA - South Atlantic Coast	Aug 10	0
	34765	Female	Jul 29	Canada - James Bay	Aug 9	0.01
	34766	Female	-	Canada/USA - Great Lakes	Jul 20	0.06
				USA - Cape Cod/Long Island	Jul 21	0.01
				USA - Delmarva Peninsula/Jersey Shore	Jul 22-Jul 23	1.25
	34768	Female	-	Canada - Maritimes	Aug 1	0.04
	34770	Female	-	Canada/USA - Great Lakes	Jul 30	0.01
				USA - Delmarva Peninsula/Jersey Shore	Aug 3	0.78
				USA - South Atlantic Coast	Aug 5	0
	34773	Male	-	USA - Delmarva Peninsula/Jersey Shore	Aug 11	0.08
	35834	Male	Jul 21	Canada - St. Lawrence River and Estuary	Jul 31	0.01
				Canada - Maritimes	Aug 2-Aug 20	18.56
	35835	Female	-	USA - Cape Cod/Long Island	Jul 30	0

Table S4. Timing and general locations of Semipalmated Plovers *(Charadrius semipalmatus)* tracked during fall migration using VHF transmitters and the Motus Wildlife Tracking System (www.motus.org). Migrants were radio-tagged at breeding sites near Burntpoint Creek, Ontario, Canada, 2015-2019 (*n* = 7). General locations are defined in Figure 2.5.

Year	Tag ID	Sex	Departure Date	General Location	Detection Dates	Detection Length (Days)
2016	19121	Male	Jul 19	Canada - Maritimes	Jul 19-20	0.02
	19124	Female	July 22	Canada/USA - Northeast Interior	Jul 24	1.15
				USA - Cape Cod/Long Island	Jul 24-28	4.79
	19127	Male	Jul 26	USA - Cape Cod/Long Island	Jul 27-Aug 15	18.96
	19114	Male	Jul 27	USA - Cape Cod/Long Island	Aug 03	0.04
				USA - Delmarva Peninsula/Jersey Shore	Aug 03	0.03
	19126	Female	Aug 1	USA - Cape Cod/Long Island	Aug 4-22	17.93
2018	28834	Male	Jul 26	Canada/USA - Northeast Interior	Aug 06	0.01
				USA - Cape Cod/Long Island	Aug 08	0.18
				USA - Delmarva Peninsula/Jersey Shore	Aug 8-19, Aug 21-Sep 5	26.42
2019	28846	Male	-	Canada/USA - Northeast Interior	Aug 03	0.01

Table S5. Results of a general linear model on variables explaining bearing of first flight track (degrees) of Semipalmated Plovers *(Charadrius semipalmatus)* departing breeding sites near Churchill, Manitoba, Canada, 2015-2019 (*n* = 61). Model included sex, nest fate, and departure date as predictors. Significant coefficients at α = 0.05 are indicated in bold. Adjusted $r^2 = 0.04$.

Variables	Estimate	SE	*t*	*P*
(Intercept)	14.5	53.1	0.3	0.90
Sex (male)	-0.9	4.1	-0.2	0.82
Nest fate (fledged)	-2.1	4.8	-0.4	0.70
Nest fate (post-hatch failure)	2.7	4.9	-0.2	0.80
Departure date	**0.6**	**0.3**	**2.2**	**<0.05**

Table S6. Results of a general linear model on variables explaining initial ground speeds (ms^{-1}) of Semipalmated Plovers *(Charadrius semipalmatus)* departing from Churchill, Manitoba, Canada, 2015-2019 (*n* = 38). Model included sex, nest fate, and departure date as predictors. Significant coefficients at α = 0.05 are indicated in bold (all ns). Adjusted r^2 = 0.00.

Variables	Estimate	SE	t	P
(Intercept)	-0.8	32.3	0.0	0.90
Sex (male)	0.9	2.3	0.4	0.70
Nest fate (fledged)	-1.2	2.8	-4.3	0.70
Nest fate (post-hatch failure)	-1.4	2.9	-0.5	0.60
Departure date	0.1	0.2	0.5	0.60

Table S7. Results of a linear mixed-effects model on variables explaining all ground speeds (ms^{-1}) of Semipalmated Plovers *(Charadrius semipalmatus)* on fall migration, 2015-2019 (*n* = 237). Model included sex, nest fate, and departure date as predictors and bird ID as a nested random factor. Significant coefficients at α = 0.05 are indicated in bold.

	Fixed effects				Random effect	
Variables	Estimate	SE	t	*P*	Variance	SD
(Intercept)	-21.9	16.7	-1.3	0.20		
Sex (male)	0.8	1.2	0.6	0.53		
Nest fate (fledged)	-0.2	1.5	-0.1	0.88		
Nest fate (post-hatch failure)	2.2	1.5	1.5	0.14		
Departure date	**0.2**	**0.1**	**2.3**	**0.03**		
Bird ID					2.7	1.6

Table S8. Timing and general regions of stopovers undertaken by Semipalmated Plovers *(Charadrius semipalmatus)* tracked during fall migration using VHF transmitters and the Motus Wildlife Tracking System (www.motus.org). Migrants were radio-tagged at breeding sites near Churchill, Manitoba, Canada (*n* = 40; 2015-2019). General regions are defined in Figure 2.5.

General Stopover Region	Tag ID	Sex	Year	Departure Date	Stopover Arrival Date	Stopover End Date	Stopover Length-of-Stay (days)
Canada - Southwestern Hudson Bay	33713	Female	2019	Jul 6	Jul 6	Jul 17	10.8
	34739	Female	2019	Jul 10	Jul 9	Jul 10	0.4
Canada - James Bay	24552	Female	2017	Jul 24	Jul 27	Jul 27	0.5
Canada - St. Lawrence River and Estuary	29286	Female	2018	Jul 22	Jul 26	Jul 26	0.4
Canada - Maritimes	35834	Male	2019	Jul 22	Aug 2	Aug 20	18.6
	14662	Male	2015	-	Aug 6	Aug 24	18.2
	29290	Male	2018	Aug 5	Aug 13	Aug 29	16.6
	34747	Male	2019	Jul 21	Jul 29	Aug 5	6.8
	33711	Female	2018	Jul 29	Jul 31	Aug 3	2.8
	29257	Female	2018	Jul 19	Jul 28	Jul 29	1.6
USA - Cape Cod/Long Island	24500	Male	2018	Jul 28	Jul 29	Aug 23	25.4
	24507	Female	2018	Jul 26	Jul 27	Aug 19	22.5
	14648	Male	2015	-	Aug 5	Aug 26	21.5
	34763	Male	2019	Jul 29	Jul 31	Aug 21	20.7
	24537	Male	2017	-	Jul 27	Aug 16	20.0
	20841	Female	2016	-	Aug 3	Aug 22	19.4
	24554	Female	2017	Jul 20	Aug 3	Aug 19	16.6
	24526	Female	2017	Jul 22	Jul 25	Jul 29	3.8
	24501	Male	2018	Jul 30	Aug 3	Aug 5	1.8
	14648	Male	2015	-	Aug 3	Aug 4	1.7
	20823	Male	2016	-	Aug 6	Aug 7	1.0
	14661	Female	2015	Jul 23	Jul 27	Jul 28	1.0

General Stopover Region	Tag ID	Sex	Year	Departure Date	Stopover Arrival Date	Stopover End Date	Stopover Length-of-Stay (days)
	29285	Female	2018	-	Jul 20	Jul 20	0.5
	34737	Male	2019	-	Jul 31	Jul 31	0.4
	29287	Male	2018	Jul 22	Jul 29	Jul 29	0.4
USA - Delmarva Peninsula/Jersey Shore	33709	Male	2019	Aug 1	Aug 4	Aug 26	21.4
	14670	Female	2015	-	Jul 31	Aug 21	21.3
	24556	Male	2017	Aug 4	Aug 6	Aug 25	19.5
	24555	Male	2017	Jul 30	Jul 31	Aug 19	18.9
	34751	Female	2019	Jul 19	Jul 21	Aug 8	18.2
	33710	Male	2019	Aug 2	Aug 5	Aug 22	16.9
	24531	Male	2017	Jul 30	Jul 31	Aug 15	15.8
	24521	Female	2018	Jul 19	Jul 20	Aug 4	15.7
	20823	Male	2016	-	Aug 9	Aug 22	12.3
	29272	Female	2018	Jul 27	Jul 28	Aug 8	11.3
	33713	Female	2019	Jul 7	Jul 24	Aug 1	8.3
	20835	Female	2016	Jul 26	Aug 5	Aug 8	2.5
	34766	Female	2019	-	Jul 22	Jul 23	1.2
	34770	Female	2019	-	Jul 30	Jul 31	0.6
	24508	Female	2017	Jul 27	Jul 28	Jul 28	0.5
	14664	Female	2015	Jul 29	Aug 1	Aug 1	0.2
	34750	Male	2019	Aug 2	Aug 4	Aug 4	0.2
USA - South Atlantic Coast	33695	Male	2019	-	Jul 31	Aug 20	19.7
Northern South America	29275	Male	2018	Aug 3	Sep 6	Sep 12	6.2

Table S9. Timing and general regions of stopovers undertaken by Semipalmated Plovers *(Charadrius semipalmatus)* tracked during fall migration using VHF transmitters and the Motus Wildlife Tracking System (www.motus.org). Migrants were radio-tagged at breeding sites near Burntpoint, Ontario, Canada (*n* = 3; 2016-2019). General regions are defined in Figure 2.5.

General Stopover Region	Tag ID	Sex	Year	Departure Date	Stopover Arrival Date	Stopover End Date	Stopover Length-of-Stay (days)
USA - Cape Cod/Long Island	19126	Male	2016	Aug 1	Aug 4	Aug 22	17.9
	19127	Male	2016	Jul 26	Jul 27	Aug 15	19.0
USA - Delmarva Peninsula/Jersey Shore	28834	Male	2018	Aug 6	Aug 8	Aug 19	11.0
					Aug 21	Sep 5	15.5

Table S10. Results of a generalized linear model with a binomial distribution on variables explaining stopover probability of Semipalmated Plovers *(Charadrius semipalmatus)* on fall migration, 2015-2019 (*n* = 84). Model included sex, nest fate and departure date as predictors. Significant coefficients at α = 0.05 are indicated in bold.

Variables	Estimate	SE	*z*	*P*
(Intercept)	**21.4**	**9.9**	**2.2**	**0.03**
Sex (male)	1.2	0.7	1.7	0.09
Nest fate (fledged)	0.2	0.7	0.2	0.82
Nest fate (post-hatch failure)	0.2	0.8	0.3	0.76
Departure date	**-0.1**	**0.0**	**-2.2**	**0.03**

Table S11. Results of a general linear model on variables explaining stopover length-of-stay of Semipalmated Plovers *(Charadrius semipalmatus)* on fall migration, 2015-2019 (*n* = 29). Model included sex, nest fate and departure date as predictors. Significant coefficients at α = 0.05 are indicated in bold. Adjusted R^2 = 0.21.

Variables	Estimate	SE	*t*	*P*
(Intercept)	-3.4	55.3	-0.1	0.95
Sex (male)	**8.9**	**3.6**	**2.5**	**0.02**
Nest fate (post-hatch failure)	-4.7	4.2	-1.7	0.27
Nest fate (fledging success)	-6.7	3.9	0.2	0.10
Departure date	0.1	0.3	0.5	0.82

Table S12. Results of a general linear model on variables explaining stopover latitude of Semipalmated Plovers *(Charadrius semipalmatus)* on fall migration, 2015-2019 (*n* = 29). Model included sex, nest fate and departure date as predictors. Significant coefficients at α = 0.05 are indicated in bold. Adjusted $R^2 = 0.23$.

Variables	Estimate	SE	*t*	*P*
(Intercept)	158.0	37.1	4.3	<0.001
Sex (male)	1.2	2.4	0.4	0.63
Nest fate (post-hatch failure)	2.6	2.6	1.0	0.32
Nest fate (fledging success)	4.2	2.8	1.5	0.14
Departure date	**-0.6**	**0.2**	**-3.1**	**<0.01**

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