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Differences in Migration Timing Along the Midcontinental Flyway in Sanderling (*Calidris alba*) from Three Gulf of Mexico Staging Areas

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Abstract.—Although there is a clear link between early arrival on the breeding grounds and fitness in migratory birds, how winter and staging site use influence the timing of migration events prior to arrival at breeding areas is not well established. Therefore, there is a need to characterize the migration phenology of long-distance migratory birds. This study investigated the northbound migration timing of Sanderlings (*Calidris alba*) along the Central and Mississippi Flyways (i.e., the 'Midcontinental Flyway'). Between 2015 and 2017, coded nanotags were attached to 120 Sanderlings in three staging areas in the USA portion of the Gulf of Mexico: North Padre and Bolivar Flats, Texas and sites in Louisiana. Individuals were then tracked northward using the Motus Wildlife Tracking System. Sanderling detections in more northern latitudes on northward migration were primarily in Saskatchewan (94%; $n = 33$), with only two individuals detected along the Atlantic coast. Sanderlings trapped in North Padre arrived later in Saskatchewan than individuals trapped in Bolivar Flats and Louisiana. Additionally, there was a negative association between Saskatchewan arrival timing and staging duration, such that later-arriving individuals from North Padre had significantly shorter staging durations and consequently departed from Saskatchewan at the same time as individuals originating from Bolivar Flats and Louisiana. These results provide new insight into the migration schedule of a declining long-distance migratory shorebird species and show how departure and arrival timing are linked across disparate staging sites. *Received 4 November 2019, accepted 9 October 2020.*

Key words.—*Calidris alba*, Midcontinental Flyway, migration timing, Motus radio-telemetry, Sanderling, shorebird.

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Every year, long-distance migratory birds travel vast distances to find better foraging opportunities, avoid predation and inclement weather, and improve fitness (Alerstam *et al.* 2003). Although the conditions at their destination (i.e., its breeding and wintering grounds) are significant determinants of fitness and survival (Rappole and McDonald 1994; Latta and Baltz 1997), there is mounting evidence to suggest that conditions encountered on migration are important drivers of population dynamics (Baker *et al.* 2004; Newton 2006; Hewson *et al.* 2016). In particular, factors that influence the timing of northbound migration, such as weather (Sinelschikova *et al.* 2007) and prey availability (Zwarts 1990), are linked to the fitness of migratory birds. This is because early arrival on the breeding grounds is associated with access to higher quality territories and mates, earlier breeding, bigger clutches, higher offspring survival, additional time for re-nesting, and, consequently, greater reproductive success (Norris *et al.* 2004; Smith and Moore 2005).

Despite the clear link between early arrival to breeding areas and fitness, a complete understanding of the migration phenology of many species is lacking. Moreover, although recent studies have revealed differences in the timing of northbound and southbound avian migration (e.g., Lislevand

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et al. 2016; Carneiro *et al.* 2018; Covino *et al.* 2020), less is known about whether or how individuals adjust their migration timing within a season. Studying long-distance migrants has been complicated by the logistical difficulty of tracking individuals (particularly small-bodied species) across widely dispersed, but biologically linked, breeding, staging, and wintering sites (Marra *et al.* 2015). Recent advances in automated radio-telemetry, including the development of automated receivers and the miniaturization of radio-tags, has facilitated the tracking of small migrants across broad geographical scales (Taylor *et al.* 2017).

Our goal was to examine the timing of northbound migration and linkages between major staging areas in Sanderling (*Calidris alba*), a long-distance migratory shorebird species that has declined at a rate of -3.3%/year since the 1970s (Environment and Climate Change Canada 2019). New World Sanderling can migrate up to 10,000 km annually between their wintering grounds in South and Central America and the Gulf of Mexico (GOM) and their breeding grounds in the Canadian Arctic (Macwhirter *et al.* 2020). We recently found that departure dates vary among Sanderling trapped in different staging sites in the GOM, which is linked to individual condition and oil spill contaminant levels (Bianchini and Morrissey 2018a). Here, we investigated whether these individuals from different GOM staging sites continue to show differences in arrival and subsequent departure timing as they migrate farther north.

Our objective was to compare the travel times and northbound migration timing of Sanderling trapped in three staging sites in the USA portion of the GOM: North Padre, Texas, Bolivar Flats, Texas, and Louisiana. Banding records suggest that most Sanderling staging in the GOM migrate north along the Central and Mississippi Flyways (hereafter the 'Midcontinental Flyway') through the Canadian Prairies (Myers *et al.* 1990), with up to 75,000 Sanderling staging at Chaplin and Reed Lakes in Saskatchewan, Canada (Howell *et al.* 2019). This represents approximately 58% of the total estimated numbers of Sanderlings using the Midcontinental Flyway or 12% of the global population (Howell *et al.* 2019). Chaplin and Reed Lakes are recognized as globally significant sites under the Important Bird Areas program (Schmutz 2000) and as sites of hemispheric importance in the Western Hemispheric Shorebird Reserve Network (Beyersbergen and Duncan 2007). In this study, travel time was defined as the total time of migration (i.e., a combination of any time spent in flight and staging) between the GOM and a more northern staging site, and migration timing was defined as the dates when individuals were migrating (i.e., arrival and departure dates). We tracked Sanderling as they travelled north using the Motus Wildlife Tracking System (Motus), an international array of automated radio-telemetry receivers (Taylor *et al.* 2017). In a previous study, we found that individuals trapped in North Padre, Texas, departed earlier from the GOM than individuals trapped in Bolivar Flats, Texas, and Louisiana (Bianchini and Morrissey 2018a). Therefore, here we examined whether Sanderling departing from North Padre would continue to exhibit differences in travel times to and departure timing from Saskatchewan relative to individuals departing from the other GOM sites.

METHODS

Study Area

Between 2015 and 2017, we trapped 120 Sanderling during northward migration from staging sites in Texas (North Padre Island: 27° 20′ 56.0″ N, 97° 19′ 49.3″ W; Bolivar Flats: 29° 24′ 05.6″ N, 94° 42′ 32.7″ W), and Louisiana (Elmer's Island Wildlife Refuge: 29° 10′ 49.4″N, 90° 03′ 58.1″ W; Grand Isle: 29° 13′ 11.2″ N, 90° 00′ 59.5″ W; Port Fourchon: 29° 05′ 51.1″ N, 90° 12″ 16.9″ W) (Fig. 1). We classified trapping sites in the GOM into three staging areas: (1) North Padre Island, Texas; (2) Bolivar Flats, Texas; and (3) Louisiana (composed of Elmer's Island, Grand Isle, and Port Fourchon) based on evidence that individuals did not make local movements between these three areas (Bianchini and Morrissey 2018a).

Animal Capture and Handling

We trapped Sanderling during the day using cannon nets and noose carpets (capture dates are

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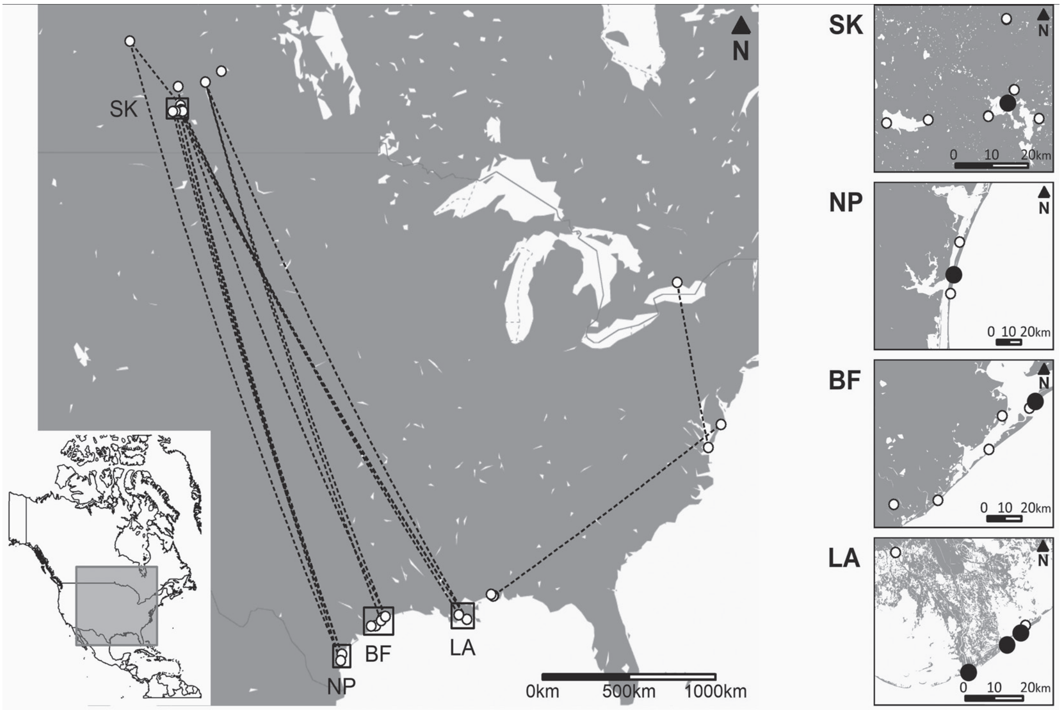

Figure 1. Migration tracks of 35 radio-tagged Sanderling (*Calidris alba*) that were detected outside of the Gulf of Mexico (white circles indicate detection locations). For these birds, dashed lines connect the great circle distances between an individual's last detection in the Gulf of Mexico and its first detection at a more northern site (lines do not necessarily indicate flight paths). The map inset indicates the area in North America shown in the larger map. Smaller panels give a higher magnification of the Chaplin and Reed Lake, Saskatchewan (SK), North Padre (NP), Bolivar Flats (BF), and Louisiana (LA) staging areas, showing the receiver locations where Sanderling were detected (smaller white circles) and trapping sites (larger black circles) within each area.

given in Table 1). Upon capture, we weighed, measured, and gave a unique numbered metal band and a coded alpha numeric flag to each individual. We attached Lotek coded nanotags (NTQB-3-2, Newmarket, Ontario, Canada) to Sanderling in North Padre ($n = 59$), Bolivar Flats ($n = 31$) and in Louisiana ($n = 30$). Tags weighed 0.67 g or < 1.5% of the estimated lean body mass of Sanderling (Scott *et al.* 2004) and were programmed with pulse lengths of 2.5 ms and pulse intervals of approximately 6 s (2015 and 2016) and 8 sec (2017), at a single frequency (166.380 MHz). Sanderling undergo extreme variations in body mass during migration (mass ranges from ~ 40 to > 100 g during a single staging event; Robinson *et al.* 2003), which makes using harnesses a poor option for attaching nanotags to Sanderlings. Therefore, we affixed nanotags to each bird's upper back by parting the feathers and gluing tags to the bird's skin using a quick-setting marine epoxy (J-B Weld ClearWeld 5 Min Epoxy). We aged Sanderlings according to Pyle (1997), and we only attached nanotags to adult after second year (ASY) individuals, as second year (SY) juvenile shorebirds can exhibit alternative migration schedules, with juveniles tending to either migrate after adults on northward migration or to forego migration and stay on the wintering grounds (Newton 2011).

Detection Data Collection and Processing

We tracked Sanderling migration movements using Motus (Taylor *et al.* 2017). Between 2015 and 2017, over 300 receiver stations were operational in North America. Nanotags were recorded by SRX receivers (Lotek Wireless, Newmarket, Ontario, Canada) or by Sensorgnome receivers (Compudata, London, Ontario, Canada), which can detect radio-tagged individuals within ~20 or ~50 km, respectively, of a receiver tower (Anderson *et al.* 2019). We removed false detections by filtering out detections with less than three consecutive bursts on a single antenna at a single receiver (Crewe *et al.* 2018). Our radio-tagged Sanderlings were detected at 26 receiver stations during their northward, spring migration (Fig. 1), giving us the time of detection and approximate location of individuals over the study period.

We tracked radio-tagged Sanderlings to Chaplin Lake (50° 26′ 28.36″ N, 106° 40′ 9.37″ W) and Reed Lake (42° 21′ 36.36″ N, 107° 6′ 7.1064″ W) in Saskatchewan by erecting six Motus receiver towers at this location. We positioned towers to give complete coverage

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Table 1. Summary of means ($\bar{x}$) and ranges of Sanderling (*Calidris alba*) capture dates, departure dates from the Gulf of Mexico (GOM), travel times from the Gulf of Mexico to Saskatchewan, arrival and departure dates in Saskatchewan, and staging durations in Saskatchewan[a].

	GOM staging area							
	North Padre		Bolivar Flats		Louisiana		GOM average	
Timing variables	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Capture date (day of year)	118	109 – 132 (n = 59)	120	114 – 126 (n = 30)	116	114 – 119 (n = 30)	118	109 – 132 (n = 119)
GOM departure (day of year)	134	123 – 159 (n = 18)	137	123 – 153 (n = 17)	136	123 – 144 (n = 13)	136	123 – 159 (n = 48)
Travel time (days)	17.4	6.3 – 34.0 (n = 10)	15.4	11.0 – 20.1 (n = 4)	11.4	3.17 – 23.3 (n = 6)	15.2	3.2 – 34.0 (n = 20)
Saskatchewan arrival (day of year)	149	140 – 159 (n = 16)	138	133 – 145 (n = 6)	146	137 – 157 (n = 6)	146	133 – 159 (n = 28)
Saskatchewan staging duration (days)	8.2	2.2 – 13.2 (n = 9)	15.8	9.9 – 19.7 (n = 6)	14.5	7.6 – 17.3 (n = 4)	11.9	2.2 – 19.7 (n = 19)
Saskatchewan departure (day of year)	156	142 – 164 (n = 9)	153	150 – 158 (n = 6)	156	154 – 158 (n = 4)	154	142 – 164 (n = 19)

[a] Arrival dates, departure dates, and staging durations in Saskatchewan only include Sanderling detections from Chaplin and Reed Lakes.

of the staging area, so that arrival and departure dates could be determined with a high level of accuracy.

We calculated Sanderling departure dates from the GOM and arrival and departure dates in Chaplin and Reed Lakes, Saskatchewan, using Motus detection data. We classified departure dates as an individual's last detection at a site (Bianchini and Morrissey 2018a). For Sanderling detected in both the GOM and Saskatchewan (n = 20), we calculated travel time between these locations as the number of days between an individual's last detection in the GOM and an individual's first detection in Saskatchewan. For individuals that staged in Saskatchewan (n = 19), we calculated staging duration as the number of days between an individual's first and last detection in Chaplin and Reed Lakes (i.e., departure – arrival date). Here, we defined a staging event as a detection period lasting at least two days, and shorter durations were considered fly-bys (a two-day cut-off has been used for staging duration calculations in previous studies; e.g., Gómez *et al.* 2017). This eliminated nine birds that were detected for a median of 34 minutes (range = 1.42 min – 22 hours). It was not possible to reliably differentiate between migratory and regional movements with the current dataset; therefore, we assumed that the last and first detections at a site corresponded to the actual departure and arrival dates of actively migrating individuals. Our departure and arrival dates are consistent with previously measured departure and arrival timing of Sanderling in the GOM and in Saskatchewan (Myers *et al.* 1990; Macwhirter *et al.* 2020; Withers 2002). However, a limitation of the Motus system is that individuals can move out of the range of receiver stations, and it is possible that actual departures are later and actual arrivals are earlier than those reported here.

Statistical Analyses

We examined whether there were differences in travel time and migration timing among Sanderling tagged in the three GOM staging areas (North Padre, Bolivar Flats, and Louisiana). We found differences in departure dates from the GOM in a previous study (Bianchini and Morrissey 2018a). In this study, we looked for the following differences among the three GOM staging areas: we compared (a) travel times to Saskatchewan; (b) arrival dates in Saskatchewan; and (c) departure dates from Saskatchewan using linear mixed effects models (LMMs), and we compared (d) staging durations in Saskatchewan using a generalized linear mixed effects model (GLMM) with a log link function, assuming a quasi-Poisson error distribution, which was appropriate given that these were overdispersed count data (Ver Hoef and Boveng 2007). We included staging area and year as fixed effects in all global models. As individuals were trapped in cohorts at each location on only a few occasions, we included capture date as a random intercept to account for seasonal variation.

We further examined the relationships among the above measures of migration timing. We used LMMs to examine the effect of (a) GOM departure date on travel time to Saskatchewan; (b) GOM departure date, travel time to Saskatchewan, and the interaction of de-

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parture date and travel time on Saskatchewan arrival date (departure date and travel time were not collinear; variance inflation factor (VIF) < 2); and (c) Saskatchewan arrival on Saskatchewan departure. A GLMM with a quasi-Poisson error distribution was used to examine (d) the relationship between Saskatchewan staging durations and arrival dates. Here, we included year as a fixed effect and capture date and staging area as random intercepts in all global models.

We observed unequal variance in residuals among years and staging areas in models where GOM departure date was the response variable. We also observed unequal variance among years in all models where Saskatchewan departure date was the response variable. In these models, we added variance structures (using the varIdent function in the nlme package; Pinheiro *et al.* 2018) for staging area and/or year to allow for heterogeneity without transforming the response variables (Zuur *et al.* 2009). We did not accommodate for spatial structure in our comparisons among staging areas, as Mantel tests (run using the mantel function in the vegan package; Oksanen *et al.* 2018) indicated that response variables were not spatially autocorrelated ($-0.06 < R^2 < 0.05$, $P > 0.20$).

All analyses were performed in R version 3.4.2 (R Core Team 2017). We ran LMMs in the nlme package (Pinheiro *et al.* 2018) and GLMMs in the MASS package (Venables and Ripley 2002), using the glmmPQL function. For LMMs, we used lower AICc scores (Akaike's information criterion corrected for small sample size), model weights, and deviance scores for model selection according to Burnham and Anderson (2002) using the bbmle package (Bolker and R Development Core Team 2017). Where models were equivalent (ΔAICc < 2), we calculated weighted model-averaged estimates for fixed effects in the top model set using model.avg in the MuMIn package (Barton 2017). Because our GLMMs used a quasi-Poisson error distribution, rather than log-likelihood, there was no AICc for model comparison. Furthermore, because the glmmPQL function does not preserve a deviance parameter in the fitted model, it is not possible to use quasi-AICc (Bolker 2017). Therefore, we performed model selection for GLMMs using backward elimination of the fixed effects based on the estimated *P*-values of the fixed effects, with $P < 0.05$ as the selection criterion (Bolker *et al.* 2008). We performed all plotting using packages ggplot2 (Wickham 2009) and cowplot (Wilke 2017). We generated maps using the packages ggmap (Kahle and Wickam 2013) and RgoogleMaps (Loecher and Ropkins 2015).

RESULTS

Thirty-five of the 120 individuals tagged in the GOM were detected again by receivers in more northern latitudes. Of these, 94% ($n = 33$) were detected in Saskatchewan, and 6% ($n = 2$) were detected in the Atlantic Flyway. Migratory movements of Sanderling trapped in the GOM therefore indicated that most northward migration occurred along the Midcontinental Flyway (Fig. 1; online Appendix: Fig. A1 for the number of tags deployed and detected in each location).

We found differences in travel times and migration timing among Sanderling trapped in three GOM staging areas (Table 1). Motus detection data suggested that relative to Sanderling trapped in Bolivar Flats and Louisiana, Sanderling trapped in North Padre departed significantly earlier from the GOM (Bianchini and Morrissey 2018a; Fig. 2a) and travelled more slowly to Saskatchewan ($\beta \pm$ SE = 15.2 ± 5.8 days, $P = 0.049$; Fig. 2b; online Appendix: Tables A1 – A8 model selection results). North Padre migrants also arrived latest in Saskatchewan ($\beta \pm$ SE = 12.2 ± 3.4 days, $P = 0.049$; Fig. 3a). However, we found that North Padre Sanderling departed from Saskatchewan at the same time as individuals from the other staging areas (GOM staging area was not retained in the top model to explain variation in Saskatchewan departure dates; Fig. 3b) by shortening their staging durations ($\beta \pm$ SE = -0.66 ± 0.17 days, $P = 0.002$; Fig. 3c). Sanderling trapped in Bolivar Flats and Louisiana had similar patterns in the timing of migration, with no significant differences in departure dates from the GOM ($\beta \pm$ SE = -0.25 ± 2.42 days, $P = 0.92$; Fig. 2a), travel times to Saskatchewan ($\beta \pm$ SE = -4.2 ± 4.1 days, $P = 0.36$; Fig. 2b), Saskatchewan arrivals ($\beta \pm$ SE = 8.0 ± 3.6 days, $P = 0.05$; Fig. 3a), or Saskatchewan staging durations ($\beta \pm$ SE = -0.088 ± 0.188 days, $P = 0.65$; Fig. 3c).

Arrival dates in Saskatchewan were positively associated with GOM departure dates ($\beta \pm$ SE = 1.01 ± 0.02, $P < 0.0001$;) and travel times to Saskatchewan ($\beta \pm$ SE = 0.99 ± 0.02, $P < 0.0001$; online Appendix: Fig. A2), such that individuals departing later from the GOM and traveling more slowly arrived later at the more northern site. Further examination of migration timing revealed no association between GOM departure date and travel time to Saskatchewan, such that Sanderling departing later from the GOM did not travel faster to the northern site. We saw no association between Saskatchewan arrival and departure dates. Instead, there was a

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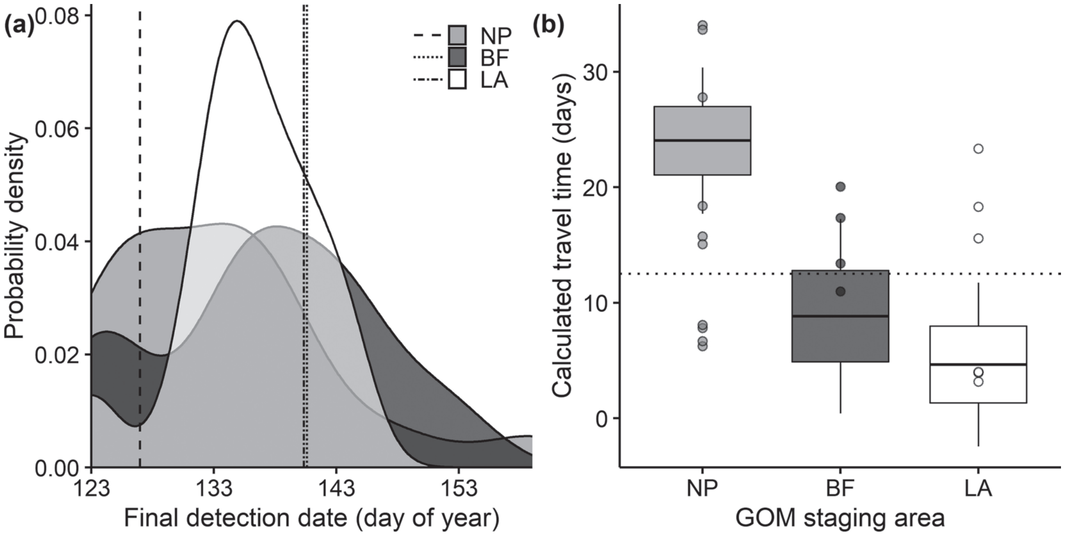

Figure 2. Final detection dates (a) and calculated travel times to Saskatchewan (b) of Sanderling (*Calidris alba*) trapped in three Gulf of Mexico staging areas (NP = North Padre, BF = Bolivar Flats, LA = Louisiana). (a) Shaded polygons (from raw data) represent the probability density of departure (area under the curves = 1), and vertical lines indicate the model-averaged mean departure date from each area (NP: *n* = 18, BF: *n* = 17, LA: *n* = 13). (b) Boxes show model-averaged means ± SE, with vertical lines indicating the 95% confidence intervals. Circles indicate raw travel time values (NP: *n* = 10, BF: *n* = 4, LA: *n* = 6). The dotted horizontal line shows the model-averaged mean travel time of all individuals (*n* = 20). Note that the difference in departure dates among staging areas was revealed in our previous paper (Bianchini and Morrissey 2018a).

negative association between Saskatchewan arrival dates and staging durations, such that later-arriving individuals spent less time staging in Saskatchewan (β ± SE = -0.046 ± 0.011, $P = 0.0005$; Fig. 4). Year explained some of the variance in GOM departure dates and travel time to Saskatchewan. On average, Sanderling tended to depart later and travel

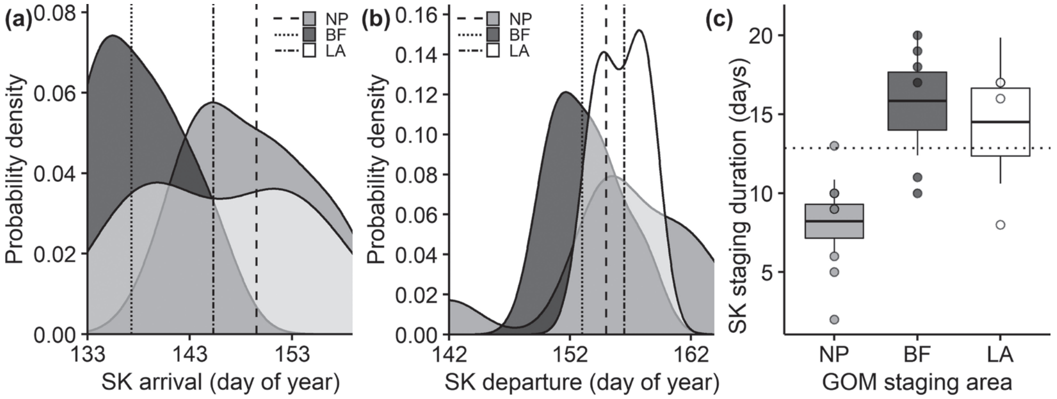

Figure 3. (a) Sanderling (*Calidris alba*) trapped in North Padre (NP, *n* = 16) arrived later in Saskatchewan (SK) relative to birds trapped in Louisiana (LA, *n* = 6) and Bolivar Flats (BF, *n* = 6). (b) There was no difference in SK departure dates among individuals from the three Gulf of Mexico (GOM) staging areas (NP: *n* = 9, BF: *n* = 6, LA: *n* = 4), as (c) NP Sanderling (*n* = 9) had shorter staging durations in SK relative to birds from BF (*n* = 6) and LA (*n* = 4). In panels a and b, shaded polygons (from raw data) represent the probability density of SK arrival and departure, respectively (area under the curves = 1). In panel a, vertical lines indicate model-averaged mean arrival dates, and in panel b, vertical lines indicate median departure dates calculated (from raw data). In panel c, boxes show model-averaged means ± SE, with vertical lines indicating the 95% confidence interval. Circles show raw staging duration values, and the dotted horizontal line shows the model-averaged mean staging duration of all individuals.

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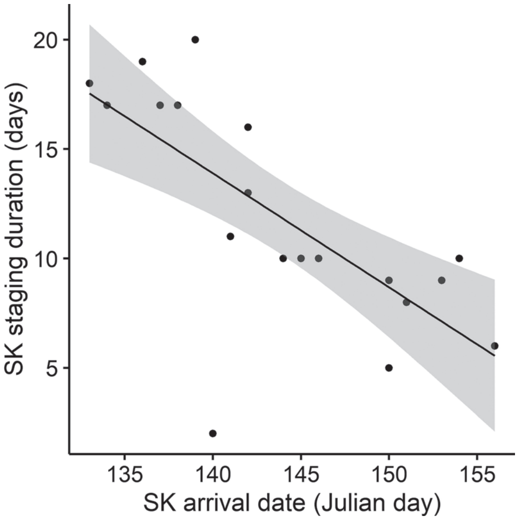

Figure 4. There was a negative association between Saskatchewan (SK) staging durations and arrival dates (*n* = 19). The line indicates a model-based estimate of the weighted model-averaged mean ± a 95% confidence interval. Each circle represents an individual.

more slowly in 2015 relative to 2016 (departure: $\beta \pm SE = -12.4 \pm 2.6$, $P < 0.0001$; travel time: $\beta \pm SE = 20.7 \pm 4.4$, $P = 0.005$) and 2017 (departure: $\beta \pm SE = -17.0 \pm 3.5$, $P < 0.0001$; travel time: $\beta \pm SE = 19.1 \pm 6.2$, $P = 0.03$). There was no difference in Saskatchewan arrival dates, staging durations, or departure dates among years.

We note that there were noticeable differences between the raw (Table 1) and model-predicted means (Figs. 2 and 3). This difference likely results from the relatively small number of detected individuals in our study. Nevertheless, our model-predicted means, which are adjusted for any other fixed effects in the best-approximating model and for the random effect of capture date, give our best prediction of the population means for each response variable given the available data.

DISCUSSION

Recent advances in automated radio-telemetry systems allowed us to track individual long-distance migrants between staging sites separated by thousands of kilometers. Here, we followed Sanderling along the Midcontinental Flyway from three staging and/or wintering areas in the GOM to a major staging area in Saskatchewan, which allowed us to capture detailed information about Sanderling migration timing across > 3000 km.

Despite greater Motus coverage along the Atlantic Flyway relative to the Midcontinental Flyway (Taylor *et al.* 2017), 33 of the 35 Sanderling detected in more northern sites (94%) were detected in Saskatchewan, and only 2 individuals were detected along the Atlantic Flyway, suggesting a strong preference for northward migration along the midcontinental route. Given the relatively high Motus coverage along the Atlantic Flyway (Tayler *et al.* 2017), it is unlikely for tagged individuals to use this route and not be detected. Conversely, there are large gaps in Motus coverage in the midcontinent (Taylor *et al.* 2017), and it is therefore more likely for tagged individuals to use this flyway undetected. Band resight data corroborate the importance of the Midcontinental Flyway for Sanderling and suggest that most individuals overwintering in Chile and Peru and staging and wintering in the Gulf Coast migrate north through the Canadian Prairies (Myers *et al.* 1990).

The small number of sites along the Midcontinental Flyway that are outfitted with Motus radio-telemetry receivers likely explains the low recovery rates of this study. Here, 29% of individuals tagged in the GOM were subsequently detected in more northern latitudes, which was lower than the recovery rates of previous studies using the Motus telemetry network (e.g., 32% in Gómez *et al.* 2017, 81% in Anderson *et al.* 2019). Sanderling have been sighted at stopover sites south of Saskatchewan in the U.S. Prairies (Myers *et al.* 1990), and shorebirds can also use dynamic wetland habitats opportunistically and can disperse broadly as they migrate across the midcontinent (Skagen and Knopf 1994). It is therefore possible that undetected individuals either lost their tags or used other staging sites along the Midcontinental Flyway that did not have Motus receivers. Regardless, the Motus network and rapid advancements in tracking technology have provided a tool that offers new

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insight into the midcontinental staging sites and migration routes of small shorebirds.

We showed that some of the variation in Sanderling migration timing along the Midcontinental Flyway was related to where individuals staged in the GOM. Overall, Sanderling trapped in North Padre appeared to use a different migration strategy than individuals trapped in Louisiana and Bolivar Flats. Our most notable result was that late-arriving individuals had shorter staging durations in Saskatchewan. Given the complete Motus receiver coverage of Chaplin and Reed Lakes, detection data from Saskatchewan reliably reflected actual arrival and departure dates. We were therefore able to evaluate actual staging durations in Saskatchewan, whereas most detection data only permit an evaluation of minimum staging duration (i.e., days between capture date and departure; e.g., Gómez *et al.* 2017; Wright *et al.* 2018). We found that Sanderling trapped in North Padre arrived in Saskatchewan later but had the shortest overall staging durations and ultimately departed from Saskatchewan at the same time as individuals trapped in Bolivar Flats and Louisiana. There are two possible explanations for these results, each of which would imply that the Sanderling trapped in North Padre use a different migration strategy.

First, it is possible that late-arriving individuals were following a time-minimization migration strategy. According to this explanation, individuals trapped in North Padre arrived later in Saskatchewan, but forwent longer stopovers, and likely refueled more quickly, in an effort to reach breeding areas earlier (Alerstam and Lindström 1990; Hendenström and Alerstam 1997). It is generally assumed that migratory birds are under pressure to arrive early on the breeding grounds (Alerstam 2006; Newton 2008), as early arrival is associated with higher quality territories and mates, earlier breeding, and additional time for renesting, which ultimately result in greater reproductive performance for earlier arriving individuals (Norris *et al.* 2004; Smith and Moore 2005).

Our first, time-minimization explanation assumes that Sanderling made a direct flight between the GOM and Saskatchewan. For all individuals, we saw large variations in travel times between the GOM and Saskatchewan. Some Sanderling made a direct flight to Saskatchewan in only 3.2 days, with the fastest individuals traveling at approximately 35 km/hr, a result comparable to the 40 km/hr ground speeds of migrating Sanderling measured by Scott *et al.* (2004). According to our travel time calculations, other individuals took up to 34 days, which would imply that some Sanderling made indirect flights, stopping over at unknown locations on route to Saskatchewan. Banding records (Myers *et al.* 1990) and survey data (Skagen *et al.* 1999), however, show that Sanderlings tend to use a "jumping" migration strategy along the Midcontinental Flyway, overflying most of the North American interior. Indeed, Sanderlings have been recorded in large numbers in Saskatchewan, but not elsewhere in the midcontinent (Skagen *et al.* 1999; Andrei *et al.* 2006). Banding records and survey data therefore suggest that Sanderling typically make a direct flight from the GOM to Saskatchewan (Myers *et al.* 1990; Skagen *et al.* 1999), which supports the possibility of a time-minimization migration strategy.

According to our first explanation, late arrivals in Saskatchewan would suggest that Sanderling departed later from North Padre than from the other two staging areas. This inference, however, contradicts the results from our previous study, which found that North Padre Sanderlings departed earliest from the GOM (Bianchini and Morrissey 2018a). It is possible that the earlier North Padre departure dates (and, consequently, the longer calculated travel times to Saskatchewan) reflected individuals in the North Padre staging area moving outside of the detection range of Motus receivers prior to departure. Unlike Bolivar Flats and Louisiana, which are more spatially discrete sites, the North Padre staging area is large and multidimensional (Withers 2002). In North Padre, shorebirds can easily access the nearby Laguna Madre, an extensive system of large tidal flats that is one of the most significant shorebird staging, wintering, and breeding habitats along the Gulf Coast

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(Withers 2002). Four Motus receivers are located along Padre Island and provide some coverage of the Laguna Madre, but most of this habitat falls outside of the range of Motus receivers (Taylor *et al.* 2017). Therefore, although an individual's last detection in North Padre was assumed to reflect its actual departure from the GOM, last detections could also reflect individuals moving outside of the range of Motus receivers prior to departure. However, we cannot reliably differentiate between actual departures and regional movements with the current dataset.

The second possible explanation for our results is that individuals trapped in North Padre departed earlier from the GOM and travelled more slowly to Saskatchewan, as was suggested by our Motus detection data. This explanation suggests that Sanderling trapped in North Padre tended to make less direct flights to Saskatchewan. Although shorebird survey and observational data from the mid-1990s suggested that Sanderling overfly much of the North American interior (Skagen *et al.* 1999), more recent eBird data report Sanderling sightings throughout the Midcontinental Flyway (eBird 2017). The Prairie wetlands of the North American interior are highly dynamic, and shorebirds tend to occupy available wetland habitats opportunistically during migration across the midcontinent (Skagen and Knopf 1994). It is therefore possible that the Sanderling trapped in North Padre staged and refuelled at unknown locations (without Motus receivers) on route to Saskatchewan, ultimately arriving later at this staging area. Individuals following an energy-minimization migration strategy are expected to stop more regularly, to make shorter flights, and to deposit less fuel than time-minimizers (Alerstam and Lindström 1990; Hedenström and Alerstam 1997). Therefore, if individuals from North Padre were following an energy-minimization migration strategy, they may have had shorter staging durations in Saskatchewan because they required less time to deposit smaller departure fuel loads.

Determining which of these two explanations is correct will require more data. For instance, Sanderling departure masses could provide evidence to support either explanation, as departure fuel loads can reflect individual refueling rates and can determine an individual's subsequent flight distance (Alerstam 2001). Individuals with faster fuel depositions rates tend to have larger departure fuel loads (Moore *et al.* 2017), and individuals with larger departure fuel loads tend to make longer and more direct flights to key staging areas (Gómez *et al.* 2017). Determining the food resources and predation risk at each location could also help to differentiate between these two explanations, as both factors can determine habitat selection during refuelling (Chudzińska *et al.* 2015). Notably, in our study, food availability or predation risk in the Laguna Madre relative to the North Padre shoreline may have influenced the likelihood of Sanderling moving into the Laguna Madre and out of range of the Motus receivers prior to departure from the North Padre staging area. Additionally, differences in food availability among years could also explain the interannual variations in GOM departure dates observed here, where higher food availability may have caused earlier departure dates in some years (Bridge *et al.* 2010).

Additionally, knowing the breeding and wintering locations of each individual could also provide evidence to support one of these explanations. A growing body of evidence suggests that breeding latitude is a key driver of northbound migration timing. Previous tracking studies in Collared Flycatchers (*Ficedula albicollis*; Briedis *et al.* 2016), Bar-tailed Godwits (Conklin *et al.* 2010), and Tree Swallows (*Tachycineta bicolor*; Gow *et al.* 2019) have found that individuals breeding in higher latitudes depart later from the wintering grounds, have longer staging durations, and arrive later on the breeding grounds. However, the breeding latitudes of Sanderling in this study are unknown. Nonbreeding latitudes, in combination with sex or age, have also been shown to affect northbound migration timing in birds, with males wintering farther north than females and juveniles and arriving earlier on the breeding grounds (O'Hara *et al.* 2005; Woodworth *et al.* 2016). Based on banding and feather

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isotope records, we have information that suggests that a proportion of the Sanderling in Chaplin Lake, Saskatchewan overwinter in the Texas Gulf Coast (Labarrere 2016), but Bolivar Flats and Louisiana also provide overwintering habitat for Sanderling (Withers 2002). Nevertheless, individuals trapped in North Padre generally had earlier capture dates than Sanderling trapped in the other two staging areas. Of the Sanderling trapped in North Padre that were subsequently detected, 20/26 (77%) individuals were captured on or before day of the year 111 (April 20/21), whereas all of the Sanderling trapped in Bolivar Flats and Louisiana were captured after day of the year 114 (April 23/24; capture date range: 114 – 126). Although capture date was added as a random effect to control for seasonal variations, it is possible that Sanderling trapped in North Padre represented an earlier cohort of birds.

It is important to acknowledge that the population structure at each site in the GOM is unknown, and individuals of different ages and sexes, for example, may have inherently different migration schedules (Morrison 1984). Equally, the quality of staging sites as shorebird refueling habitat is not fully characterized in the GOM. The GOM hosts over one million wintering and migrating shorebirds every year (Cohen *et al.* 2017). Due to the oil extraction and transportation activities in this region, shorelines along the Gulf coast are exposed to frequent and repeated oil pollution from numerous oil leaks (Burger 2017) and from large-scale spills, like the Deepwater Horizon oil spill (Beyer *et al.* 2016). Oil pollutants have the potential to impair pre-migratory fueling (Bianchini and Morrissey 2018b) and we previously determined that this can delay departure (Bianchini and Morrissey 2018a). We also acknowledge that our sample size of detected individuals is low, and additional research (i.e., data from more individuals and years) will help inform the differences in migration timing among Sanderling from these three GOM staging areas.

Further research is therefore required to fully understand why differences in migration timing among Sanderling trapped in different GOM staging areas occur and to identify the factors driving the observed variations in migration pace. Our study underscores the need for more extensive Motus coverage in key shorebird habitats, like the Laguna Madre and North Padre areas in Texas. Our study also highlights the great potential of the Motus network to track shorebird migration, particularly along the relatively understudied Midcontinental Flyway that has revealed new insights into differential migration schedules and linkages across distant staging areas.

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