Exploring the strategies of first migration in the subarctic-nesting shorebird, *Calidris alpina hudsonia*

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Abstract

Compared with adult conspecifics, juvenile Dunlin undertaking their first migrations experience higher rates of mortality. Despite the significant impact of juvenile shorebirds on population dynamics, little is known about young birds' maiden migrations. For the first time, we present the migratory strategies of juvenile Dunlin (*Calidris alpina hudsonia*) during their inaugural journeys to non-breeding grounds using the Motus radio telemetry network. We analyze the migrations of adult Dunlin tracked via the Motus system, and compare strategies between age groups. Juveniles preferentially over-wintered in discrete sections of the Eastern Seaboard – sites exclusive to this age demographic. We also elucidate vital juvenile staging sites in Southeastern Ontario, and potential mortality hotspots within Ontario and Nova Scotia. We postulate genetic influences on the migrations of juveniles. Three novel non-breeding sites of adults were documented, in Colombia, Alaska, and Indiana. We also emphasize the ecological importance of select stopover sites along the Atlantic USA.

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Introduction

Evolutionary Incentives of Migration

Long distance migrations are coordinated and patterned seasonal mass movements of animals that span great distances and have evolved in a multitude of taxa. The driving forces behind migratory movements are complex and vary among taxonomic groups (Dingle 1991), however, be it via land, water, or air, the primary advantage of migrations is simple: organisms change locations in response to fluctuating seasonal resource availability (Fryxell and Sinclair 1988). North Pacific populations of Blue whales (*Balaenoptera musculus*), for instance, have been recorded to follow seasonal blooms of phytoplankton, which occur progressively later at higher latitudes, from the Gulf of California to the Gulf of Alaska - journeys totaling more than 6000 km per year (Abrahms, et al. 2019). Many terrestrial animals, such as the Barren-ground caribou (*Rangifer tarandus granti)*, likewise traverse vast distances in pursuit of optimal resource availability. The annual migrations of herds in continental North America, which are driven primarily by forage quality, span from non-breeding grounds south of the North American tree line up to Arctic calving grounds and measure, at minimum, 5000 km (Fancy et al. 1989).

By moving to regions with increased food availability, and more favorable environmental conditions, organisms may significantly increase their reproductive output (Alerstam et al. 2003). The seasonally-driven migrations of the Atlantic salmon (*Salmo salar*), during which individuals cover distances exceeding 2000 km while travelling between marine habitats and upstream freshwater spawning grounds, may be best interpreted as an adaptation to improve foraging profitability and thus lifetime reproductive success (Quinn and Dittman

1990). At higher latitudes, marine productivity generally exceeds that of freshwater systems, therefore male Atlantic salmon may take advantage of this productivity and return to spawn again at a much larger body mass (Quinn and Dittman 1990). The White-crossed seed bug (*Neacoryphus bicrucis*), is another long-range migrant whose reproductive success has been strongly linked to resource abundance (Solbreck and Pehrson 1979). Egg production in this species is a direct function of food availability (i.e., number of dandelion seeds per adult female; Solbreck and Pehrson 1979).

Yet another evolutionary driver of migration is predation risk (McKinnon et al. 2010). The hypothesis of predation as a driving factor for migratory movements in prey species implies that despite the large energetic expenses associated with migration, individuals who travel to areas with lower predation rates experience improved survival (White et al. 2014). This may be especially true for vulnerable neonates. Certain subpopulations of moose (*Alces alces*) inhabiting the Gustavus forelands along the Southern coast of Alaska have been known to undergo seasonal migrations to island archipelagos or subalpine ridge systems, while other sympatric subpopulations remain in coastal regions year-round (White et al. 2014). Mountainous terrain and isolated archipelagic geography are thought to reduce predation risk when compared to the coastal systems of Alaska, throughout which there are greater densities of large carnivores (Bergerud et al.1984). Accumulated fat reserves of adult females, which are an indicator of the bioenergetics of the environment experienced by an individual, do not differ between migratory and resident subpopulations during the post-migratory summer growing season, yet calf survival may be as much as 2.9 times higher in migrants than in residents (White et al. 2014). Migration in this subpopulation therefore likely confers fitness benefits in the form of predator avoidance rather than improved access to nutrients (White et al. 2014).

Risk of parasitic infection has also been theorized to spur long-distance migratory movements in numerous taxa (Altizer et al. 2011; Kelly et al. 2016). Parasitic loads often accumulate in individuals over time in habitats where parasites are transmitted via environmental modes (parasitic life stages that exist outside of hosts; fecal-oral transmission; (Altizer et al. 2011). Migration, in this context, may allow species to temporarily leave heavily contaminated environments, reducing accumulation of parasites, only to return after harsh conditions (i.e., low temperatures, fewer available hosts) have reduced parasite abundance (Altizer et al. 2011). Monarch butterflies (*Danaus plexippus*), one of the longest migrating insect species in the world, have been known to fly up to 5000 km annually from regions as far north as Canada to Central Mexico (Altizer et al. 2011). Comparisons between subpopulations which winter along the coast of California and those which remain year-round residents have shown that non-migratory individuals are as much as nine times more likely to be infected by *Ophryocystis elektroscirrha,* a specialist protozoan parasite that has been found in monarch populations in North America, Hawaii, Australia, Cuba, Central and South America and often causes wing deformities (Satterfield et al. 2016). Large ungulate herbivores such as Red deer (*Cervus elaphus*) likely migrate to escape high parasitic infection rates as well (Mysterud et al. 2015). On the South coast of Norway, subpopulations that migrate farther distances between breeding and non-breeding grounds to higher elevations exhibit lower average tick (*Ixodes ricinus*) loads than those that remain stationary at lower elevations, where environmental conditions are more favorable to ticks (Mysterud et al. 2015).

Drivers of Avian Migration

Birds exhibit some of the longest migrations in the Animal Kingdom. Arctic terns (*Sterna paradisaea*), the furthest recorded migrating species on the planet, may travel an annual distance of over 80,000 km to and from their Arctic breeding grounds at an average rate of 520 km per day (Egevang et al. 2010). Some species, like the White stork (*Ciconia ciconia*), migrate for up to 270 days between Europe and Africa each year, and total upwards of 24,000 km (Berthold et al. 2004). One of the largest groups of migratory birds, comprised of up to 361 species, are the Neotropical migrants, which spend non-breeding periods in South and Central America and migrate North to temperate zones, where they produce and raise offspring (DeGraaf and Rappole 1995). The biological impetus primarily responsible for driving such extensive, perilous, and metabolically expensive migrations in birds is similar to that which shapes migrations of non-avian taxa: fluctuations in resource availability, predation rates, and parasitism.

A multitude of herbivorous, insectivorous, and carnivorous bird species alike have adapted to take advantages of brief windows of peak food abundance that occur in select geographical regions each year. Wood warblers (*Phylloscopus sibilatrix*) time their northward migrations to coincide with peak spring fluctuations of caterpillar biomass (Graber and Graber 1983), while the phenologies of their southward migrations are strongly correlated with fruiting phenology (Thompson and Wilson 1979). Brent geese (*Branta bernicla*) fly thousands of kilometers to the High Arctic every year to match breeding phases with peak abundances of high-quality mosses and grasses, and Honey buzzards (*Pernis apivorus*) travel from Southeast Asia to Japan where they produce and raise offspring in mid-summer, when bee nests reach their annual maximum sizes (Both 2010). Carnivorous species like Eleonora's falcons (*Falco eleonorae*) migrate to the Mediterranean Islands in the fall in order to synchronize nesting with mass influxes of migratory songbirds (Passeriformes; Both 2010).

In birds, predation risk is also an important factor in shaping the evolution of migratory behavior. Nest predation rates of Arctic ground-nesting shorebirds (Charadriiformes) may decrease as much as 3.6% for every 1° increase in latitude (McKinnon et al. 2010), and likewise, clutches of tropical forest-nesting species may be twice as likely to be depredated if individuals migrate to and breed at lower altitudes than higher ones (Boyle 2008). Clutches of migratory passerines may be 1.78 times larger in northern (34° N) versus southern (26° N) breeding sites due to the fact that predation risk constrains parental food provisioning to offspring, and is thus inversely correlated with clutch size (Martin et al. 2000).

Migration is theorized to decrease parasitic loads in at least two ways: migratory culling and/or escape from habitats with elevated rates of parasitism (Bush and Clayton 2018). Individuals with heavy parasitic loads may be less likely to survive migratory journeys due to compromised immune function and reduced flight capacity, thus decreasing prevalence of parasites in sampled populations (Bush and Clayton 2018). Seasonal movements to breeding grounds may also grant individuals spatial and temporal refuge from high rates of parasitism, reducing the accumulation of endo- and ectoparasite loads (Bush and Clayton 2018). A comparison between two North American sympatric populations of dark-eyed Juncos (*Junco hyemalis*), one migratory and the other sedentary, revealed significantly higher frequency of infections by protozoans of the Order Haemosporidia in the sedentary population, both during the breeding and non-breeding seasons (Slowinski et al. 2018). Likewise, the prevalence of infestation by Chigger mites (Acarina: Trombiculidae) in 26 Neotropical species (belonging to 17 genera) inhabiting Mexican coffee agroecosystems may be as much as 1.4 times greater in year-round residents than in long-distance migrants; individuals that do not regularly migrate and thus do not periodically escape the environments in which they become parasitized most heavily, accumulate larger parasitic loads over time

than do the birds that undergo annual migrations to areas with lower parasitic densities (Dietsch 2005).

Migration in Juvenile Birds

Regardless of how migration has evolved, it is still viewed as a metabolically costly and highly dangerous endeavor for birds, especially for young undergoing their first journeys from breeding to non-breeding grounds (Rotics et al. 2016). Mortality during migration is significantly higher for juveniles than adults across a large array of taxa including White storks (Schaub and Pradel 2004), Greater snow geese (*Chen Caerulescens Atlantica*; Menu et al. 2005), Barnacle geese (*Branta leucopsis*; Owen and Black 1989), Osprey and Honey buzzards (*Pandion haliaetus* and *Pernis apivorus*, respectively; Strandberg et al. 2009), Black kites (*Milvus migrans*; Sergio et al. 2011), and Eurasian widgeons (*Mareca Penelope*; Guillemain et al. 2013). The disproportionately high mortality rates of juveniles may be attributed to experience-related differences in migratory performance, namely: inferior navigation abilities (Perdeck 1958) and more variability in orientation (Moore 1984), poorer predator avoidance (Dierschke 1998), competitive disadvantages while foraging at stop over sites (Heise and Moore 2003), and higher sensitivity to weather-related navigation disruptions (Owen and Black 1989). Young birds likely also expend greater amounts of energy while in flight due to smaller wing surface areas compared to adults, and thus have greater wing loadings (Perez-Tris and Telleria 2001).

The greater challenges of first migration for juveniles may explain, at least in part, the fact that in many species, juvenile and adult birds exhibit contrasting migratory tactics in regard to phenology and route choice. Generally, for most avian taxa, the arrival of young birds to non-breeding grounds follows that of adults (Hockey et al. 1998; Stewart et al. 2002; Newton 2008). Aside from inferior migratory performance in comparison to adults, later

juvenile arrival dates may also be ascribed to several advantageous processes, such as detours to avoid regions of high predation (Lindstrom et al. 2011), and large expanses of water over which long periods of sustained flight are required (Crysler et al. 2016), as well as longer stopover durations (Mellone et al. 2013; McKinnon et al. 2014) and more frequent stopovers to allow for improved re-fueling and rest (Yong et al. 1998; Rguibi-Idrissi et al. 2003). Juveniles of some species also depart from breeding grounds later than adults in order to maximize feeding period and energy stores before embarking on migration (Hendenstrom 2004).

Given the temporal and spatial segregation of adults and juveniles during fall migration, the young of many avian taxa do not travel together with their parents as family units (Hendenstrom 2004; Zduniak and Yosef 2008; Henningsson and Karlsson 2009; Lindstrom et al. 2011; Crysler et al. 2016). Since members of these taxa do not have guidance from older conspecifics on their first migrations, their route choices may primarily be determined by genetics rather than learning (Henningsson and Karlsson 2009). Some taxa, however, do migrate in large, mixed juvenile-adults flocks with close association to siblings and parents, such as certain species of storks (Ciconiidae: Rotic et al. 2016), geese (Anatidae: Elder and Elder 1949), hawks (Accipitridae: Maransky and Bildstein 2001), bustards (Otididae: Palacin et al. 2011), and cranes (Gruidae: Stevenson and Griffith 1946). In species that migrate in groups of mixed age classes, the transfer of navigational information from more experienced individuals to young is likely crucial for migratory success (Mueller et al. 2013). The fitness advantages which young birds acquire from following older conspecifics during their first migrations is an obvious driver of the evolution of mixed-aged flocks in many species; the mortality rates of inexperienced juveniles, which are by nature, more prone to navigational errors and predation, likely decrease when young birds follow the pathways

dictated by birds that have already undergone successful migrations in the past (Henningsson and Karlsson 2009).

Investigating the migratory patterns of juvenile birds may be of critical importance to conservation strategies for two reasons. First, it is well known that mortality is particularly high during first migration from breeding to non-breeding grounds, as previously mentioned. Anthropogenic impacts may further reduce naturally low survivorship (Thomas et al. 2006). The juvenile demographic may thus regulate population sizes and may be a significant source of recent population declines (Owen and Black 1989; Schaub and Pradel 2004; Zduniak and Yosef 2008; Sergio et al. 2011; Burger and Olla 2013; Guillemain et al. 2013; Rotics et al. 2016). Despite its potential importance, surprisingly little is known about the migratory patterns of juvenile birds and the factors that shape them (Vansteelant et al. 2017). The majority of existing studies track large species that undergo their first migrations together with older conspecifics, and exclude smaller species that do not rely on socially learned navigational information (Vansteelant et al. 2017). In-depth analyses of the migratory patterns (i.e., geographic bottlenecks, unique stopovers, migration phenology) of juveniles may differ from that of adults within a species (Lindstrom et al. 2011) and may consequently provide novel information with important conservation implications.

Shorebird Migration

Shorebirds, a paraphyletic group within the order Charadriiformes, undergo some of the furthest seasonal migrations of all avian taxa. Each spring, a multitude of arctic-nesting shorebirds journey thousands of kilometers from their non-breeding grounds, across multiple biomes, expending great amounts of metabolic energy (Wikelski et al. 2003) to reach high latitude (60 - 90°) breeding grounds in the Northern Hemisphere (Myers 1983). Some species such as the Red Knot (*Calidris canutus*) are known to travel 14,000 km twice a year from

their non-breeding grounds in South America to their breeding grounds in Northern Canada (Niles et al. 2010). Other species, such as the Bar-tailed Godwit (*Limosa lapponica*), have been recorded to travel for over 10,000 km in a single flight (Gill et al. 2010). Such impressive migratory feats position this fascinating taxonomic group as ideal candidates for studying long-distance migration.

As a whole, shorebirds are estimated to have declined by 70% within the past four decades (North American Bird Conservation Initiative 2016) and 61% of North American populations have long term, negative trends (Smith et al. 2020). Pinpointing causes of shorebird declines is difficult due to the migratory nature of these taxa, and the fact that threats to their populations may span entire continents. Indeed, unlike resident species, the population sizes of migrants are often influenced by factors in more than one region (Newton 2004). Several major threats have been linked to declines of worldwide shorebird populations. Habitat degradation and fragmentation as a result of the expansion of public beaches (Lafferty et al. 2013), and the transformation of wetlands into farms for instance, are significant factors in the declines of many shorebird taxa worldwide (Czech and Parsons 2002). Pesticide use (White et al. 1983; Braune and Noble 2009), unsustainable hunting practices (Watts and Turrin 2016), invasive species such as raccoons and feral swine (Engeman 2010), exotic snakes (Engeman et al. 2011), and climate change-induced phenological asynchrony between timing of breeding and peak food availability at breeding sites (McKinnon et al. 2010) are also highly important contributing factors resulting in globally dwindling shorebird populations in the modern day. Other biological characteristics that make shorebirds vulnerable to population decline include a dependence on spatially discrete habitats for breeding and foraging, low reproductive rates, specialized foraging strategies, and gregariousness on the migratory staging sites and non-breeding grounds (Piersma and Baker 2000). It is clear that migration heavily influences the population dynamics of long-distance migrants (Klassen et

al. 2014) therefore, studying the details of avian migrations is thus of high value in terms of conservation.

Shorebirds are considered to be valuable ecological indicators of ecosystem decline for a variety of different habitats, such as coastal bays and lakes, oyster reefs, mudflats, beaches, seasonal wetlands, and salt flats (Ogden et al. 2014). Shorebirds are irrevocably linked to discrete habitats for foraging and breeding - intertidal areas, wetlands, estuaries, and salt flats, and as a result, any form of ecological change to these habitats, such as release of contaminants, changes in primary consumer abundances, or even slight increases in temperature, can strongly influence shorebird populations. Shorebirds are also important ecological components that regulate mass and energy fluxes across wetland food webs; during migration shorebirds have a predatory impact on the biomass of invertebrate populations in a variety of ecosystems, and they remove a significant percentage of annual production of benthic macrofauna (Moreira 1997).

Objectives

The three central objectives of my thesis are to 1) map the migratory flyways and stopover sites of juvenile Dunlin (*Calidris alpina*) on their first migrations from their breeding to their non-breeding grounds using the Motus radio telemetry system, 2) investigate inter-annual and intra-annual variation in juvenile migration pathways, and 3) compare the spatial details of juvenile migratory routes to those of adults, particularly differences in stopover sites, general migratory directionality, and final wintering sites.

I hypothesize that juvenile migration tracks will differ from those of adults, both spatially and temporally. Although the mechanisms that shorebirds use to navigate during migration are multi-faceted, complex, and not fully understood, it is theorized that this taxa likely utilizes a combination of internal circadian rhythm cues, visual cues of sun orientation, and the Earth's magnetic fields to successfully reach the non-breeding grounds (Alerstam et al. 2001). Due to the well-supported concept that these crucial navigational mechanisms are underdeveloped in juvenile shorebirds compared to mature birds (Grönroos et al. 2012), I predict that young Dunlin will exhibit more meandering routes with greater total distances and more instances of reverse migration, while experienced adults will take more direct flights to their non-breeding grounds. Young Dunlin will exhibit more variation in final detections sites, due to their inexperience with navigation and higher rates of mortality. Juvenile migration, on average will also occur later than adult migration; young will depart from breeding grounds and arrive to non-breeding grounds at later dates than adults.

I also predict that brood will have an effect on migratory route choice in juvenile Dunlin; migration tracks will be more similar within broods than among broods. Also, the routes of related birds will be more similar to one another than to the routes of unrelated birds migrating the same year.

Methodology

Study Site

Fieldwork (i.e., nest searching and monitoring; tagging of individuals) was conducted within the 850 000 ha Churchill Wildlife Management Area (58.66°N, 93.81°W), in the transitional zone between boreal forest and tundra, in Churchill, Manitoba, Canada (Figure 1). This region is managed by the provincial government and has a long history of wildlife research (Jehl and Lin 2004). The Churchill Wildlife Area provides essential nesting habitat for a wide variety of arctic-nesting birds, including 15 species of shorebirds, and is the Southernmost point of the Dunlin breeding range (Jehl and Lin 2001). Shorebird nesting densities are high in the Churchill Wildlife Management Area as well, making it an ideal location to study shorebirds during the breeding season.

Nests were monitored at three specific sites during the summers of 2016-2018; the Golf Balls (58.75°N, 93.92°W), Gun Range (58.74°N, 93.96°W), and Fen (58.66°N, 93.81°W) (Figure 1). These sites are wetlands dominated by grasses and sedges with scattered shrubs and very few trees, and are characterized by small ephemeral ponds, as well as countless peat mounds known as hummocks (Skeel 1983). The Golf Balls, Gun Range, and the Fen are located at straight-line distances of 16.3, 13.5, and 32.0 km, respectively, from the town center of Churchill. Each site is accessible by gravel road from the Churchill Northern Studies Center (58.73°N, 93.81°W; Figure 1).

Study Species

Dunlin are migratory circumpolar breeding shorebirds within the Scolopacidae family. This species is among the most common and wide spread of all shorebirds, with breeding

grounds covering the coastal grasslands and saltmarshes of the temperate zone, mires in the boreal zone and tundra of the subarctic and Arctic (Birdlife International 2017), and very large worldwide population of approximately 4,295,000-6,800,000 individuals (Engelmoer and Roselaar 1998).

Dunlin make their nests on the ground by scraping shallow depressions among vegetation, often atop of hummocks or grassy mounds (Kaufman 2001). Nest cups measure, on average, 9.9 centimeters wide and 3.2 centimeters deep, and clutches usually consist of four eggs, but sometimes two to three. Pairs are usually monogamous, and both sexes incubate as well as protect young throughout the breeding season. In the instance of nest predation, Dunlin have high rates of renesting during early incubation stages (82-95%) and moderate rates later in the season (35-50%; Jamieson 2011). Renesting typically occurs 5 to 7 days after a nest has been destroyed, and mates usually stay together during the process. Dunlin incubate for an average of 22 days (Kaufman 2001). During the breeding season, Dunlin feed mainly on adult and larval insects, as well as gastropods and arachnids, while during non-breeding season, their diets consist largely of polychaete worms, bivalves, and crustaceans, but also insects (Birdlife International 2017).

The subpopulation nesting in Churchill, MB is *Calidris alpina hudsonia.* Three Dunlin subspecies occur in the coastal and wetland regions of North America and breed in North American Arctic and sub-Arctic regions: *Calidris alpina hudsonia, Calidris alpina articola,* and *Calidris aplina pacifica*. *Calidris alpina hudsonia* breeds in the Hudson's Bay area, and winters along the Eastern coast of the United States, down through the coast of Florida, and as far down as the East coast of Mexico (Warnock and Gill 1996). Population estimates of *C. a. articola*, *hudsonia,* and *pacifica* are 500 000, 450 000, and 550 000 respectively (Andres et al. 2012). A 2012 report suggests that populations of *C. a. arcticola* and *C. a. hudsonia* may be stable. Dunlin are considered by the Canadian Shorebird Conservation Plan as a Species of

Moderate Concern that warrant conservation planning due to high rates of habitat loss in their non-breeding range and their vulnerability to an array of anthropogenic impacts, given its strong tendency to aggregate (Fernandez et al. 2010).

Radio tracking

There are several means through which bird migrations can be tracked, including light-level geolocators (Costantini and Moller 2013), GPS-based satellite telemetry (Chan et al. 2019), and radio telemetry (Lyn et al. 2018). Modern radio telemetry typically uses Very High Frequency (VHF) radio transmitters. Individuals are equipped with VHF transmitter tags, which are then detected by radio tower networks (Ogden et al. 2014). This technology grants researchers the ability to track individual animals on their migratory pathways, and investigate nest fidelity, as well as stopover site use. Since their first use in the late 1960s on elephant seals, radio tag technology has become increasingly miniaturized with the development of smaller electronic components, circuit boards, and power sources. Small sized radio transmitters are essential for use on many bird species, since tags can weigh no more than three to five percent of a bird's overall mass, as not to significantly impede flight dynamics. Radio transmitters sized eleven by five by three millimeters and weighing less than 0.3 g can now be produced, allowing for the tracking of even the smallest avian taxa (Ogden et al. 2014).

In our study, we took advantage of the Motus Network, a collaborative network of international researchers using automated radio telemetry arrays to track large and small-scale movements of a variety of small aerial species, from butterflies to bats (Taylor et al. 2017). Since 2012, the Motus system of automated receiver towers in North America has been used to track over 87 species and boasts upwards of 250 million individual detections.

In order to deploy radio tags on Dunlin chicks, nests were found by means of thorough, exhaustive systematic searches on foot between 5 June and 15 July during 2016, 2017, and 2018. When nests were found, two eggs were floated in order estimate hatch dates using the floatation method (Liebezeit et al. 2007). The floatation method provides an estimate of hatch date based on size and positioning of the air sac in a developing egg; as eggs develop, the air sac increases in size and changes position so that eggs will float at a specific height and angle based on their stage of development. Nests were revisited every five days to monitor for signs of imminent hatch. Hatch dates were recorded, and upon hatch, chicks were fitted with leg bands depicting unique numerical series and weighed on the nest.

In order to recapture chicks of sufficient size for tag deployment (a minimum weight of 22 grams, as tags cannot exceed 3% of a chick's body mass), we searched for banded chicks during the brood rearing season (10 July to 15 July) along predefined transect lines intersecting the area of highest nesting density. Transect line surveys were conducted every two days by a minimum of two observers walking approximately 50 m apart from one another. Adult dunlin performing distraction displays were first located during transects, and chicks were found within close proximity. Chicks were also captured during haphazard searches conducted around nests known to have hatched days prior. Unbanded families were found during these searches as well and chicks weighing 22 grams or more were tagged regardless of whether or not their age was known or whether their parents were identified.

A total of 46 chicks of sufficient weight were equipped with NTQB-3-2 Lotek radio tags. The NTQB-3-2 Lotek radio transmitter model weighs 0.67 grams, allows for detection readings every ten seconds, and has an estimated battery life of 124 days. Tags were attached to birds according to field protocols approved by the York University Animal Care Committee. Rump feathers were gently clipped and tags were glued to skin and stubble on chicks' rumps. A waterproof permanent marker was used to color the attached radio tags

black, rendering them less conspicuous. Once chicks were outfitted with tags, the area was abandoned promptly so to reduce further disturbance.

Data Analysis

Full project data, including all detections and related metadata, as well as all receiver station metadata, were downloaded using the package *motus* (Brzustowski and Lepage 2018), in R version 3.2.4 (R Core Team 2016). All juvenile Dunlin tag detections from 2016 to 2018 were first coalesced into a single subset of data under the unique Motus species code 'DUNL' using the *tidyverse* collection of packages (Wickham 2017). In order to simplify the Dunlin data table, the package *motus* was used to extract only the following essential pieces of tag detection metadata: tag ID, tag deployment latitude and longitude, receiver location and name, species ID, detection run length, time stamp, receiver static noise level, port/antenna at which detection occurred, signal strength, and tag life span. Time stamps of each tag detection were rounded to the nearest minute and transformed into an easily interpretable format of month-day-hour-minute with *tidyverse*. Receiver deployment dates and locations as well as tag deployment dates and locations were then validated by generating maps and simple date versus receiver/tag ID plots using packages *rworldmap* (South 2011) and *ggmap* (Kahle and Wickman 2013).

Tag detections were filtered using the following criteria. First, false positive detections were removed from the dataset, and were deemed as such if they occurred outside of the predicted battery lifespans of tags (124 days, from time of activations for NTQB-3-2 tags). Predicted battery spans, provided by the tag manufacture as well as Motus, are considered accurate estimates given that tags are exposed to expected degrees of environmental conditions, but may be longer or shorter *in vivo* (Crewe et al. 2001). Detection were also removed if they implied highly improbable flight speeds of 30 $m \cdot s^{-1}$ or greater, sustained for a

day or more, between receivers. While the average Dunlin flight speed is 16 $m \cdot s^{-1}$ during migration to non-breeding grounds (Gronroos et al. 2012), individuals have been recorded to reach 25 ms^{-1} while preforming aerial displays (Davis 1980). The average static noise of receivers in this project was calculated to be 71.46 ±7.47 dB. Since static noise, usually due to a variety of interfering anthropogenic communication signals, may increase the possibility of false positives, detections associated with static noise levels above the average range were eliminated from the dataset (detections which occurred in the presence of exceptionally low noise levels were included).

Run lengths and the number of detections at a given receiver were two central factors determining the inclusion of tag detections in the dataset. As a tagged bird travels from one point to another, its transmitter releases VHF coded pluses at regular intervals. When a tagged individual then passes within the detection radius of a Motus tower, the VHF pulses emitted by the tag are then picked up. However, in order for an individual to become registered at any given tower (i.e., become officially detected at a location), a minimum of two consecutive pulses from its tag must be picked up by a tower, corresponding to the tag's particular pulse interval (how often a tag emits a pulse varies based on tag model and preferred programming). The "run length" of a registered detection is defined as the number of consecutive pulses from a particular tag that is recorded by a receiver. The run lengths of individual detections can thus vary greatly, depending on how many successive pulses are recorded from a tag. Each receiver may also record multiple detections from one tag, each with its own unique run length.

The chance that a tag was erroneously detected at a receiver due to random noise decreases with increasing run length, and likewise, with a greater number of consecutive detections, given that static noise levels are within the norm.

The variability of which ports (antennae) detections occurred on was also considered. Each Motus telemetry tower possesses three antennae/ports, which are oriented in three different directions, and are often times evenly spaced apart. Each antenna corresponds to its own lobe-shaped detection radii. If a bird is detected in a consecutive manner at more than one port of a receiver, it was deemed more likely to be a true positive, as movement between antennae detection zones may indicate local movements or a flight path of a bird, thus reducing the probability that the detection was caused by a random noise event.

Detections that fulfilled the following requirements were included in the final dataset:

1. Detections with maximum run lengths of 4 or greater (Crewe et al. 2018).
2. Detections with a maximum run length of 3 that exhibited greater than 40 consecutive hits at a given receiver.
3. Detections with run lengths of 2 or 3 that exhibited 4 or more consecutive hits and also occurred at two or more different ports of receiver.

The above filtering criteria should be considered less conservative than the filtering guidelines recommended by Motus (Crewe et al. 2001). Typically, all detections that have run lengths of 2 are discarded, as to ensure the elimination of all false positives, however, it is also advised that individual detections be analyzed on a case-by-case basis as some detections with low run lengths may be valid. The majority of juvenile detections we recorded were of low run length and were thus filtered using my unique criteria. This adapted filtration criteria was created in response to both the low sample sizes of tracked juvenile Dunlin, as well as the fact that run lengths of three or under were exceedingly common throughout all juvenile detections across the Motus network. Each individual tag was closely examined in the context of known adult Dunlin migratory patterns as well.

Adult Dunlin tracks on the other hand, were obtained from three different pre-compiled datasets: 1) mature birds that were tagged on their established breeding grounds in

Churchill, Manitoba (these birds all belonged to one known genetic population; Nol et al. 2015), 2) James Bay, Ontario (these birds were captured at an important stop over site during their migration, and it is not known what genetic populations they may have belonged to; Friis et al. 2015), and 3) the Mingan Islands Archipelago in Southern Quebec (likewise, these birds were tagged on a stopover site, and thus their genetic population ties are unknown; Aubry et al. 2014). Adult birds tracked from Churchill were equipped with NTQB-2 tags, while birds tagged in James Bay and Quebec were equipped with NTQB-3-2 models (Table 1). Thirty birds were equipped with radio transmitters in Churchill, Manitoba (58.7°N, 93.85°W), eight in Grand-Ile, Quebec (50.2°N, 63.75°W), and 20 in James Bay, Ontario (51.82°N, 80.69°W). Ten adults were successfully tracked from Churchill, five from Quebec, and fifteen from James Bay.

The filtered tag detections of juveniles and adults were plotted on a map of North America using QGIS version 2.18.26 (QGIS Development Team. 2019).

Migration Parameters

Given that body condition of chicks at the time of capture may influence tracking success, we tested for differences in body mass between successfully and unsuccessfully tracked individuals using a Mann-Whitney-Wilcoxon test. Unsuccessfully tracked individuals were deemed as such if they were detected within the breeding grounds only, while all successfully tracked birds were recorded on the Motus network in at least one location outside of the breeding grounds. As birds hatching earlier in the season may have time to acquire more resources for a successful first migration, we also tested for differences in median hatch dates of successfully and unsuccessfully tracked broods using a Mann-Whitney-Wilcoxon test.

Total distances of migratory routes were measured as the sum of all distances between detection sites, starting from the locations that birds were originally tagged to the locations at which they were last detected. Individual migration timespans (days) and rates (kilometers per hour) for both age groups were calculated based on the date a bird was last detected on the breeding grounds, as well as the date of final recorded detection. The migratory departure dates of adult birds from their breeding site of Churchill, and those from stopover sites of James Bay and Quebec were calculated using the date each bird was last detected at its associated tagging location. Neither the timespan of migration nor the migration rate could be calculated for the majority of tracked juvenile birds, as only three departure dates from the breeding grounds were recorded successfully for juveniles. Calculating migration timespans using the date at which chicks were equipped with radio tags as a starting date would likely result in falsely inflated migration durations since juveniles, still flightless at the time of tagging, remain on the breeding grounds up to sixteen days before departure. It should still be noted however, that even using the last recorded detections on the breeding grounds, the calculated migratory timespans could be overestimated if juvenile birds did not embark on migration promptly after this last detection.

To help ascertain if juvenile tracks ended prematurely - that is, whether or not the final detection locations of young birds coincided with actual non-breeding sites, or if radio tags simply never reached the non-breeding grounds - the latitudinal values of final detection locations were contrasted between age groups and populations via a Kruskal-Wallis test. The final detection latitudes of adult Dunlin populations were used here as a template of likely complete migratory tracks, to which juvenile tracks were compared.

Route trajectory was a numerical metric that was created in order to quantitatively compare the general directionality trends of different migratory tracks. Two trajectory values were established for each documented migratory route: latitudinal and longitudinal trajectory.

These values were established by calculating the net latitudinal and net longitudinal displacements of migratory tracks in decimal degrees, between the origin of tagging and the final detection locations of each bird on the Motus network (using Mercator projection). Positive latitudinal displacement values indicated general southbound migratory trends, while negative values indicated northbound trajectories, relative to tagging origin. Likewise, positive longitudinal displacement values implied overall Eastward trajectories, and negative longitudinal displacement values implied Westward trajectories. Route trajectory, unlike final detection latitude, takes into account tagging location as well as the often indirect, meandering nature of migrations. It must be noted however, that neither of these trajectory values can be conflated with or are representative of true ground distances, as ground distances are not consistent for degrees of longitude that depend on latitude. Thus, the trajectory values mentioned here are only meaningful when used as direct comparisons of the general directionality of birds' migratory routes. Inter-annual variations in migratory distances as well as route trajectories were compared for juvenile birds using one-way ANOVA and/or Kruskal-Wallis tests when data were not normally distributed.

Differences in migration distance, timespan/duration of migration, migration rate, as well as trajectory were analyzed among age groups and populations using Kruskal-Wallis tests, while differences in these parameters between male and female adult birds within different populations were examined via Mann Whitney Wilcoxon tests. Since mature birds were radio-tagged at different locations each year, the aforementioned parameters were compared between different adult populations/tagging sites. Potential annual differences in migratory hotspots (i.e., regions in which Dunlin were frequently detected) were identified for both age groups.

To elucidate the potential role of genetic relatedness in shaping the spatial migratory patterns of juvenile Dunlin, differences in migration distance as well as latitudinal and

longitudinal route trajectory among three identified broods were investigated via ANOVA and Kruskal-Wallis tests when data were not normally distributed.

Results

During the summers of 2016 - 2018, 84 chicks belonging to 37 different broods were banded, and 46 juveniles were equipped with Lotek NTQB-3-2 radio telemetry tags (Table 2; Table 5). Of the 46 juveniles tagged from 2016 - 2018, migration pathways of eleven individuals were successfully documented (Table 3; Figure 2). A total of 30 adult Dunlin were tagged during 2015 in Churchill, MB, of which 10 were tracked successfully (Table 1; Figure 3). Fifteen of 20 birds tagged in James Bay, ON in 2015 were successfully tracked (Table 1; Figure 4; Figure 5). Five of eight birds tagged in Grand-Ile, Quebec in 2014 were tracked successfully (Table 1; Figure 6).

Juvenile Migration Parameters

Approximate migration departure dates are known for only three juveniles: one bird, tagged in 2016, likely departed on or around 12 July, another, tagged in 2017, departed on 24 July, and the third, tagged in 2018, departed close to or on July 14 (Table 3). The average duration of migration exhibited by these three juvenile Dunlin was 108.3±68.81 days. The longest timespan over which a tag was detected was 186 days (from 14 July 2018 - 16 January 2019). Juvenile birds were detected at one to three different receivers on their migratory routes outside of their breeding grounds (Table 3), between the months of July and October.

Juvenile Dunlin tagged in 2016 were first detected on migration on the median date of 2 September while the median date of first detection for birds tagged in 2017 and 2018 were 21 August and 15 August, respectively. The median dates of final detection for birds tagged in 2016, 2017, and 2018 were 13 September, 14 November, and 10 November, respectively (Table 3).

The eleven juvenile migrations documented across the years of 2016 to 2018, averaged 2507±445.16 kilometers. The longest recorded migration was observed in 2017 and spanned a total of 3298 kilometers. Juveniles averaged 2239±269.2 kilometers in 2016, 2839±714.9 kilometers in 2017, and 2526±201.1 kilometers in 2018. There were no significant differences found in total migratory distance among the three study years (Kruskal-Wallis, h=10, df=9, $p > 0.05$).

Tracking Success

The median hatch date of broods from which juvenile birds were successfully tracked on Southward migration across the years of 2016 - 2019 was 26 June, while the median hatch date of broods of undetected individuals was 28 June (Table 4). Hatch dates of tracked and untracked birds did not significantly differ (Mann-Whitney-Wilcoxon test, $p > 0.05$, z=1.47).

Body masses of the eleven successfully tracked juveniles averaged 34.18±7.26 g at the time of capture and subsequent attachment of radio tags. The 35 tagged juveniles that were never detected weighed an average of 34.73±5.40 g. Both the tracked and untracked groups included similar outliers in terms of chick mass - the heaviest chick that was tracked successfully weighed 45 grams at the time of tagging, while the largest chick that was not detected weighed 44 grams. Chick body mass data met the assumptions of normality (Shapiro-Wilk, $p > 0.05$) as well as homogeneity of variance (Levene's test, $p > 0.05$), thus a T-test was conducted. There was no significant difference in body mass at the time of radio tag equipment between birds whose migrations were later documented and the birds that were not recorded by the Motus network (Two-sample T-test, $p > 0.05$, t=0.27).

Intra-Annual and Inter-Annual Juvenile Migratory Trends

All recorded juveniles routes exhibited southeastward trajectory trends from Churchill, Manitoba during fall migration. Among the three years, the routes of birds tagged in 2016 were most similar to one another in terms of latitudinal trajectory from the breeding grounds. Two birds tagged in 2016 flew to Southeastern Ontario (44.14°N, 76.38°W; Figure 2), and two others migrated to the East coast of the USA (41.15°N, 71.55°W and 41.29°N, 72.32°W) with an average latitudinal trajectory of 15.98±1.69°, that is, the net displacement of these two routes averaged a span of nearly 16° latitude from Churchill, and their respective final detection sites. The average longitudinal trajectory for routes in 2016 was 19.65±2.59°. Migratory tracks recorded in this year also exhibited the least amount of longitudinal distance between their most distal detection locations (405 km).

Two juveniles tagged in 2017 were last detected in Southern Ontario (42.58°N, 80.40°W), while the third migrated through this region and was last recorded in Florida (31.30°N, 81.34°W). Migratory paths of birds tagged in 2017 flew an average of 19.84±6.52° South, and showed the greatest variation in latitudinal trajectory, but the lowest variation in longitudinal trajectory (average 13.09±0.55°).

The routes of juveniles tagged in 2018 were divided into two distinct trends - two birds followed identical paths to Pennsylvania (40.32°N, 75.90°W), and two migrated to Nova Scotia (43.93°N, 60.02°W and 45.21°N, 64.40°W). The average latitudinal trajectory between the breeding grounds and final detection sites of birds tracked in 2018 was 16.22±2.51°, and the corresponding average longitudinal trajectory was 24.75±8.10°, which was the greatest recorded longitudinal variation in final detection site location.

Juvenile migratory route trajectory did not significantly differ among the three years in latitudinal trends (One-way ANOVA, f=1.09, df=10, $p > 0.05$) or in longitudinal trends (Kruskal-Wallis, h=10, df=7, $p > 0.05$).

Brood-Dependent Trends in Juvenile Migratory Routes

Of the eleven juvenile Dunlin that were successfully tracked, three pairs of individuals were related (broods A, B, and C; one brood per consecutive year), and three individuals were from separate families. Two of the eleven birds belonged to unidentified broods (Table 5). Brood A exhibited the least amount of variation in migratory trajectory, as both birds took identical paths on their southbound migrations and were last detected in Southeastern Ontario (44.14°N, 76.389°W; Figure 7). The two other birds tracked during the same year each exhibited unique migratory routes, both of which were further eastward compared to the mutual route of brood A. Individuals of brood A flew 14.42° East and 17.42° South from their breeding grounds. Birds of brood B both migrated to Southern Ontario (42.58°N, 80.40°W), and one of these individuals was last detected in Georgia, Florida (31.30°N, 81.34°W). The track of the third, unrelated juvenile tagged that year was positioned considerably further eastward than the routes of brood B. Brood B exhibited the furthest Southward migrations, with an average latitudinal trajectory of 21.72±7.98°, but travelled the shortest Eastward distance (longitudinal trajectory of 12.94±0.67°). Juveniles belonging to brood C, which migrated in 2017, flew to the East coast of Canada, and were both last detected in Nova Scotia (43.93°N, 60.02°W and 45.21°N, 64.40°W). The two other non-related juveniles which were tracked in 2017, did not travel to Canada's East coast, but instead to Southern Ontario, displaying significantly more westerly paths than birds of brood C. On average, brood C

travelled 14.09±0.90° south, and 31.60±3.09° East from the breeding grounds - the furthest Eastward migratory trend of all three broods.

Two juveniles tagged in 2018, belonging to unidentified broods, shared identical migratory paths from Churchill, Manitoba to Pennsylvania as well (Figure 2). It is not known whether these two individuals were genetically related.

Migratory distances did not differ significantly among the three identified broods (Kruskal-Wallis, h=5, df=4, $p > 0.05$) nor did latitudinal trajectory (Kruskal-Wallis, h=5, $p > 0.05$, df=4). There was however, a notable difference in the longitudinal trajectory trends between families (One-way ANOVA, f=56.84, df=2, $p < 0.05$). Birds of brood C took significantly more eastward migratory routes than birds of brood A or B. Longitudinal route trajectory did not differ between broods A and B.

Potential Geographic Hotspots of Juvenile Migration

Nine of our eleven recorded juvenile migratory routes passed through a section of Southern and Southeastern Ontario, spanning from South-West Oxford to Cornwall (Figure 2). Throughout all three years, the most common regions at which birds were detected were Long Point Provincial Park located on a peninsula off the North shore of Lake Erie and Wolfe Island, on the Northern-most tip of Lake Ontario. Individuals remained at these sites for an average of 7.2±9.9 days and 4.3±11.9 days respectively. The two most frequented detection spots were located in Ontario: Wolfe Island, and Long Point. The furthest Southward detection site of all eleven tracked juveniles was in St. Simons, Georgia.

Several possible annual variations in migratory hotspots were apparent. In 2016, all four tracked birds travelled through a relatively narrow passageway in Southeastern Ontario, spanning from 44.14°N, 76.39°W to 43.93°N, 60.03°W - a geographic corridor that was exclusive to juveniles migrating in 2016. The three birds that were tagged in 2017 were all

detected at the Long Point Bird Observatory in Southern Ontario (42.58°N, 80.40°W), two of which were last detected there. None of the individuals migrating in 2016 or 2018 were observed to fly through this area. A third possible migratory hotspot for juvenile Dunlin migrating from Churchill, Manitoba was observed in the East coast of Canada; only individuals that were tagged in 2018 were detected in Nova Scotia.

Adult Dunlin Migration Parameters

Median fall migration departure dates for adult Dunlin tagged on their breeding grounds of Churchill was 15 July 2015. The median fall migration departures of the other adults tagged on their migratory stop over sites in James Bay and Quebec were 11 September 2015, and 5 September 2014, respectively. Median dates of arrival to the first stop over site for adults migrating from Churchill was on 11 August 2015, while the subsequent stop over dates of birds tagged in James Bay, and Quebec were 11 November 2015, and 27 November 2014, respectively. The median date of final detection for adults tagged in Churchill was 20 August 2015, while adults captured in Quebec reached their final detection locations on the median date of 28 December 2014, and adult birds tagged in James Bay did so on the median date of 16 January 2016.

Adult Dunlin were detected at two to eleven different receiver locations along their migratory routes. Individuals were tracked for an average of 76.3±46.4 days from first detection at the site of tagging to first detection at their final migratory destination. The longest recorded adult migration spanned a total of 180 days from 11 September 2015 to 8 March 2016. However, the migration duration of this particular individual is based on an exceptionally late, single, and possibly erroneous final detection. The longest recorded migration that is based instead on several detections at the final detection site, and is more likely to be valid, lasted a total of 51 days, from 8 September to 1 November 2015. It should

be noted that due to the fact that Dunlin tagged in James Bay and Quebec were simply using these locations as migratory stop overs, their total migratory distances are not known, as their natal breeding grounds are unknown as well.

Of the 29 recorded migratory routes of adult Dunlin, 21 belonged to males and eight to females. The average migratory distance, calculated as the ground distance from tagging origin to final detection location, travelled by male birds tagged in Churchill was 2898±170.57 kilometers, and that of females tagged at this location was 2750±372.2 km. There was no significant difference in migratory distances between male and female birds (Mann-Whitney-Wilcoxon tests, z=0, $p > 0.05$). Males and females tagged in James Bay travelled an average of 2331±547.5 km, and 1879±788.2 km, respectively. Again, no difference in route distance was found between sexes (Mann-Whitney-Wilcoxon tests, z=0.46, $p > 0.05$). Adult males that were tagged in Southern Quebec flew a mean distance of 2936±1184 km, while females flew 5296±60.19 km, and likewise were not significantly different from one another (Mann-Whitney-Wilcoxon tests, z=0.25, $p > 0.05$).

On average, males travelled at a speed of 2.03±1.62 kilometers per hour, while females flew at a rate 1.6±0.83 kilometers per hour during southbound migration. Males and females tagged in Churchill migrated at average rates of 2.414±0.56 and 1.731±0.59 km per hour, respectively (Mann-Whitney-Wilcoxon test, z=0.67, $p > 0.05$). Males and females captured in James Bay flew at average speeds of 1.2014±0.24 and 1.570±0.58 km per hour, respectively (Mann-Whitney-Wilcoxon test, z=-0.31, $p > 0.05$). Males and females from Southern Quebec travelled at mean rates of 4.204±1.34 and 1.512±0.01 km per hour (Mann-Whitney-Wilcoxon test, z=82.3, $p > 0.05$). The differences in migration speed were not significant between sexes of any of the three tagging locations.

Potential Adult Migratory Hotspots

Of the ten adults tagged in Churchill, five were last detected in Alaska; four of these birds flew identical routes - first to an area 40 kilometers East of York Factory, Manitoba (57.1°N, 91.65°W), then to Mentasta Lake, Alaska (62.9°N, 143.7°W) - while another travelled straight to Mentasta Lake (Figure 5). Four birds were last detected in Wyandotte, Indiana (38.25°N, 86.3°W), although they took varying routes, and one individual was last detected in Formosa, Ontario (44.05°N, 81.2°W).

For birds tagged in James Bay, the Mingan Archipelago National Park Reserve was a highly frequented detection site (Figure 3; Figure 4). Eight individuals were last detected in this region, and one flew through. Two birds were last detected in Cundinamarca, Colombia, one of which exhibited the longest recorded migratory track, at 5669.35 kilometers, and 180 days. Two individuals were last detected in Mississippi.

Cundinamarca, Colombia (4.32°N, 74.54°W), was a common final detection location for adult Dunlin tagged in Quebec; three of five birds flew to this non-breeding site (Figure 6). Two other individuals were last detected much farther northward, along the East coast of Massachusetts and Rhode Island.

Comparisons of Migratory Parameters by Age and Population

There were no differences detected in migratory rates among juvenile birds and the adults migrating from the same breeding ground in Churchill (Kruskal-Wallis, h=31, df=31, $p > 0.05$). Latitudinal trajectory from the breeding grounds to final detection sites did not differ among ages of Churchill-tagged birds either (Kruskal-Wallis, h=3.51, df=40, $p > 0.05$). Significant differences in longitudinal trajectory, however, were detected (Kruskal-Wallis, h=25.6, df=40, $p < 0.05$). Juveniles exhibited more Eastward migratory route trends compared

to adults tagged in Churchill. Adults tagged in Churchill exhibited significantly more Westward routes than adults from James Bay.

Juveniles were last detected at an average of 41.5±1.14° latitude while adult birds that were tagged in Churchill were last recorded at 51.2±3.95° latitude, on average. Birds tagged on the stopover site of James Bay were last detected at 39.4±4.10° latitude. Quebec-tagged individuals exhibited an average final detection latitude of 19.1±9.05°. The average latitudes of the non-breeding grounds of juveniles did not differ from those of Churchill adults, but were significantly farther North than the final detection sites of adults tagged in Quebec (Kruskal-Wallis, h=35.97, df=20, $p < 0.05$). The final detection locations of adult individuals tagged in Churchill as well as in James Bay were also farther north than those of Quebec-tagged birds. Churchill and James Bay adult populations did not significantly differ in terms of average final detection latitude (Kruskal-Wallis, h=35.97, df=20, $p < 0.05$).

Discussion

Taking advantage of the recent advances in tracking technologies, we were able to track, for the first time ever, the migratory routes of North American-breeding juvenile Dunlin from their subarctic breeding grounds to their non-breeding grounds. In general, juvenile Dunlin departed from their natal breeding grounds in Churchill in mid- to late July, traveling southeastward to non-breeding areas located along the Northeastern coast of the United States. Young birds seemed to congregate in and over-winter in a discrete section of the Eastern Seaboard, where few adults were ever detected. Southeastern Ontario appeared to be a migratory hotspot for juvenile birds across all three years, with Long Point Provincial Park and Wolfe Island, Ontario noted as highly frequented detection sites during migration. The routes of related birds were more spatially similar to one another than to those of unrelated birds. The trajectories of juvenile birds were also notably more eastward than those of adult birds from the same Churchill-breeding population. The final detection locations of juveniles were further north than the final detection regions of the adult Dunlin tracked from Churchill as well. It should be noted, however, that due to small sample sizes our results should be interpreted with caution.

Age based segregation of non-breeding sites

Our data indicate a clear distinction in the selection of final, non-breeding site destinations between juvenile and adult birds as juveniles migrated to and spent their first non-breeding season in a relatively small, geographically discrete zone situated within the Northeastern extent of the currently documented non-breeding range of Dunlin (Fernandez et al. 2010; Birdlife International 2017). Over 45% of juveniles were last detected within this Northern section of the Eastern Seaboard - an area spanning from Rhode Island to New

Jersey. No Churchill-breeding adults were last detected there, and only 1% of adults tagged at stopover sites (James Bay and Quebec) were last detected in this specific region. Juveniles were rarely recorded to reach the Southern United States, and only one young bird was recorded in Georgia. In contrast to juvenile birds, 40% of the Churchill adults were detected in Indiana. Approximately 50% of Churchill-tagged adults were last detected in Southeastern Alaska; no recorded juveniles were ever detected at either Alaska or Indiana. If the final recorded detections of our juveniles are reliable endpoints for migration, our data provides clear evidence of age-based segregation of non-breeding sites for the *hudsonia* subspecies of Dunlin.

Age-based segregation of non-breeding areas has been observed in a wide variety of avian species, from diurnal birds of prey (order Accipitriformes; Reading et al. 2020; Henriques et al. 2017), to songbirds (Order Passeriformes; Woodworth et al. 2016; Prescott and Middleton 1990). Evidence as to which age group migrates farther from the breeding grounds is generally mixed, however, in avian taxa breeding in the Northern Hemisphere, juveniles typically tend to over-winter farther South than adults (Ketterson and Nolan 1976; Holberton and Able 2000; Catry et al. 2004). On one extreme, adults may not even migrate at all, and instead remain on the breeding grounds year-round, as is the case for Cinereous vultures (*Aegypius monachus*; Reading et al. 2020). The juveniles of other species, such as those of Savannah sparrow populations breeding in the Bay of Fundy, New Brunswick, migrate significantly longer distances during southbound migration, and pass the winter season in locations considerably farther from the breeding grounds than adults (Woodworth et al. 2016). Contrastingly, in taxa such the American Goldfinch, whose breeding range spans from central Canada to Nebraska and whose non-breeding range reaches as far South as central Mexico, older conspecifics tend to fly farther South and over-winter near the southern

extent of their non-breeding range, while immature individuals do not migrate as far and stop significantly Northward of adults (Prescott et al. 1990).

Our finding that juvenile Dunlin end their migrations at higher latitudes than adults contradicts the general aforementioned migratory trends of North American birds. Our results are however, in agreement with documented age-based segregation of non-breeding sites of other shorebird species. For instance, juvenile Western Sandpipers (*Calidris mauri*), which breed in Western Alaska, spend their first non-breeding season in one of two strikingly distinct geographic regions - they either over-winter near the northern-most extent of their non-breeding range (the Atlantic coast of the USA), or at its southern-most extent, in Peru. Adult Western Sandpipers on the other hand over-winter throughout Central America (Nebel et al. 2002). Contrastingly, juveniles of both Red Knot as well as Sanderling (*Calidris alba*) populations breeding in Northwest Australia tend to migrate further South and over-winter in lower latitudes of Southeastern Australia than do the adults of their respective populations (Minton at al. 2001). Yet, several shorebird species do not exhibit any age-based segregation during the non-breeding season at all. Juvenile and adult Ruddy Turnstones (*Arenaria interpres*), Bar-tailed Godwits, Red-necked Stints (*Calidris ruficollis*), and Great Knots (*Calidris ruficollis*) that migrate via the East Asian-Australasian Flyway (a vast geographic stretch that encompasses Alaska to Russia, and as far south as Australia, through which a great number of avian taxa fly during annual migrations) exhibit heavily overlapping non-breeding ranges (Nebel 2007).

Several hypotheses may explain the age-based segregation of non-breeding sites that we observed in our study. Predation pressure, for example, may play an important role in influencing the evolution of differing non-breeding sites between adult and juvenile Dunlin. Migratory patterns of many sandpipers (Scolopacidae) are strongly shaped by the migrations of raptors, both temporally and geographically (Lank et al. 2003). The southbound migrations

of sandpipers typically precede those of falcon species by nearly a month. By migrating early, birds maintain a distance between predator populations during migration. Despite considerably larger energy requirements, sandpipers that over-winter in British Colombia tend to take meandering routes along the Alaskan panhandle as they fly northward during spring migration, instead of migrating in straighter, more direct paths. These lengthier, more complex migratory routes however, do not overlap with the migratory routes of raptor species to a high degree, thus decrease individuals' exposure to larger numbers of migrating raptors, ultimately reducing mortality rates due to predation, (Lank et al. 2003).

Juvenile shorebirds are particularly susceptible to predation compared with adults. In certain populations of Bar-tailed Godwits, Red Knots, and Dunlin, juveniles have been shown to experience significantly higher predation-related mortality; discrepancies in predation rates between age groups may be as much as ten times greater for juveniles (Van Den Hout et al. 2008). Juvenile shorebirds may be at greater risk of predation largely due to a lack of experience. Not only are young birds less experienced in detecting and reacting to predatory attacks, but they also tend to use unrefined foraging strategies; whereas adult shorebirds aggregate in large flocks when feeding in order to deter predators, juveniles tend to feed in much smaller groups (Van Den Hout et al. 2008).

The most significant predators of shorebird species, including Dunlin, outside of the breeding grounds, are falcons (family Falconidae) and accipiters (family Accipitridae) (Page and Whitacre 1975; Kus et al. 1984; Cresswell and Whitfield 1994). Eight raptor species commonly found throughout North America, belonging to these two taxa likely account for the majority of predation pressure on North American Dunlin populations: Peregrine falcons (*Falco peregrinus*), American Kestrels (*Falco sparverius*), Merlins (*Falco columbarius*), Gyrfalcons (*Falco rusticolus*), Prairie falcons (*Falco mexicanus*), Sharp-shinned hawks (*Accipiter striatus*), Cooper's hawk (*Accipiter cooperii*), and Northern Goshawks (*Accipiter*

gentilis). Interestingly, the established ranges (breeding and non-breeding) of most of the aforementioned North American falcon and accipiter species largely exclude sections of the Eastern Seaboard region in which juvenile Dunlin were frequently last detected and likely over-wintered (Cornell University 2020). Only the American Kestrel, Cooper's hawk, and Sharp-shinned hawk are known to inhabit Maine, Massachusetts, Connecticut and Rhode Island year-round or during non-breeding seasons. The known ranges of Gyrfalcons and Prairie falcons share no overlap with the particular coastal areas our juvenile Dunlin tended to over-winter, and Peregrine falcons as well as Merlins are only known to pass through these locations during migration. Northern Goshawks may be found in Rhode Island and Connecticut during the non-breeding season, however, their populations there are considered scarce (Cornell University 2020). It is possible that the non-breeding destination selections of young Dunlin are heavily shaped by predation from the aforementioned raptor species.

Considering the large role predation pressure plays in shaping shorebird migrations, and given the disproportionate degree of vulnerability of juveniles to predation, it may be that juvenile Dunlin have evolved to preferentially select pockets along the coasts of Massachusetts, Connecticut, and Rhode Island as optimal non-breeding sites in order to avoid spending the winter in areas which host a greater variety of raptor species, thus avoiding potentially higher predation rates.

It is also important to mention that although winter conditions in the aforementioned northern section of the Eastern Seaboard are not as accommodating as the winter conditions experienced in more southern states, the average daily high in winter throughout Rhode Island to New Jersey sits at a relatively mild 8°C, even during the coldest months. Such temperatures are likely sufficiently warm enough for wintering Dunlin to stay above thermoneutrality (especially considering that certain closely physiologically related subspecies such as *pacifica* and *articola* winter in Alaska, where winter temperatures are considerably more marsh). The

coastal expanse ranging from Rhode Island to New Jersey also hosts an abundance of aquatic invertebrate biomass all year round, on which Dunlin can feed freely - several species of insects, like winter stoneflies (Family: Taeniopterygidae), a wide diversity of mollusk taxa, as well as ample quantities of dormant invertebrate egg masses of many fauna such as a species of fresh water jellyfish (*Craspedacusta sowerbyi*), for example, and an array polychete worms (Class: Polychaeta), and several common amphipods species (*Onyctidae erangonvx*; *Crangonvx gracilis*; *Svnurella chamberlain*, etc.) (Nehls and Tiedemann 1993). The Northern section of the Eastern Seaboard at which many of our tracked juveniles were last detected, in theory, may be more than sufficient in its environmental qualities to accommodate flocks of wintering Dunlin.

A well-established, widely applicable ecological concept known as the theory of social dominance, lends further support to the geographic segregation of adult and juvenile Dunlin non-breeding sites that we report here. This long-standing, parsimonious theory states that, in general, larger, more experienced (older), and more dominant individuals of a species tend to out-compete subordinates for resources, prompting subordinate conspecifics to instead migrate to different habitats, which may contain suboptimal resource quantity or quality (Gauthreaux 1978). Food resources on the non-breeding habitats of shorebirds are of course finite, and stark differences in predation rates may exist between localities within a given non-breeding region (Van Den Hout et al. 2008). Consequently, some degree of competition between adult and juvenile conspecifics is a common phenomena observed in a diverse array of avian taxa, from Wandering albatrosses (*Diomedea exulans*; Riotte-Lambert and Weimerskirch 2013), to American Robins (*Turdus migratorius*; Vanderhoff and Eason 2008), to Roseate terns (*Sterna dougallii*; Watson and Hatch 1999).

The coastal non-breeding areas Dunlin typically aggregate on consist of a variety of distinct habitats. For instance, intertidal zones rich with bivalve, mollusk, and annelid prey

items upon which shorebirds rely, and saltmarshes or wetlands, which contain different prey fauna and are located farther inland (Van Den Hout et al. 2008). Although these two ecotypes are usually geographically proximal, they may differ in the quantity of prey items, the nutritional value of common prey, as well as levels of predation. Juvenile shorebirds may be forcibly excluded by adults from ideal foraging sites and may frequently be forced to forage in locations of less optimal resource access, (e.g., regions with overall lower invertebrate densities or areas where the substrate under which prey hides is harder and is thus more difficult to probe into), and at sites where exposure to predation is considerably higher, as has been documented in Red Knots over-wintering at Banc d'Arguin, France. Here, adults regularly chase off younger conspecifics from farshore foraging sites, forcing young birds to aggregate at less ideal sites farther inland (Van Den Hout et al. 2008). Furthermore, adult birds may simply outcompete younger birds in foraging rates (Marchetti and Price 2008). Several characteristics vital for prey acquisition, both physiological and neurological, are naturally underdeveloped in immature shorebirds, such as beak innervation (the nerve networks of young birds that spread throughout their bills, and are responsible for sensory input, and allow birds to locate prey underneath substrate, are not yet fully developed), and skeleto-muscular systems (underdeveloped musculature; reduced brain-to-muscle connections). Optimized foraging strategies are also products of experience, and younger individuals typically exhibit much less refined foraging techniques (Marchetti and Price 2008).

In birds that breed in the Northern Hemisphere, it has been commonly observed that subordinate individuals, which are often times younger, are forced to migrate even further southward from their breeding grounds than their dominant conspecifics, and in the process, sacrifice greater metabolic costs and enhance their exposure to migratory dangers, in order to find adequate food sources (Ketterson and Nolan 1976; Holberton and Able 2000; Catry et al.

2004). Despite this general trend, the theory of social dominance does not imply that subordinate individuals always migrate farther southward, or to more distal locations from their breeding origins compared to adults. At its core, the social dominance theory simply predicts that subordinates are pressured to find alternative resources, regardless of direction or distance (Gauthreaux 1978). Perhaps, if resources and environmental conditions are more advantageous at higher latitudes than at lower latitudes juveniles of certain species may have evolved to over-winter northward of adult conspecifics instead, such as in the instance of Alaskan-breeding Western Sandpipers mentioned above. It is thus plausible that in Dunlin, immature birds tend to over-winter in locations at higher latitudes, which are poorer in habitat quality in order to avoid intense intra-species competition with mature birds, as well as to avoid higher densities of raptors.

The biological and evolutionary rationale behind the existence of age-based distinctions of Dunlin non-breeding sites are clear and lend support to our identification of such geographical regions. We emphasize the importance of focusing conservation efforts on the juvenile-specific non-breeding regions we highlight, since juveniles play a large role in the regulation of shorebird population dynamics. The Northern part of the Eastern Seaboard may be of particular conservation importance due to the fact that a large portion of our tracked juveniles ended their southbound migration there.

Our results must, of course, be interpreted with caution, as the sample size of juveniles in our study was small. Much of our results should be considered largely exploratory, especially in terms of the identification of a novel, Northern section of the Eastern Seaboard as a preferred wintering site for juveniles. Nonetheless, these findings provide a substantial basis and rationale for future juvenile shorebird migration studies to be concentrated on this specific coastal region.

Juvenile Migratory Hotspots

Several potentially novel migratory hotspots of juvenile Dunlin are elucidated in our study. During southbound migrations, juveniles were detected with high frequency (relative to our sample size of tracked juvenile birds) in regions of Southeastern Ontario, in particular Wolfe Island and Long Point Provincial Park - locations in which adult birds were not commonly detected. The increased frequency of detections in regions of Southeastern Ontario may imply that juvenile Dunlin migrating from Churchill rely heavily on discrete geographic areas such as these for migratory staging, and that these vital stopover sites (or at the least migratory passage ways) differ from those of adult birds. Staging or stop over sites are vital for shorebirds of any age group, as migrating individuals must stop to refuel and accumulate essential energy reserves required to continue their arduous migrations. Not only must stop over sites provide habitats appropriate to the specialized foraging strategies of shorebirds, such as wetlands or shorelines, but they must also host an adequate abundance of food resources (Harrington 1995). Given the tendency for this taxa to aggregate at high densities at these localities, and their importance as sources of energy during migration, anthropogenic impacts such as habitat alteration of stopover sites likely play extensive roles in the population declines of shorebirds; several shorebird taxa have even been known to avoid staging sites which are heavily altered via natural forces or human disturbance, and disperse broadly during migration to find better quality sites in response (Ross et al 2012).

Many high-quality shorebird habitats are located in Southern Ontario, namely large and medium-sized wetlands, which typically tend to remain relatively consistent in size and resource quality from year to year, in spite of annual fluctuations in precipitation levels or other volatile climactic factors (Ross et al. 2012). Although large-scale, anthropogenic habitat changes have occurred in the wetlands of Southern Ontario during modern times, many of these remaining, intact wetland habitats are now of high conservation value, and most are

protected from future disturbance; certain southern Ontario wetland and shoreline regions, such as Long Point Provincial Park on the shore of Lake Erie, are currently considered keystone stop over sites for migratory birds, and are thus closely managed (Ross et al. 2012). Considering the contemporary reduction in anthropogenic impacts on key shorebird stop over habitats in southern Ontario, the resistance of these habitats to natural fluctuations of annual climatic events and the consistently high quantity of habitat and resource availability, it is understandable why our tracked juvenile Dunlin were often detected in these regions on the way to their non-breeding sites. Although our data cannot decisively confirm Southeastern Ontario as a vital juvenile Dunlin stop over site on account of our low sample sizes and limited number of study years, we can suggest that significant numbers of young Dunlin may stop over in Southeastern Ontario annually, and in turn, suggest that continued conservation efforts in these sites may be beneficial to Arctic-breeding shorebird populations.

Potential Juvenile Mortality Hotspots and Anomalous Final Detections

We cannot ignore the possibility that the northern coastal area of the Eastern Seaboard where juveniles were frequently last detected was actually a mortality hotspot, and that a disproportionately large number of juveniles may have perished there. Migratory mortality hotspots are common for an array of fauna, and can be defined as any region or point in the continuity of an organism's migration where mortality rates are abnormally high in relation to natural mortality rates throughout the migratory route (Seidler et al. 2018). Particularly busy roadways that intersect animals' typical migratory pathways, for example, have been known to cause significantly high rates of mortality in several species such as Pronghorns (*Antilocapra Americana*) migrating through the Western USA (Seidler et al. 2018), and even Monarch butterflies, which were found to suffer casualties of upwards of 2 million individuals in 2016 and 2017 as a result of vehicle collisions (Kantola et al. 2019). Migratory birds have likewise been documented to die at disproportionately high rates in specific geographic

regions due to certain environmental hazards like fields of electrical lines (Loss et al. 2014), wind farms (Smallwood 2007), large assemblages of structures with large windows (Hager et al. 2008), pesticides (Parsons et al. 2010), and high densities of invasive predatory species (Loss et al. 2013). The northern region of the Eastern Seaboard where many juveniles were last detected may have harbored hidden risks to juvenile survival, and may have in reality been of poorer habitat quality than may be observed upon preliminary inspection. Such is the problem with ecological traps - habitats to which animal populations are initially attracted as a result of biological cues that advertise high habitat quality, however, which also harbor hidden fitness detriments, and may result in high mortality rates (Kristan 2003).

Ecological traps, for example, may be associated with heavy agricultural runoff, which leads to high levels of saturation by pesticides or other contaminates - such ecological traps have been previously illustrated in over 30 avian species (Lopez-Anita et al. 2012). Agricultural sites with large stretched of crop fields for instance, may attract high densities of invertebrates from surrounding habitats due to ample vegetation, to which many insectivorous bird species are in turn drawn (Taft and Haig 2005). Birds then feast on pesticide-laden invertebrate prey, resulting in either sub lethal fitness declines or direct mortality (Lopez-Anita et al. 2012). One family of pesticides commonly used today as insecticides, known as ChE-inhibitors, have been shown to directly induce mortality in several different sandpiper species (Flickinger et al. 1986). Pesticide toxicity is a particularly significant environmental hazard for shorebird populations due to the specificity of habitats on which shorebirds rely for refueling during migration. Nearshore habitats and coastlines (beaches, tidal flats), as well as wetlands are common habitat types that shorebirds, including Dunlin, use as vital stopover sites (Clark et al. 1993), as are flooded agricultural areas (Strum et al. 2010). These kinds of habitats tend to be recipients of heavy pesticide runoff from upland agricultural and forest sites, and/or are directly treated with chemical agents (Flickinger et al. 1986).

An array of commonly used toxic compounds can be found in high levels within the bodies of many common aquatic invertebrates living in North American wetlands, like larval Dipterans and Odonates (Schepker et al. 2020), as well as in common bivalve and crustacean species that inhabit beaches and intertidal zones of the USA (Feldman et al. 2000) - the most significant prey items consumed by shorebirds on non-breeding grounds (Birdlife International 2017). Given their high urban densities, it is possible that the northern section of the Eastern Seaboard in which juvenile Dunlin were frequently last detected receives considerable quantities of pesticide runoff. This is even more likely the case since, unlike Delaware Bay, most of the sites our juveniles were last detected are not commonly regarded as key staging sites for migrating Dunlin, and may therefore not be given high conservation efforts (Burger et al. 1997).

The juvenile tracks that ended in Southern Ontario and on Canada's East Coast are likely to have been terminated early given that these regions are well north of the accepted boundaries of Dunlin non-breeding ranges, and exhibit harsh winter conditions. The average temperatures in Southern Ontario and on Canada's East Coast during the winter months are sufficiently low to significantly impact the thermoregulatory energy costs of even adult Dunlin, and are thus not conducive to survival. The thermoregulatory processes of adult Dunlin account for about 59% of daily energy requirements (Kelly et al. 2002). Dunlin have been found to begin incurring thermostatic energy costs at ambient temperatures of 20°C and below (Kelly et al. 2002) - temperatures far above the seasonal averages of Southeastern Ontario and Canada's East Coast during the winter months (Environment Canada 2019). Despite the fact that basal metabolic rate is strongly positively correlated with body mass in shorebirds, the daily energy expenditures of juvenile Dunlin have previously been shown to be significantly higher than those of adult birds, likely due to the increased metabolic requirements of a longer gastrointestinal tract (Kvist and Lindstrom 2001). Furthermore, low

temperatures and harsh environmental conditions (e.g., wind, rain, snow, etc.) compromise the immune systems of individuals, resulting in increased susceptibility to bacterial and parasitic infection (Kelly et al. 2016).

There are several potential explanations as to why these several juveniles were last detected at such improbable non-breeding sites in Ontario, and likely never reached their true non-breeding grounds. As previously detailed, Southern Ontario may have acted as yet another ecological trap and mortality sink for young birds. Since the 1700's, Southern Ontario has been subjected to centuries of increasingly intensive agricultural and urban processes; more than 64% of its land is currently agricultural (Hanief and Laursen 2019). As a result, this region harbors many pesticide-treated moist-soil agricultural fields to which shorebirds are naturally drawn to refuel during migration, and are thus inadvertently exposed to heavy amounts of pesticides via the consumption of contaminated prey items. The abundant wetland and coastal habitats that characterize southern Ontario are also essential stop over sites during migration, however, are also likely to be heavily contaminated with agricultural run-off and harmful chemicals from nearby farmlands (Sultana et al 2018).

Environmental factors may not be the only reason juvenile Dunlin were last detected at improbable non-breeding sites; intrinsic elements such as inherently suboptimal, age-related navigational inadequacies of juvenile birds may have contributed to the significant numbers of juveniles that failed to reach their appropriate non-breeding sites. Migratory orientation is a complex, multi-dimensional process requiring the coordination of many neural centers in birds' brains (Wiltschko and Wiltschko 2001), and the navigational abilities of immature birds are often underdeveloped relative to those of adults (Rotrics et al. 2016). The underdeveloped spatial orientation functions of young birds have been observed in many species including, but not limited to, Common starlings (*Sturnus vulgaris*; Perdeck et al. 1967), White-crowned sparrows (*Zonotrichia leucophrys*; Thoroup et al. 2007), and

Whooping cranes (*Grus Americana*; Meuller at al. 2013). Juvenile birds may be less able to successfully re-adjust their migratory routes in response to being blown off course by severe storms, as is well-documented in Eurasian Sparrowhawks (*Accipiter nisus;* Mayr 1952), common starlings and Common Chaffinches (*Fringilla coelebs;* Perdeck 1958). Like other taxa, immature shorebirds exhibit suboptimal migratory navigation as well - juvenile Dunlin of the *schinzii* subspecies, which breed in southeastern Greenland, Iceland, the British Isles, Scandinavia and throughout several regions in the Baltics, may take considerably more meandering, south-oriented routes than adults, and often travel longer distances to reach their non-breeding grounds, independent of the effect of wind systems (Grönroos et al. 2012). It is yet unknown whether juvenile *Calidris alpina hudsonia* share these age-related navigational deficits.

Juvenile birds likely also expend proportionally more energy during active flight than older birds during migration. More experienced individuals, regardless of species, tend to use more refined, energy-efficient flight mechanics than do young (Rotrics et al. 2016). For instance, a significant portion of flight activity in young white storks consists of flapping, which burns upwards of 14% more energy than the flight patterns of adults, which incorporate more soaring. Immature individuals of most avian taxa, including shorebirds, possess significantly smaller wing surface areas compared to adults as well, and consequently have poorer capacities to sustain long distance flights, on account of greater energy expenditures, proportional to their body mass, required to travel at sufficient rates during migration (Perez-Tris and Telleria 2001). The relatively subpar navigational abilities of juvenile birds, combined with poorer flight capabilities on account of undeveloped morphological traits, may have influenced the migratory patterns of our juvenile Dunlin, and resulted in the termination of tracks at sites improbable to be true non-breeding spots. The possibility of radio

transmitters detaching from the backs of birds, or batteries failing early is also discussed in more detail below.

Genetic Influence on Juvenile Migratory Patterns

This study suggests a potential genetic influence on the migratory patterns of juvenile Dunlin during their first migrations. Within any given year, the spatial patterns of juveniles' migratory routes were more similar between related individuals than among non-related birds. One brood's route choice stood out in particular - this pair of related Dunlin took a significantly more Eastward route than the other two family groups, and were the only tracked birds, regardless of age, that were ever detected on the East coast of Canada, in Nova Scotia.

A wide variety of avian taxa, from hawks to cranes, migrate from their breeding grounds to their non-breeding sites in mixed-age flocks (Stevenson and Griffith 1946; Elder and Elder 1949; Maransky and Bildstein 2001; Palacin et al. 2011; Rotic et al. 2016). In such cases, it is possible that the routes used by birds undergoing their very first migrations are, at least in part, learned from older conspecifics, since young birds follow adults to the non-breeding grounds and may later recall navigational choices during subsequent migrations (Mueller et al. 2013). In other species, young birds do not travel together with older conspecifics during their first migrations, and therefore cannot learn migratory patterns; route choices may be instead shaped by external factors like weather (Richardson 1985), as well as environmental pressures encountered at key stopover sites, namely predation rates and food availability (Bauer et al. 2010). Migratory route patterns in these species may also be partially intrinsic and hereditary (Henningsson and Karlsson 2009). For instance, in European Blackcaps (*Sylvia atricapilla*), a species in which there exists age-based segregation during autumn migration, breeding experiments that crossed individuals from one population that exhibit Southeastern migratory routes with individuals from another population which use

distinctively Southwestern routes, produced birds that displayed geographically unique migration patterns, intermediate between the route choices of both parental populations (Helbig 1991).

Juvenile Dunlin depart from their natal subarctic territories at different times of the season than do adults, and thus do not have the opportunity to learn migratory routes from older birds (Henningsson and Karlsson 2009). It is possible that, like the routes of juveniles of other species in which adult and young birds do not migrate together, the pathways Dunlin take on their first migrations are predicted by not only external factors, but are also shaped by intrinsic, hereditary elements.

Novel Adult Non-Breeding Areas

We revealed three distinct, noteworthy and potentially novel non-breeding destinations of Canadian-breeding adult Dunlin: one in northern Colombia, another in Indiana, and a third in southern Alaska. A great deal of contemporary data exists on the migratory routes of North American-breeding Dunlin. Subpopulations breeding in the subarctic regions of Canada typically spend the winter along the East coast of the USA and Mexico, while Alaskan-breeding subpopulations migrate to the West coast of the USA to Mexico (Birdlife International 2017; Audubon Society 2019; Fernández et al.). The vast majority of modern records of Dunlin ranges seem to indicate that the absolute southern-most limit of this species' non-breeding range reaches only to areas as far South as the coasts of Mexico's Yucatan Peninsula (Birdlife International 2017; Audubon Society 2019; Fernández et al.). There is no contemporary, conclusive body of evidence supporting the existence of non-breeding Dunlin populations in South American localities. However, our adults that were tagged at staging sites in James Bay and Quebec were frequently last detected in South America. Albeit rarely, vagrancy during migration in adult Dunlin has been recorded, and

some studies have documented Dunlin specimens as far southern Nicaragua and Costa Rica (Wayne et al. 1981). An exceptional vagrant was once documented in French Guiana, and eyewitness sightings of Dunlin have even been made in Ecuador, Peru, Argentina, Venezuela and Paraguay (Fagan and McMullan 2013). Nonetheless, these are relatively rare, isolated phenomenon involving only lone birds.

Considering the immense migratory distance and the massive amounts of energy a subarctic-nesting bird must exert in order to reach sites as far as northern Colombia, spending the non-breeding season in such a region must provide significant biological advantages that compensate for exceptionally arduous journeys (Alerstam et al. 2003). Approximately 27% of Colombia is covered by a diversity of unique, tropical, resource-rich wetland habitats, of which there are a multitude of different types. Upwards of 89 macrohabitats exist within the country's borders, ranging from marine, marsh, coastal, inland, and human-made wetlands (Ricaurte et al. 2019). Given the wide diversity of Colombian ecotypes conducive to Dunlin foraging strategies, as well as the species diversity and biomass of aquatic invertebrates found within them, Dunlin are likely to thrive in northern South America during the non-breeding season. Additionally, Colombia has seen a substantial increase in country-wide conservation efforts in the modern era, focused specifically on managing the country's many ecologically invaluable wetland habitats; environmental policy makers, managers, and scientists have put into motion many pro-conservation policy changes in recent years (Ricaurte et al 2014). The body of research on these vital wetland ecosystems is rapidly expanding, and increasingly more natural areas are registered as protected land (Pinilla 2010; Ruiz et al. 2011; Ricaurte et al. 2014; Ramirez et al 2019). With greater quantities of protected wetland habitats, reductions in pesticide use, and other conservation efforts seen in recent years, northern Colombia has arguably now become a desirable, hospitable non-breeding site for Dunlin populations.

A significant number of adult Dunlin that were tagged in Churchill, exhibited rather unexpected migratory routes after departing from their breeding grounds - these individuals did not travel southbound like most other Dunlin we tracked, but rather flew directly west, across continental Canada, through northern sections of Saskatchewan and Alberta, and eventually stopping in southeastern Alaska. No studies could be found in the current body of literature that help explain the atypical migratory paths we documented; adult Dunlin of the *hudsonia* subspecies have never previously been tracked via any technology from Churchill to Alaska during autumn migration.

Other seemingly anomalous migratory route patterns of *Calidris alpina hudsonia* populations have however, been observed in past studies. Significant portions of adult *hudsonia* from subarctic Canadian breeding populations have been recorded to migrate to and over-winter in a variety of uncommon non-breeding sites, quite far from the well-known, long-established non-breeding grounds of this subspecies. *Hudsonia* individuals have been spotted and verified during the non-breeding season in countries such as Panama, Costa Rica, and Paraguay, for example (Lesterhuis and Clay 2003), whereas considerably large congregations of other closely related subspecies, such as the *Calidris alpina schinzii*, (which historically breed in Greenland and over-winter in southwest Africa) have been occasionally observed spending the non-breeding season in ostensibly abnormal localities as well, namely along the Atlantic coast of the USA (Curry et al. 2003). Although largely speculative, given the genetic and physiological similarities between Dunlin subspecies, our tracked adult Dunlin that were tagged in Churchill may truly have spent the winter season in Alaska, despite this region being an atypical non-breeding destination for *Calidris alpina hudsonia*.

The environmental conditions in high latitude regions during the non-breeding months are often exceedingly harsh. Along the southern coast of Alaska, where several of our adult Dunlin were last detected, the average daily high temperatures from November to March can

reach well below freezing for up to 140 consecutive days (Ruthrauff et al 2013), which means individuals must expend high amounts of energy in order to thermoregulate (Kelly et al. 2002). Nonetheless, shorebird species that spend the non-breeding season in coastal Alaska are able to reach daily energy requirements through behavioral adaptations, like partitioning greater quantities of their daily activity budgets to foraging, physiological changes in digestive organ sizes and pectoral muscle mass, as well as through the meticulous selection of foraging sites that are highest in invertebrate prey densities (Ruthrauff et al. 2018). Although *hudsonia* populations have not been previously observed to over-winter in Alaska, other subspecies have well-documented non-breeding sites in these regions. Significant numbers of Dunlin of the *arcticola* and *pacifica* subspecies over-winter along the southwestern and central coastal areas of the state (Birdlife International 2017; National Audubon Society 2019). Considering the similarities in physiological characteristics (Gates et al. 2013), and the high degree of genetic similarity among Dunlin subspecies (Marthinsen at al. 2007), *hudsonia* individuals are likely also able to tolerate and even thrive in the conditions experienced in coastal Alaska during the winter months, as do *arcticola* and *pacifica* populations.

Despite low winter temperatures, coastal Alaska offers vast high-quality habitats throughout the annual cycle, and the advantages of over-wintering in these regions are clear. The mudflats and coastal meadows of the Yukon-Kuskokwim Delta on the West coast of Alaska, for example, host millions of migrating shorebirds each year due to their ideal foraging habitats and abundance of prey items (Warnock et al. 2013). During spring, daily shorebird number estimates in the Copper-Bering River Delta on the southern coast of Alaska reach well over a million individuals, and the Yakutat Forelands, situated along the eastern Alaskan Gulf, contain some of the most extensive continuous wetland and tidal flat habitats found in the subarctic latitudes of North America (Andres and Browne 1998). Much of Alaska's coastal regions are also currently designated as protected land, and the populations

of many resident species that were once endangered have rebounded in recent years as a result (Womble and Gende 2013). Thus, Dunlin populations spending the winter in these areas may experience relatively lower levels of anthropogenic disturbance than populations over-wintering in unprotected coastal sites in Mexico or the southern USA. Furthermore, over-wintering at higher latitudes also reduces rate of parasitic infection and transmission from individual to individual (Altizer et al. 2011). Such fitness advantages may be enough to sufficiently offset the great energetic costs and associated dangers of migrating from Churchill to Alaska.

Several other adult birds that were tracked from their natal grounds of Churchill shared yet another abnormal final detection site in southern Indiana. Currently, there exists no concrete data that designates Indiana as a non-breeding destination for *hudsonia* populations, nor any other Dunlin subspecies. This region is also upwards of 850 km away from the nearest Atlantic coast. Although some *hudsonia* individuals may occasionally disperse slightly further inland to forage in nearby wetlands, this subspecies has historically been almost exclusively confined to coastal regions like shorelines and tidal flats, during the non-breeding season (Warnock and Gill 1996). Several other Dunlin subspecies, however, have been observed to over-winter in inland regions, far away from coastal habitats. The subspecies *pacifica* for example, frequently spends the winter months in the marshes of Willamette Valley, Oregon, which is approximately 100 kilometers from the Californian coastline (Sanzenbacher et al. 2002). The *arcticola*, *sakhalina*, *kistchinski*, and *actites* Dunlin subspecies typically spend their non-breeding seasons deep within the Yangtze River floodplain, over 900 kilometers away from China's Pacific coast, as well as in the Poyang Hu freshwater wetlands, over 500 kilometers from the closest coastal habitat (Bentzen et al. 2016). Clearly, it is common for many Dunlin subspecies to over-winter in areas far away from the coastal regions that typically define the non-breeding sites used by this species.

The next question that should be asked is whether the landscapes of southern Indiana include adequate expanses of shorebird-specific foraging habitats, sufficient abundances of invertebrate prey, and tolerable winter conditions. Average Indiana temperatures in November rarely drop below -1.1°C and often reach 16°C. The lowest average temperatures during December and in the coldest month of January reach -6.7°C and -9.4°C, respectively (American Weather Atlas 2020). *Arcticola* and *pacifica* Dunlin subspecies that winter in coastal Alaska likely endure much harsher conditions, yet have long-established non-breeding populations in Alaska (Birdlife International 2017; National Audubon Society 2019).

An array of favorable, shorebird-friendly habitats can be found throughout the state of Indiana in proximity to the site at which many adult Dunlin were last detected. In fact, Indiana is widely considered in the ornithological community to be a historically important staging site for many migratory shorebird species, as its lands are decorated not only by rich wetlands and shallow lakes abundant in invertebrate prey, but also by large areas of periodically flooded farmlands, shallow enough for shorebirds to wade through while foraging on aquatic invertebrates (Mast and Dunning 2000). Even in winter months, Indiana's many wetlands host substantial invertebrate biodiversity and biomass beneath their layers of mud and clay. Larval Snow Craneflies (*Chionea scita*), larvae of several species of wingless limoniid flies (genus Chionea) (Jacobus 2014), small but very abundant freshwater isopods (*Lirceus fontinalis*), and common freshwater amphipod species (*Crangonyx forbesi*) are all plentiful year round in the wetland habitats of Indiana (Clifford 1966). Due to the high degree of phenotypic and genetic similarity shared among Dunlin subspecies, the remarkable ability of Dunlin to fine-tune physiological and behavioral mechanisms in response to changes in environmental conditions, Indiana's tolerable winter temperatures, and adequate habitat types as well as the food resources present in Indiana during the winter months, it is at least possible that the few adult

hudsonia birds we tracked did in fact over-winter in central areas of this state, despite not having been previously documented to do so.

Although these findings cannot be used as strong support or even a basis on which to substantiate any new theories about population-level divergences of migratory strategies in Dunlin due to our study's short duration and small sample sizes, we can propose the possibility that *hudsonia* Dunlin, may be remarkably genotypically plastic and highly adaptable to changes in their environment. On account of the geographic diversity of the three unique, novel adult final detection sites mentioned above, it may be possible that a given population of *hudsonia* Dunlin are be capable of diverging into multiple new migratory strategies, in a relatively rapid timeframe. The five adult birds which were last detected in Alaska and the four adults that were last detected in Indiana might belong to two distinct, newly diverging subsets of the *hudsonia* Churchill population. The adults that migrated to Alaska and those that migrated to Indiana may be part of the early stages of a microevolutionary event through which two novel, divergent migratory strategies are emerging, and through which distinct subspecies may eventually arise.

Shorebirds, as a taxon, are theorized to be capable of relatively rapid population-level microevolution events; drastically divergent migratory patterns have been known to emerge in some shorebird populations in less than 100 generations (Piersma 2011). Red Knots, a shorebird within the Scolopacidae family, to which Dunlin also belong, are comprised of six recognized subspecies, whose ranges generally do not share high degrees of overlap with one another, are separated by significant geographical distances, and exhibit distinct migratory patterns (Buehler and Baker 2005). The most recent split between two Red Knot subspecies involves the subspecies *rufa* and *islandica.* While it is thought that most avian subspecies diverge gradually over long periods, the division between *rufa* and *islandica* is theorized to be

a historic rather than pre-historic phenomenon, as this phylogenetic divergence likely developed less than 1000 years ago (Piersma 2011).

Furthermore, the phenotypic traits that differentiate most subspecies of shorebirds from one another generally do not overlap (e.g., length, timing, and direction of migration, as well as certain morphological traits), thus suggesting that the divergence of subspecies in this taxon, and perhaps development of new migratory patterns, likely arises in the form of sudden evolutionary novelties rather than gradual variation, as described by traditional concepts of natural selection (Piersma 2011).

The rate at which large-scale environmental changes are unfolding in the modern era may spur unprecedented rates of adaptation and divergence of migratory behaviours in shorebirds, contributing to the accelerated emergence of novel population-level migratory patterns (Piersma 2011). Considering the potential aforementioned advantages of migrating from Churchill to non-breeding grounds in Alaska (which are further enhanced by warming subarctic temperatures on account of lower thermoregulatory requirements), and the high-quality wetland habitats as well as abundant prey availability found year-round in southern Indiana, it is plausible that these two novel migratory strategies were strongly and quickly selected for in Dunlin populations breeding in subarctic Canada.

However, it is important to emphasize that, due to the absence of any population genetic data, the small sample size of tracked adults, and the fact that individuals were only tracked over the course of one year, evidence for the proposed migratory microevolution hypothesis is not strong, but certainly warrants further research. Only by tracking a significantly greater number of Dunlin from the same breeding population over multiple years, and testing for genetic differentiation between migratory groups, will we be able to determine whether *hudsonia* populations are currently undergoing any microevolutionary divergences in migratory patterns. Regardless, if the novel adult non-breeding sites we

suggest here are valid, future conservation strategies should prioritize both the wetland and estuarine habitats of southern Alaska as well as the inland marsh ecosystems found in Indiana to help reduce population declines of North American Dunlin.

Adult Migratory Hotspots

Our study highlights several migratory hotspots of adult Dunlin during their post-breeding migrations. Adult birds tagged on their Churchill breeding grounds, and birds tracked from stopover sites in Quebec and James Bay, were all frequently detected along the East and Northeast coastal regions of the United States, in a region spanning from New Hampshire to Virginia. Particularly high numbers of detections were recorded in Connecticut and Delaware. In most cases, our adult Dunlin appeared to be staging at these coastal sites along the East coast of the USA, which was evident through the high number of detections per individual at each site as well as the duration birds remained within these vicinities. It is not surprising that such large numbers of our tracked adult Dunlin utilized areas of Delaware Bay as a key stopover site. Delaware Bay is a well-established staging site of utmost importance for a multitude of shorebird species during spring and autumn migrations (Tsipoura and Burger 1999); upwards of 270,000 shorebirds can be counted on any given day during the autumn and spring seasons (Burger et al. 1996). Dunlin are among the most abundant species found in Delaware during both spring and autumn migrations; at peak times of the season, conservative population estimates of Dunlin foraging along the shoreline of Delaware Bay can surpass 11,000 individuals (Clark and Niles 1993). The Bay attracts vast densities of shorebirds not only due to its consistently high abundance of mollusk and annelid prey, but also because of the mass spawning events of Horseshoe crabs (Family Limulidae), the eggs of which are easy to find, are present in vast quantities during the period of time shorebirds are migrating, and are very nutrient dense (Tsipoura and Burger 1999). Many birds that arrive at

Delaware Bay too late into the season and miss the short phenological window of greatest food abundance peaks, often do not accumulate sufficient energy reserves to continue migration and are significantly more likely to die during their journeys (Tsipoura and Burger 1999). Accordingly, Delaware Bay is currently receiving high levels of conservation efforts, not only in terms of minimization of further urban development, but also in regard to increased eco-friendly ecotourism programs, the development of new frameworks for sustainable commercial harvest of Horseshoe crabs, and extensive coastal habitat restoration initiatives (McGowan et al. 2015).

Our adult Dunlin were also detected with high frequency in coastal Virginia, New Jersey, Rhode Island, and Massachusetts, all of which are regions established as important shorebird staging sites by contemporary research. The Western Hemisphere Shorebird Reserve Network, in collaboration with the National Fish and Wildlife Foundation, have identified eleven of the most ecologically important stopover sites for *hudsonia* Dunlin in all of North America (Frenandez et al. 2010). Three of these eleven vital staging sites support exceptionally large numbers of migratory Dunlin during southbound migration and are therefore of especially high conservation value. One such crucial staging region is located in Virginia, in the Chincoteague National Wildlife Refuge, another is the Edwin B. Forsythe National Wildlife Refuge on the coast of New Jersey, and the third is Duxbury Beach, in coastal Massachusetts.

Our results confirm the ecological value of previously identified stopover areas in Delaware Bay and in coastal regions of Virginia, New Jersey, Rhode Island, as well as Massachusetts. These regions offer migrating Dunlin ideal habitat types for foraging as well as high quality and abundant food resources, all of which are critical for sufficient accumulation of energy during migration, and thus for survival (Frenandez et al. 2010).

The Atlantic coast however, also contains some of the USA's most densely populated urban areas, which poses the ever-present threat of coastal habitat alteration (Clark and Niles 2000). The Atlantic as well as is the Pacific sides of the coastal USA are also under constant risk of catastrophic oil spills, and the potential subsequent, inevitable destruction of essential Dunlin habitat (Clark and Niles 2000). Fortunately, many key Dunlin stopover sites along the USA's Atlantic Coast share a high degree of overlap with public land ownership (approximately 60 to 95 percent in most states), which grants conservation authorities significant influence over these regions (Clark and Niles 2000). Although the majority of the aforementioned coastal areas already receive conservation attention, they must be continually and closely managed in order to mitigate future Dunlin population declines.

Limitations of Tracking Migrations Via Radio Telemetry and Solutions

While our research provides important, novel insights into Dunlin migration and further supports established data found in contemporary research, we also bring to light here the many limitations and downfalls of using VHF radio tracking technology for the study of shorebird migrations. The majority of migratory routes of our tagged birds were not successfully recorded during southward migration by the Motus network. A large number of tagged individuals were only detected within the immediate localities in which they were originally tagged (within several kilometers of tagging origin), and significant portions of birds were not detected at all. The possibility of tag failure may also explain certain improbable or anomalous final detection sites of juvenile birds as well as adults (e.g., previously mentioned detections in Canada's East Coast, Southern Ontario, and Alaska). We propose several explanations as to why tracking may have been unsuccessful, and offer several potential improvements for future studies.

The high rate of migratory tracking failure we observed might be in part due to increased susceptibility of individuals to predation during periods of acclimation to radio tags. During these brief windows of adjustment following tag equipment, which are estimated to last roughly three days in several shorebird species, shorebirds may experience the highest rates of predation-related mortality of the breeding season, as has been documented in North American Dunlin populations (Warnock and Warnock 1993). The most significant and morbid effects of tag application may have largely been due to the fact that older transmitter models were significantly heavier, bulkier, arguably less conspicuous, and less aerodynamic than modern versions. However, it is still likely that the application of even modern tag models may cause birds' some level of initial discomfort, resulting in temporary behavioral changes, such as increased preening and altered locomotion, which may ultimately lead to increased predation rates, although to a significantly lesser degree compared to older transmitter designs (Streby et al. 2015).

Tag acclimation periods may be a reason as to why so many individuals that were tagged on the breeding grounds in Churchill, as well as at staging sites in James Bay and Quebec, exhibited numerous detections within their immediate localities, but were never detected outside regions of tagging origin. Juvenile Dunlin are already at a greater risk of predation than adults due to inexperience (Van Den Hout et al. 2008) - naturally higher rates of predation in young birds may have been exacerbated further by the periods of acclimation individuals go through after being equipped with a radio tag, during which birds were easier to locate and hunt. This may help explain the disproportionate numbers of our juveniles that were only detected within the immediate areas in which they were originally tagged, compared with adult birds.

Susceptibility to predation on the breeding grounds decreases as shorebirds age, since individuals become more experienced at foraging and avoiding predation, and also develop

stronger flight skills (Colwell et al. 2007). In future studies that track juvenile Dunlin, radio tags should therefore be equipped at the latest possible stages of birds' physiological development in order to ensure individuals are as least vulnerable to predation as possible, thus minimizing predation-related mortality.

The method we used to attach radio tags may have also played a role in low tracking success. The use of fast-drying adhesives to equip tracking devices onto birds' backs is common and widely accepted due its minimally invasive nature, low cost, and because the gluing of tags is non-permanent, as many avian species undergo annual full body molts and shed tags in the process (Warnock and Takekawa 2003). However, this mode of radio tag application also presents the possibility of adhesive failure and the consequential premature detachment of tags. The mean retention time of glued radio tags likely varies from species to species and even between individuals, but may be as low as 24 hours in some species, as seen in radio tagged Bobolinks (*Dolichonyx oryzivorus*; Diemer et al. 2014).

In response to tag applications, birds often increase the intensity and durations of preening activities, leading to the breakage or complete removal of the devices (Diemer et al. 2014). Retention rates of glued tags have been negatively correlated with increased foraging times in wet habitats; as adhesives are exposed to moisture for longer periods of time and undergo greater amounts of mechanical stress due to birds' physical movements during foraging, tags are more likely to fall off (Loring 2016). Since Dunlin typically allot significant portions of their daily time budgets to foraging at staging sites, and exclusively use aquatic, exceedingly wet habitats, tag adhesive failure may be particularly likely to occur in this species as well as in other shorebirds. We therefore emphasize the importance of using the strongest and most water-resistant glues available to attach radio tags onto the backs of Dunlin. Alternatively, the tracking of Dunlin may prove to be more successful if tags are attached via avian harnesses instead, that are modified to fit the specific morphology of

shorebirds. The continual attachment of a radio tag using this method does not depend on adhesive success as it uses sturdy straps to safely secure tracking devices onto to birds' bodies, and granted that a harness transmitter is of equal or nearly equal weight compared to a Lotek radio transmitter, this newer technology may prove to yield far greater tracking success. (Sanzenbacher et al. 2000).

The completeness of our recorded migratory routes as well as their spatial resolutions greatly depend on the presence and density of Motus radio towers throughout the migratory range of Dunlin, since birds must fly within proximity of a receiver station in order to be detected. Although the Motus network is currently growing and the density of receivers is increasing worldwide, there still remain significant barren areas in the global network of Motus towers, especially in remote locations that are difficult to access (Taylor et al 2017). Furthermore, maximum detection radiuses of towers within which birds must enter in order to be detected, shrink whenever adverse weather conditions occur, such as cloudy skies, dense fog, or heavy precipitation (Taylor et al 2017). Consequently, never-before discovered Dunlin staging sites and unknown non-breeding areas located in exceptionally remote regions, which also frequently experience adverse weather events, might not be documented, despite possibly being important for the conservation of Dunlin populations.

A possible alternative to tracking Dunlin via VHF radio telemetry is satellite technology. The use of satellite-based tracking devices likely yields higher spatial resolution of migratory movements and would likely produce fewer gaps in spatial data, even in the most remote areas, as satellite technology does not depend on the construction of receiver stations on the Earth's surface (Scarpignato et al 2016). Of course, using satellites to track wildlife is a significantly more expensive endeavor, and requires greater degrees of multi-disciplinary work to establish a sufficient detection network, and likely poses greater technical challenges. Nonetheless, the use of satellite technology in wildlife tracking is rapidly

developing, and the increasing miniaturization of GPS devices means smaller and smaller avian species can be tracked, including the smallest of shorebird species (Scarpignato 2016).

Conclusions and Implications

This study is the first to provide an in-depth analysis of the geographic movements of juvenile *Calidris alpina hudsonia* during their first autumn migrations from subarctic regions of Canada to their southern non-breeding grounds - a crucial life history event that is arguably the most difficult and risky endeavor in the life of a Dunlin.

Clear differences in migration strategies between adults and juveniles were observed - juveniles generally over-wintered at higher latitudes than adult conspecifics and were detected frequently in a highly specific northern section of the Eastern Seaboard, where very few adults were last detected. Two critical migratory staging sites used almost exclusively by juvenile birds were also identified within Southern Ontario: Wolfe Island and Long Point Provincial Park. These novel juvenile non-breeding grounds and unique migratory staging sites should be investigated further and likely be given high conservation priority.

A considerable proportion of our tagged juvenile Dunlin exhibited tracks that terminated in seemingly anomalous locations, namely in southern Ontario and Nova Scotia. These two Canadian localities, in which many young birds were last detected, are highly unlikely to support shorebirds throughout the non-breeding season due to harsh winter conditions and low prey densities, and it is probable that the juveniles last detected there all perished. The discovery of these sites of high mortality may provide us the opportunity to investigate a possible mortality hotspots of juvenile Dunlin, and ultimately better understand the reasons why disproportionate numbers of young birds die in such particular areas. Identifying any sources of large-scale Dunlin mortality is undoubtedly essential to prevent, or at the very least, slow down rapid shorebird population declines that are transpiring in the modern era at alarming rates.

Lastly, several novel non-breeding sites of adult Dunlin were discovered, all of which have not yet been established in current literature. The three novel adult non-breeding sites we documented included northern Colombia, Alaska, and Indiana. It may be possible that some subarctic-nesting Dunlin populations are experiencing adaptive shifts in their non-breeding ranges in response to modern environmental changes. Nonetheless, these potentially newly discovered non-breeding regions must be further investigated, as they may prove to be vital sites for shorebird populations.

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Table 1: Sample sizes of adult Dunlin equipped with two different models of Lotek radio telemetry tags at three deployment locations. NTQB-2 tags weigh 0.35 g and have battery lifespans of up to 71 days, while NTQB-3-2 tags weigh 0.67 g and can last up to 170 days.

Site of Tag Deployment				
		Churchill, MB	James Bay, ON	Grand-Ile, QC
Tag Model	NTQB-2	10	0	0
	NTQB-3-2	0	15	5

Table 2: Summary of the total number of Dunlin nests found (n=37), chicks banded (n=83), and juveniles equipped with NTQB-3-2 radio telemetry tags (n=46) per year from 2016 - 2018.

Year	*Dunlin Nests Found Per Year*	*Chicks Banded*	*Juveniles Tagged*	*Proportion of Dunlin Tagged*
2016	15	34	16	0.47
2017	13	38	19	0.50
2018	9	11	11	1.0

Table 3: Summary of deployment and detection dates of successfully tracked tags equipped on juvenile Dunlin (n=11) during the years of 2016 - 2018. Julian date 187 = July 5

Tag ID	*Year of Deploy-ment*	*Deploy-ment Date (Julian)*	*Total Number of Detection Sites*	*Last Detection at Breeding Grounds (Julian)*	*First Detection Outside of Breeding Grounds (Julian)*	*Final Detection (Julian)*
18854	2016	187	1	NA	215	236
18853	2016	187	1	NA	236	279
18852	2016	189	1	NA	249	277
18849	2016	190	2	194	278	278
20845	2017	193	3	210	244	265
20847	2017	193	3	NA	223	7 (2018)
20848	2017	193	3	NA	217	280
14689	2018	191	1	NA	248	248
33138	2018	195	2	NA	201	248
31489	2018	195	2	195	229	16(2019)
31488	2018	195	1	NA	254	259

Table 4: Summary of hatch dates of broods from which juveniles were successfully tracked (n=5) on Southward migration compared to hatch dates of broods from which juveniles were not detected (n=8). Both tracked and untracked birds were equipped with NTQB-3-2 radio telemetry tags. Julian date 175 = June 23.

Brood ID	*Hatch Date (Julian)*	*Year*
Successfully Tracked		
16Dunl02	176	2016
16Dunl03	179	2016
16Dunl09	176	2016
17Dunl06	180	2017
17Dunl101	178	2017
18Dunl101	?	2018
Untracked		
16Dunl12	181	2016
16Dunl103	180	2016
16Dunl104	180	2016
17Dunl01	180	2017
17Dunl02	183	2017
17Dunl05	181	2017
17Dunl09	175	2017
17Dunl10	176	2017

Table 5: Codes of successfully tracked tags deployed in 2016, 2017, and 2018. Birds bearing tags 18854 and 18853 were related (brood A), as were individuals equipped with tags 20845 and 20847 (brood B). Juveniles outfitted with tags 31489 and 31488 belonged to a third family (brood C). Birds bearing tags 18852, 18849, 20848 were not related. Tagged birds marked with asterisks (14689, 33138) belonged to unidentified families, and their genetic relatedness is unknown.

Brood ID	*Brood Label*	*Year Tagged*	*Tag ID(s)*
16Dunl02	A	2016	18854, 18853
16Dunl03		2016	18852
16Dunl09		2016	18849
17Dunl101	B	2017	20845, 20847
17Dunl06		2017	20848
18Dunl101	C	2018	31489, 31488
N/A		2018	14689*
N/A		2018	33138*

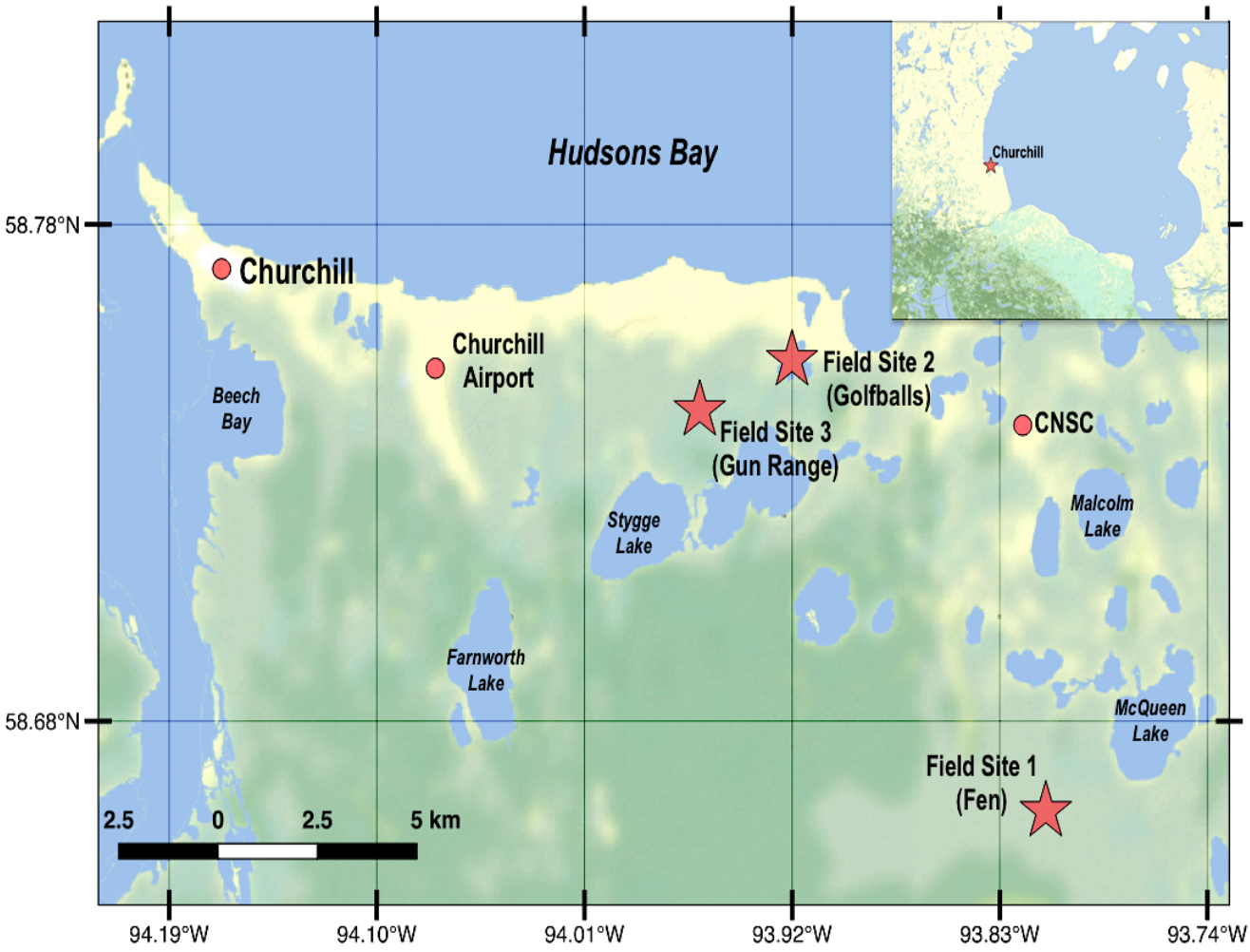


Figure 1: Map of Churchill, MB, and the surrounding area. Depicted are the Churchill Northern Studies Center (CNSC; 58.73°N, 93.81°W) as well as each of the three main study sites where Dunlin nests were found and monitored, and juveniles were equipped with radio telemetry tags: site one (Fen; 58.66°N, 93.81°W), site two (Golf Balls; 58.75°N, 93.92°W), and site three (Gun Range; 58.74°N, 93.96°W).

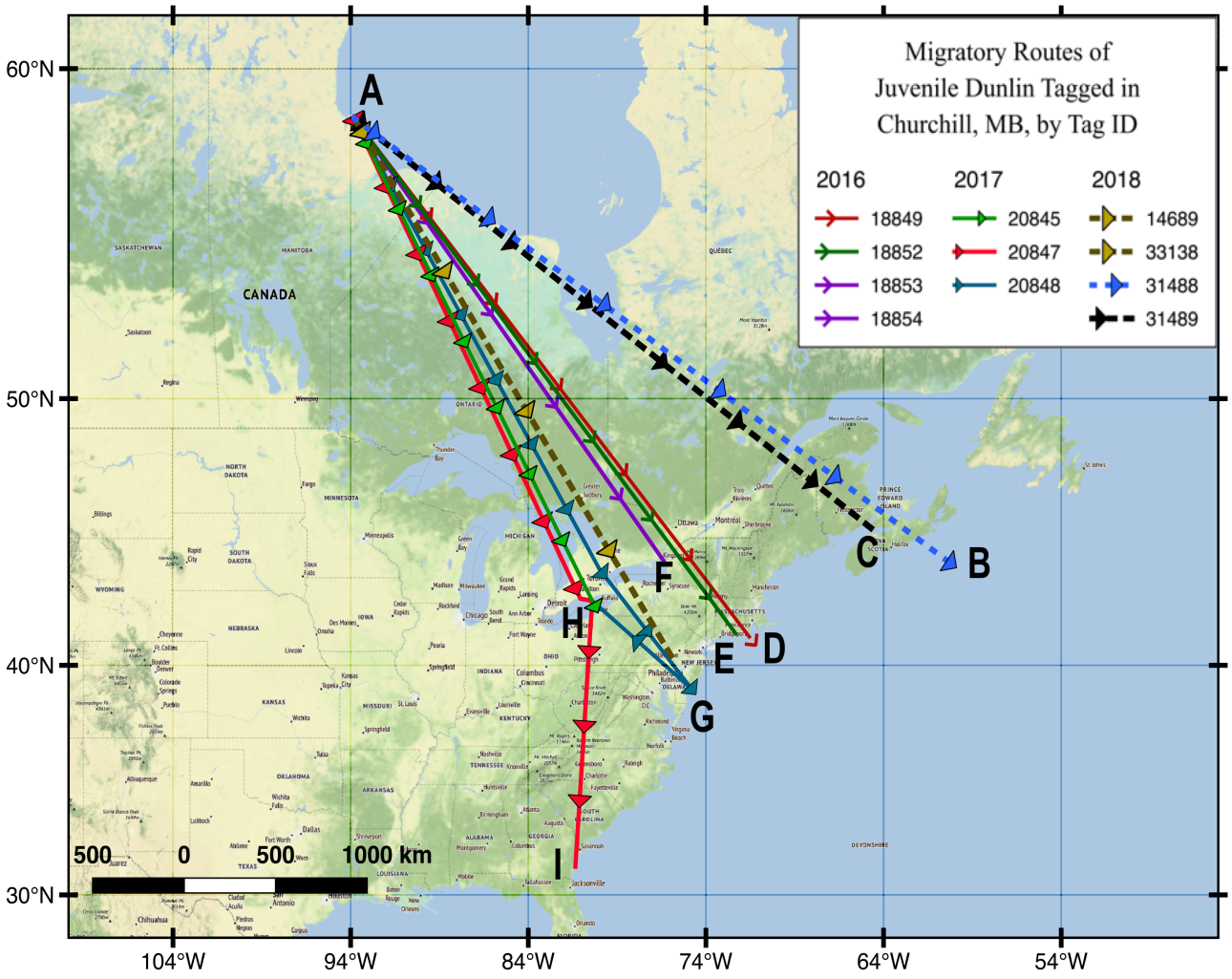


Figure 2: Migratory tracks of eleven juvenile Dunlin equipped with Lotek radio telemetry tags during the summers of 2016, 2017, and 2018. The following detection sites are labeled: Churchill, Manitoba (A; 58.7 °N, 98.3° W), Sable Island, Nova Scotia (B; 43.9 ° N, 59.9° W), Delhaven, Nova Scotia (C; 45.2 °N; 63.4 °W), New Shoreham, Rhode Island (D; 41.1 ° N, 75.1° W), Old Lyme, Connecticut (E; 41.2 ° N, 72.3° W), Wolfe Island, Ontario (F; 44.1 ° N, 76.4° W), Reading, Pennsylvania (G; 40.3 ° N, 79.9° W), Longpoint, Ontario (H; 42.6 ° N, 80.4° W), and St Simon's, Georgia (I; 31.3° N, 81,3° W). Several migratory routes overlap, and thus share the same line pattern. Birds bearing tags 18854 and 18853 both travelled to Wolfe Island, and birds carrying tags 14689 and 33138 were both last detected in Pennsylvania.

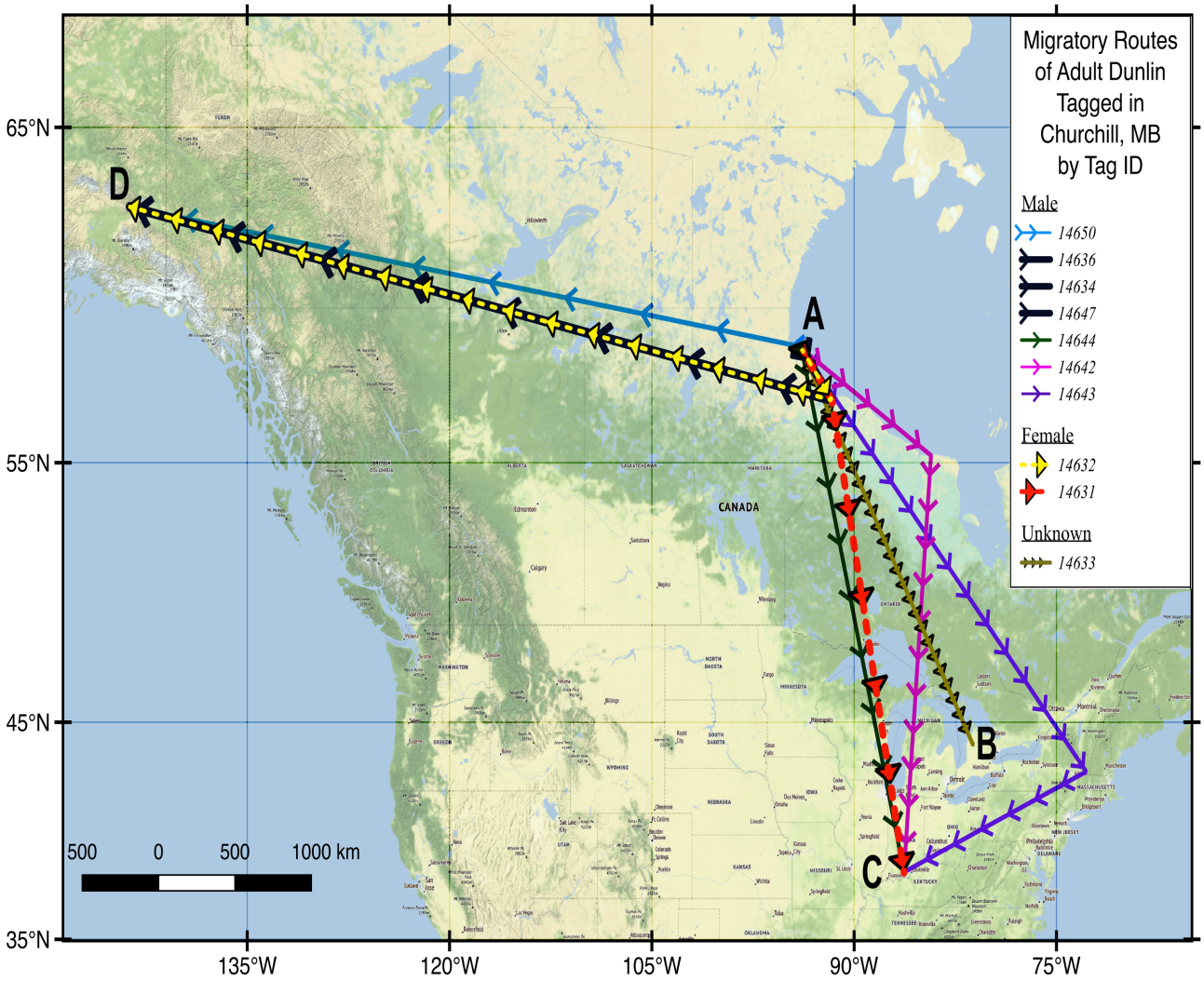


Figure 3: Migratory tracks of ten adult Dunlin equipped with Lotek radio telemetry tags in Churchill, Manitoba during the summer of 2015. The following final detection sites are labeled: Churchill, Manitoba (A; 58.7 °N, 98.3° W), Formosa, Ontario (B; 44.0 °N, 81.2° W), Wyandotte, Indiana (C; 38.3 °N, 86.3° W), Mentasta Lake, Alaska (D; 62.9 °N, 143.7° W). Several migratory routes overlap, and are thus share the same line pattern. Dunlin equipped with tags 14632, 14634, 14636, and 14647 each travelled from Churchill to Nanuk, Manitoba to Mentasta Lake.

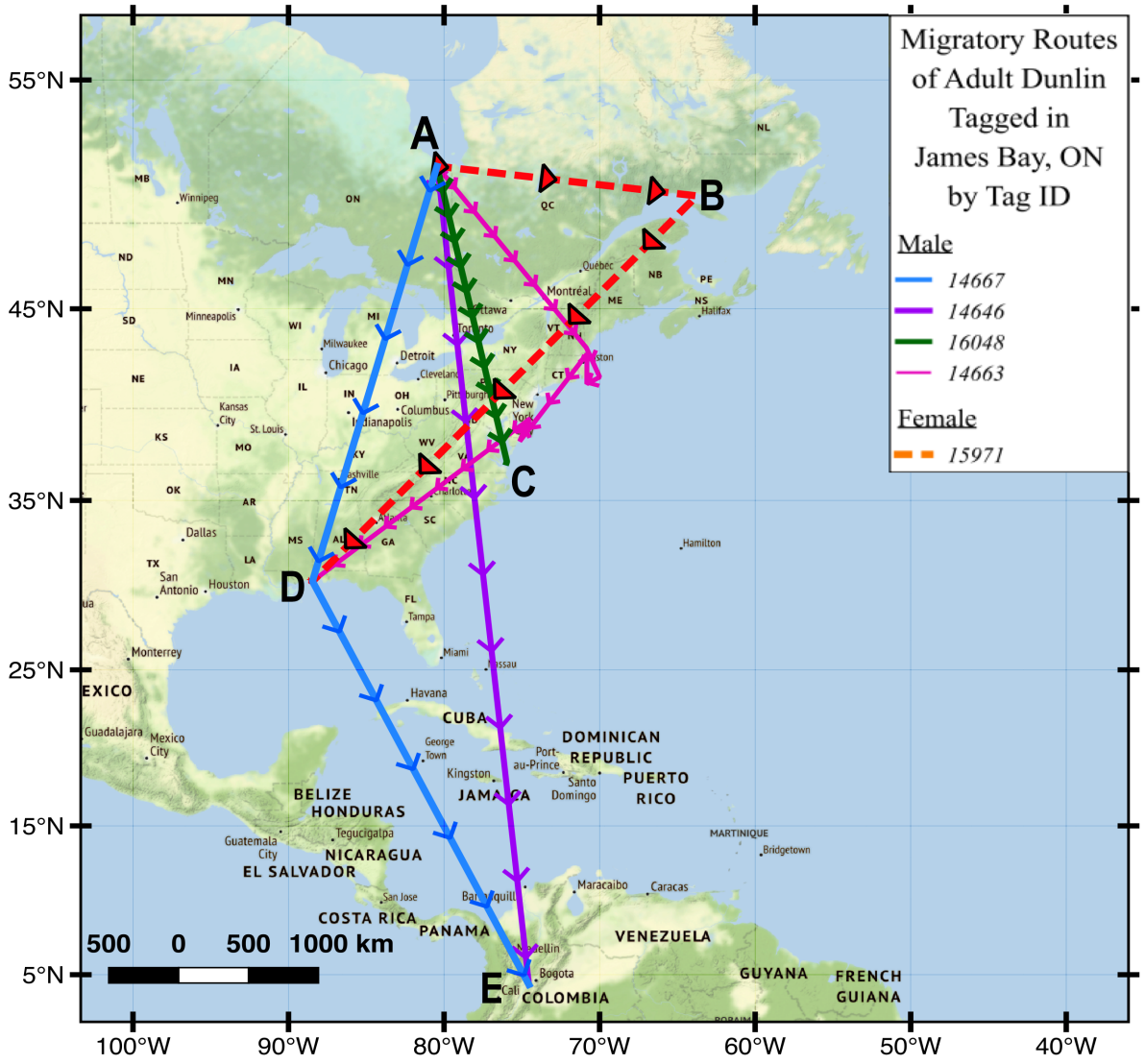


Figure 4: A large-scale image of migratory tracks of adult Dunlin equipped with Lotek radio telemetry tags in James Bay, Ontario in 2014. Of fifteen birds tagged in James Bay, only five are pictured here. Only these individuals exhibited detections Southward of 44°N. The following detection sites are labeled: James Bay, Ontario (A; 51.0 °N, 80,0° W), Grand Ile, Quebec (B; 50.2 °N, 63.9° W), Virginia Beach, Virginia (C; 37.1 °N, 75.9° W), Pascagoula, Mississippi (D; 30.4 °N, 88.5° W), and Cundinamarca, Colombia (E; 4.32 °N, 74.5° W).

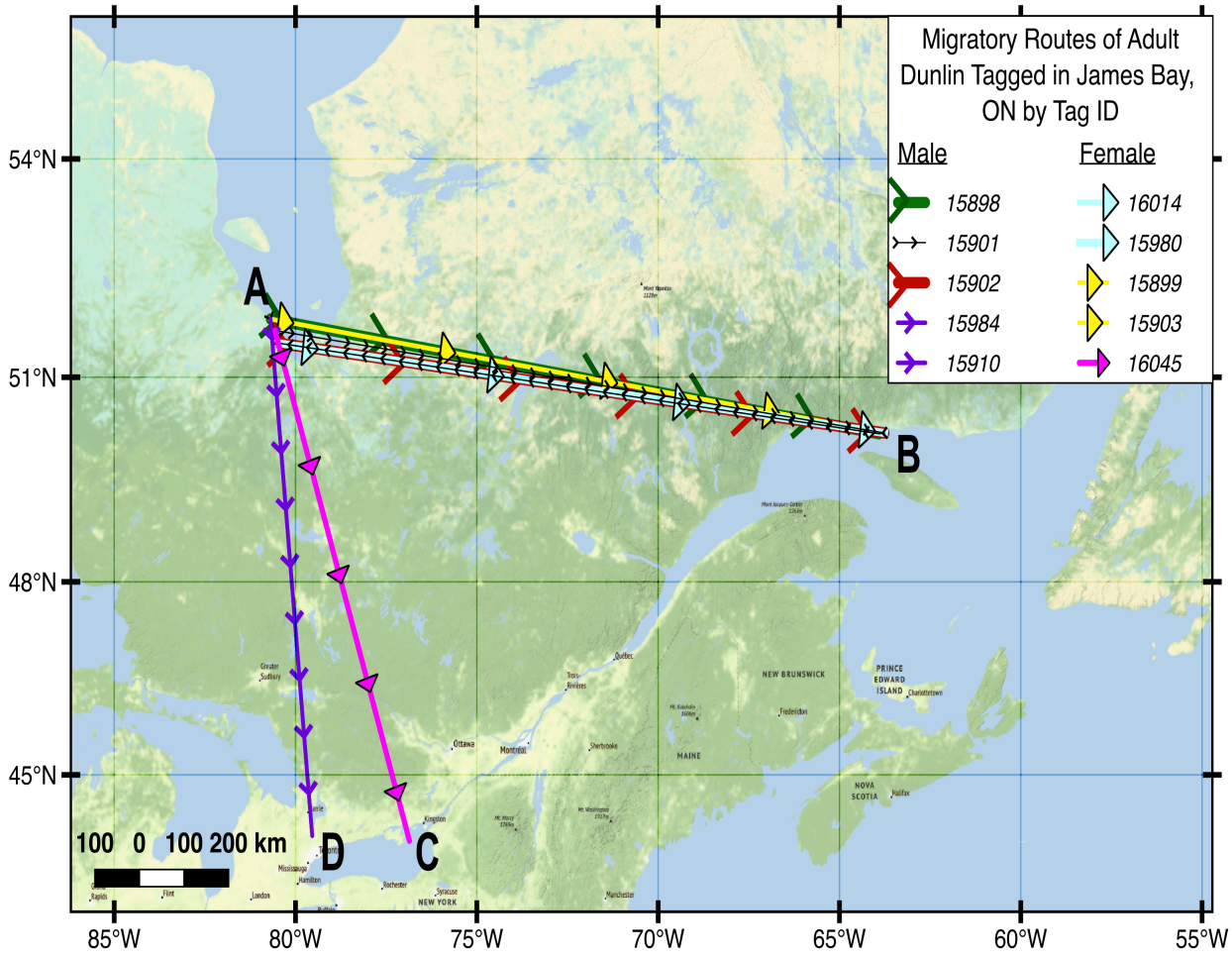


Figure 5: A small-scale image of migratory tracks of adult Dunlin equipped with Lotek radio telemetry tags in James Bay, Ontario in 2014. Of fifteen birds tagged in James Bay, ten are pictured here, as these individuals were not detected farther South than 44°N. The following detection sites are labeled: James Bay, Ontario (A; 51.0 °N, 80,0° W) Grand Ile, Quebec (B; 50.2 °N, 63.9° W), Milford, Ontario (C; 43.9 °N, 76.8° W), Koffler, Ontario (D; 44.0 °N, 79.5° W). Several routes overlap. Birds bearing tags 15903, 15898, 15999 were all tagged at Longridge in James Bay, Ontario and were last detected at Grande-Ile, Quebec. Birds carrying tags 15902, 15980, and 16014 were tagged at North Bluff in James Bay, Ontario, and were last recorded at Niapisakau, Quebec. The bird bearing tag 15901 was tagged at Longridge in James Bay and was last detected at Piskwamish in James Bay. Individuals with tags 15910 and 15984 were tagged in Longridge in James Bay, and shared a final detection site at Koffler, Ontario.

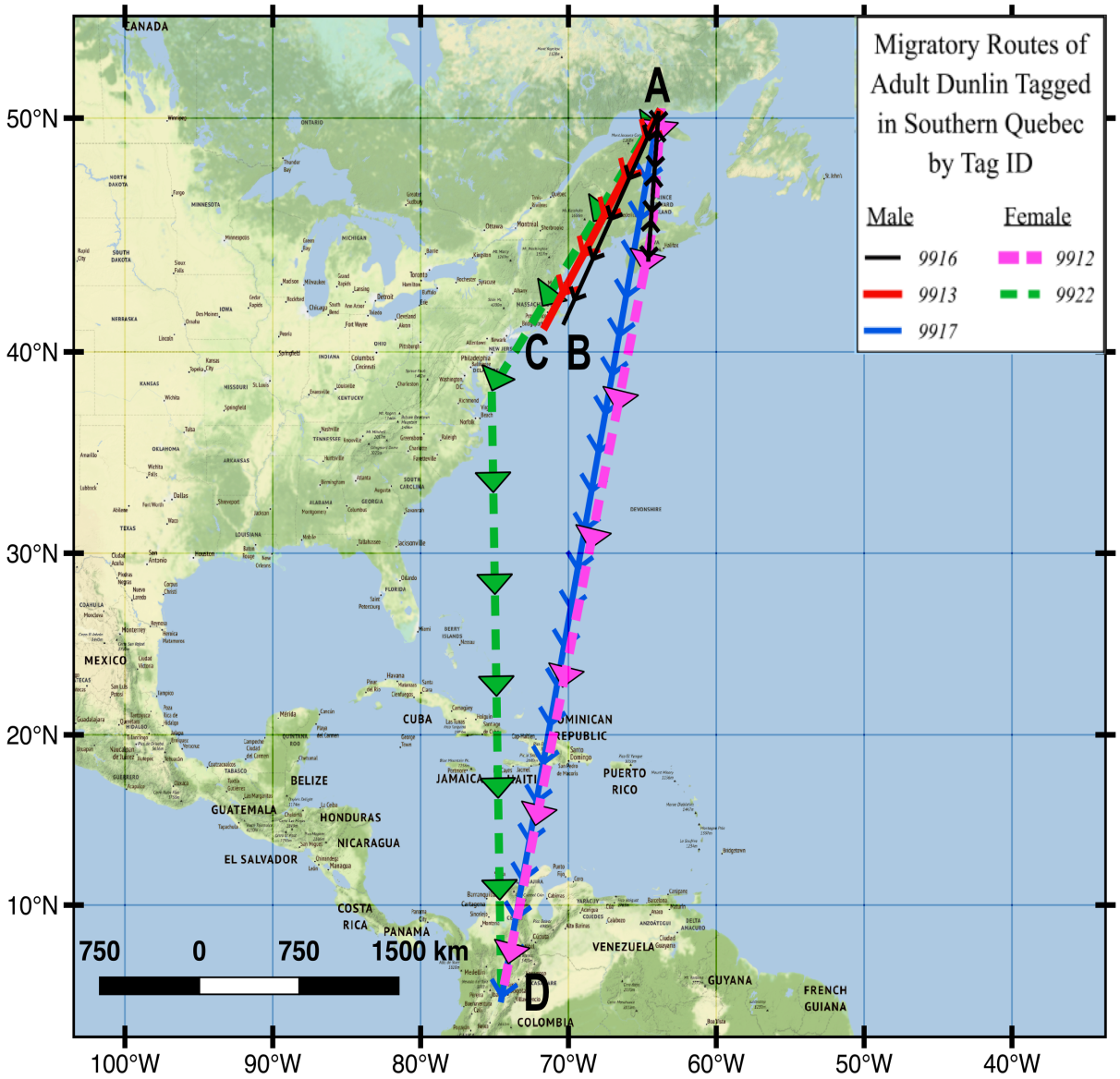


Figure 6: Migratory tracks of five adult Dunlin equipped with Lotek radio telemetry tags in Southern Quebec in 2014. The following final detection sites are labeled: Grand Ile, Quebec (A), Musk, Massachusetts (B), New Shoreham, Rhode Island (C), and Cundinamarca, Colombia (D).

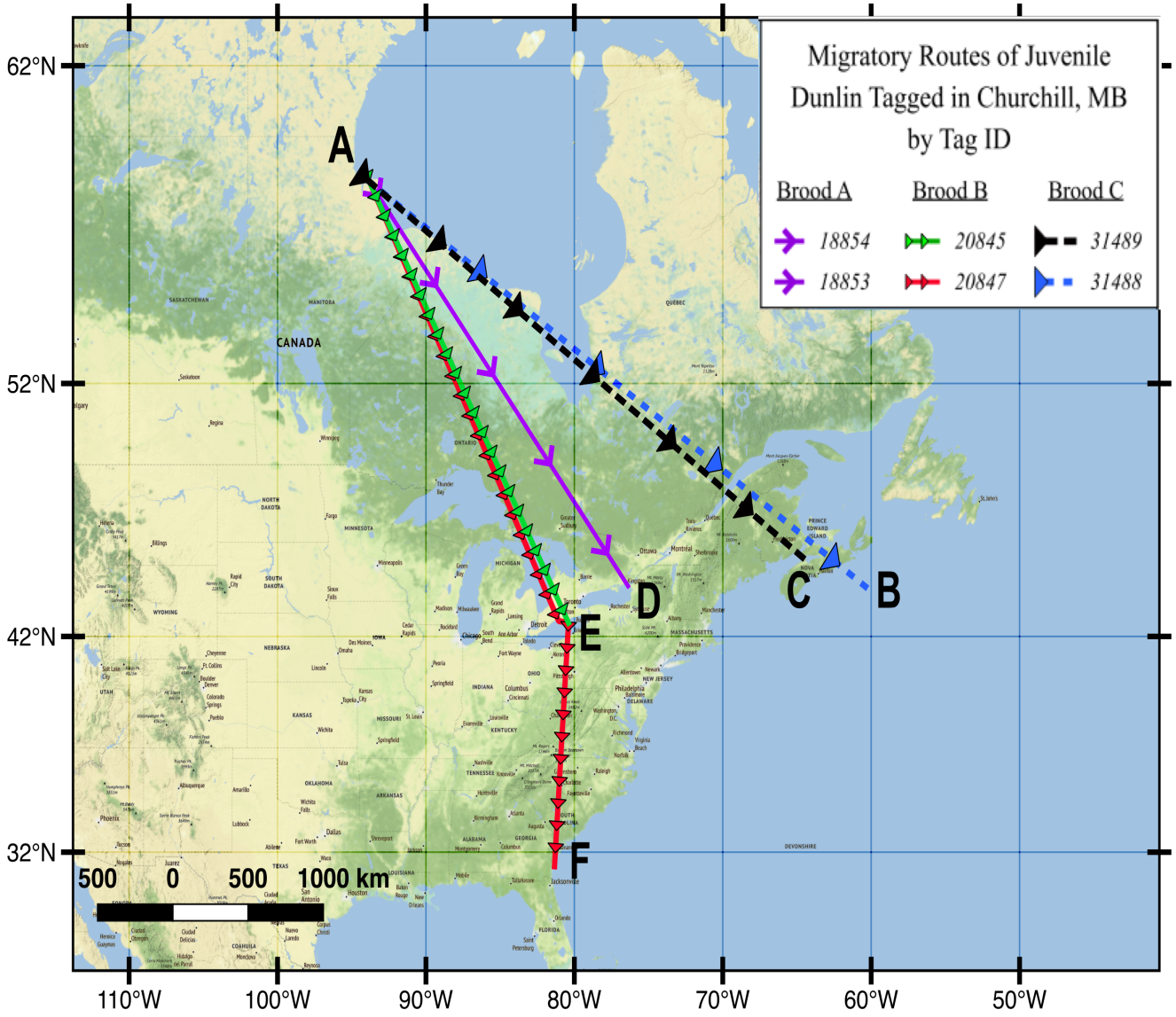


Figure 7: Migratory tracks of six juvenile Dunlin belonging to three different broods, equipped with Lotek radio telemetry tags in Churchill, Manitoba. The following final detection sites are labeled: Churchill (A), Sable Island (B), Delhaven, Nova Scotia (C), Wolfe Island, Ontario (D), Long Point, Ontario (E), and St Simon's, Georgia (F)