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Rushing in the spring and relaxing in the fall: seasonal and sex-specific migration profiles of Dunlin

Apurados en la primavera y relajados en el otoño: perfiles de migración estacionales y específicos al sexo en *Calidris aplina hudsonia*

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ABSTRACT. Developing effective species conservation strategies relies on our ability to understand the spatiotemporal distribution of birds across their annual cycle. Assessing the connectivity between breeding and non-breeding areas remains challenging in migratory species that may exhibit intraspecific variation in migration strategies. Here we use light-level geolocation to test for sex-specific differences in the migration strategies (i.e. migration routes, stopovers, and wintering sites) of a population of Dunlin (*Calidris alpina hudsonia*) that breeds in Churchill, Manitoba, Canada. Churchill Dunlin exhibited relatively weak connectivity, as birds spread out evenly across the Atlantic Coast south of New Jersey, U.S.A, and the Gulf Coast from Mexico to Florida, U.S.A., the entire known non-breeding range of the species. We did identify important concentrated stopovers in James Bay, ON, Canada and along the coast of Delaware, U.S.A. Overall migration and stopover durations were significantly shorter during spring (northward) compared to fall (southward) migration. During spring migration, males followed a more direct migration route than females. In fall, male Dunlin departed breeding grounds earlier and spent more time on migration than females, likely driven by a trend of longer stopover durations. These sex-specific differences suggest that in spring, males deploy an energy minimization strategy to reach breeding grounds quickly and select the highest quality mating territories, whereas in fall, males take a much more relaxed migration. This research sheds light on the least understood period of the avian life cycle and informs our ability to target conservation initiatives to locations most important for this species.

RESUMEN. Desarrollar estrategias de conservación de especies efectivas reposa en nuestra habilidad de comprender la distribución espacio-temporal de las aves a través de su ciclo anual. Determinar la conectividad entre áreas de reproducción y no reproductivas es todavía un reto para especies migratorias que muestran variación intraespecífica en las estrategias migratorias. Aquí usamos geolocalizadores de niveles de luz para comprobar diferencias específicas al sexo en las estrategias de migración (i.e. rutas de migración, parada y sitios de invierno) en una población de *Calidris alpina hudosnia* que se reproduce en Churchill, Manitoba, Canadá. La población de Churchill de *C. a. hudsonia* mostró una conectividad relativamente débil pues las aves se dispersan a través de la costa Atlántica al sur de Nueva Jersey, EEUU y la costa del Golfo desde México hasta Florida, EEUU, la totalidad del rango reproductivo de la especie. Identificamos puntos de parada importantes concentrados en la bahía de James, ON, Canadá y a lo largo de la costa de Delaware, EEUU. En general la duración de la migración y de las paradas fueron significativamente más cortas durante la primavera (con dirección norte) comparado con la migración de otoño (con dirección sur). Durante la migración de primavera, los machos siguieron rutas de migración más directas que las hembras. En el otoño, los machos de *C. a. hudsonia* partieron de sus sitios de reproducción más temprano y pasaron más tiempo migrando que las hembras, probablemente determinado por una tendencia en tener una mayor duración en las paradas. Estas diferencias específicas al sexo sugieren que en la primavera, los machos despliegan una estrategia de minimización en la energía para alcanzar los sitios de reproducción rápidamente y seleccionar los territorios de apareamiento de mayor calidad, mientras que en el otoño, los machos toman una migración mucho más relajada. Esta investigación da luces sobre el periodo menos comprendido del ciclo anual de las aves e informa nuestra habilidad para focalizar la iniciativas de conservación a las localidades con mayor importancia para esta especie.

Key Words: *annual cycle, Calidris alpina, Dunlin, geolocators, migration, sex-specific, stopovers*

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 (Shaw 2016) and to reduce exposure to predators (Hope et al. 2014) and parasites (Kelly et al. 2016). Migration strategies among birds are diverse, with great interspecific and intraspecific differences (Newton 2011). 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). For species that exhibit intraspecific differences in migration strategies, determining the connectivity between breeding and non-breeding areas remains challenging, as it requires tracking of individual movements of both males and females throughout the entire annual cycle.

Selection pressures that differ by season may cause migratory strategies to change in fall versus spring (Nilsson et al. 2013). Many birds exhibit a time-minimization migration strategy in spring when there is fitness pressure to arrive early to the breeding grounds, and a slower, less energetically costly migration in fall (Hedenström and Alerstam 1997, Horton et al. 2016, Duijns et

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al. 2019; although see also Schmaljohann 2018, Carneiro et al. 2019). Early spring arrival may be especially important for Arctic breeding shorebirds, as the breeding window at these high latitude sites is relatively short and food availability generally follows a narrow seasonal peak (Smith et al. 2010, Saalfeld et al. 2019). Additionally, some shorebirds may adjust their southbound migratory timing to avoid risk of predation. Since some raptor species migrate during a more constrained period of time during southbound versus northbound migration, migratory shorebirds are exposed to greater danger of predation from these avian predators during the post-breeding season (Duijns et al. 2019). While most shorebirds time their southbound migration to start before the migration of these predators (Hope et al. 2011), some shorebirds such as Pacific Dunlin (*Calidris alpina pacifica*), may remain at sites near the breeding ground until after peak raptor migration has commenced (Jamieson 2011). Intraspecific differences in seasonal migration strategy may also differ by age (Anderson et al. 2019). In some shorebird species, adults that moult at post-breeding staging sites tend to migrate before juveniles (McKinnon et al. 2022). Juvenile shorebirds have also been shown to have fall (southward) migrations of longer duration and less direct routes than older individuals (Evans and Davidson 1990, Anderson et al. 2019) and may opt to stay in wintering sites year-round, rather than migrate to breeding grounds (Branson et al. 1979, Goss-Custard et al. 1982).

Sex-specific differences in migration also exist. For instance, differential breeding functions between sexes may influence timing of migration. Some male shorebirds migrate to breeding grounds earlier than females to select the highest quality mating territories, whereas females may spend more time on stopover sites gaining energy stores for reproduction (Pitelka 1959, Farmer and Weins 1999). Additionally, fall migration phenology may differ between sexes in species where males and females provide different levels of parental care or have different parental duties post-hatch (Newton 2008). Sexual dimorphism can also result in large-scale geographical differences in wintering distributions of male and female shorebirds (Nebel 2005, Mathot et al. 2007). For example, female Western Sandpipers (*Calidris mauri*) have larger bills than their male counterparts, and winter further south where invertebrate food resources are buried more deeply in the sediment (Mathot et al. 2007). Additionally, Fernández and Lank (2007) showed that Western Sandpipers have sexual variation in wing morphology and predict that the longer and more pointed wings of females may increase flight efficiency and allow for longer migration distances than males. Shorebirds may also exhibit sex-specific and age-specific preferences for wintering sites based on habitat quality (Shephard and Lank 2004). As variable environmental conditions and habitats encountered during these energy-intensive journeys may have important implications for the population dynamics of a species (Webster et al. 2002, McDuffie et al. 2022), identifying migration routes, stopover sites, and wintering sites is an important first step for targeting full life cycle conservation initiatives (Hobson 1999). The identification of individual migration routes may also provide valuable information on the nature and extent of biological carry-over effects across the annual cycle (Marra et al. 2015).

Dunlin are intermediate to short-distance migratory shorebirds with 5-13 recognized subspecies (Warnock and Gill 2020), most of which breed in the Arctic or Subarctic. Dunlin tend to follow

a "skip" or "jump" migration strategy, where they refuel small-to-medium energy stores intermittently at a series of quick stops at sites that are short-to-medium distances from one another (Warnock et al. 2004, Warnock 2010, Catry et al. 2022), although there is evidence that this strategy may change seasonally for some subspecies (Pakanen et al. 2018). The subspecies *C.a.hudsonia* breeds in northern Canada, from Victoria Island, Northwest Territories to the western coasts of Hudson and James Bays (Warnock and Gill 2020). *C.a.hudsonia*'s winter range is along the Atlantic coast from New Jersey south to Florida, and along the Gulf Coast west to Texas and Mexico (Warnock and Gill 2020). Using light-level geolocators, we investigated sex-specific and seasonal differences in the migration profiles of Dunlin (*Calidris alpina hudsonia*), breeding in Churchill, Manitoba, Canada, including migration routes, stopover sites, and overwintering sites. *C. a. hudsonia* are well suited to the present study because they exhibit breeding site fidelity across years (see Tomkovich 1994, Thorup 1999), 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). As our current understanding of *C.a.hudsonia* migration comes from individual observations and a small number of band resightings during migration and at non-breeding sites (see Skagen et al. 1999, Warnock and Gill 2020), this study is the first to track individuals throughout their full annual cycle. Identifying the sex-specific, seasonal differences in migration profiles and the degree of migratory connectivity of this breeding population will be important for the development of full life cycle conservation initiatives in this species, as it provides a more informed understanding of where individuals are located year-round.

METHODS

Study sites
The study was conducted near the town of Churchill, Manitoba (58.76841°N, 94.16496°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 territories are abundant and easily accessible. The first site (Fen; 58.67029° N, 93.83457°W) was located about 7.7 km southwest of the Churchill Northern Studies Centre (CNSC) on a plot bordering Twin Lakes Road, and the second site (Gun Range; 58.74604° N, 93.96801° W) was located about 8.9 km northwest of the CNSC (Fig. 1). The nesting area is characterized primarily by fen and sedge meadow habitats (Holmes et al. 2020).

Field methods
We monitored Dunlin during the 2010, 2011, 2016, and 2017 breeding seasons. During each year, nest searching occurred from approximately June 5th to July 20th. Field crews located nests by walking the tundra daily until Dunlin were flushed from the nest or could be followed back to their nests after observing distraction displays. After adults returned to their nest to continue incubation, they were caught with a bownet. 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 100g Pesola spring balance. Dunlin were sexed using a discriminant function analysis (DF = 0.589 x (head length) = 0.096 x (body mass) - 0.051 (tarsus

Fig. 1. Location of our two main field sites (Fen and Gun Range [GR]) near Churchill, Manitoba where geolocators were attached and removed from Dunlin (*Calidris alpina hudsonia*) in 2010, 2011, 2016 and 2017.

length); Koloski et al. 2016), 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 (Mk12A; British Antarctic Survey [BAS], n = 35) and 2016 (W65A9; Migrate Technology, n = 30). The geolocators were glued onto a plastic leg flag and attached to the tibiotarsus (see Figure 1 in Pakanen et al. 2015). Geolocators were removed in the subsequent breeding season after finding nests and recapturing birds.

Geolocator analysis
BAS geolocators recorded light-level readings every minute and recorded maximum light measures from these intervals every 2 minutes, and the Migrate Technology devices took readings every minute and recorded maximum light measures every 5 minutes. Data from recovered BAS geolocators were offloaded in BASTrak (Biotrak Ltd, Wareham, UK), and data from Migrate Technology geolocators were offloaded using IntigeoIF software (Migrate Technology Ltd, Cambridge, UK). To avoid skewing the

estimation of longitude, which depends on comparing time of local noon to this internal clock, internal clock drift was corrected when light-level data were downloaded. For initial twilight selection, we used the R package *TwGeos* (Lisovski 2016) to automatically identify sunrises and sunsets (transitions from light to dark) using a light threshold value of 2.5 for BAS tags and 1.5 for Migrate Technology tags. Transitions from light to dark were edited using an automated process, where twilights occurring 45 minutes before or after the 4 neighboring twilights were considered outliers and removed from analysis. All further geolocator analysis was completed using the package *FlightR* (Rakhimberdiev and Saveliev 2017). When generating movement models within FLightR, 1 million particles were used to optimize reconstruction of a bird's migratory movements (Rakhimberdiev et al. 2016). Since Dunlin 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 southward migration was initiated. 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 traveled between all consecutive twilights for every day that the geolocator was active. Only distances traveled 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. These error estimates allow for easy filtering of reliable positions. Although *FlightR* estimates positions with greater accuracy than other tools used to analyze geolocators, estimates of latitude are still less precise than estimates of longitude (Rakhimberdiev et al. 2017). Latitudinal estimates are particularly poor during the fall and spring equinoxes when there is almost no latitudinal variation in day length (Knight et al. 2018). To increase the accuracy of our dataset, we excluded all stationary position estimates with latitude credible intervals that fell within the top decile (CI > 8.1 degrees). 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 that appeared to be north of the breeding grounds (and thus highly unlikely), or direct north-south-north movements approximately 2 weeks preceding or following fall and spring equinoxes. Questionable latitude estimates were excluded based on interpretation that they represented unlikely movements. We understand that there may be some user bias in doing so. The migratory routes presented in this study are therefore the best approximation of the actual tracks traveled by Dunlin.

Determining migration profiles

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

in the fall or the breeding grounds in the spring. Stopover duration was defined as the total number of days that an individual remained stationary at a single location (or merged locations discussed above) during migration. Based on the geolocator data alone, there is no way to differentiate between a stopover site (i.e., any site where a shorebird stops to feed or rest during migration; Warnock et al. 2010) and a staging site (i.e., sites that have consistent food resources that birds can rely on to refuel before energetically demanding migratory feats; Warnock et al. 2010). Therefore, we use the term stopover site throughout the manuscript unless we provide references to support evidence of staging.

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 (i.e., wintering) site was considered as the location where birds remained stationary for the longest period between October and April (Hobson et al. 2015). In four cases, a second, later, pre-migratory wintering region was identified for birds that made extensive, non-local, movements within this time period. For these four cases, the end of fall migration was determined by arrival to the first wintering region and the start of spring migration was determined by departure from the second wintering region. Movements between these two wintering regions 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 (mean departure date from first wintering site = March 13; mean departure date for spring migration = April 29), and also because these individuals were traveling to locations south of the main wintering site (i.e., moving away, not towards, the breeding grounds).

Fall migration distance was calculated by summing distances Dunlin moved on days between the date of departure from the breeding grounds and date of arrival on the wintering grounds (excluding local movements during stationary periods). Spring migration distance was calculated using the same methods, using days of travel after departure from the wintering site 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. Travel rate was then calculated by dividing migration distance by the travel time. We also calculated the great circle distance (i.e., straight-line distance, GCD) between the breeding and non-breeding sites. We determined the migratory route directness by dividing the GCD by the distance traveled 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).

All analyses were conducted using R Statistical Computing Software* 3.5.1 (R Core Team 2018). Due to limited sample sizes, data for both time periods (2010/2011 and 2016/2107) were combined for analyses. Non-parametric tests were conducted due to violations of the assumptions of homogeneity of variance and/or normality. Seasonal differences in migration strategies were tested using the Wilcoxon signed-rank test and sex differences in

Table 1. Summary of non-breeding stationary periods and fall and spring migration characteristics of 26 Dunlin (*Calidris alpina hudsonia*) from a breeding population in Churchill, MB. Values were derived from geolocator data and represent means over years 2010 - 2011 and 2016 - 2017. Data were 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. Statistically significant differences in migration parameters between seasons are bolded (Bonferonni corrected α = 0.05/3 = 0.016).

Parameter	Fall			Spring			*W*	*P* value
	Mean ± SE	Range	*n*	Mean ± SE	Range	*n*		
Migration initiation date	August 26 ± 7	July 7 - Oct. 23	26	April 29 ± 5	March 18 - May 25	22	NA	NA
Migration end date	Nov. 3 ± 3	Oct. 8 - Dec. 28	25	May 29 ± 1	May 24 - June 3	17	NA	NA
Migration duration (days)	69 ± 9	4 - 142	25	26 ± 5	3 - 75	17	**150**	**<0.001**
Number of stopovers	1.0 ± 0.1	1 - 3	25	1.4 ± 0.2	0 - 3	17	20	0.82
Stopover duration (days)	48 ± 7	3 - 112	25	15 ± 3	3 - 63	17	**148.5**	**<0.001**
Travel time (days)	4.9 ± 0.4	2.1 - 8.5	25	4.1 ± 0.4	1.6 - 7	17	103.5	0.21
Migration speed (km/day)	786 ± 51	352 - 1994	25	963 ± 95	528 - 2145	17	43	0.12
Migration distance (km)	3457 ± 146	2328 - 4810	25	3551 ± 146	2619 - 4812	17	62	0.52
GCD (km)	2878 ± 87	2084 - 3813	25	3043 ± 118	2084 - 4218	25	0	0.10
Migration directness	0.85 ± 0.02	0.62 - 1.00	25	0.86 ± 0.03	0.51 - 1.00	17	78	0.96

migration strategies were tested using the Mann-Whitney U test. Due to the presence of multiple statistical tests per dependent variable, p-values were adjusted using Bonferroni correction (Cabin and Mitchell 2000). Values reported in the result section are means ± SE.

RESULTS

Geolocator recovery
Thirty-five geolocators were deployed in 2010 and 17 of these geolocators were recovered in 2011. Thirty geolocators were deployed in 2016 and 10 were recovered in 2017. These recaptures resulted in device recovery rates of 49% in 2011 and 33% in 2017. Data from one unit recovered in 2017 could not be salvaged. In this same year, one individual carrying a geolocator was resighted but could not be recaptured. Of the 26 geolocators that had usable data, 15 were on females and 11 were on males. Nine devices collected partial track lines, failing sometime before birds returned to their breeding site. In total, we retrieved data for 26 breeding ground departure dates (*n* = 15 females, *n* = 11 males), 25 fall migrations (*n* = 15 females, *n* = 10 males), 22 non-breeding, non-migratory periods (*n* = 13 females, *n* = 9 males) and 17 spring migrations (*n* = 9 females, *n* = 8 males).
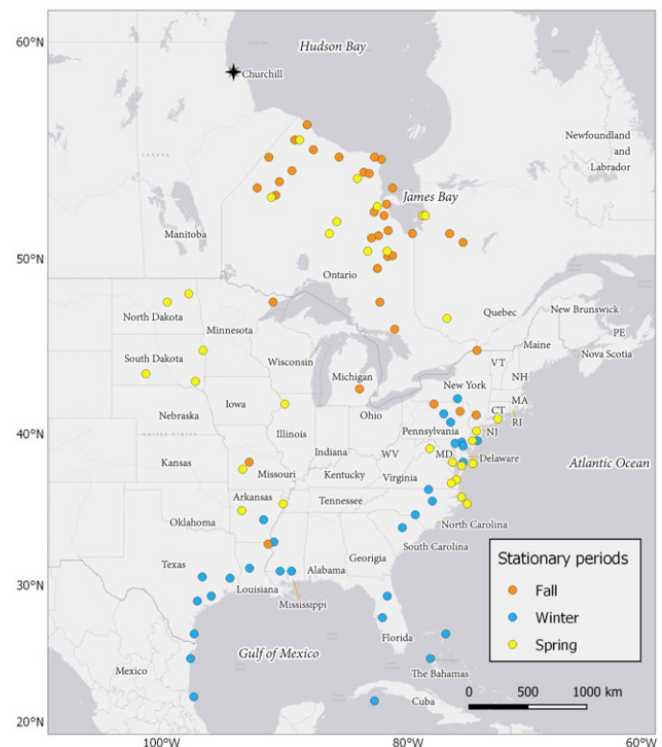
Migration patterns and timing
Dunlin breeding in Churchill departed for fall migration between July 7 and October 23 and arrived at wintering areas between October 8 and December 28 (Table 1). The mean length of fall migration was 69 ± 9 days (range: 4-142 days, *n* = 25). On average, Dunlin used 1.4 ± 0.2 stopover sites and spent 48 ± 7 days refueling at these sites on their southward migration (Table 1). The individual with the longest fall migration flew ~4810 km before arriving at a wintering site in Florida, compared to the shortest migration of ~2328 km to a site in New York (mean distance of all individuals = 3457 ± 146 km, *n* = 25).

Twenty-four (96%) Dunlin migrated south by flying southeast to stopover sites in northern Ontario, along the southwest coast of Hudson Bay or near James Bay (Figure 2). From there, Dunlin wintering at sites along the Atlantic Ocean flew across southeastern Ontario into New York State, before following a coastal route to final overwintering sites (Figure 3). In contrast,

Dunlin wintering at sites along the Gulf of Mexico either flew to these wintering sites directly from James Bay or stopped over in southwestern Ontario before traveling the Mississippi Flyway (across Illinois, Missouri, and Arkansas; Figure 3) to reach these wintering sites.

Fig. 2. Map of stationary position estimates of Dunlin (*Calidris alpina hudsonia*; n = 26) migrating to and from Churchill, Manitoba during the years 2010/2011, and 2016/2017.

Dunlin spent the wintering season at sites along the Atlantic Coast ranging from New York to Florida, and along the Gulf of Mexico

Fig. 3. Migratory tracks of two individuals demonstrating the predominant migration patterns taken by Dunlin (*Calidris alpina hudsonia*) across one annual cycle. Dunlin overwintering at sites bordering the Atlantic Ocean tended to migrate along the border of the Mississippi and Atlantic flyways (A). Dunlin overwintering in Texas often migrated through the centre of the Mississippi flyway on their southbound migration and then migrated through the Central flyway on their return journey (B). Points on the maps are the most probable latitude and longitude for each recorded twilight and lines show direct connections between these positions, not necessarily paths taken by birds.
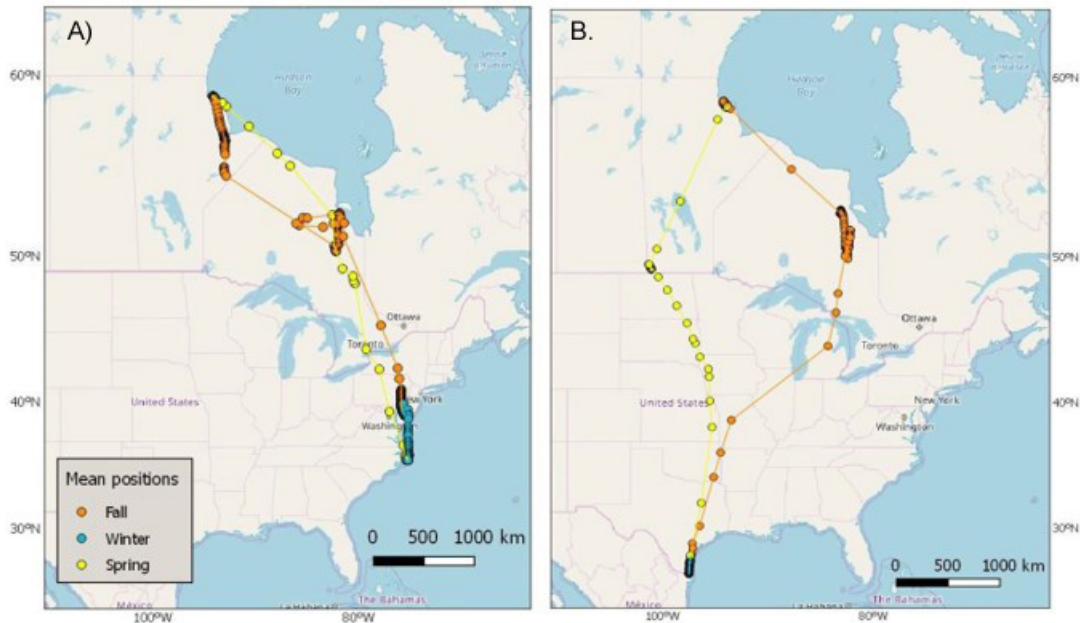
ranging from Mississippi to Mexico (Figure 2). The mean number of days spent at wintering sites was 177 ± 6 (range: 114-220, *n* = 22). Four birds made nonlocal, southward movements in February and March and took prolonged stops at second wintering locations in the Bahamas (*n* = 2), Cuba (*n* = 1), and Mexico (*n* = 1). These Dunlin stayed an additional 41 ± 11 days at this second wintering site (range: 28-48 days).

Dunlin initiated spring migration between March 18 and May 25 and arrived back to the breeding grounds between May 24 and June 3 (Table 1). Spring migration duration (26 ± 5 days, *n* = 17) was significantly shorter than fall migration (69 ± 9 days, *n* = 25; *W* = 150, *P* <0.001). More than half of this spring migration period was spent stopping over at an average of 1.4 ± 0.2 stopover sites (range: 1-3) for an average of 15 ± 3 days (range: 3-63, *n* = 17). Stopover durations were significantly shorter during spring migration (*W* = 148.5, *P* <0.001, Table 1) than fall migration. The average distance traveled during spring migration was 3551 ± 146 km (range: 2619-4812 km, *n* = 17).

Dunlin that overwintered at sites bordering the Atlantic Ocean took similar routes and used similar stopover locations when migrating north as they did south (Figure 3). Despite having migrated through the center of the Mississippi Flyway on their southbound migration, birds overwintering in Texas and Louisiana typically migrated along the eastern boundary of the Central Flyway on their return journey (Figure 3). Eighty-three percent of all individuals that flew through the Central Flyway (*n* = 6) stopped over in North or South Dakota. Dunlin that

stopped in the Dakotas did not make any further stops before arriving at the breeding grounds. 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.

Sex differences in migration strategy

Date of departure from the breeding grounds varied significantly by sex; on average, males departed earlier (August 9 ± 10, range: July 8 to October 14) than females (September 7 ± 9, range: July 23 to Oct 23; *U* = 131, df = 24, *P* = 0.01). Male Dunlin also had a fall migration of longer duration (90 ± 13 days) than females (55 ± 10; *U* = 38.5, df = 23, *P* = 0.05; Table 2). Despite males departing the breeding grounds earlier than females, there was no sex difference in timing of arrival to wintering sites (*U* = 53.5, df = 23, *P* = 0.24; Table 2). During spring migration, males took a more direct route from wintering sites to the breeding grounds than females (males = 0.94 ± 0.02, females = 0.78 ± 0.05; *U* = 10, df = 15, *P* = 0.01; Table 2). There was no evidence to suggest sex differences in any other spring migration parameters (Table 2).

We did find evidence of sex-specific migration patterns in Dunlin during the 2016/2017 study year. Males tended to favor the Mississippi Flyway route on their way to wintering sites along the Gulf Coast, taking the Central Flyway on their return journey (3 of 4 males; Figure A1.4 b,c,d), whereas females opted to take the more easterly route, along the border of the Mississippi and

Table 2. Comparison of the migration strategies of male and female Dunlin (*Calidris alpina hudsonia*). Statistically significant sex differences in migration parameters are bolded (Bonferonni corrected α = 0.05/3 = 0.016).

Parameter	Fall						Spring					
	Females Mean ± SE	n	Males Mean ± SE	n	U	P value	Females Mean ± SE	n	Males Mean ± SE	n	U	P value
Migration initiation date [†]	Sept. 7 ± 9	15	Aug. 9 ± 10	11	131	**0.01**	April 29 ± 6	13	April 28 ± 8	9	62	0.84
Migration end date [†]	Nov. 2 ± 5	15	Nov. 4 ± 4	10	53.5	0.24	May 28 ± 1	9	May 30 ± 1	8	23.5	0.25
Migration duration (days)	55 ± 10	15	90 ± 13	10	38.5	0.05	25 ± 3	9	27 ± 8	8	33	0.81
Number of stopovers	1.0 ± 0.2	15	2.0 ± 0.2	10	69.5	0.74	1.0 ± 0.3	9	2.0 ± 0.3	8	34	0.60
Stopover duration (days)	38 ± 8	15	62 ± 11	10	40.5	0.06	15 ± 5	9	14 ± 4	8	32.5	0.77
Travel time (days)	4.9 ± 0.5	15	4.8 ± 0.6	10	75.5	1.00	4.2 ± 0.5	9	4.0 ± 0.5	8	42.5	0.56
Migration speed (km/day)	780 ± 73	15	794 ± 68	10	71	0.85	987 ± 162	9	936 ± 101	8	35	0.96
Migration distance (km)	3360 ± 177	15	3603 ± 254	10	60	0.43	3640 ± 243	9	3451 ± 159	8	38	0.89
GCD (km)	2809 ± 107	15	2982 ± 148	10	58	0.37	2993 ± 163	15	3119 ± 170	10	62	0.50
Migration directness	0.85 ± 0.03	15	0.85 ± 0.04	10	72	0.89	0.78 ± 0.05	9	0.94 ± 0.02	8	10	**0.01**

[†]Bonferroni corrections for these two variables are α = 0.05/2 = 0.025

Atlantic Flyways, on their way to and from wintering sites along the Atlantic Coast (4 of 5 females; Figure A1.2 b,c,d,e). Six female Dunlin in 2010/2011 took this same route, although one individual (ID 659; Figure A1.1 g) used the Mississippi Flyway on the way south and then used a more coastal route through the Atlantic Flyway on the way north. Another female flew through the center of the Mississippi Flyway in both directions (ID 647; Figure A1.1 e). In 2010/2011, no females used the Central Flyway in the spring, although one individual that died before returning to the breeding grounds could have migrated along this route (ID 675; Figure A1.1 a). In 2010/2011, males used both routes equally (Figure A1.3).

DISCUSSION

To our knowledge, this is the first time *hudsonia* Dunlin have been tracked throughout their complete annual cycle, filling an important knowledge gap in the migration ecology of this species. Despite high concentration of individuals at a few key stopover sites in northern Ontario and the midwestern and eastern United States, adults were spread out evenly across the entire known non-breeding range, covering the Gulf of Mexico and Atlantic coasts.

On their southbound migration, Dunlin used two distinct migration routes after departing from stopover sites in northern Ontario; Dunlin either flew along the border of the Atlantic and Mississippi Flyways to wintering sites bordering the Atlantic Ocean, or through the center of the Mississippi Flyway to wintering sites along the Gulf of Mexico. The most frequented wintering locations along the Gulf of Mexico were in Texas and Mississippi, and along the Atlantic Coast were in Maryland and Delaware, as well as in coastal North and South Carolina.

Dunlin also followed two apparent migration routes during northward migration. Individuals that wintered along the Atlantic Coast followed similar routes when flying north and south. Conversely, those Dunlin that overwintered in sites close to Texas tended to migrate farther west during their northward migration, visiting portions of the Dakotas and Manitoba. Our geolocator data confirm previously reported observations of *C. a. hudsonia* at stopovers along these two northward routes (Skagen et al. 1999, Warnock and Gill 2020) but we are the first to

geographically link this migrating population between seasons. However, not all Dunlin followed these two routes; three individuals overwintering in Texas flew east along the Atlantic coast before migrating through the Mississippi and Atlantic Flyways to reach the breeding grounds.

Migratory connectivity describes the links between breeding and non-breeding sites of individuals and populations. Migratory connectivity is considered high when individuals from a single breeding population move exclusively to a localized area in the migratory range, with little mixing of individuals from other breeding populations, or low when individuals from a breeding population winter over a wide area, mixing with individuals from other breeding populations (Webster et al. 2002). Despite tracking birds from a single, small breeding site, the non-breeding, non-migratory sites identified in this study were spread across most of the known wintering range (Massachusetts to Mexico) for this subspecies (Fernández et al. 2010, Warnock and Gill 2020). This suggests weak migratory connectivity for the *hudsonia* subspecies of Dunlin breeding in Churchill, as these birds appear to diffuse to many locations along the Gulf and Atlantic Coasts during the wintering months. Stopover sites also varied considerably among individuals, but we identified three areas where many of the tracked Dunlin stopped. The first locations occur during southbound migration, when nearly all Dunlin move to areas in northern Ontario, along the coast of Hudson Bay and James Bay. The wetland and coastal habitat of southwestern Hudson Bay and James Bay is a concentration area for up to 25 shorebird species migrating from the Arctic and Subarctic (Friis et al. 2013). Two other important and consistently used stopover sites occur in the spring when Dunlin stop over in North or South Dakota or at sites along the coasts of Virginia and Delaware. The Dakota sites are well known as spring staging areas; every year, thousands of birds stop to gain muscle protein and fat to fuel their migrations north (Skagen et al. 1999, Tsipoura and Burger 1999, Fernández et al. 2010). Warnock and Gill (2020) used resighting observations to suggest that Dunlin overwintering along the Gulf Coast of Mexico likely fly directly to the breeding grounds after stopping over in the Dakotas, and our geolocator data are consistent with this "jump" migration pattern (i.e., long, non-stop flights between sites; Piersma 1987, Warnock 2010), as no stopover areas were

detected between the Dakotas and the breeding grounds in Churchill. The identification of these important sites in our research lends further support for dedicating conservation efforts to these areas.

Timing of migration
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. This post-breeding migration strategy may be explained by Dunlin undergoing pre-basic 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). *C. a. arcticola* breeding in western Alaska and Canada complete pre-basic wing moult during the breeding and post-breeding season, prior to migrating to the wintering grounds (Engelmoer and Roselaar 1998, Warnock et al. 2013), and *C.a. hudsonia* initiate pre-basic wing moult during breeding (L. McKinnon unpublished data). A possible advantage of this moult timing is that these individuals require fewer resources once reaching their wintering grounds, as they are not recovering from migration and regrowing feathers at the same time (Taylor et al. 2011). The delayed departure from Subarctic sites noted in this study could also be related to predator avoidance, where *C.a. hudsonia* may time southbound migration to avoid onset of the constrained raptor migration, as other studies have described in the closely-related *pacifica* subspecies (Lank et al. 2003, Jamieson 2011). For some shorebird species, inter-individual differences in post-breeding migration phenology may be explained by reproductive effort; those individuals that breed successfully may depart later or spend more time recouping costs of a long breeding season, whereas unsuccessful breeders can refuel more quickly for an early departure (Hooijmeijer et al. 2014). The high inter-individual variation in departure dates, travel rates, migration durations and stopover durations documented in our study suggest that Dunlin have migration strategies that are flexible to local, within-year conditions.

Spring migration of shorebirds is typically 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 on northern breeding grounds, where there is a narrow window of time for favorable breeding conditions (O'Reilly and Wingfield 1995). This proved to be the case for *C. a. hudsonia*, as spring migration was, on average, 43 days shorter than fall migration (Table 1). The results from this population of Dunlin support previous interpretations 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 from wintering areas (March 18 - May 25), variable travel rates (528 - 2145 km day^{-1}), and mean stopover durations (3- 63 days) during spring migration, arrival dates to the breeding grounds were confined to an 11-day interval (May 24 - June 3). This suggests that shorebirds can compensate for later spring migration dates through flexibility in other aspects of migration, such as increasing travel rates or having fewer, shorter stopovers (Warnock et al. 2004, Lindstorm et al. 2016, Rakhimberdiev et al. 2018). Long-term monitoring of shorebird arrival dates in Alaska suggests that shorebirds may adjust spring migration schedules to local environmental conditions both on the breeding

grounds and during migration, such as time of ice break up and snowmelt, as well as temperatures during the final portions of their migratory trips (Ely et al. 2018). The northward 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.

Surprisingly, there were no sex differences in timing of arrival to the breeding grounds. This result was somewhat unexpected, as male shorebirds often arrive on the breeding grounds before females to establish the best breeding territories (Kokko 1999, Lanctot et al. 2000), to increase or decrease extrapair copulation opportunities (Kokko et al. 2006, Lanctot et al. 2000), and because, for some species, 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 males appeared to arrive earlier than females due to sex-biased resightings, rather than actual differences in timing of arrival. Warnock et al. (2004) also failed to find a relationship between arrival dates and sex in radio-tagged Pacific Dunlin and Western Sandpipers, although authors note that sample sizes were small and the listening schedule for tracked individuals may not have captured all significant differences between sexes. Another explanation for the lack of sex differences in timing of arrival could be that these females are not delayed on prolonged stopover 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).

In fall, male Dunlin departed from the breeding grounds significantly earlier than females. We expect that males were able to depart earlier because of potential earlier moult timing. Though we did not investigate sex-specific timing of moult in our study, male moult 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, at which time chicks are close to fledging (Jamieson 2011). The males 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.

Conservation implications
This research has identified the coast of Delaware and James Bay area as critical stopover sites that *C. a. hudsonia* rely upon during both south and northward migration. Delaware Bay is known as an important staging site for thousands of shorebirds (Newton 2006) including the endangered Red Knot (*Calidris canutus rufa*; Baker et al. 2004). Unfortunately, collapsing horseshoe crab populations at this site have been linked to declines in some shorebird species that depend on the eggs of this invertebrate to fuel their lengthy northward migrations (Baker et al. 2004, Mizrahi et al. 2012). 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 staging sites are thought to be critically important for "skip" migrants like Dunlin, that must refuel for longer periods of time before departing on their short

to medium migratory flights. The wetland and coastal habitat of southwestern Hudson Bay and James Bay is a known concentration area for up to 25 shorebird species migrating from the Arctic and Subarctic (Friis et al. 2013). Our study confirms that *C. a. hudsonia* are among the many shorebirds that use these two stopover sites and adds to the body of research that stresses the importance of maintaining the quality of these sites for future conservation efforts.

The southern Atlantic and Gulf Coast of Mexico, where nearly half of the tracked Dunlin overwinter, provides essential habitats that are not only important for the Dunlin studied in this project, but are also frequented 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 destabilize the arctic-nesting shorebird populations that occupy these areas during the nonbreeding seasons. That said, the presence of two distinct migration routes (interior and coastal) in this subspecies, in combination with weak migratory connectivity between the breeding and wintering sites, could prove beneficial for the conservation of Dunlin. Variation in migratory strategies and wintering sites may make Dunlin more resilient to habitat modification and predicted changes in climate, as not all sites will be subject to the same degree of change. However, this same variation could complicate targeted conservation efforts as important sites may be more difficult to identify and the spread of sites across the non-breeding range may make them difficult to protect.

There was some evidence for sex-specific differences in migration routes in 2016/2017, with females primarily taking the coastal migration route, while most males migrated along the interior route. In 2010/2011, most females used the same coastal route, although a few females diverged from the two typical routes identified, whereas most males used both routes equally. This further complicates conservation planning, as female and male Dunlin appear to have different habitat requirements during the migratory seasons and care will need to be taken to consider the needs of both sexes when developing effective conservation strategies.

CONCLUSIONS
This study successfully tracked the round-trip journey of Dunlin from a breeding site near Churchill, Manitoba to overwintering locations along the Gulf and Atlantic Coasts. We 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). Focused conservation is difficult to implement for the *C.a. hudsonia* population, as the non-breeding locations identified in this study are not concentrated in one location, but instead span across a large geographic range.

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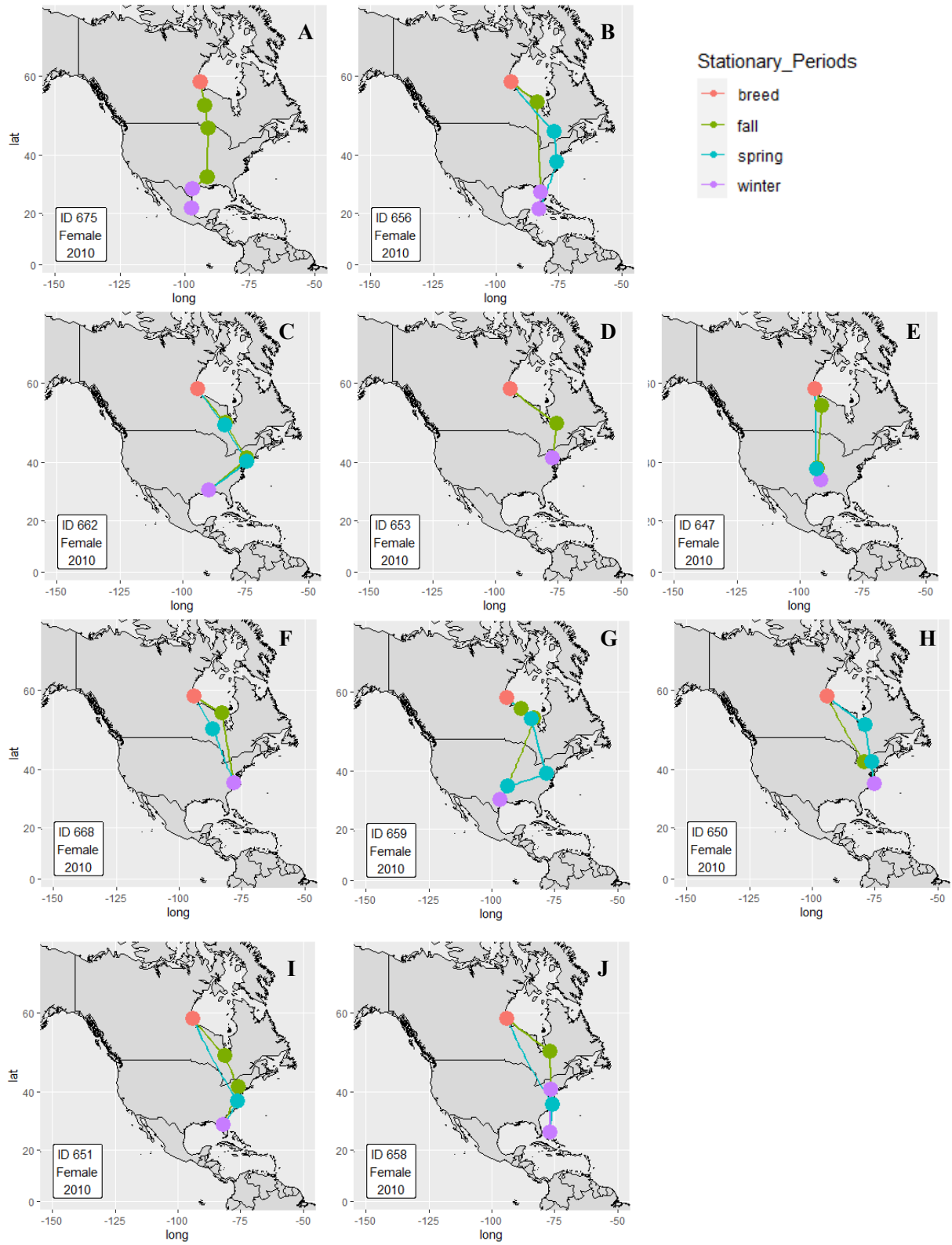
Figure A1.1. Stationary periods of female Dunlin tracked from 2010-2011.
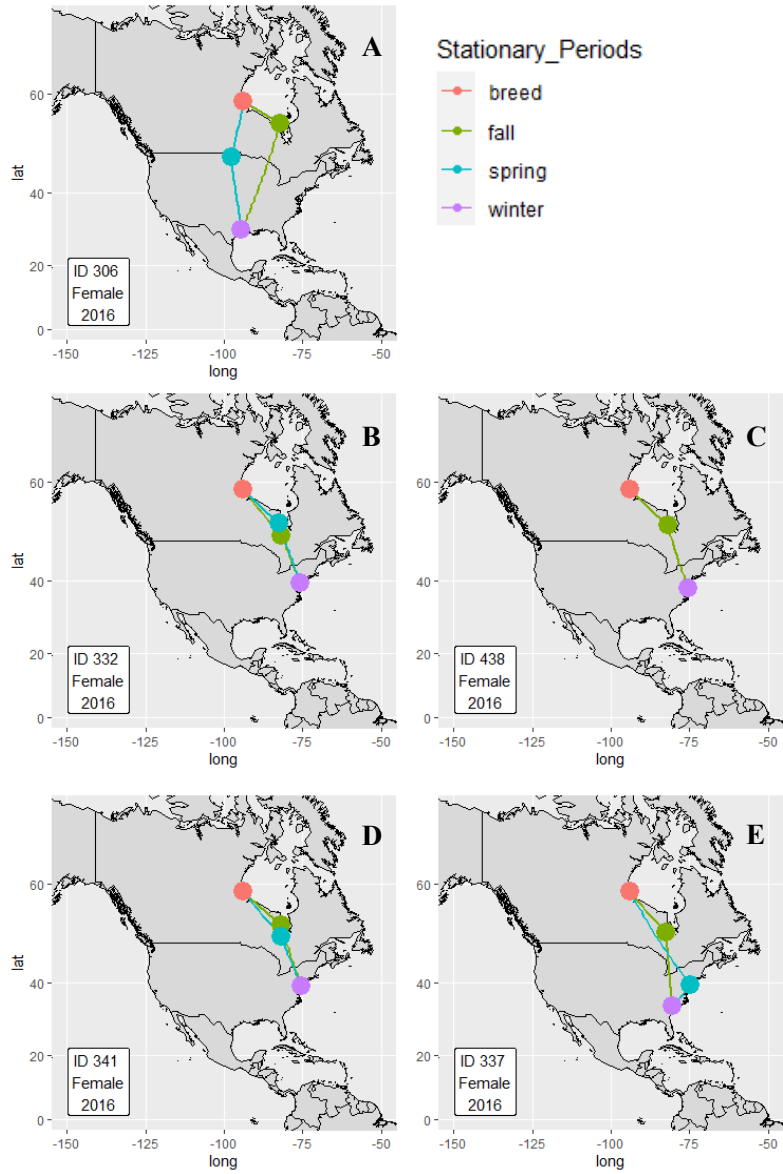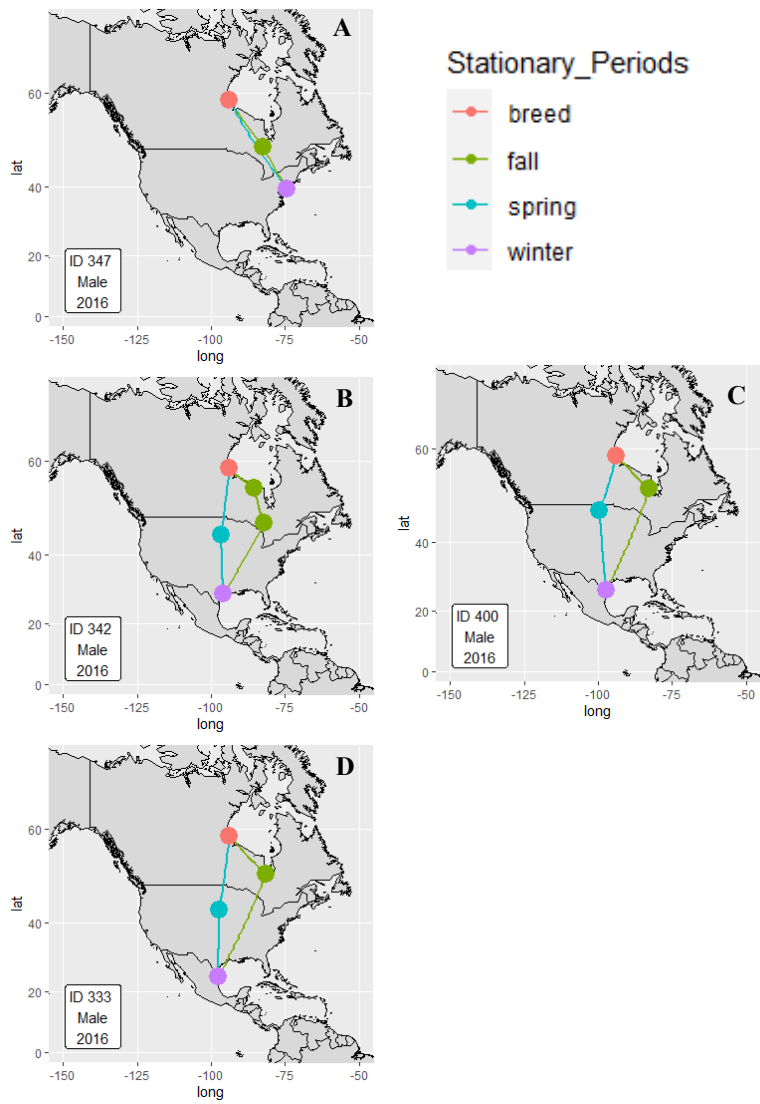
Figure S2. Stationary periods of female Dunlin tracked from 2016-2017.
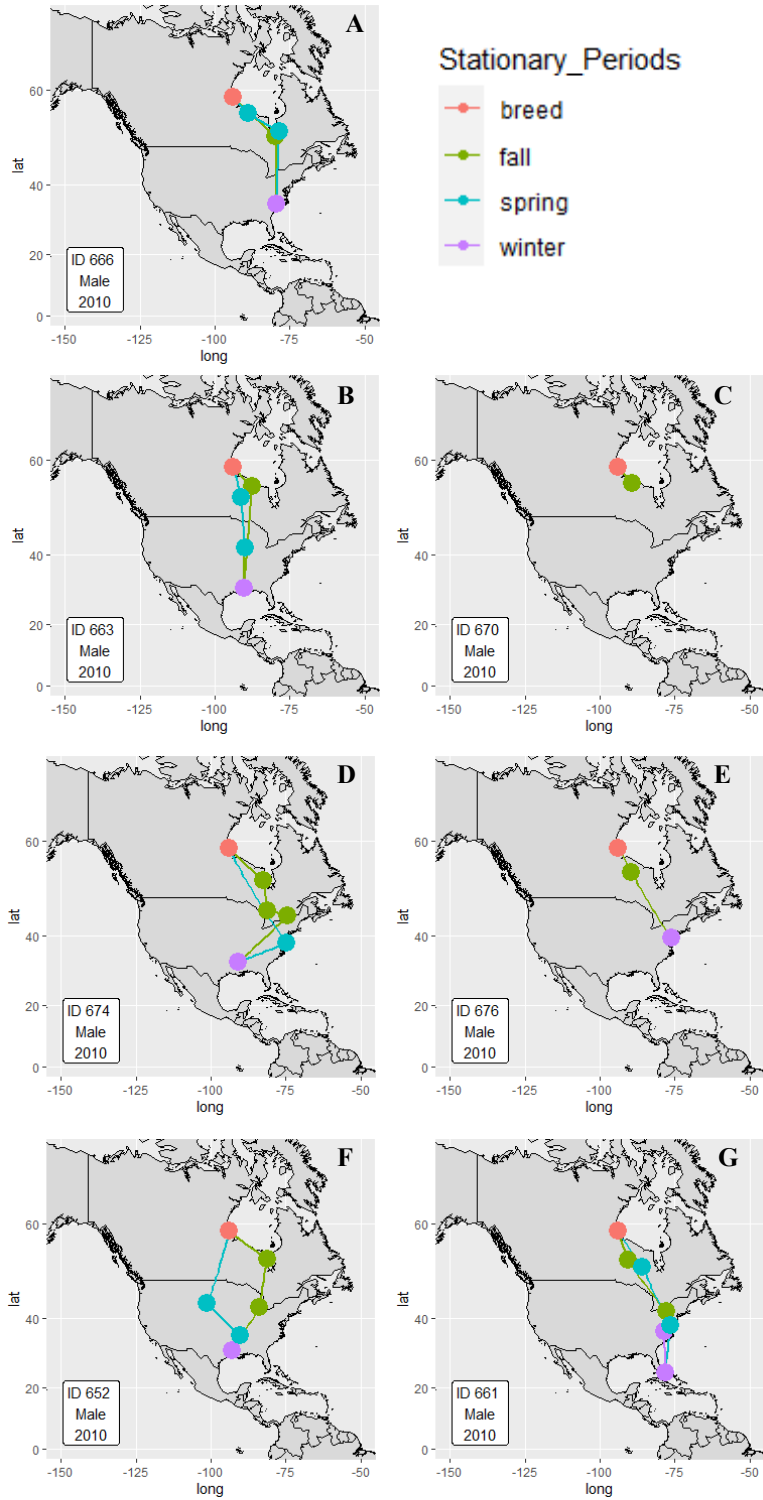
Figure S3. Stationary periods of male Dunlin tracked from 2010-2011.

Figure S4. Stationary periods of male Dunlin tracked from 2016-2017.