USING LIGHT-LEVEL GEOLOCATION TO INVESTIGATE THE CARRY-OVER EFFECTS OF LONG-DISTANCE MIGRATION ON THE REPRODUCTIVE SUCCESS OF DUNLIN (*CALIDRIS ALPINA HUDSONIA*)

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Abstract

Avian migration strategies can have lasting effects on individual fitness in subsequent seasons. These carry-over effects are difficult to study in migratory species because of the geographical separation between breeding and non-breeding sites. I used light-level geolocation to examine, for the first time, how individual spring migration strategy affects reproductive success in a subarctic-nesting shorebird. I showed that female Dunlin (*Calidris alpina*) breeding in Churchill, MB laid eggs of increased volume after migrating longer distances at decreased speeds. Nest survival increased for female Dunlin that migrated longer distances along less direct routes, but the opposite relationship was found for males. There was no evidence for effects of timing of arrival or migration duration on reproductive success. This research highlights the potential fitness consequences of different migration strategies and will be imperative for informing full life-cycle conservation for subarctic-nesting shorebirds.

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Introduction

Migration is a strategy used by animals to take advantage of habitats that are seasonally rich in resources but are undesirable to live in year-round. Migration strategies are diverse, and both interspecific and intraspecific differences occur. Variation may exist in the directness of routes taken, whether all populations within a species are migratory, the distance and duration of the trip, and the motivations behind the seasonal movements (Dingle 1991). The decision to migrate or remain a resident is a critical factor of life history strategy (Stearns 1989).

The primary advantage of migration is moving locations to take advantage of a seasonal fluctuation in resource availability (Fryxell and Sinclair 1988). These increases in seasonal productivity and habitat quality may be beneficial during the breeding season because they can improve an animal's reproductive success (Alerstam et al. 2003). Further, it has been shown that migratory behaviour in fish and ungulates may occur as a form of predator avoidance (Hebblewhite and Merrill 2007, Skov et al. 2013). Migration may be considered worthwhile if the benefits of this long-distance journey outweigh the incurred costs (Alexander 1998).

Despite these advantages, there are also certain risks associated with these seasonal movements. Avian migration is especially risky; mortality rates are highest during migration than any other period throughout the annual cycle (Sillett and Holmes 2002, Lok et al. 2015). This may be explained by dangers encountered along the migratory pathway, including predation, collision with man-made structures, adverse weather patterns and stopping over at areas with scarce food resources, which can lead to starvation (Klaassen et al. 2014). Long-distance flights are physiologically expensive for birds; many experience changes to body condition, increased metabolic rates and increased energy expenditure during migration (Alerstam et al. 2003, Altshuler and Dudley 2006, Akesson and Hedenstrom 2007,

Tulp et al. 2009). Birds breeding in polar locations may experience additional metabolic and thermoregulatory demands following migratory flights due to severe weather conditions that they may encounter upon arrival to the breeding grounds (Fort et al. 2013). In turn, these demands can negatively affect immune defense, making individuals more susceptible to parasite infection and disease (Kelly et al. 2016). Exposure to a range of new environments along the migratory route is challenging because conditions are highly variable and may be unfamiliar from one location to the next.

Carry-over effects of migration

In spring, many shorebirds migrate long distances to arctic breeding grounds to take advantage of increased food availability and decreased predation risk, competition and parasite exposure (McKinnon et al. 2010, Aharon-Rotman et al. 2016). However, the long-distance spring migration of many shorebird species is a physiologically demanding feat (Alerstam et al. 2003, Altshuler and Dudley 2006) that can have residual effects on breeding performance and survival at later stages of the annual cycle (Webster et al. 2002). For example, a shorebird that experiences a more energetically demanding migration (e.g., longer migration) may arrive to the breeding grounds in poorer physical condition, which in turn could negatively affect the energy-intensive processes of reproduction, including breeding performance, egg production and incubation (Tulp et al. 2009, Bulla et al. 2016). Moreover, poor over-wintering habitat quality may cause an individual to delay departure for spring migration, which can then affect timing of arrival to the breeding grounds (Tonra et al. 2011). Similarly, conditions encountered at stopover sites such as availability of food, harsh weather, levels of competition and habitat disturbance are considered to affect fitness in later stages of life (Newton 2006). The duration of these stops is also related to stopover quality, where refueling rates are expedited if birds have access to

increased, better quality resources (Piersma 1987). The different components of migration may have interactive effects on an individual's reproductive timing and success in the following breeding season.

Migration strategies

There are different and sometimes competing goals when animals make behavioural decisions during migration: speed, energy conservation and safety (Alerstam and Lindstrom 1990). Depending on the circumstances, an animal may adjust its migration strategy to encompass all or some of these parameters (Akesson and Hedenstrom 2000). For example, male shorebirds tend to exhibit a time-minimization strategy during the spring, when they will skip over or spend less time at stopover sites to reach breeding grounds earlier, gaining access to the best breeding territories and mates (Farmer and Weins 1999). In contrast, females may depart for spring migration later and spend more time at stopover sites to gain additional energy stores in preparation for reproduction (Farmer and Weins 1999). However, early arrival in the spring is important for both sexes to coordinate breeding with favorable weather conditions. Optimal timing of breeding for arctic-nesting shorebirds occurs after 50% snowmelt, when thermoregulation costs are lower (Smith et al. 2010) and nests are initiated in time for eggs to hatch synchronously with the seasonal increase in food availability (Perrins 1969). Timing of breeding also affects brood quality; larger broods and heavier chicks tend to be produced earlier in the season (Borgmann et al. 2013). Migration strategies that allow for early arrival to the breeding grounds should thus increase reproductive success by allowing for early onset of breeding, when environmental conditions are optimal for egg laying and chick-rearing.

Avian reproductive success

Lifetime reproductive success is defined as the number of offspring an individual successfully rears throughout its lifetime. For birds, the first critical stage of reproductive success is nesting; eggs must survive the incubation period in order for chicks to hatch. Nest survival may be affected by factors such as timing of breeding, predation rates, nest habitat quality, and parental breeding experience (Svensson 1997, Møller 2000, Borgmann et al. 2013, Dunn and Møller 2014, Weithman et al. 2017). Increased egg size is known to positively affect hatching and juvenile survival (Michel et al. 2003); larger eggs retain more heat when adults are disturbed from incubating (Perrins 1996) and provide increased nutrient stores to hatching chicks (Weidinger 1996). Larger eggs give rise to larger chicks, which is especially important in the Arctic, where chick survival depends on early thermoregulatory independence (Schekkerman et al. 2003). As many shorebirds are "income" breeders, they rely on nutrients and energy obtained during reproduction (i.e., after arrival to the breeding grounds) to support egg production rather than energy stores formed prior to reproductive investment (Klassen et al. 2001). Migration strategies that permit early arrival to the breeding grounds (e.g., shorter distance, faster pace, shorter duration) would afford female shorebirds increased refueling time before the onset of energy intensive reproductive activities. It is assumed that these females would exhibit improved body condition prior to egg production and could thus lay larger eggs of increased quality.

Tracking avian migration

Mapping the large-scale movements of avian migrants is a challenging endeavour because most are too small to carry satellite or cellular trackers (Bridge et al. 2011). Before the miniaturization of tracking devices, researchers relied heavily on capture-mark-recapture methods for collecting movement

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data (Bächler et al. 2010). These methods are limiting because they depend on the resighting of previously banded birds at nonbreeding and breeding sites. In the 1960s, weather radar was adapted for ornithological studies, and has been used to predict timing of migration, flight speeds and density of migrants (Gauthreaux and Belser 2003). More recently, very high frequency (VHF) radio-transmitters were made light enough to be carried by songbirds as small as 6 g (Hadley and Betts 2009). However, tracking birds throughout migration remained difficult and was seldom done, as it required researchers holding antennae to follow birds over vast distances and for long periods of time (Wikelski et al. 2003).

Light-level geolocators are tracking devices that use daylight to estimate geographic locations. Light-level geolocation is based on the principle that the timing of sunrise and sunset vary across the globe. Astronomical equations are used to calculate geographical coordinates, where local noon predicts longitude and length of day predicts latitude (Hill and Braun 2001). These devices are archival, so recovery of the tags post-deployment is necessary to offload light-level data that has been measured and stored. The first geolocators designed for large seabirds weighed 28 g (Anderson et al. 1991) and successfully tracked the migration of the Wandering Albatross (*Diomedea exulans*) and Sooty Shearwater (*Ardenna grisea*) (Croxall et al. 2005, Shaffer et al. 2006). The miniaturization of these devices to less than 2 g facilitated their application to small songbirds. Stutchbury et al. (2009) were the first to use geolocators to track songbirds for one full annual cycle. This research laid the foundation for the use of geolocators on other avian taxa, including shorebirds, raptors and waterfowl (Catry et al. 2010, Conklin and Battley 2010, Solovyeva et al. 2014). Geolocators have since revealed extraordinary avian flights, including the longest animal migration ever recorded (Egevang et al. 2010) and a 3-day non-stop flight by a warbler weighing less than 12 g (DeLuca et al. 2015).

The identification of individual migration routes is critical for understanding the population dynamics of migratory bird species because it impacts our ability to identify the nature and extent of

biological carry-over effects. The recent miniaturization of light-level geolocators, VHF radio-transmitters, and archival GPS tags has facilitated the mapping of large-scale movements of small avian migrants. Tracking individual birds from the breeding grounds to non-breeding sites permits us to understand the seasonal interactions of migration and reproduction. Connecting these periods enables us to quantify the biological trade-offs acting throughout the annual cycle.

Research objectives and predictions

To investigate the carry-over effects of spring migration on the breeding success of shorebirds, I used light-level geolocation to track Dunlin (*Calidris alpina hudsonia*) throughout one full annual cycle. The objectives of this study are to identify migratory routes, stopovers and overwintering sites of these Dunlin, and to use these data to determine how individual migration strategies affect reproductive success. Late arriving migrants are predicted to have lower reproductive success, defined by later lay dates, decreased egg volumes (females only), and reduced nest survival, than migrants that arrive to the breeding grounds earlier. I further predict that individuals migrating for a shorter duration (through combinations of increased migration speed, fewer and shorter stationary periods, and shorter distance; which may reduce energetic costs) will have increased reproductive success.

Methodology

Study site

  The study was conducted near the town of Churchill, Manitoba (58° 46' 09" N, 94° 10' 09" W) on the west coast of Hudson Bay. Churchill is located in an eco-zone at the southern limit of subarctic tundra and the northern limit of the boreal forest treeline. Field work was conducted at two sites where Dunlin breeding territory is abundant and easily accessible. The first site (Fen; 58° 40' 03" N, 93° 49' 00" W) was located southwest of the Churchill Northern Studies Centre (CNSC) on a plot bordering Twin Lakes Road, and the second site (Gun Range; 58° 44' 34" N, 93° 57' 59" W) was northwest of the CNSC, and approximately 1 km from road access (Figure 1). The nesting area was characterized primarily by fen, hummock bog and lichen heath habitats.

Figure 1: Map of Churchill, MB with emphasis on the two main field sites where Dunlin nest. Geolocators were attached and removed at both the Fen and Gun Range (GR) breeding territories.

Focal Species

Dunlin are a long-distance migratory shorebird with 11 recognized subspecies (Fernández et al. 2010), most of which breed in the Arctic or Subarctic. Their wintering sites span from the Pacific Coast to the Atlantic Coast in North America, as well as coastal areas in Europe, Asia and Africa (Birdlife International 2017). Dunlin typically form monogamous pair-bonds during the breeding season, although these pairs usually do not remain together throughout the non-breeding season (Van Leeuwen and Jamieson 2018). Dunlin nest on the ground, where nesting habitat is characterised by dry patches of

tundra surrounded by marshy wetland. Females will normally produce one 4-egg clutch per year and both sexes incubate these eggs, although males spend more time caring for offspring post-hatch (Borowik and McLennan 1999). Shorebirds are precocial and as such Dunlin chicks will typically leave the nest 24 hours post-hatch, but still rely on their parents to brood until they gain thermoregulatory independence (Ricklefs and Williams 2003).

Overall, Dunlin population trends are declining, especially in populations from countries surrounding the Baltic Sea due to habitat loss and degradation, as well as reduction in adult survival (Blomqvist et al. 2010). The subspecies studied in this project, *C. a. hudsonia,* is listed as a Shorebird of Conservation Concern, with a population size estimated at 450,000 individuals (U.S. Shorebird Conservation Plan Partnership 2016). The breeding range for this subspecies is from Northwest Territories to Hudson and James Bays in northern Canada and the wintering range is from Massachusetts to Mexico along the Gulf and Atlantic Coasts (Warnock and Gill 1996, Fernández et al. 2010).

Dunlin are an exemplary species to model the effects of migration on reproductive parameters because migration strategies are often variable between individuals. As previously mentioned, male shorebirds tend to exhibit a time-minimization strategy during northwards migration, whereas females may minimize both time and energy by staying longer at high quality stopovers to gain larger energy stores (Farmer and Wiens 1999). Individual differences in body condition and refuelling rates may impact how long an individual remains at nonbreeding sites, and how fast or far an individual can fly (Henkel and Taylor 2015). In addition, *C. a. hudsonia* are well suited to the present study because they exhibit site fidelity across years, which makes recovery of geolocator tags more likely, and because no effects of geolocators on breeding performance or return rates have been identified for this subspecies (Weiser et al. 2016).

Field methods

A population of Dunlin breeding in Churchill, MB was monitored from summer 2010 through summer 2011, and again from summer 2016 through summer 2017. During each of these study periods, nest searching occurred from approximately 5 June to 20 July. Field crews walked the tundra daily until incubating Dunlin were flushed from the nest or observed during distraction displays. After each adult returned to its nest to continue incubation, it was caught with a bownet (Weiser et al. 2016). Morphological measurements of bill, total head and tarsus length were measured to the nearest 0.01mm with digital calipers and the mass of each bird was measured to the nearest gram with a 100 g Pesola spring balance. Dunlin were sexed by discriminant function analysis (Koloski et al. 2016):

$$DF = -0.589 * (head\ length) - 0.096 * (body\ mass) - 0.051 * (tarsus\ length)$$

where individuals with *DF* scores < -44.8 were classified as female and > -43.7 were classified as male. Individuals with scores falling between the cut-off were assigned a sex based on the DF score of their mate (i.e., opposite sex) or classified as unknown when this was not possible. Captured adult Dunlin were equipped with tibia-mounted geolocators in both 2010 (British Antarctic Survey (BAS), model MK12A, BioTrak) and 2016 (Intigeo, model W65A9, Migrate Technology Ltd.). In summers following deployment, nest searching efforts were repeated to locate nests of geolocator equipped birds, and geolocators were recovered from recaptured birds. Clutch initiation dates for nests that were found during laying were determined by counting 1 day backwards for each egg found in the nest cup. Incubation was assumed to commence on the day that the fourth egg was laid, and hatch date was then estimated by counting forward 21.5 days (i.e., *C. alpina* incubation period; Weiser et al. 2017) from the incubation initiation date. If a nest was found during incubation, clutch initiation and hatch dates were estimated using the egg flotation method described by Liebezeit et al. (2007). Egg

length and breadth were measured at the widest point using digital calipers to the nearest 0.1mm. Egg volume was then determined using the geometric mean regression equation:

$$V = K_v * (LB)^2 + 0.1332$$

where *Kv* is the species-specific volume coefficient (K_v for Dunlin is 0.4679), *L* is the egg's length and *B* is the egg's breadth (Governali et al. 2012). Nest locations were recorded by GPS, and further identified by placing wooden tongue depressors 2 m and 5 m from the nest. With the aid of these markers, nests were revisited and monitored every 4 to 5 days until the outcome of a nest (i.e., nest fate) was determined. Field personnel determined that eggs hatched if nestlings were observed in a nest, or if banded adults were encountered with fledglings post-hatch. A nest was considered successful if at least one egg hatched. Nest failure was determined by observing indices of depredation near an empty nest cup (e.g., fox urine or shells with holes and remnants of yolk), or by observing abandoned, cold eggs for 2 consecutive nest checks past the estimated hatch date.

Geolocator analysis

   BAS geolocators recorded light level readings every minute and recorded maximum light measures from these intervals every 2 minutes, and Intigeo devices took readings every minute and recorded maximum light measures every 5 minutes. Data from recovered Intigeo geolocators were offloaded using IntigeoIF software (Migrate Technology Ltd., Coton, Cambridge), and data from BAS geolocators were offloaded in BASTrak (Biotrack Ltd., Wareham, UK). The internal clocks of the geolocators drifted an average of 159 seconds per year. To avoid skewing the estimation of longitude, which depends on comparing time of local noon to this internal clock, this drift was corrected when light-level data were downloaded. I used the *TwGeos* (v.0.0-1, Lisovski 2016) R package to

automatically identify sunrises and sunsets (transitions from light to dark) using a light threshold value

of 1 for Intigeo tags and a threshold of 2.5 for BAS tags. Transitions from light to dark were edited using

an automated process, where twilights occurring 45 minutes before or after the four neighbouring

twilights were considered outliers and removed from analysis. All further geolocator analysis was

completed using the R package *FlightR* (v.0.4.6, Rakhimberdiev and Saveliev 2017).

Accuracy of position estimates using geolocators relies upon the ability to precisely discern

twilight times. The template fit model used in *FlightR* can estimate positions with higher accuracy than

programs which depend on the threshold method because it utilises all available measurements around

twilight (i.e., not simply the exact point when light-levels pass a certain threshold at twilights;

Rakhimberdiev et al. 2016). The template fit model compares recorded light intensities to expected light

intensities at different global positions. In this model, a particle filter algorithm is used to compare the

probability of occurrence in one location compared to another, as well as the probability of traveling

between these inferred locations (Rakhimberdiev et al. 2015). Each particle represents a possible

location, and the particle filter selects the most likely position estimates for each twilight

(Rakhimberdiev et al. 2015). This program further refines position estimates by computing a hidden

Markov chain model, which uses positional information from neighbouring twilights when estimating

current positions (Patterson et al. 2008). When generating these movement models, 1 million particles

were used to optimize reconstruction of a bird's migratory movements (Rakhimberdiev et al. 2016).

Since Dunlin are shorebirds (i.e., do not spend any part of the lifecycle at sea), a spatial-behavioral mask

was also used so that the probability of assigning a stationary position on land was greater than that of a

position over water.

FlightR calibrates geolocator tags by determining the linear relationship between recorded light

levels and expected light levels for a known location. On-bird (in-habitat) calibration was used for the

period when Dunlin were known to be on the breeding grounds directly following incubation and before migration initiation. The function *stationary.migration.summary* was used to differentiate stationary periods from periods when birds were flying. This function also estimates when a bird begins and ends a stationary period. Stationary periods were conservatively defined as periods of non-flight when a bird remained in the same location for at least 2 days, as this increases the probability of identifying stopovers correctly (Schmaljohann et al. 2017). Consecutive stationary periods that were estimated to occur within a 200 km radius of one another were considered the same stopover event and were thus merged (Schmaljohann et al 2017). In such cases, a single point estimate was determined by averaging the latitude and longitude of point estimates for the overlapping stationary periods (Kramer et al. 2017). These stationary periods were then used to describe departures from and arrivals to the breeding grounds and wintering sites, length of stopovers and duration of fall and spring migration. Migration distances were estimated with the function *get_ZI_distances*, which estimates the distance travelled between all consecutive twilights for every day that the geolocator was active. Only distances travelled on days occurring between the start and end of migration, excluding any distance accumulated within defined stationary periods, were considered when calculating total migration distance.

Filtering of outlier positions

An advantage of the package *FlightR* is that error estimates (95% credible intervals) for both latitude and longitude of every stationary position are provided; this allows for easy filtering of reliable positions. Although *FlightR* estimates positions with a higher accuracy than other tools used to analyse geolocators, latitude estimates are still less precise than longitude estimates (Rakhimberdiev et al. 2017). During fall and spring equinox there is almost no latitudinal variation in daylength, which increases the

error associated with latitudes estimated during this period (Knight et al. 2018). To increase the accuracy of my dataset, I excluded all stationary position estimates with latitude credible intervals that fell within the top decile (CI > 8.1 degrees; Figure 2). The reliability of position estimates paired with such a high level of uncertainty is questionable and could lead to misinterpretation of geolocator data; therefore, these positions were treated as outliers and removed from further analysis. In this study, the excluded positions were most often associated with movements arbitrarily north of the breeding grounds, or direct north-south-north movements approximately 2 weeks preceding or following fall and spring equinoxes.
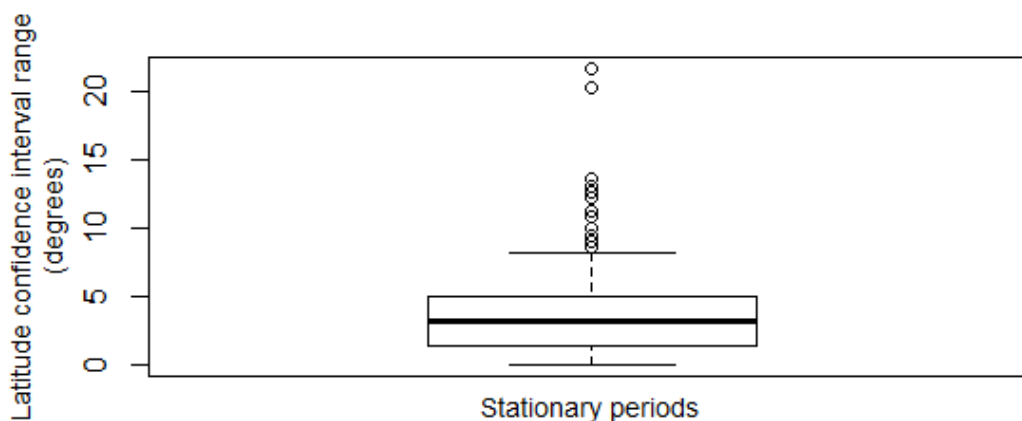
Figure 2: Boxplot of confidence intervals for all latitudes of estimated stationary periods. Whiskers represent 10th and 90th percentiles. Outliers correspond to positions that had a confidence interval outside of the 8.1 degree range. These positions were removed from further analysis.

Determining migration profiles

Light-level data were used to derive details about the non-breeding migratory and stationary periods. Migration initiation dates were identified as the first day that Dunlin took flights of at least 200 km south of the breeding grounds in the fall, or north of the wintering grounds in the spring (Bracey et al. 2018). Similarly, migration was considered complete on the first day that an individual remained

stationary at either the main wintering site in the fall or breeding grounds in the spring. All stationary periods of two or more days occurring during migration were defined as stopover locations. Stopover duration was defined as the total number of days that an individual remained stationary at a single location.

The wintering period was defined as the interval between the end of fall migration and the beginning of spring migration (Bracey et al. 2018). The main non-migratory, non-breeding site was considered as the location where birds remained stationary for the longest period between the "wintering months" of October to April (Hobson et al. 2015). In a few cases ($n = 4$), a second, pre-migratory wintering area was identified for birds that made non-local movements within this interval. These movements were distinguished from the start of spring migration because departure dates from the first wintering site occurred before the average northward migration of the other Dunlin sampled ($\bar{x}_{departure}$ from first wintering site = March 13, $\bar{x}_{departure}$ for spring migration = April 29), and also because these individuals were travelling to locations south of the main wintering site (i.e., moving away, not towards, the breeding grounds).

Fall migration distance was calculated by summing all cumulative tracks occurring outside of stationary periods, on days of travel after departure from the breeding grounds and before arrival to the wintering sites. Spring migration distance was calculated using the same methods, using days of travel after departure from the wintering sites and before arrival to the breeding grounds. Migration duration was defined as the total number of days between migration initiation and migration termination. Travel time was calculated by summing all hours of flight (i.e., total time excluding stationary periods) between migration initiation and termination. Migration speed was then calculated by dividing migration distance by the travel time. Great circle distance (GCD) was measured as the shortest distance along the surface of the earth that links the breeding and non-breeding sites (i.e., straight line distance). Migratory route

directness was then determined by dividing the GCD by the actual distance travelled by an individual

during fall or spring migration (Kramer et al. 2017). Individuals with a score close to 1.0 were

considered to have taken a more direct migratory route than individuals with scores < 1.0 (Kramer et al.

2017).

Statistical analysis

To ensure that spring migration covariates were non-correlated, I ran a principal component

analysis (PCA) to generate a set of synthetic orthogonal variables (Juillet et al. 2012) using the *psych*

package (v.1.8.4, Revelle 2018) in the program R (v. 3.5.1, R Core Team 2018). Spring migration

covariates were obtained from geolocator data, and 13 were included in the PCA: first wintering site

latitude, first wintering site longitude, duration of wintering period, spring migration initiation date,

number of stopovers, mean stopover duration, migration duration, total migration distance, distance

from final stopover to the breeding grounds, travel time, migration speed, directness, and arrival date to

the breeding grounds. For individuals with incomplete migratory tracks, missing values for each variable

were replaced using mean imputation. Axes with eigenvalues greater than 0.9 were retained and varimax

rotation was used to improve biological interpretation (Juillet et al. 2012).

Five rotated components, or factors, were retained from the PCA (Table 1). Migration

covariates with loading values > absolute values of 0.70 were considered to contribute the most to each

factor, and interpretation of the 5 factors was based on combinations of these variables (Juillet et al.

2012). The rotated components were reordered in *psych* based on the amount of variance accounted for.

The first factor (RC1) was considered an index of non-breeding period duration; high RC1 values are

indicative of decreased wintering period duration and earlier departure dates, as well as increased

migration duration and mean stopover duration (Table 1). The second factor (RC4) was considered a

mixed index of arrival date to the breeding grounds, number of stopovers and distance from final

stopover to the breeding grounds: high RC4 values are indicative of later arrival dates, increased number

of stopovers and decreased distance from final stopover to the breeding grounds. The third factor (RC2)

was considered an index of wintering site location; high RC2 values are indicative of a wintering site

that is further northeast. The fourth factor (RC3) was considered an index of migration speed; high RC3

values are indicative of increased travel time and decreased speed. The fifth factor (RC5) was

considered an index of migration distance; high RC5 values are indicative of a migration of longer

distance and less direct route.

To test the main hypotheses regarding effects of migration duration and breeding site arrival on

Dunlin lay dates and mean egg volumes, 28 additive linear models were constructed *a priori* using

different combinations of the 5 rotated components (Table 2). When building these models, I only

considered the most biologically relevant combinations of migration variables known to affect shorebird

reproduction (e.g., Gill et al. 2001, Baker et al. 2004, Gunnarson et al. 2005). Given that many

shorebirds have sex-specific migration strategies (e.g., Kokko et al. 2006, Duijns et al. 2014), models

where migration covariates interacted with sex were also included. Additionally, I tested for the random

effects of nest ID and year. For models that included egg volume as the response variable, only female

Dunlin were included, as male contribution to egg formation was considered negligible. In such cases,

models with interactive effects of sex (models 15 - 28; Table 2) were not tested. Breeding parameter

measurements were only included for years following spring migration (i.e., in years 2011 and 2017).

Model selection occurred in three steps (Zurr et al. 2009). First, the inclusion of random effects

was determined by comparing model scores of the most complex model (model 28 and 28b for the

response variable of lay date and egg volume, respectively) with and without each random effect. If

random effects improved model fit in the first step, they were included in all subsequent models. Linear

mixed effects models with random effects were constructed using the function *lme* and fitted with the Maximum Likelihood (ML) method in the R package *nlme* (v.3.1-137, Pinheiro et al. 2018). When random effects were not included, all subsequent models were built using the function *lm*. Bayesian Information Criterion (BIC) was used to select the top model for mixed effects models, and Akaike's Information Criterion for small sample sizes (AIC_c) to select the top model for fixed effects models. BIC is considered more conservative for use with mixed models because it assigns higher penalty for models with more parameters (Zurr et al. 2009). The model with the lowest BIC/AIC_c score was considered the best fitting model (Burnham and Anderson 2002) to predict variation in Dunlin lay dates or mean egg volumes. Models that were within 2 BIC/AIC_c units (ΔBIC/ ΔAIC_c < 2) of the best fitting model were considered competitive (Burnham and Anderson 2002). Finally, the top model was validated by plotting the spread of residuals against fitted values and normality of residuals was assessed visually, as well as with a Shapiro-Wilks test.

To describe variation in nest survival, I built competing models using the R package *RMark* (v.2.2.5, Laake 2013). Daily nest survival (DSR) is the probability of a nest surviving 1 day of the nesting season. The nesting season was considered to commence the day that the first nest was found and to end on the last day any nest was checked. I considered the earliest (June 10) and latest (July 21) dates between both 2011 and 2017, and thus defined a nesting season of 42 days. Minimally, five pieces of information are needed to create each model: 1) the day of the nesting season on which the nest was found 2) the last day the nest was checked and found to be alive 3) the last day the nest was checked 4) the fate of the nest (0 = successful, 1 = depredated), and 5) number of nests with this nest fate (Dinsmore et al.2002). Individual rotated principal component values and the sex of each bird (Table 2) were also included to estimate how DSR varies with different migration strategies, while accounting for potential migration differences between sexes. The top model was selected using the

Akaike's Information Criterion corrected for a small sample size (AIC_c; Burnham and Anderson 2002) using the same methods described above.

All analyses were conducted using R Statistical Computing Software version 3.5.1 (R Core Team 2018). Sex differences in migration strategies were evaluated using two-sample *t*-tests. Results of all tests were considered statistically significant at an alpha level of 0.05. All methods in this study were reviewed and accepted by the Animal Care Committee of York University.

Table 1: List of migration covariates and their loadings on the 5 rotated components (RC). These axes were interpreted by selecting variables with loadings > absolute values of 0.70, as shown in bold. The last two rows show the proportion of variance and cumulative variance explained by each rotated component, respectively.

Covariate	Loadings				
	RC1	RC4	RC2	RC3	RC5
Migration initiation	**-0.91**	-0.16	-0.04	-0.06	-0.14
Breeding arrival	0.03	**0.81**	-0.05	0.00	0.22
Migration duration	**0.83**	0.40	0.09	0.11	0.23
# stopovers	0.35	**0.80**	-0.11	-0.04	0.26
Mean stopover duration	**0.89**	0.04	0.01	0.18	0.06
Travel time	0.08	0.02	-0.24	**0.91**	0.26
Speed	-0.13	-0.02	-0.08	**-0.95**	0.15
Distance	0.25	0.34	-0.37	0.12	**0.74**
Directness	-0.16	-0.11	-0.23	0.01	**-0.90**
Winter longitude	0.07	-0.13	**0.94**	-0.04	-0.10
Winter latitude	-0.12	-0.04	**0.95**	-0.07	0.14
Winter duration	**-0.87**	-0.13	0.18	0.03	-0.06
Distance final leg	-0.21	**-0.87**	0.07	-0.08	0.07
Proportion explained	0.30	0.21	0.18	0.16	0.15
Cumulative variance	0.26	0.44	0.60	0.74	0.87

Table 2: Complete list of *a priori* models used to explain differences in Dunlin reproductive parameters. Models with interactive or additive effects of sex (15 - 28) were not tested with the response variable of mean egg volume. Model 28b was tested as the fullest model with the response variable of mean egg volume. Note: the explanatory variable of *wintering site latitude and longitude* has been written more simply as *wintering site*.

	Hypotheses	*Candidate model*
1	Null	Intercept
2	Non-breeding duration	Intercept+RC1
3	Wintering site	Intercept+RC2
4	Migration speed	Intercept+RC3
5	Breeding site arrival/ distance last leg of migration/ # stopovers	Intercept+RC4
6	Migration distance	Intercept+RC5
7	Migration distance and wintering site	Intercept+RC5+RC2
8	Migration distance and speed	Intercept+RC5+RC3
9	Migration distance and breeding site arrival/ distance final leg/# stopovers	Intercept+RC5+RC4
10	Migration speed and wintering site	Intercept+RC3+RC2
11	Migration speed and breeding site arrival/ distance final leg/ # stopovers	Intercept+RC3+RC4
12	Wintering site, breeding site arrival/ distance final leg/ # stopovers and migration distance	Intercept+RC2+RC4+RC5
13	Wintering site, breeding site arrival/ distance final leg/# stopovers and migration speed	Intercept+RC2+RC4+RC3
14	Wintering site, breeding site arrival/ distance final leg/ # stopovers and non-breeding duration	Intercept+RC2+RC4+RC1
15	Non-breeding duration variable by sex	Intercept+RC1*sex
16	Wintering site variable by sex	Intercept+RC2*sex
17	Migration speed variable by sex	Intercept+RC3*sex
18	Breeding site arrival/ distance final leg of migration/ # stopovers variable by sex	Intercept+RC4*sex
19	Migration distance variable by sex	Intercept+RC5*sex
20	Migration distance and wintering site variable by sex	Intercept+RC5*sex+RC2*sex
21	Migration distance and speed variable by sex	Intercept+RC5*sex+RC3*sex
22	Migration distance and breeding site arrival/ distance final leg/ # stopovers variable by sex	Intercept+RC5*sex+RC4*sex
23	Migration speed and wintering site variable by sex	Intercept+RC3*sex+RC2*sex
24	Migration speed and breeding site arrival/ distance final leg/ # stopovers variable by sex	Intercept+RC3*sex+RC4*sex
25	Wintering site, breeding site arrival/ distance final leg/# stopovers and migration distance variable by sex	Intercept+RC2*sex+RC4*sex +RC5*sex

Table 2 continued

	Hypotheses	Candidate model
26	Wintering site, breeding site arrival/ distance final leg/ # stopovers and migration speed variable by sex	Intercept+RC2*sex+RC4* sex+RC3*sex
27	Wintering site, breeding site arrival/ distance final leg/ # stopovers and non-breeding duration variable by sex	Intercept+RC2*sex+RC4* sex+RC1*sex
28	All variables, variable by sex	Intercept+RC1*sex+RC2* sex+RC3*sex+RC4*sex+ RC5*sex
28b	All variables, no interaction of sex	Intercept+RC1+RC2 +RC3+RC4+RC5

RC1= Index of non-breeding duration
RC2= Index of wintering site location
RC3= Index of migration speed
RC4=Index of # stopovers, arrival to breeding and distance of the final leg of migration
RC5= Index of migration distance
 * indicates an interactive effect
 + indicates an additive effect

Results

Geolocator recovery

Thirty-five geolocators were deployed in 2010 and 17 of these geolocators were recovered in 2011. Of the 30 geolocators deployed in 2016, 10 were recovered in 2017. These recaptures resulted in device recovery rates of 49% in 2011 and 33% in 2017. One unit recovered in 2017 was corroded and suffered penetrative damage, such that no light-level data could be salvaged. In this same year, one individual carrying a geolocator was resighted but could not be recaptured. Of the 26 geolocators that captured usable data, 15 were carried by females and 11 were carried by males. Nine devices stopped collecting data sometime before they could be recovered. In total, I retrieved data for 26 breeding ground departure dates, 25 fall migrations, 22 wintering periods and 17 spring migrations.

Migration patterns and timing

Dunlin breeding in Churchill departed for fall migration between July 7 and October 23 and arrived at wintering areas between October 8 and December 28 (Table 3). The mean length of fall migration was 69 ± 8.52 days (range: 4 - 142 days; $n = 25$) and was 62% longer than spring migration ($\bar{x} = 26 \pm 5.25$; range: 3 - 75 days; $n = 17$). On average, Dunlin used 1.44 ± 0.13 stopover sites and spent 48 ± 6 days refueling at these sites on their southward migration (Table 3). James Bay and the adjacent southwest coast of Hudson Bay were identified as important (i.e., commonly used) stopover areas for Dunlin during both fall and spring migration (Figure 3). Percentages of migrating individuals that stopped in this area were 96% in the fall, and 47% in the spring. The individual with the longest fall migration flew 4812 km before arriving at a wintering site in Florida, compared to the shortest migration of 2328 km to a site in New York ($\bar{x} = 3457 \pm 145.6$ km; $n = 25$).

Dunlin spent the wintering season at sites along the Atlantic Coast ranging from New York to Florida, and along the Gulf of Mexico ranging from Mississippi to Mexico (Figure 3). The most frequented wintering locations were in Texas, Maryland and North Carolina. The percentages of Dunlin that remained stationary at these sites were 20%, 12% and 12%, respectively (Table 4). The mean number of days spent at wintering sites was 177 ± 6.32 (range: 114 - 220; $n = 22$). Four birds made non-local, southward movements in February and March and took prolonged stops ($\bar{x} = 41$ days) at second wintering locations in the Bahamas, Cuba, and Mexico.

Dunlin initiated spring migration between March 18 and May 25 ($\bar{x} =$ April 29 ± 5.32; $n = 22$) and arrived back to the breeding grounds between May 24 and June 3 ($\bar{x} =$ May 29 ± 0.73; $n = 17$). The average length of spring migration was 26 ± 5.25 days, 15 ± 3.13 of which were spent stationary at stopover sites (Table 3). Dunlin tended to migrate along the boundary of the Mississippi and Atlantic flyways (Figure 4) when overwintering at sites bordering the Atlantic Ocean (Table 4; Figure 5). Many of the birds overwintering in Texas migrated through the centre of the Mississippi flyway on their southbound migration, and then migrated along the eastern boundary of the Central flyway on their return journey (Table 4; Figure 5). Eighty-three percent of all individuals that flew through the Central flyway ($n = 6$) stopped over in North or South Dakota. The average distance travelled during spring migration was 3551 ± 146.3 km (range: 2619 – 4812 km; $n = 17$).

Table 3: Summary of non-breeding stationary periods and fall and spring migration characteristics of 26 Dunlin from a breeding population in Churchill, MB. Values were derived from geolocator data and represent means over years 2010-2011 and 2016-2017. Data is only included from geolocators that successfully captured entire tracks for either fall or spring migration. Parameter terms are further defined in the text of methodology.

Parameter	*Fall*			*Spring*			*Non-breeding, non-migratory*		
	Mean ± SE	Range	*n*	Mean ± SE	Range	*n*	Mean ± SE	Range	*n*
Migration initiation date	August 26 ± 7.08	July 7 – October 23	26	April 29 ± 5.32	March 18- May 25	22	-	-	-
Migration end date	November 3 ± 3.16	October 8 - December 28	25	May 29 ± 0.73	May 24 - June 3	17	-	-	-
Wintering duration (days)	-	-	-	-	-	-	177 ± 6.32	114 - 220	22
Migration duration (days)	69 ± 8.52	4 - 142	25	26 ± 5.25	3 - 75	17	-	-	-
Number of stopovers	1.44 ± 0.13	1 - 3	25	1.0 ± 0.21	1 - 3	17	-	-	-
Stopover duration (days)	48 ± 6.82	3 - 112	25	15 ± 3.13	3 - 63	17	-	-	-
Travel time (days)	4.86 ± 0.38	2.08 - 8.5	25	4.13 ± 0.35	1.58 – 7.0	17	-	-	-
Migration speed (km/day)	786 ± 50.6	352 - 1994	25	936 ± 95.4	528 - 2136	17	-	-	-
Migration distance (km)	3457 ± 145.6	2328 - 4810	25	3551 ± 146.3	2619 - 4812	17	-	-	-
GCD (km)	2878 ± 87.0	2084 - 3594	25	3049 ± 119.6	2273 - 4676	25	-	-	-
Migration directness	0.848 ± 0.02	0.623 - 1.0	25	0.853 ± 0.03	0.491 - 1.0	17	-	-	-

Table 4: Details about the migratory routes of Dunlin flying to and from breeding grounds in Churchill, MB. Wintering areas are arranged in order of descending latitudes (north to south). "NA" was used in instances where a migratory track was not captured in its entirety, and information is missing in these cases. Locations of migratory tracks are described using the boundaries of North American flyways (see Figure 4 for map of flyway locations).

		Fall migration			Non-breeding, non-migratory		Spring migration		
Bird ID	Sex	Migration initiation date (Julian)	Stopovers (#)	Migration route (flyway location)	Wintering area (longitude, latitude; DD)	2nd wintering area (longitude, latitude; DD)	Migration initiation date (Julian)	Stopovers (#)	Migration route (flyway location)
650	F	265	1	Border of Mississippi/ Atlantic flyway	New York (-75.73, 43.37)	-	100	2	Border of Mississippi/ Atlantic flyway
653	F	289	1	Border of Mississippi/ Atlantic flyway	Pennsylvania (-77.12, 41.25)	-	NA	NA	NA
658	F	291	1	Border of Mississippi/ Atlantic flyway	Pennsylvania (-76.57, 40.74)	The Bahamas (-76.93, 26.55)	98	NA	NA
347	M	287	1	Border of Mississippi/ Atlantic flyway	New Jersey (-74.4, 39.6)	-	145	0	Border of Mississippi/ Atlantic flyway
332	F	210	1	Border of Mississippi/ Atlantic flyway	Delaware (-75.67, 39.5)	-	141	1	Border of Mississippi/ Atlantic flyway
676	M	188	1	Centre of Mississippi/ Centre of Atlantic flyway	Maryland (-76.21, 39.43)	-	NA	NA	NA

Table 4 continued

Bird ID	Sex	Migration initiation date (Julian)	Stopovers (#)	Migration route (flyway location)	Wintering area (longitude, latitude; DD)	2nd wintering area (longitude, latitude; DD)	Migration initiation date (Julian)	Stopovers (#)	Migration route (flyway location)
		Fall migration			*Non-breeding, non-migratory*		*Spring migration*		
438	F	264	1	Border of Mississippi/ Atlantic flyway	Maryland (-75.55, 38.25)	-	142	0	Border of Mississippi/ Atlantic flyway
341	F	204	1	Border of Mississippi/ Atlantic flyway	Maryland (-75.45, 38.25)	-	141	1	Centre/Eastern border of Mississippi flyway
661	M	237	2	Border of Mississippi/ Atlantic flyway	North Carolina (-78.36, 36.49)	The Bahamas (-78.2, 24.75)	116	2	Border of Mississippi/ Atlantic flyway
668	F	266	1	Centre of Mississippi/ Western border of Atlantic flyway	North Carolina (-78.05, 35.73)	-	139	1	Border of Mississippi/ Atlantic flyway
666	M	256	1	Border of Mississippi/ Atlantic flyway	North Carolina (-79.43, 34.83)	-	77	3	Border of Mississippi/ Atlantic flyway
647	F	296	2	Centre of Mississippi flyway	Arkansas (-91.73, 34.50)	-	145	1	Centre of Mississippi flyway
337	F	266	1	Centre of Mississippi flyway	South Carolina (-80.48, 33.97)	-	92	1	Border of Mississippi/ Atlantic flyway
674	M	192	3	Border of Mississippi/ Atlantic flyway	Mississippi (-90.89, 33)	-	80	NA	NA
652	M	192	2	Centre of Mississippi flyway	Louisiana (-92.87, 31.2)	-	128	2	Eastern border of Central flyway

Table 4 continued

		Fall migration			Non-breeding, non-migratory		Spring migration		
Bird ID	Sex	Migration initiation date (Julian)	Stopovers (#)	Migration route (flyway location)	Wintering area (longitude, latitude; DD)	2nd wintering area (longitude, latitude; DD)	Migration initiation date (Julian)	Stopovers (#)	Migration route (flyway location)
663	M	242	1	Centre of Mississippi flyway	Louisiana (-90.39, 31)	-	129	2	Eastern border of Central flyway
662	F	208	2	Border of Mississippi/Atlantic flyway	Mississippi (-89.46, 31)	-	94	2	Border of Mississippi/ Atlantic flyway
659	F	217	2	Centre of Mississippi flyway	Texas (-96.55, 30.6)	-	119	3	Centre/Eastern border of Mississippi flyway
306	F	272	1	Centre of Mississippi flyway	Texas (-94.45, 30.51)	-	130	1	Eastern border of Central flyway
342	M	189	2	Centre of Mississippi flyway	Texas (-95.97, 29.25)	-	122	1	Eastern border of Central flyway
651	F	257	2	Border of Mississippi/Atlantic flyway	Florida (-81.7, 29.25)	-	111	NA	NA
675	F	245	3	Centre of Mississippi flyway	Texas (-97.1, 28.9)	Mexico (-97.39, 21.9)	NA	NA	NA
656	F	209	1	Border of Mississippi/Atlantic flyway	Florida (-82.09, 27.72)	Cuba (-82.74, 21.6)	93	NA	NA
400	M	200	1	Centre of Mississippi flyway	Texas (-97.36, 26.55)	-	130	1	Eastern border of Central flyway
333	M	198	1	Centre of Mississippi flyway	Mexico (-97.65, 24.75)	-	135	1	Eastern border of Central flyway
670	M	247	NA	NA	NA	NA	NA	NA	NA
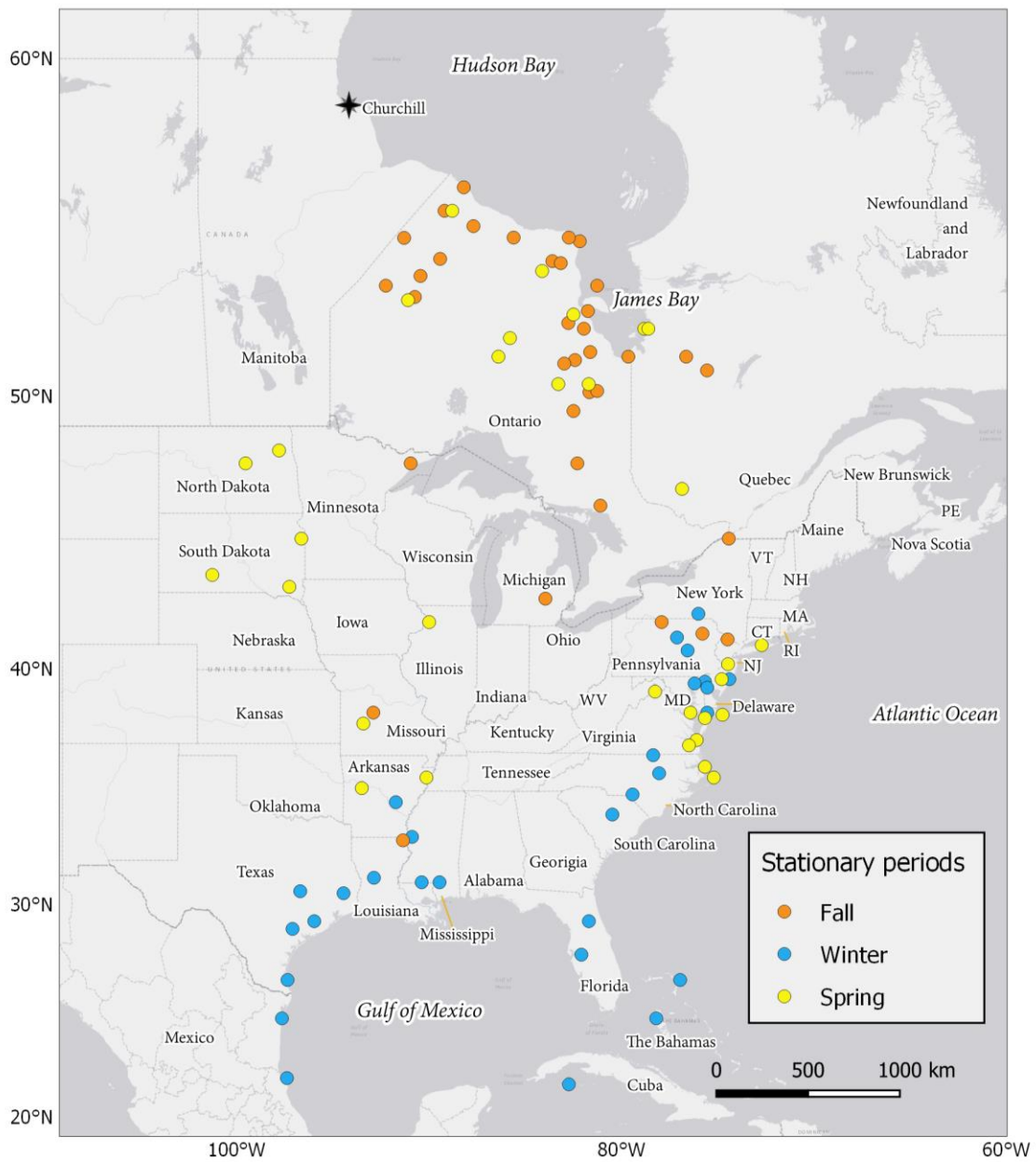
Figure 3: Map of non-breeding stationary positions of Dunlin (*n* = 26) migrating to and from Churchill, MB during the years 2010 - 2011, and 2016 - 2017.
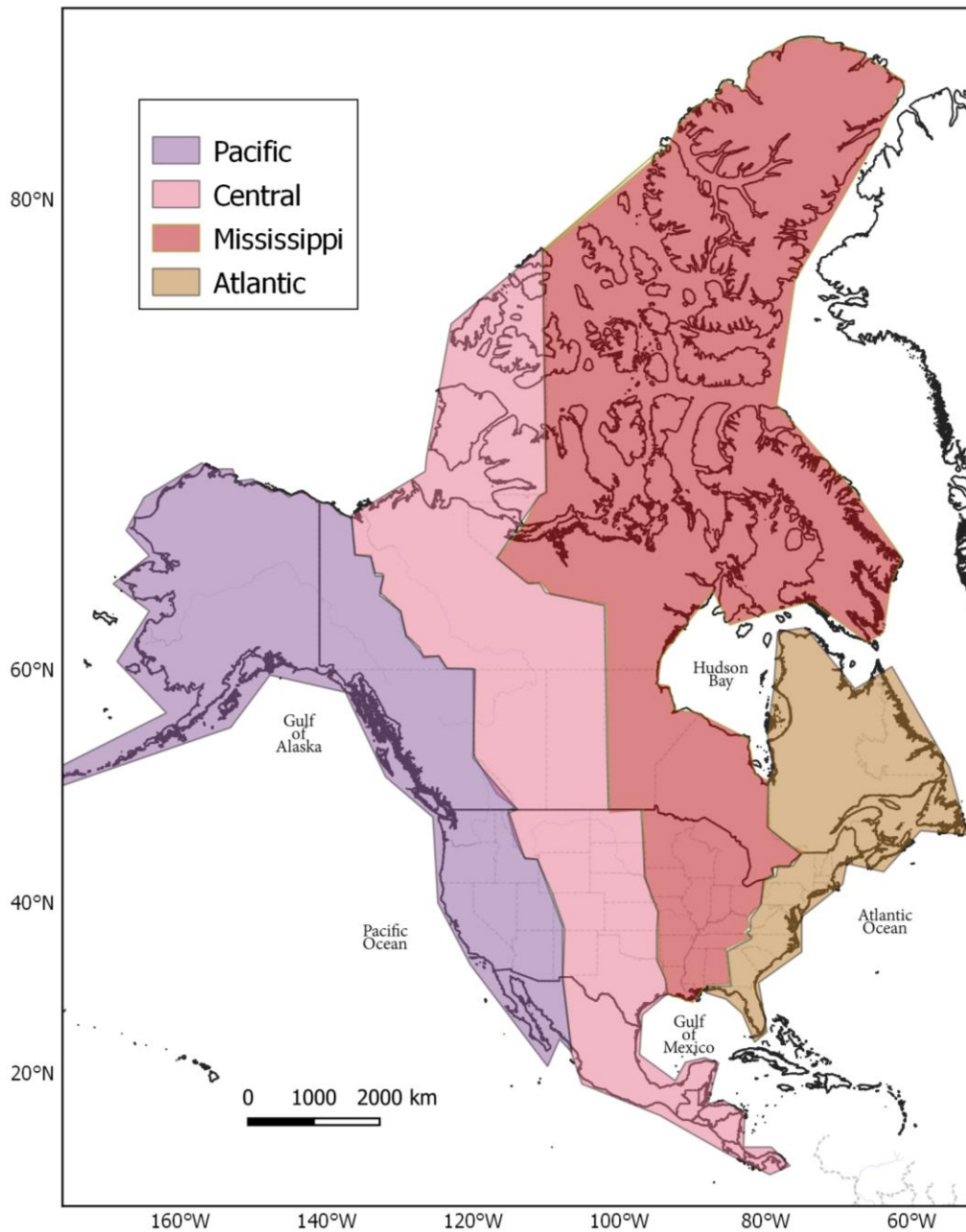
Figure 4: Map of North American flyways (i.e., pathways that birds commonly take while migrating). North American flyways were used to categorize and describe the migratory routes taken by the Dunlin in this study. Flyway boundaries interpreted from U.S. Fish & Wildlife Service (2018).
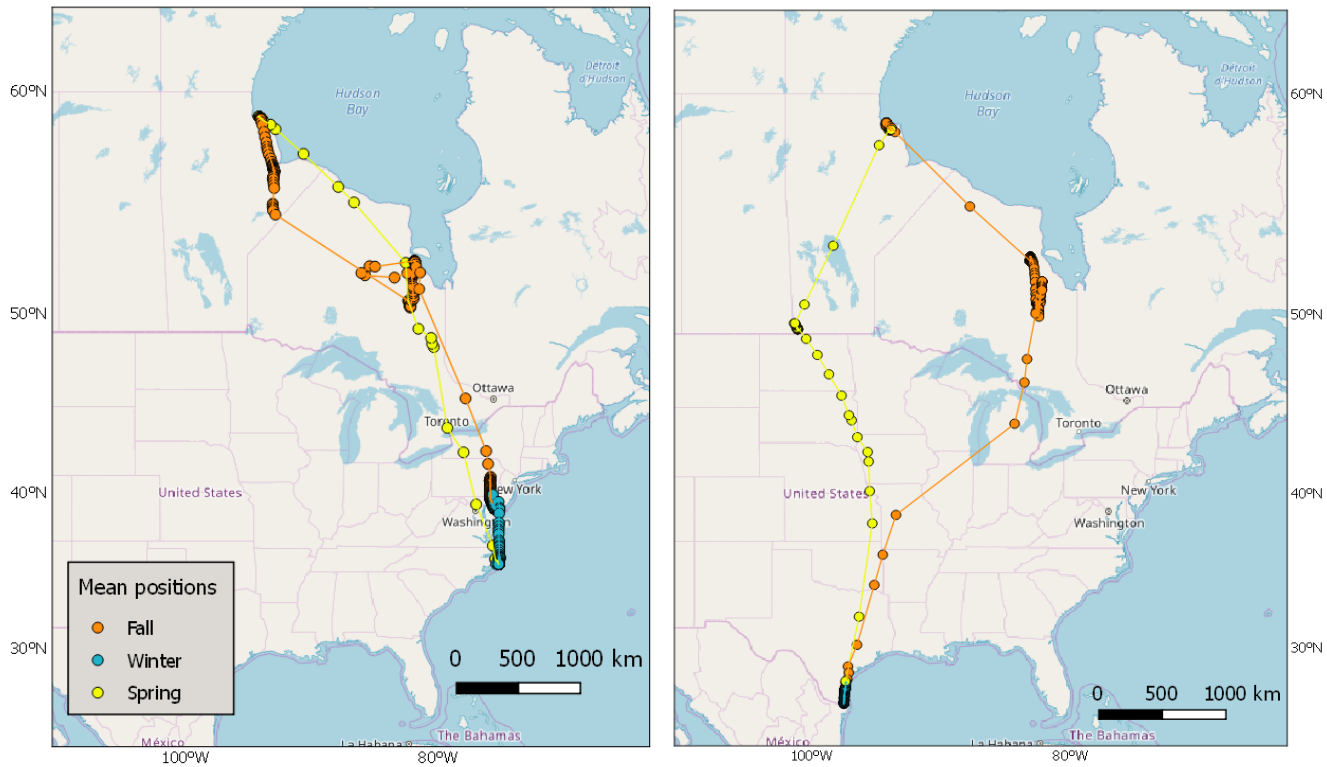
Figure 5: Migratory tracks of two exemplary Dunlin showing mean positions across one full annual cycle. North American flyways (Figure 4) were used to describe the geographic scope of different movement patterns of Dunlin during fall and spring migration. Dunlin tended to migrate along the border of the Mississippi and Atlantic flyways when overwintering at sites bordering the Atlantic Ocean (left panel). Many of the birds overwintering in Texas migrated through the centre of the Mississippi flyway on their southbound migration, and then migrated through the Central flyway on their return journey (right panel). Points on the maps are the most probable latitude and longitude for each recorded twilight and lines show direct connections between these positions, not paths taken by birds.

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Sex differences in migration phenology

Date of departure from the breeding grounds varied significantly by sex; on average, males departed earlier (August 9) than females (September 7) ($t = 2.25_{df=24}$, $p = 0.034$; Table 5). Male Dunlin also had a fall migration of longer duration ($t = 2.11_{df=23}$, $p = 0.044$; Table 5). Despite males departing the breeding grounds earlier than females, there was no sex difference in timing of arrival to wintering sites ($t = -0.295_{df=23}$, $p = 0.770$; Table 5). There was no evidence to suggest differences in timing of spring migration between sexes (Table 5).

Table 5: Comparison of the phenology of migration between sexes. Sex differences in migration parameters that are statistically significant at an alpha level of 0.05 are bolded.

	Females		Males			
	n	*Mean ± SE*	*n*	*Mean ± SE*	*t- value*	*p- value*
Fall migration initiation date	15	September 7 ± 8.47	11	August 9 ± 10.32	**2.25**	**0.034**
Duration of fall migration (days)	15	55.3 ± 10.41	10	90.3 ± 12.98	**2.11**	**0.044**
Mean fall stopover duration (days)	15	38.2 ± 7.87	10	62 ± 11.33	1.78	0.088
Fall migration end date	15	November 2 ± 4.87	10	November 4 ± 3.54	-0.30	0.770
Spring migration initiation date	13	April 29 ± 5.99	9	April 28 ± 7.93	0.09	0.930
Duration of spring migration (days)	9	25.3 ± 7.61	8	27 ± 7.71	0.15	0.880
Mean spring stopover duration (days)	9	15.4 ± 5.23	8	14.3 ± 3.52	-0.16	0.870
Spring migration end date	9	May 28 ± 0.97	8	May 30 ± 1.06	-1.22	0.240

Effects of migration strategy on lay dates

The most complex model describing variation in lay dates, with year as a random effect (BIC_{year} = 120.396), fit the data better than the most complex model with nest ID as a random effect (BIC_{nest} = 122.428, ΔBIC = 2.03), as well as the most complex fixed model (BIC_{fixed} = 125.494, ΔBIC = 5.10). Thus, year was included as a random effect in all subsequent *a priori* models. Variation in lay dates was best described by an index of wintering location (RC2 in model 3; Tables 6, 7). Birds that overwintered at locations of increasing latitude (i.e., further north; increasing RC2 scores) and increasing longitude (i.e., further east; increasing RC2 scores) laid nests later in the season (Figure 6). However, the null model fell within 2 ΔBIC of the top model (model 1; Table 6), thus decreasing support for an effect of the index of wintering location on Dunlin lay dates. My original predictions that individuals arriving to the breeding grounds earlier and migrating for a shorter duration of time (through combinations of increased migration speed, fewer and shorter stationary periods, and shorter distance) will have earlier lay dates were not supported by the data; none of the factors interpreted as indices of migration duration, timing of arrival to the breeding grounds and number of stopovers, migration speed or migration distance were included in the top-ranking model (Table 6).

Table 6: Model selection results for linear mixed effects models illustrating the effect of spring migration on Dunlin lay dates ($n = 20$). All models include year as a random effect. Models are ranked by ascending ΔBIC, and models with ΔBIC < 2 are considered competitive as the best fitting models (bolded). The candidate model, number of parameters (k), Bayesian Information Criterion (BIC), the difference between the BIC value of the highest ranked model and all other candidate models (ΔBIC) and model weights (w_i) are shown.

#	Model	k	BIC	ΔBIC	w_i
3	**Intercept+RC2**	**4**	**101.566**	**0.000**	**0.264**
1	**Intercept**	**3**	**102.080**	**0.514**	**0.204**
2	Intercept+ RC1	4	103.907	2.341	0.082
10	Intercept+RC3+RC2	5	104.257	2.691	0.069
4	Intercept+RC3	4	104.326	2.760	0.067
7	Intercept+RC5+RC2	5	104.527	2.961	0.060
6	Intercept+RC5	4	104.996	3.430	0.048
5	Intercept+RC4	4	105.017	3.451	0.047
28	Intercept+RC1*sex +RC2*sex +RC3*sex+RC4*sex+RC5*sex	14	106.456	4.890	0.023
14	Intercept+RC2+RC4+RC1	6	106.819	5.253	0.019
16	Intercept+RC2*sex	6	107.182	5.616	0.016
8	Intercept+RC5+RC3	5	107.201	5.635	0.016
13	Intercept+RC2+RC4+RC3	6	107.252	5.685	0.015
11	Intercept+RC3+RC4	5	107.320	5.754	0.015
12	Intercept+RC2+RC4+RC5	6	107.489	5.923	0.014
9	Intercept+RC5+RC4	5	107.922	6.356	0.011
15	Intercept+ RC1*sex	6	108.330	6.764	0.009
19	Intercept+RC5*sex	6	108.890	7.324	0.007
17	Intercept+RC3*sex	6	109.615	8.049	0.005
18	Intercept+RC4*sex	6	109.744	8.178	0.004
21	Intercept+RC5*sex+RC3*sex	8	111.201	9.635	0.002
20	Intercept+RC5*sex+RC2*sex	8	112.417	10.851	0.001
23	Intercept+RC3*sex+RC2*sex	8	112.848	11.282	0.001
22	Intercept+RC5*sex+RC4*sex	8	114.317	12.751	0.000
24	Intercept+RC3*sex+RC4*sex	8	114.894	13.328	0.000
27	Intercept+RC2*sex +RC4*sex +RC1*sex	10	117.688	16.122	0.000
25	Intercept+RC2*sex+RC4*sex +RC5*sex	10	117.703	16.137	0.000
26	Intercept+RC2*sex +RC4*sex +RC3*sex	10	117.845	16.279	0.000

Table 6 Continued

RC1= Index of non-breeding duration and winter departure date
RC2= Index of wintering location
RC3= Index of migration speed
RC4=Index of # stopovers, arrival to breeding and distance of the final leg of migration
RC5= Index of migration distance
[1]* indicates an interactive effect
[1]+ indicates an additive effect

Table 7: Parameters of the top ranked model explaining variation in Dunlin lay dates.

Dependant variable	Parameter	Estimate	SE	t-value	p-value	df
Lay date	Intercept	157.180	1.256	125.165	<0.001	17
	RC2	0.891	0.479	1.858	0.081	
	Year	Intercept	Residual			
	(Random)	SD= 1.541	2.072			

RC2= Index of wintering location
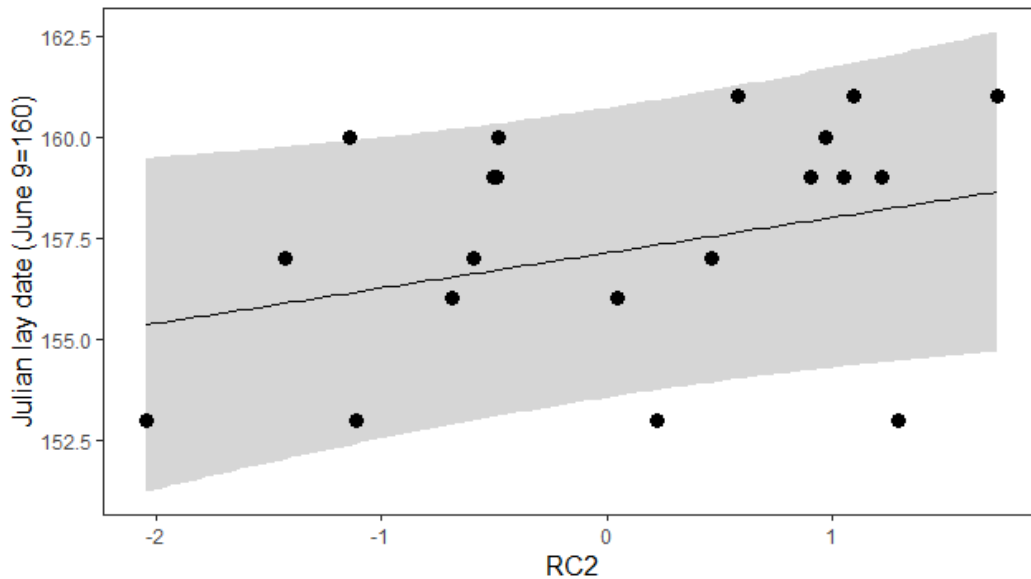
Figure 6: The effect of an index of wintering site location (RC2) on the lay dates of Dunlin nests. Black

line and shading represent regression line and 95% confidence intervals. Dunlin that wintered further

northeast (i.e., higher RC2 scores) had lay dates later in the season.

Effects of migration strategy on egg volume

No random effects were retained during the first step of model selection; therefore, all subsequent *a priori* models are linear fixed effects models. Variation in mean Dunlin egg volume was best described by model 8, which included additive effects of indices of migration speed (RC3) and migration distance (RC5) (Tables 8, 9). Female Dunlin that migrated longer distances along less direct routes (i.e., increasing RC5 scores) and spent more time flying at lower speeds (i.e., increasing RC3 scores), laid eggs of greater volume (Figure 7). The predictions that individuals migrating for a shorter duration of time and arriving early to the breeding grounds will lay eggs of larger volume were not supported by the data; effects of the indices of migration distance and speed were opposite to those predicted, and the indices of other variables (timing of arrival to the breeding grounds and number of stopovers, as well as migration duration) were not included in the highest ranked model (Table 8).

Table 8: Model selection results for candidate models predicting variation in mean egg volume of female Dunlin ($n = 11$) breeding in Churchill, MB. Models are ranked by ascending ΔAIC_c, and models with $\Delta AIC_c < 2$ are considered competitive as the best fitting models (bolded). The candidate model, number of parameters (k), Akaike's Information Criterion with adjustment for small sample sizes (AIC_c), the difference between the AIC value of the highest ranked model and all other candidate models (ΔAIC_c), and Akaike weights (w_i) are shown.

#	Model	k	AIC_c	ΔAIC_c	w_i
8	**Intercept+RC5+RC3**	**3**	**21.612**	**0.000**	**0.767**
4	Intercept+RC3	2	27.546	5.933	0.039
28b	Intercept+RC1+RC2+RC3+RC4+RC5	6	27.584	5.972	0.039
10	Intercept+RC3+RC2	3	28.476	6.864	0.025
1	Intercept	1	28.767	7.155	0.021
12	Intercept+RC2+RC4+RC5	4	29.285	7.673	0.017
11	Intercept+RC3+RC4	3	29.469	7.857	0.015
5	Intercept+RC4	2	29.531	7.919	0.015
6	Intercept+RC5	2	29.717	8.105	0.013
13	Intercept+RC2+RC4+RC3	4	30.052	8.440	0.011
3	Intercept+RC2	2	30.227	8.615	0.010
2	Intercept+ RC1	2	30.334	8.722	0.010
7	Intercept+RC5+RC2	3	30.701	9.089	0.008
9	Intercept+RC5+RC4	3	31.148	9.536	0.007
14	Intercept+RC2+RC4+RC1	4	33.110	11.498	0.002

RC1= Index of non-breeding duration and winter departure date
RC2= Index of wintering location
RC3= Index of migration speed
RC4=Index of # stopovers, arrival to breeding and distance of the final leg of migration
RC5= Index of migration distance
[1]+ indicates an additive effect

Table 9: Parameters of the top ranked model explaining variation in mean Dunlin egg volume.

Dependant variable	Parameter	Estimate	SE	t-value	p-value	df
Egg volume	Intercept	10.775	0.185	58.302	<0.001	8
	RC5	0.554	0.191	2.908	0.020	
	RC3	1.215	0.350	3.471	0.008	

RC3= Index of migration speed
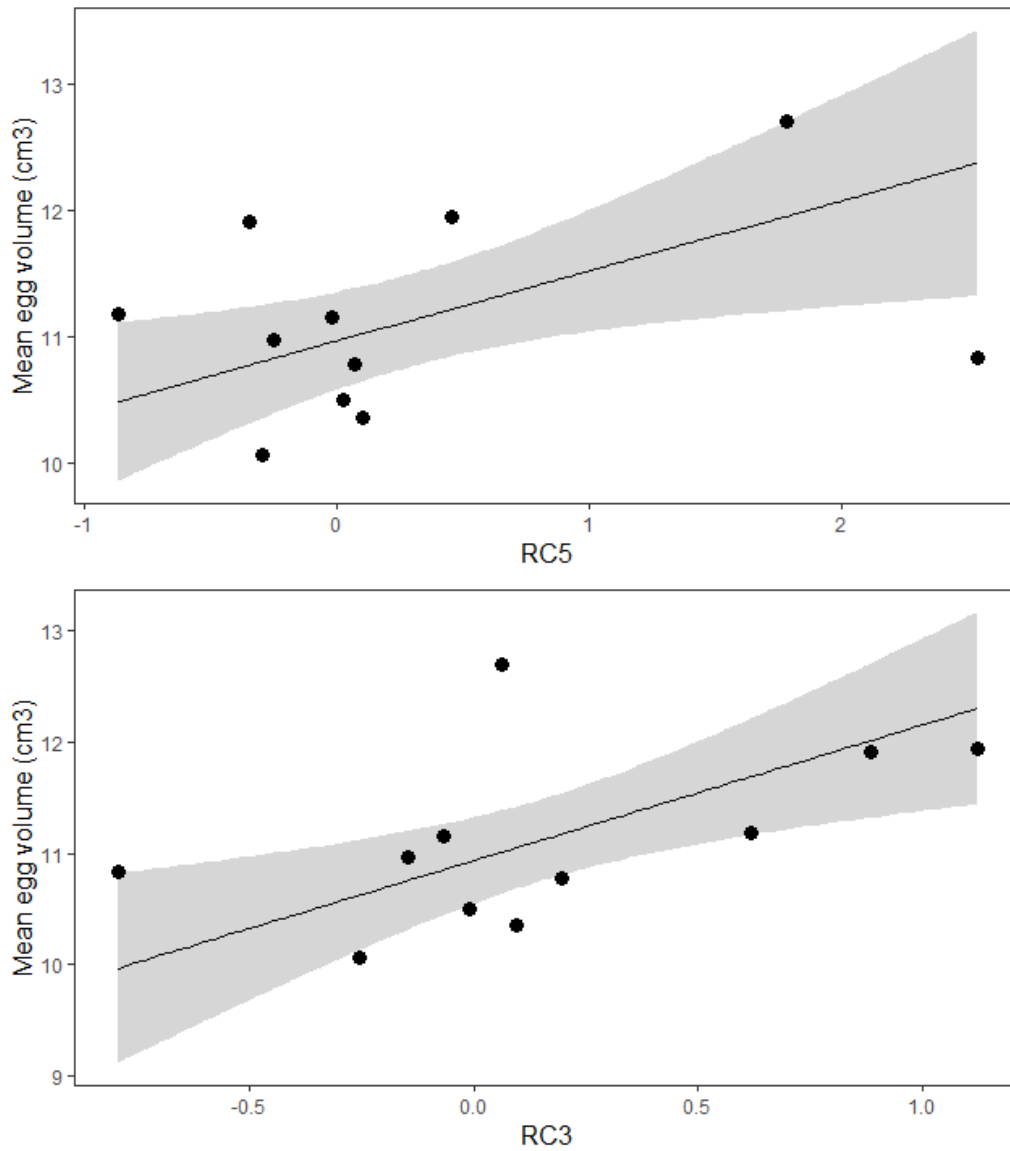RC5= Index of migration distance

Figure 7: The effects of indices of migration distance (RC5) and migration speed (RC3) on mean egg volume. Black line and shading represent regression line and 95% confidence intervals. High RC5 scores represent individuals that migrated further distances and high RC3 scores represent individuals that migrated at lower speeds.

Variation in daily nest-survival rates (DSR) was best described by model 19, with an interactive effect of our index of migration distance (RC5) and sex (Tables 10, 11). DSR decreased for male Dunlin that migrated further distances, along less direct routes (i.e., increasing RC5 scores; Figure 8). In contrast, opposite effects were observed for female Dunlin, with longer spring migration distance and decreased directness having a positive effect on DSR (Figure 8). The original predictions that earlier timing of arrival and decreased migration duration (through combinations of increased migration speed, fewer and shorter stationary periods, and shorter distance) would positively affect DSR were only partially supported; the effect of distance on DSR was as predicted for male Dunlin but was opposite to the prediction for females. No support was found for effects of arrival to the breeding grounds, migration duration, migration speed or number and length of stopovers on nest survival, as indices of these variables were not included in the top model (Table 10).

Table 10: Model selection results for models predicting changes in nest survival of Dunlin ($n = 19$) breeding in Churchill, MB. Models are ranked by ascending ΔAIC_c, and models with $\Delta AIC_c < 2$ are considered competitive as the best fitting models (bolded). The candidate model, number of parameters (k), Akaike's Information Criterion with adjustment for small sample sizes (AIC_c), the difference between the AIC value of the highest ranked model and all other candidate models (ΔAIC_c), and Akaike weights (w_i) are shown.

#	Model	k	AIC_c	ΔAIC_c	w_i
19	**Intercept+RC5*sex**	**4**	**35.029**	**0.000**	**0.305**
1	Intercept	1	37.192	2.162	0.103
21	Intercept+RC5*sex+RC3*sex	6	37.345	2.315	0.096
22	Intercept+RC5*sex+RC4*sex	6	38.276	3.247	0.060
4	Intercept+RC3	2	38.404	3.374	0.056
20	Intercept+RC5*sex+RC2*sex	6	38.807	3.778	0.046
5	Intercept+RC4	2	39.007	3.977	0.042

Table 10 continued

#	Model	k	AIC_c	ΔAIC_c	w_i
2	Intercept+RC1	2	39.014	3.984	0.042
3	Intercept+RC2	2	39.195	4.165	0.038
6	Intercept+RC5	2	39.204	4.174	0.038
8	Intercept+RC5+RC3	3	40.297	5.267	0.022
10	Intercept+RC3+RC2	3	40.441	5.411	0.020
11	Intercept+RC3+RC4	3	40.441	5.412	0.020
15	Intercept+RC1*sex	4	40.838	5.808	0.017
9	Intercept+RC5+RC4	3	40.988	5.958	0.016
7	Intercept+RC5+RC2	3	41.221	6.192	0.014
18	Intercept+RC4*sex	4	41.336	6.306	0.013
17	Intercept+RC3*sex	4	41.656	6.626	0.011
25	Intercept+RC5*sex+RC2*sex+RC4*sex	8	42.183	7.154	0.009
13	Intercept+RC2+RC4+RC3	4	42.479	7.450	0.007
16	Intercept+RC2*sex	4	42.595	7.565	0.007
14	Intercept+RC2+RC4+RC1	4	42.939	7.909	0.006
12	Intercept+RC2+RC4+RC5	4	42.968	7.938	0.006
24	Intercept+RC3*sex+RC4*sex	6	44.112	9.083	0.003
23	Intercept+RC3*sex+RC2*sex	6	45.491	10.461	0.002
27	Intercept+RC1*sex+RC2*sex+RC4*sex	8	46.963	11.933	0.001
26	Intercept+RC2*sex+RC4*sex+RC3*sex	8	47.625	12.595	0.001
28	Intercept+RC1*sex+RC2*sex+RC3*sex+RC4*sex+RC5*sex	12	47.704	12.675	0.001

RC1= Index of non-breeding duration and winter departure date
RC2= Index of wintering location
RC3= Index of migration speed
RC4=Index of # stopovers, arrival to breeding and distance of the final leg of migration
RC5= Index of migration distance
[1] * indicates an interactive effect
[1] + indicates an additive effect

Table 11: Logit link function parameters of the top ranked model predicting variation in Dunlin nest survival.

				95% confidence intervals	
Dependant variable	Parameter	Estimate	SE	Lower	Upper
Daily nest survival	Intercept	3.119	0.764	1.622	4.616
	RC5	-3.934	2.310	-8.637	0.770
	sex	0.945	1.082	-1.176	3.065
	RC5*sex	6.156	2.780	0.707	11.604

RC5= Index of migration distance
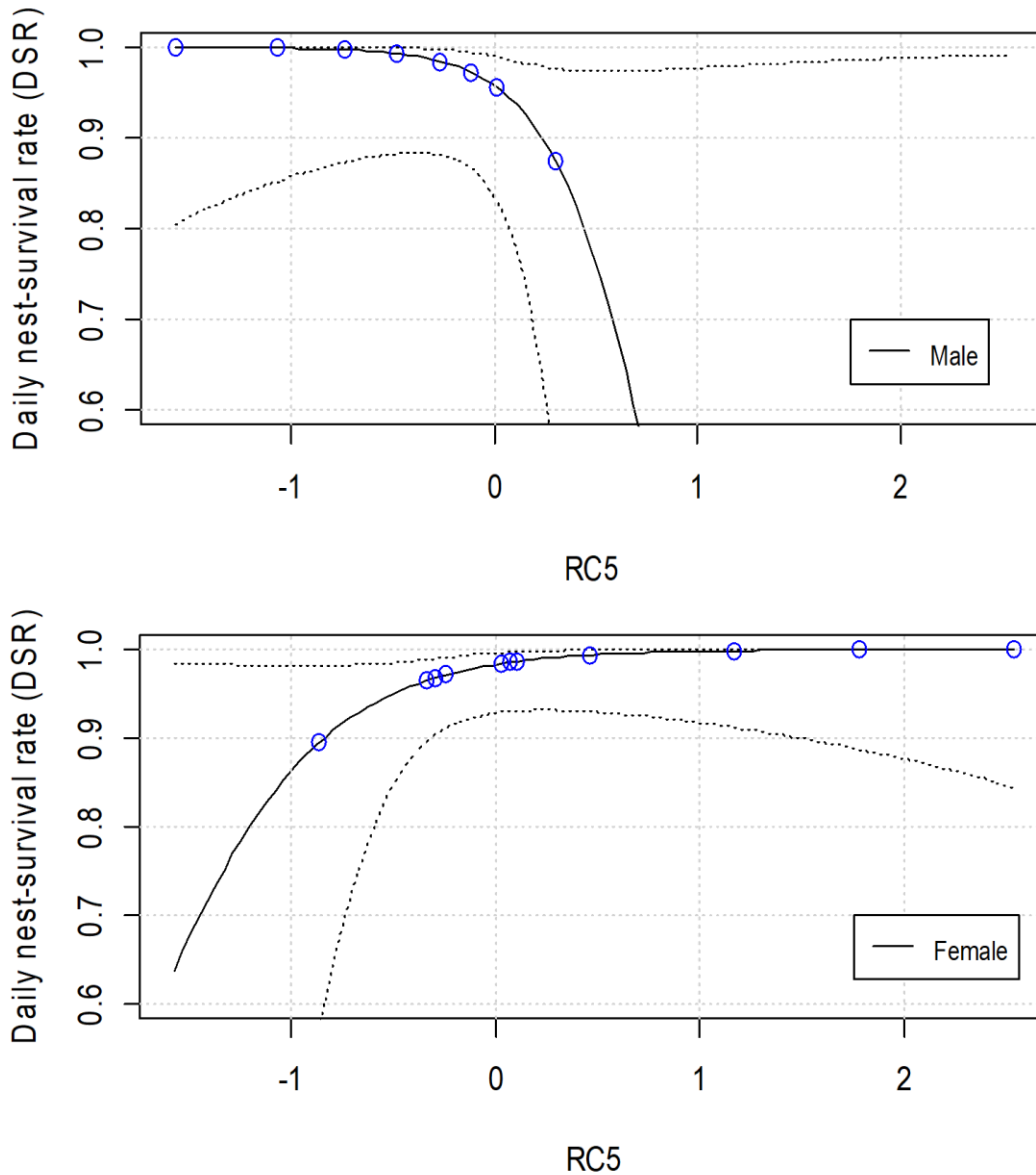
Figure 8: Model estimates of Dunlin daily nest-survival rates showing the effect of an index of migration distance (RC5) in interaction with sex. Middle, solid line represents DSR estimated using beta parameters from the best fitting model. Dotted lines represent upper and lower 95% confidence intervals.

Discussion

Using light-level geolocation, I successfully tracked 17 Dunlin throughout a complete migration cycle. This study provides a better understanding of the migratory ecology of Dunlin that are breeding in a region that is currently undergoing amplified climatic changes (Zhang 2010). By identifying migration scheduling, routes, and stopovers, we learn more about a shorebird species' spatiotemporal distribution during the least understood phase in the avian lifecycle (Cooper et al. 2017). As of 2018, there have only been 7 publications that use geolocators attached to landbirds to investigate seasonal interactions (McKinnon and Love 2018) and, to the best of my knowledge, none on arctic-nesting shorebirds to date. Thus, my research is the first to do so, thereby allowing me to identify the carry-over effects of migration on breeding parameters within the *C. a. hudsonia* subspecies. Indices of migration speed and distance were included in the top model explaining variation in mean Dunlin egg volume, but effects were opposite to those hypothesized; female Dunlin that migrated at slower speeds and spent more hours travelling, as well as travelled further distances along less direct routes, laid eggs of greater volume. Indices of migration distance were included in the top model explaining variation in daily nest-survival rates (DSR), with effects differing by sex; DSR decreased for male Dunlin that migrated longer distances along less direct routes, as predicted, but increased for females as migration distance increased. The prediction that late timing of arrival negatively affects reproductive success was not supported; the index of timing of arrival to the breeding grounds was not included in any of the top models predicting variation in the three reproduction parameters. In addition, I did not find evidence for effects of migration duration or the number and length of stationary periods on reproductive success.

Connectivity of the non-breeding season

These tracking data identify the links between the breeding grounds in Churchill, stopover sites in northern Ontario, stopover sites in midwestern and eastern United States of America and non-breeding, non-migratory sites in American states bordering the Gulf of Mexico and Atlantic Ocean. On their southbound migration, it is apparent that Dunlin use two distinct migration routes. Nearly all Dunlin started their migration by flying southwest to stopover sites in northern Ontario, near the coast of Hudson Bay and James Bay. From there, Dunlin flying to overwintering sites along the coast of the Atlantic Ocean flew across southeast Ontario into New York state, before following a coastal heading further south. Those Dunlin wintering at sites along the Gulf of Mexico flew across southwestern Ontario through the Mississippi flyway (across Illinois, Missouri, and Arkansas). The most frequented wintering locations along the Gulf of Mexico were in Texas and Mississippi, and along the Atlantic Coast, Maryland and Delaware, as well as North and South Carolina. There do not appear to be any sex differences in wintering locations, as both female and male Dunlin wintered at each of these locations.

Dunlin also followed two apparent migration routes during northwards migration. Individuals that flew along the border of the Mississippi and Atlantic flyways on their southbound migration followed a similar route when flying north. Conversely, those Dunlin that overwintered in sites close to Texas tended to migrate directly north through the midwestern United States. The geolocator data from the present study confirm previously reported observations of these two northward routes for the *C.a. hudsonia* subspecies (Warnock and Gill 1996, Skagen et al. 1999). That said, three Dunlin wintering in Texas and Louisiana did not follow these patterns; each took a more easterly route along the Atlantic Coast, stopping over in Delaware before migrating north along the border of the Mississippi and Atlantic flyways.

Although the position estimates from geolocators do not allow us to obtain extremely high-resolution movement data, the general locations (states/provinces) identified as non-breeding sites for these Dunlin are consistent with our previous understanding, as determined by resightings and band recoveries, of Dunlin migratory movements (Fernández et al. 2010). Interestingly, the non-breeding, non-migratory sites identified in this study are spread across most of the known wintering range (Massachusetts to Mexico) for this subspecies (Warnock and Gill 1996). This suggests weak migratory connectivity for Dunlin breeding in Churchill, as these birds appear to diffuse to many locations along the Gulf of Mexico and Atlantic Coast during the wintering months. Stopover sites also varied considerably among individuals, but I identified three areas where many of the tracked Dunlin remained stationary. Nearly all Dunlin ($n = 25$) moved to areas in northern Ontario, along the coast of Hudson Bay and James Bay, directly following the breeding season. In the spring, 6 Dunlin stopped over in North or South Dakota and 7 stopped over at sites along the coasts of Virginia and Delaware. The wetland and coastal habitat of southwestern Hudson Bay and James Bay is a known staging hotspot for up to 25 shorebird species migrating from the Arctic and Subarctic (Friis et al. 2013). Initiated in 2009, the Western James Bay Shorebird Project now operates 3 field sites to estimate population trends and movement patterns for shorebird species staging in these areas. Similar shorebird monitoring projects exist in Delaware Bay (Delaware Shorebird Project) and the Dakotas (Northern Great Plains Joint Venture), where thousands of shorebirds stage to gain muscle protein and fat to fuel their migrations north (Tsipoura and Burger 1999). Warnock and Gill (1996) used resighting observations to suggest that Dunlin overwintering along the Gulf Coast likely fly directly to the breeding grounds after stopping over in the Dakotas, and our geolocator data are consistent with this "jump" migration pattern. This research identifies a high concentration of Dunlin at these important staging sites and lends further support for dedicating conservation efforts to these areas.

Dunlin remained on the breeding grounds, or at sites adjacent to the breeding site (e.g., the coasts of Hudson Bay and James Bay), for an average of 6 weeks after the breeding season prior to completing their fall migrations. This may be explained by Dunlin undergoing prebasic moult, where birds may need longer to prepare before leaving the Subarctic because they are amassing fuel stores and regrowing feathers simultaneously (Taylor et al. 2011). It has previously been shown that subspecies of Dunlin breeding in western Alaska and Canada complete prebasic moult in the post-breeding season, prior to migrating to the wintering grounds (Engelmoer and Roselaar 1998, Warnock et al. 2013). An advantage of this moult timing is that these individuals require fewer resources once reaching their wintering grounds; this allows them to stay in the Subarctic for prolonged periods, without the pressure of arriving at their wintering destinations ahead of other migrants competing for the same resources (Taylor et al. 2011).

Timing of migration

In general, the timing of migration varied considerably among individuals. The migration periods for *C.a. hudsonia* identified in this study are mostly consistent with those reported by Skagen et al. (1999), although the range of arrival dates to the wintering grounds extends later than those previously described. Songbird tracking studies have shown that some species can adapt migration phenology in response to weather events or conditions on the non-breeding grounds; Red-backed Shrikes (*Lanius collurio*) delayed spring migration by 2 weeks after encountering a drought at a stopover site (Tøttrup et al. 2012) and Semi-collared Flycatchers (*Ficedula semitorquata*) slowed the final phase of their spring migration in response to cold weather en-route (Briedis et al. 2017). The high inter-individual variation in departure dates, speeds, migration durations and stopover durations may suggest that these Dunlin have migration strategies that are flexible to local, within-year conditions.

It is typical for the spring migration of shorebirds to be of a shorter duration than fall migration (Jehl 1979, Alerstam and Lindstrom 1990, Colwell 2010). This is likely because individuals are more rushed in the spring to arrive to northern breeding grounds, where there is a narrow window of time for favourable breeding conditions (O'Reilly and Wingfield 1995). On average, Dunlin had a fall migration that was 62% longer than spring migration. The results from this population of Dunlin support previous understanding that pre-breeding movements are more time-constrained than post-breeding movements (Alerstam et al. 2006, Egevang et al. 2010, Conklin et al 2013, Johnson et al. 2016). Despite a large range of departure dates (March 18 - May 25), arrival dates to the breeding grounds were confined to an 11-day interval (May 24 - June 3). This suggests that shorebirds can compensate for constrained timing of arrival through flexibility in other aspects of migration, such as increased speeds or fewer, shorter stopovers (Hooijmeijer et al. 2014, Lindstorm et al 2016, Rakhimberdiev et al. 2018).

In the fall, male Dunlin departed from the breeding grounds significantly earlier than females. I expect that males were able to depart earlier because of their earlier moult timing, which has been shown to start before and end sooner than females in a closely related species (Barshep et al .2013, Dietz et al. 2013). Although males do invest more time than females caring for chicks post hatch, this investment only lasts about 19 days, when chicks are close to fledging (Jamieson 2011). The male Dunlin tracked in this study had a longer fall migration duration than females, but there was no significant difference in arrival times to the wintering grounds. Surprisingly, there were no sex differences in timing of arrival to the breeding grounds. This last result is unexpected, as male shorebirds often arrive to the breeding grounds before females to establish the best breeding territories (Kokko 1999), to increase their extrapair copulation opportunities (Kokko et al. 2006), and because their larger body size allows them to withstand adverse weather conditions of the early season (Moller 2004). Nonetheless, the present study had results consistent with those reported in Brown et al. (2017), in which the authors speculated that the

theory that males arrive earlier than females could be attributed to sex-biased resightings, rather than actual differences in timing of arrival. Another explanation for the lack of sex differences in timing of arrival could be that these females are not delayed on prolonged staging events because Dunlin are considered to be "income" breeders; females rely on energy gained concurrently while breeding rather than financing reproduction from energy stores gained prior to arrival on the breeding grounds (Klaassen et al. 2001).

Although the spring migration strategies of these Dunlin were highly variable, including the range of departure dates (March 18th - May 25th), speeds (528 - 2136 km/day), and mean stopover durations (3- 63 days), arrival times to the breeding grounds were constrained to an 11-day interval. These results are mirrored in songbird migration phenology research; it has been shown that overwintering environmental conditions affect departure dates from these sites, but arrival dates to breeding grounds remain unaffected (McKinnon et al. 2015, Pedersen et al. 2016).

Effects of migration strategy on reproductive parameters

Contrary to my results, the timing of arrival to breeding grounds has previously been shown to influence reproductive success, as early arriving migrants have a competitive advantage in choosing breeding territories and mates (Farmer and Weins 1999). Even if migrants arrive in poor body condition due to a rushed migration, early arriving birds may have increased time to recover before breeding. These individuals can start breeding early, which increases the time available to raise young while environmental conditions on the breeding grounds are still favorable (Perrins 1969, Møller 1994, Moore et al. 2005). This is especially important for birds nesting in the north, since the window for breeding is shortened; as the season progresses, the resources available for egg formation and chick development decrease. Breeding success in other species has also been shown to decline

later in the breeding season (Gienapp and Bregnballe 2012). Chicks hatching early in the season may have increased survival because they can gain thermoregulatory independence earlier (Schekkerman et al. 2003), as well as experience being independent from their parents before the onset of migration. Weiser et al. (2018) conducted a study across 25 taxa of migratory shorebirds to assess seasonal declines in reproductive traits of clutch size, daily nest survival rates, incubation duration and egg volume. Although they found strong seasonal declines in many species, the *C.a. hudsonia* subspecies of Dunlin did not have significant declines for any of the reproductive traits measured. It is possible that timing of arrival was not an important predictor of variation in any of the reproductive parameters because Dunlin exhibited very little flexibility in arrival dates to the breeding grounds.

Despite all the evidence supporting arrival date as an important indicator of the onset of nesting, weather conditions upon arrival to northern breeding grounds also influence the timing of reproduction (Smith et al. 2010). Inclement weather conditions upon arrival such as delayed snowmelt or cold temperature can delay nesting or, if the weather is severe enough, can stop breeding attempts all together (Troy 1996). These conditions may also delay the emergence of invertebrate prey (Tulp and Schekkerman 2008), which translates to reduction in energy reserves for egg production. This indicates that early arrival may not always be conducive for earlier breeding; if spring weather in a particular year is delayed, then nesting will likely be delayed as well. To better assess reproductive success and variability within and among years, future research should focus on assessing effects of weather variables and resource availability on reproduction throughout the breeding season.

The model with the lowest BIC score explaining variation in Dunlin lay dates included an index of wintering site location. Dunlin that spent the wintering months at sites further northeast initiated nests later in the breeding season. However, it is important to note that the null model was competitive, suggesting that none of the migration variables are good predictors of the variation in lay dates. Since

we did not measure any variables on the wintering grounds that may affect an individual's ability to migrate, such as habitat quality, predation pressure, heterospecific competition, or climatic conditions, it is difficult to pinpoint what factors on the wintering grounds may be affecting lay dates. There has been much research to suggest that non-breeding site conditions may have carry-over effects on reproductive success of shorebirds and waterfowl. Poor site quality can decrease fuel store deposition, which can delay timing of arrival to the breeding grounds and decrease reproductive success (Ebbinge and Spanns 1995, Baker et al. 2004, Gunnarson et al. 2005). In addition, high prey intake at wintering sites has been linked to increased reproductive success for Black-tailed Godwits (*Limosa limosa*) (Gill et al. 2001). My results contradict previous research showing that nesting success increases for several shorebird species that winter at sites closer to the breeding grounds (Hotker 2002, Bregnballe et al. 2006). Other indirect effects of the wintering grounds could include the conditions at proximate stopover sites or the difficulty of routes taken from these different locations. There was a strong divide in migration routes of Dunlin wintering along different coasts; most birds wintering along the Gulf of Mexico flew through the Central flyway on their northward migration, whereas birds wintering along the Atlantic Coast flew along the border of the Atlantic and Mississippi flyways. The Atlantic Coast, from Virginia to Delaware, is a site that is shared by thousands of shorebirds during the non-breeding seasons (Newton 2006), and it is possible that this increase in bird densities causes a cascade of negative effects, such as increased competition resulting in a depletion of food resources, insufficient fuel reserves, and delayed onset of migration.

Contrary to my predictions, female Dunlin that migrated at slower speeds and travelled along less direct routes laid eggs of greater volume. It was assumed that females would exhibit a fast paced, more direct route in order to reach the breeding grounds earlier. Dunlin and other small shorebirds are "income" breeders and arrive to the breeding grounds with a high refueling requirement before they can

begin egg production (Klaassen et al. 2001). Early arrival would allow more time to forage and deposit nutrients in preparation for the onset of breeding. The observed results may be explained by different strategies for migratory flight optimization; maximizing time or energy efficiency (Lindström and Alerstam 1992). The flight strategies of female Dunlin may involve decreased travel speed but incur benefits of reduced energy expenditure (Vincze et al. 2018). As such, there may exist a trade-off between arriving early to the breeding grounds and arriving in good body condition (Norris et al. 2004, Smith and Moore 2005, Paxton and Moore 2015). I speculate that a slow-paced, less direct route may improve body condition by avoiding geographical regions with higher movement costs (Flack et al. 2016) and decreasing the energy necessary for powerful, fast paced flight (Pennyquick 1969). It is also possible that female Dunlin are moving off-course to access stopovers that offer high quality resources, thereby maximizing energy intake (e.g., as hypothesized for swifts by Åkesson et al. 2012). Since the mass of total eggs produced in a single clutch can nearly reach females' body mass, female body condition prior to breeding may be especially indicative of egg volume (Weiser et al. 2018). Future work should assess female body condition (e.g., mass and macro/micronutrient stores) prior to egg production to better understand how migratory strategy may be related to body condition.

Spring migration distance was again included in the top model describing variation in daily nest-survival rates (DSR). Female Dunlin that flew farther and along less direct migratory routes had increased DSR. The effect was opposite for male Dunlin; DSR decreased as migration distance increased. It was expected that shorebirds of both sexes that took longer migrations, and consequently had greater energetic demands, would have decreased reproductive success. Birds that have longer migrations have increased chances of encountering conditions that increase the cost of flight, such as adverse weather en-route or physical barriers (Fox and Gitay 1991, Lok et al. 2015). These birds were expected to arrive in poorer body condition and to be less equipped for the energy intensive reproductive

behaviours that might affect nest survival (e.g., defending a breeding territory, attracting a high-quality mate, incubation and predator defence). While this prediction was supported for male Dunlin, it is noteworthy that increasing migration distance had positive effects on the daily nest survival of female Dunlin, as it did for egg volume in females (see above). McKinnon et al. (2015) found that Wood Thrushes that occupied moisture rich, food abundant non-breeding sites flew significantly farther during spring migration than those leaving drier sites. They suggest that high quality non-breeding sites can compensate for longer distance migration. It would be meaningful to test if the geographical separation of non-breeding sites used by *C.a. hudsonia* males and females correlates with differential habitat productivity, and if this condition is driving the detected carry-over effect of migration distance on nest survival.

Geolocator accuracy and tracking advances

Geolocators are useful tools to capture movement data because they can provide location estimates for each day that they are active and can store enough data to capture start-to-finish, year-round migration. The main limitation of geolocators are that they are archival, so recapture of geolocator carrying birds is pivotal for retaining any usable data. In addition, their ability to capture high resolution movement patterns is limited. Further, many bird migrations overlap with the fall and spring equinoxes, when geographic variation in day length is minimal. Since latitudinal estimates are based on varying lengths of daylight, accuracy of these estimates is negatively affected during these periods, which also happen to be the most critical periods for migration studies. Shading of the light sensor may also introduce bias, where light levels may cross the threshold into darkness prematurely if there is cloudy weather or when birds move into shaded habitats. This shading of sensors can result in position

estimates being displaced northwards or southwards from their true positions, where daylengths are shorter depending on the time of year (Porter and Smith 2013).

In this study, geolocator analysis was completed in *FlightR*, which allowed refinement of position estimates using a template fit observation model and an improved movement model (Rakhimberdiev et al. 2016). However, some tracks still had unlikely position estimates (e.g., far north from the breeding grounds or latitudinal jumps south then directly north again). Unlikely latitude estimates were excluded based on interpretation that they represented unlikely movements and I understand that there may be some user bias in doing so. The migratory routes presented in this study are meant to be a best approximation of the actual tracks travelled by Dunlin. For the purposes of this study, the potential error associated with position estimates was not seen as an issue, as the same error across all the tracked Dunlin is assumed. In addition, only individuals from this sample are compared to answer questions about the carry-over effects of migration on reproductive success. Exact site locations were not required, as I only needed to compare relative migration distance, speed, number of stopovers, stopover duration and migration duration, as well as all other migration covariates.

In addition to geolocators, there exists other technologies that will advance our ability to track small avian migrants in the near future. The International Cooperation for Animal Research using Space (ICARUS) is a satellite network that will combine a large antenna attached to the International Space Station with transmitters that can be worn by small migrant birds, fish, and mammals. ICARUS is revolutionary because it is a tracking system that can provide position data in real-time, and can collect environmental data such as temperature, humidity, air pressure and height in addition to movement data (Gesellshaft 2019). This tracking technology can provide new insight into where birds are encountering fatal threats along their migration routes and data will no longer only be representative of those individuals that survive their annual migrations and are recaptured by researchers (McKinnon and Love

2018). It is anticipated that ICARUS will be open for use by the scientific community in 2019. Current limitations are the anticipated high cost of tags (> 1000 CAD), as well as the large size of transmitters (5 g) (McKinnon and Love 2018).

Another popular tool used in movement research is automated telemetry systems, which uses a network of static radio telemetry towers to detect digitally encoded tags worn by birds, bats and insects within a 20 km radius (Taylor et al. 2017). One benefit of this system is that it allows multiple tags to be detected on a single radio frequency, thus eliminating the need to search for the correct frequency for a specific tag. One of the biggest networks of these automated radio telemetry towers, Motus Wildlife Tracking System, was developed in Canada and currently has over 325 active towers in 11 countries. This system is beneficial because it allows researchers to gather information about small migrants on various temporal and spatial scales and has promising applications for survival studies because it reduces bias associated with only recapturing birds that survive migration. Current limitations are the geographical scale of tower placement, as towers are currently most concentrated in the Western Hemisphere, but spatial expansion is underway with plans to strategically place towers at known migratory hotspots (Taylor et al. 2017).

Conservation implications

Over 80% of shorebird populations in North America are declining (Andres 2012) and studies have shown that this decline is ongoing and occurring across their geographic range (Austin et al. 2000). Shorebirds are especially vulnerable to population declines due to several factors, including their long migratory flights, dependence on wetland habitats during their annual cycles, and slow reproductive rates (Bart et al. 2007). Breeding habitats in northern regions are particularly susceptible

to global warming induced climatic shifts, including changes such as asynchrony of chicks hatching with peak insect abundance (Tulp and Schekkerman 2006) and drying of tundra ponds (Smol and Douglas 2007). These vulnerabilities make shorebirds a group of conservation concern (Bart et al. 2007) and highlights the urgency to better understand ecological processes that are contributing to these risks.

This research has identified the coast of Delaware and James Bay as critical stopover sites, and habitats close to the Gulf of Mexico and Atlantic Coast as wintering sites that *C. a. hudsonia* rely upon during the non-breeding season. Delaware Bay is known as an important staging site for thousands of shorebirds species (Newton 2006). Unfortunately, collapsing horseshoe crab populations at this site have been linked to declines in species such as Red Knot (*Calidris canutus*) (Baker et al. 2004) and Semipalmated Sandpiper (*Calidris pusilla*) (Mizrahi et al. 2012), who depend on the eggs of this invertebrate to fuel their lengthy northward migrations. In addition, Galbraith et al. (2002) projected concerning intertidal habitat loss at this site. This decline in resources and loss of intertidal habitat in Delaware Bay is particularly concerning, since stopover sites are thought to be critically important for "jump" migrants like Dunlin, who must refuel for longer periods of time before departing on their migratory flights. In addition, the Northern Gulf of Mexico, where nearly half of the tracked Dunlin overwinter, is experiencing one of the worst coastal wetland habitat losses in the United States (Henkel and Taylor 2015). Changes to the wetland habitat can be best explained by rising sea levels, climate change and dredging human-made channels (Turner 1997, Henkel and Taylor 2015). These habitats are not only important stopover and overwintering sites for the Dunlin studied in this project, but they are also relied upon by over 34 species of shorebirds (Henkel and Taylor 2015). These habitats are expected to experience increased degradation as the processes of global warming accelerate (Burger et al. 2012),

which may destabilise the arctic-nesting shorebird populations that occupy these areas during the non-breeding seasons.

Conclusions

This study successfully tracked the round-trip journey of Dunlin from a Churchill, MB breeding site to overwintering locations along the Gulf of Mexico and Atlantic Coast. I identified individual migration routes, stopovers and overwintering locations, as well as estimated 13 different variables describing the migration strategies of these Dunlin. Identifying the links between breeding and non-breeding sites is important because it allows for conservation initiatives to be targeted at locations where shorebirds are known to be located throughout the annual cycle (Hobson 1999). This remains difficult for the *C.a. hudsonia* population, as the non-breeding locations identified in this study are not concentrated to one location, but instead span across a large geographic range. On the other hand, this research increases understanding of the effects of migration strategies on the reproductive ecology of shorebirds that breed in northern regions, which is increasingly important as climate change threatens to desynchronise the phenology of these events. This study identified indices of spring migration speed and spring migration distance as important predictors of reproductive success. I found no evidence for the effects of arrival time to the breeding grounds, migration duration or number and length of stopover sites on Dunlin reproductive success. Future work should attempt to quantify conditions encountered during migration (e.g., wintering site habitat quality, weather conditions or predation pressures en-route), as well as body condition of breeding birds prior to reproduction in order to assess the mechanisms driving the detected carry-over effects. This research identifies how events occurring at different stages of the annual cycle are correlated and is critical for the complete understanding of the biology of this migratory species.

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