ANTIPREDATOR NEST-DEFENSE BEHAVIOUR AND POST-BREEDING MIGRATION OF TWO POORLY UNDERSTOOD SUBARCTIC BREEDING SHOREBIRDS, THE SHORT-BILLED DOWITCHER (*LIMNODROMUS GRISEUS HENDERSONI*) AND THE STILT SANDPIPER (*CALIDRIS HIMANTOPUS*)

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"The nests (of these trustful and confiding birds) must be about the hardest of all shore-birds to find."

– Rowan 1927, on Short-billed Dowitchers

ABSTRACT

Olivia R. Maillet

Antipredator Nest Defense Behaviour and Post-breeding Migration of Two Poorly Understood Subarctic Breeding Shorebirds, the Short-billed Dowitcher (*Limnodromus griseus hendersoni*) and the Stilt Sandpiper (*Calidris himantopus*).

Understanding threats to declining species at multiple stages of their annual cycle is important for determining the cause of their declines and conserving their populations. To assess potential responses to changing habitat and predators under climate change, I compared the nest site characteristics, responses to human intruders, and migratory patterns between Short-billed Dowitchers and Stilt Sandpipers breeding in Churchill, MB. I conducted behavioural observations and habitat surveys and deployed radio transmitters on birds during incubation. Short-billed Dowitcher nests had higher concealment and adults were more aggressive than Stilt Sandpipers. Short-billed Dowitchers took an eastern migratory route and stopped in the southeast US, whereas Stilt Sandpipers migrated west. Short-billed Dowitchers displayed relatively high connectivity during migration with nearly 1/3 of confirmed stopovers occurring at a single site in Georgia. These findings highlight the importance of considering varying antipredator defense and migration strategies in the face of climate change.

Keywords: incubation, nest concealment, Motus, migratory connectivity, Midcontinent, Central Flyway

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CHAPTER 1 – GENERAL INTRODUCTION

Shorebirds are declining rapidly, and for many species, the causes of these declines are not well understood (Rosenberg et al. 2019, Smith et al. 2023a). Anthropogenic effects, including climate change, are increasingly threatening to shorebirds at all stages of their annual cycle. During breeding in the subarctic and arctic, habitat change due to the encroaching treeline may influence available nest sites (Ballantyne and Nol 2015), a habitat change that could benefit boreal-nesting species and adversely affect species that breed in open tundra. Anthropogenic disturbance and changes to sensitive coastal wetlands and barrier islands required for stopovers and wintering (Pfister et al. 1992, Iwamura et al. 2013), and hunting potentially exceeding sustainable limits during the non-breeding season (McDuffie et al. 2022a), may influence shorebird populations. Carry-over effects from the migration period can also influence reproductive success in arctic shorebirds (Clements et al. 2022). Examining threats to shorebirds at multiple stages of the annual cycle is crucial to developing a clear understanding of conservation priorities.

Responses to climate change in the north are expected to differ amongst taxa (Green 2010). Species at the edges of their range may be especially vulnerable to changes in habitat availability (Cobben et al. 2012, Wheeler et al. 2018, Orme et al. 2019) or shifting predator communities (Elmhagen et al. 2017). These distributional changes have already been documented in arctic-breeding shorebirds, with evidence that some warmer-breeding shorebirds may be moving in and colder-breeding shorebirds may be moving out of survey areas, suggesting a northward shift (Anderson et al. 2023). Therefore, examining the ecology of species breeding at the leading and trailing edges of their ranges may provide insight into the causes of population decline. In the Churchill, Manitoba, Canada region, the Short-billed Dowitcher

(*Limnodromus griseus hendersoni*) is at the leading edge of its range, and the Stilt Sandpiper (*Calidris himantopus*) is at the trailing edge of its range, so their responses to climate change may differ. In this thesis, I compare the behaviour of these two understudied shorebirds during two stages of the annual cycle: breeding and post-breeding migration at a site where one is at the northern part of its breeding range (Short-billed Dowitcher) and the other is at the southern part (Stilt Sandpiper).

The Stilt Sandpiper is an arctic-nesting long-distance migrant bird species that has declined significantly (Jehl 2004, Klima and Jehl 2020, Smith et al. 2023a). The Short-billed Dowitcher is a subarctic and boreal-nesting intermediate-distance migrant bird species that has been studied at only a few breeding locations and is also showing indications of declining populations (Jehl and Hussell 1966, Harris 1989, Jehl et al. 2020, Smith et al. 2023a). Both birds are regular breeders in wet sedge meadows or fens in the Churchill, Manitoba region of Canada, a site that sits on the ecotone between boreal forest and tundra habitats in the western Hudson Bay Lowlands (Dredge and Dyke 2020). Most observations of both species are from the 1970s-1990s and are summarized in Klima and Jehl (2020) and Jehl et al. (2020). Their populations may be particularly vulnerable to both shrub and tree encroachment into previously open wetland habitats in the sub-arctic. Also, little is published about their migration, their stopovers, or their final non-breeding locations.

Both Short-billed Dowitchers and Stilt Sandpipers are monogamous, biparental incubators (Jehl 1973, Harris 1989, Jehl et al. 2020, Klima and Jehl 2020). Both species typically lay 4 eggs in a small nest cup on or on the side of hummocks and incubate for ~3 weeks before eggs hatch synchronously. Their first nest attempts are initiated in late May to early June and hatch mid-June to early July, with second attempts hatching in mid-July. Their incubation is divided approximately equally between males and females with some diel patterns; female Stilt Sandpipers and male Short-billed Dowitchers incubate mainly during the night (Jehl et al. 2020, Klima and Jehl 2020). After hatch, males take on most chick-rearing responsibilities in both species, with the female leaving after 1-3 (maximum 7 in Stilt Sandpiper) days, presumably to migrate (Jehl and Smith 1970, Jehl et al. 2020, Klima and Jehl 2020).

Despite significant declines in abundance during migration (Smith et al. 2023a), Short-billed Dowitchers may be increasingly common in the Churchill region, though increases could be due to changes in search effort. Historical impressions suggested that they were rare to uncommon in the 1930s-1940s (Taverner and Sutton 1934, Grinnell and Palmer 1941), uncommon to common in the 1970s-1990s (Jehl and Smith 1970, Jehl 2004), and during the Arctic Shorebird Demographic Network surveys (2010-2014), a period when there was intensive searching of potential shorebird habitats in the Churchill region by up to 6 researchers (E. Nol pers. comm), 44 nests were found over 4 years. Based on these historical impressions, Short-billed Dowitchers appear to be increasingly common in the Churchill region. However, because their nests can be difficult to find, nest searching methods differ, and effort within a single season may differ, trends in the density of nests found over time may not reflect true population trends. Contrary to the trends observed in Short-billed Dowitchers, Stilt Sandpipers are declining in the Churchill region. Since early studies in the 1930s when Stilt Sandpipers were described as one of the most common shorebirds in Churchill (Taverner and Sutton 1934), they have been later described as common in the 1960s (Jehl and Smith 1970), and increasingly uncommon in the 1990s (Jehl 1997). In 1999, just one nest was found, and no nests were found in 2000 (Jehl 2004). During the Arctic Shorebird Demographic Network surveys, 10 nests were found over 4 seasons of dedicated shorebird nest searching ("Churchill 2010-2014 Arctic Shorebird Demographic Network" 2014). Just one nest was found in 2018 (Brown et al. 2022).

Over three breeding seasons in June and July of 2021-2023 over approximately 7 km^2 of search area I found and monitored nests of Short-billed Dowitchers and Stilt Sandpipers breeding in the Churchill, Manitoba, region. I tracked their nest success, attempted to individually mark each bird, conducted behavioural observations during nest checks, and conducted habitat surveys, with special reference to the degree to which they are concealed by vegetation or associated with nearby trees and shrubs (Holmes et al. 2020). In addition to banding for resighting purposes, I deployed a small radio transmitter on each adult I banded to track their migration south.

This research is significant because it is still largely unknown, for either species, why their populations have declined, their sensitivity to encroaching trees and shrubs from lengthening growing seasons, and the stage of their annual cycle where they are most vulnerable to mortality. The Churchill region is especially interesting to this study as it is one of the only locations in the world at which both species breed and are accessible for research (Jehl et al. 2020, Klima and Jehl 2020). This provides an opportunity to compare the differing potential responses to climate change between bird species that breed at opposite edges of their ranges.

Objectives

This thesis contains two data chapters; first, in Chapter 2, I examine events occurring during the breeding season. The objectives for Chapter 2 are to compare the nest site characteristics and incubation behaviour between an arctic breeder at the southern limit of its range (Stilt Sandpiper) and a boreal breeder at the northern limit of its range (Short-billed Dowitcher) by 1) determining how their nest site characteristics, especially concealment, differ between species, 2) comparing their antipredator nest-defense behaviour, and 3) assessing how these factors may influence their individual responses to climate change. Second, in Chapter 3, I examine events occurring during post-breeding migration. The objectives for Chapter 3 are to 1) examine the effect of sex and nest hatch date on departure date, 2) track the pathways, speed, and timing of post-breeding migration of Short-billed Dowitchers and Stilt Sandpipers using the international and collaborative Motus Wildlife Tracking System, 3) and describe stopover sites. Finally, in a concluding Chapter 4, I summarize the findings of my thesis, discuss potential conservation implications, and emphasize the research priorities for both species.

CHAPTER 2 – NEST CONCEALMENT AND ANTIPREDATOR BEHAVIOUR OF THE SHORT-BILLED DOWITCHER AND STILT SANDPIPER

ABSTRACT

Changing vegetation and animal communities in the subarctic may influence the behaviour and nest success of breeding shorebirds. Nest site characteristics and antipredator defense behaviour in two cryptic shorebirds, Stilt Sandpipers (*Calidris himantopus*) and Short-billed Dowitchers (*Limnodromus griseus hendersoni*), are known only by qualitative descriptions. At a treeline site in Churchill, Manitoba, Canada, the Stilt Sandpiper is breeding at the southern limit of its largely arctic range, whereas the Short-billed Dowitcher is breeding at the northern limit of its largely boreal range. My objective was to determine if Short-billed Dowitchers and Stilt Sandpipers have differing nest site characteristics, especially concealment, and if, as a result, they employ different antipredator defense strategies to minimize detection during incubation. I measured nest site vegetation and the extent of concealment at nest sites and scored behavioural responses to human intruders at regular visits to Short-billed Dowitcher and Stilt Sandpiper nests at fens in the Churchill, Manitoba, Canada region. Water depth and vegetation height within 1 m^2 of Short-billed Dowitcher nests were significantly higher than those around Stilt Sandpiper nests, but there was no difference in habitat cover types at or around the nest. Vertical (from above) and horizontal (from the sides) concealment were significantly greater at Short-billed Dowitcher nests. While both species exhibited a range of defense behaviours, Short-billed Dowitchers flushed nearly underfoot and engaged in significantly more aggressive defense behaviours, such as distraction displays, whereas Stilt Sandpipers typically flushed from their nests or departed

before we arrived, but there was substantial individual variation. These differences highlight the importance of considering such nuanced behaviors in the context of ongoing environmental changes in the subarctic.

INTRODUCTION

Shorebirds are experiencing some of the steepest and most concerning declines of all North American birds (Rosenberg et al. 2019, Smith et al. 2023a). These declines may be linked to events that occur during their breeding season, for example, events that reduce nest success. Nest success in arctic shorebirds can be explained by a variety of factors including habitat characteristics (Laidlaw et al. 2020), incubation behaviour (Meyer et al. 2020), predation pressure (Smith et al. 2007), and nest-defense behaviour (Smith and Wilson 2010). Because predation is the primary cause of nest failure for arctic shorebirds (Smith et al. 2007), nest success is directly related to predation risk.

Habitat selection in shorebirds is non-random. It is based on concealment to avoid predation and maintenance of a suitable microclimate to incubate eggs (Amat and Masero 2004, Miller et al. 2014). Shorebirds tend to nest in open areas with high visibility to allow them to detect predators but, across species, they employ differing strategies for nest concealment. For example, Upland Sandpipers (*Bartramia longicauda*) select nest sites with fewer trees and greater herbaceous cover (Miller et al. 2014) than what is available in the landscape. Poorly concealed nests of ground-nesting shorebirds may have higher predation rates than those that are well-concealed (Laidlaw et al. 2020). Nonetheless, because nest habitat selection is related to predation risk, shorebirds should select nests in locations that maximize the success of their breeding attempt.

Shorebird breeding habitat in the arctic and subarctic is threatened by climate change and grazing by hyperabundant light geese (i.e. Snow Goose, *Anser caerulescens*), both of which are significantly altering tundra ecosystems and may be limiting suitable nesting habitat for shorebirds that require open and graminoid-covered nest sites (Wauchope et al. 2017, Flemming et al. 2019). Climatic changes to subarctic habitats are reducing the amount and quality of preferred nesting sites for shorebirds (Swift et al. 2017) through interactions between warmer growing seasons, increased shade, and snow accumulation, colloquially known as 'shrubification' (Cutler 2011). These changes include a shift from graminoid-dominated vegetation to a drier, shrub-dominated community through an increase in biomass of willow (*Salix spp.*), alder (*Alnus spp*.), and birch (*Betula spp.*) (Chapin III et al. 2000, Myers-Smith et al. 2011, Fraser et al. 2014).

Although the effects of habitat change may be slow and difficult to observe over a short period of time, studies have already demonstrated a change in nesting habitat for shorebirds by both shrubification and grazing by hyperabundant geese. For example, encroaching shrubs and trees have reduced suitable breeding habitat for Whimbrel (*Numenius phaeopus*) near Churchill, Manitoba, reducing the number of breeding pairs in a historically high-density nesting area (Ballantyne and Nol 2011). These vegetation changes at this subarctic site are also expected to reduce the extent of available nesting habitat for Dunlin (*Calidris alpina*) and Hudsonian Godwit (*Limosa haemastica*) (Swift et al. 2017, Holmes et al. 2020). Additionally, densities of cover-nesting and open-nesting shorebirds have been reduced at sites with high goose density (Flemming et al. 2019). Understanding the factors that influence habitat availability and nest success in lesser-understood shorebirds is increasingly important as it may enable us to identify drivers of their population changes.

Nest habitat influences nest success in many studies, however, in some shorebird species, there is little support for the hypothesis that variation in nest success is related to habitat characteristics (Holmes et al. 2020), and instead, incubation behaviour influences nest outcomes (Miller et al. 2014). Antipredator nest-defense is defined as any behaviour by a parent that decreases the likelihood of nest predation (Montgomerie and Weatherhead 1988). This behaviour either obscures the nest location in the first place or actively distracts the predator from the nest once it is located. Many shorebirds perform some form of antipredator defense behaviour but the effectiveness of these behaviours in preventing predation is poorly known (Smith and Edwards 2018).

Shorebirds employ a variety of flushing behaviours. Upon detecting an intruder, they may either flush or sit tight and remain undetected. Those who flush at a relatively short distance between the intruder and the nest may engage in aggressive antipredator behaviour by either calling, feigning injury to distract from the nest ("broken-wing display") or performing a "rodent run" in which the parent scurries away from the nest on foot. Each of these behaviours shift the focus from the nest location to the adult bird (Armstrong 1954). In some arctic-breeding shorebirds, short-distance flushes are associated with birds that actively defend their nest, and lower levels of predation (Smith and Edwards 2018). Long-distance flushes are also associated with lower levels of nest predation because the predator must search a larger area to find the nest. These long-distance flushes, along with those who do not actively defend their nest, are sometimes referred to as "passive defense", although they do involve an active decision by the incubator (Sanchez-Gomez et al. 2024). Finally, intermediate-distance flushes are associated with higher levels of nest predation (Smith and Edwards 2018).

These flushing and defense behaviours may vary between and within a species. Biparental shorebirds may flush at a greater distance than uniparental species (Smith and Wilson 2010). In some biparental shorebird species such as Semipalmated Plovers (*Charadrius semipalmatus*), Black-bellied Plovers (*Pluvialis squatarola*), and Ruddy Turnstones (*Arenaria interpres*), incubators react to nest intruders with greater intensity as nests age. As the time, and therefore energy invested in eggs increases as they approach their hatch date, biparental shorebirds may be less willing to flee the nest, displaying stronger antipredator defense behaviour than earlier in incubation (Smith and Wilson 2010). These aggressive reactions to predators can result in successful nest-defense and therefore higher nest survival (Larsen et al. 1996).

The impacts of shrubification on shorebirds and other birds are expected to vary between species as each has a unique set of habitat requirements and geographical ranges. While some boreal-nesting bird species at the edge of their ranges may experience range expansions past the historical treeline (Wheeler et al. 2018), arctic-nesting species living in these transitionary treeline habitats may be limited by suitable nest sites or forced to abandon historic nesting sites entirely (Ballantyne and Nol 2015). Because shorebirds have varying levels of cover at their nests and different strategies for defending their nests, habitat change may influence their ability to breed successfully. Therefore, it will be important to address the impacts of shrubification on population change not only at the core but at the leading and trailing edges of a species' geographical range where they may be most sensitive to habitat change (Wheeler et al. 2018).

The Short-billed Dowitcher (*Limnodromus griseus*) is a medium-sized intermediate-distance migrant shorebird breeding in the boreal and subarctic regions of Canada and Alaska. At the Churchill study site in northern Manitoba, Canada, the *hendersoni* subspecies is expected.

Due to the inaccessibility of its breeding sites to visiting Western scientists and the difficulty in locating its nests, the basic breeding biology of the Short-billed Dowitcher remained poorly documented in published literature until the mid-19th century. Despite being commonly observed during its annual migration (Skagen et al. 1999) the Short-billed Dowitcher is still one of the least understood of the North American shorebirds. Our limited knowledge of its breeding biology comes from a small number of nests from only four locations across its entire breeding range: Alberta, Canada (e.g., (Rowan 1927)), southern Alaska, U.S. (e.g., (Hurley 1932)), Schefferville, Quebec, Canada (e.g., (Harris 1989)), and Churchill, in northern Manitoba, Canada (e.g., (Jehl and Hussell 1966)). Although currently listed as Least Concern, they have been identified as a ‘tipping point species’, defined as one of 70 bird species that have lost two-thirds of their population in the last 50 years, and are on track to experience a further 50% decline in the next 50 years (North American Bird Conservation Initiative 2022) and their population is estimated to have declined by ~85% between 1985-2019 (Smith et al. 2023a).

The Stilt Sandpiper (*Calidris himantopus,* previously monotypic *Micropalama himantopus,* now included in the genus *Calidris*) is a medium-sized shorebird breeding in arctic and subarctic tundra across Canada and Alaska. Most of the limited published literature describing the behaviour and migration of the Stilt Sandpiper comes from studies in the 1970s (Jehl 1973) and 1990s (Jehl and Lin 2001) and observations published in Klima and Jehl (2020). Like Short-billed Dowitchers, Stilt Sandpipers have also been identified as a ‘tipping point species’ (North American Bird Conservation Initiative 2022) and their population is estimated to have declined by ~75% between 1985-2019 (Smith et al. 2023a). In the Churchill region, the number of breeding pairs declined by 80% between studies in the 1960s-1990s (Jehl 1973, Jehl and Lin 2001). In Churchill, Short-billed Dowitchers and Stilt Sandpipers nest in flooded meadows dominated by sedge hummocks. However, the microhabitat characteristics of their nests are not well known, with current knowledge primarily based on qualitative descriptions (Jehl et al. 2020, Klima and Jehl 2020).

Antipredator defense behaviour in Stilt Sandpipers and Short-billed Dowitchers and their responses to human intruders are also known by qualitative descriptions. Stilt Sandpipers are described to leave nests inconspicuously and are rarely surprised off nests (Jehl 1973). When flushed at the nest, they may challenge the intruder with a wing-up display, threat song, and less commonly, distraction displays (Jehl 1973). By contrast, Short-billed Dowitchers are described to only occasionally leave the nest when humans are far away, and almost invariably flush underfoot (Jehl et al. 2020). Other descriptions of parental behaviour approximately a week before hatch suggest that the incubating Short-billed Dowitcher will leave the nest to confront a human intruder (Jehl et al. 2020). Both species freeze on their nests in response to avian predators (Jehl et al. 2020, Klima and Jehl 2020). In other species, nest age does influence reaction strength (Smith and Wilson 2010), but this has not been investigated for Short-billed Dowitchers and Stilt Sandpipers.

In this study, I compared the nest site characteristics, nest concealment, and antipredator nest behaviour between the Short-billed Dowitcher at the northern part of its breeding range and the Stilt Sandpiper at the southern part of its breeding range, both nesting at a subarctic site at the treeline. Because their breeding range mostly encapsulates the boreal forest and subarctic, I expected Short-billed Dowitchers to select nest sites associated with more cover: taller vegetation types, closer to trees, and at a macrohabitat scale, taller trees and a higher density of trees, and as a result, flush at a closer distance and employ active antipredator defense such as calling, distraction displays, or aerial attacks. I expected that Stilt Sandpipers, typically breeding at higher latitudes, would select nest sites with shorter vegetation types, further from trees, and at a macrohabitat scale, shorter trees/shrubs and a low density of trees around the nest, and would flush at a far distance, employing passive defense such as an unobservable departure from the nest or a flush to minimize detection. Because close flushes may force direct confrontation of the intruder, as opposed to far flush distances where the incubating bird can avoid the intruder, reaction strength should decrease with flush distance similarly in both species. As nests progressed and approached hatch, I expected the commitment to the nesting attempt to increase, and that it would correspond to stronger reaction strength, and therefore a closer flush distance.

METHODS

Study Area

The Churchill, Manitoba region (58°45’N, 95°04’W) is a transitionary zone at the northern edge of the western Hudson Bay Lowlands of Canada, an ecoregion stretching along the coast from northern Manitoba to southern James Bay. The region is characterized by its coastal beach and greywacke and quartzite cliffs near the ocean, gravel ridges, subarctic tundra, wetland complexes, sedge and grass fens, and boreal forest inland (Dredge and Dyke 2020). In this region, cover-nesting shorebirds breed in fens and wet meadows dominated by sedges (*Carex sp.*) and grasses, small flowering vegetation (e.g., *Andromeda polifolia*, *Rhododendron lapponicum*) with shrubs (*Betula sp.*, *Salix sp.*) and sparse trees (*Larix laricina*, *Picea mariana*). Within these habitats, shorebirds nest on hummocks or dry areas. Early in the spring, these hummocks are typically surrounded by water, which later dries to mud and the grass surrounding the hummocks becomes denser by mid-to-late July.

Fieldwork was conducted at two main sites in the Churchill area where Short-billed Dowitchers and Stilt Sandpipers have nested and/or have been observed in recent years (Jehl and Lin 2001, Sullivan et al. 2009) (Figure 2.1, Figure 2.3). The first site (Twin Lakes Fen; 58.67029°N, 93.83457°W) is a large 4.4 km^2 wet sedge meadow north of the Twin Lakes and the second site (Airport; 58.741354°N, 94.063753°W) is a smaller 2.3 km^2 wet sedge meadow beside the runway at the Churchill Airport. Several nests were also found outside these sites by other researchers during their research activities.

Figure 2.1. Survey sites for Short-billed Dowitcher (*Limnodromus griseus hendersoni*) and Stilt Sandpiper (*Calidris himantopus*) nests in 2021-2023. The general location of all searched sites is indicated with a white circle, and sites with success in finding nests of either species are indicated with a triangle. Nests were found incidentally at Landing Lake Road and Twin Lakes Road by other research teams but were not surveyed by us.

The Twin Lakes Fen and Airport Fen have similar habitats (Figure 2.3). Both are large, flooded meadows with hummocks and interspersed with small ponds and emergent palsas, both of which are more common at the Airport Fen. Trees are sparse and stunted but become taller and denser along the southern edges of both plots where the transition to boreal forest begins. The raised and paved airport runway marks the north and west edges of the Airport Fen plot, and a gravel road marks the south edge. Past the southern edge is more wetland habitat that I did not search because it was much drier and lacked displaying shorebirds early in the season. The gravel Twin Lakes Road marks the west edge of the Twin Lakes Fen plot, separating it from the west side of the fen, which was drier, more treed, and with fewer shorebirds displaying early in the season. The eastern edge of the Twin Lakes Fen is McQueen Lake, and the northern and southern edges are more densely treed and lacked shorebird nests.

Figure 2.2. Short-billed Dowitcher (*Limnodromus griseus hendersoni*) and Stilt Sandpiper (*Calidris himantopus*) nest sites in 2021-2023 in the Churchill, Manitoba area. Short-billed Dowitcher nests are indicated with a triangle, and Stilt Sandpiper nests are indicated with a circle.

Figure 2.3. Typical wet sedge fen habitat in Churchill, Manitoba, where Short-billed Dowitchers and Stilt Sandpipers nest. This photo is from early in the season (early June), around the time when nest-site selection would occur. Nests are placed on hummocks.

Predators that have been confirmed to depredate either nests or artificial nests of shorebirds in the Churchill area include avian predators such as Parasitic Jaegers (*Stercorarius parasiticus*), Common Ravens (*Corvus corax*), Herring Gulls (*Larus argentatus smithsonianus*), and other raptors, and mammalian predators such as red foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) (Brown et al. 2022). At the Twin Lakes Fen site, predators of real shorebird nests recorded on camera traps are Parasitic Jaegers and arctic foxes, whereas at the Airport Fen, just predation by a red fox has been recorded on camera traps (Brown et al. 2022). The same study reports the average distance to a shorebird nest from an active fox den as 3.32 ± 0.28 km in 2018 and 2.81 ± 0.20 km in 2019 (Brown et al. 2022)

Casual observations of potential predators of shorebird nests for the duration of this study differed between plots. At the Twin Lakes Fen only, I regularly observed one (possibly two) nesting pairs of Parasitic Jaegers and up to seven individuals at once. Parasitic Jaegers were often aggressively chased by shorebirds, almost invariably Whimbrel and Hudsonian Godwits. I once observed a nesting Parasitic Jaeger catch and eat a juvenile, but fully fledged Lesser Yellowlegs (*Tringa flavipes*) after a short aerial chase. One Short-eared Owl (*Asio flammeus*), one Northern Harrier (*Circus hudsonicus*) and 1-6 Sandhill Cranes (*Antigone canadensis*) were occasionally observed at the Twin Lakes Fen. At the Airport Fen, Herring Gulls were commonly observed (2-3 individuals) and a territorial pair of Merlins (*Falco columbarius*) was uncommonly observed. Common Ravens were relatively common at both sites early in incubation (1-3 individuals) when Canada Goose (*Branta canadensis*) nests were abundant. I observed ravens carrying Canada Goose and Whimbrel eggs. An aggressive Arctic Tern (*Sterna paradisaea*) colony prevented any predators from remaining in the Airport Fen area for more than a couple of minutes. I observed one polar bear (*Ursus maritimus*) at each site, but no other mammalian predators at these plots in any year during our fieldwork.

Nest Searching and Monitoring

Nests were located by teams of 2-5 people (most often 2) walking through wet sedge meadow plots in the study area approximately 5-10 m apart. Because these shorebird nests are difficult to find, especially those of the Short-billed Dowitcher, I employed many different methods of finding nests of both species with varying success (Table 2.1). Our methods of finding nests included 1) walking through suitable habitat (sedge meadow hummocks surrounded by pools of water with sparse shrubs and spruce trees) and flushing incubating birds, 2) two observers each holding an end of an 8-12 m rope that had plastic bottles half-filled with rocks attached at each meter, walking through sedge meadows and lightly bouncing the rope in the air to create a rattling sound to flush incubating birds, 3) watching behavioural cues and following a single adult bird to a nest, 4) listening to chick calls and adult "hush" and alarm calls to locate an adult brooding chicks in a freshly hatched nest, and 5) visiting previous nest sites recorded during the years 2010-2022 as territorial fidelity is very high in Stilt Sandpipers (Jehl 1973).

Table 2.1. Methods for finding Short-billed Dowitcher (*Limnodromus griseus hendersoni*) and Stilt Sandpiper (*Calidris himantopus*) nests during incubation and their success in the Churchill, Manitoba region in 2021-2023.

Method	Short-billed Dowitcher	Stilt Sandpiper
Incidental (walking)	23	2
Dragging rope (2022/23 only)	9	1
Follow to nest site	1	3
Adult brooding fresh chicks in nest (calling)	2	0
Returning to old nest site	0	3

When I found nests, I marked them with a small wooden stick (20 mm wide and 50-100 mm above the ground) about 5 m away to help relocate the nests, as this was sometimes difficult with Short-billed Dowitchers who did not flush until I stepped 0.5 m away. I marked each nest location with a handheld Garmin GPS (accurate to ± 3 m). If a nest was found during lay or hatch, I estimated the initiation and hatch dates based on the laying and incubation period for each species. If a nest was found with a full clutch, I floated 2-4 eggs (Liebezeit et al. 2007) to determine the approximate initiation date and hatch date. Because no specific tool exists for the Short-billed Dowitcher, I used the hatch date estimation based on the closely related Long-billed Dowitcher (*Limnodromus scolopaceus*, Say, 1822) (Liebezeit et al. 2007).

Once a nest was thought to be complete and past early incubation (~1 week) I attempted to capture both parents using a bow-net ground trap (diameter = 61 cm, net gauge = 1.5 cm x 1.5 cm). I captured one incubating bird at a time due to the tendency of the off-duty Short-billed Dowitchers and Stilt Sandpipers to forage outside of their territory (Jehl et al. 2020, Klima and

Jehl 2020). Each bird received a metal band and a unique combination of colour bands or an engraved alpha-number-number flag over a single colour band for later identification during nest checks and resighting in future years. All markers were applied to the upper legs to increase visibility during nest checks and limit corrosion, as both species tend to wade in water (Gratto-Trevor 2018). Aluminum bands, stainless steel bands, and colour bands applied in 2021 and 2022 were still field-readable on all resighted birds (3 individuals in 2022, 12 individuals in 2023) (Supplementary Table S1). The sex of Stilt Sandpipers was determined using blood samples (n = 5), the sex of the partner (n = 1), recaptures of previously sexed birds (n = 4), and cloacal protuberance of the female and/or behaviour (n = 2) (Pyle 2008) (Supplementary Table S3). Blood samples were analyzed by O. Haddrath of the DNA laboratory, Royal Ontario Museum, Toronto, Ontario, Canada. The sex of Short-billed Dowitchers was determined by comparing the culmen length to ranges published in Pyle (2008) (n = 26) as the female's culmen averages longer, and if measurements were ambiguous (n = 16), the likely sex was determined with the likely sex of the mate (Supplementary Table S4). The work was conducted under the Bird Banding permit #10515 AT and a protocol approved by the Animal Care Committee at Trent University.

I visited each nest at an interval of approximately every 3 days to check the status and check for any signs of hatch. I chose this interval to minimize disturbance to incubating birds (MaCivor et al. 1990, Kurucz et al. 2015). Although it is unclear whether human scent trails made while monitoring nests may attract mammalian predators (Weldon 2022), I limited the directness of our trail towards the nest, the reuse of our trails towards nests, and the trampling of vegetation surrounding the nest. Each nest check lasted about 10-30 seconds to determine if a parent was incubating, the colour band combination of the parent, the strength of reaction to our visit, and closer to hatch, whether any eggs showed signs of hatch. Our presence at the nest was longer (up to one minute at the nest and 20 minutes in the vicinity) if I was setting a trap to capture the adult birds.

If any avian or mammalian predators were seen in the area (most commonly Common Raven (*Corvus corax*) and Parasitic Jaeger (*Stercorarius parasiticus*), I postponed nest checks until the next day or until the predator was no longer in the area. Because both shorebird species can nest very close to Parasitic Jaeger nests (as close as ~150 m away in this study), I did not drag a rope in any area defended by jaegers, so as not to flush birds and alert predators to nest locations. I conducted nest searching and nest checks in mild weather using both predetermined cut-offs and judgment based on perceived weather for the safety of the birds and their nests: temperature of 5° - 25°C, wind of <60 km/hr, no heavy rain or snow. I did not flush birds off nests if they were shading eggs on hot and sunny days.

I checked nests more frequently 3 days before the estimated hatch date, where possible, every day once pipped, and checked eggs for hatch signs. Short-billed Dowitcher eggs show star cracks 2-3 days before hatch, and pip 1 day before hatch (Jehl et al. 2020). In Stilt Sandpipers, eggs show hairline cracks 3-4 days before hatch, and pip 10-14 hours before hatch (Klima and Jehl 2020). I used these signals and known timing to accurately determine the hatch date and nest fate. I considered nests to have been depredated if there were no eggs, large eggshells, or membranes in the nest or nearby prior to the estimated hatch date (Mabee 1997). I considered nests to be successful if I observed at least one fully hatched chick or if there was evidence of hatched eggshells (tiny pieces from hatching in the nest, or hatched shells carried and dropped away from the nest cup) and parents were located acting defensively. Nests lacking evidence for either a successful hatch or depredation were recorded as unknown fate. When eggs hatched, I attempted to band all chicks in the nest with a metal band and a single colour band combination specific to that nest. I attempted to resight chicks during habitat surveys later in the season (approximately 1 July – 1 August) but this was rarely successful as the chicks and adults of both species depart the nest area as soon as they are dry (Jehl et al. 2020, Klima and Jehl 2020).

Nest Habitat and Concealment Measurements

All habitat data were collected after the nest fate was determined to avoid disturbance to incubating adults and chicks and to avoid trampling of vegetation during incubation (between 3 July – 5 August). I attempted to measure all parameters as soon as possible after hatch, sometimes prior to the emergence of new green vegetation, so that they would better reflect the conditions at nest site selection and during incubation. To measure horizontal concealment, I stood a 7 cm x 7 cm cardboard checkerboard square on the North, East, South, and West walls of the nest cup and counted the number of visible squares at a crouching position of 0.5 m tall, at 5, 10, and 20 m away from the nest cup (Smith et al. 2007, Holmes et al. 2020). To measure vertical concealment, I placed this same checkerboard square flat on the center of the nest cup and counted the number of visible squares from 1 m directly above the nest. I calculated the extent of each measure of concealment by dividing the number of concealed squares by total squares (for example if 5 squares were visible, 44/49 = 0.898 of the checkerboard concealed).

I defined the scale within a 1 m^2 quadrat centred on the nest cup as the microhabitat (Holmes et al. 2020). At each microhabitat scale, I estimated the percent cover of 1) graminoid (grass, sedge), 2) shrub/tree including dwarf birches, willows, black spruce, and tamarack, 3) woody-stemmed plants such as Lapland rosebay, black crowberry (*Empetrum nigrum*), and bog rosemary, 4) herbaceous plants such as bogbean (*Menyanthes trifoliata*) and any other greenstemmed plant, 5) lichens, 6) moss, 7) mud or dead vegetation, and 8) standing water. I measured the natural height of the tallest vegetation, which was always old, dry grass from the previous year. I measured the distance from the nest cup or unused site point to the nearest tree or shrub over 0.5 m. I measured water depth (cm) around the nest cup with a ruler at 2-4 randomly generated points.

At the mesohabitat scale, which I defined as 5 m^2 around the nest, I measured water depth with a ruler at 2-4 points generated blindly with one person spinning at the nest cup and on the command of another person, tossing a meter stick and measuring water where it landed. Following the same methods I used for the microhabitat, I estimated percent cover within a 1 m^2 quadrat centred at four points 5 m away from the nest cup, each in North, West, East, and South directions.

I defined the macrohabitat scale as a 40 m radius around the nest as in Holmes et al. (2020). I counted the number of trees or shrubs, defined as woody vegetation ≥ 0.5 m tall, within a 40 m radius from the nest cup and measured the height of each tree or shrub ≥ 0.5 m tall in this radius. The species or genera of shrub/tree that were counted included dwarf birches (*Betula sp*.), willows (*Salix sp.*) black spruce (*Picea mariana*), and tamarack *(Larix laricina*). Due to time constraints in 2023, I counted and measured trees only in one randomly selected quarter and multiplied the # trees by 4 to estimate the total in the entire 40 m radius. The number and height of trees were not counted at one Short-billed Dowitcher nest (22SBDO07, Figure 2.2, "Landing Lake Road") because it was located on a hummock in the middle of a pond surrounded by forest and the terrain was impossible to traverse. The habitat characteristics of two Stilt Sandpiper nest sites first used in 2022 and reused in 2023 were assessed in both years.

Measuring Antipredator Nest-defense Behaviour

At each nest visit, I recorded the behaviour of the incubating bird. Using a handheld GPS to navigate to the nest site, I began watching for signs of movement or flushing at approximately 100 m away from the nest. For consistency between visits, 2 observers walked towards active nesst together, though the inaccuracy of handheld GPS units in determining the exact nest location made this difficult at times. We watched carefully for movement, and I recorded the distance between us and the nest when the bird flushed with either the handheld GPS unit or pacing if we were close enough (<15 m). When the bird flushed, I also scored its reaction strength on a scale of 0-4: 0 = unattended nest upon arrival, 1 = flush but no vocal or active response (a "pure flush"), 2 = alarm calling only (no distraction display), 3 = distraction display (either "rodent-running" or a broken-wing display which typically includes calling (Gochfeld 1984)), and 4 = aerial attack (similar to (Smith and Wilson 2010) and adapted for these species).

Statistical Analysis

All analyses were conducted in R through RStudio version 4.3.0 (R Core Team 2023). Data were filtered and processed with the package 'dplyr' (Wickham et al. 2023). All plots were generated in R (R Core Team 2023) using packages 'ggplot2' (Wickham 2023) and 'cowplot' (Wilke 2020), and all maps were generated in QGIS (QGIS Development Team 2023) with basemaps by Bing (Bing Maps 2023). To compare the extent of vertical and horizontal concealment between Short-billed Dowitcher and Stilt Sandpiper nests, I ran a Beta Regression Model for each horizontal and vertical concealment (with logit link) using package 'betareg' (Cribari-Neto and Zeileis 2010). The model for horizontal concealment included average concealment at 5 m (averaged from N, E, S, and W measurements) as a proportion from 0-1 as the response variable and species as the explanatory variable. The model for vertical concealment included vertical concealment as a proportion from 0-1 as the response variable and species as the explanatory variable. Because much of the concealment data were close to or on the boundaries of 0 and 1, I transformed the concealment data using the following equation (Smithson and Verkuilen 2006), where N is the sample size and s is a constant between 0 and 1 (0.5 is suggested):

$$y' = y(N - 1) + 0.5$$

I assessed the fit of the models using residual plots. There was a low sample size and insufficient variance in concealment to test the effect of direction (N, E, S, and W) and distance (5, 10, and 20 m away), so I tested the average across 4 directions at 5 m away only. I conducted a PERMANOVA with the package 'vegan' (Oksanen et al. 2024) to determine if there was a difference in vegetation cover type at nests of Short-billed Dowitchers and Stilt Sandpipers at the microhabitat (1 m^2) and mesohabitat (the average percent covers of the four directions at 5 m^2 away from the nest) scales. All other comparisons of nest habitat between species were conducted using two-sample t-tests: tallest vegetation (cm), average tree/shrub height in a 40 m radius around the nest (m), number of trees in a 40 m radius around the nest, distance to the nearest tree (m), and water depth within 1 m^2 and 5 m^2 around the nest.

To assess the relationship between flush distance and reaction strength, I ran a linear model for each species with reaction strength as the response variable and flush distance as the explanatory variable. To compare flush distances and reaction types between species, I fit Linear Mixed Effects Models for each response variable using package 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017). Species, horizontal concealment, vertical concealment, and nest age were fixed effects. Measures of horizontal concealment were the average of N, E, S, and

W directions at 5 m from the nest. For the flush distance model, I included 2-way interaction terms between species and horizontal concealment, vertical concealment, and nest age, but lacked the power to include 3-way interactions. There were no significant interaction terms explaining reaction strength, so I excluded these from the final model. There were not enough observations of female Stilt Sandpipers to include sex as a covariate in the models. Due to a low sample size, I decided to include all observations, including repeat observations for marked individuals, though not all observations were individually identifiable. To account for repeat measures, and to assess the impact of individual personality (added variance component), I added individual ID as a random effect in the models explaining reaction strength and flush distance.

To compare the distributions of reaction strength between species, I conducted a two-sided Kolmogorov-Smirnov Test through the package ‘stats‘ (R Core Team 2023). To maximize the sample size, I used all observations for which reaction strength was recorded which included repeat observations from some individuals (max = 6 observations/individual, mean = 2). I converted the histograms of counts of each reaction type to proportions for visualization purposes because the sample sizes were different between species. A summary of all questions and statistical tests used in Chapter 2 is provided in Table 2.2.

Table 2.2. Summary of all questions and statistical tests used in Chapter 2.

Question	Statistical Test	Predictor (Covariates)	Response
Does concealment differ between nests of Short-billed Dowitchers and Stilt Sandpipers?			
Horizontal concealment	Beta regression	Species	Average horizontal concealment in 4 directions at 5 m away from the nest (proportion)
Vertical concealment	Beta regression	Species	Vertical concealment from 1 m above the nest (proportion)
Do vegetation types differ between nest sites of Short-billed Dowitchers and Stilt Sandpipers at the micro- and meso-habitat scales?			
Vegetation cover at microhabitat scale	PERMANOVA	Species	Cover represented by grass, mud, water, herbaceous plants, woody plants, shrubs, trees, lichen, and moss within 1 m^2 of nest cup
Vegetation cover at mesohabitat scale	PERMANOVA	Species	Cover represented by grass, mud, water, herbaceous plants, woody plants, shrubs, trees, lichen, and moss within 1 m^2 of nest cup
Vegetation height	t-test	Species	Height (cm) of the tallest vegetation (cm) within 1 m^2 of nest cup
Do tree characteristics differ between nest sites of Short-billed Dowitchers and Stilt Sandpipers?			
Tree height	t-test	Species	Height (m) of all trees (>0.5 m) in 40 m radius around the nest cup
Tree distance	t-test	Species	Distance (m) from the nest cup to the nearest tree (>0.5 m)
Tree density	t-test	Species	Number of trees in 40 m radius around the nest cup
Does water depth differ between nest sites of Short-billed Dowitchers and Stilt Sandpipers?			
Water depth at microhabitat scale	t-test	Species	Water depth (cm) within 1 m^2 around the nest cup
Water depth at mesohabitat scale	t-test	Species	Water depth (cm) within 5 m^2 around the nest cup

Does reaction strength vary with flush distance in incubating Short-billed Dowitchers and Stilt Sandpipers?			
Flush distance x Reaction strength	Linear model (for each species)	Flush distance (m)	Reaction strength (0-4)
What affects flush distance?			
Flush distance	Linear mixed effects model	Species, nest age (days), vertical concealment (proportion), horizontal concealment (proportion), species *nest age, species*vertical concealment, species*horizontal concealment, random effect: individual (incubator) ID	Flush distance (m)
What affects reaction strength?			
Reaction strength	Linear mixed effects model	Species, nest age (days), vertical concealment (proportion), horizontal concealment (proportion), random effect: individual (incubator) ID	Reaction strength (0-4)

RESULTS

Nests

From 2021-2023, I found 35 Short-billed Dowitcher nests and nine Stilt Sandpiper nests at four sites (Figure. 2.1, Figure 2.2). Two Stilt Sandpiper nests found in 2023 were in the same nest cups from 2022, and no Short-billed Dowitcher nest cups used in 2021-2022 were reused in

2022-2023. Nine Short-billed Dowitcher nests were found in the Airport Fen and 24 were found in the Twin Lakes Fen (Figure. 2.3). Another two Short-billed Dowitcher nests were found in non-focal plot locations by another research team searching deeper in the forested areas for Lesser Yellowlegs nests. All Stilt Sandpiper nests were found in the Twin Lakes Fen.

Active nests were visited an average of 3.9 (SD ± 2.6, range = 1-9) times across the incubation period at an average interval of 2.6 (SD ± 1.5, range = 0-8) days in 2021 and 2022 and 5.1 (SD ± 3.2, range 1-10) days in 2023. The earliest known hatch date for Short-billed Dowitchers occurred on 20 June 2023, and the latest known hatch date was 16 July 2021 (Supplementary Table S2). The earliest known hatch date for Stilt Sandpipers occurred on 26 June 2023 and the latest occurred on 11 July 2022. In 2023, one Stilt Sandpiper nest hatched between 23-25 June but the exact date was not observed. Of nests across all years found before hatch, 22/26 (85%, unknown = 6) Short-billed Dowitcher nests and 4/7 Stilt Sandpiper (57%, unknown = 2) nests were successful (Table 2.3).

Table 2.3. Nest success for Short-billed Dowitchers (*Limnodromus griseus hendersoni*, *n* = 32) and Stilt Sandpipers (*Calidris himantopus*, *n* = 9) breeding in the Churchill, Manitoba region in 2021-2023. Includes only nests found before hatch. S = Successful, F = Failed, U = Unknown fate.

	All years			2021			2022			2023		
	S	F	U	S	F	U	S	F	U	S	F	U
Short-billed Dowitcher	22	4	6	5	0	1	6	4	0	11	0	5
Stilt Sandpiper	4	3	2	1	3	0	2	0	1*	1	0	1

* Abandonment due to unviable nest

Nest Habitat and Concealment

All nest cups were on the ground, typically on isolated hummocks surrounded by mud and water (examples of Short-billed Dowitcher nests: Supplementary Figure S1, and Stilt Sandpiper nests: Supplementary Figure S2), except for one Short-billed Dowitcher nest along a small pond in the Airport Fen where the cup was created in an elongated stretch of low hummocks. Vertical concealment was significantly higher at Short-billed Dowitcher nests (58.5% ± 29.3 (mean ± SE), range 2-100%) than at Stilt Sandpiper nests (21.3% ± 29.3, range 0.1-93.9%) ($P < 0.01$) (Table 2.4, Figure 2.4). Just one Stilt Sandpiper nest was over 30% concealed (at 93.9% vertical concealment). This nest was covered from above by a small dwarf birch (*Betula nana*) (Supplementary Figure S3).

Table 2.4. Results of beta regression models (with logit link) explaining average horizontal concealment (%) at 5 m away and vertical concealment (%) from 1 m above between Short-billed Dowitcher (*Limnodromus griseus hendersoni*) (n = 35) and Stilt Sandpiper (*Calidris himantopus*) (n = 9) nests. Significant results indicated in bold and evaluated at α = 0.05.

Coefficients	Estimate	SE	*Z*	*P*
Horizontal Concealment				
(Intercept)	3.15	0.15	21.50	<0.01
Species (Stilt Sandpiper)	-1.67	0.20	-8.16	**<0.01**
Vertical Concealment				
(Intercept)	0.27	0.19	1.47	0.14
Species (Stilt Sandpiper)	-1.31	0.42	-3.11	**<0.01**

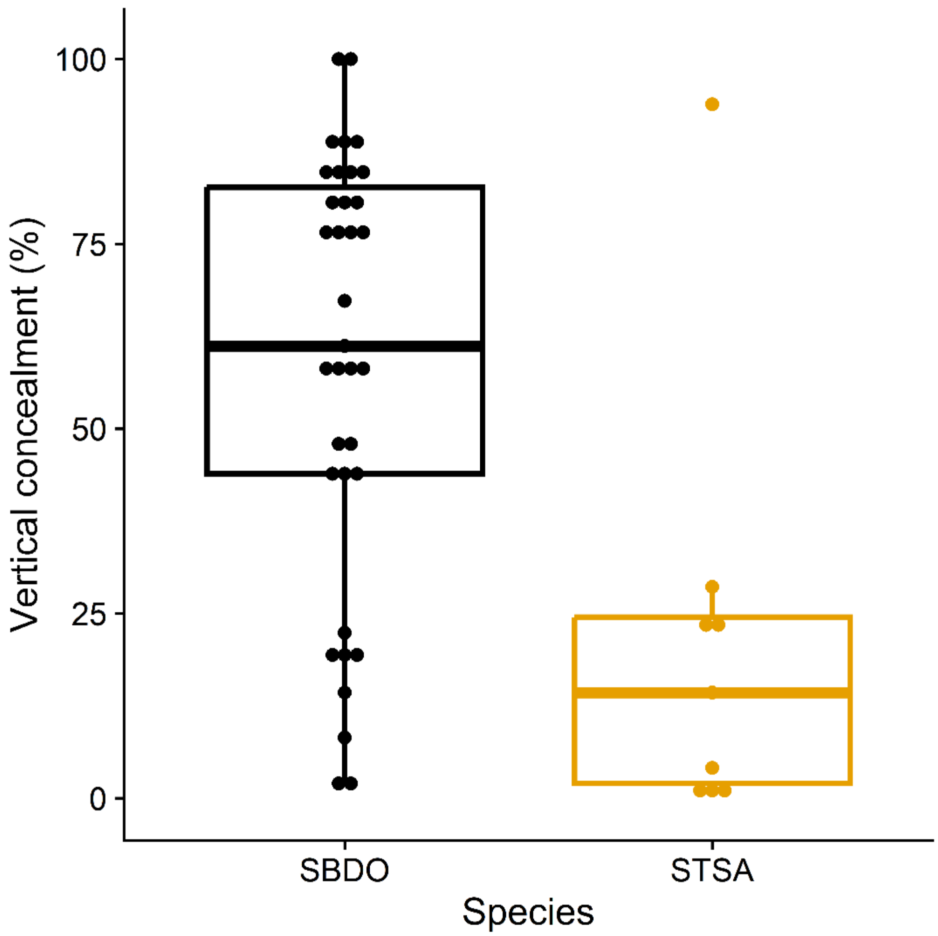

Figure 2.4. Vertical concealment (%) from 1 m above at Short-billed Dowitcher (*Limnodromus griseus hendersoni*) and Stilt Sandpiper (*Calidris himantopus*) nests. Dots represent each nest, the median is indicated by the thick middle line, boxes represent interquartile interval where 50% of data is found, length of whiskers represent maximum and minimum values within 1.5x interquartile range and dots outside of whisker range represent potential outliers.

Average horizontal concealment at 5 m away from the nest was significantly higher in Short-billed Dowitcher nests (97.1% ± 3.96) than in Stilt Sandpiper nests (81.9% ± 9.10) ($P <$ 0.01, Table 2.4, Figure. 2.5). Due to insufficient variance in concealment within species, I did not test differences in concealment at 10 and 20 m away although at each direction, STSA nests were typically less concealed than those of SBDO (Figure 2.5). At 10 m away, nests of Short-billed Dowitchers were concealed with an average of 98.9% and Stilt Sandpipers at an average of 95.6% across all directions. At 20 m away, nests of both species were almost entirely concealed with an average of 99.5% concealment across all directions, with the least concealed nest having an average of 90.2% concealment across all directions (Figure 2.4). At 10 and 20 m away, all Short-billed Dowitcher nests were 100% concealed from the north. At 20 m away, nests of both species were 100% concealed from the west.

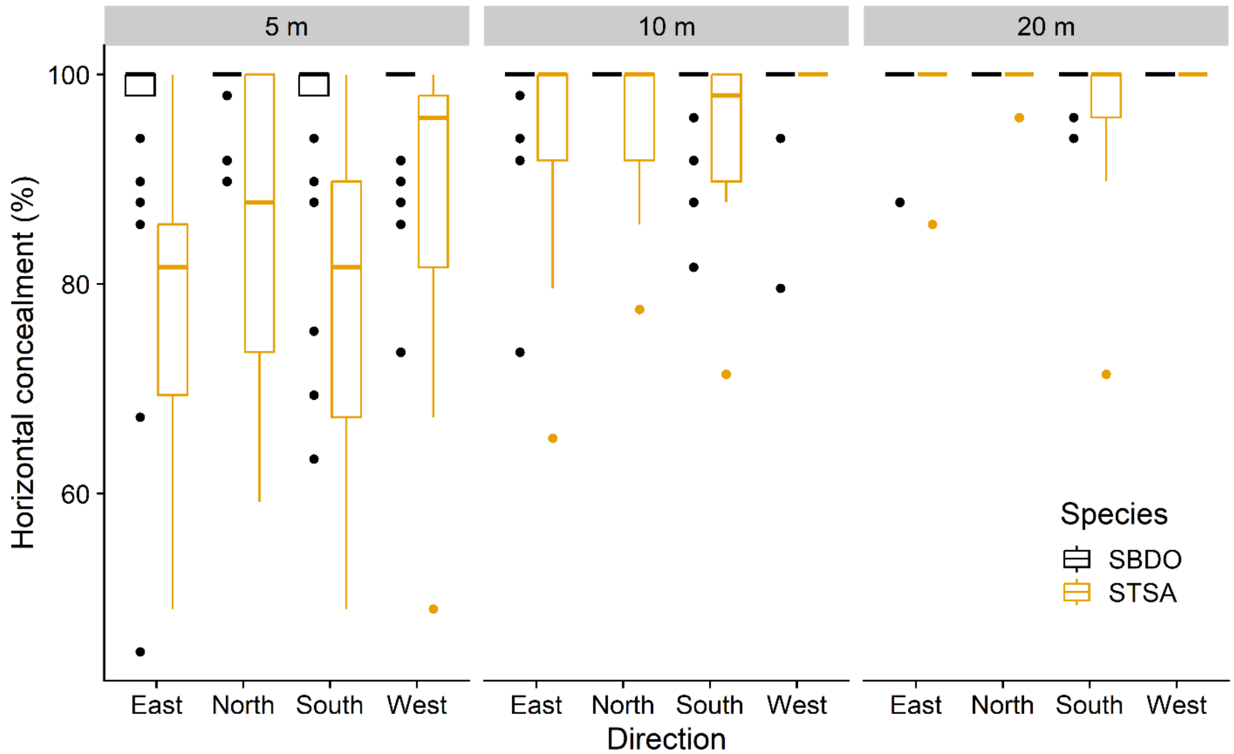

Figure 2.5. Horizontal concealment (%) of Short-billed Dowitcher (*Limnodromus griseus hendersoni*) and Stilt Sandpiper (*Calidris himantopus*) nests from 0.5 m high at 5, 10 and 20 m away in four directions. The median is indicated by the thick middle line, boxes represent interquartile interval where 50% of data is found, length of whiskers represent maximum and minimum values within 1.5x interquartile range and dots outside of whisker range represent potential outliers.

There were no differences in the vegetation cover types (Moss, Lichen, Woody plant, Herbaceous plant, Shrub, Mud, Water, Grass) at the microhabitat (R^2 = 0.03, P = 0.29) and the mesohabitat (R^2 = 0.02, P = 0.68) scale, but the tallest vegetation was higher at Short-billed Dowitcher nests (45.3 ± 1.8 cm) than at Stilt Sandpiper nests (37.1 ± 2.6 cm) (Table 2.5, P = 0.02). Water was significantly deeper within 1 m^2 of Short-billed Dowitcher nests (5.8 ± 0.6 cm) than Stilt Sandpiper nests (3.2 ± 0.8 cm) (P = 0.02), but not significantly different within 5 m^2 (Table 2.5). Stilt Sandpiper nests were significantly closer to the nearest tree or shrub than Short-billed Dowitchers (P < 0.01), however, there were three dowitcher nests with trees <1 m away from the cup, typically atop the hummock. There were no significant differences in the average tree height or number of trees in a 40 m radius of the nest between species (Table 2.5). There was high variation in the number of trees in a 40 m radius within species; for Short-billed Dowitchers, there were 4 - 268 trees and for Stilt Sandpipers there were 31 – 92 trees within a 40 m radius of the nest.

Table 2.5. Average ± SE (*n*) habitat characteristics and results of t-tests for Short-billed Dowitcher *(Limnodromus griseus hendersoni*) and Stilt Sandpiper (*Calidris himantopus*) nests. Significant (α = 0.05) differences tested by t-tests are indicated in bold.

	Short-billed Dowitcher	Stilt Sandpiper	*P*
Tallest vegetation (cm)	45.3 ± 1.8 (*36*)	37.1 ± 2.6 (*9*)	**0.0213**
Tree height in 40 m radius (m)	87.1 ± 3.5 (*25*)	80.3 ± 3.7 (*5*)	0.1988
Distance to tree (m)	9.0 ± 1.6 (*35*)	3.1 ± 0.6 (*9*)	**0.0013**
Number of trees in 40 m radius	49.0 ± 9.0 (*34*)	40.0 ± 6.4 (*9*)	0.4224
Water depth within 1 m^2 (cm)	5.8 ± 0.6 (*25*)	3.2 ± 0.8 (*5*)	**0.0233**
Water depth within 5 m^2 (cm)	7.0 ± 0.6 (*26*)	5.1 ± 1.1 (*5*)	0.1860

Antipredator Nest-defense Behaviour

Thirty-five Short-billed Dowitcher nests were visited 130 times, during which time flush distance was recorded 83 times and reaction strength (0-4) was recorded 94 times. Nine Stilt

Sandpiper nests were visited 40 times, during which flush distance was recorded 24 times and defense behaviour was recorded 33 times. All nests were visited between 0900 and 2130 h. Males were recorded incubating during more visits than females in both Short-billed Dowitchers (average 58%, 20-100% of visits) and Stilt Sandpipers (average 84%, 57-100% of visits).

Flush distance and reaction strength were negatively related for Short-billed Dowitchers (estimate = -1.84, $R^2 = 0.12$, $P < 0.01$, $n = 74$, Figure 2.6) but the relationship was not statistically significant for Stilt Sandpipers probably due to lower power (estimate = -5.18, $R^2 = 0.06$, $P = 0.15$, $n = 20$, Figure 2.6). Stilt Sandpipers flushed at further distances (11.9 m ± 15.8) than Short-billed Dowitchers (3.6 m ± 4.7) (Figure. 2.7). There were significant interaction effects between species and nest age (estimate = 1.42, $P < 0.01$, Table 2.6), and species and vertical concealment (estimate = 0.23, $P < 0.01$, Table 2.6) on flush distance. Stilt Sandpiper flushed at closer distances with lower vertical concealment, whereas Short-billed Dowitchers flushed at similar distances across a gradient of vertical concealment (Figure 2.8). Short-billed Dowitchers flushed at similar distances across the incubation period, whereas Stilt Sandpipers flushed at further distances as the nest age increased (Figure 2.8). There was no significant relationship between flush distance and horizontal concealment in either species. Individual as random effect explained 5% of the variation in the flush distance model (Table 2.6).

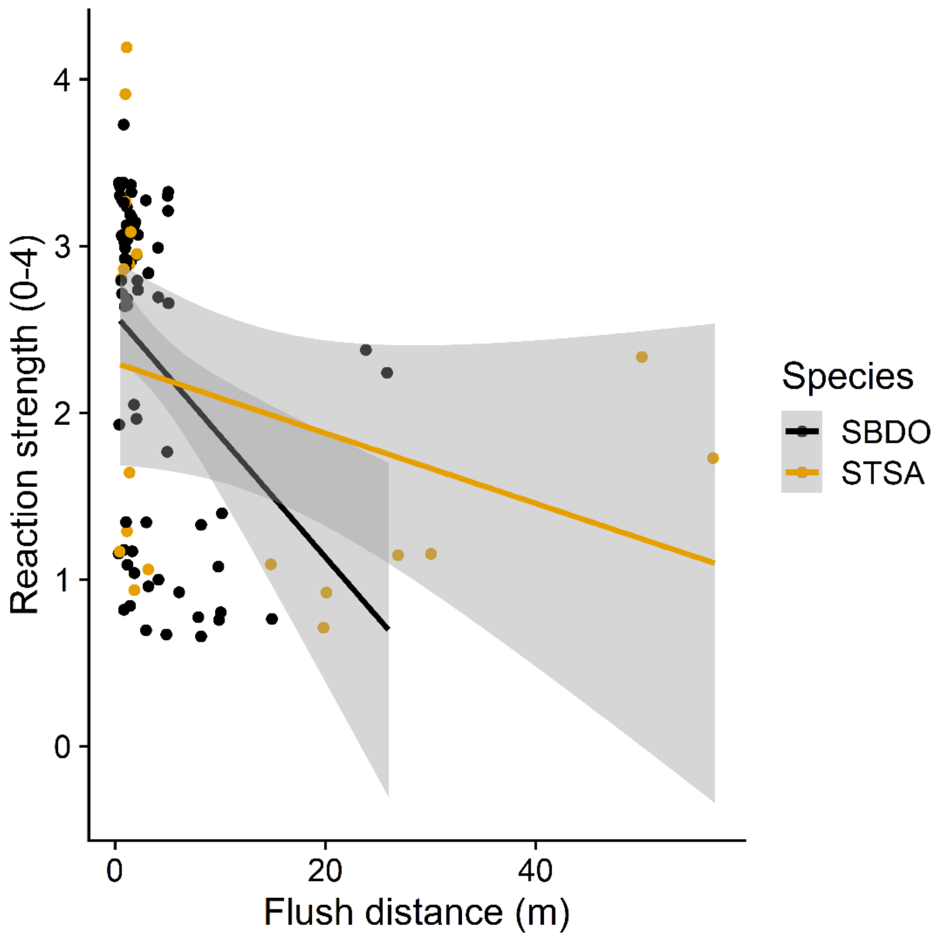

Figure 2.6. Relationship between flush distance (m) and reaction strength during visits to Short-billed Dowitcher (*Limnodromus griseus hendersoni*, SBDO) and Stilt Sandpiper (*Calidris himantopus*, STSA) nests. Points have been jittered to better display areas with overlapping values.

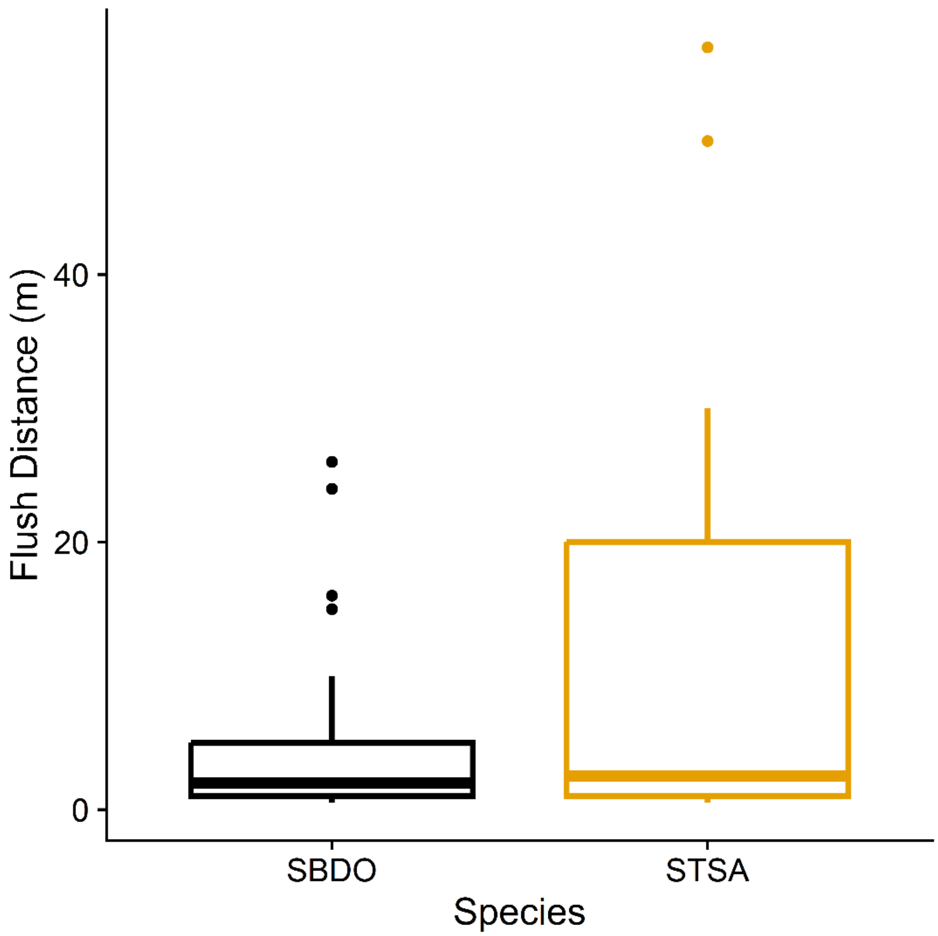

Figure 2.7. Flush distance (m) during visits to Short-billed Dowitcher (*Limnodromus griseus hendersoni*, SBDO) and Stilt Sandpiper (*Calidris himantopus*, STSA) nests. The median is indicated by the thick middle line, boxes represent interquartile interval where 50% of data is found, length of whiskers represent maximum and minimum values within 1.5x interquartile range and dots outside of whisker range represent potential outliers.

Table 2.6. Linear Mixed Effects Model of variables affecting flush distance (m) of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) (*n* = 83) and Stilt Sandpipers (*Calidris himantopus*) (*n* = 24). The model includes interactions of species and nest age, vertical concealment, and horizontal concealment as explanatory variables and incubator ID as a random effect. Significant (α = 0.05) effects are indicated in bold.

Random Effects	Variance	SD		
IncubatorID (Intercept)	1.88	1.37		
Residual	36.21	6.02		
Fixed Effects	Estimate	SE	*t*	*P*
(Intercept)	3.02	91.02	0.03	0.97
Species (Stilt Sandpiper)	7.49	91.37	0.08	0.94
Nest Age	0.12	0.12	1.02	0.31
Vertical Concealment	0.00	0.03	0.15	0.88
Horizontal Concealment	-0.02	0.91	-0.02	0.99
Species*Nest age	1.42	0.26	5.54	**<0.01**
Species*Vertical Concealment	0.23	0.05	4.76	**<0.01**
Species*Horizontal Concealment	-0.25	0.91	-0.27	0.79

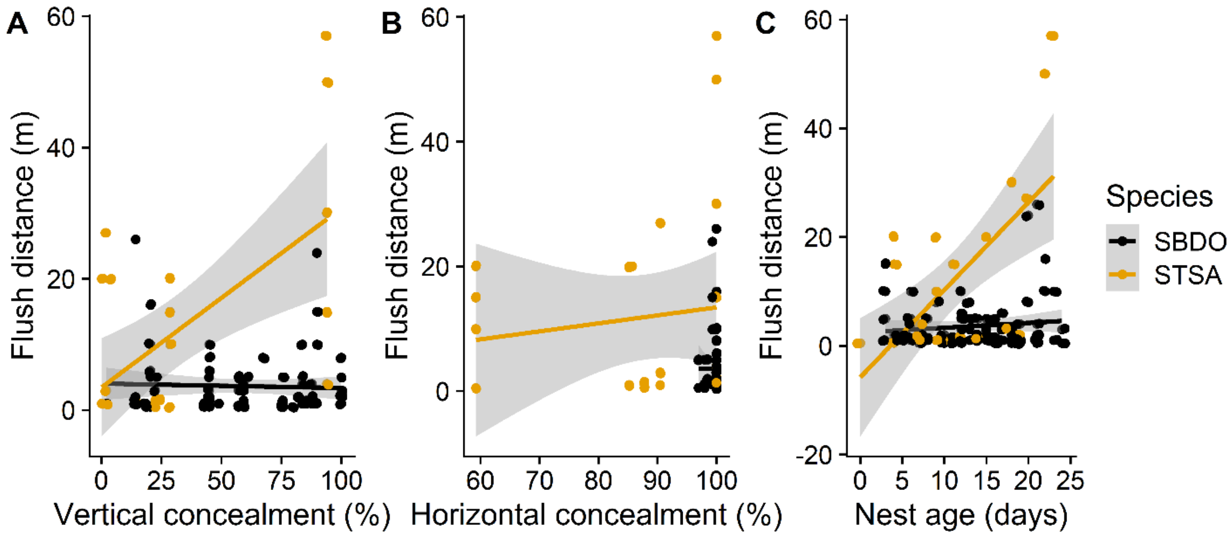

Figure 2.8. Relationships between flush distance and vertical concealment, horizontal concealment, and nest age during visits to Short-billed Dowitcher (*Limnodromus griseus hendersoni*, SBDO) and Stilt Sandpiper (*Calidris himantopus*, STSA) nests. Points have been jittered to better display areas with overlapping values. Significant interactions are indicated with *.

While both species exhibited a full range of defense behaviours, there was a significant difference between the distributions of reaction strength between Short-billed Dowitchers and Stilt Sandpipers (D = 0.29, $P = 0.01$, Figure 2.9). Short-billed Dowitchers displayed an average reaction strength code of 2.2 ± 0.1 ($n_{obs} = 94$, mean ± SE), and Stilt Sandpipers displayed an average reaction strength code of 1.5 ± 0.2 ($n_{obs} = 33$, mean ± SE). The most common nest-defense behaviour during nest visits was a distraction display for Short-billed Dowitchers and a flush for Stilt Sandpipers. Both Short-billed Dowitchers ($n = 1$) and Stilt Sandpipers ($n = 2$) rarely performed aerial attacks. During 27% of nest visits for Stilt Sandpipers and 5% for Short-billed Dowitchers, eggs were unattended upon our arrival at the nest and no incubating birds were present in the area. Active defense, including calling, distraction display or aerial attack was the predominant behaviour for Short-billed Dowitchers (68%), and passive defense was the predominant behaviour for Stilt Sandpipers (60%: 33% flush, 27% unattended).

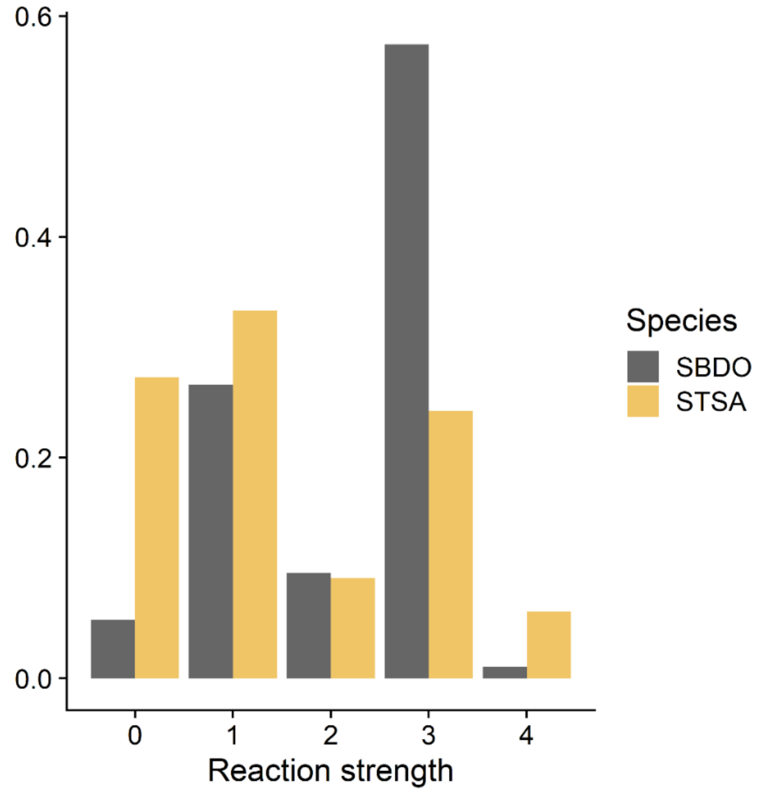

Figure 2.9. Proportion of antipredator defense behaviours exhibited during visits to Short-billed Dowitcher (*Limnodromus griseus hendersoni*) and Stilt Sandpiper (*Calidris himantopus*) nests. Antipredator defense behaviours range from flush to aerial attack (0 – unattended, 1 – pure flush, 2 – alarm calling, 3 – distraction display, 4 – aerial attack).

Short-billed Dowitchers and Stilt Sandpipers had weaker reactions to intruders at nests as vertical concealment increased (estimate = -0.01, P = 0.04, Table 2.7, Figure 2.10). Nest age and horizontal concealment were not significant predictors of reaction strength (Table 2.7, Figure 2.10). Individual variation explained 21% of the total variation in the model (Table 2.7).

Table 2.7. Linear Mixed Effects Model of variables affecting reaction strength (0-4) of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) (*n* = 94) and Stilt Sandpipers (*Calidris himantopus*) (*n* = 33). The model includes reaction strength as the response variable, nest age, vertical concealment, and horizontal concealment as explanatory variables, and incubator ID as a random effect. Significant (α = 0.05) effects are indicated in bold.

Random Effects	Variance	SD		
IncubatorID (Intercept)	0.26	0.51		
Residual	0.98	0.99		
Fixed Effects	Estimate	SE	*t*	*P*
(Intercept)	3.25	1.46	2.23	**0.03**
Species (Stilt Sandpiper)	-0.92	0.31	-2.87	**0.01**
Nest Age	-0.03	0.02	-1.67	0.10
Vertical Concealment	-0.01	0.00	-2.10	**0.04**
Horizontal Concealment	-0.00	0.01	-0.03	0.97

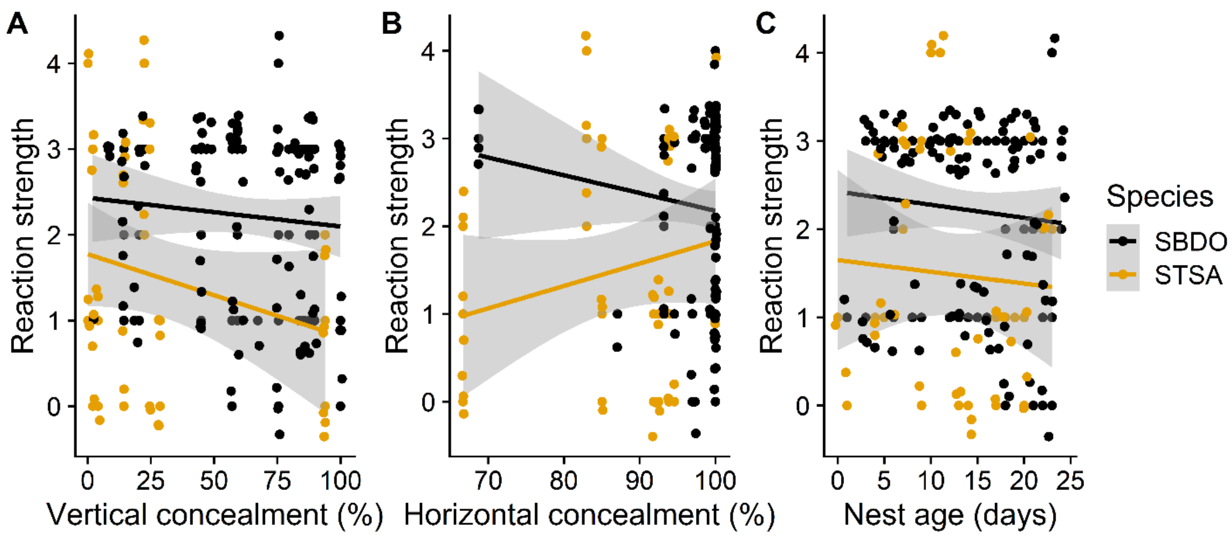

Figure 2.10. Relationships between reaction strength and vertical concealment, horizontal concealment, and nest age during visits to Short-billed Dowitcher (*Limnodromus griseus hendersoni*, SBDO) and Stilt Sandpiper (*Calidris himantopus*, STSA) nests. Points have been jittered to better display areas with overlapping values.

DISCUSSION

I provide some of the first quantitative descriptions of the nesting habitat and its relationship to antipredator behaviour in two poorly studied shorebirds breeding at the ecotone between the northern boreal forest and the sub-arctic tundra. Short-billed Dowitcher nests had taller vegetation at the nest cup and higher vertical and horizontal concealment (at 5 m away) than Stilt Sandpiper nests although the general larger scale characteristics of the habitats were similar between the two species. Tree height, tree abundance, and vegetation types (grass, woody etc.) around nests did not differ between species, although low sample sizes for Stilt Sandpipers may have affected the results. Stilt Sandpiper nest cups were closer to the nearest tree or shrub than Short-billed Dowitcher nest cups. Finally, water within 1 m^2 of Short-billed Dowitcher nests was deeper than at Stilt Sandpiper nests, but there was no difference in water depth within 5 m^2 of the nest cup. Though both species exhibited a range of flush distances and antipredator nest-defense behaviours, given their greater nest concealment, Short-billed Dowitchers flushed closer to human intruders and chose more active defense strategies than Stilt Sandpipers, which flushed from further away and chose passive defense strategies. Reaction strength decreased with flush distance for Short-billed Dowitchers but not for Stilt Sandpipers, which may be due to power issues from a small sample size. Stilt Sandpipers flushed further as vertical concealment and nest age increased, but Short-billed Dowitchers flushed at similar distances across a gradient of concealment and nest ages. Reaction strength decreased with vertical concealment similarly for both species and did not vary with horizontal concealment nor nest age.

Our measurements of concealment and habitat characteristics are generally consistent with what has been qualitatively described in previous work on these species. Stilt Sandpiper nests found at Churchill, Manitoba, during studies in the 1960s, were mostly open from above, occasionally with rhododendron or dwarf birch beside the nest cup (Jehl 1973). Short-billed Dowitcher nests are generally described as well concealed from above (Jehl et al. 2020). In our study, although Short-billed Dowitchers had more concealed nests than Stilt Sandpipers, they ranged from just 2% to 100% concealed from above, suggesting that there is some degree of variation in vertical concealment, though all nests were highly concealed from the sides. Nests of typically well-concealed species could be poorly concealed due to inexperience in breeding (Hatchwell et al. 1999) or springs with low temperatures resulting in low vegetation height (Laidlaw et al. 2020). Comparing nest concealment between nest attempts throughout a season or between marked individuals of different ages could test whether concealment is a learned behaviour in this species or whether individual behaviours are consistent over time.

Compared to flush distances of other biparental Arctic-breeding shorebirds observed at East Bay, Nunavut, such as Black-bellied Plovers (mean = 115.6 m), Semipalmated Plovers (mean = 39.1 m), and Ruddy Turnstones (mean = 56.1 m) (Smith and Wilson 2010), Short-billed Dowitchers and Stilt Sandpipers had relatively close flush distances, with a maximum of 57 m recorded for a Stilt Sandpiper. Distraction displays were almost always limited to “rodent-running” in both species, though occasionally both species attempted to feign “broken-wing” injury. The close flush distances displayed by Short-billed Dowitchers and Stilt Sandpipers, are similar to other biparental *Calidris* sandpipers, such as the Least Sandpiper observed in the Magdalen Islands, Quebec, which flushed when human intruders were less than 5 m away (*Calidris minutilla*) (Moore 1912).

Greater than 20% of the variation in reaction strength could be explained by the random effect of individual. This suggests that individual variation in boldness may explain some of the differences in nest-defense responses. For some individuals, personality was consistent throughout incubation (personal observation), and for some species, these nest-defense behaviours can be consistent across years (Burtka and Grindstaff 2013). Consistent personality may limit plasticity and therefore has the potential for negative consequences for the parent and offspring (Dall et al. 2004), which is important to consider with changing environmental conditions.

Flush distance increased with vertical nest concealment for Stilt Sandpipers but not for Short-billed Dowitchers. Stilt Sandpipers may have more behavioural plasticity in antipredator defense strategies than Short-billed Dowitchers. Horizontal concealment was not a predictor of flush distance for either species, consistent with some other concealed nesting species such as Wood Thrush (*Hylocichla mustelina*) (Israel et al. 2023). In a study of Kentish Plovers (*Charadrius alexandrinus*), nest concealment was only a predictor of female, but not male flush distance (Kwanye et al. 2024). In a uniparental incubator, bold female Common Eiders (short flush distance) were found in concealed nests (Seltmann et al. 2014). Our dataset includes a single observation of flush distance (30 m) from just one female Stilt Sandpiper, at a highly vertically concealed nest (Supplementary Figure S3), so testing for female boldness in these biparental incubators is not possible with the data I collected.

Klima and Jehl (2020) suggested that differences in Stilt Sandpiper flush behaviours may be related to habitat differences between sites. At Churchill in the mid-1960s, Stilt Sandpipers were rarely "surprised" off nests and instead flushed when a human approached 75-100 m away (Jehl 1973). At Cambridge Bay in 1960, Stilt Sandpipers nesting in willowy tundra flushed at short distances, whereas one incubating a nest on a dry exposed slope flushed "well in advance" (Parmelee 1967). At a site in Wapusk National Park, Stilt Sandpipers nested on dry exposed rocky slopes and from casual observations at three nests in 2023, appeared to flush from nearly underfoot. However, as we studied flush distance at just one site where Stilt Sandpipers nest in Churchill, we are not able to examine these patterns quantitatively. In Temminck's Stint (*Calidris temminckii*), flush distance was related to visibility from the nest but only with calls and behavioural cues from sentinels of other species (Koivula and Rönkä 1998). A parallel study of Stilt Sandpipers nesting in more open, arctic habitats, including the recording of the reactions of sentinels during nest checks, could demonstrate differences in decision-making between individuals of the same species nesting in different habitats.

Smith and Wilson (2010) observed that as the season progressed and nests approached hatch, other biparental shorebird species at East Bay, Nunavut defended their nests with greater intensity, but flush distance did not change. In this study, Stilt Sandpipers initiated a flush further from human intruders as the season progressed, but like Short-billed Dowitchers, their reaction strength did not change over time. Because of their poorly concealed nests, Stilt Sandpipers may have greater selection to remain on their nests to avoid exposing eggs to cold early in the season. They also may be better able to detect human intruders approaching from far away and may learn that they are able to leave undetected before we arrive. Habituation to humans can show an opposite pattern, for example, in Two-banded Plovers (*Anarhynchus falklandicus*) flush distances decreased in areas where exposure to humans was high (St Clair et al. 2010). In this study, Short-billed Dowitchers did not exhibit a pattern of flush distance and reaction strength over time, suggesting that their reaction may remain similar across the nesting period, probably because they could not see the intruder or always rely on cryptic colouration. Gradual habituation to the human intruders in this study could also weaken the relationship between flush distance and nest age.

Increasing vegetation growth in the subarctic and Arctic may influence the application and effectiveness of existing defense behaviours. For species that rely on visual detection of incoming predators for early, undetected departure, increasing overgrowth of vegetation in previously open habitats can increase nest predation (Koivula and Rönkä 1998). In open shore-breeding Temminck's Stint (*Calidris temminckii*), visibility around the nest and cues from sentinels influence the effectiveness of their nest-defense strategy. Because Stilt Sandpipers have poorly concealed nests, they may rely on a similar "leave early" strategy, explaining why at 27% of visits, their nests were unattended upon our arrival. Stilt Sandpipers did not always employ a “leave early” strategy, sometimes flushing underfoot. Employing close flush distances should be beneficial to individuals who can effectively chase or distract predators from the nest location because conspicuous behaviour is related to increased nest predation (Smith et al. 2012b). If Stilt Sandpipers continue to nest in areas where vegetation changes are occurring, this may reduce the effectiveness of their nest-defense by limiting their ability to detect predators and leading to a potential mismatch between their habitat and nest-defense strategy when flushed at close range. Therefore, like Temminck’s Stint, their nest-defense and success may be influenced by shrubification at subarctic nest sites.

Encroaching woody vegetation at the Churchill, Manitoba site may impact Short-billed Dowitchers differently than Stilt Sandpipers. We recorded high nest success for Short-billed Dowitchers nesting near Churchill, with 22 successful nests of 26 known nest fates, compared to 4 of 7 nests hatching for Stilt Sandpipers. As a species that appears to rely mainly on concealment and aggressive nest-defense behaviour rather than leaving early, increased vegetation growth at these wet sedge meadows at the treeline may not influence the effectiveness of the Short-billed Dowitcher’s nest-defense strategy. In fact, sometimes the deep water surrounding their nests (up to 15 cm within 1 m^2, and up to 17 cm within 5 m) may preclude them from sneaking off nests the way Stilt Sandpipers could be able to.

Though Stilt Sandpipers generally nested in drier areas, one nest cup used both in 2022 and 2023 by the same pair was surrounded by water. In 2022, this nest was discovered with two eggs floating nearby, and in the nest, one empty but intact egg and one cracked and rotting egg. This nest was discovered after a heavy rainfall event during which The Fen site appeared flooded, so the eggs appeared to have floated out of the nest. This nest was incubated until at least 3 July and the male incubating the nest departed the Churchill region on 12 July. The nest cup was very low to the ground and would have likely hatched in a drier area with better drainage. In 2023, this nest cup was reused, and the eggs successfully hatched. Future studies of this species could investigate their nest site selection and nest success across a gradient of sites throughout their range to examine potential influences of increasing extreme weather events and shrubification under climate change.

Another potential consequence of climate change with the potential to impact shorebird nest success in the subarctic is shifting predator communities. Predators increasing in abundance in the Churchill region include Common Ravens and Herring Gulls (Jehl 2004), both of which are predators of shorebird nests (Brown et al. 2022). The northward expanding range of red foxes (*Vulpes vulpes*) makes them a novel predator to the Arctic, in some areas replacing arctic foxes (Elmhagen et al. 2017, Gallant et al. 2020). Studies testing the aggressive responses to stuffed models of different predators by Red-wattled Lapwing (*Vanellus indicus*) and Northern Lapwing (*Vanellus vanellus*) suggest that they distinguished between predator species and reacted accordingly (Elliot 1985, Sládeček et al. 2019). Many of the predators of shorebird nests in the Churchill region are avian, representing 78% and 36% of predation events at artificial and real nests in a previous study (Brown et al. 2022). Distraction displays, demonstrated in American Golden Plovers (*Pluvialis dominica*) breeding in Churchill, Manitoba, are usually directed at human, or mammalian intruders, rather than avian predators, to which American Golden Plovers displayed cryptic behaviour (Byrkjedal 1989). Because shorebird nest success in Churchill can be impacted by proximity to avian predators (Brown et al. 2022), it may be important to consider other antipredator defense strategies such as actively chasing predators away, or the effectiveness of camouflage of both eggs and the incubator or incubation recesses (Smith et al. 2012b).

Future research on the behaviour of Short-billed Dowitchers and Stilt Sandpipers could investigate cooperation within and between species. In some cases, Short-billed Dowitchers nested 20-40 m away from other pairs, and in two instances, 10-15 m away from active Whimbrel nests. Upon nest visits, especially to those with hatched chicks, apparent non-breeders and breeders with chicks nearby would sometimes come to defend other pairs. Also, because both Short-billed Dowitchers and Stilt Sandpipers nest in these areas where auditory and visual cues about predators are often provided by loud sentinels such as Hudsonian Godwit and Whimbrel, evaluating their responses to predators with and without aid from sentinels as in Temminck's Stint (Koivula and Rönkä 1998) may provide information on their flexibility to changing communities of conspecifics and predators.

Conclusion

Our ability to compare defense behaviour and concealment between successful and unsuccessful nests at this site is limited by a low number of successful nests in Stilt Sandpipers and a low number of failed nests in Short-billed Dowitchers. There was substantial variation within species, and individual behaviours may play a role in their decision-making, especially for Stilt Sandpipers.

Because both Stilt Sandpipers and Short-billed Dowitchers are experiencing steep population-level declines measured during migration (Smith et al. 2023a), understanding factors that influence breeding success, and therefore reproductive output may be important to conserving these species. Forecasting changes in available habitat throughout both of their ranges may indicate whether their ranges are shifting and if they will be limited by nesting habitat in the subarctic or encounter novel or increasing predator abundance under different climate scenarios. Like other arctic breeding shorebirds, the distribution of nesting Stilt Sandpipers could be changing or moving further north and contracting out of Churchill. This may also be important for Short-billed Dowitchers because although Churchill sits near the north edge of their breeding range, very few studies of this subspecies occur outside of this area. Additionally, because three subspecies of Short-billed Dowitchers exist, assessing population trends and threats during the breeding season would require more coordinated effort across sites. However, because of the inaccessibility of their breeding sites and the difficulty of locating their nests, more information from their breeding grounds may not be easily obtained.

CHAPTER 3 – POST-BREEDING MIGRATION OF THE SHORT-BILLED DOWITCHER AND STILT SANDPIPER

ABSTRACT

Migration is costly and dangerous and assessing the threats shorebirds encounter during this period of their annual cycle and the connectivity of their populations can be important to their conservation. Short-billed Dowitcher and Stilt Sandpiper populations have declined significantly, and their post-breeding migration patterns are known mainly by shorebird surveys, qualitative descriptions and estimates of flight capabilities. Despite recent advances in tracking technology, no studies have tracked the post-breeding migration of these species. From 2021-2023, I detected tracks from VHF radio-transmitters deployed on Short-billed Dowitchers (n = 35) and Stilt Sandpipers (n = 10) during the breeding season in Churchill, Manitoba, to be tracked by the Motus Wildlife Tracking System. Short-billed Dowitchers generally made non-stop flights through the Great Lakes to the Southeast Atlantic Coast where their stopover duration was 9.4 ± 6.0 days (median ± SE, range = 1-24 days), with key stopover sites in South Carolina and Georgia. Females departed the breeding grounds ~10 days earlier than males. Barrier islands and saltmarshes along the Southeast Atlantic coast are important to the post-breeding migration of Short-billed Dowitchers from Churchill, Manitoba. Stilt Sandpipers migrated from their breeding grounds through the prairies to stopover sites between southern Manitoba and Missouri, with just one confirmed stopover location in the Midwest with a duration of 5.73 days during migration. Short-billed Dowitchers displayed relatively high connectivity during the migration period with nearly one third of confirmed stopovers occurring at a single site in Georgia. Tag loss and low

network coverage prevented the identification of more stopover sites between the breeding grounds and central North America and South America. Thus, I was not able to identify any wintering sites.

INTRODUCTION

Shorebirds are declining at alarming rates in the Western hemisphere (Rosenberg et al. 2019, Smith et al. 2023a). Migratory shorebirds are at a higher risk of declines than resident species (Koleček et al. 2021). Because migratory species inhabit numerous different places, environments, and jurisdictions throughout their annual cycle, they may encounter more threats than those who do not migrate (Sutherland et al. 2012, Koleček et al. 2021). For example, migrating shorebirds may encounter anthropogenic disturbance at stopover sites (Burger et al. 2007), loss of wintering habitat (Fernández and Lank 2008), hunting (Atlantic Flyway Shorebird Initiative 2016), sea-level rise (Convertino et al. 2012), and infectious disease (Krauss et al. 2010). Among migratory species, these threats are expected to differ. Those with overlapping breeding and non-breeding ranges may be less likely to be declining (Gilroy et al. 2016), and those who migrate over North America are more associated with population declines than oceanic migrants (Thomas et al. 2006). Differences may occur even within a species, for example, eastern-breeding Lesser Yellowlegs (*Tringa flavipes*) are more likely to visit areas with high shorebird hunting than western breeders (McDuffie et al. 2022a).

Understanding the movement and links between breeding, non-breeding, and stopover sites for migratory birds is crucial to addressing conservation issues at any stage of their annual cycle. The concept of migratory connectivity is becoming increasingly important with the threat of habitat loss and climate change in each of the habitats they encounter along their migratory pathway (Webster et al. 2002, Jetz et al. 2007). By examining factors controlling winter habitat quality, researchers can address the interactions between non-breeding grounds, survival, and reproduction in breeding grounds within and between subpopulations (Gill et al. 2001). Breeding populations with low migratory connectivity spread out in the wintering grounds and may be more resilient to threats, but possibly harder to conserve (Wilcove and Wikelski 2008), whereas populations with high migratory connectivity (lower dispersion) may rely on a few breeding sites and are more sensitive to changes at those sites (Webster et al. 2002, Gilroy et al. 2016).

Though we can derive estimates of population trends (Smith et al. 2023a) or distribution and range shifts (Bart et al. 2007, Rushing et al. 2020) from surveys and mark-recapture data, rapid advances in wildlife tracking technologies have enhanced our ability to track the movements of small migratory birds (Cohn 1999, Ryder et al. 2011). Shorebirds tracked with devices such as radio-transmitters (Anderson et al. 2019), light-level geolocators (Wright et al. 2022), and GPS transmitters (McDuffie et al. 2022a), can provide information that is otherwise difficult or impossible to obtain such as stopover duration (Howell et al. 2019), winter movements (Linhart et al. 2022), and migratory routes and connectivity of breeding populations (Brown et al. 2017, McDuffie et al. 2022a). Despite this, the movements of many migratory shorebirds are still unknown.

The Short-billed Dowitcher (*Limnodromus griseus)* is a medium-sized intermediate distance migrant shorebird breeding in the boreal and subarctic regions of Canada and Alaska, U.S. It is divided into three subspecies with distinct plumages, measurements, and ranges: *L. g. griseus* (Atlantic), *L. g. hendersoni* (central), and *L. g. caurinus* (pacific). Due to the inaccessibility of its breeding sites and the difficulty in locating its nests, the basic biology of the

Short-billed Dowitcher remained poorly understood by scientists until the mid-19th century. Despite being commonly observed during migration (Jehl 1963, Skagen et al. 1999), the Short-billed Dowitcher is still one of the least understood of the North American shorebirds and no tracking studies of the central subspecies, *L. g. hendersoni* have been published. *L. g. hendersoni* breeds in Canada inland from central Alberta (Rowan 1932) through northern Manitoba (Jehl and Smith 1970), northern Ontario and possibly Akimiski Island, Nunavut (Carpentier 1989), with a possible zone of intergradation with *L. g. griseus hendersoni* on the western coast of James Bay, Ontario. The wintering range of the Short-billed Dowitcher includes the Pacific Coast of North America, mostly from northern California, U.S. (Small 1994) to Baja California, Mexico, along the coast of Central America south of Mexico (Russell and Monson 1998) through to Panama (Ridgely and Gwynne 1989) and along the northwestern coast of South America from Colombia to Peru (American Ornithologist's Union 1998). On the Atlantic Coast, it winters mostly from southern Virginia to southern Florida along the Gulf of Mexico Coast to Texas in the United States, from Tamaulipas, Mexico south to Panama (Ridgely and Gwynne 1989), in the Bahamas, Greater Antilles, Cayman Islands, and Barbados, and along the Atlantic coast of Colombia and Venezuela to Brazil (American Ornithologist's Union 1998).

Flocks of Short-billed Dowitchers are common on both coasts of North America during fall and spring migration. During fall migration *L. g. hendersoni* are rare north of Long Island, New York, U.S., and represent 10-12% of migrants in New Jersey, U.S., where the Atlantic subspecies dominates (Jehl 1963, Jehl et al. 2020). The proportion of *L. g. hendersoni* to *L. g. griseus* during fall migration increases southward along the Atlantic coast (Pitelka 1950, Jehl 1963). However, Short-billed Dowitchers are also widespread, but uncommon, in the interior of North America during migration. For example, Short-billed Dowitchers (mostly *hendersoni*) peak in abundance during post-breeding migration in northern Oklahoma, U.S., in the first three weeks of July (Paulson 1993, Hoffman 1999), *L. g. hendersoni* are the most common subspecies migrating through Ontario, Canada (Jaramillo et al. 1991) and large numbers have been reported in Ohio, U.S. (Peterjohn 1989).

Several aspects of migration of the central subspecies, *L. g. hendersoni*, and more specifically, those breeding at the far eastern edge of their range in Churchill, are not well known. Based on estimated flight bearings for dowitchers leaving Churchill, they appear to depart eastward, potentially towards James Bay, Ontario then towards the Atlantic coast (personal comment in Jehl et al. 2020). Their relative rarity inland in eastern and northeastern U.S. states suggests they may do a direct flight, with historical data suggesting weights of approximately 125 g at breeding grounds in Churchill could sustain flight to mid-Atlantic without refuelling, though their flight capability is largely unknown (personal comment in Jehl et al. 2020). Estimated flight range from energetics and body mass suggests distances as low as 1900-2000 km (Jehl 1963) from birds at stopover sites on the east coast and as high as 2700-3500 km from birds in Saskatchewan, Canada (Alexander and Gratto-Trevor 1997). The exact wintering ranges of each subspecies are not well known due to their non-distinct basic plumages but *L. g. hendersoni* is expected to winter broadly on the northern coast of South America (American Ornithologist's Union 1957).

Another subarctic-breeding shorebird, the Stilt Sandpiper (*Calidris himantopus*), is a long-distance migrant with an extensive but disjunct breeding range stretching from the subarctic regions of James Bay, and as far northwest as the low-arctic regions of northern Alaska, U.S. and Yukon, Canada (Salter et al. 1980, Klima and Jehl 2020). This species has been studied in detail at only a few of its breeding sites, including a sub-arctic site near Churchill (Jehl 1970, Jehl

1973). Historically, the Churchill breeding population consisted of a high density of 12-16 pairs/100 ha in the 1960s but has since declined significantly (Jehl 2004). At a species level, an analysis of their abundance during migration suggests that the Stilt Sandpiper has also declined significantly since the 1980s by an estimated 75% (Smith et al. 2023a).

Based on counts during migration, the Stilt Sandpiper's main post-breeding migration route appears to follow a narrow band pattern that includes major stopover sites in the prairies and continues to their non-breeding sites primarily in freshwater wetlands in interior South America, with smaller numbers wintering in coastal North America (Alexander and Gratto-Trevor 1997, Skagen et al. 1999, Klima and Jehl 2020). Numbers of Stilt Sandpipers at saline lakes in the Great Plains of the U.S. show peak abundance in late July (Andrei et al. 2006). The region spanning Saskatchewan, Canada to Kansas, U.S. is expected to include major staging areas after a non-stop flight from the breeding grounds due to the lower numbers observed in the south-central U.S. (Klima and Jehl 2020). Specific stopover sites may vary with water conditions but typically they use wetlands during migration (Skagen and Knopf 1994). A previous study recorded Stilt Sandpipers stopping for 4-13 days at a major staging area in Quill Lakes, Saskatchewan (Alexander and Gratto-Trevor 1997).

This study will focus on three main topics regarding the migration of Short-billed Dowitchers and Stilt Sandpipers: the migratory pathways, the timing (departure dates and speed), and their stopover locations. As these are some of the least understood of the shorebirds and the migration pathway of the birds nesting at this site is unknown, tracking the migration of these populations may provide insight for future conservation efforts during non-breeding periods. Understanding migratory connectivity may be especially important for species that have disjunct breeding ranges, such as the Stilt Sandpiper (Klima and Jehl 2020), or distinct subspecies, such as the Short-billed Dowitcher. Also, the migration routes of the Short-billed Dowitcher are of interest because the Churchill site is the furthest east known breeding grounds of the *L. g. hendersoni* subspecies, where a zone of intergradation with *L. g. griseus* has long been debated by naturalists (Jaramillo et al. 1991).

The objectives of this chapter are to 1) examine the effect of sex and nest hatch date on departure date, 2) track the pathways, speed, and timing of post-breeding migration of Short-billed Dowitchers and Stilt Sandpipers using the international and collaborative Motus Wildlife Tracking System, 3) and describe stopover sites. I predicted that Short-billed Dowitchers breeding in Churchill would take an eastern route during post-breeding migration based on flight direction observations (observation in Jehl et al. 2020) and that Stilt Sandpipers would take a central route based on high survey counts in the prairies of Canada (Alexander and Gratto-Trevor 1997). Though environmental factors could influence departure dates such as wind (Grönroos et al. 2012), I was interested in identifying nest-level characteristics that influence departure dates. Due to higher post-hatch parental care displayed by males (Jehl and Smith 1970, Jehl et al. 2020, Klima and Jehl 2020), I predicted that for both species, females would depart the breeding grounds earlier than males and that the nest hatch date should explain departure date.

METHODS

Study Area

The Churchill, Manitoba region is a unique transitionary zone at the northern edge of the western Hudson Bay Lowlands of Canada, an ecoregion stretching along the coast from northern Manitoba to southern James Bay. The region is characterized by its coastal beach and greywacke and quartzite cliffs near the ocean, gravel ridges, subarctic tundra, wetland complexes, sedge and grass fens, and boreal forest inland (Dredge and Dyke 2020). Radio-transmitters were deployed at three sites in the Churchill, Manitoba area where we found nests of Short-billed Dowitchers and Stilt Sandpipers (Figure 3.1). The first site (Twin Lakes Fen; 58.67029°N, 93.83457°W) was a large wet sedge meadow north of the Twin Lakes, the second site (Airport; 58.741354°N, 94.063753°W) was a smaller wet sedge meadow beside the runway at the Churchill Airport, and the third site (Landing Lake; 58.711216°N, 94.057384°W) was a small pond approximately 75 meters into the forest from Airport Road north of Landing Lake (Figure 3.1)

Motus Receiving Stations

The transmitters used in this study (see Tag Deployment) are detected by the Motus Wildlife Tracking Network, an international, collaborative system of receiving towers that detect unique signals from VHF radio transmitters as tagged birds fly by (Taylor et al. 2017). A VHF radio-tagged bird flying by a Motus receiving station can sometimes be detected at up to 50 km (Anderson et al. 2019) but the estimated detection range of Motus receiving stations is often closer to 5-15 km due to conditions such as adverse weather, topography, or vegetation (Taylor et al. 2017). There is a relatively high density of Motus receiving stations in eastern North America, fewer in the west and fewer in Central and South America (motus.org; Figure 3.2). Transmitters are relatively inexpensive (~$200) and lightweight (~0.66g), but the fine resolution of migration tracks is limited by the number and distribution of receiving stations in the area where the bird is migrating or stopping over.

I defined the ‘northern array’ of towers as any tower within 200 km of Churchill, Manitoba. One tower was within 8 km of the breeding area to detect shorebirds while breeding and departing and was deployed from 18 July 2021 to 28 July 2023 (Table 3.1). Five more towers were deployed between 30-200 km away in south, east, and north directions (Table 3.1**,** Figure 3.1): a – ‘Prince of Wales Fort’, b – ‘CNSC 21’ (Churchill Northern Studies Centre), c – ‘Nester 1’, d – ‘Broad River Research Compound’ (Broad River), e – ‘Owl River Research Compound’ (Owl River), f – ‘York Factory National Historic Site’ (York Factory). I defined the ‘Southern Array’ of towers to include any tower south of the Northern Array.

Figure 3.1. Map of study area, Motus tower and tag deployments in Churchill, Manitoba region. Red points indicate nests (*n* = 35) with tag deployments (*n* = 42) of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) and yellow points indicate nests (*n* = 9) with tag deployments (*n* = 10) of Stilt Sandpipers (*Calidris himantopus*) in 2021-2023. Green points indicate Motus receivers. Towers in the Northern Array include a – Prince of Wales Fort, b – CNSC, c – Nester 1, d – Broad River, e – Owl River, f – York Factory.

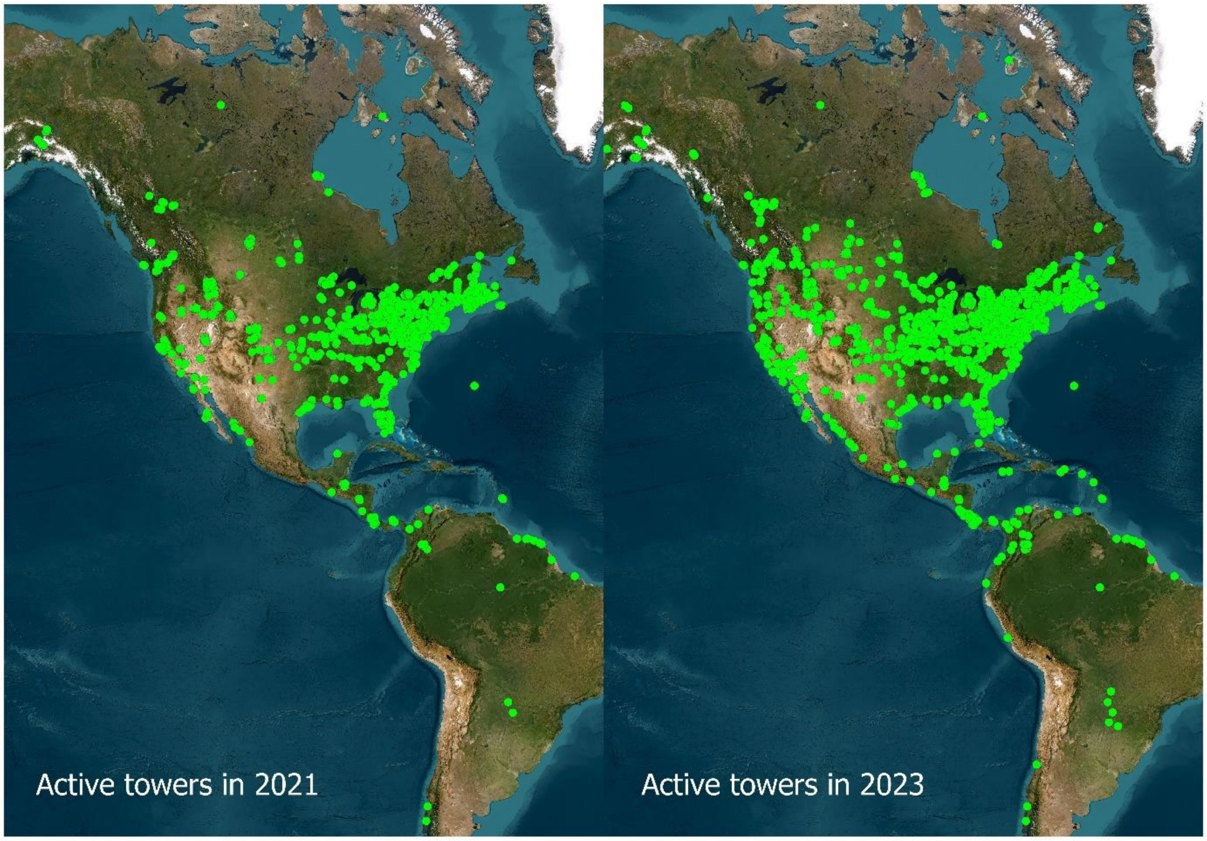

Figure 3.2. Map of active Motus receiving stations active in the first year (2021, left) and the last year (2023, right) of this study. Motus receiving stations have increased substantially in North America, Central America, and South America.

Table 3.1. Motus receiving tower deployments in the northern array and distance from the main study site, The Twin Lakes Fen. Dates represent deployments and in 2023, the most recent date with recorded data.

Tower name	Distance (km)	Direction	Deployments
Churchill Northern Studies Centre	8	S	18 July 2021 – 28 July 2023
Prince of Wales Fort	30	NW	25 July 2022 – 21 September 2022
			22 June 2023 – 19 October 2023
Nester 1	33	E	18 June 2021 – 21 September 2022
Broad River	76	SE	10 June 2022 – 18 October 2023
Owl River	108	SE	9 June 2022 – 18 October, 2023
York Factory	200	SE	7 June 2022 – 18 October, 2023

Tag Deployment

This work was conducted under the Bird Banding permit #10515 AT and an approved animal care protocol. Between 6 June – 5 July 2021-2023, I captured adult Stilt Sandpipers and Short-billed Dowitchers incubating full clutch nests (typically 4 eggs) using a bow-net ground trap (Figure 3.1). I deployed VHF radio tags (“Nanotags”, NTQB2-3-2(M), Lotek, Inc.) attached with LePage® Ultra Gel™ Control® cyanoacrylate glue according to the shorebird glue method (https://motus.org/wp-content/uploads/2020/02/tag_deployment_methods.pdf). Feathers above the uropygial gland were trimmed and the tags were glued to feather stubs and skin (Warnock and Warnock 1993). This method is relatively non-invasive, as tags are expected to fall off naturally during the bird’s prebasic moult. The tags weighed 0.67 g and varied from 1.1%-1.4% of the Stilt Sandpipers body weight (46.5-61 g) and 0.6-0.8% of the Short-billed Dowitchers body weight (83-114 g); both percentages are substantially lower than the recommended tag weight limit of 3-5% of a bird's body weight (Barron et al. 2010). Tags were programmed to transmit every 8.9-10.5 seconds, offering a predicted tag life of 169-191 days.

I deployed 12 tags on 8 Stilt Sandpipers (male: n = 5, female: n = 3) and 42 tags on 41 Short-billed Dowitchers (male: n = 22, female: n = 15, unknown: n = 4). Over three years, one Short-billed Dowitcher was tagged twice but only detected in 2023. Two Stilt Sandpipers were tagged twice during the study: one was tagged in 2021 and 2022 (ID: 54783 and 65693), and one was tagged in 2022 and 2023 (ID: 65687 and 63523). One Stilt Sandpiper was tagged each of the three years (ID: 54779, 65702, and 65705). The sex of Stilt Sandpipers was determined using blood samples (n = 5), the sex of the partner (n = 1), recaptures of previously sexed birds (n = 4), and cloacal protuberance of the female and/or behaviour (n = 2) (Pyle 2008) (Supplementary Table S3). Blood samples were analyzed by O. Haddrath of the DNA laboratory, Royal Ontario Museum, Toronto, Ontario, Canada. The sex of Short-billed Dowitchers was determined by comparing the culmen length to ranges published in Pyle (2008) (n = 26) as the female's culmen averages longer, and if measurements were ambiguous (n = 16), the likely sex was determined with the likely sex of the mate (Supplementary Table S4).

An additional Stilt Sandpiper of unknown sex was tagged in Wapusk National Park, approximately 30 km east of the Twin Lakes Fen on 18 June 2023 (tag 63541). The tagging location was within 1 km of the Nester 1 Motus receiving station, though this tower was not active at the time (Figure 3.1). I included this individual's migratory pathway in a supplementary map to examine the migratory connectivity of Stilt Sandpipers.

Data Cleaning

All analyses were conducted using R Version 4.3.2 (R Core Team 2023). I used the R packages motus (Birds Canada 2022) and dplyr (Wickham et al. 2023) to process and filter data, lubridate (Grolemund 2011) to format dates and times within the Motus data, ggplot2 (Wickham 2016) and cowplot (Wilke 2020) to generate plots. I generated maps in QGIS (QGIS Development Team 2023). Figure 3.1 was created with Bing Maps base map (Bing Maps 2023), and Figures 3.2, 3.5, 3.7, 3.8, 3.10, 3.12, and 3.13 were created with ESRI base maps (ESRI 2023).

I applied the strictest built-in filter in the motus package (Birds Canada 2022) which removed potential false hits with a run length (series of detections of an individual at a tower) of less than 3 and a run length of less than 5 at noisy receiving stations (those with >100 runs in an hour where 85% have a run length of 2). After the strictest filter was applied, I inspected each detection event individually and checked for several issues to ensure that the pathway and timing based on theoretical migration speeds was biologically possible. Of the detections assigned to be removed by the filter, any detections that were likely legitimate were added back to the dataset.

To assess legitimacy, I checked that the time between subsequent detections at a single antenna at a tower was divisible by the burst interval of the tag, e.g., if the tag's burst interval was 8.89 seconds, it was acceptable if detections were 17.78 ± 0.5 and 26.67 ± 0.5 seconds apart, but not acceptable if detections were 6 or 15 seconds apart. Next, I checked that plots of the change in detection latitude and longitude over time were acceptable. I removed any detections that strayed far out of the presumed migration pathway either by time or space, e.g., a detection in Florida, and then in Kamloops, British Columbia on the same day. I checked that the timing of the detections made sense biologically, e.g., removing detections that occurred when I knew that the individual was still in Churchill by creating a filter to remove any detections before the last resight of the bird in Churchill or the last date it was observed incubating if the nest was successful. I checked that the distance covered between two subsequent receiving station detections was biologically possible by comparing the approximate distance between receiving stations over time with the recorded flight speeds of each species (McNeil 1970). Finally, I identified and removed problematic receiving stations from the dataset when detections occurred for every bird in the study and when detections that may have been accepted were also occurring before migration was initiated.

In some cases, a subjective decision had to be made. For example, I removed any detection for which a plot of the signal coming from the tag over time appeared unacceptable, e.g., if there was only one burst recorded, if patterns arose that could not explain a bird moving closer and further away from the receiving station. However, detections with poor signal plots that may have been initially removed but that made sense with the timing and pathway created by accepted detections may have been allowed. To check the validity of questionable locations or in a few cases longer detections, e.g., where a bird was detected by receiving stations for multiple days suggesting a stopover, I visually cross-referenced this location with eBird data (ebird.org, Sullivan et al. 2009). I checked a radius of approximately 15 km and decided whether it was likely that the detection was true based on the effort that occurred in an area and how many individuals of the species were typically seen. If there were no observations of the species in the radius but still some checklist effort, I typically removed the detection. I used this mainly for areas with high eBird coverage such as southern Canada or the northeastern United States. For consistency of detections during flyovers, I assigned the time of detection as the average point during a series of hits at a tower, which may have corresponded to the time at which the bird was closest to the tower.

Departure Dates

I considered any tag with a detection at the Owl River, Broad River, or York Factory Motus receiving stations (Table 3.1, Figure 3.1) to be an individual departing the breeding area. For two individuals I used departures from the CNSC station because subsequent detections further south confirmed these as departures. I used the average time of detections at these departure stations as the departure time. To further support that these detections were during a migration flight, I checked that the detections at the Broad River Research Compound Motus receiving station (76 km south of the tagging site and 32 km north of the Owl River Research Compound Motus receiving station) occurred on the same night and earlier than those at the more southern Owl River Research Compound Motus receiving station for tags detected at multiple stations.

To meet my first objective, I tested two factors that may affect the departure date of Short-billed Dowitchers. I fit a linear mixed effects model to the relationship between departure date as the response variable and estimated hatch date (doy) and likely sex (M or F) and included year as a random effect. I used the estimated hatch date based on either actual hatch evidence or float estimates. I used the departure dates of 16 individuals (male = 9, female = 7). Only one departure was detected for Stilt Sandpipers, so they were excluded from this analysis.

Migratory Pathways

Locations of detections (stations) were connected with the Points to Path function in QGIS ordered by time to represent the approximate migratory pathway of each individual. For the purpose of broadly describing migratory pathways and stopover locations given the uneven distribution of Motus stations (Figure 3.2), and the filtering steps required and described above, I divided the areas of North America in which Short-billed Dowitchers and Stilt Sandpipers were detected into 11 regions: 1) Northern Array (Churchill area, Wapusk National Park, York Factory in northern Manitoba), 2) Prairies – Canada (southern Manitoba), 3) Northern Ontario, 4) Great Lakes – Canada/U.S. (area around all 5 Great Lakes, including the state of Michigan), 5) Midwest U.S. (east North Dakota east to the Great Lakes, Minnesota, southwest Wisconsin, Iowa, Missouri, Illinois, Kentucky, and Ohio), 6) Northeast Interior U.S. (New York and Pennsylvania south of Great Lakes region, eastern Ohio, West Virginia, interior Virginia and Maryland), 7) Mid-Atlantic U.S. (coastal New York, New Jersey, Delaware, Maryland, and Virginia), 8) Southeast Interior U.S. (Tennessee, Mississippi, Alabama, interior Georgia, South Carolina and North Carolina), 9) Southeast Atlantic U.S. (coastal North Carolina, South Carolina, Georgia, and eastern Florida), 10) Gulf Coast (coast of Gulf of Mexico, western Florida, Florida Keys), 11) Central America (Figure 3.3). I calculated departure bearings as the angle between the tagging site and the first tower detection after departure.

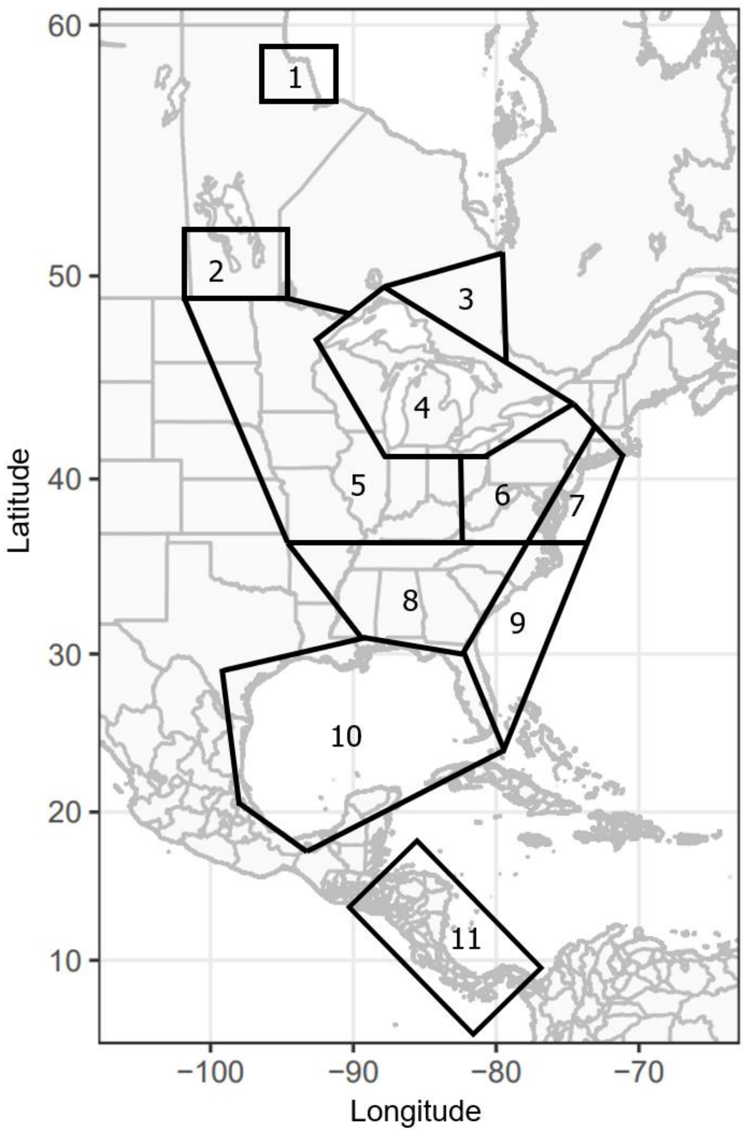

Figure 3.3. Map of the broad regions of North America where VHF-tagged Stilt Sandpipers (*Calidris himantopus*) and Short-billed Dowitchers (*Limnodromus griseus hendersoni*) were detected by the Motus Wildlife Tracking System in 2021-2023. 1) Northern Array, 2) Prairies – Canada, 3) Northern Ontario, 4) Great Lakes – Canada/U.S., 5) Midwest U.S., 6) Northeast Interior U.S., 7) Mid-Atlantic U.S., 8) Southeast Interior U.S., 9) Southeast Atlantic U.S., 10) Gulf Coast, 11) Central America.

Migration Timing and Speed

I counted the number of unique individuals of each species that were detected at least once in each of the broad regions (Figure 3.3). I defined 'length of passage' as the time spent in a region, whether the bird was passing through or if it stopped for any amount of time, as I could not always definitively separate these two phenomena. I estimated the minimum length of passage (days or hours) in each region for each bird that visited by subtracting the time/date of the last detection from the time/date of the first detection in the region. I estimated only length of passage after the northern array because it was not possible to track post-breeding movements before southward movement. Because the Motus system of receiving stations does not have perfect coverage, these length of passage numbers are expected to be low estimates in many cases. For instance, birds stopping over in North America may complete their pre-basic moult and drop their VHF tag but remain at the stopover site. Additionally, some stopover sites in the southeast U.S. could potentially be wintering sites, as some Short-billed Dowitchers and Stilt Sandpipers can winter in these areas (Norling et al. 2012, Wallover et al. 2015).

I calculated migration speed by dividing the haversine distance between stations (km) by the time (hr) between subsequent detections. I included towers for which detections lasted <1 hr. I removed any detections at towers <62.3 km from each other as simultaneous detections are known to occur below this distance (upper 97.5% from Anderson et al. 2019). I removed any speeds over 42 m/s as these may represent simultaneous detections at multiple nearby towers and any speeds under 9 m/s as these may indicate a lack of movement (Grönroos et al. 2012, Anderson et al. 2019). To determine the initial migration speed from the breeding area in Churchill, I selected the last detection in the breeding array (Figure 3.1) and the first detection in the southern array. I divided the haversine distance between stations (km) by the time (hr) between the last detection in the northern array and the first detection in the southern array.

Stopovers

I considered any repeated detections occurring at a single receiving station for >24 hours to be a confirmed stopover event, and I summarized other potential stopover locations where the time between detections between subsequent stations were >12 hours. I removed any potential stopovers where the speed between subsequent towers was <57.6 km/hr based on previously reported air and ground speeds for shorebirds (Grönroos et al. 2012). I calculated the minimum stopover length using the date and time of the first and last detections at the receiving station. To meet my third objective, I described stopover locations by visually inspecting the estimated range of the tower where the individual stopped over (available on motus.org), and qualitatively describing potential stopover habitat, proximity to human development, or any other relevant landscape features.

RESULTS

Departure Dates

Short-billed Dowitchers

Seventeen dowitchers were detected departing the breeding grounds, representing 53% of tags with detections. The average departure date for Short-billed Dowitchers was 17 July ± 2.0 (mean ± SE, range = 3 July-August 2). Female Short-billed Dowitchers departed the breeding grounds 10.5 ± 3.4 days (estimate ± SE) earlier than males ($P < 0.01$, Table 3.2, Figure 3.4). Hatch date was not a significant predictor of departure date (estimate = 0.39, $P = 0.32$). Dowitchers departed at an initial bearing of 149° ± 2.8 (mean ± SE). Two dowitchers were detected leaving the breeding site by the CNSC station: at 2052 h and 1933 h local time (CDT), approximately 52 and 170 minutes before sunset, respectively. An average of 26 minutes (17-42) elapsed between detections at the Broad River and Owl River stations, which are about 30 km apart ($n = 6$). Two confirmed failed breeders departed Churchill on the evening of 12 July 2022. One was a female from a nest attempt that failed between 14-17 June (ID: 65688), and the other was a male from a nest attempt that failed between 24-26 June (ID: 65690). The time elapsed between nest failure and departure was 25-28 days and 15-17 days respectively, but it is unclear if these were the last nesting attempts made by these individuals.

Table 3.2. Linear mixed effects model relating sex (male or female) and hatch date (estimated or actual) to departure date (day of year) of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) ($n = 16$). Significant ($\alpha = 0.05$) effects are indicated in bold. Year as a random effect explained 10% of the variation in the model.

	Estimate	SE	*t*	*P*
Departure date ~ presumptive sex + hatch date + (1|year)				
(Intercept)	122.64	62.42	1.97	0.10
Sex (Male)	10.55	3.37	3.13	**<0.01**
Hatch date	0.39	0.35	1.11	0.32

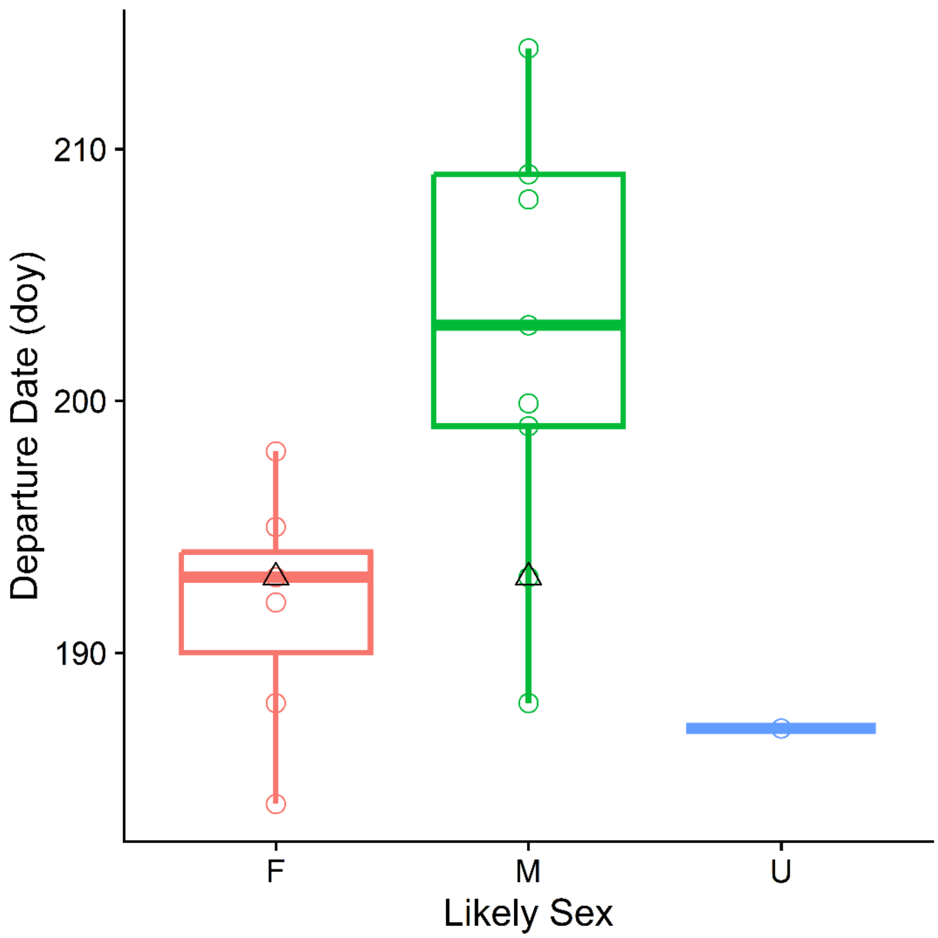

Figure 3.4. Assumed post-breeding migration initiation date (ordinal day of year) of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) after breeding in Churchill, Manitoba (male: *n* = 9; female: *n* = 7, unknown: *n* = 1). Open circles represent individual Short-billed Dowitchers, triangles indicate departure dates of two failed breeders, the median is indicated by the thick middle line, boxes represent interquartile interval where 50% of data is found, length of whiskers represent maximum and minimum values within 1.5x interquartile range.

Stilt Sandpipers

One Stilt Sandpiper (1/12 tags, 8%) was confirmed to have departed the breeding grounds at 1900 h on 12 July when it was last detected at the CNSC station before subsequent detections in the southern array. No other Stilt Sandpipers were detected leaving the area.

Migratory Pathways

Short-billed Dowitchers

Of 42 tags deployed on Short-billed Dowitchers in 2021-2023, 35 (83%) were detected by the Motus Wildlife Tracking System. In 2021, two dowitchers were observed later in the breeding season without tags. Of the dowitchers tagged in 2022 and 2023 when towers were active in the Northern Array (Table 3.1), 23/29 (79%) were detected either in the Churchill, Manitoba region or departing further south in the Northern Array, most commonly at the CNSC station 8 km north of The Fen site (16/29, 55%). At Broad River, 76 km east, 9/29 (31%) tags were detected, and 12/29 (41%) were detected 108 km southeast at Owl River (12/29). When the Nester 1 tower was active in 2021-2022, 1/28 (4%) tags were detected, and when the York Factory station was active in 2023, 1/14 (7%) tags were detected.

Thirty-two of all thirty-five detected tags (91%) were detected in the Southern Array. Short-billed Dowitchers were detected migrating as far west as Galveston, Texas, U.S., as far east as Atlantic City, New Jersey, U.S., and as far south as Big Pine Key, Florida, U.S. (Figure 3.5). After departing the breeding grounds, most individuals (30/32, 94%) were detected by at least one tower in the Great Lakes region, however, based on the estimated pathways in Figure 3.5, it is possible that all individuals moved through the Great Lakes region. After moving through the Great Lakes region, Short-billed Dowitchers were sometimes detected in the Midwest (8/32, 25%) and/or the Northeast Interior U.S. (17/32, 53%), before arriving at either the Mid-Atlantic Coast (5/32, 16%), the Southeast Atlantic Coast (20/32, 63%), and/or the Gulf Coast (7/32, 22%). Few individuals (4/32, 13%) were detected in the Southeast Interior, and of these, one was later detected in the Southeast Atlantic Coast, and two were detected in the Gulf Coast. After Short-billed Dowitchers were detected in the Mid-Atlantic Coast, they were typically not detected elsewhere (4/5, 80%), except for one individual that was later detected stopping over in the Southeast Atlantic Coast (ID: 65698). The Southeast Atlantic Coast was the final detection region for 17/20 (85%) of the Short-billed Dowitchers detected in the region, but 3/20 (15%) were later detected in the Gulf Coast. Just one tag (2%) was detected in the Northern Ontario region (ID: 63555) (Figure 3.5).

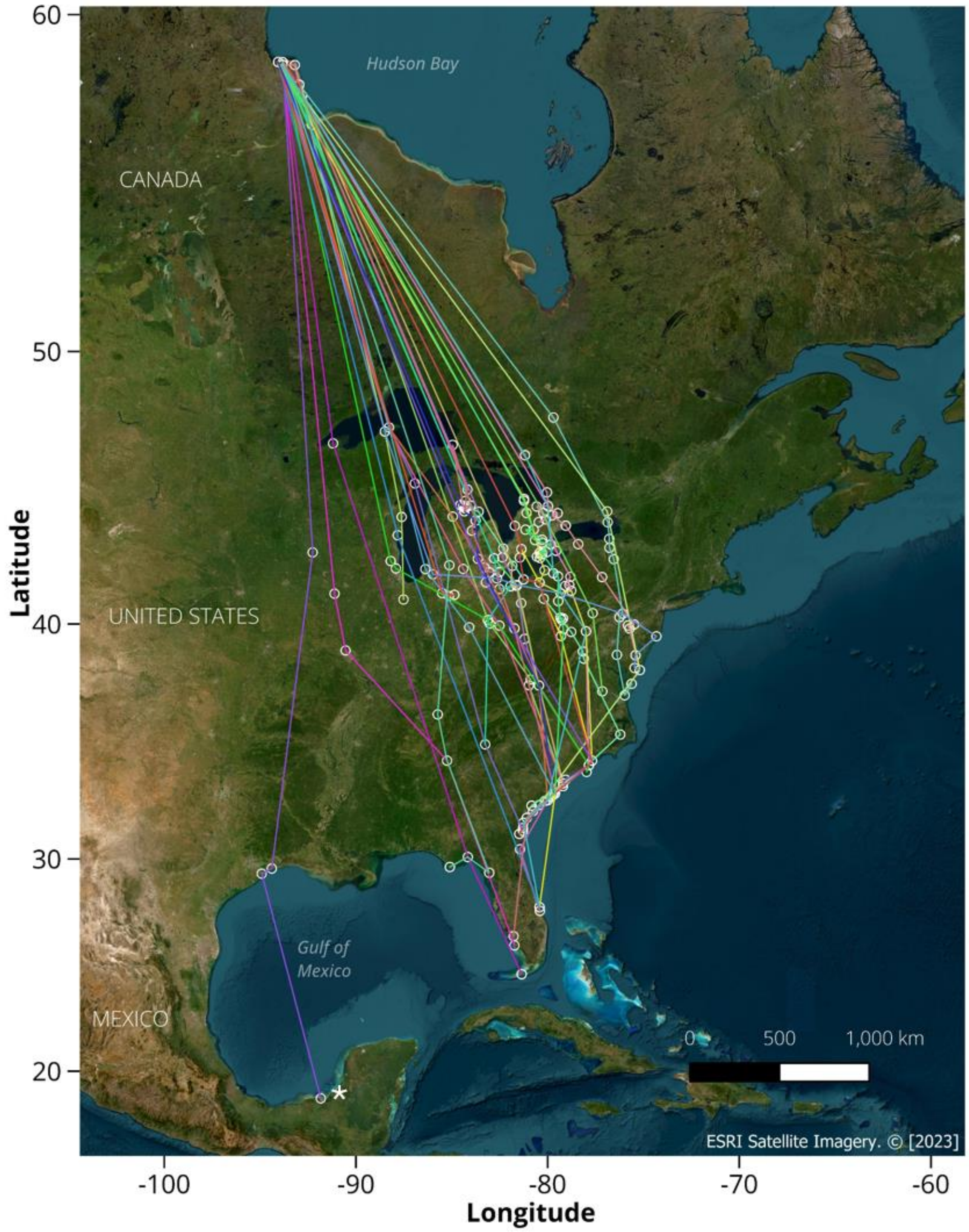

Figure 3.5. Detections and approximate pathways of VHF tags deployed on Short-billed Dowitchers (*Limnodromus griseus hendersoni*) in Churchill, Manitoba in 2021-2023 by the Motus Wildlife Tracking System. Each coloured line represents the approximate pathway of an individual's southbound migration (n = 35), and each white circle represents a Motus receiving station at which one or more detection occurred. Circle with * indicates location of a flagged bird resighted by birders but not detected by the Motus Wildlife Tracking System.

Seven of one hundred seventy-one of the towers in the Southern Array at which dowitchers were detected recorded ≥ 5 individuals. In West Virginia, U.S., 5/32 (16%) of tags were detected at the 'Hanging Rock' receiving station. On the southeast coast of North Carolina, U.S., 8/32 (25%) of all tags were detected at 'NCNERR – Masonboro Island', and 5/32 (16%) were detected at 'CFA Motus tower' on Lea-Hutaff Island. On the northeast coast of South Carolina, U.S., 5/32 (16%) of tags were detected at 'North Intent – Winyah Bay NERR'. Another 8/32 (25%) of all tags were detected at 'Cape Romain NWR, SC (Bulls Island)' and 7/32 (22%) at the 'Little Bear' receiving station on Kiawah Island on the mid-east coast of South Carolina. Finally, 5/32 (16%) were detected at the Georgia DNR Dock near Brunswick, Georgia, U.S. No Short-billed Dowitchers were detected taking a western interior route through the Prairies region of Canada nor in the Central America region.

No Short-billed Dowitchers were detected by the Motus Wildlife Tracking System outside of Canada and the U.S., however, one bird (ID: 63528) was photographed at Playa Norte in Ciudad Del Carmen, Campeche, Mexico on 13 November 2023 (https://ebird.org/checklist/S154410096, Macaulay Library ML 611122498). This dowitcher was tagged on 11 June 2023 and successfully hatched a nest on 20 June. It was detected at the 'CNSC 21' station on 30 June until 1 July at 1751 h (CST). On 10 July, it was detected for 5 minutes in northeastern Iowa, and 2 d 8h later it was detected moving west along the Gulf Coast between two towers in the Galveston, Texas area for 4 and 5 minutes each. After these detections, this dowitcher was not detected again until it was photographed at Playa Norte on 13 November. To date, this individual has not been seen again at Playa Norte.

The minimum length of passage was longest in the Southeast Atlantic, where Short-billed Dowitchers stayed for 9.60 ± 1.66 d (median ± SE, max = 27.19 d, n = 20) (Figure 3.6). Short-billed Dowitchers generally had very short stays in the Midwest (0.01 ± 0.80 d, max = 6.45 d, *n* = 8), Northeast Interior (0.02 ± 0.02 d, max = 0.24 d, *n* = 17), Northern Ontario (0.01 d, *n* = 1), Southeast Interior (0.01 ± 0.04 d, max = 0.15 d, *n* = 4), and Gulf Coast (0.01 ± 0.48 d, max = 3.44 d, *n* = 7) (median ± SE, *n*). The length of passage was longer in the Mid-Atlantic (0.30 ± 1.27 d, max = 6.59 d, *n* = 5) and Great Lakes (0.31 ± 0.14 d, max = 3.75, *n* = 29) (Figure 3.6).

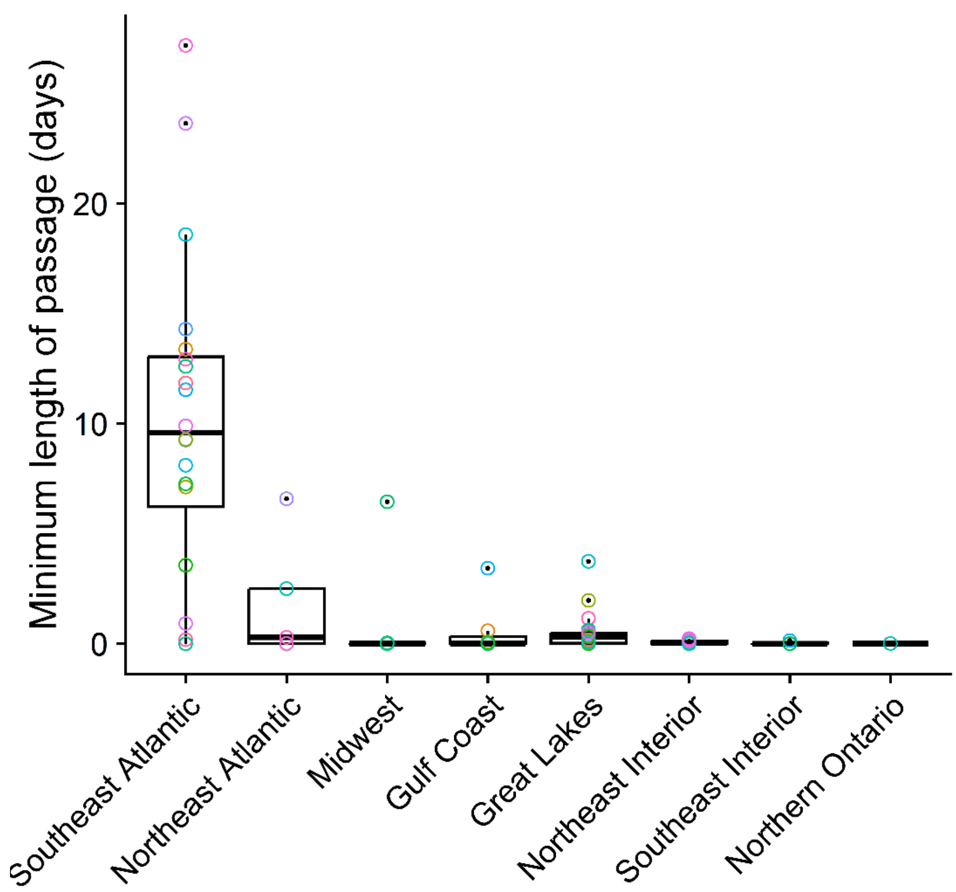

Figure 3.6. Minimum length of passage of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) (*n* = 35) during post-breeding migration (see Supplementary Table S5, Supplementary Figure S5).

Stilt Sandpipers

Of the 12 tags deployed in Churchill in 2021-2023, 10 (83%) tags on 6 individuals were detected by the Motus Wildlife Tracking System. Of the sandpipers detected in 2022 and 2023 when towers were active in the Northern Array, 6/7 (86%) were detected by the CNSC station 8 km north of the Twin Lakes Fen site where all tags were deployed. No tags were detected at towers southeast of Churchill in the Northern Array. Eight of ten (80%) tags were detected in the Southern Array (Figure 3.7). No Stilt Sandpipers were detected in or departing the Churchill region. Three of eight (38%) individuals detected in the Southern Array were detected in the Prairies region, and then 8/8 (100%) individuals were detected in the Midwest region. Only two individuals were detected further south after being detected in the Midwest region. One Stilt Sandpiper was detected in Costa Rica at the Estación Biológica Maritza receiving station (10.9576°N, 85.4966°W), located in Parque Nacional Guanacaste in the northernmost province and 22.6 km east of the closest inlet of the Pacific Ocean, the Gulf of Santa Elena. Another individual was detected on the coast of Georgia, U.S., and then on the coast of Florida, U.S.

One individual (ID: BuOr, tags 54783 and 65693) was tagged twice during the study and was detected at two towers 172 km apart in 2021 and 2022. One individual (ID: YJE/Ba, tags 54779, 65702, and 65705) was tagged and detected in each year of the study, and over three years, the trajectory of its post-breeding migration was approximately the same (Figure 3.8). This individual was detected at the same station ‘MDC PURDIN’, Missouri, U.S., for two years in a row: it was detected flying by on 16 July 2021 and 20 July 2022.

The Stilt Sandpiper tagged in Wapusk National Park at the Nester 1 Research Station took at first a similar route to those tagged in Churchill (Supplementary Figure S4). It was detected in Grand Forks, North Dakota, U.S., at the same location where several Stilt Sandpipers tagged in Churchill were also detected. It then moved southeast across the Midwest, being detected in Chicago, Illinois, U.S. before final detections occurring in coastal Virginia, U.S. at Fisherman's Island.

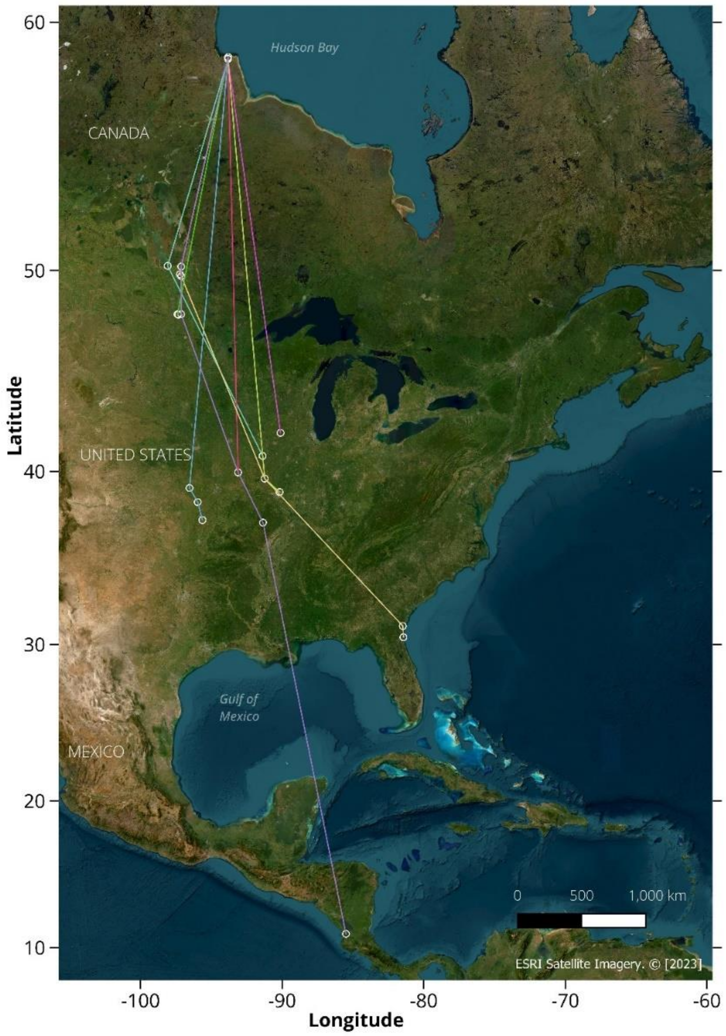

Figure 3.7. Detections and approximate pathways of VHF tags deployed on Stilt Sandpipers (*Calidris himantopus*) in Churchill, Manitoba in 2021-2022 by the Motus Wildlife Tracking System. Each coloured line represents the approximate pathway of an individual's southbound migration (n = 10), and each white circle represents a Motus receiving station at which one or more detection occurred.

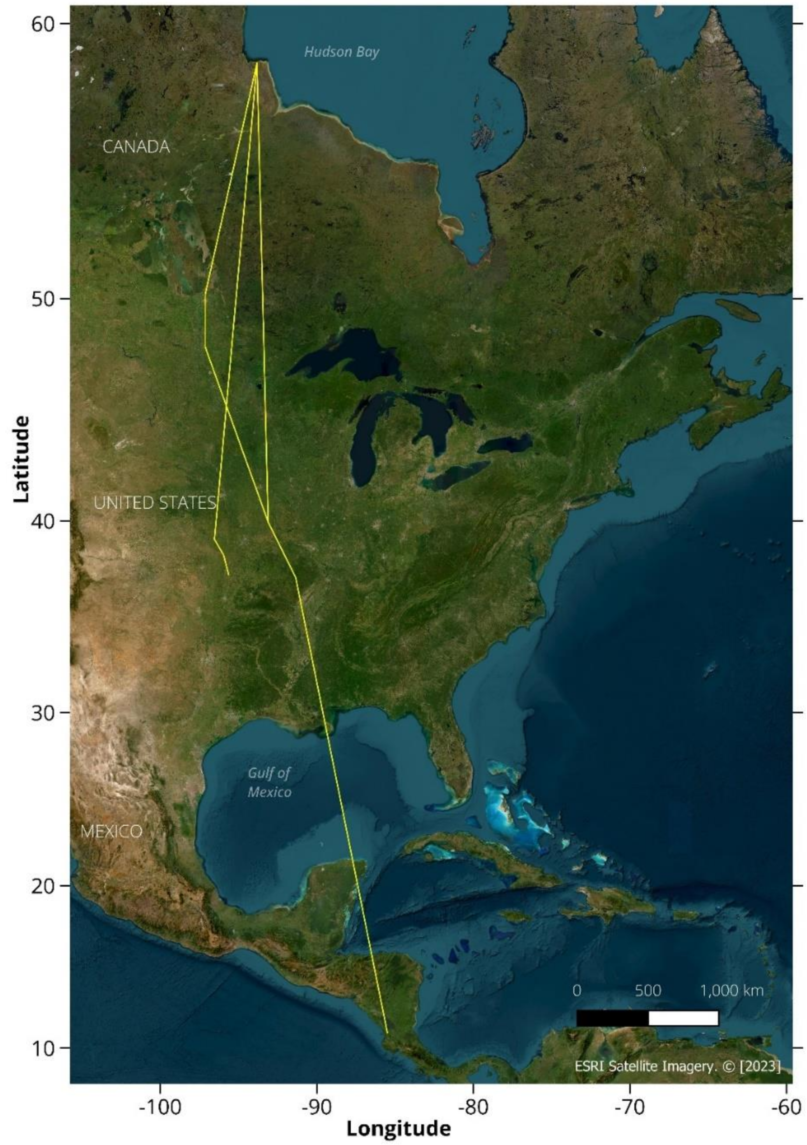

Figure 3.8. Approximate pathway of post-breeding migration in 2021, 2022, and 2023 of a single individual Stilt Sandpiper (*Calidris himantopus*) flag "YJE" tagged across multiple years and detected by the Motus Wildlife Tracking System migrating from Churchill, Manitoba.

The minimum length of passage was the longest in the Midwest, where Stilt Sandpipers were detected for 0.03 ± 1.02 d (median ± SE; max = 6.72 d, *n* = 8) (Figure 3.9). In the Prairies region, Stilt Sandpipers were detected for 0.01 ± 0.01 d (median ± SE; max = 0.03 d, *n* = 3). One Stilt Sandpiper was detected for 5 min in Central America (northwestern Costa Rica), and another was detected for 1.82 d in the Southeast Atlantic Coast region (Figure 3.9).

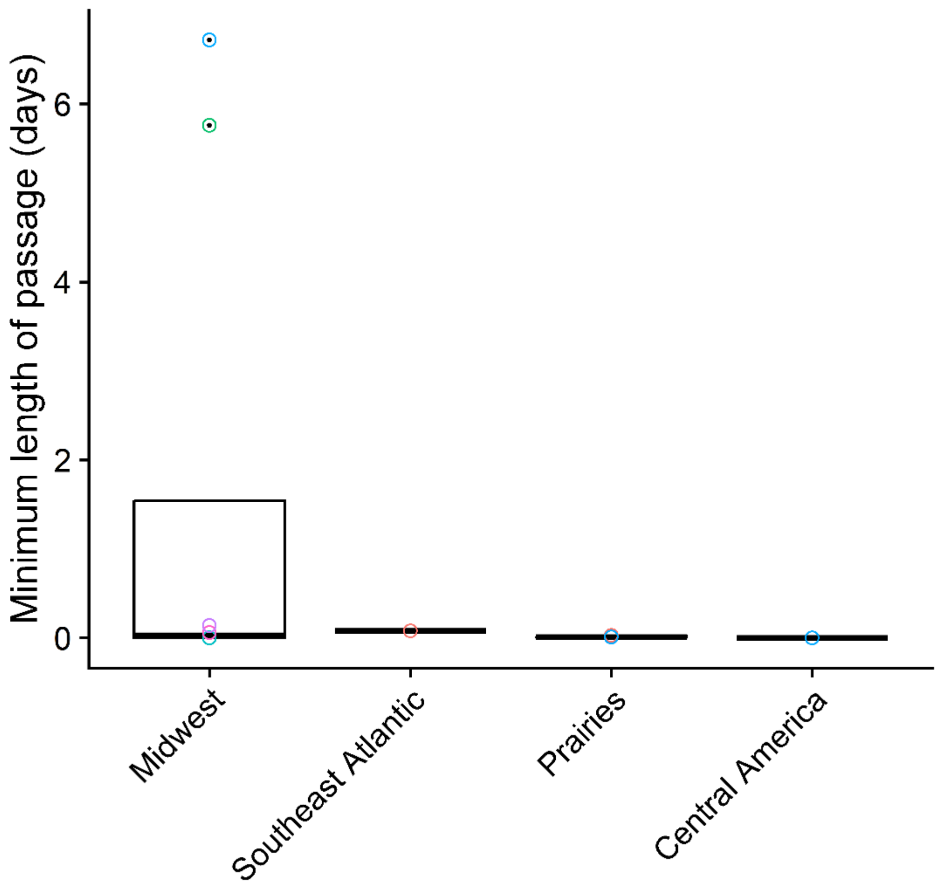

Figure 3.9. Minimum length of passage of Stilt Sandpipers (*Calidris himantopus*) (*n* = 10) during post-breeding migration (see Supplementary Table S5, Supplementary Figure S5).

These are low estimates in many cases for both species. For example, Stilt Sandpiper ID 65702 was detected on 13 July 2022, in the Prairies region and then in the Midwest region approximately 4 hours later. This individual spent 6.52 d somewhere between northeast North Dakota and Missouri, before flying by two stations across Missouri on 20 July 2022. After these detections, it was not detected again in North America before being detected flying by a station in northwestern Costa Rica on 13 August 2022.

Migration Timing and Speed

Short-billed Dowitchers migrated at an estimated average ground speed of 19.0 ± 0.6 m/s or 68.2 ± 2.0 km/hr (mean ± SE, n = 115). The initial estimated migration speed between the last detection in the northern array and the first detection in the southern array was 20.51 ± 2.13 m/s (median ± SE) (Table 3.3). Thirteen of twenty (65%) Short-billed Dowitchers had an initial migration speed of > 57.6 km/hr and therefore likely did not stop between the northern and southern array, whereas 7/20 (35%) had an initial estimated migration speed of < 57.6 km/hr and therefore likely stopped between the northern array and their first detection in the southern array for 4.37 ± 2.13 d (median ± SE, min = 1.58, max = 17.4 d, n = 7) before being detected by stations in the southern array (Table 3.3). Of flights from breeding grounds to the first stop or end of detections in the southern array, Short-billed Dowitchers flew 2941 ± 80 km (median ± SE, n = 15) and up to 3102 km before stopping or no longer being detected.

Table 3.3. Post-breeding migration speed (median ± SE (*n*)) of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) breeding in Churchill, Manitoba in 2021-2023. Migration initiation characteristics calculated based on detections from the Motus receiving stations in the Northern Array south of the tagging sites (see Figure 3.1).

	Short-billed Dowitcher	Stilt Sandpiper
Migration initiation ground speed (m/s)	20.51 ± 2.13 (16)	6.9 (1)
Migration initiation distance (km)	2941 ± 80 (15)	1217 (1)
Migratory ground speed (m/s)	19.0 ± 0.6 (115)	18.0 ± 1.3 (7)

Stilt Sandpipers migrated at an average ground speed of 18.0 ± 1.3 m/s or 64.6 ± 4.7 km/hr (Table 3.3, mean ± SE, *n* = 7). Just one Stilt Sandpiper was confirmed leaving the northern array (Tag65702) on 12 July when it was last detected at the CNSC tower at 1910 h. The Stilt Sandpiper then flew past a tower ~977 km southwest at Oak Hammock Marsh in southern Manitoba, Canada 39 hours later (estimated speed of 25 km/hr). It was then detected in North Dakota, U.S. 4 hours later (estimated speed of 61 km/hr). Six days later, it was detected flying south between two towers in Missouri, U.S. 2 hours apart (estimated speed of 75 km/hr). It was then undetected until 13 August flying by a tower in Costa Rica (Figure 3.8).

Stopovers

Single-tower Short-billed Dowitcher stopover locations were recorded in Georgia (*n* = 6), South Carolina (*n* = 5), Florida (*n* = 1), North Carolina (*n* = 1), and Virginia (*n* = 1) (Table 3.4, Table 3.5, Figure 3.10). Most stopovers occurred between 35°N and 30°N (Figure 3.11). Six of fourteen Short-billed Dowitcher stopovers occurred on the coast of Georgia, including the longest minimum stopover duration of 24.0 days in 2023 (Table 3.5, Figure 3.10). Four stopovers occurred at the same Motus tower, the Georgia Department of Natural Resources (DNR) Dock, three of which were in 2023 and lasted a minimum of 8.8-24.0 days. Five of fourteen stopovers occurred on the coast of South Carolina (Table 3.5, Figure 3.10). Stopovers began as early as 11 July for a failed breeder (likely a male, Tag65689) and as late as 4 August for three successful breeders and began on average on 23 July (Table 3.5, Figure 3.10). Stopovers began approximately 7 days earlier in 2023 than in 2022.

Stopovers for Short-billed Dowitchers generally occurred on barrier islands and saltmarshes on the southeast Atlantic coast of the United States (Table 3.4). Many stopover locations were accessible to the public, some only by boat access. Four of fourteen stopovers occurred within tower ranges of National Wildlife Refuges. The Georgia DNR Dock tower, which represented the location of four of fourteen stopovers, was the closest to a city, Brunswick, Georgia, but is surrounded by saltmarshes and barrier islands (Table 3.4).

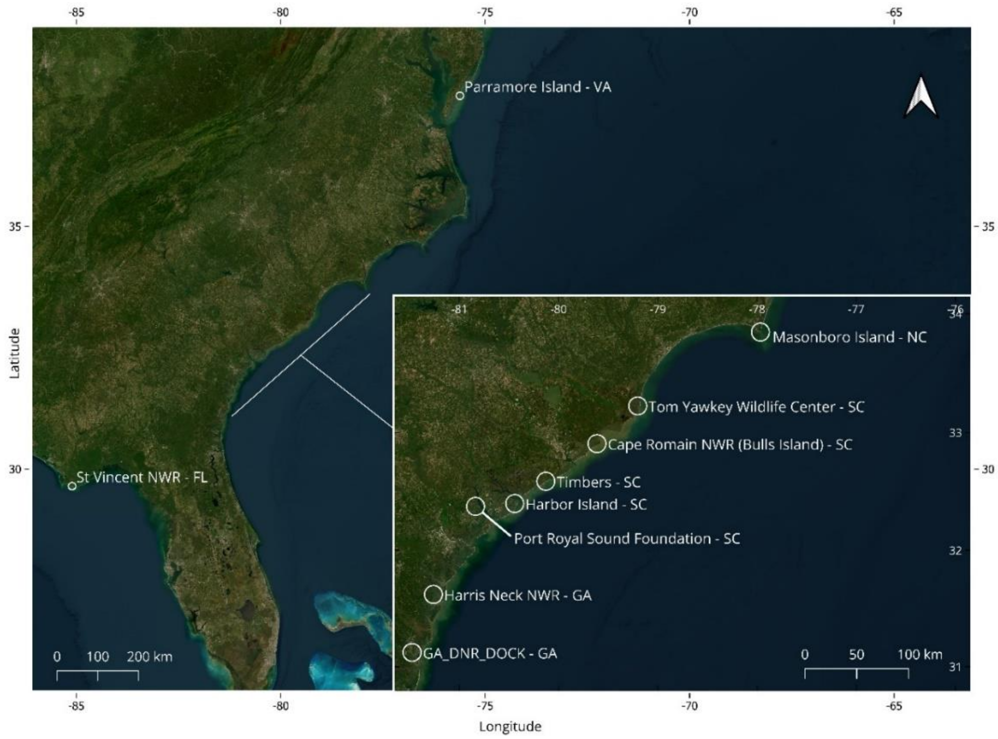

Figure 3.10. Stopover sites of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) during post-breeding migration from Churchill, Manitoba, Canada in 2021-2023 by the Motus Wildlife Tracking System. Each white circle represents a Motus receiving station at which at least one stopover occurred.

Table 3.4. Description of stopover sites of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) during post-breeding migration from Churchill, Manitoba in 2021-2023 detected by the Motus Wildlife Tracking System. IBA = Important Bird Area, WHSRN = Western Hemisphere Shorebird Reserve Network, NWR = National Wildlife Refuge

Stopover location	Dates	Duration (days)	Potential habitat	Ownership and development
Parramore Island, Virginia	12-13 July 2023	1.39	Barrier island, salt marshes (Raff et al. 2018)	Owned by The Nature Conservancy, uninhabited, and open to the public (VDCR 2024)
Masonboro Island, North Carolina	14-21 July 2023	7.26	Barrier island, salt marshes, tidal flats (NCDEQ n.d.)	State-owned reserve, uninhabited, open to the public via boat access (NCDEQ n.d.)
Tom Yawkey Wildlife Center, South Carolina	26-29 July 2023	3.27	Salt marshes, managed wetlands, open beach (SCDNR 2016)	State-owned reserve, uninhabited, limited to guided tours (SCDNR 2016)
Cape Romain National Wildlife Refuge, Bulls Island, South Carolina	18-25 July 2022	7.50	Barrier island, salt marshes, intertidal mud and sandflats (WHSRN 2019b, USFWS (n.d.) a)	State-owned NWR, uninhabited, Bulls Island accessible by ferry/boat (USFWS (n.d.) a)
Timbers, Kiawah Island, South Carolina	4-17 August 2021	13.16	Barrier island, salt marshes	Developed, private property and one public beach (Charleston County Parks and Recreation n.d.), Deveaux Bank (within tower range) uninhabited and limited access
Harbor Island, South Carolina	4-9 August 2022	5.49	Barrier island, salt marshes (National Audubon Society 2010)	Developed, private gated community (National Audubon Society 2010)
Port Royal Sound Foundation, South Carolina	31 July-18 August 2022	17.72	Tidal flats, salt marshes (Port Royal Sound Foundation n.d.)	Uninhabited and low development (Port Royal Sound Foundation n.d.)

Harris Neck National Wildlife Refuge, Georgia	25 July-2 August 2022, 26 July-7 August 2022	8.09, 12.28	Barrier island, salt marshes (USFWS (n.d.) b)	State-owned NWR, uninhabited, open to the public (USFWS (n.d.) b),
Georgia DNR Dock, Brunswick, Georgia	12-20 July 2023, 23 July-16 August 2023, 27 July-6 August 2023, 4-13 August 2022	8.80, 24.02, 9.35, 10.33	Barrier island, salt marshes (National Audubon Society 2024)	Close to a large city, some barrier islands are state-owned with varying levels of development (National Audubon Society 2024)
St Vincent National Wildlife Refuge, Florida	11-14 July 2022	3.00	Barrier island	Uninhabited (NWR)

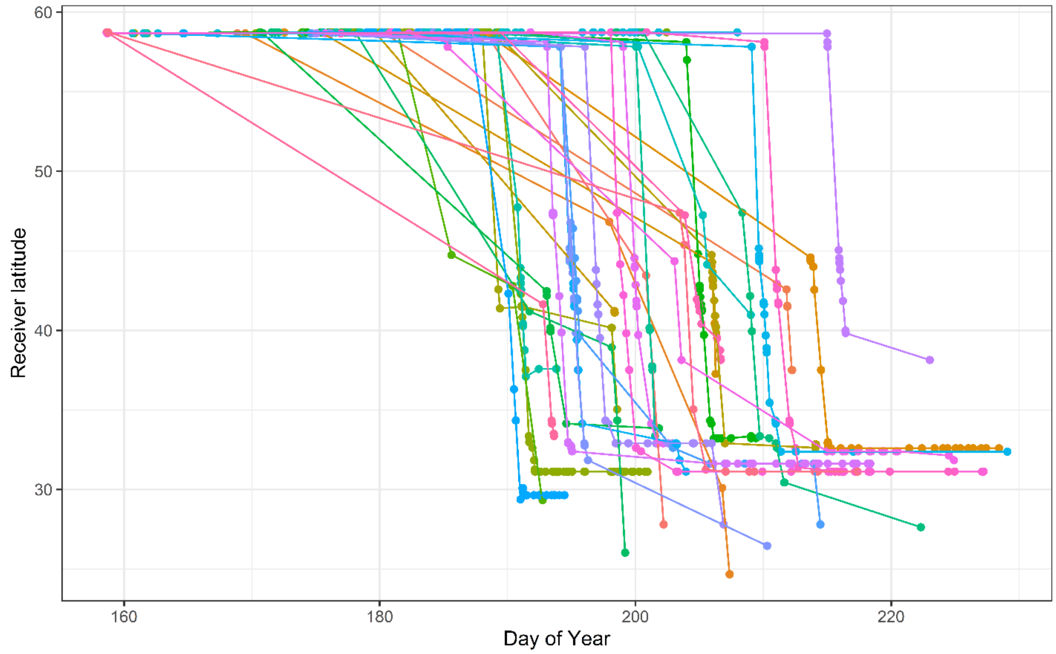

Figure 3.11. Receiver latitude of tower detections and approximate pathways of VHF tags deployed on Short-billed Dowitchers (*Limnodromus griseus hendersoni*) in Churchill, Manitoba in 2021-2023 by the Motus Wildlife Tracking System. Each coloured line represents the approximate pathway of an individual's southbound migration (*n* = 35), each open circle represents a Motus receiving station at which one or more detection occurred, and each closed circle represents the tagging date.

Table 3.5. Confirmed (at a single tower) stopover characteristics of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) during post-breeding migration from Churchill, Manitoba, Canada, to sites in the southeastern United States in 2021-2023 (*n* = 14).

Parameter	*n*	Mean ± SD	Range
Stopover start date	14	23 July ± 8.9	11 July – 4 August
Stopover duration (minimum days)	14	9.4 ± 6.0	1.4 – 24.0
South Carolina	5	9.4 ± 5.9	3.3 – 17.7
Georgia	6	12.1 ± 6.0	8.1 – 24.0
Florida	1	3.0	
North Carolina	1	7.3	
Virginia	1	1.4	

Another 26 potential stopovers were identified (where dowitchers were undetected for >12 hours, Figure. 3.12, Supplementary Table S6). Of those, 14 dowitchers remained in one U.S. state for the duration of the time they were undetected. Four of fourteen (29%) of these stopovers occurred in Ohio for 4.36 ± 1.75 d, 4/14 (29%) occurred in Georgia for 2.83 ± 2.18 d, 2/14 (14%) (median ± SE) occurred in South Carolina for 1.56 and 7.08 days, and one each in North Carolina (7.26 d), Florida (10.67 d), Virginia (1.02 d) and Michigan (0.94 d). The additional 12 potential stopovers occurred between various U.S. states and lasted for 4.69 ± 1.33 d (median ± SE).

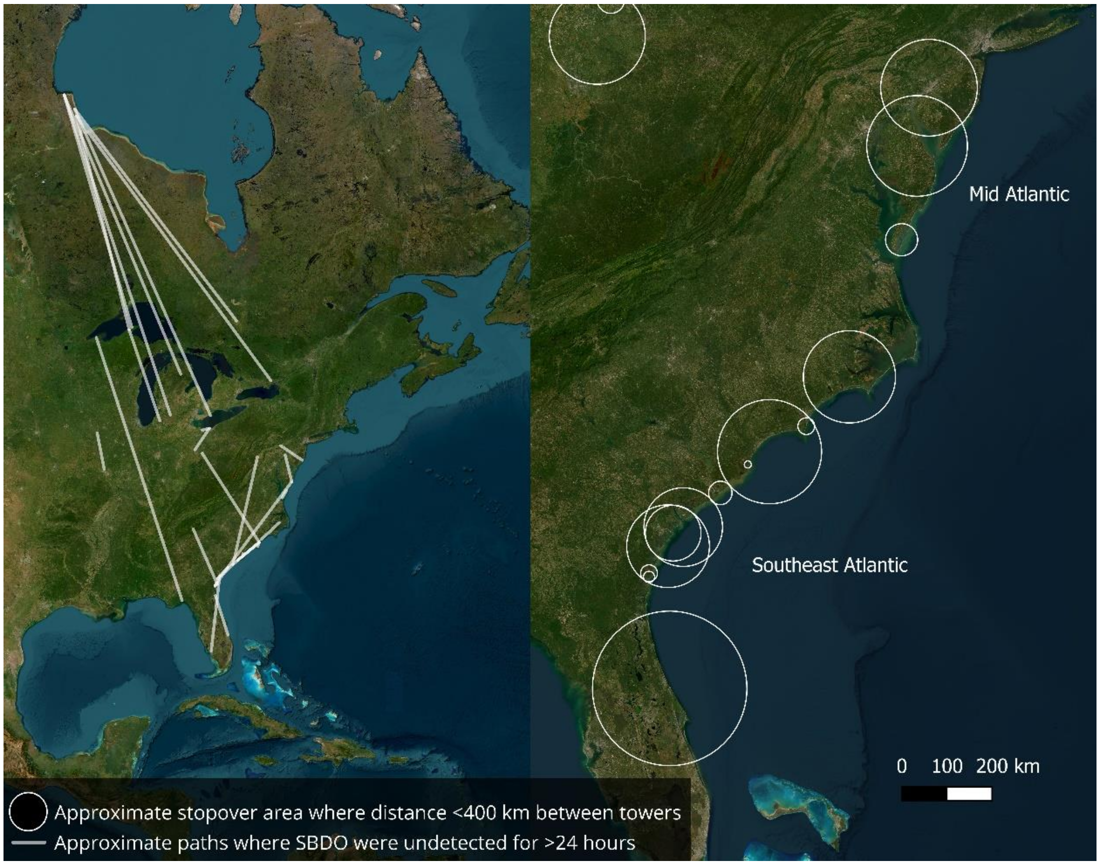

Figure 3.12. General locations of Short-billed Dowitcher (*Limnodromus griseus hendersoni*) stopovers where the time between two subsequent towers was >24 hours. Lines indicate the approximate paths and circles indicate the receiving range between towers <400 m apart (the approximate area in which the bird stopped).

One stopover was confirmed for a Stilt Sandpiper (Tag65687) where it remained between two stations (5 km away from each other) in North Dakota for 5.73 d from 26 September – 2 October 2022 (Figure 3.13). The tower was located at a sewage lagoon, nearby an airport and military base. An additional two potential stopovers occurred between the Prairies and Midwest region (11.87 d and 12.68 d, Figure 3.13), and one more within the Midwest region for 6.53 d (Figure 3.13, Supplementary Table S7), but exact locations were not attainable.

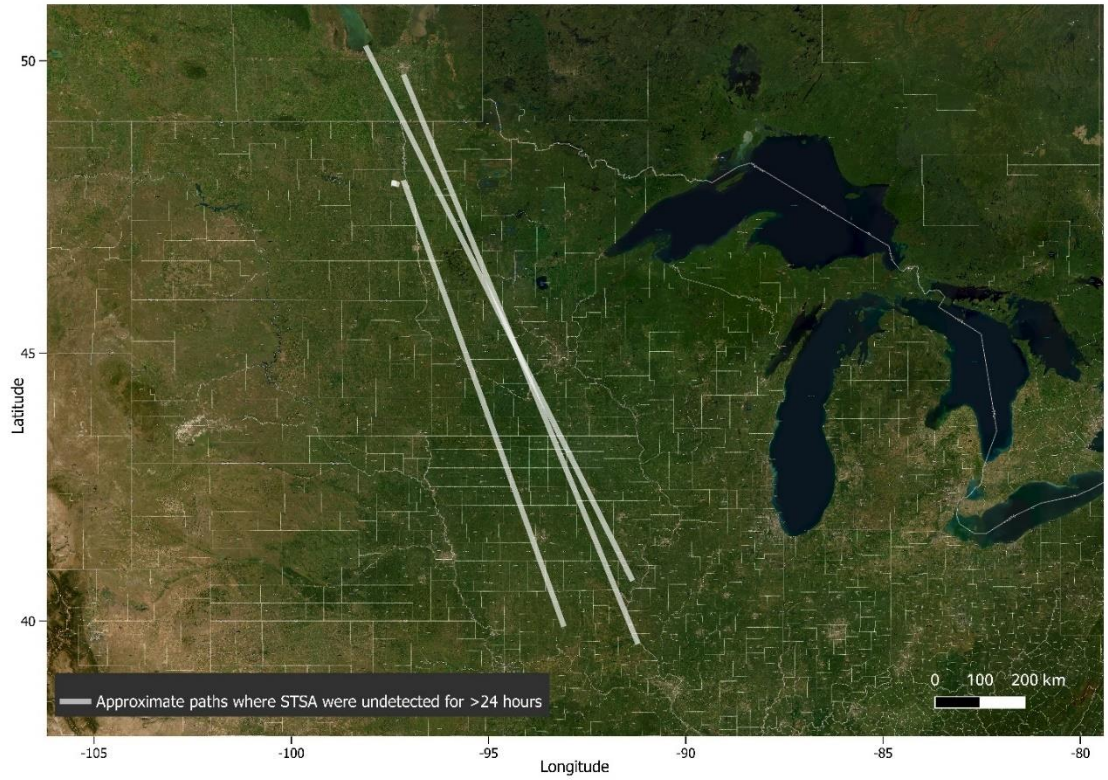

Figure 3.13. Approximate area in which Stilt Sandpipers (*Calidris himantopus*) stopped during post-breeding migration from Churchill, Manitoba in 2021-2023 by the Motus Wildlife Tracking System. Each white line represents a range between two Motus receiving stations where a stopover (<24 hrs) occurred.

DISCUSSION

I documented the first data on departure dates, migratory routes, and stopover locations for two poorly understood shorebird species using the Motus tracking array. Short-billed

Dowitchers began post-breeding migration in mid-July (range from 3 July – 2 August), females departed before males, and failed breeders left mid-July. The two species used very distinct migratory routes from Churchill, Manitoba, Canada with Short-billed Dowitchers bearing east and Stilt Sandpipers bearing west after leaving Churchill. Stopover lengths ranged widely but, for Short-billed Dowitchers, they can be relatively long, especially in the southeastern U.S.

Departure Dates

Short-billed Dowitchers breeding in Churchill departed the region in early July to early August, with the median occurring on 17 July, consistent with estimates from dowitchers arriving in coastal New Jersey, U.S. (Jehl 1963). Females departed over a week earlier than males (Jehl 1963, Jehl et al. 2020). Though female Short-billed Dowitchers appear to share incubation duties equally in Churchill (Jehl et al. 2020), female dowitchers provide little parental care after hatch (Harris 1989). This supports a "female-first" hypothesis recognized in other sandpipers: female Short-billed Dowitchers are the non-caring parent so they initiate migration before males (Myers 1981, Ydenberg et al. 2005). Two failed breeders left on 12 July, which is later than has been suggested (Jehl et al. 2020). These individuals may have initiated another nest attempt after their initial nest failures. Similar to estimates of failed breeders (Klima and Jehl 2020), we detected just one departure date of a Stilt Sandpiper on 12 July of a male from a nest that was abandoned sometime after 3 July. Examining factors influencing departure dates such as body condition or pre-departure winds may explain variation in departure dates within sexes and among successful breeders (Grönroos et al. 2012, Anderson et al. 2019).

Migratory Pathways

Short-billed Dowitchers departed their breeding grounds in the Churchill, Manitoba region and headed east, where many were detected by towers southeast of the tagging site. Nearly all tagged Short-billed Dowitchers were then detected at least once in the Great Lakes region, consisting mostly of fly-bys. In contrast, two Short-billed Dowitchers instead appeared to fly straight south from Churchill before diverging to the Gulf Coast of Mexico. Some dowitchers flew through to the Great Lakes region to the Mid-Atlantic, while others flew to the Gulf Coast, and the majority arrived at the Southeast Atlantic Coast. Previous suggestions based on initial flight bearings that Short-billed Dowitchers departed towards James Bay to the Atlantic Coast were not supported for most individuals (Jehl et al. 2020). According to approximate flight pathways, no Short-billed Dowitchers passed through James Bay, Ontario, Canada. However, 7 Short-billed Dowitchers were not detected for several days after departure before appearing in the southern array. It is possible that they could have stopped in Northern Ontario, possibly on James Bay, but there were no detections of dowitchers tagged in this study at any of the three towers on western James Bay that were active during our study.

Compared to the other subspecies of Short-billed Dowitchers, *L. g. griseus*, which is observed migrating along the North to Mid-Atlantic coast (Jehl 1963), and *L. g. caurinus*, which migrates almost exclusively along the Pacific coast (Paulson 1993), *L. g. hendersoni* generally takes a central pathway south. *L. g. hendersoni* breeding in Churchill take an intermediate route between *L. g. hendersoni* migrating through the prairies and interior U.S. (Peterjohn 1989, Alexander and Gratto-Trevor 1997, Hoffman 1999), and *L. g. griseus* migrating primarily on the Atlantic Coast. This pathway is therefore consistent with observations that *L. g. hendersoni* is the dominant subspecies migrating through Ontario (Jaramillo et al. 1991). An intermediate pathway is interesting given the debate of the Western coast of Hudson Bay as a zone of intergradation between *L. g. griseus* and *L. g. hendersoni*, but studies confirming the subspecies of breeding individuals in this area would be needed to propose this as a possible explanation.

The banded Short-billed Dowitcher observed by photographers in Ciudad Del Carmen, Campeche, Mexico in November migrated further to the west than any other individual in the study. It is unclear if it moved through the Great Lakes, and because it was undetected for two days between Iowa and Texas, it may be the only individual that stopped for any amount of time in the interior U.S. Additionally, the movement between the Gulf Coast in Texas, U.S. in July to Campeche, Mexico in November suggests that Short-billed Dowitchers continue migrating after their initial stopovers where they appear to lose their tags. Finally, this sighting highlights the benefit of flagging shorebirds as it provided movement information for an individual in an area lacking Motus receiving stations.

Although we did not obtain information on wintering grounds, the migration pathways of Short-billed Dowitchers still indicate some level of migratory connectivity. Nearly all individuals migrated through the Great Lakes, and 63% ended up in the Southeast Atlantic Coast, a number which may be higher without tag loss. Two Motus receiving stations, Masonboro Island in North Carolina, U.S., and Cape Romain NWR in South Carolina, U.S., each detected 25% of Short-billed Dowitchers in this study. A receiving station on Kiawah Island, South Carolina detected 22% of Short-billed Dowitchers. These high proportions of individuals banded at the same location in Churchill and subsequently detected at single towers >2000 km away indicates the importance of these sites during this subpopulation’s migration and suggests relatively high migratory connectivity.

No Stilt Sandpipers banded in Churchill were detected by towers southeast of Churchill at Wapusk National Park, Manitoba, Canada, which suggests that, unlike Short-billed Dowitchers, they do not follow along the coast of western Hudson Bay from Cape Churchill to York Factory, Manitoba. Stilt Sandpipers generally migrated through the Canadian prairies in Manitoba through the Prairie Potholes region and further south into the interior of the United States with most detections occurring in the central flyway. After stopovers in these regions, most individuals stopped being detected, but two individuals were detected again in Georgia then Florida in the United States, and Costa Rica. Further evidence for this spread comes from the Stilt Sandpiper tagged in Wapusk National Park, ~30 km east of the Twin Lakes Fen that initially followed the central flyway to the prairies and interior U.S., before making a flight across the Midwest and detections ending in coastal Virginia, U.S. Of Stilt Sandpipers banded at Quill Lakes, Saskatchewan, Canada, resights and band recoveries occurred in Montana, New Jersey, and Texas, U.S., and two in Venezuela (Alexander and Gratto-Trevor 1997). Together with previous band recoveries (Alexander and Gratto-Trevor 1997) and tracks from a nearby breeding site (Wapusk National Park), this indicates a wide spread of their migratory pathways. This may indicate that individuals of the same breeding population migrate in different areas and may not winter in the same locations. Lesser Yellowlegs breeding in Churchill, Manitoba similarly migrate through the prairie Potholes region, before moving east to make a transatlantic flight to where many winter in the Argentine Pampas Region in South America (McDuffie et al. 2022b). During the non-breeding season, there is mixing between Lesser Yellowlegs breeding populations of different origins resulting in low migratory connectivity. Low migratory connectivity is more common in long-distance migrants (Finch et al. 2017), but exploring this for the Stilt Sandpiper will require different tracking methods (e.g., satellite tags) that provide consistent location data into the non-breeding period and tagging effort across their breeding range.

Migration Timing and Speed

These tracking data confirm that Short-billed Dowitchers breeding in Churchill, Manitoba are capable of non-stop, direct flight to the Southeast Atlantic. Though their relative rarity inland in the northeast suggests they may do a direct flight, and historical data suggesting weights of approximately 125 g at breeding grounds in Churchill could sustain flight to the Mid-Atlantic without refuelling (personal comment in Jehl et al. 2020), their ability to do so had not been confirmed. Non-stop initial flight distances of up to 3100 km exceed estimates from energetics and fat content from previous studies in New Jersey, U.S., of 1900-2000 km of individuals expected to complete a non-stop flight originating from Labrador, Canada (Jehl 1963) and are consistent with estimates of 2700-3500 km from individuals migrating through Saskatchewan (Alexander and Gratto-Trevor 1997). Just seven individuals that were detected in the Northern and Southern Arrays may have stopped during their initial flight from Churchill, and many other individuals lacked detections to confirm whether their flights were non-stop. Tracks from just one Stilt Sandpiper confirm that they are capable of non-stop flight from the breeding grounds to at least North Dakota (>1200 km).

Stopovers

Short-billed Dowitchers breeding in Churchill typically had stopovers of up to 24 days on the southeastern Atlantic coast which is dominated by barrier islands, inlets, and saltmarshes. Despite their many different stopover sites, stopovers of four individuals occurred within range of the Georgia DNR Dock tower in Brunswick, Georgia, U.S., two of which overlapped. An additional two stopovers are suspected in this area where they were undetected between nearby towers for several days. Therefore, this represents at least 19% of tagged individuals detected in the southern array and is the location of 29% of all confirmed stopovers, indicating that this site is important to the Churchill breeding Short-billed Dowitchers. Approximately 20 km north of the tower site is the Altamaha River Delta, a Site of Regional Importance recognized by the Western Hemisphere Shorebird Reserve Network (WHSRN) as important to several shorebird species (designated 1999, (Western Hemisphere Shorebird Reserve Network 2019a). Much of this area is protected and closed to public access (Western Hemisphere Shorebird Reserve Network 2019a). This suggests high connectivity between at least breeding and stopover areas.

Four other stopovers occurred along a ~175 km stretch of the coast of South Carolina, U.S. In the north, the Santee Delta-Cape Romain region has been recognized as a Site of International Importance by WHSRN (designated 1995, (Western Hemisphere Shorebird Reserve Network 2019b)), and as an Important Bird Area by the National Audubon Society (National Audubon Society 2007), with important habitat for breeding, migrating, and wintering shorebirds. As of 2018, this region covers 484 km^2 of mixed forest, beaches, mudflats, salt marshes, and wetlands that support over 100,000 migratory shorebirds annually, including 11% of all Short-billed Dowitchers (Western Hemisphere Shorebird Reserve Network 2019b). A study in the Cape Romain National Wildlife Refuge in 2016 found that Short-billed Dowitcher densities were positively correlated with horseshoe crab (*Limulus polyphemus)* egg abundance (Takahashi et al. 2021). In a 2007-2010 shorebird survey in the Cape Romain National Wildlife Refuge area, Short-billed Dowitchers were the second most abundant species (9% of total shorebird abundance) and were most abundant in the winter but are present in the area in all seasons (Wallover et al. 2015). Due to a sudden drop in detections, typically during the first couple weeks of August, it is unclear whether these sites are all stopovers or whether they may also be wintering sites for Short-billed Dowitchers breeding in Churchill.

Just south of the Santee Delta-Cape Romain, the "Timbers" tower on Kiawah Island, South Carolina detected a Short-billed Dowitcher's 13-day stopover from 4-17 August 2021. Tag54776 was detected arriving at Kiawah Island at the "Little Bear" tower before being detected at the "Timbers" tower for most of the 13 days during a stopover on or around Kiawah Island in South Carolina. Signal plots from approximately 600 and 2130 h (± 30 min) on several days suggest that these detections occurred when the dowitcher was flying back and forth from roost sites at approximately civil twilight, as large numbers of Whimbrel have been recorded to do at the same location (Sanders et al. 2021). All detections were from the antenna pointed 245° (southwest) with an estimated range that covers the southwest area of Seabrook Island, the southeast corner of Edisto Island, and Deveaux Bank, a small ephemeral sandbar long known as important for migrating and nesting waterbirds (Jodice et al. 2007). Recently, Deveaux Bank was identified as a nocturnal roosting site for nearly 20,000 Whimbrel (*Numenius phaeopus*) each spring migration, representing ~50% of the eastern population (Sanders et al. 2021). These detections highlight that some Short-billed Dowitchers from the Churchill area are also likely using this site as a nocturnal roost.

Stopovers to refuel after and before continuing long flights are critical to successful migration (Duijns et al. 2017). Because the Short-billed Dowitchers tagged in this study rely on coastal stopover sites on barrier islands and saltmarshes, threats to their migration and stopover sites may include sea-level rise and disturbance by humans. Short-billed Dowitchers may be especially sensitive to sites with human disturbance (Drever et al. 2016), as they flush in response to personal watercraft (Rodgers Jr. and Schwikert 2002) and are relatively sensitive to disturbance by vehicles (Pfister et al. 1992). Sea-level rise is expected to reduce habitat availability for shorebirds by 20-70% in some areas of the Atlantic coast (Galbraith et al. 2002). Observations of dowitchers migrating through Saskatchewan (likely *L. g. hendersoni*) suggest they could migrate inland, but their ability to change their migration routes in response to habitat change is unknown and probably unlikely based on their almost strictly coastal winter range (Alexander and Gratto-Trevor 1997, Jehl et al. 2020)

Fewer stopover events for Stilt Sandpipers were detectable through the Motus network, but they suggest a somewhat unexpected hazard to the migration of this Stilt Sandpiper subpopulation may be bird-aircraft strikes. Nearby an airport and military airfield, two constructed lagoons west of Grand Forks, North Dakota host Motus receiving stations to examine movements of birds around airfields (U.S. Fish & Wildlife Service n.d.). This area attracts migrating waterbirds (Maxson 1981) and bird deterrence strategies occur to reduce bird-aircraft collisions (Allen 2018). These towers provided the only confirmed stopover location for a Stilt Sandpiper and an area in which an additional individual was detected. Many Stilt Sandpiper detections occurred at towers along the Mississippi River, where shorebirds use aquaculture ponds and agricultural areas, in addition to natural habitat (Twedt et al. 1998, Lehnen and Krementz 2013). Though constructed wetlands such as these may provide habitat for migratory birds, including Calidrine sandpipers, they may also create ecological traps for migrating birds (Zhang et al. 2020) through hazards such as pollutants (Zala and Penn 2004). These shallow, sometimes nutrient-dense wetlands are likely attractive to wading shorebirds who need to feed on invertebrates during migration (Spieles and Mitsch 2000), so they may pose a risk to migrating species such as the Stilt Sandpiper if they are ecological traps.

Limitations

Some deployed tags on both Short-billed Dowitchers and Stilt Sandpipers were not detected. I am cautious to attribute a lack of detection by the Motus network to mortality. A Stilt Sandpiper tagged in 2021 was never detected in the Northern or Southern Arrays but was later resighted guarding chicks in 2023 (Supplementary Table S1). Six dowitchers tagged in 2021 were never detected by the Motus network, 2/6 were resighted without Motus tags 3 and 6 days later, and 3/6 of these dowitchers were resighted in 2022-2023 (Supplementary Table S1). In 2022, 16/16 dowitchers tagged were detected, and in 2023, 13/14 dowitchers tagged were detected. Because we observed premature tag loss at the deployment site in the first year of the study, we may not have affixed tags well enough to remain on until migration was initiated.

For most stopovers, the end date is unclear, therefore they are low estimates in some cases. Also, it is unlikely that Short-billed Dowitchers and Stilt Sandpipers remain at their initial stopover sites as we might expect detections to continue longer until their transmitter's battery dies. After migration was initiated, I suggest two possible explanations of why detections stopped occurring after initial stopovers despite their sufficient battery life. First, Short-billed Dowitchers begin head moult in the breeding grounds and are often in heavy body moult during migration in Quebec, Canada (McNeil and Cadieux 1972) and on the Mid-Atlantic coast (Jehl 1963). Because the Short-billed Dowitchers in this study spent up to 24 days at stopover sites, they are likely moulting transmitters off. The temporary method of affixing transmitters with cyanoacrylate glue can lead to transmitter loss long before the battery is dead and this is a significant limitation of this attachment method (Loring et al. 2021). Another possibility, especially for those that were detected at other towers further south after leaving a stopover site, is that both Short-billed Dowitchers and Stilt Sandpipers are departing the Mid-Atlantic, Southeast Atlantic and Gulf Coast to arrive at wintering grounds in areas with no Motus Network coverage. For example, limited band-recovery data suggest that Stilt Sandpipers banded during fall migration in Saskatchewan arrive in Venezuela (Alexander and Gratto-Trevor 1997), but no Motus coverage existed in Venezuela until one receiving station was deployed in 2022 and another in 2023 (Matta 2024). Similarly, the lack of network coverage between the Churchill region and the Great Lakes, and the imperfect nature of tag detection, prevent the identification of stopover sites before arrival to the Southern Array.

Although gluing tags is a relatively non-invasive and quick method of applying small transmitters to shorebirds, their application to Short-billed Dowitchers and Stilt Sandpipers may result in tag loss. Like other shorebirds, this tag loss can occur before migration is initiated or soon afterwards (Smith et al. 2023b), and therefore should be avoided for studies aiming to identify wintering locations. Alternatively, the lack of detections could be attributed to migration through areas with low Motus network coverage, in which case, this also highlights the need for more receiving stations in Central and South America. Tracking studies with alternative attachment methods and the ability to obtain locations through satellite or GPS could determine whether the lack of detections after stopover events is attributable to tag loss or migration through areas with low network coverage.

Conclusion

This is the first study to characterize the post-breeding migration routes, timing, and stopovers of central Short-billed Dowitchers (*L. g. hendersoni*) and Stilt Sandpipers breeding in Churchill, Manitoba, Canada. Both species were capable of long non-stop flights from the breeding grounds of >1000 km for Stilt Sandpipers and >3000 km for Short-billed Dowitchers.

The Southeast Atlantic coast provided most stopover sites for Short-billed Dowitchers migrating from Churchill Manitoba, with key sites in Georgia and South Carolina, with one near Brunswick, Georgia hosting 29% of all stopovers. This highlights the importance of this region for Short-billed Dowitchers migrating from Churchill, as many of these sites have already been identified as important for other declining migratory shorebirds (Sanders et al. 2021, Pelton et al. 2022). A supplementary band resight in Campeche, Mexico of a Short-billed Dowitcher in November suggests that some either stopover or may winter in this area, though this individual's track was an outlier compared to others migrating further east. The threats Short-billed Dowitchers encounter during migration are likely related to stopping over in coastal systems on barrier islands and salt marshes, which are susceptible to anthropogenic disturbance (Feagin et al. 2010) and climate change (Zinnert et al. 2017). Stopover sites for Stilt Sandpipers were harder to identify but occurred between southern Manitoba, Canada and Missouri, U.S. and are consistent with previous studies identifying the area between Saskatchewan and Kansas as a major stopover area (Klima and Jehl 2020).

This study confirmed some existing hypotheses about migratory connectivity, at least during migration, but led to new questions. One site hosted 29% of all stopovers for Short-billed Dowitchers, suggesting relatively high connectivity, but it is unclear if and where these individuals moved after stopping at this location. Regardless, high connectivity at stopover sites could pose a threat to Short-billed Dowitchers with increasingly frequent and severe storms that may impact barrier island habitat. Individual Short-billed Dowitchers bearing relatively far east and west compared to the majority of tagged individuals may raise questions about their subspecies and whether Churchill is an area of intergradation for *L. griseus hendersoni* (Central) and *L. griseus griseus* (Atlantic), and further complicate our understanding of their migratory connectivity. Based on our limited tracking data for Stilt Sandpipers, migratory connectivity appeared low with some individuals fanning out after initial flights, possibly confirming the existing hypothesis that low migratory connectivity is more common among long-distance migrants (Finch et al. 2017), however, tag loss prevented investigating this further. To overcome limitations due to tag loss, future studies could use alternative attachment methods or satellite tags.

CHAPTER 4 – CONCLUSION

In Chapter 1, I provided a general introduction to my research questions and the study species, the Short-billed Dowitcher and Stilt Sandpiper. In this thesis, I examined events during two stages of the annual cycle, the breeding season (Chapter 2) and post-breeding migration (Chapter 3) for birds breeding in Churchill, Manitoba, Canada.

In Chapter 2, I compared the nest habitat characteristics, nest concealment, and antipredator defense strategies between Short-billed Dowitchers and Stilt Sandpipers. I made behavioural observations of 35 Short-billed Dowitcher and 9 Stilt Sandpiper nests during incubation and collected habitat data after hatch. Short-billed Dowitcher nests had taller vegetation at the nest cup, higher concealment from the sides and above, and therefore seemed to rely on camouflage, short flush distances, and aggressive displays to deter human intruders. Stilt Sandpipers had low nest concealment from the sides and above and therefore relied on detecting human intruders and some employed a "leave-early" behaviour to remain undetected. Despite differences between species, individual personality was also important to the boldness of some Stilt Sandpipers during interactions with humans. The effects of changing habitat and predator communities may vary between species with different concealment and antipredator defense strategies.

These differences in flush distance should be interpreted with caution due to the small sample size available for Stilt Sandpipers: 24 observations, for which incubator ID was only known for 2/3 of observations, as identification was sometimes impossible when trying to minimize disturbance at the nest site. At peak hatch during each breeding season, I observed many unbanded parents with chicks in our study plots. The resighting of eight Short-billed

Dowitchers in 2023 banded in previous years (2021-2022), half of them guarding chicks, suggests that I did not locate many of the nests that occurred in our study plots (Supplementary Table S1). Possible explanations could be that we only searched habitats that we deemed suitable and missed key nesting areas, or birds may have sat so tightly on nests that they didn't flush at all as we passed by.

Within our Churchill area study sites, the broader habitat preferences of Short-billed Dowitchers and Stilt Sandpipers are similar, and both species show some diversity in nest sites. I searched for nests in wet sedge meadow habitat, but Jehl (1973) also describes some Stilt Sandpiper nest locations as open, dry tundra, or on low, well-drained gravel ridges that cross the sedge meadows. At a site ~36 km east of Churchill, near the Nester 1 Research Station in Wapusk National Park, we found three Stilt Sandpiper nests on completely exposed, dry, *Dryas integrifolia*-dominated slopes. Additionally, two Short-billed Dowitcher nests in this study were found by other research teams at small ponds and meadows in openings within dense coniferous forests. Detecting true differences in habitat characteristics between species may require a larger sample of Stilt Sandpiper nests, which is not likely forthcoming at the Churchill study site. However, Holmes et al. (2020) only detected minor habitat cover differences between nests and random sites for Dunlin at The Fen, so these species may select nest sites using factors other than vegetation types.

Several species that once nested in the Churchill region have been extirpated. The Semipalmated Sandpiper (*Calidris pusilla*), which according to personal notes in Jehl (2007) was the most common breeding shorebird in the area prior to the 1960s, was last documented nesting at a single site in 2001. Population declines during migration and non-breeding counts have not been supported by studies in the breeding season for the western and central subspecies (Smith et al. 2012a). However, further east at Cape Churchill along the coast of Hudson Bay, Semipalmated Sandpipers appear to have increased between surveys in 1984 and 2000 (Sammler et al. 2008). Because Stilt Sandpipers have declined significantly in the Churchill region but are still relatively common in that colder, more upland tundra area, their distribution may be changing similarly to Semipalmated Sandpipers.

In Chapter 3, I characterized the post-breeding migration pathways, departure dates, speed, and stopovers using radio-transmitters and received data from 35 tagged Short-billed Dowitchers and 10 tagged Stilt Sandpipers through the Motus Wildlife Tracking Network. Short-billed Dowitchers generally migrated through the Great Lakes before arriving in the Mid-Atlantic, the Gulf Coast, and most commonly, the Southeast Atlantic Coast. Stilt Sandpipers migrated through the Prairie Potholes Region and along the Mississippi River and were then detected on coasts in Georgia, U.S. and northwestern Costa Rica. An additional Stilt Sandpiper tagged in Wapusk National Park, east of Churchill, migrated first through North Dakota, U.S. before flying across the Midwest with final detections in coastal Virginia U.S. Non-stop flights from the breeding grounds were recorded for both species. I summarized their stopover events and highlighted potential threats to both species during their post-breeding migration. Wintering sites were not obtainable either due to tag loss or movement into areas with no Motus coverage, so stopover and wintering sites for these species could be identified using alternative attachment methods.

Based on the timing of migration in this study, current survey techniques for shorebirds in the Northern U.S. and Canada may not be effective for Short-billed Dowitchers. Many Short-billed Dowitchers departed the Churchill, Manitoba region and arrived at their first stopover sites before the International Shorebird Survey for fall migration begins (Northern U.S. and Canada:

11 July, Southern U.S., Mexico, and Caribbean: 15 July (Program for Regional and International Shorebird Monitoring (PRISM) 2018, Manomet 2019)). Almost all Short-billed Dowitchers in this study migrated through the Great Lakes, and some moved through as early as 9 July (median date = 20 July). Nearly half (14/29) of these Short-billed Dowitchers moved through Ontario, Canada before the Ontario Shorebird Survey begins on 20 July (Program for Regional and International Shorebird Monitoring (PRISM) 2018). The Ontario Shorebird Survey detected declines of dowitchers (mostly Short-billed) of 31.3% between 1974-1989 and 27% between 1989-2009 (Ross et al. 2012). As *L. g. hendersoni* is the most common subspecies in southern Ontario (Jaramillo et al. 1991), these surveys could potentially miss the migration of Short-billed Dowitchers of this subspecies. The results from these surveys may also be misleading because they start in mid-late July, when they may mostly record numbers of juveniles of unknown subspecies and successful breeding males.

Most Short-billed Dowitchers migrating through Ontario did not stop, which could contribute to their population decline in Ontario Shorebird Surveys. Populations that may have previously stopped in the Great Lakes region may no longer find it desirable. This could be due to increased human disturbance, as Short-billed Dowitchers may be especially sensitive to people, dogs (Drever et al. 2012), vehicles (Pfister et al. 1992), and watercraft (Rodgers Jr and Schwikert 2002). Feeding conditions may also influence whether shorebirds return to previous stopover sites (Minias et al. 2010). In addition, Short-billed Dowitchers are generally associated with water levels of <5 cm at stopover sites (Potter et al. 2007). Water levels fluctuate in cycles on the shorelines of the Great Lakes Lake Huron and Lake Michigan, but Lake Erie water levels have consistently been above long-term averages since approximately 2015 (Great Lakes Environmental Research Laboratory 2024), which could limit available shoreline habitat for migrating shorebirds and force them to stopover further inland. Future studies investigating stopover decisions in Short-billed Dowitchers may help to determine if declines in surveys should be attributed to shifting stopover sites or true population declines.

Both Stilt Sandpipers and Short-billed Dowitchers have declined significantly across many surveyed migration sites since the 1980s (Smith et al. 2023a). Due to the difficult terrain, the cryptic nature of their nests and likely an increasingly small population of Stilt Sandpipers, the number of nests I located and monitored, and tags I deployed were lower than desired, especially for Stilt Sandpipers. Despite these issues, I documented differences between their nest site concealment, compared their antipredator defense strategies, and characterized their post-breeding migration. Future studies investigating Short-billed Dowitchers and Stilt Sandpipers should focus on identifying wintering sites and characterizing their propensity to threats such as hunting during migration and non-breeding seasons. Various types of hunting occur in different locations, such as commercial hunting, subsistence hunting, or sport hunting, and each may impact shorebird populations differently. Understanding the migratory connectivity of these species is important to knowing which specific breeding populations could be affected by different levels and types of hunting to appropriately target management actions. The consequences of events during the breeding season to migration (Clements et al. 2022) and estimating adult survival could be important to these species, however more information from their subarctic and arctic breeding grounds is difficult and costly to obtain and would necessitate long-term studies.

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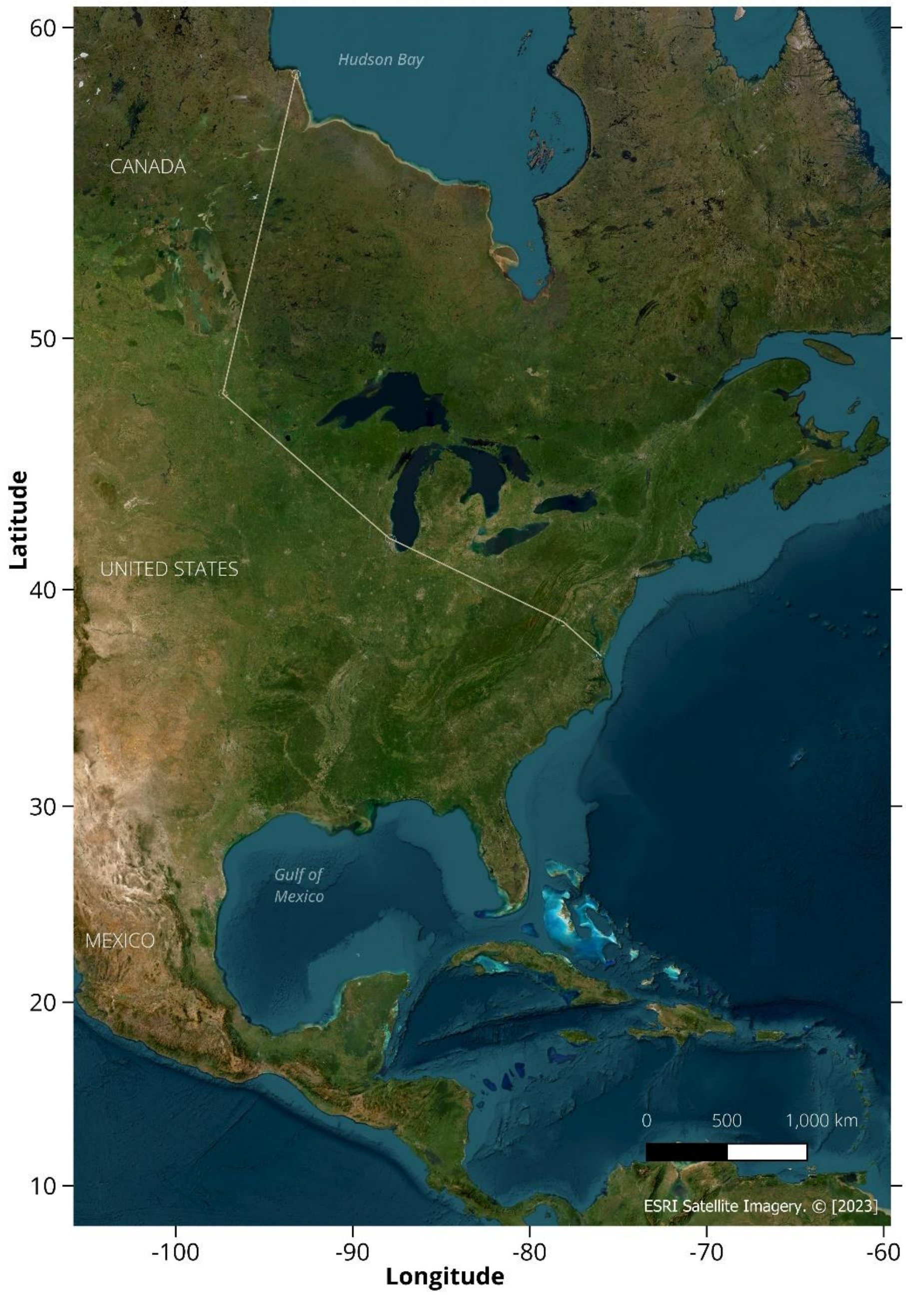
SUPPLEMENTARY MATERIAL

Figures

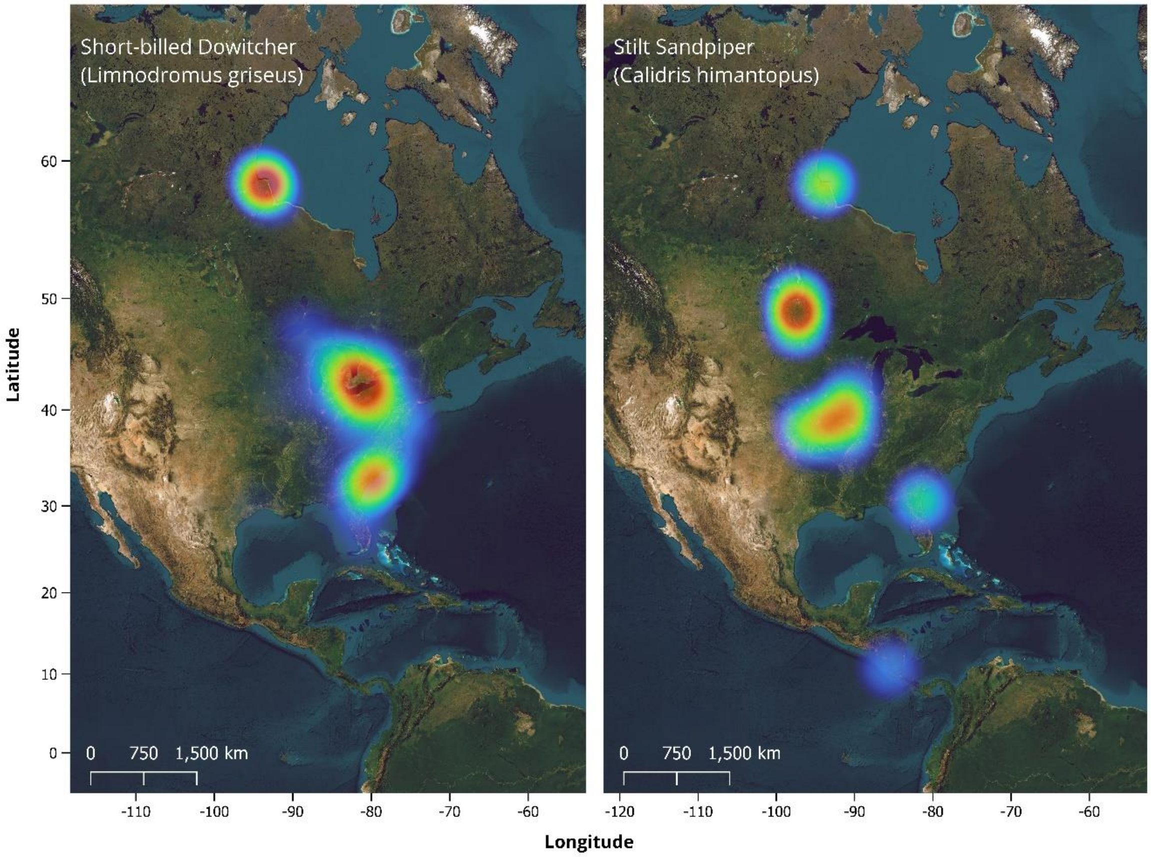
Supplementary Figure S1. Typical Short-billed Dowitcher (*Limnodromus griseus hendersoni*) nest with eggs. The nest cup is lined with dry grass.

Supplementary Figure S2. Typical Stilt Sandpiper (*Calidris himantopus*) nest with eggs. The nest cup is lined with dry grass and *Betula* sp. leaves.

Supplementary Figure S3. Stilt Sandpiper (*Calidris himantopus*) crouching in nest cup during hatch at nest 22STSA02. This nest had 93.9% vertical concealment due to a small dwarf birch (*Betula nana*) growing directly above the cup. Photo by Andrew Brown.



Supplementary Figure S4. Approximate pathway of post-breeding migration of a single Stilt Sandpiper (*Calidris himantopus*) tagged in Wapusk National Park, Manitoba and detected by the Motus Wildlife Tracking System. Basemap by ESRI (ESRI 2023) and map generated in QGIS (QGIS Development Team 2023).



Supplementary Figure S5. Heatmap displaying the frequency of individual tags affixed to Short-billed Dowitchers (*Limnodromus griseus*) and Stilt Sandpipers (*Calidris himantopus*) detected at each Motus receiving station.

Tables

Supplementary Table S1. Resights in 2022-23 of Short-billed Dowitchers (*Limnodromus griseus hendersoni*, SBDO) and Stilt Sandpipers (*Calidris himantopus*, STSA) banded in 2021-22.

Species	Individual ID	Plot	Resight year	Original banding year	Distance (m)	Notes
Nesting						
STSA	BuOr	Fen	2022	2021	315	With BuGr in 2021
STSA	YJEBa	Fen	2022	2021	456	Never saw partner in 2022
SBDO	E03Ye	Airport	2023	2021	21	Never saw partner in 2023
STSA	YJEBa	Fen	2023	2021	0	Same nest cup as 2022
STSA	YJHGr	Fen	2023	2022	0	Same nest cup as 2023
SBDO	GrPi	Fen	2023	2022	157	True divorce from WhBa, nesting with E06Ba
Seen with chicks						
SBDO	PuPi	Fen	2023	2021	353	With unbanded dowitchers
SBDO	BuBu	Fen	2023	2022	187	Associating with YeYe
SBDO	YeYe	Fen	2023	2022	173	Associating with BuBu
SBDO	WhBa	Fen	2023	2022	424	Associating with E08Ba
STSA	BaGr	Fen	2023	2021	456	Associating with YJEBa
SBDO	PiPi	Fen	2023	2022	648	With unbanded dowitchers
Seen foraging						
SBDO	BaPi	Fen	2022	2021	1485	Never found nest
SBDO	WhPi	Airport	2023	2021	95	Never found nest
SBDO	OrBu	Fen	2023	2022	40	Never found nest

Supplementary Table S2. Summary of nest initiation (mean ± SD (range)) and nest hatch (mean ± SD (range)) of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) and Stilt Sandpipers (*Calidris himantopus*) breeding in the Churchill, MB region from 2021-2023. Estimated initiation and hatch dates were calculated using the Arctic Shorebird Float Tool (Manomet 2021) and include nests that did not hatch but for which a hatch estimate was generated. For Short-billed Dowitchers, estimates were calculated using the Long-billed Dowitcher (*Limnodromus scolopaceus*) parameters.

	Short-billed Dowitcher	Stilt Sandpiper
Estimated initiation date based on floating	4 June ± 7.4 (24 May – 22 June) *n* = 27	8 June ± 10.6 (27 May – 22 June) *n* = 5
Estimated hatch date based on floating	28 June ± 7.4 (17 June – 16 July) *n* = 27	1 July ± 10.6 (19 June – 15 July) *n* = 5
Actual hatch date based on chicks or eggshell evidence	30 June ± 7.3 (20 June – 16 July) *n* = 18	30 June ± 7.6 (26 June – 11 July) *n* = 3

Supplementary Table S3. Sexing measurements of Stilt Sandpipers (*Calidris himantopus*) during incubation in Churchill, Manitoba in 2021-2023.

NestID	Sex (by partner or cloacal protuberance)	Sex (by DNA)	Presumptive sex
21STSA02	M	M	M
21STSA03[1]	-	M	M
21STSA03	-	F	F
21STSA04	-	F	F
21STSA04[2]	-	M	M
22STSA01[3]	F	-	F
22STSA01[2]	M	M	M
22STSA02	M	-	M
22STSA02	F	-	F
22STSA03[1]	M	M	M
23STSA02[3]	F	-	F
23STSA01[1]	M	M	M

[1,2,3] indicate same individuals across years.

Supplementary Table S4. Sexing measurements of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) during incubation in Churchill, Manitoba in 2021-2023, based on ranges for males and females published in Pyle (2008).

NestID	Culmen (mm)	Sex (by culmen)	Partner's presumptive sex	Presumptive Sex
21SBDO01	59.7	U	M	F
21SBDO01	53.9	M	U	M
21SBDO02	57.3	M	F	M
21SBDO02	60.6	U	M	F
21SBDO03[1]	52.5	M	U	M
21SBDO04	59.1	U	F	M
21SBDO04	62.5	F	F	F
21SBDO05	59.4	U	U	U
21SBDO05	58.2	U	U	U
21SBDO06	62.5	F	M	F
21SBDO06	55.9	M	F	M
21SBDO07	59.1	U	U	U
21SBDO08	61.8	F	U	F
22SBDO02	51.5	M	U	M
22SBDO11	60.6	U	M	F
22SBDO03	59.5	U	M	F
22SBDO03	54.6	M	U	M
22SBDO04	55.2	M	F	M
22SBDO04	61.8	F	M	F
22SBDO05	54.0	M	U	M
22SBDO05	60.5	U	M	F
22SBDO06	53.8	M	F	M
22SBDO06	64.6	F	M	F

22SBDO07	51.3	M	U	M
22SBDO08	62.1	F	U	F
22SBDO08	59.8	U	F	M
22SBDO09	61.2	U	M	F
22SBDO09	53.0	M	U	M
23SBDO01[1]	57.3	M	U	M
23SBDO02	56.1	M	U	M
23SBDO04	51.5	M	U	M
23SBDO05	56.0	M	U	M
23SBDO05	59.9	U	M	F
23SBDO06	61.2	U	U	U
23SBDO07	55.6	M	U	M
23SBDO08	54.5	M	U	M
23SBDO08	60.2	U	M	F
23SBDO09	54.2	M	U	M
23SBDO10	60.7	U	M	F
23SBDO11	64.2	F	U	F
23SBDO11	58.4	U	F	M
23SBDO12	52.8	M	U	M

[1] indicates same individual across years.

Supplementary Table S5. Summary of minimum length of passage (median +/- SE, n, max) in days for Short-billed Dowitcher (*Limnodromus griseus hendersoni*) and Stilt Sandpiper (*Calidris himantopus*).

	Short-billed Dowitcher			Stilt Sandpiper		
	median +/- SE (days)	*n*	max (days)	median +/- SE (days)	*n*	max (days)
Prairies	-	0	-	0.01 ± 0.01	3	0.03
Northern Ontario	0.01	1	0.01	-	0	-
Great Lakes	0.31 ± 0.14	29	3.75	-	0	-
Midwest	0.01 ± 0.8	8	6.45	0.03 ± 1.02	8	6.72
NE Interior	0.02 ± 0.02	17	0.24	-	0	-
Midatlantic	0.3 ± 1.27	5	6.59	-	0	-
SE Interior	0.01 ± 0.04	4	0.15	-	0	-
SE Atlantic	9.6 ± 1.66	20	27.19	0.08	1	0.08
Gulf Coast	0.01 ± 0.48	7	3.44	-	0	-
Central America	-	0	-	0.00	1	0.00

Supplementary Table S6. Summary of potential stopovers of Short-billed Dowitchers (*Limnodromus griseus hendersoni*) where birds went undetected for >12 hours between stations in the southern array. Those >24 hours are indicated in bold. GL = Great Lakes, MW = Midwest U.S., NEI = Northeast Interior U.S., MA = Mid-Atlantic U.S., SEI = Southeast Interior U.S., SEA = Southeast Atlantic U.S., GC = Gulf Coast.

TagID	Time undetected (days)	Distance (km)	Region	
			Start	End
54774	**8.81**	1957	GL	GC
54788	**7.08**	48	SEA	SEA
63517	**1.84**	50	GL	GL
63517	**6.89**	178	GL	MW
63530	**1.56**	14	SEA	SEA
63543	**1.22**	767	NEI	SEA
63543	**7.26**	34	SEA	SEA
63547	**6.44**	256	MW	MW
63550	**10.67**	328	SEA	SEA
63555	**1.02**	62	MA	MA
65688	**7.32**	213	GL	MW
65690	**7.30**	809	NEI	SEA
65690	**2.94**	162	SEA	SEA
65691	**14.00**	602	SEA	GC
65694	0.58	213	SEA	SEA
65695	**6.57**	193	NEI	MA
65696	**11.05**	116	SEA	SEA
65697	0.51	213	SEA	SEA
65698	**11.39**	796	MA	SEA
65699	**2.77**	172	SEA	SEA

65700	**2.89**	35	SEA	SEA
65701	0.94	621	GL	GL
65701	**1.22**	180	NEI	MA
65704	0.98	458	SEI	SEA
65704	**1.53**	23	SEA	SEA

Supplementary Table S7. Summary of confirmed and potential stopovers of Stilt Sandpipers (*Calidris himantopus*) where birds went undetected for >24 hours between stations. Those in bold are confirmed stopovers (at one station or between two nearby). PR = Prairies Canada, MW = Midwest U.S.

TagID	Time undetected (days)	Distance (km)	Region	
			Start	End
54775	11.87	1220	PR	MW
65687	5.73	5	MW	MW
65693	12.68	1166	PR	MW
65702	6.53	948	MW	MW