

ARTICLE

Animal Ecology

Migration strategy and constraint in migration behavior vary among shorebird species with different life histories

Sarah J. Clements^{1,2}  | Jason P. Loghry³ | Jennifer A. Linscott⁴ |
Jorge Ruiz^{5,6} | Joe C. Gunn⁷ | Juan G. Navedo^{5,6,8}  | Nathan R. Senner⁴  |
Bart M. Ballard³ | Mitch D. Weegman⁹ 

¹School of Natural Resources, University of Missouri, Columbia, Missouri, USA

²Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, Maine, USA

³Caesar Kleberg Wildlife Research Institute, Texas A&M University – Kingsville, Kingsville, Texas, USA

⁴Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, USA

⁵Bird Ecology Lab, Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Valdivia, Los Ríos, Chile

⁶Estación Experimental Quempillén, Facultad de Ciencias, Universidad Austral de Chile, Chiloé, Chile

⁷Department of Plant and Soil Science, University of Vermont, Burlington, Vermont, USA

⁸Millennium Institute Biodiversity of Antarctic and Subantarctic Ecosystems (BASE), Santiago, Chile

⁹Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

Correspondence

Sarah J. Clements

Email: sjclements9@gmail.com

Funding information

Waterbird Society; University of Missouri; Animal Behavior Society; National Science Foundation Graduate Research Fellowship Program; Environment and Climate Change Canada; Missouri Birding Society (Audubon Society of Missouri); Upper Mississippi River/Great Lakes Joint Venture; Robert J. Kleberg, Jr. and Helen C. Kleberg Foundation; Webster Groves Nature Study Society; Fondo Nacional de Desarrollo Científico y Tecnológico; Texas A&M - Kingsville; University of South Carolina

Handling Editor: Robert R. Parmenter

Abstract

Migration strategy is a key behavioral characteristic guiding how migratory species time their annual cycles and use habitat. Understanding variation in migration strategy within and among species and individuals can be useful for understanding how birds navigate energetic trade-offs and designing or modifying conservation plans meant to benefit multiple species and life histories. We compared migration strategies among three migratory shorebird species with variable life history traits and short, medium, and long migration distances, respectively: American avocets (*Recurvirostra americana*), black-bellied plovers (*Pluvialis squatarola*), and Hudsonian godwits (*Limosa haemastica*). Avocets (short distance) exhibited the most within-species variation in migration duration, proportion of migration time spent at stopovers, and stopover duration. Plovers (medium distance) and godwits (long distance) showed less variation in these metrics, but godwits showed the most variation in the number of stopovers used. There were significant differences among species in migration distance, number of stopovers used, proportion of time stopped over, departure and arrival dates, and migration duration, but not mean stopover duration. We also found that avocets spent more time stopped over relative to migration distance than plovers or godwits, indicating that avocets showed the most energy-minimizing strategy of the three species. Our findings

This is an open access article under the terms of the [Creative Commons Attribution License](#), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

set the stage for future work assessing the effects of climate change and land use on characteristics associated with different migration strategies for additional migratory species.

KEY WORDS

migration timing, movement ecology, stopover, tracking, wader

INTRODUCTION

Shorebird populations are vulnerable to the effects of anthropogenic development and climate change (Galbraith et al., 2014; Robinson et al., 2009; Wauchope et al., 2017) largely because of their dependence on a broad range of habitat types. Over half of North American shorebird species are listed as species of conservation priority (Rosenberg et al., 2014), and population sizes have declined precipitously over the past several decades (Rosenberg et al., 2019; Smith et al., 2023). Due to their vulnerability and declining population trends, conservation and management actions focused on shorebirds are increasingly important and useful in the context of global change (Koleček et al., 2021; Piersma & Lindström, 2004). However, the implementation of management plans is often limited by a lack of specific knowledge about how shorebirds use habitats and move through landscapes (Faaborg et al., 2010).

Migration strategy refers to decisions with respect to use of migratory pathways, stopover sites, timing of movements, and balance of energy acquisition and expenditure (Colwell, 2010). The collective migration strategies of individuals, in turn, inform our understanding about how and why species and populations move. Migration strategies and outcomes, as well as their degree of variability or constraint within and among populations and species, are shaped by both species-level characteristics and individual responses to resource availability and environmental pressures (Alerstam & Lindström, 1990; Lindström, 2020; Shuert et al., 2023). For example, migration routes and movement patterns (i.e., frequency and duration of stopovers) are shaped by the distribution of stopover habitat (Piersma, 1987). If stopover habitat is abundant, there may be high variability in migration routes, or birds may take short, frequent stops; but if it is more limited, birds may take more constrained migration routes and may need to take fewer, longer stops. A well-studied example of this pattern is variation among species in migratory connectivity (Webster et al., 2002). American woodcock (*Scolopax minor*), for instance, have relatively diffuse stopover requirements and therefore display very low migratory connectivity (Moore et al., 2019). Conversely, far-eastern curlews (*Numenius madagascariensis*) require specific stopover conditions and therefore show strong migratory

connectivity (Morriss et al., 2022). Additionally, physiological or resource constraints can influence migration behavior and strategy. For example, birds may display time-minimizing (i.e., faster migration, less time refueling) or energy-minimizing (i.e., slower migration, more time refueling) migration strategies (Hedenstrom & Alerstam, 1997). Across many shorebird species, smaller body size and shorter migrations are associated with energy minimization, while larger body size and longer distance migrations are associated with time minimization (Anderson et al., 2019; Zhao et al., 2017). Other elements of life history, such as foraging strategy and habitat associations, can influence migration behavior, route, and strategy (e.g., Végvári et al., 2010). Until recently, many elements of migration strategy were very difficult to study, but the availability of tracking technology for smaller species allows opportunities to investigate additional aspects of migration strategy in greater detail, including phenology and stopover dynamics.

Migratory behavior and migration distance are often considered risk factors for population decline due to constraints associated with longer migration distances or less predictable habitat availability (Both et al., 2010; Galbraith et al., 2014). Moreover, differences in migration strategies have been associated with differences in population trends (Lisovski et al., 2021). In North America, shorebirds migrating through the mid-continent are thought to be declining due to changes in wetland dynamics across the landscape (Thomas et al., 2006). Mid-continental migrants vary in the types of wetlands they are likely to use, and their migration strategy and resource availability are therefore hypothesized to be strongly linked (Skagen et al., 2005). For example, species depending on unpredictable ephemeral wetlands to feed, such as American avocets (*Recurvirostra americana*; Ackerman et al., 2020), may need more flexibility in migration strategy than species with more flexible feeding strategies, such as black-bellied plovers (*Pluvialis squatarola*), which can feed in wetland or upland habitats (Poole et al., 2020). Associations between life history and migration strategies are important for understanding stopover habitat requirements and assessing species vulnerability to anthropogenic change. Variability in migration strategy within and among strategies is an important

contributor to population and species resilience and can have demographic consequences (Gilroy et al., 2016). For example, longer migration distances have been associated with negative population trends (Hewson et al., 2016; Laaksonen & Lehikoinen, 2013; Sanderson et al., 2006). In addition, species with low within-species variability in migration phenology or strategy in general may be more vulnerable to stopover habitat loss than species with high within-species variability (Briedis & Bauer, 2018; Iwamura et al., 2013). It is also possible that strategies using fewer stopovers relative to migration distance could be more vulnerable to habitat loss due to the importance of the few stopovers that do exist. However, relatively little is known about the movement patterns of shorebirds in mid-continent North America, and survey coverage at consistent sites is minimal (Smith et al., 2023). Therefore, tracking data can provide novel information about shorebird behavior and migration strategies in the mid-continent.

We used lightweight, automated tracking devices to collect northward migration movement data for three shorebird species that represent migrations beginning in both North and South America and passing through mid-continent North America, but differ in migration distances and life histories: American avocets (*R. americana*), black-bellied plovers (*P. squatarola*), and Hudsonian godwits (*Limosa haemastica*). Our objective was to describe variation in migration strategies within and among these three species. In general, we expected that (1) shorter migrations would be less constrained (i.e., more within-species variation in strategy) than longer migrations; (2) shorter distance migrants would follow an energy-minimizing strategy, while longer distance migrants would follow a time-minimizing strategy; and (3) there would be significant differences among species in the number of stopovers used, migration duration, proportion of time spent stopped over, and departure and arrival dates, reflecting the substantial life history differences among species.

METHODS

Study species

We chose our study species, American avocets (avocets), black-bellied plovers (plovers), and Hudsonian godwits (godwits), to represent a gradient of migration distances and life history strategies. Avocets are short-distance migrants that breed near ephemeral wetlands over a large portion of the central and western United States and southern Canada, from Texas, USA, to southern Alberta and Saskatchewan, Canada, and spend the nonbreeding

season in Mexico and the southern United States (Ackerman et al., 2020). Individuals from different breeding populations migrate through coastal and inland North America, but specific routes are not well known (Ackerman et al., 2020). American avocets feed on invertebrates and occasionally small fish and seeds and usually feed in the water column (Ackerman et al., 2020; Boettcher et al., 1995; Dinsmore, 1977). Black-bellied plovers have an intermediate migration distance. They are globally distributed (also known as gray plovers), and, in the Western Hemisphere, breed across the Alaskan (USA) and Canadian arctic and spend the nonbreeding season on the coasts of southern North America, Central America, and northern South America (Poole et al., 2020). Black-bellied plovers feed on aquatic and terrestrial invertebrates and are visual foragers (Poole et al., 2020). Hudsonian godwits are long-distance migrants. They breed in boreal bogs and tundra sedge meadows in Alaska and Canada and spend the nonbreeding season in southern South America (Walker et al., 2020). Hudsonian godwits forage on invertebrates by probing in mud and moist soil (Walker et al., 2020).

Bird movement data

We captured avocets at Rockefeller Wildlife Refuge in Louisiana, USA, in January and February 2020 and 2021 and the Laguna Madre area of Texas, USA, in April 2021. We captured plovers at Rockefeller Wildlife Refuge in January, February, and March 2019 and 2020 and at Laguna Madre in March, April, and May 2019, 2020, and 2021. We captured godwits at two bays on Isla Chiloé in Chile in January and March 2019, 2020, and 2021. We captured all birds during the nonbreeding season (Figure 1) using cannon and rocket nets, with the exception of avocets in Louisiana, which we captured by spotlighting. Plovers were banded with a US Geological Survey (USGS) metal band, avocets were banded with a USGS metal band and green flag with field-readable alphanumeric characters, and godwits were banded with a plastic band and a red flag with field-readable alphanumeric characters. Bird captures in Louisiana and Texas were conducted under USGS permit (number 21314), Texas Parks and Wildlife Scientific Research Permit (number SPR-812-965), and Louisiana Department of Wildlife and Fisheries Scientific Research and Collection Permit (number WDP-019-016) to B. Ballard. Work on Padre Island National Seashore in Texas was conducted under a Research and Collection Permit (number PAIS-2021-SCI-0002) to D. Newstead. Louisiana and Texas captures were approved by the University of Missouri (ACUC number 9502) and Texas A&M

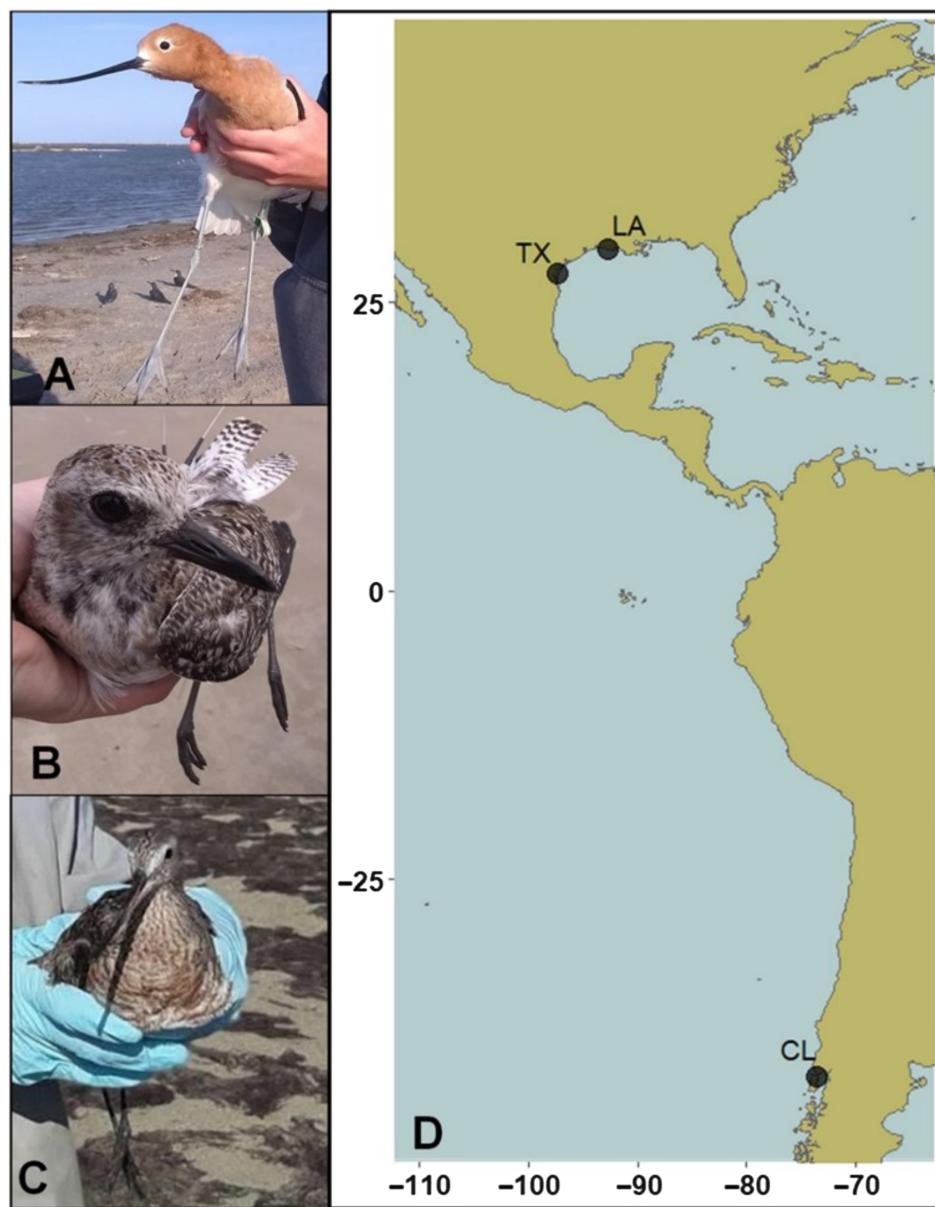


FIGURE 1 (A) An American avocet (photo credit J. Loghry), (B) black-bellied plover (photo credit: S. Clements), and (C) Hudsonian godwit (photo credit: J. Navedo), and (D) a map of capture sites. Avocets and plovers were captured in Texas (TX) and Louisiana (LA) in the United States, while godwits were captured on the Chiloé Archipelago in Chile (CL).

University—Kingsville (ACUC number 2018-10-30A). Captures in Chiloé took place under licenses (number 7625/2018 and number 296/2020) from the Government of Chile to Juan G. Navedo and Bioethics Approval (number 355/2019) from the Universidad Austral de Chile.

We used four different models of GPS, GPS-acceleration (ACC), and Platform Transmitter Terminal (PTT) tracking devices from three different manufacturers: Lotek (Newmarket, Ontario, Canada), Ornitela (Vilnius, Lithuania), and Microwave Ltd. (Columbia, MD, USA). The GPS and PTT devices transmitted data via the Argos satellite system, while the GPS-ACC devices transmitted

through the Global System for Mobile Communication (GSM; i.e., cell phone) network. We used a different set of devices on each species depending on device and bird size (Appendix S1: Table S1) to ensure that device mass would be approximately $\leq 3\%$ of bird mass. In total, we deployed 136 tracking devices: 37 Pinpoint Argos Solar S and 8 Pinpoint Argos 75 devices on plovers, 37 Ornitrack-10 devices on avocets, and 29 Argos Solar PTTs and 25 Pinpoint Argos Solar S transmitters on godwits. We recorded mean bird mass ($\pm SD$) for avocets (368.8 ± 43.1 g), plovers (213.4 ± 19.4 g), and godwits (327.3 ± 53.0 g). In general, bird weight was lower earlier in the catching period and higher later in the catching period

(birds were heaviest closer to northward migration). We attached tracking devices with a leg loop harness made of silicone, nylon, or elastic shock cord (Rappole & Tipton, 1991; Sanzenbacher et al., 2000). We collected morphometrics from each bird and aged and sexed birds according to morphology and plumage characteristics as well as molecular methods (Gherardi-Fuentes et al., 2020; Meissner & Cofta, 2014; van der Velde et al., 2017).

The Pinpoint Argos Solar S devices placed on plovers and godwits were programmed to collect a GPS fix every 2 h (12 locations per day), while the Pinpoint Argos 75 devices on plovers were programmed to begin collecting one location every 3 days from mid-April to mid-May, one point daily from mid-May to mid-July, and subsequently one point every 3 days. The Argos Solar PTTs on godwits transmitted Argos locations according to a duty cycle of 5 h of transmitting opportunistically according to satellite configuration, followed by 24 h of charging. All Ornitrack-10 devices on avocets in Louisiana in 2020, along with the nine deployed in Texas in 2021, were initially programmed to collect one GPS fix per hour (24 per day) and one ACC fix every 6 min. For those in Louisiana in 2020, the GPS duty cycle was reduced to once every 4 h (six per day) during the winter season due to excessive battery drainage and later increased to once every 2 h (12 per day). ACC duty cycles were unchanged except if the device battery fell below 25% capacity, at which point devices stopped collecting ACC data. In 2021, tracking devices in Louisiana were programmed to collect one GPS fix every 2 h and one ACC fix every 20 min. The changes in duty cycle were due to differences in battery capacity given differences in specific device model (some were a newer version and had larger memory capacity) and GSM coverage between sites. We programmed devices to last through one northward migration and breeding season, and harness materials were not expected to last more than 1 year.

Data from Lotek and Microwave devices were stored in Movebank (Kranstauber et al., 2011). We used Movebank to filter location quality based on Lotek Cyclic Redundancy Check status for Lotek device data and the Douglas Argos Filter (Douglas et al., 2012) for Microwave device data. Then, we used the “SDLFilter” package (Shimada et al., 2012) in the R Programming Environment (R Core Team, 2021) to remove duplicate points and outliers based on a speed threshold of 150 km/h. The “SDLFilter” package calculates travel speeds based on GPS locations and timestamps and can detect duplicate points in space and time. For the Ornitela devices, we filtered by removing GPS points with HDOP > 10. Finally, we visually identified and removed several remaining outlier points, most of which showed erroneous future times or were located at 0° latitude and

longitude. We did not use ACC data in this analysis because not all devices collected them.

Characterizing migration strategies

We used movement data from the three species to quantify migration metrics and represent migration strategies. We used only complete migratory tracks for this study and only complete migratory tracks with high-resolution (2-h duty cycle) data for the migration strategy analysis (see Table 1 for sample sizes and Appendix S1: Section S1 for discussion of deployment outcomes). First, we subset the data to include only tracks with at least one full northward migration and no multiday data gaps between nonbreeding and breeding areas. In the very few cases where an individual’s device recorded more than one northward migration, we retained only the first migration following deployment (resulting in only one migration per individual). Then, for all Pinpoint Argos Solar S and Ornitrack-10 devices, we aligned duty cycles to retain one location every 2 h using the “move” package (Kranstauber et al., 2020) in R. We used the dataset that comprised birds with 2-h duty cycles (Pinpoint Argos Solar S and Ornitack-10 devices) for the full analysis. For the Pinpoint Argos 75 and Argos Solar PTT, we aligned duty cycles to retain one location approximately every 24 h. For birds with these 24-h devices (Pinpoint Argos 75 and Argos Solar PTT), we present results for migration duration as well as departure and arrival dates, but, due to our small sample sizes for the 24-h duty cycles (Table 1), we did not use the 24-h duty cycle data to compare migration strategies. We identified the migration period by using kernel density estimates to determine breeding ranges and using distance and latitude thresholds. We identified stopovers based on a 30-km distance threshold (following Clements et al., 2022; see Appendix S1: Section S2 for additional details on delineation of breeding,

TABLE 1 Sample sizes of full migration tracks (complete data from nonbreeding to breeding area with no data gaps) broken down by species and duty cycle.

Species	Full migration tracks		
	Total	2-h duty cycle	24-h duty cycles
Black-bellied plover	33	25	8
American avocet	14	14	0
Hudsonian godwit	10	6	4

Note: Only the 2-h duty cycle tracks were used in statistical comparisons of migration strategies, but limited results from the 24-h duty cycle were also presented.

migration, and stopover periods). Using these data, we then calculated total migration distance, number of stopovers used, average stopover duration, proportion of time spent at stopovers, and nonbreeding area departure and breeding area arrival dates.

Migration metrics

We calculated total migration distance as the sum of all daily steps between the beginning and end of migration. The number of stopovers was the total number of stopovers identified for each bird. Migration duration was the time (in days) between the first and last point in migration (including all stopping events; Lindström et al., 2019). Proportion of time spent stopped over was the total time spent at stopover sites divided by the total time spent in migration. Departure and arrival dates were the ordinal dates on which birds departed nonbreeding areas and arrived at breeding areas. Mean stopover duration for each bird was the mean of the time (in hours) spent at stopovers. Travel-to-stopover ratio was the migration distance (in kilometers) divided by the total time stopped over in days (Anderson et al., 2020). All of these metrics are described in Table 2.

Comparing migration strategies

For the devices with 2-h duty cycles, we used a one-way ANOVA to quantify differences among species in each migration metric and Bonferroni-adjusted pairwise *t* tests to identify which species were significantly different ($p < 0.05$) from one another within each metric. All tests were run in the R Programming Environment. For the devices with 24-h duty cycles, we did not conduct an ANOVA or pairwise *t* tests due to the small sample size of godwits, but we summarized the results of each

migration metric. To address our first objective, which was to examine patterns in within-species variability of migration metrics in relation to migration distance, we calculated the mean and standard deviation for each migration metric and plotted the means and the 50% and 95% quantiles around them. To address our second objective related to time-minimizing and energy-minimizing migration strategies, we compared the results of our migration metric calculations in addition to the results of one-way ANOVA and pairwise *t* tests specifically for migration distance, migration duration, number of stopovers used, stopover duration, and the ratio of distance traveled to time spent stopped over. These characteristics are variable along the continuum of time- to energy-minimizing migration strategies and are related to flight distance and fuel load (Hedenstrom & Alerstam, 1997). To address our third objective, we used the results of one-way ANOVA and pairwise *t* tests for all of our migration metrics to evaluate whether differences among species were significant.

RESULTS

Comparing migration strategies

We mapped northward migration routes and locations of nonmigratory individuals for the three species between January and July (Figure 2). Of the birds for which data were collected through to the breeding season, two avocets remained in southern Texas and eight godwits did not migrate or breed and instead spent the breeding season in Argentina (e.g., Navedo & Ruiz, 2020). Mean migration distance (\pm SD) was significantly different among avocets (2234.7 ± 450.4 km), plovers (5807.8 ± 900.4 km), and godwits ($13,324.6 \pm 1219.3$ km; $p < 0.001$; Table 3; Figure 3A). Mean number of stopovers was lowest for avocets (4.9 ± 2.0), intermediate for plovers (6.1 ± 1.7), and highest for godwits (8.4 ± 4.4). Number of stopovers

TABLE 2 Definitions of several metrics used to quantify migration strategy in shorebirds, along with their definitions and units in which they were measured for the purposes of this multispecies study.

Metric	Definition	Units
Migration distance	Sum of all daily steps between the beginning and end of migration	Kilometer
No. stopovers	Total no. stopovers	Count
Migration duration	Time between first and last point in migration	Days
Proportion of time in stopover	Total time spent at stopover sites divided by total time in migration	Days
Departure/arrival dates	Dates on which birds departed nonbreeding areas and arrived at breeding areas	Ordinal date
Stopover duration	Mean amount of time spent at stopovers	Hours
Travel to stopover ratio	Migration distance divided by the total time stopped over	Kilometer per day

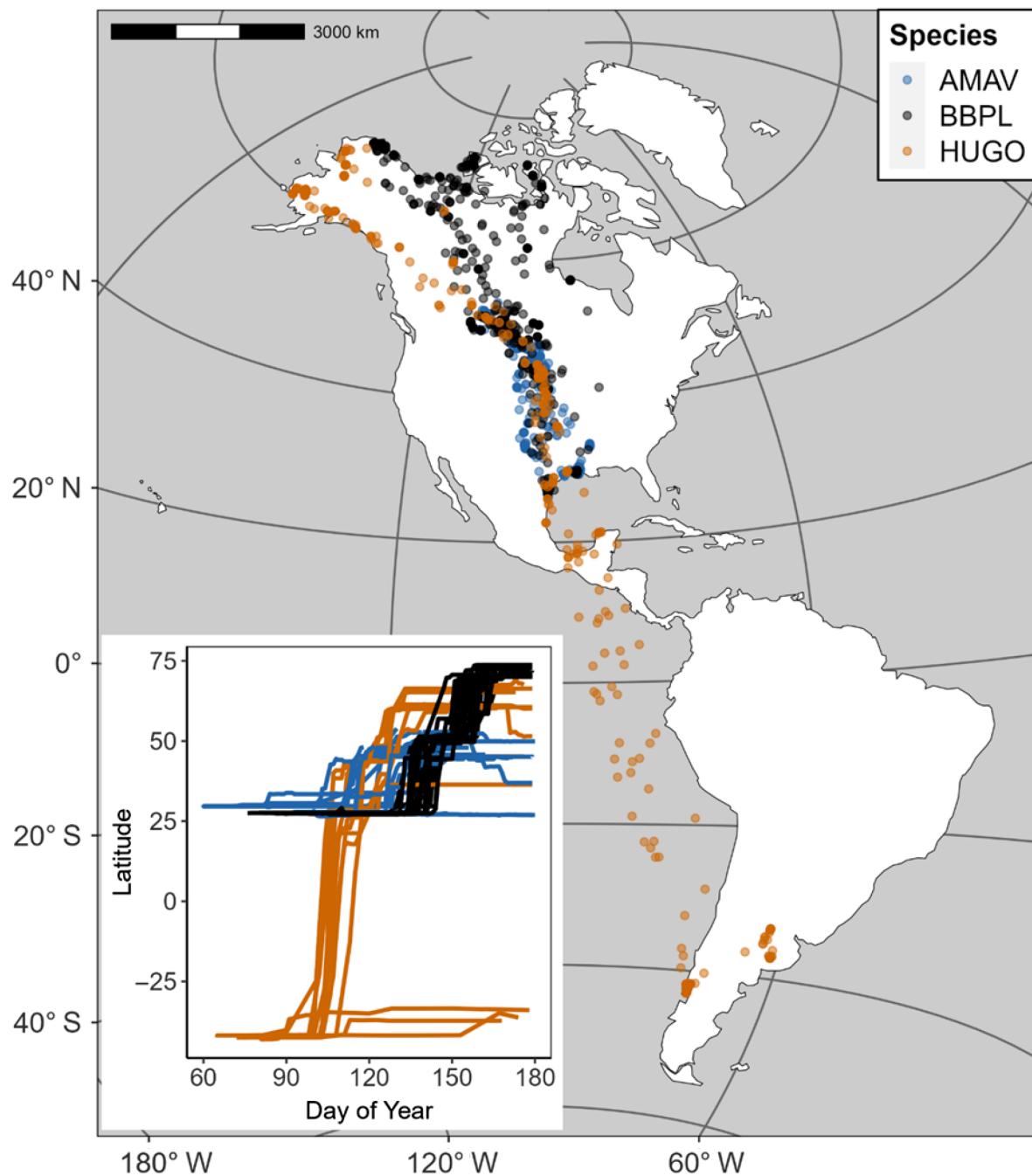


FIGURE 2 Map of daily locations between March and July 2019–2021 and inset plot of latitude by date for 62 American avocets (AMAV), black-bellied plovers (BBPL), and Hudsonian godwits (HUGO). In the map, each point represents the daily location of a bird, and in the inset plot, each line represents an individual bird.

differed among species ($p = 0.01$; Table 3), with godwits differing from avocets ($p < 0.001$; Figure 3B).

Mean migration duration differed ($p = 0.002$) among avocets (19.6 ± 15.2 days), plovers (22.8 ± 4.1 days), and godwits (35.4 ± 6.2 days; Table 3; Figure 3C). Godwits had a significantly longer migration duration than avocets ($p < 0.001$) and plovers ($p = 0.01$). Mean proportion of time stopped over did not differ for avocets (0.59 ± 0.25) and plovers (0.68 ± 0.12) or godwits (0.46 ± 0.14 ;

$p = 0.49$; Figure 3E; Table 3), but plovers spent a significantly higher proportion of time stopped over than godwits ($p = 0.02$).

Mean departure date from nonbreeding areas differed among avocets (20 April; ordinal day 110 ± 15), plovers (17 May; ordinal day 137 ± 4), and godwits (11 April; ordinal day 101 ± 6 ; $p < 0.001$; Table 3; Figure 4). Departure date was significantly earlier for godwits than for both avocets ($p < 0.001$) and plovers ($p < 0.001$), as

well as earlier for avocets than for plovers ($p < 0.001$). Mean arrival date on breeding areas also differed among species ($p < 0.001$; Table 3; Figure 4; Appendix S1: Figure S1), with avocets arriving earliest (Day 130 ± 11 ; ~10 May), followed by godwits (136 ± 8 ; ~16 May) and finally plovers (159 ± 4 ; ~8 June). Plovers had significantly later arrival dates than both avocets ($p < 0.001$) and godwits ($p < 0.001$), but avocets and godwits were

not different ($p = 0.23$). Mean stopover duration did not differ among avocets (52.0 ± 46.3 h), plovers (66.0 ± 28.1 h), or godwits (56.8 ± 33.3 h; $p = 0.49$; Table 3; Figure 3E).

The ratio of distance traveled to time spent stopped over was significantly different ($p = 0.04$; Table 3; Figure 3F) between plovers (399.2 ± 115.8) and godwits (882.1 ± 248.7). Avocets (590.3 ± 751.5) did not differ significantly from the other two species, although one individual completed an exceptionally fast migration relative to the others (Figure 3F). We chose to include this individual in the analysis, because our visual inspection of the bird's track indicated that there were no issues or gaps in the migration data.

TABLE 3 Results of one-way ANOVA to identify differences in seven migration metrics among three species—American avocets, black-bellied plovers, and Hudsonian godwits.

Migration metric	<i>p</i>	<i>F</i>	df
Migration distance	<0.001	399.19	2
No. stopovers	0.012	4.96	2
Migration duration	0.002	7.12	2
Proportion time in stopover	0.018	4.48	2
Mean stopover duration	0.496	0.71	2
Departure time	<0.001	61.524	2
Arrival time	<0.001	72.474	2
Travel to stopover ratio	0.04	3.47	2

Migration duration for birds with 24-h duty cycles

Based on findings from testing the effects of reduced data, we chose to present only migration duration and departure/arrival information from our devices with 24-h duty cycles. However, we chose not to completely exclude our birds with less frequent duty cycles and to present

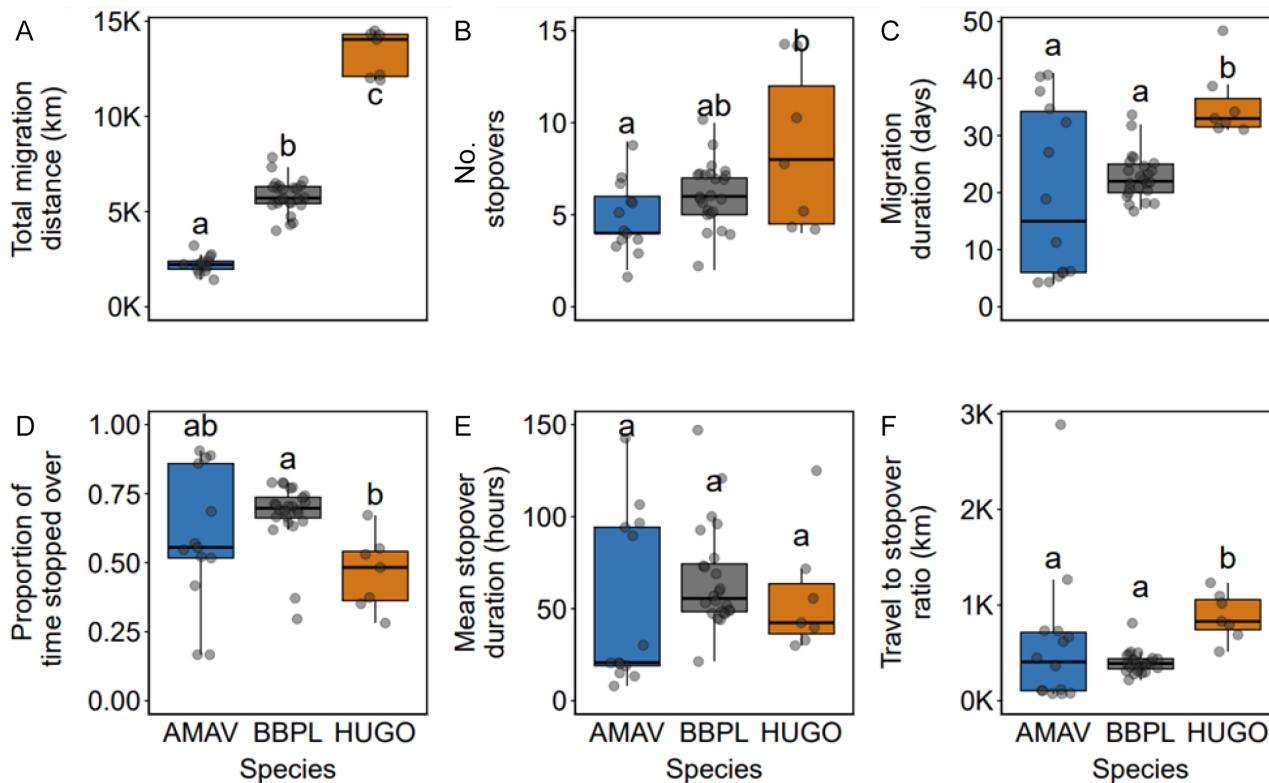


FIGURE 3 Boxplots of migration metrics summarized across all individuals of each species—American avocet (AMAV), black-bellied plover (BBPL), and Hudsonian godwit (HUGO). The gray points represent the raw data points, the boxes represent the middle 50% quantile, the midline represents the median, and the whiskers approximately show the 95% CIs. Letters above boxes indicate significantly different groups based on the results of pairwise *t* tests ($p < 0.05$).

the raw data for migration duration, departure date, and arrival date, as there is evidence that these metrics are the least influenced by duty cycle (Clements, 2022). The sample sizes differed for plovers ($n = 8$) and godwits ($n = 4$). Mean migration duration varied for plovers (23.1 ± 8.0 days) and godwits (30.5 ± 7.6 days). Mean

departure date from nonbreeding areas also varied for plovers (ordinal day 133 ± 6 ; ~13 May) and godwits (ordinal day 111 ± 21 ; ~21 April). Mean arrival date to breeding areas also varied for plovers (ordinal day 157 ± 7 ; ~6 June) and godwits (ordinal day 141 ± 14 ; ~21 May; Figure 5).

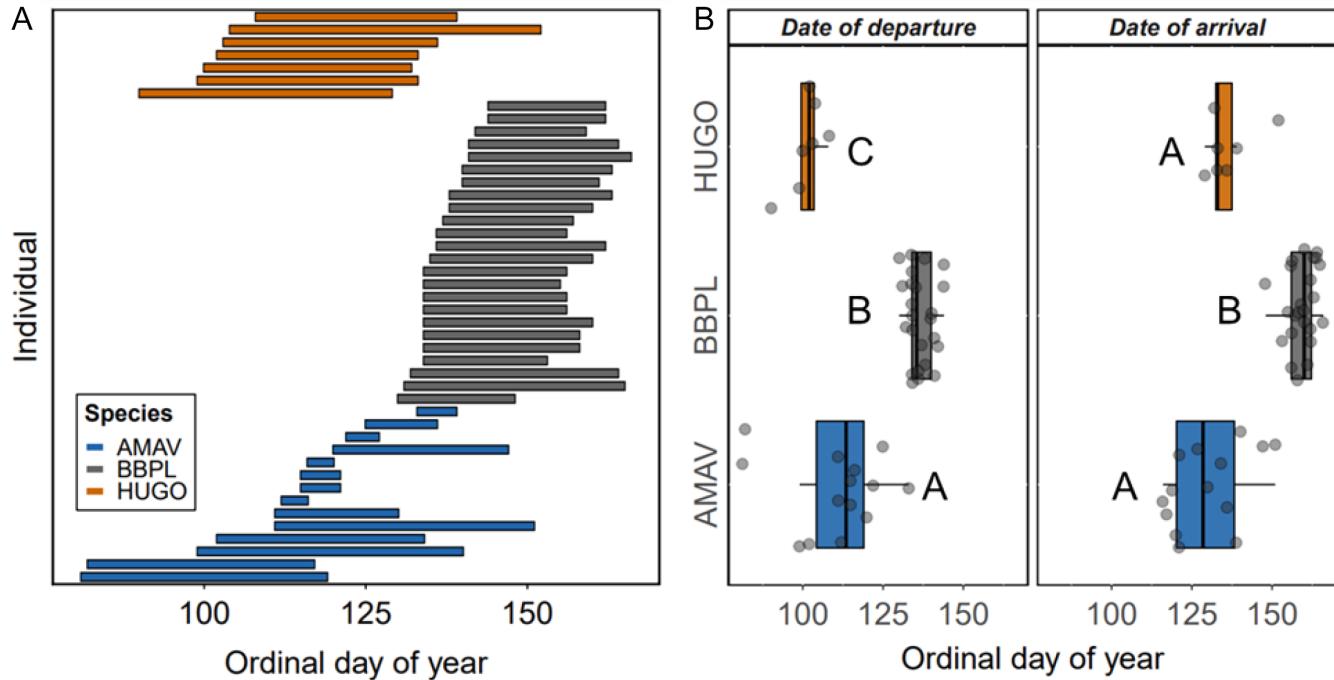


FIGURE 4 (A) Migration period across day of year for each of 45 individual American avocets (blue), black-bellied plovers (black), and Hudsonian godwits (orange) with 2-h duty cycles and complete migrations, where each bar represents one bird, with the leftmost end of the bar showing the departure date and the rightmost end showing the arrival date. (B) Boxplots of departure and arrival dates summarized across all individuals of each species, American avocet (AMAV), black-bellied plover (BBPL), and Hudsonian godwit (HUGO). The gray points represent the raw data, the boxes represent the middle 50% quantile, the midline represents the median, and the whiskers approximately show the 95% CIs. Letters next to boxes indicate significantly different groups based on the results of pairwise t tests ($p < 0.05$).

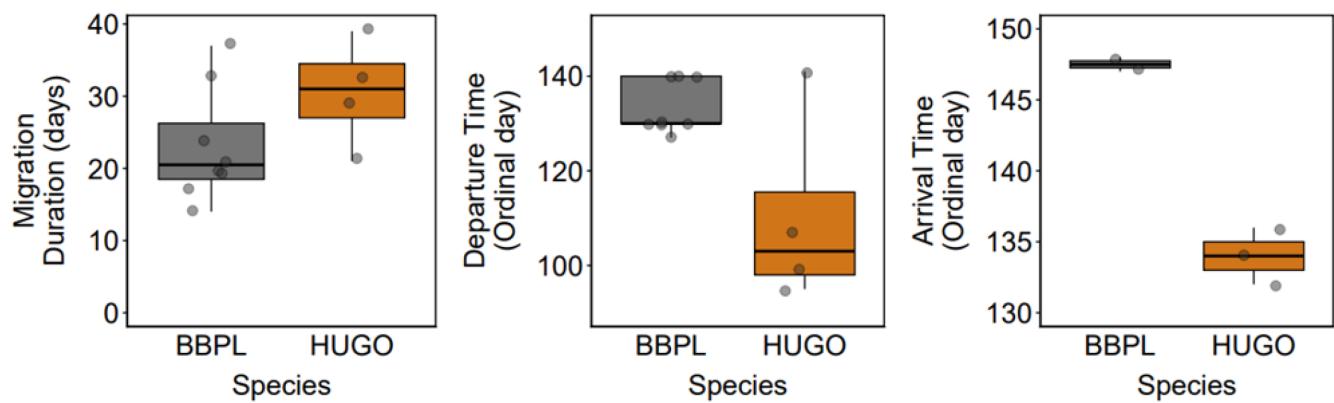


FIGURE 5 Results for migration metrics from devices with 24-h duty cycles and complete migration data for black-bellied plovers (BBPL) and Hudsonian godwits (HUGO). The gray points represent the raw data, the boxes represent the middle 50% quantile, the midline represents the median, and the whiskers approximately show the 95% CIs. No statistical analyses were conducted due to small sample sizes.

DISCUSSION

We compared migration strategies among American avocets, black-bellied plovers, and Hudsonian godwits, which were chosen for their short, medium, and long migration distances, respectively. As expected, we saw the highest variability in most migration metrics for avocets, which had the shortest migration distance, and less variability in migration metrics in plovers and godwits, which had longer migration distances. On the spectrum of time- to energy-minimizing, godwits were the most time-minimizing, with the farthest distance traveled per unit time spent stopped over due to their long, nonstop flights at the beginning of migration (Linscott et al., 2022). Toward the middle of the spectrum were plovers, with fewer and longer stopovers than avocets. While avocets showed high variability in the ratio of distance traveled to time spent stopped over, their shorter migration distances and frequently longer migration durations suggest that they tend the most toward an energy-minimizing strategy out of the three species. We found a substantial difference between at least one pair of species in all migration metrics with the exception of mean stopover duration, suggesting that, as predicted, migration strategies are variable across species with different migration distances and life histories.

Migration strategies and patterns

Our results augment previous knowledge of migration routes for our three focal species. Plovers and avocets are far less studied in central North America than their coastal-migrant counterparts, so our study adds new insight into these species' migrations. For avocets, little has been known about specific migration routes, and our data showed that they often stop over in and pass through areas farther east of their breeding range than commonly thought (Ackerman et al., 2020). Additionally, we add to previous studies about Hudsonian godwit movements (e.g., Linscott et al., 2022; Navedo & Ruiz, 2020; Senner et al., 2014). As expected, some godwits did not breed and spent the breeding season in Argentina instead of migrating to the Northern Hemisphere (Navedo & Ruiz, 2020). Avocets are known to breed in the Texas coastal bend (Rappole & Blacklock, 1985). Some of our birds remained there through the breeding season, suggesting that avocets exhibit a partial migration strategy in this area (*sensu* Chapman et al., 2011).

We expected that godwits would have the most constrained migration strategy (i.e., least variation in migration metric values among individuals), plovers would be intermediate, and avocets would be the least

constrained, according to their varying migration distances (Zhao et al., 2017). For avocets, which have a broad latitudinal breeding range and relatively short migration, it appears that a variety of migration strategies are used (i.e., for many metrics, there was a substantial spread in the distribution, rather than having most individuals clustered around the mean). Longer migrations may necessitate constrained strategies, but more variation could occur in response to environmental conditions, such as poor weather (e.g., Briedis et al., 2017) or suboptimal stopover conditions (e.g., Herbert et al., 2022). This could explain why godwits showed more within-species variation than plovers, even though we expected the opposite. Because godwits migrate over more space and time, there may be more opportunity for environmental factors to influence migration strategy and cause variability among individuals. In addition, on longer, evolutionary timescales, there could be stronger selection on some species than others to exhibit certain behavioral traits. For example, in godwits, some degree of flexibility in migration phenology may enable adequate refueling at stopover sites that can vary in quality (Senner et al., 2014). This possible pattern of long-term selection for variability in phenology may apply to other characteristics of migration strategy (but see Conklin et al., 2017).

There were no significant differences in stopover duration among the three species, but each species had different rates of individual variation within species. For example, black-bellied plovers had high variability in mean stopover duration, and this may have been a reflection of the tendency of some plovers to consistently make an extended stop in southern Saskatchewan (Figure 2). This area is likely high-quality habitat for the species, reflected by the long stopover durations there. Semipalmated sandpipers (*Calidris pusilla*), which are also known to follow a time-minimizing migration strategy, have a longer stopover duration at high-quality stopover sites (Herbert et al., 2022). In addition, within-individual variation (i.e., differences in stopover duration among a given individual's stopovers) was not examined, and this variation could also contribute to the lack of significant differences among species in stopover duration. When comparing and applying our results to other species, it is important to note that larger bodied shorebirds are more likely to have time-minimizing strategies for northward and southward migration (Zhao et al., 2017), and our focal species are all relatively large shorebird species. Smaller species with similar migration distances and morphology may have to stop more often or have otherwise different strategies.

Continuing climate and land use change may further constrain migration strategies for all three species we

studied. Plovers and godwits travel through and stop over in the Prairie Pothole Region (PPR) and the Central and Southern Great Plains, while avocets stop over and breed there. Wetlands in these areas are dynamic and expected to become more unpredictable as climate change advances (Mullens & McPherson, 2019; Rashford et al., 2016). Consequently, habitat may be reduced in quality, quantity, or both, and these effects will be highly variable across the region (Johnson et al., 2005, 2012). In the future, changes in wetland availability and productivity in the mid-continent could alter our three species' migration strategies and could influence their survival and reproductive success (Johnson et al., 2005; Steen et al., 2018). Furthermore, our study revealed a relatively small number of stopovers made by many of the birds we tracked along full migrations, highlighting the importance of identifying and managing stopover sites in mid-continent North America and elsewhere for long-term shorebird conservation efforts (Navedo & Piersma, 2023).

Given that plovers and godwits seem the most constrained in migration strategy (i.e., metrics were most consistent across individuals), they could be at risk if key stopover areas are degraded or destroyed (Studds et al., 2017) or if change occurs at different rates during different parts of the annual cycle (Both & Visser, 2001; Wilde et al., 2022). Although avocets appear to have the most flexible migration strategy, plovers and godwits have more flexibility in feeding habitats. Plovers and godwits can feed in soil or mud (Poole et al., 2020; Walker et al., 2020), while avocets typically feed in the water column (Ackerman et al., 2020). Studies focused on an array of life history characteristics such as foraging strategy, habitat associations, and social behavior would provide a more holistic picture of the likely effects of global change on species with different migration strategies.

Comparisons with other concepts and frameworks in the study of migration strategy

Although we were only able to study three species in depth, there are many other studies investigating questions about migration strategy in other species, so our results can be considered in the context of this body of literature. For example, migration strategy can reflect patterns in population trends and be an indicator of species resilience. Lisovski et al. (2021) investigated stop-over dynamics in curlew sandpipers (*Calidris ferruginea*) and red-necked stints (*Calidris ruficollis*) in the East-Asian-Australasian flyway and found that curlew sandpipers have a heavier dependency on a smaller

number of sites, while red-necked stints are more flexible in sites and less dependent on specific areas. Curlew sandpipers and red-necked stints are closely related, but curlew sandpipers are experiencing rapid population decline, while the red-necked stint population trend is stable, so in this case differences in migration strategy could be associated with population trend and therefore species resilience to change (Lisovski et al., 2021). We saw similar patterns in our study, particularly regarding the comparison between Hudsonian godwits and American avocets. Due to their long-distance migrations with a substantial distance occurring over water, Hudsonian godwits require stopover areas in south-central North America (Walker et al., 2020). In contrast, we found that avocets generally stop more often relative to their shorter migration distance and appear to find stopover habitat more opportunistically, with greater flexibility in site use. Similar to the patterns found by Lisovski et al. (2021), godwits have a more negative population trend than avocets (Smith et al., 2023), which parallels the higher dependence of godwits on a smaller number of stopover areas. In addition, American woodcock, a short-distance migratory shorebird, have high variability in migration distance, duration, phenology, and number of stopovers (Clements et al., 2024), and our study also found high variability in many metrics for avocets. American woodcock have a similar latitudinal range (and therefore potential migration distance) to avocets, but a much smaller latitudinal range than Hudsonian godwits or black-bellied plovers. This pattern also suggests that shorter migration distances may be associated with greater flexibility in migration strategy and that for long-distance migrants, identifying and prioritizing key stopover sites may be particularly important.

There is also evidence that in some species, differences in migration strategy exist between ages, sexes, or breeding populations, but our study did not capture the full range of these characteristics (see *Methods*) for all of our focal species. For example, differential migration, when age or sex classes vary in times or places they migrate, is common in migratory birds and has been observed in many shorebird species, including black-bellied plovers (Cristol et al., 1999). We only captured male black-bellied plovers at our sites, which are located at the northern edge of the species' nonbreeding range (Poole et al., 2020), meaning that female black-bellied plovers likely have farther migration distances than the males we captured. This context should be considered in the interpretation of results related to black-bellied plover migration distance. The other focal species we studied appeared to be in mixed-sex groups, but the skewed sex ratios in our samples of avocets suggest the potential for spatial differences in nonbreeding sites.

Similarly, we know that different breeding populations of Hudsonian godwits have shown differences in migration phenology (Senner, 2012) but that variation was not captured in this study. Differential migration and its drivers remain poorly understood and could be important components of migration strategy, so future studies on differential migration would enhance our understanding of migration strategy (Paprocki & Conway, 2024).

More broadly, it is important to consider that there are many ways migration strategy has been characterized in the literature and many ways to measure it. Researchers can think of migration strategy in terms of energetics, for example, as time-minimizing and energy-minimizing strategies, and they may measure it by quantifying or finding proxy metrics for energy acquisition and expenditure (Hedenstrom & Alerstam, 1997). Whether or not to migrate at all can also be a key measure of migration strategy (Newton, 2012); we saw evidence for facultative migration in a small number of American avocets in Texas in our study, but this suggests that some individuals breeding in the areas where the nonbreeding and breeding ranges overlap may not be migrating. This is not common in shorebirds and would be an interesting area of future research. Migration strategy can also be characterized by the distance between and time spent at stopover sites; these measures allow researchers to examine the spectrum between a “hop” strategy, where short stopovers are taken a short distance apart, to a “skip” strategy, where birds move farther and spend more time at each stop, to a “jump” strategy, where birds are making long, nonstop flights and must spend more time at sites to refuel (Piersma, 1987). In our study, avocets appeared closest to the “hop” end of the spectrum, godwits appeared closest to the “jump” end of the spectrum, and plovers appeared to be closest to the intermediate “skip” strategy (similar to the findings of Catry et al., 2024). We make these interpretations by considering our results as a whole but did not attempt to set thresholds for these strategies because we interpret them as a continuum rather than as discrete strategies. Finally, although there are many ways to categorize migration strategy, we emphasize the importance of considering many elements of migratory behavior when investigating migration strategy, as every species will have a unique combination of characteristics making up its strategy, and the degree of variability in migration characteristics within species is also a key component of understanding it. We recommend that the results of this study and other studies of migration strategy be interpreted in the context of the broad and complex continuum of migration strategy that exists in migratory birds.

Considerations for deployment outcomes

We encourage consideration of deployment outcomes (e.g., device failure, bird mortality) when planning studies, as device effects on birds can be a significant issue in avian movement ecology (Bodey et al., 2018; Brlik et al., 2020; Whidden et al., 2007). We deployed 136 devices in the nonbreeding season with the intention of collecting data through the subsequent breeding season. Of our 136 deployments, 67 (49%) resulted in complete data from the nonbreeding season through the breeding season with no substantial time gaps, including the avocets and godwits that did not migrate. Success in obtaining complete migration data differed by species (43% for avocets, 70% for plovers, 31% for godwits). These differences could be due to differences in performance between device types (Clements et al., 2021), differences in device effects on birds, or a combination of both, but we were not able to glean this information from our data. Additional details of deployment outcomes are described in Appendix S1: Section S1. A 48% deployment failure rate has been reported across animal ecology (Hofman et al., 2019), so we did not expect to acquire quality data from every device deployment. As more sophisticated tracking devices continue to be developed, it may be more feasible to understand the causes of deployment failure. More evaluation of the causes of device failure and the effects of devices on birds across species and device types is important and should be undertaken in future studies.

Conclusions

Shorebirds with different migration distances and life history strategies will be vulnerable to climate and land use change in different ways in the future, so it is important to characterize bird movement and behavior across species. Our results show that avocets, with a relatively short migration distance, have greater flexibility in their migration behavior. Plovers and godwits exhibited less within-species variation, which could mean that their longer migrations constrain their behavior. Further work is needed to determine whether birds with constrained migratory behaviors are more susceptible to climate and land use change. Variability in strategy among birds with different migration distances highlights the need for community-level research and conservation efforts.

ACKNOWLEDGMENTS

This work was conducted under the following permits: USGS banding permit number 21314; Texas Parks and Wildlife scientific research permit number SPR-812-965;

Louisiana Department of Wildlife and Fisheries Scientific Research and Collection Permit number WDP-019-016; Texas A&M University-Kingsville IACUC approval number 2018-10-30A, University of Missouri ACUC protocol number 9502; Captures licenses (number 7625/2018 and number 296/2020) from the Government of Chile; and Bioethics Approval (number 355/2019) from Universidad Austral de Chile. Funding for this study was provided by a National Science Foundation Graduate Research Fellowship awarded to Sarah J. Clements; the Robert J. Kleberg, Jr. and Helen C. Kleberg Foundation, Upper Mississippi River/Great Lakes Joint Venture, University of Missouri, Texas A&M University—Kingsville, Audubon Society of Missouri, and Environment and Climate Change Canada awarded to R. Clark; Webster Groves Nature Study Society, The Waterbird Society, and the Animal Behavior Society; University of South Carolina; and Fondo Nacional de Desarrollo Científico y Tecnológico. We thank J. Olszak, R. Temple, J. Marty (Louisiana Department of Wildlife & Fisheries), and D. Newstead (Coastal Bend Bays & Estuaries Program) for providing logistical frameworks and assistance for fieldwork, and E. Basso, B. Benvenuti, G. Biscarra, F. Farley, C. Gherardi, J. Gutiérrez, B. Hill, J. LeClaire, C. Navarrete, T. Rodkey, A. Schindler, G. Torres, C. Verdugo, J. Vergara, M. Verhoeven, and K. Wojtusik for their work on bird capture efforts. We also thank T. Bonnot, L. Eggert, and F. Thompson for helpful comments on a previous version of this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code and data (Clements et al., 2024) are available from Zenodo: <https://doi.org/10.5281/zenodo.14549031>.

ORCID

Sarah J. Clements  <https://orcid.org/0000-0001-9572-0032>

Juan G. Navedo  <https://orcid.org/0000-0003-3451-1792>

Nathan R. Senner  <https://orcid.org/0000-0003-2236-2697>

Mitch D. Weegman  <https://orcid.org/0000-0003-1633-0920>

REFERENCES

- Ackerman, J. T., C. A. Hartman, M. P. Herzog, J. Y. Takekawa, J. A. Robinson, L. J. P. Oring, P. Skorupa, and R. Boettcher. 2020. "American Avocet (*Recurvirostra americana*), Version 1.0." In *Birds of the World*, edited by A. F. Poole. Ithaca, NY: Cornell Lab of Ornithology.
- Alerstam, T., and Å. Lindström. 1990. "Optimal Bird Migration: The Relative Importance of Time, Energy, and Safety." In *Bird Migration* 331–351. Berlin, Heidelberg: Springer.
- Anderson, A. M., S. Duijns, P. A. Smith, C. Friis, and E. Nol. 2019. "Migration Distance and Body Condition Influence Shorebird Migration Strategies and Stopover Decisions During Southbound Migration." *Frontiers in Ecology and Evolution* 7: 251.
- Anderson, C. M., H. G. Gilchrist, R. A. Ronconi, K. R. Shlepr, D. E. Clark, D. A. Fifield, G. J. Robertson, and M. L. Mallory. 2020. "Both Short and Long Distance Migrants Use Energy-Minimizing Migration Strategies in North American Herring Gulls." *Movement Ecology* 8: 1–12.
- Bodey, T. W., I. R. Cleasby, F. Bell, N. Parr, A. Schultz, S. C. Votier, and S. Bearhop. 2018. "A Phylogenetically Controlled Meta-Analysis of Biologging Device Effects on Birds: Deleterious Effects and a Call for More Standardized Reporting of Study Data." *Methods in Ecology and Evolution* 9: 946–955.
- Boettcher, R., S. M. Haig, and W. C. Bridges. 1995. "Habitat-Related Factors Affecting the Distribution of Nonbreeding American Avocets in Coastal South Carolina." *The Condor* 97: 68–81.
- Both, C., C. A. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, and R. P. Foppen. 2010. "Avian Population Consequences of Climate Change Are most Severe for Long-Distance Migrants in Seasonal Habitats." *Proceedings of the Royal Society B: Biological Sciences* 277: 1259–66.
- Both, C., and M. E. Visser. 2001. "Adjustment to Climate Change Is Constrained by Arrival Date in a Long-Distance Migrant Bird." *Nature* 411: 296–98.
- Briedis, M., and S. Bauer. 2018. "Migratory Connectivity in the Context of Differential Migration." *Biology Letters* 14: 20180679.
- Briedis, M., S. Hahn, and P. Adamík. 2017. "Cold Spell en Route Delays Spring Arrival and Decreases Apparent Survival in a Long-Distance Migratory Songbird." *BMC Ecology* 17: 1–8.
- Brlík, V., J. Koleček, M. Burgess, S. Hahn, D. Humple, M. Krist, J. Ouwehand, et al. 2020. "Weak Effects of Geolocators on Small Birds: A Meta-Analysis Controlled for Phylogeny and Publication Bias." *Journal of Animal Ecology* 29: 207–220.
- Catry, T., E. Correia, J. S. Gutiérrez, P. Bocher, F. Robin, P. Rousseau, and J. P. Granadeiro. 2024. "Low Migratory Connectivity and Similar Migratory Strategies in a Shorebird with Contrasting Wintering Population Trends in Europe and West Africa." *Scientific Reports* 14: 4884.
- Chapman, B. B., C. Brönmark, J. Å. Nilsson, and L. A. Hansson. 2011. "The Ecology and Evolution of Partial Migration." *Oikos* 120: 1764–75.
- Clements, S. J., B. M. Ballard, G. R. Eccles, E. A. Sinnott, and M. D. Weegman. 2021. "Trade-Offs in Performance of Six Lightweight Automated Tracking Devices for Birds." *Journal of Field Ornithology* 92: 506–517.
- Clements, S. J., L. A. Berigan, A. C. Fish, R. L. Darling, A. M. Roth, G. Balkcom, B. Carpenter, et al. 2024. "Satellite Tracking of American Woodcock Reveals a Gradient of Migration Strategies." *Ornithology* 141: ukae008.
- Clements, S. J., and J. C. Gunn. 2024. "sjclements9/Midcontinent-Shorebird-Migration-Strategies: Data: Migration Strategy and Constraint in Migration Behavior Vary Among Shorebird Species with Different Life Histories (v1.0)." Zenodo. <https://doi.org/10.5281/zenodo.14549032>.

- Clements, S. J., J. P. Loghry, B. M. Ballard, and M. D. Weegman. 2022. "Carry-Over Effects of Weather and Decision-Making on Nest Success of a Migratory Shorebird." *Ecology and Evolution* 12: e9581.
- Clements, S. J. 2022. Ecology of Mid-Continent Migratory Shorebirds, Performance of Tracking Devices, and Modelling Animal Social Structure and Demography. Dissertation, University of Missouri, Columbia, Missouri, USA.
- Colwell, M. A. 2010. *Shorebird Ecology, Conservation, and Management*. Berkeley: University of California Press.
- Conklin, J. R., N. R. Senner, P. F. Battley, and T. Piersma. 2017. "Extreme Migration and the Individual Quality Spectrum." *Journal of Avian Biology* 48: 19–36.
- Cristol, D. A., M. B. Baker, and C. Carbone. 1999. "Differential Migration Revisited: Latitudinal Segregation by Age and Sex Class." *Current Ornithology* 1999: 33–88.
- Dinsmore, J. J. 1977. "Notes on Avocets and Stilts in Tampa Bay, Florida." *Florida Field Naturalist* 5: 25–30.
- Douglas, D. C., R. Weinzierl, S. C. Davidson, R. Kays, M. Wikelski, and G. Bohrer. 2012. "Moderating Argos Location Errors in Animal Tracking Data." *Methods in Ecology and Evolution* 3: 999–1007.
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, Jr., P. Heglund, et al. 2010. "Conserving Migratory Land Birds in the New World: Do We Know Enough?" *Ecological Applications* 20: 398–418.
- Galbraith, H., D. W. DesRochers, S. Brown, and J. M. Reed. 2014. "Predicting Vulnerabilities of North American Shorebirds to Climate Change." *PLoS One* 9: e108899.
- Gherardi-Fuentes, C., J. Ruiz, C. Verdugo, and J. G. Navedo. 2020. "Male-Biased Adult Sex Ratio in Non-breeding Areas of an Extreme Long-Distance Migratory Shorebird Population." *Acta Oecologica* 105: 103560.
- Gilroy, J. J., J. A. Gill, S. H. M. Butchart, V. R. Jones, and A. M. A. Franco. 2016. "Migratory Diversity Predicts Population Declines in Birds." *Ecology Letters* 19: 308–317.
- Hedenstrom, A., and T. Alerstam. 1997. "Optimum Fuel Loads in Migratory Birds: Distinguishing between Time and Energy Minimization." *Journal of Theoretical Biology* 189: 227–234.
- Herbert, J. A., D. Mizrahi, and C. M. Taylor. 2022. "Migration Tactics and Connectivity of a Nearctic–Neotropical Migratory Shorebird." *Journal of Animal Ecology* 91: 819–830.
- Hewson, C. M., K. Thorup, J. W. Pearce-Higgins, and P. W. Atkinson. 2016. "Population Decline Is Linked to Migration Route in the Common Cuckoo." *Nature Communications* 7: 12296.
- Hofman, M. P., M. W. Hayward, M. Heim, P. Marchand, C. M. Rolandsen, J. Mattisson, F. Urbano, et al. 2019. "Right on Track? Performance of Satellite Telemetry in Terrestrial Wildlife Research." *PLoS One* 14: e0216223.
- Iwamura, T., H. P. Possingham, I. Chadès, C. Minton, N. J. Murray, D. I. Rogers, E. A. Treml, and R. A. Fuller. 2013. "Migratory Connectivity Magnifies the Consequences of Habitat Loss from Sea-Level Rise for Shorebird Populations." *Proceedings of the Royal Society B: Biological Sciences* 280: 20130325.
- Johnson, L. A., D. A. Haukos, L. M. Smith, and S. T. McMurry. 2012. "Physical Loss and Modification of Southern Great Plains Playas." *Journal of Environmental Management* 112: 275–283.
- Johnson, W. C., B. V. Millett, T. Gilmanov, R. A. Voldseth, G. R. Guntenspergen, and D. E. Naugle. 2005. "Vulnerability of Northern Prairie Wetlands to Climate Change." *Bioscience* 55: 863–872.
- Koleček, J., J. Reif, M. Šálek, J. Hanzelka, C. Sottas, and V. Kubelka. 2021. "Global Population Trends in Shorebirds: Migratory Behaviour Makes Species at Risk." *The Science of Nature* 108: 1–8.
- Kranstauber, B., A. Cameron, R. Weinzerl, T. Fountain, S. Tilak, M. Wikelski, and R. Kays. 2011. "The Movebank Data Model for Animal Tracking." *Environmental Modelling & Software* 26: 834–35.
- Kranstauber, B., M. Smolla, and A. K. Scharf. 2020. "Move: Visualizing and Analyzing Animal Track Data." R Package Version 4.0.6.
- Laaksonen, T., and A. Lehikoinen. 2013. "Population Trends in Boreal Birds: Continuing Declines in Agricultural, Northern, and Long-Distance Migrant Species." *Biological Conservation* 168: 99–107.
- Lindström, Å. 2020. "Migration Tracks of Waders: Avoiding the Pitfalls of Speed Estimates and Inferred Strategies." *Wader Study* 127: 2–3.
- Lindström, Å., T. Alerstam, and A. Hedenstrom. 2019. "Faster Fuelling Is the Key to Faster Migration." *Nature Climate Change* 9: 288–89.
- Linscott, J. A., J. G. Navedo, S. J. Clements, J. P. Loghry, J. Ruiz, B. M. Ballard, M. D. Weegman, and N. R. Senner. 2022. "Compensation for Wind Drift Prevails for a Shorebird on a Long-Distance, Transoceanic Flight." *Movement Ecology* 10: 1–16.
- Lisovskyi, S., K. Gosbell, C. Minton, and M. Klaassen. 2021. "Migration Strategy as an Indicator of Resilience to Change in Two Shorebird Species with Contrasting Population Trajectories." *Journal of Animal Ecology* 90: 2005–14.
- Meissner, W., and T. Cofta. 2014. "Part 10: Ageing and Sexing the Grey Plover *Pluvialis squatarola*." *Wader Study Group Bulletin* 121: 9–14.
- Moore, J. D., D. E. Andersen, T. R. Cooper, J. P. Duguay, S. L. Oldenburger, C. A. Stewart, and D. G. Kremetz. 2019. "Migratory Connectivity of American Woodcock Derived Using Satellite Telemetry." *The Journal of Wildlife Management* 83: 1617–27.
- Morriss, Z. N., A. Lilleyman, R. A. Fuller, R. Bush, J. T. Coleman, S. T. Garnett, Y. N. Gerasimov, et al. 2022. "Differential Population Trends Align with Migratory Connectivity in an Endangered Shorebird." *Conservation Science and Practice* 4: e594.
- Mullens, E. D., and R. A. McPherson. 2019. "Quantitative Scenarios for Future Hydrologic Extremes in the US Southern Great Plains." *International Journal of Climatology* 39: 2659–76.
- Navedo, J. G., and T. Piersma. 2023. "Do 50-Year-Old Ramsar Criteria Still Do the Best Possible Job? A Plea for Broadened Scientific Underpinning of the Global Protection of Wetlands and Migratory Waterbirds." *Conservation Letters* 16: e12941.
- Navedo, J. G., and J. Ruiz. 2020. "Oversummering in the Southern Hemisphere by Long-Distance Migratory Shorebirds Calls for

- Reappraisal of Wetland Conservation Policies.” *Global Ecology and Conservation* 23: e01189.
- Newton, I. 2012. “Obligate and Facultative Migration in Birds: Ecological Aspects.” *Journal of Ornithology* 153: 171–180.
- Paprocki, N., and C. J. Conway. 2024. “The Underlying Causes of Differential Migration: Assumptions, Hypotheses, and Predictions.” *Biological Reviews*. <https://doi.org/10.1111/brv.13160>
- Piersma, T. 1987. “Hop, Skip, or Jump? Constraints on Migration of Arctic Waders by Feeding, Fattening, and Flight Speed.” *Limosa* 60:3 185–194.
- Piersma, T., and Å. Lindström. 2004. “Migrating Shorebirds as Integrative Sentinels of Global Environmental Change.” *Ibis* 146: 61–69.
- Poole, A. F., P. Pyle, M. A. Patten, and D. R. Paulson. 2020. “Black-Bellied Plover (*Pluvialis squatarola*), Version 1.0.” In *Birds of the World*, edited by S. M. Billerman. Ithaca, NY: Cornell Lab of Ornithology.
- R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Rappole, J. H., and G. W. Blacklock. 1985. *Birds of the Texas Coastal Bend: Abundance and Distribution*. College Station, TX: Texas A&M University Press.
- Rappole, J. H., and A. R. Tipton. 1991. “New Harness Design for Attachment of Radio Transmitters to Small Passerines (Nuevo Diseño de Arnés para Atar Transmisores a Passeriformes Pequeños).” *Journal of Field Ornithology* 62: 335–37.
- Rashford, B. S., R. M. Adams, J. Wu, R. A. Voldseth, G. R. Guntenspergen, B. Werner, and W. C. Johnson. 2016. “Impacts of Climate Change on Land-Use and Wetland Productivity in the Prairie Pothole Region of North America.” *Regional Environmental Change* 16: 515–526.
- Robinson, R. A., H. Q. Crick, J. A. Learmonth, I. M. Maclean, C. D. Thomas, F. Bairlein, M. Forchhammer, et al. 2009. “Travelling Through a Warming World: Climate Change and Migratory Species.” *Endangered Species Research* 7: 87–99.
- Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, et al. 2019. “Decline of the North American Avifauna.” *Science* 366: 120–24.
- Rosenberg, K. V., D. Pashley, B. Andres, P. J. Blancher, G. S. Butcher, W. C. Hunter, D. Mehlman, et al. 2014. *The State of the Birds 2014 Watch List*. Washington, DC: North American Bird Conservation Initiative, U.S. Committee.
- Sanderson, F. J., P. F. Donald, D. J. Pain, I. J. Burfield, and F. P. J. Van Bommel. 2006. “Long-Term Population Declines in Afro-Palearctic Migrant Birds.” *Biological Conservation* 131: 93–105.
- Sanzenbacher, P. M., S. M. Haig, and L. W. Oring. 2000. “Application of a Modified Harness Design for Attachment of Radio Transmitters to Shorebirds.” *Wader Study Group Bulletin* 91: 16–20.
- Senner, N. R. 2012. “One Species but Two Patterns: Populations of the Hudsonian Godwit (*Limosa haemastica*) Differ in Spring Migration Timing.” *The Auk* 129: 670–682.
- Senner, N. R., W. M. Hochachka, J. W. Fox, and V. Afanasyev. 2014. “An Exception to the Rule: Carry-Over Effects Do Not Accumulate in a Long-Distance Migratory Bird.” *PLoS One* 9: e86588.
- Shimada, T., R. Jones, C. Limpus, and M. Hamann. 2012. “Improving Data Retention and Home Range Estimates by Data-Driven Screening.” *Marine Ecology Progress Series* 457: 171–180.
- Shuert, C. R., N. E. Hussey, M. Marcoux, M. P. Heide-Jørgensen, R. Dietz, and M. Auger-Méthé. 2023. “Divergent Migration Routes Reveal Contrasting Energy-Minimization Strategies to Deal with Differing Resource Predictability.” *Movement Ecology* 11: 31.
- Skagen, S. K., S. Brown, and R. Johnson. 2005. “Implications of Different Shorebird Migration Strategies for Habitat Conservation.” In *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference*, Vol. 191, edited by C. J. Ralph and T. D. Rich, 680–83. Albany, CA: United States Department of Agriculture, Forest Service, Pacific Southwest Research Station.
- Smith, P. A., A. C. Smith, B. Andres, C. M. Francis, B. Harrington, C. Friis, R. I. G. Morrison, et al. 2023. “Accelerating Declines of North America’s Shorebirds Signal the Need for Urgent Conservation Action.” *Ornithological Applications* 125: duad003.
- Steen, V., S. K. Skagen, and B. R. Noon. 2018. “Preparing for an Uncertain Future: Migrating Shorebird Response to Past Climatic Fluctuations in the Prairie Potholes.” *Ecosphere* 9: e02095.
- Studds, C. E., B. E. Kendall, N. J. Murray, H. B. Wilson, D. I. Rogers, R. S. Clemens, K. Gosbell, et al. 2017. “Rapid Population Decline in Migratory Shorebirds Relying on Yellow Sea Tidal Mudflats as Stopover Sites.” *Nature Communications* 8: 1–7.
- Thomas, G. H., R. B. Lanctot, and T. Székely. 2006. “Can Intrinsic Factors Explain Population Declines in North American Breeding Shorebirds? A Comparative Analysis.” *Animal Conservation* 9: 252–58.
- van der Velde, M., O. Haddrath, Y. I. Verkuil, A. J. Baker, and T. Piersma. 2017. “New Primers for Molecular Sex Identification of Waders.” *Wader Study* 124: 147–151.
- Végvári, Z., V. Bokony, Z. Barta, and G. Kovacs. 2010. “Life History Predicts Advancement of Avian Spring Migration in Response to Climate Change.” *Global Change Biology* 16: 1–11.
- Walker, B. M., N. R. Senner, C. S. Elphick, and J. Klima. 2020. “Hudsonian Godwit (*Limosa haemastica*), Version 1.0.” In *Birds of the World*, edited by A. F. Poole. Ithaca, NY: Cornell Lab of Ornithology.
- Wauchope, H. S., J. D. Shaw, Ø. Varpe, E. G. Lappo, D. Boertmann, R. B. Lanctot, and R. A. Fuller. 2017. “Rapid Climate-Driven Loss of Breeding Habitat for Arctic Migratory Birds.” *Global Change Biology* 23: 1085–94.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. “Links Between Worlds: Unraveling Migratory Connectivity.” *Trends in Ecology & Evolution* 17: 76–83.
- Whidden, S. E., C. T. Williams, A. R. Breton, and C. L. Buck. 2007. “Effects of Transmitters on the Reproductive Success of Tufted Puffins.” *Journal of Field Ornithology* 78: 206–212.
- Wilde, L. R., J. E. Simmons, R. J. Swift, and N. R. Senner. 2022. “Dynamic Sensitivity to Resource Availability Influences

Population Responses to Mismatches in a Shorebird." *Ecology* 103: e3743.
Zhao, M., M. Christie, J. Coleman, C. Hassell, K. Gosbell, S. Lisovski, C. Minton, and M. Klaassen. 2017. "Time Versus Energy Minimization Migration Strategy Varies with Body Size and Season in Long-Distance Migratory Shorebirds." *Movement Ecology* 5: 1–12.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Clements, Sarah J., Jason P. Loghry, Jennifer A. Linscott, Jorge Ruiz, Joe C. Gunn, Juan G. Navedo, Nathan R. Senner, Bart M. Ballard, and Mitch D. Weegman. 2025. "Migration Strategy and Constraint in Migration Behavior Vary among Shorebird Species with Different Life Histories." *Ecosphere* 16(1): e70161. <https://doi.org/10.1002/ecs2.70161>