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Spring Shorebird Migration Chronology and Stopover Duration at an Important Staging Site in the North American Central Flyway

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Abstract.—Staging, an essential part of shorebird migration, is when birds concentrate in large numbers to rest and refuel. Abundance estimates at key staging sites offer promise to monitor many transient migrant populations; however, stopover chronology is needed. Point counts were conducted of all shorebirds staging at Chaplin and Reed Lakes, Saskatchewan, Canada (May-June 2014-2017). Stopover durations of individual Sanderlings (*Calidris alba*) were obtained using automated radio telemetry of individual Sanderlings tagged both locally and in the Gulf of Mexico (April-May 2015-2017). Seventeen Arctic-breeding shorebird species were recorded during point counts. Sanderlings were the most abundant and reached peak numbers during the last week of May. Estimates of Sanderling stopover duration varied by year and estimation method: "true stopover duration" (radio-tagged in Gulf of Mexico with known arrival and departure) was 11.1 days (95% CI = 8.6-13.6); "minimum stopover duration" (radio-tagged at Chaplin Lake with unknown arrival but known departure) was 11.9 days (95% CI = 11.1-12.7); and "estimated stopover duration" (Pradel Survival and Seniority models) was 19.9 days (95% CI = 17.5-22.7). Assuming an average 11-day stopover, we estimated ~75,000 Sanderlings (Range = 56,000-91,000) or 12% of the global population use this site during spring migration. These findings highlight the importance of accurate migration chronology to monitor Arctic-breeding shorebird populations. *Received 18 May 2018, accepted 5 September 2018.*

Key words.—*Calidris alba*, Central Flyway, migrating shorebirds, migration chronology, Motus automated telemetry, population estimation, Sanderling, stopover duration.

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Migration is a crucial phase of many birds' annual cycles, and populations are vulnerable when concentrated at a single staging site where they need to rest and refuel. Shorebirds are particularly susceptible since they are known to use communal staging areas at high densities, often employing a "jumping" strategy (i.e., long distance flights) interspersed with staging periods of one or more weeks to replenish fat stores (Warnock 2010). Sixty-one percent of studied Arctic-breeding shorebird populations in North America are exhibiting long-term declines (declining for > 30 years), and it is unclear whether these declines are related to factors during migration or other phases of the annual cycle (Andres *et al.* 2012). Therefore, shorebird use of and timing and duration of stopovers at key staging sites remain important research areas for shorebird conservation.

Length of stay at staging sites (stopover duration) can strongly influence overall migration pace, which can exert carry-over effects for reproduction (Newton 2006; Harrison *et al.* 2011). Stopover duration is influenced by various factors including seasonal timing, weather, predators and prey abundance. Individuals staging later in the season are often under pressure to "catch up" by accumulating fuel deposits two to three times faster than individuals arriving earlier in the season (Atkinson *et al.* 2007a). Poor weather (i.e., storms, rain, strong headwinds) may delay departure and extend stopover duration even after birds have deposited enough fuel to make their next flight (Richardson 1990). Increased predation risk and decreased prey availability can decrease fueling rates and shorten or lengthen stopover duration (Ydenberg *et al.* 2004; Jonker *et al.*

2010). This variation in stopover timing and transience at staging sites makes abundance and use patterns difficult to estimate. Therefore, changes in stopover duration could be responsible for apparent shorebird declines if unaccounted for in staging population estimates (Ydenberg *et al.* 2004).

Since staging populations are transient, stopover duration must be considered along with raw abundance when estimating population size. For example, some individuals will be double-counted if a survey interval is shorter than stopover duration or missed if a survey interval is longer (Farmer and Durbian 2006). Mark-recapture techniques are typically used to estimate "minimum stopover duration" as the number of days from capture to last sighting of locally captured individuals (Myers *et al.* 1990; Scott *et al.* 2004) or "estimated stopover duration" using Cormack-Jolly-Seber survival models (Lehnen and Krementz 2007; Gillings *et al.* 2009; Gómez *et al.* 2017). However, these methods often overestimate or underestimate stopover length because the duration that locally marked individuals are present prior to capture is unknown. Additionally, detectability may be low in large or inaccessible sites or when individuals are marked with leg bands only. Radio telemetry can greatly improve stopover estimates of small birds because detectability is limited by equipment range rather than observer error (Chernetsov 2012). Stopover durations of radio-tagged individuals with known arrival dates (e.g., individuals tagged elsewhere prior to arrival), "true stopover duration", is likely the most reliable and accurate method although rarely compared to other estimation methods.

The Central Flyway of North America is used by almost 40 species of shorebirds (Morrison *et al.* 2001), although stopover durations and population estimates at key inland sites are lacking for this region. Large numbers have been reported from some Arctic-breeding species, including Sanderling (*Calidris alba*), Semipalmated Sandpiper (*C. pusilla*), and Red-necked Phalarope (*Phalaropus lobatus*), in the Prairie Pothole Region (PPR) of the Central Flyway during northward migration. Total shorebird numbers migrating through the USA PPR are estimated at 7.3 million in spring and 3.9 million in fall (Skagen *et al.* 2008). Numbers during fall migration are generally lower due primarily to the elliptical migration pattern of some Arctic-breeding shorebirds (Myers *et al.* 1990). Peak daily spring shorebird counts at single sites in the Canadian PPR are often over 25,000 and occasionally over 100,000 (Alexander and Gratto-Trevor 1997; Beyersbergen and Duncan 2007; Beyersbergen 2009a, 2009b).

One major shorebird staging area in the North American PPR is Chaplin and Reed Lakes of southern Saskatchewan, Canada. These saline lakes are recognized as a Western Hemispheric Shorebird Reserve Network site of hemispheric importance used by 100,000 shorebirds or more each spring (Beyersbergen and Duncan 2007). Despite its designation, temporal patterns and population sizes of staging shorebirds at this site are unknown. Our objectives were to: 1) characterize temporal patterns of shorebird abundance for three common Arctic-breeding species during spring migration; and 2) estimate spring stopover duration and population size of the most numerous species, Sanderling (*Calidris alba*), using multiple estimation methods including data from radio-tagged individuals.

METHODS

Study Area

Spring surveys, banding, and telemetry were conducted at Chaplin (50° 26′ 22.52″ N, 106° 38′ 34.98″ W) and Reed (50° 23′ 22.562″ N, 107° 02′ 08.12″ W) Lakes in southern Saskatchewan, Canada (Fig. 1). The lakes are located within the PPR of the Great Plains of North America, an area characterized by millions of shallow wetlands formed by glacial retreat (Winter 1989). Chaplin Lake is the second largest saline lake in Canada, approximately 35 km long and 10 km wide. The lake is divided by roads and dykes into a number of sections that are used for sodium sulphate extraction by a mine on the north shore. As such, water levels on the lake are regulated by activities of the mining operation, but are also influenced by natural precipitation and evaporation. Reed Lake, located approximately 30 km to the west of Chaplin Lake, is another shallow saline lake approximately 13 km long and 3.5 km wide. Water levels

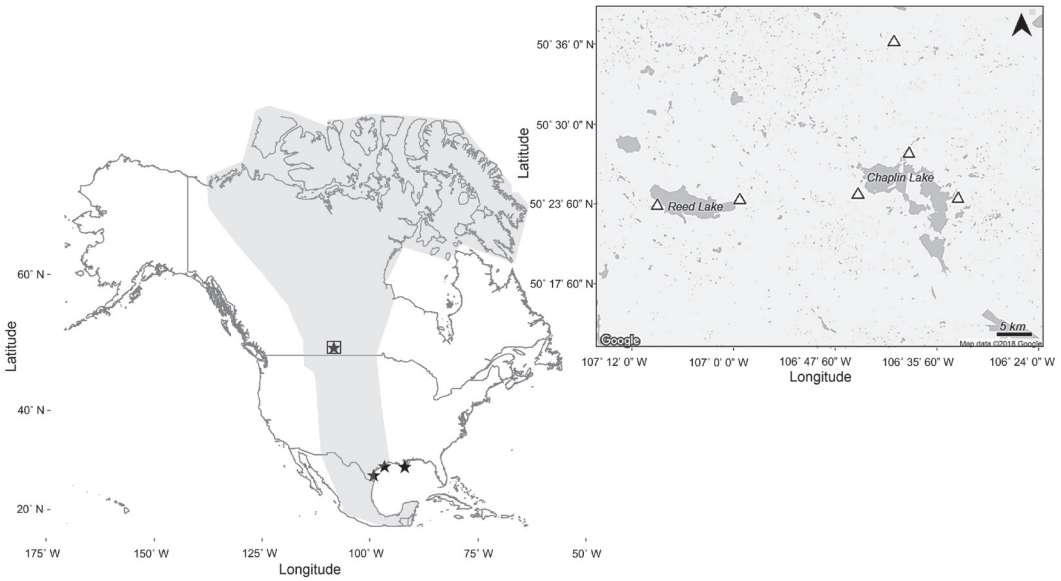

Figure 1. Study sites within the Central Flyway of North America. Shown are the location of trapping and tagging sites in the Gulf of Mexico, USA, and Saskatchewan, Canada (stars), and six Motus telemetry tower locations in proximity to Chaplin and Reed Lakes, Saskatchewan, Canada (empty triangles).

at Reed Lake are influenced by spring runoff, precipitation, and evaporation.

Based on banding and band re-sight records, Sanderlings staging at Chaplin and Reed Lakes were also using the coastal marine beaches throughout the USA Gulf of Mexico earlier in migration as a more southerly staging area (C. A. Morrissey, unpubl. data). We captured, banded and radio-tagged a subset of Sanderlings at three sites in the Gulf of Mexico: North Padre Island, Texas, USA (27° 20′ N, 97° 20′ W), Bolivar Flats, Texas, USA (29° 22′ N, 94° 43′ W), and Grand Isle, Louisiana, USA (29° 10′ N, 90° 04′ W).

Point Count Surveys

Weekly point count surveys of all shorebird species (n = 32 species) at Chaplin and Reed Lakes were conducted during spring (May-June 2014 - 2017) migration. Eighteen point stations were established along the shoreline and roads running through Chaplin Lake, and six along the shoreline of Reed Lake (total = 24 point stations). Each point had an observation radius of 200 m (n = 8) or 500 m (n = 16) depending on topography and proximity to other points. Points were selected systematically along the shoreline and roads such that they encompassed suitable shorebird habitat that was representative of the larger area, were accessible by foot or vehicle, and did not overlap with adjacent points. The spring migration period was defined as 1 May to 15 June, with all 24 points being surveyed once within a 4-day window each week for a total of six spring surveys each year. Surveys were conducted any time between sunrise and sunset, during wind speeds of 0 to 40 kmph, and with zero to light precipitation.

Capture and Radio Telemetry of Sanderlings

From 2015-2017, we captured Sanderlings in the Gulf of Mexico early in spring migration (19 April-12 May), and at Chaplin Lake later in spring migration (13 May-7 June) (Table 1; Fig. 1). We used several capture techniques, depending on time of day and location: mist nets from dusk to dawn (Chaplin Lake only), cannon net (Gulf of Mexico only) or noose carpets (all locations) during daylight hours (Gosler 2004). We did not trap during adverse weather conditions (high winds and/or rain). We banded individuals with one aluminium band, one color band, and one alpha numeric coded plastic

Table 1. Number of individuals tagged, detections, and tagging dates (Julian) for radio-tagged Sanderlings in the Gulf of Mexico, USA, and Chaplin and Reed Lakes, Saskatchewan, Canada, by study year.

Year	No. Tagged in Gulf of Mexico	No. (%) Tagged in Gulf of Mexico and Staging at Chaplin/Reed Lakes	Mean (Range) of Tagging Dates in Gulf of Mexico	No. Tagged at Chaplin Lake	Mean (Range) of Tagging Dates at Chaplin Lake
2015	24	7 (29)	110 (109-110)	38	146 (133-158)
2016	37	4 (11)	115 (111-119)	40	151 (140-159)
2017	59	13 (22)	125 (117-132)	39	149 (139-152)

flag (green for USA, white for Canada), in a combination unique to each year. We glued coded radio transmitters (Lotek Avian NanoTag Model NTQB-3-2), with a 6-8 sec burst rate, 0.67 g mass and ~90-105 day battery life, directly onto the skin and feathers between the scapulae of each bird with a 5 min curing marine epoxy.

We used radio telemetry (Motus Wildlife Tracking System) to monitor individuals' daily presence. This is an expanding network of automated radio-telemetry towers operated primarily in North America and used in combination with miniature long life avian coded transmitters (Taylor *et al.* 2017). These receivers continuously scanned for tags and logged data when a tagged individual was in the immediate area. Our local telemetry array consisted of six towers surrounding Chaplin and Reed Lakes (Fig. 1), each with three nine-element Yagi antennas (Model: Laird PLC1669) oriented 120° from one another and a SensorGnome receiver (Compudata) that scanned on all antennas continuously. Towers operated from at least 5 May-10 October, with most towers operating as of mid-April each year. Towers were approximately 7 m tall, at elevations ranging from ~660 to 725 m above sea level, and with an approximate 12 km range based on test tags flown with unmanned aerial vehicles (J. E. Howell unpubl. data; Taylor *et al.* 2011). For each individual detected by the tower, the tag number (id), date, time (hr:min:sec), antenna, and signal strength (dBm) were automatically recorded. Analyses using raw radio telemetry data were restricted to the spring periods when tagging occurred (2015-2017), but we applied results (mean stopover duration) to population size analysis of all years of the study (2014-2017).

Relative Abundance and General Chronology of Shorebird Migration

We obtained arrival and departure flights of radio-tagged Sanderlings staging at Chaplin and Reed Lakes. We isolated sets of detections of radio-tagged individuals in flight using the following criteria: 1) at least 50% of detections inside the set were separated from each other in time by the interval between transmitter signals (6 or 8 sec in this study); 2) detections inside the set were separated from detections outside the set by 5 or more minutes; and 3) detections inside the set had a curved shape when plotted as signal strength vs. time (Mitchell *et al.* 2012). We defined an arrival as the moment of maximum signal strength during the first set of detections at the study site of an individual radio-tagged in the Gulf of Mexico. We defined a departure as the moment of maximum signal strength during the last set of detections at the study site of an individual radio-tagged either in the Gulf of Mexico or at the study site (Mitchell *et al.* 2012). We identified non-stop flight detections or "fly-overs" (individuals that pass over the towers and site without landing) as single sets of detections; we excluded these individuals (n = 7) from our analyses of stopover duration. Arrivals, departures, and fly-overs were identified for individuals tagged in the Gulf of Mexico, whereas only departures were identified for individuals tagged at Chaplin Lake.

We report relative abundance of all spring staging birds combined, Sanderling, and the two next most common Arctic migrants after Sanderling: Red-necked Phalarope and Semipalmated Sandpiper. We identified peaks in migrating shorebird abundance using histograms of raw bird numbers over time for data from each year of the study. We examined average total abundance across all years using locally weighted regression to identify patterns in staging based on point counts using a LOESS-smoothing function ("ggplot2") in the statistical program R (R Core Development Team 2017). Locally weighted regression is a non-parametric method that is useful for exploring patterns when a specified model may not fit the data well, such as during migration surveys when birds continually enter and exit the area and a fixed pattern of abundance over time may not be expected (Knudsen *et al.* 2007). We assessed consistency in temporal trends among years through visual inspection of confidence intervals; narrow confidence intervals indicate a more consistent trend.

Sanderling Stopover Duration and Population Size Estimates

We used radio telemetry to estimate stopover duration, and both radio telemetry and point count data to estimate population size of Sanderlings staging at Chaplin and Reed Lakes. We were also able to compare stopover duration of individuals tagged in the Gulf of Mexico to those tagged at Chaplin Lake. We calculated "true stopover duration" (TSD) of individuals tagged in the Gulf of Mexico and detected at Chaplin and Reed Lakes as the difference between their dates of departure and arrival. We calculated "minimum stopover duration" (MSD) of individuals tagged at Chaplin Lake as the difference between their dates of departure and capture. Because individuals tagged at Chaplin Lake were present prior to capture for an unknown period of time, MSD may not equal TSD. We tested for a difference between MSD of Chaplin-tagged individuals and TSD of Gulf-tagged individuals using an analysis of variance (ANOVA).

We used Pradel Survival and Seniority models (Pradel 1996) on Chaplin-tagged individuals to obtain "estimated stopover duration" (ESD) (Schaub *et al.* 2001) using program MARK (White and Burnham 1999). Models estimate survival (φ), recapture (p), and seniority parameters (γ). The survival parameter (φ) is equal to the product of probabilities true survival (S) and site fidelity (F). All radio-tagged birds successfully departed from Chaplin or Reed Lake (based on examination of signal strength vs. time plots), so we assumed $S = 1$. Therefore, we were able to define φ as equal to site fidelity (F) (i.e., the probability of remaining at the site after capture) (Sandercock 2006). Recapture probability (p) was assumed to be 1 because the telemetry towers constantly detected any tagged individual in the vicinity at any time. The seniority parameter γ was the probability of having been at the site before capture. Both φ and γ were held constant over time in models such that we could calculate ESD. Data from each year (2015-2017) were analyzed separately, with all encounter histories

beginning on the date that the first individual was captured and ending on the date after the last tagged individual departed the area. We included capture date as a covariate to test for an effect of capture date on φ; individuals captured later in the season often remain for a shorter period after capture (Gillings *et al.* 2009).

To estimate population size of Sanderlings at our study site (Chaplin and Reed Lakes, 2014-2017) while accounting for population turnover throughout migration and among years, we corrected raw point count abundance data for: 1) total number of bird-days; 2) TSD to account for individuals arriving and departing between sampling dates; 3) detectability of Sanderlings at each lake to account for individuals not seen; and 4) an estimate of sampled vs. total available habitat on each lake to account for area not covered during surveys (Farmer and Durbian 2006; Drever *et al.* 2014).

Because not every day of the migration season was surveyed, we modeled the total number of birds over the spring season and then bootstrap-sampled to generate random numbers of birds for each day (Drever *et al.* 2014). We calculated a total number of "bird-days" by modeling number of birds by Julian day for each year, generating random numbers of birds from the models, and then summing the predicted count numbers for all days for each year. Julian date was centered on 145 (25 May) for modeling. This information was entered into a random slopes and intercept linear mixed effects model where count was the response variable and fixed effects included year, Julian date, and a polynomial year term. Random slopes included Julian date and the polynomial term, and the random intercept term was year. This model assumes a fixed migration chronology but allows for variation between years (Drever *et al.* 2014).

To estimate detectability, we reviewed the literature for detectability rates reported in other studies of shorebird migration in similar habitat. Based on published detectability rates (Farmer and Durbian 2006; Brown *et al.* 2007; Ellis *et al.* 2014), we used 0.75 as our detectability rate for Sanderlings in population estimates, which we judged to be a conservative estimate based on the open habitat and high visibility at Chaplin and Reed Lakes. To estimate sampled habitat, we first calculated total area of usable habitat on the lakes. We included all of the roads and dykes on both lakes, 200 m into the lake on each side of the road or dyke, and a 200-m inner buffer around the perimeter of two smaller wetland segments on Chaplin Lake where there was no road. We believe this was a conservative approach and likely a minimum estimate given that there was more available habitat that was not accessible. We calculated the proportion of habitat that we sampled during surveys by dividing the sampled area by the total usable area (Farmer and Durbian 2006). Therefore, the estimated number of birds on each survey date incorporated raw counts from surveys, detectability, and sampled habitat.

We divided the above total bird-day estimates by mean TSD, which accounts for random variation and mean length of stay, and used bootstrapping to obtain 2,000 estimates of population size. We then applied the percentile method for generating the median, 0.025, and 0.975 percentiles as population estimates and confidence intervals for each year of the study (Drever *et al.* 2014). All mixed effects models were fit with package "lme4" in statistical program R (R Core Development Team 2017).

RESULTS

Spring migration was characterized by high species richness (17 Arctic-breeding species), high abundance (highest counts of the most common species in thousands or tens of thousands), and relative consistency in timing among years (Fig. 2; Appendix). The three most common species (Sanderling, Semipalmated Sandpiper, and Red-necked Phalarope) peaked in abundance at different times during spring migration, but mean total abundance of all Arctic-breeding shorebirds combined was highest during the third week of May (raw mean peak count = 13,988 ± 4,336 (mean ± SE), predicted mean peak count = 13,924 ± 2,140, 95% CI = 9,423-18,424).

Sanderling and Red-necked Phalarope contributed most to the overall pattern, each being several times more abundant than any other species (Appendix). Spring Sanderling numbers peaked during the fourth week of May on average (raw mean peak count = 7,297 ± 1,742, predicted mean peak count from LOESS-smoothed mean = 6,584 ± 1,264, CI = 3,935-9,232) (Fig. 2). Red-necked Phalarope abundance peaked during the third week of May (raw mean peak count = 7,720 ± 2,007, predicted mean peak count from LOESS-smoothed mean = 7,711 ± 1,074, CI = 5,461-9,962). Semipalmated Sandpiper abundances were the most variable among years, showing either a single or bimodal peak between the first and fourth weeks of May (raw mean peak count = 964 ± 330, predicted mean peak count from LOESS-smoothed mean = 665 ± 226, CI = 191-1,139) (Fig. 2).

On average, 20% (n = 24/120) of the Sanderlings radio-tagged in late April or early May in the Gulf of Mexico were later detected at Chaplin or Reed Lakes (Table 1). Of these, 82% arrived within the 7-day window of the Chaplin/Reed staging popu-

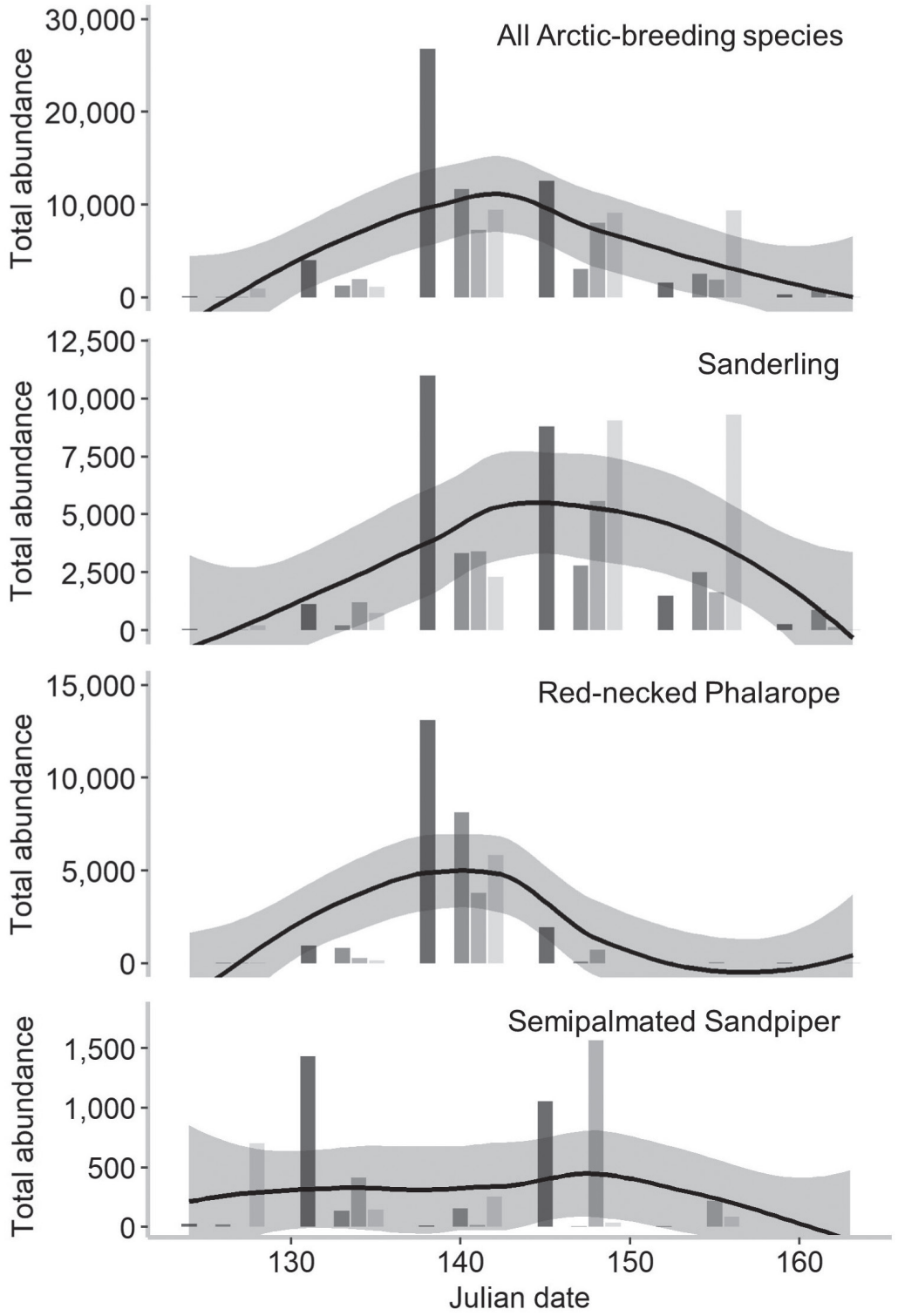

Figure 2. Point count numbers of staging shorebirds observed during spring migration at Chaplin and Reed Lakes, Saskatchewan, Canada, by Julian date for all Arctic-breeding species combined (top) as well as Sanderling, Red-necked Phalarope, and Semipalmated Sandpiper. Bars are shaded light to dark by year (2014-2017). The black line is a total (all years) LOESS-smoothed mean with surrounding 95% CIs (gray).

lation peak. Deviations between the radio-tagged individual arrivals and staging population peak primarily occurred in the 2017 cohort (Fig. 3). Departures based on radio-tagged individuals were concentrated during the first week of June and corresponded with declines in numbers of the staging population detected using point counts (Fig. 3).

Calculated stopover duration for Sanderlings at Chaplin and Reed Lakes varied by year and depended on the method used. TSD ranged from 6.3-14.8 days (mean = 11.1 days), MSD ranged from 10.0-14.8 days (mean = 11.9 days) and ESD from Pradel models ranged from 16.4-23.2 days (mean = 19.9 days) (Table 2). MSD and TSD did not differ significantly by tagging location ($F = 0.549$, df = 138, $P = 0.46$), but did significantly differ among years for both Chaplin ($F = 23.9$, df = 114, $P < 0.001$) and Gulf of Mexico-tagged individuals ($F = 4.40$, df = 22, $P = 0.05$). Mean TSD of Gulf of Mexico-tagged Sanderlings was longer than mean MSD of Chaplin-tagged Sanderlings in 2016 and 2017 but not 2015 (Table 2). MSD and TSD were significantly negatively related to capture/arrival date for both Chaplin ($R^2 = 0.312$, $F = 51.7$, df = 114, $P < 0.001$, $\beta = -0.689$) and Gulf of Mexico-tagged individuals ($R^2 = 0.447$, $F = 17.8$, df = 22, $P < 0.001$, $\beta = -0.612$), suggesting that stopover duration was shorter for individuals that arrived or were captured later in the season (Fig. 3).

We estimated that surveys covered 21% and 23% of total available habitat on Chaplin and Reed Lakes, respectively. Given this, the predicted detectability of Sanderlings (0.75), and an 11-day stopover duration from radio-tagged individuals, we estimated that the Chaplin and Reed Lakes site supports a migrant population of Sanderlings averaging ~75,000 individuals each spring. We caution that Sanderling population estimates were highly variable among the four study years (as were raw counts) and had large confidence intervals (Table 3). The median Sanderling population estimate was lowest in 2016 at 55,617 (CI = 45,309-68,441) and highest in 2014 at 90,832 (CI = 70,005-120,477).

DISCUSSION

This study confirmed the importance of Chaplin and Reed Lakes as a shorebird staging site given the diversity of species and high abundance of spring migrants, particularly Sanderling. Other sites such as Delaware Bay on the Atlantic Coast are known for similarly high shorebird richness and Sanderling counts (Clark *et al.* 1993); however, no other continental inland site in North America has recorded similar concentrations of Arctic migrants. Despite its importance as a shorebird staging area, Chaplin and Reed Lakes had not been formally surveyed since 1993-1994 (Beyersbergen and Duncan 2007). Ground surveys (different from our survey design) conducted on 20 and 26 May 1993 recorded 13,795 individuals (19 species) and 73,358 individuals (16 species), respectively. In 1994, weekly surveys throughout the spring migration reported a peak of 66,820 on 29 May 1994 (24 species). Consistent with those surveys, we detected 17 of the same migrant species. Sanderling was the most numerous species in most years (with the exception of 2016), with 11,000 Sanderlings counted in the third week of May 2017. However, compared to 1993-1994, we detected relatively fewer Semipalmated Sandpipers and Stilt Sandpipers (*C. himantopus*) while Red-necked Phalarope numbers were apparently much higher in 2017 than other years (peak count of 13,123, 170% higher than the mean peak count of all years). This suggests that migration chronology at Chaplin and Reed Lakes has been relatively consistent among years but interannual changes in relative abundance for specific species are notable.

Our data confirmed that Sanderling abundance follows a unimodal distribution with a peak abundance that was consistent with arrival and departure dates from radio-tagged individuals staging for approximately 11.1 days. The unimodal abundance pattern of Sanderling extending over the entire 6-week spring survey period may represent a single population or an inflow and outflow from different populations that overlap during the peak. Sanderling migration is considered heterogeneous, with populations

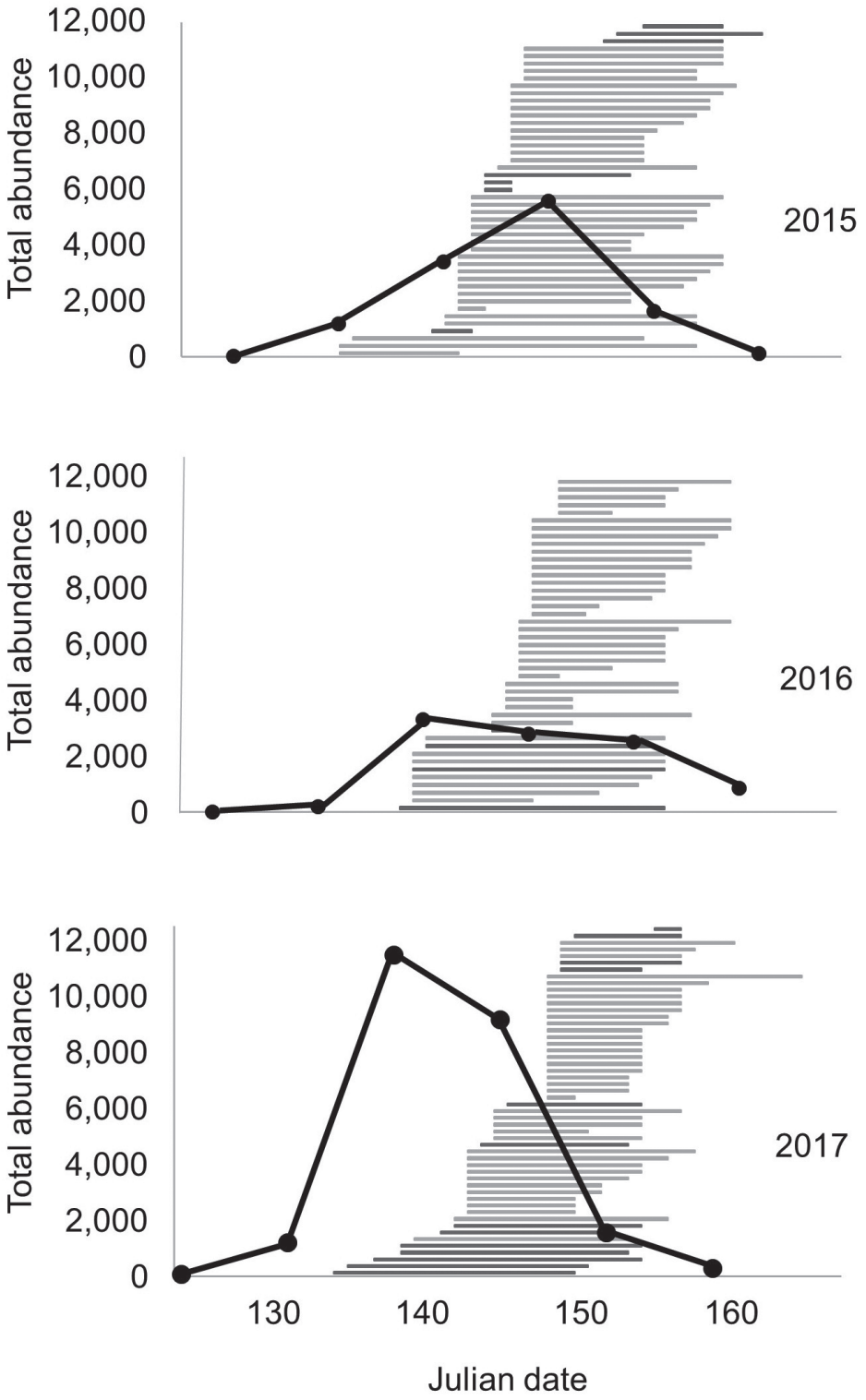

Figure 3. Spring stopover duration of individually radio-tagged Sanderlings marked at Chaplin Lake, Saskatchewan, Canada (light gray), or in the Gulf of Mexico, USA (dark gray). The length of each horizontal line indicates time from capture/arrival date to departure date. Overlaid are total numbers of Sanderlings counted during weekly point counts (black line with points) at Chaplin and Reed Lakes for each year of the study.

wintering over an exceptionally broad range along both coasts of the United States and the Pacific Coast of South America (Myers *et al* 1990). Sanderlings from different wintering origins may have different refueling requirements, which could contribute to the wide range in stopover duration. Stable isotope analysis of feathers from Sanderlings at Chaplin Lake in 2012-2015 suggested there were three general winter origins (populations) that overlapped in time at Chaplin Lake with no reported difference in arrival or staging duration (Labarrère 2016).

A similar unimodal abundance pattern was seen in Red-necked Phalaropes at Chaplin and Reed Lakes. Although no information is known about their wintering origins, fall migrants at nearby Quill Lakes, Saskatchewan (approximately 230 km northwest of Chaplin Lake), were linked to a single breeding population in Prudhoe Bay, Alaska, USA, through DNA cluster analysis (Haig *et al.* 1997). Conversely, the bimodal trend in some years in Semipalmated Sandpiper abundance could be indicative of multiple breeding or wintering populations. A multiyear study using light-level geolocators found that migrating Semipalmated Sandpipers breeding at sites in western Alaska, northern Alaska, and the Mackenzie Delta, Northwest Territories, Canada regularly used the Central Flyway for both northward and southward migration (Brown *et al.* 2017). Semipalmated Sandpipers that staged at Chaplin Lake and other prairie lakes in Saskatchewan and Alberta in spring also appeared to originate from multiple wintering populations in Central America, the Caribbean, Western South America, and northeastern South America (Brown *et al.* 2017). Further analysis of the breeding and wintering origins of Chaplin Lake and Reed Lake shorebird populations using large-scale tracking and isotope analysis may be useful in differentiating populations and their associated migration chronologies and population trends (Atkinson *et al.* 2007b).

The transience of staging shorebird populations can make stopover duration and population size difficult to estimate, but our study provides novel insight comparing individuals radio-tagged prior to arrival at the study site with those tagged locally. We were able to obtain accurate (true) stopover durations from Sanderlings tagged in the Gulf of Mexico. We expected the mean TSD of Gulf-tagged individuals to be closer to ESD of Chaplin-tagged individuals, but TSD was actually closer to the MSD of Chaplin-tagged individuals. Inclusion of stopover duration as well as detectability and habitat use area yielded population estimates ~10 times higher than raw peak counts. Furthermore, adjusting stopover duration by ±1 day yielded mean population estimates 8% lower (12 day stopover) or 10% higher (10 day stopover) whereas using the model based mean ESD of 20 days reduced the population estimate by

Table 2. True, minimum, and estimated spring stopover durations of Sanderlings staging at Chaplin and Reed Lakes derived from original radio-tagging location in the Gulf of Mexico, USA, or Chaplin Lake, Saskatchewan, Canada, for each year of the study (2015-2017) and all years combined. The mean is shown with 95% confidence intervals (CI) with sample sizes (*n*) for true and minimum stopover durations.

Year	True Stopover Duration	Minimum Stopover Duration	Estimated Stopover Duration
2015	6.3	14.8	23.2
	(3.3-9.3)	(13.4-16.2)	(17.2-31.3)
	(*n* = 7)	(*n* = 38)	
2016	14.8	11.0	18.6
	(7.0-22.6)	(9.6-12.4)	(13.8-25.3)
	(*n* = 4)	(*n* = 39)	
2017	12.6	10.0	16.4
	(9.6-15.6)	(8.9-11.1)	(12.3-22.1)
	(*n* = 13)	(*n* = 39)	
All years	11.1	11.9	19.9
	(8.6-13.6)	(11.1-12.7)	(17.5-22.7)
	(*n* = 24)	(*n* = 116)	

Table 3. Median (0.5), lower (0.025), and upper (0.975) annual population size estimates for Sanderlings staging at Chaplin and Reed Lakes during spring 2014-2017. Estimates are based on raw abundance from point count surveys corrected for the sampled proportion of suitable habitat on each lake, detectability (0.75), and a mean stopover duration (11 days).

Year	Highest Raw Count	Median (0.5) Population Estimate	Lower (0.025) Population Estimate	Upper (0.975) Population Estimate
2014	9,303	90,832	70,005	120,477
2015	5,583	71,591	58,003	89,858
2016	3,316	55,617	45,309	68,441
2017	10,987	81,698	61,483	148,639
Mean (all years)	**7,297**	**74,935**	**58,700**	**106,854**

45%. Therefore, the estimation method used for determining stopover duration can have substantial effects on population estimates.

There are several possible explanations for the mismatch between TSD and ESD and the apparent similarity in MSD and TSD: different wintering origins of individuals tagged in the Gulf of Mexico vs. Chaplin Lake, capture stress delaying departures of Chaplin-tagged individuals, or biased capture timing of Chaplin-tagged individuals. Sanderlings trapped in the Gulf of Mexico may be a unique population with shorter staging requirements (e.g., wintering in the Gulf of Mexico instead of South America with a shorter overall migration distance). Alternatively, the longer MSD may have been caused by local capture and handling effects on Chaplin-tagged individuals. Stress of capture, handling and transmitter attachment could have short-term effects on mass and reduced fuel deposition rates (Sykes *et al.* 1990; Schaub and Jenni 2000), resulting in longer stopover durations. Indeed, of 35 individuals captured at Chaplin Lake with a subcutaneous fat score of > 4 (scale of 0-5), only one bird departed the following day and the majority remained on average 9.4 days (95% CI = 8.5-10.3) following capture. We do not suspect any longer-term capture effects occurred in our study because individuals tagged in the Gulf of Mexico migrated to and staged at Chaplin and Reed Lakes and other sites successfully, all individuals detected at Chaplin and Reed Lakes departed the area (no mortality observed), and multiple spring-tagged individuals were detected during fall migration at Motus tower locations or through band re-sightings in the Central and Atlantic Flyways. Alternatively, Chaplin Lake captures could have been biased toward early arriving individuals, especially as these individuals may be more active and therefore more likely to be caught (Smith and McWilliams 2014). Any capture bias toward early staging individuals could have led the Pradel models to overestimate stopover duration. Because the seniority parameter is estimated by inverting the capture history, it effectively assumes that individuals are captured in the middle of their stopover rather than the start or end. Given the potential biases that we were unable to account for in stopover duration estimates from locally tagged individuals, we maintain that data from individuals tagged prior to arrival at a staging site provides the most accurate stopover duration and population estimates.

The staging population of ~75,000 Sanderlings at Chaplin and Reed Lakes represents 58% of the total estimated numbers of Sanderlings using the Central Flyway, 25% of North America's population, and 12% of the global population (Morrison *et al.* 2001; Andres *et al.* 2012). With shallow and stable water levels, abundant food supply (brine shrimp), and generally uninterrupted airspace (few large structures that birds could collide with), Chaplin and Reed Lakes are an attractive staging site to Sanderlings and other migrating shorebirds. However, because Chaplin and Reed Lakes are consistently used as a staging site by a globally significant number of Sanderlings, it means that habitat disturbances at the lakes carry potential population-wide impacts (War-

nock 2010). Climate change predictions include increased drought and lower primary productivity, with the most significant changes in the Canadian PPR (Mitsch and Hernandez 2013; Werner *et al.* 2013). Future increased industrial developments, wind energy projects, water conflicts, and intensified agriculture may exacerbate habitat loss with negative consequences for globally significant numbers of shorebirds (Payne 2010; Sutherland *et al.* 2012; Werner *et al.* 2013). Given the importance of staging site quality and the effect of migration delays on survival and productivity (Finch *et al.* 2014; Schmalojohann *et al.* 2017), we recommend ongoing population monitoring of this and other interior staging sites to evaluate trends and conditions for migratory shorebirds in a changing world.

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Appendix. Peak single counts of all shorebird species during point count surveys conducted during spring migration (May-June 2014-2017) at Chaplin and Reed Lakes, Saskatchewan, Canada. Arctic-breeding species (migrants) are in bold.

		Peak Spring Count			
Common Name	Latin Name	2014	2015	2016	2017
Black-necked Stilt	*Himantopus mexicanus*	2	5	7	1
American Avocet	*Recurvirostra americana*	503	459	183	250
Black-bellied Plover	***Pluvialis squatarola***	0	35	34	256
American Golden Plover	***Pluvialis dominica***	0	0	0	10
Snowy Plover	*Charadrius nivosus*	1	0	0	0
Semipalmated Plover	***Charadrius semipalmatus***	9	10	8	27
Piping Plover	*Charadrius melodus*	20	20	14	10
Killdeer	*Charadrius vociferus*	5	20	24	15
Upland Sandpiper	*Bartramia longicauda*	3	4	0	5
Whimbrel	***Numenius phaeopus***	1	0	0	0
Hudsonian Godwit	***Limosa haemastica***	3	2	1	2
Marbled Godwit	*Limosa fedoa*	14	24	87	15
Ruddy Turnstone	***Arenaria interpres***	0	2	17	11
Red Knot	***Calidris canutus***	22	26	115	95
Stilt Sandpiper	***Calidris himantopus***	1,000	147	78	2,500
Sanderling	***Calidris alba***	9,303	5,583	3,316	10,987
Dunlin	***Calidris alpina***	0	1	11	90
Baird's Sandpiper	***Calidris bairdii***	7	1	16	1
Least Sandpiper	***Calidris minutilla***	2	0	2	0
White-rumped Sandpiper	***Calidris fuscicollis***	1	0	0	30
Pectoral Sandpiper	***Calidris melanotos***	0	2	7	62
Semipalmated Sandpiper	***Calidris pusilla`***	702	1,567	154	1,434
Short-billed Dowitcher	*Limnodromus griseus*	8	0	39	0
Long-billed Dowitcher	***Limnodromus scolopaceus***	7	25	0	43
Wilson's Snipe	*Gallinago delicata*	0	0	1	0
Spotted Sandpiper	*Actitis macularius*	8	4	5	0
Solitary Sandpiper	*Tringa solitaria*	0	1	4	0
Lesser Yellowlegs	*Tringa flavipes*	0	0	7	1
Willet	*Tringa semipalmata*	17	11	33	25
Greater Yellowlegs	*Tringa melanoleuca*	1	0	1	0
Wilson's Phalarope	*Phalaropus tricolor*	454	145	156	123
Red-necked Phalarope	***Phalaropus lobatus***	5,846	3,788	8,125	13,123