Movement and habitat use of non-breeding Semipalmated Sandpiper (Calidris pusilla) at the Banco dos Cajuais in Northeast Brazil

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Abstract
Semipalmated sandpipers are Arctic breeding shorebirds that migrate to South America during the non-breeding season. Little work has been done to understand the daily movements, foraging habits and metabolic state of this species on stationary nonbreeding grounds. Our work was conducted at the Banco dos Cajuais Western Hemisphere Shorebird Reserve Network (WHSRN) site in Northeast Brazil. We captured semipalmated sandpipers in February and March 2019 and 2020 and attached nanotags to monitor their daily movements. Blood samples were taken to measure plasma triglycerides (an index of fattening rate). We also conducted behavioral observations on foraging birds. Using tracking data we determined that most semipalmated sandpipers appeared to use sunrise/sunset as an indicator for movement between salina and tidal flat habitats, and a smaller portion used tidal height. We found birds spent similar amounts of time foraging on tidal flats and in salinas, though different foraging modes were used. Plasma triglyceride measures suggest semipalmated sandpipers had not started preparing to migrate when sampled. We successfully tracked semipalmated sandpipers to North America during northward migration in 2020, detecting eight within the United States. Tracking results suggest many stopped elsewhere in South America to fuel for migration, though some may have fueled at the Banco dos Cajuais. By demonstrating substantial use of both natural and altered habitats in the region by migrant semipalmated sandpipers, these data highlight the need for broader conservation measures throughout coastal regions of South America.

KEYWORDS
foraging behavior, Motus Wildlife Tracking System, radio tracking, shorebirds, shrimp farms, South America
1 | INTRODUCTION

Shorebird populations throughout the Western Hemisphere are in decline (Andres et al., 2012; Morrison et al., 2012; Rosenberg et al., 2019). Causes of population declines in migratory species can be difficult to pinpoint, and waning numbers of shorebirds have been recorded at breeding, stopover and non-breeding sites (Andres et al., 2012; Gratto-Trevor et al., 2012; Jehl, 2007; Morrison et al., 2012). This is especially true for semipalmated sandpipers (Calidris pusilla), a Nearctic breeding shorebird that migrates to South America each year. There are three identified breeding populations of semipalmated sandpipers across the Arctic which can be distinguished by a cline in bill length, with shorter bills in the west and longer bills in the east (Gratto-Trevor et al., 2012). Disproportionate population declines have been recorded for eastern breeding semipalmated sandpipers, especially on the non-breeding grounds (Gratto-Trevor et al., 2012; Morrison et al., 2012) prompting studies throughout the species’ range to determine sources of declines.

In the West Atlantic Flyway, migratory shorebirds spend a large portion of the non-breeding season in South America. Observed declines of eastern breeding semipalmated sandpipers could be related to habitat changes there (Morrison et al., 2012). Changes in habitat in non-breeding areas of the East Asian-Australasian flyway are responsible for the largest negative effect on reproductive success and survival in Ruddy Turnstones (Arenaria interpres), a long-distance migrant (Aharon-Rotman et al., 2016). Duriez et al. (2012) obtained similar results with Eurasian Oystercatchers (Haematopus ostralegus) in the East Atlantic Flyway. Aerial surveys of the northern coast of South America suggest that shorebird habitats are being lost and altered (Morrison et al., 2012), partially as a result of human activities. This may also be related to climate change, as coastal sites are highly susceptible to the effects of sea level rise and large storm events, risking their future availability to shorebirds which depend on them (Galbraith et al., 2002). Further, human presence is a factor; for example, in Brazil ~40% of the population lives near the coast, highlighting the economic importance of these coastal areas (Ferreira & Lacerda, 2016).

Coastal areas of Northeast Brazil are important to multiple sectors of the economy including local subsistence activities, large-scale tourism, and industrial development. This creates pressure to convert certain habitats like mangroves and salt flats for human activities including shrimp and tilapia aquaculture, and salt evaporation ponds (known in Brazil as salinas) (Ferreira & Lacerda, 2016). Northeast Brazil, particularly the states of Ceará and Rio Grande do Norte, produces 98% of all domestically consumed shrimp (Litopenaeus vannamei; Ferreira & Lacerda, 2016), much of which is grown in converted mangroves and salt flat habitats (i.e., salt pans known in Brazil as apicums or salgados), typically leading to extensive habitat changes (Lacerda et al., 2021). Recent estimates suggest that 20,000–30,000 ha of coastal habitat was being used for shrimp production in 2020 (Lacerda et al., 2021). While shrimp farms have provided alternative foraging habitats for shorebirds in some cases (Basso et al., 2018; Navedo et al., 2015; Navedo & Fernández, 2019), the actual importance and potential impacts of these highly modified habitats for shorebirds in other locations is relatively unknown (Burger et al., 2019).

The Banco dos Cajuais, located in the state of Ceará in northeastern Brazil, is a Western Hemisphere Shorebird Reserve Network site of regional importance (WHSRN Sites, n.d.) designated in 2017. This WHSRN site supports a diverse assemblage of resident and Nearctic migratory shorebirds, including semipalmated sandpipers, and is characterized by extensive tidal flats, beachfront, dunes, coastal scrub, mangrove forest and a mosaic of salt flats mixed with salt evaporation ponds and shrimp farms (Albano et al., 2007; Fedrizzi et al., 2016; Meireles & Santos, 2011; Valente et al., 2011). Although the area is relatively small, the diversity of habitats at the Banco dos Cajuais is representative of other coastal areas in northeastern South America (Campos et al., 2003). While we know this site is important for non-breeding shorebirds, we lack information on site fidelity and movements for generalist species such as semipalmated sandpipers in the region. An in-depth understanding of movement patterns and habitat use will be key to implementing effective and targeted shorebird conservation activities in northeastern Brazil, and throughout coastal areas in northern South America.

To address these knowledge gaps, we used radio-tracking and behavioral observations to examine habitat use and individual movements of semipalmated sandpipers using the Banco dos Cajuais. We also examined fueling rates through measurement of plasma triglyceride levels. We hypothesized that shorebird movements would be heavily influenced by tides, and that tidal flat habitat would be used primarily for foraging while the highly modified salt flat area of the Banco dos Cajuais, dominated by salinas and shrimp farms, would be used primarily for roosting and body maintenance.

2 | METHODS

2.1 | Bird capture and sample collection

Semipalmated sandpipers were captured in Icapuí, Ceará, Brazil (−4.694, −37.360) in 2019 (12–19 February, 21–22
March) and 2020 (17–18 February, 17 March) during the non-breeding season. Birds were captured using mist nets set up on dykes among evaporation ponds during periods at night when the rising tide made tidal flats inaccessible, and birds were moving inland to roost in the salinas. We marked each bird with an individually numbered metal leg band on the upper left leg and a dark blue flag with white engraving and a unique alpha-numeric code on the upper right leg. We recorded mass (±0.1 g), flattened straightened wing chord (±1 mm), bill (culmen to tip) and tarsus length (±0.1 mm) of each bird. Birds were aged as second year (SY) or after second year (ASY) by examining wing plumage (Gratto-Trevor, 2004). If age was ambiguous, birds were recorded as after hatch year (AHY).

We attached digitally encoded 0.67-g Lotek VHF nanotags (NTQB-3-2, Lotek Wireless Inc., Newmarket, ON, Canada) onto a subset of ASY birds. In 2019 we deployed 45 nanotags on birds captured in February; in 2020, 20 nanotags were deployed in February and 39 in March with the objective of detecting local movements and northward migration. Feathers were trimmed on the lower back just above the uropygial gland, and tags were attached using cyanoacrylate glue (Loctite Super Glue Control UltraGel) following methods described in Sprague et al. (2008).

To assess metabolic state through analysis of plasma triglycerides, we collected blood samples within 20 minutes of capture to avoid the impact of handling stress (Guglielmo et al., 2002). In 2019 we collected 14 samples, and in 2020 we collected 23 samples. The average bleed time after capture was 9.9 min (SD 4.1 min). We collected blood from the brachial vein of birds using 27-gauge needles and heparinized capillary tubes. A maximum of 140 µL of blood was collected from each bird. Blood was transferred from the capillary tubes to Eppendorf tubes in the field and kept on ice until the samples could be centrifuged at the end of each capture effort, no more than 6 h after the blood was drawn. Blood samples were centrifuged at 10,000 RPM for 1 min (myS-PIN12 Mini Centrifuge, Thermo Fisher Scientific) to separate plasma and red blood cells. We pipetted off the plasma layer into separate Eppendorf tubes and stored samples at −20°C until used for analyses.

All bird sampling was conducted in compliance with state and federal environmental law (MMA/ICMBio/ SISBIO Permit No. 66348-2) and Mount Allison University Animal Care requirements (protocol #102336) under guidelines from the Canadian Council on Animal Care.

2.2 | Automated radio telemetry

We used automated radio telemetry through the Motus Wildlife Tracking System (Taylor et al., 2017, www.motus.org) to track movements and determine habitat use for semipalmated sandpipers at the Banco dos Cajuais. Nanotags are digitally encoded and operate at a fixed frequency of 166.380 MHz, each transmitting a unique signal that is decoded by the tracking system. The nanotags had a burst rate of 10.1 s and were expected to function for ~120 days, allowing us to track the birds throughout the latter portion of their time on the non-breeding grounds and potentially upon their arrival in North America during northward migration.

The Motus system uses stationary receivers that automatically record data when tagged birds are in range (up to 20 km, depending on conditions), though bird elevation and line of sight to receivers can affect detections. In 2019 and 2020 there were two active receivers at our study site, one located on a beachfront property adjacent to the main tidal flat, and a second located on a shrimp farm, ~1200 m inland from the first receiver, adjacent to the main shorebird roosting areas in the salinas. The beachfront receiver had antennas directed N and ENE to cover the central area of the tidal flats which extend up to ~3 km offshore at low tide (Figure 1). The shrimp farm receiver, located to the SW behind the mangrove and lacking a direct line of sight to the tidal flats, was strategically located to detect tagged birds using the salinas and shrimp farm environments (Figure 1). The antennas were directed NW and ESE to detect birds moving into shrimp farm and salina habitats. These areas are at quite a low elevation, resulting in the birds mostly being detected in short bursts while moving between the shore and inland habitats, unless they were foraging directly beneath the receiver.

Due to observed gaps in detections for birds tagged in 2019, we supplemented our detections from the Motus receivers with hand tracking in 2020. We used a Yagi-antenna paired with a hand-held Lotek wireless receiver (Lotek SRX600, Lotek Inc., Newmarket, ON, Canada) to track birds in areas not adequately covered by the Motus receivers. For consistency, we drove transects throughout the study area during day and nighttime hours, and at varying tidal heights. Using this approach, we confirmed that semipalmated sandpipers were in the salina environment when there were gaps in detections and that only entries and exits to these habitats were captured by the Motus receivers.

Tracking data were downloaded and processed using R statistical software version 4.0.3 (R Core Team, 2020) with an R Studio interface. We cleaned data using guidelines provided in the Motus R Book (Crewe et al., 2020). Detections were filtered to exclude those that had a run length of less than three consecutive bursts to minimize the frequency of false positives. Antenna signal plots were examined for each nanotag to remove suspect
detections, specifically detections with short durations (3–10 hits consecutively). Cleaned data were retained and used for further analyses.

2.3 | Foraging behavior

We collected behavior data using scan observations to estimate daily activities (Altmann, 1974). Scans involved observing individual semipalmated sandpipers sequentially throughout a flock and recording their behavior once every minute for 15-min sampling periods. Foraging behaviors were categorized as follows: peck, probe, skim, preen, rest, and locomotion. Observations were completed in both tidal flat and salina habitats.

To compile the scan samples, we calculated the proportion of time spent engaged in each activity by summing the number of times a particular behavior was observed during each 15-min sample and dividing it by the total number of observations. Time spent foraging was determined by combining pecking, probing and skimming (running the bill along the surface of the sediment [MacDonald et al., 2012] or continually sifting through sediment with bill in shallow water).

2.4 | Plasma metabolites

Plasma triglycerides (TRIG) were quantified for undiluted plasma samples using a commercially available assay kit from Sigma Aldrich (Triglyceride Determination Kit; Sigma-Aldrich, TR0100-1KT, Oakville, ON, Canada). The samples were analyzed in duplicate on a 96-well plate spectrophotometer (Bio-Rad, Benchmark Microplate Reader, Hercules California). If duplicate samples had >20% difference in results they were run a second time (if possible), or the data were excluded from the analysis. Duplicate samples within the acceptable variation were averaged, and the average value was considered as the metabolite measure for each individual.
2.5 | Statistical analyses

2.5.1 | Movement and habitat use

All analyses were completed using R statistical software, version 4.0.3 (R Core Team, 2020) with an R Studio interface. Throughout our analyses we tested the assumption of normality using a Shapiro test and visual inspection of Q-Q plots, and homogeneity of variance using Cochran’s test. To account for unbalanced data we used type II sums of squares (Langsrud, 2003). We set α at .05 for main effects, and 0.1 for interactions to ensure that main effects were not inappropriately interpreted in the presence of a potential interaction (as in Hamilton et al., 2006).

Birds detected for <4 days were removed from analyses (N2019 = 2, N2020 = 4), as they were outliers in the distribution of tracking lengths. These birds likely dropped their tags shortly after release or left the detection area. Our objective was to track local and long-distance migratory movements, and these data did not contribute to our understanding of habitat use. There were also some birds for which there were few detections or did not appear to use the local habitats regularly (N2019 = 2, N2020 = 6), which were not included in strategy analyses. These birds had frequent flybys or would disappear from the region for extended periods but did not use the habitat regularly.

We identified three distinct movement strategies by visually inspecting detection timelines from Motus tracking data (Supporting Information, Appendix S1). These timelines show detections by time of day and date, revealing consistent patterns that were clearly distinguishable into groups. Birds following a tidal pattern moved between habitats according to tide cycle, arriving on the tidal flats approximately 2 h after high tide regardless of time of day (Supporting Information, Appendix S1b). This regular movement led to a pattern in which birds arrived on the tidal flats roughly 1 h later each subsequent day, following the temporal progression of the tidal cycle. Conversely, birds using a sunrise/sunset pattern were not detected on the tidal flats at all during daylight hours, but were present during nighttime hours (between 18:00 and 05:00) during periods when the tidal flats were exposed (Supporting Information, Appendix S1a). Finally, a smaller subset of birds used a mixed strategy including both sunrise/sunset and tidal cycle as indicators (Supporting Information, Appendix S1c). The mixed strategy presented timelines that were more variable, but in all cases showed responses to both tidal height and daylight, so was easily distinguished from the other strategies.

To determine time spent on the tidal flat we used cleaned Motus data from the tidal flat receiver and calculated the time spent using this habitat each day. We examined days individually for each bird and determined conservative estimates for the amount of time spent on tidal flats. We included short gaps (<1 h) in detections in our estimates, as these may have stemmed from birds turning away from the receiver while foraging. However, time associated with gaps in detections bordered by detections on the shrimp farm receiver, indicating they left the coastal habitat, was removed. We also removed times when detection gaps were greater than 1 h, as individuals may have left the habitat.

To investigate possible explanations for the different movement strategies employed by individuals, we used an analysis of variance (ANOVA) to examine the relationship between bill length and movement strategy. Previous work in South America hypothesized that bill length may affect shorebird foraging during daytime low tides because high temperatures may cause prey to retreat deeper into the sediment, limiting their availability to birds with shorter bills (Nebel & Thompson, 2005). We tested the hypothesis that birds with differing bill lengths, and therefore differing abilities to access burrowing prey, may be using local habitats in different ways.

2.6 | Behavior

We analyzed behavior data using a permutational multivariate analysis of variance (PERMANOVA) with the adonis function from the vegan package in R (Oksanen et al., 2020). Behaviors (pecking, probing, skimming, resting, preening and locomotion) were the dependent variables and site and year were predictors. Significant results were examined using similarity percentages (SIMPER) and homogeneity of multivariate dispersion (PERMDISP) analyses (vegan; Oksanen et al., 2020) to assess how behaviors contributed to the overall result. To further assess identified differences in foraging we completed a separate linear model with logit transformed proportion of time spent feeding as the dependent variable and site, year, and day of year as the response variables.

2.7 | Plasma metabolites and northward migration

We used a two-way fixed factor ANOVA to compared size adjusted mass of all captured birds between the two capture times (February and March) and years (2019 and 2020) to examine differences in fattening among birds in these groups. Size adjusted mass corrects for the structural size of a bird and represents the fat content of a
bird, which was calculated using the following formula taken from Winker et al. (1992)

\[
\text{Size adjusted mass} = \frac{\text{Mass (g)}}{(\text{wing chord})^{3/2} (\text{mm})} \times 10,000
\]

We did two separate analyses of plasma metabolites, one using values from tagged birds and a second using a larger sample size, including tagged and untagged birds. To analyze tagged birds we completed an ANOVA with log transformed plasma triglyceride values as the dependent variable, and strategy and year as the predictors. For our analyses of all bled birds we completed a two-way ANOVA using log transformed plasma triglyceride values as the dependent variable and year and time of sample collection (February or March) as the predictors. We initially included size adjusted mass and time between capture and bleeding as covariates in both models, but there was no relationship \((p > .55)\) so they were removed. To see if there were differences in size adjusted mass between months and years, we completed a two-way ANOVA with size adjusted mass as the dependent variable, and year and time of sample collection (February or March) as predictors.

3 | RESULTS

3.1 | Movement strategies and northward migration

Both sunrise/sunset and tide influenced the daily movements of semipalmated sandpipers at the Banco dos Cajuais, however most of the radio-tagged birds (2019: 61%, 2020: 65.3%) moved with sunrise and sunset. These shorebirds were detected on the tidal flats during low tides at night and spent all daylight hours in the salinas (Figure 2a, Supporting Information, Appendix S1a). Given its location near the equator, at the Banco dos Cajuais each day has roughly 12 h of light which remains almost constant throughout the year. Birds using this strategy typically left the salinas and arrived at the tidal flats from 30 min before to 30 min after sunset and returned close to sunrise. Occasional detections in the salinas during daylight hours suggested they were moving within the salinas and spending the day there. They were rarely detected on the tidal flats during daylight hours.

Approximately one fifth of our tagged birds (2019: 24.4%, 2020: 16.3%) followed the tidal cycle, relocating to the tidal flats as soon as the tide began falling and returning to the salinas only when the tidal flats were covered (Figure 2b, Supporting Information, Appendix S1b). This movement was independent of daylight. These birds appeared on the tidal flats 1 h later each day, closely tracking the temporal progression of the tidal cycle, occurring twice daily with a period of approximately 12.5 h between high tides (Figure 2b). Finally, the smallest subset of birds seemed to use a mixed strategy (2019: 14.6%, 2020: 18.4%), appearing to roost during daytime high tides on the beachfront adjacent to the tidal flats or changing their movement strategy for short periods of time (Supporting Information, Appendix S1c). For many of these birds it was clear that they responded to both tidal height and sunrise/sunset (Supporting Information, Appendix S1c). Regardless of the strategy employed, the individuals were highly consistent over time in their movement patterns (Supporting Information, Appendix S1).

The average amount of time spent on the tidal flats daily varied with movement strategy. Birds moving with the tide spent 11.24 (SD 2.8) h/day on the tidal flats,
which represents nearly all available time for foraging. This is similar for birds using a mixed strategy, which spent 11.77 (SD 4.40) h/day on the tidal flats. Birds using sunrise/sunset as a movement indicator spent only 9.15 (SD 2.5) h/day on the tidal flats. The movements of these birds were still restricted by tide, which is evident by the forward temporal shift in detection gaps that were observed each night (Figure 2a). When high tide occurs at night, the available time for foraging on the tidal flats is further constrained, resulting in a lower average time spent in this habitat.

The mean bill length of all semipalmated sandpipers captured in 2019 and 2020 was 20.4 mm (SD 1.89). Bill lengths among tagged birds varied with movement strategy ($F_{2,87} = 9.87, p = .0001$) (Figure 3). Birds using the tidal strategy had longer bills than those using the sunrise/sunset strategy (Tukey’s test, $p = .0001$). Mixed strategy birds fell between the groups but did not differ significantly from either (tide vs. mixed, $p = .13$; sunrise/sunset vs. mixed, $p = .20$).

In 2020 we detected eight of our tagged birds in North America during northward migration (Table 1). One bird was detected 5 days after leaving our study site, suggesting it completed most of its migratory preparation at the Banco dos Cajuais. All others had detection gaps ranging from 15 to 51 days, and likely refueled elsewhere before departing for North America. All but one semipalmated sandpiper was detected on the Atlantic Coast of North America. Of those detected on the Atlantic Coast, the average bill length was 20.75 mm (SD 2.0), making them consistent with the rest of the population sampled at the Banco dos Cajuais.

### 3.2 | Behavior

Based on our scan sampling, bird behavior differed between sites and years (Table 2). All behaviors differed significantly between sites, though pecking and skimming drove most of the observed differences (peck: 31%

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**Figure 3** Bill lengths (mm) of semipalmated sandpipers exhibiting different movement strategies at the Banco dos Cajuais in 2019 and 2020; tidal strategy refers to birds that moved to and from the tidal flats based on tide level, sunrise/sunset strategy refers to birds that moved to the tidal flats at sunset and returned to the salinas at sunrise, and the mixed strategy involved birds that used a combination of the two methods.

**Table 1** Tagging and detection dates of semipalmated sandpipers detected on northward migration in spring 2020

| Tagging date (2020) | Last detection Banco dos Cajuais | First detection in North America | Location of arrival in North America | Time between detections (days) |
|---------------------|----------------------------------|----------------------------------|-------------------------------------|------------------------------|
| 1 17 Feb            | 7 April                          | 13 May                           | Mackay Island NWR, NC, USA, Atlantic Coast | 35                           |
| 2 17 Feb            | 19 April                         | 19 May                           | Chesapeake Bay, VA, USA, Atlantic Coast | 20                           |
| 3 17 March          | 8 May                            | 14 May                           | Kiawah Island, SC, USA, Atlantic Coast | 5                            |
| 4 17 March          | 9 May                            | 27 May                           | Pittsville, MD, USA, Atlantic Coast | 17                           |
| 5 17 March          | 30 April                         | 16 May                           | Hurley Township, MO, USA, Mississippi Flyway | 15                           |
| 6 17 March          | 8 May                            | 23 May                           | Assateague Island, MD, USA, Atlantic Coast | 17                           |
| 7 17 March          | 12 April                         | 30 May                           | Harbor Island, SC, USA, Atlantic Coast | 50                           |
| 8 17 March          | 24 March                         | 14 May                           | Harbor Island, SC, USA, Atlantic Coast | 51                           |
dissimilarity $p < .001$; skim: 25% dissimilarity $p < .001$) (Figure 4, Supporting Information, Appendix S2). Pecking and probing were more common on the tidal flats, while skimming was seen exclusively in the salinas (Figure 4). Additionally, we found dispersion of observed behaviors differed significantly between sites ($F_{1,46} = 81.6, p < .001$), with more variability in behavior in the salinas (Figure 4). Overall, the average dissimilarity in behaviors between the two sites was 56.9%.

To further investigate identified differences in foraging behaviors we assessed foraging activity separately from the other behaviors. There was no detectable difference between the tidal flats and salinas in proportion of time birds spent foraging (Site: $F_{1,44} = 2.78, p = .10$), though there was a difference between years (Year: $F_{1,44} = 16.71, p < .001$), with more foraging observed in 2019 than 2020 (Figure 5). Most often, birds foraging in the salinas appeared to prefer low salinity ponds with lower water levels, but occasionally they would be observed in high salinity evaporation ponds with higher water levels, actively “fishing” for Artemia spp.

### 3.3 | Plasma metabolites

We found no difference in plasma triglyceride levels of tagged birds between movement strategies or years (Strategy: $F_{2,14} = 2.3, p = .14$; Year: $F_{1,14} = 1.5, p = .24$), and differences between strategies and years were consistent (Strategy × Year: $F_{2,14} = 1.0, p = .39$). However,
when we included both tagged and untagged birds, years were different (Year: $F_{1,34} = 9.47$, $p = .004$), likely as a result of increased statistical power. TRIG values were lower in 2020 than they were in 2019 (Figure 6), but values in samples taken in February and March were similar (sample month: $F_{1,34} = 1.18$, $p = .29$) (Figure 6). Additionally, there was no difference in size adjusted mass of birds between the capture months and years (capture month: $F_{1,188} = 0.23$, $p = .63$; Year: $F_{1,188} = 0.18$, $p = .68$), suggesting that the birds were not gaining weight during this period.

4 | DISCUSSION

4.1 | Habitat use and movement strategies

Our tracking data indicate that semipalmated sandpipers using the Banco dos Cajuais in Northeastern Brazil make extensive use of both beachfront and tidal flats, as well as human-altered environments such as salinas and shrimp farms. We found that sunrise/sunset and tidal height were the two main factors influencing daily movements of semipalmated sandpipers at the Banco dos Cajuais. We expected the tidal cycle to be the major driver of local shorebird movements at this site, as its influence has been reported in other similar habitats (Basso et al., 2018; Dias, 2009), and because the tidal flats at the Banco dos Cajuais are mostly unavailable during peak high tide periods. Additionally, tides are a common feature of the landscape for shorebirds at many points during their annual cycle, often dictating their movements (Burger et al., 1977; Rogers et al., 2006). We were surprised to find that semipalmated sandpiper movements at this location were primarily driven by sunrise and sunset. Birds using this strategy visited the tidal flats only at night and therefore had reduced access to the tidal flats, especially when high tides occurred at night. Thus, they spent more time in human-manipulated areas dominated by salinas, and shrimp growing basins.

Although our data do not explain the existence of these different strategies, we hypothesize that changes in prey availability between day and night may be causing birds to move at sunrise and sunset. The Banco dos Cajuais is characterized by a hot, tropical climate. Even during the rainy season, it typically rains in heavy bursts of short duration during the predawn and early morning period, with comparatively less rainfall during the day. This results in higher sediment temperatures during daytime low tide periods. It is known that sediment temperature affects the vertical zonation of different marine invertebrates, some of which are potential prey items for shorebirds (Brown, 1960; Gilroy, 2012). A study in Panama found Western Sandpipers (Calidris mauri) adjusted their foraging strategies in relation to sediment temperature, probing more when temperatures were highest, possibly because invertebrates moved deeper into the sediment (Nebel & Thompson, 2005). Additionally, there is some evidence to suggest that foraging at night may lead to increased prey availability. McNeil et al. (1995) found that many shorebird prey items in Venezuela, including profitable items such as polychaetes and amphipods, were located closer to the sediment surface and therefore more available to shorebirds at night. In our study, shorter-billed birds were more likely to avoid tidal flats during the day, supporting the notion that prey availability may be determining when these birds can forage on the tidal flats. The differences in bill length that we observed among strategies may also reflect some level of habitat segregation among different groups of birds. In semipalmated sandpipers, females have longer bills (Gratto-Trevor et al., 2012), suggesting there may be differences in strategy use based on sex. Similarly, bill length varies by breeding origin, with eastern breeders having longer bills than those from central or western areas (Harrington & Morrison, 1979). While the average bill length of sandpipers sampled in our study suggests they are eastern breeders, previous work suggests central breeders may also be found in this region (Gratto-Trevor et al., 2012). Thus, while we consider it unlikely, it is possible that strategy may vary with breeding origin. Future work should investigate the relationship between habitat use strategy, sex and breeding origin.

The availability of Artemia spp. in saltwater evaporation ponds may also explain daytime use of the salinas by semipalmated sandpipers observed in our study. Semipalmated sandpipers and other shorebirds are known to use...
visual cues in finding prey items (Ashmole, 1970; Hicklin & Smith, 1984; MacDonald, 1987), which requires daylight. *Artemia franciscana* plays an important role in the aquaculture industry in northeastern Brazil, in some cases being cultured in salinas and used as a feeding supplement at shrimp farms (Valenti et al., 2021; Wainberg et al., 2011). Léger et al. (1987) found that *Artemia* are high in protein and can be a nutritious food source. Semipalmated sandpipers are opportunistic generalist foragers (Kober and Barlein 2006, Gerwing et al., 2016), and may be taking available *Artemia* during daytime. This would explain the observed “fishing” behavior in high-saline, *Artemia* dense ponds in salinas. Availability of *Artemia* at the Banco dos Cajuais may be especially beneficial to shorter-billed semipalmated sandpipers. Future research should examine its importance as a food resource for shorebirds at this location and consider the potential for incorporating such information into best management plans.

Anthropogenic disturbance may also contribute to the movement patterns we observed. It is well established that anthropogenic disturbance and habitat degradation can negatively impact shorebirds (Li et al., 2019; Pfister et al., 1992). Models developed by Aharon-Rotman et al. (2016) suggest that changes on the wintering grounds of Ruddy Turnstones (*A. interpres*) in South Australia resulting in reduced food intake would lead to reduced survival and reproductive success. Similarly, Gibson et al. (2018) found that annual survival of non-breeding Piping Plovers (*Charadrius melodus*) was negatively related to exposure to anthropogenic disturbance, and that avoiding human disturbance was advantageous for survival. It is possible that many birds are avoiding tidal flats during daylight hours, or salinas in nighttime hours, because of disturbance. In addition to tourism, subsistence and commercial fishing are common activities in Northeast Brazil. There is a particularly prolific lobster fishery at the Banco dos Cajuais (Cruz et al., 2013) which contributes significantly to the level of boat, foot and vehicle traffic during daylight hours on and adjacent to tidal flats. Furthermore, fishers often collect baitfish in the salinas at night, which may disturb birds. There is also a large feral cat population at the Banco dos Cajuais, particularly in parts of the salinas which are close to the local human population (Camboim, 2019). Feral cats have been well documented preying on wild birds in other parts of Brazil and throughout the world (Campos et al., 2007; Doherty et al., 2016). At the Banco dos Cajuais we have observed cats stalking shorebirds in the salinas at night. Although our presence may have to some extent attracted cats to the area during banding sessions, threat of predation at night, when birds are less likely to detect predators, may be another factor encouraging shorebirds to leave the salinas when it is dark.

### 4.2 Foraging behavior

Although they use different foraging modes, our results suggest that semipalmated sandpipers forage similar amounts in salinas and tidal flats. The observable differences in foraging modes are likely a response to prey availability (Kalejta & Hockey, 1994; Kuwae et al., 2008; MacDonald et al., 2012) and habitat characteristics (Kuwae et al., 2010).

Previous work in other regions has suggested salinas may be important for conserving shorebirds, with many species showing a preference for foraging in salinas (Dias, 2009; Masero, 2003), especially during premigration (Masero, 2003). While water depth and salinity are thought to be important indicators explaining shorebird use of salinas (Dias, 2009; Tripp & Collazo, 2003), little work has examined the influence of other habitat characteristics or invertebrate abundance in such environments. Future studies should investigate the availability of potential prey in salinas and tidal flats to help explain the different foraging modes and movement strategies displayed by semipalmated sandpipers at the Banco dos Cajuais.

### 4.3 Plasma triglycerides and northward migration

Our data suggest that non-breeding semipalmated sandpipers present at the Banco dos Cajuais in February and March were not yet gaining weight in preparation for their northward migration. We observed no change in size-adjusted mass from February to March, and plasma triglyceride values were much lower than what has been detected at stopover sites where birds are known to be actively gaining weight (Linhart, 2021; Lyons et al., 2008; Thomas & Swanson, 2013). Our values are similar to estimates from other non-breeding grounds (Guglielmo et al., 2002; Lyons et al., 2008) where birds were also not gaining weight.

Although there is some understanding of migration patterns for the different breeding populations within North America (Gratto-Trevor et al., 2012; Herbert et al., 2022), little is known about stopover locations in South America, with only a few complete pathways recorded (Brown et al., 2017). Semipalmated sandpipers overwintering at the Banco dos Cajuais are likely fueling for migration at other important locations in South America. Reentrâncias Maranhenses in Maranhão
(northern Brazil), ~800 km NW from the Banco dos Cajuais, is a WHSRN site of hemispheric importance (WHSRN Sites, n.d.) used by semipalmated sandpipers during southbound migration. Although there is little evidence to suggest its importance as a stopover location for this species during northbound migration (Rodrigues, 2000), it is likely that other important coastal sites in northwestern Brazil, French Guiana and Suriname could be used by semipalmated sandpipers to prepare for their migration to the breeding grounds (Brown et al., 2017; Spaans, 1978). Our tracking data support this hypothesis as many birds detected in North America had departed the Banco dos Cajuais weeks before their arrival in the northern hemisphere. However, one sandpiper was detected in North America only 5 days after departing the Banco dos Cajuais on May 8. This short time period is indicative of a non-stop flight and suggests that the Banco dos Cajuais may be used by some proportion of semipalmated sandpipers to prepare for long-distance migration, further highlighting the importance of this site. Future work should include blood sampling and tagging semipalmated sandpipers throughout the non-breeding season and pre-migration to learn more about the physiological preparation and flight pathways that characterize this species migratory behavior. It should also focus on expanding the Motus network throughout South America and employing new satellite tracking technologies as they become available. This would improve our ability to detect migration pathways and identify important stopover locations, which should be considered a shorebird conservation priority.

4.4 | Conservation implications

Large-scale anthropogenic changes and loss of coastal habitats in South America are considered to be among the main factors contributing to the global population declines observed in various shorebirds species (Morrison et al., 2012). Limited information is available to suggest this in the Western Atlantic flyway, but in other flyways habitat loss and change has been found to have large negative impacts on the survival of migrant species (Duriez et al., 2012; Aharon-Rotman, 2016). In many areas of South America, changes to shorebird habitats in coastal areas are a direct result of human activities, and in northeast Brazil the main impacts are related to the conversion of mangroves and associated habitats into salinas and shrimp farms (Ferreira & Lacerda, 2016; Valenti et al., 2021). Although some previous studies have suggested that shrimp farms can be important to shorebirds and other waders (Basso et al., 2018; Masero, 2003; Navedo & Fernández, 2019), such heavily altered habitats, including both shrimp farms and salinas, may also present a greater overall risk via general habitat reduction, exposure to predators such as feral cats, environmental degradation and exposure to contaminants like heavy metals during non-breeding periods (Burger et al., 2019).

Our data highlight remarkable consistency in daily movement and habitat use by individual semipalmated sandpipers on the non-breeding grounds as well as the identification of distinct movement strategies. Regardless of movement strategy, our findings suggest that semipalmated sandpipers are making notable use of habitats that have been heavily modified by humans, in most cases spending >50% of their time on the non-breeding grounds in salinas or shrimp farms. We hypothesize that prey availability, possibly combined with human and predator disturbance, influences habitat use by semipalmated sandpipers throughout the day and night. Additional research will be required to test this hypothesis and determine the relative importance of these influences in driving the observed patterns in movement strategies and habitat use. The broader implications of semipalmated sandpipers spending so much time in these habitats that have been modified for human use are also unknown, and more work is needed to understand the quality and quantity of the prey base, diets of birds throughout the region, and threats facing birds when using these areas. This could help guide future conservation planning and restoration efforts to ensure quality food items and safe, productive habitats are available.

The variety of habitats within our study system is representative of many other coastal areas in South America. As such, our findings suggest broader habitat protections are required throughout the region and highlight the importance of preventing future habitat changes and loss for shorebirds across the continent. Based on patterns of habitat use observed in our study, we recommend that protected area management plans for important coastal areas in Northeast Brazil and elsewhere in the region be broadened to include salgado or apicum habitats, as well as intertidal lagoons, estuaries, beachfront and other areas modified by human activity. This should particularly consider salinas and shrimp farms, which could represent useful habitat for shorebirds where best management practices are implemented. These practices should include managing salinity and water depth to support prey items (Tripp & Collazo, 2003). Currently, water levels at our study site are managed for salt production, making habitat availability in the salinas unpredictable, and therefore undependable for foraging and roosting sandpipers. Future work should focus on developing specific management recommendations for this area that would support the local prey base and promote habitat...
availability for shorebirds. Given the importance of coastal areas to shorebirds and the economy of Northeast Brazil, we suggest that concerted efforts to engage local communities with shorebird conservation in the region continue and expand. Efforts should include public policy discussion and the promotion of sustainable use of coastal environments, which represents the best way to advance conservation in the region. Additionally, recommendations of best management practices for extractive activities and tourism uses, aimed at maximizing shorebird use of the habitat while minimizing risk to the birds, should be developed.

Future work should also examine the daily movements and habitat use of other long-distant migrants at the site, which may have different habitat requirements. Semipalmated sandpipers are generalist foragers (Kober & Bairlein, 2006) that may be able to adapt to using altered habitats as long as there is a suitable food source available. Conversely, other species like Red Knot (Calidris canutus rufa), which are common at the Banco dos Cajuais and are globally threatened (Fedrizzi et al., 2016), are potentially less flexible. These birds have a more specialized diet (Kober & Bairlein, 2006), preferring to forage on bivalves (Martínez-Curci et al., 2015). Their ability to use disturbed habitats is less clear, and ongoing work at this site suggests that such environments may be used only for roosting at high tide (Mobley et al., 2019). Ultimately, conservation decisions in the region should integrate the needs of the full shorebird community, and additional work like that reported here will contribute to a well-rounded approach to conservation and management throughout this WHSRN site and other similar coastal areas of South America.

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CONFLICT OF INTEREST
The authors declare no potential conflict of interests.

AUTHOR CONTRIBUTIONS
Rebeca C. Linhart completed all data analyses and wrote the manuscript. Diana J. Hamilton assisted with data analysis and writing the manuscript. Julie Paquet and Jason A. Mobley provided substantial feedback on the manuscript. All authors participated in data collection and offered advice and feedback throughout the study. Diana J. Hamilton, Julie Paquet, Rebeca C. Linhart and Jason A. Mobley contributed to study design.

DATA AVAILABILITY STATEMENT
All movement data have been made available on Mov eBank. The code has been made available on GitHub in the following repository: https://github.com/reblin/Brazil-SESA. All other data are available from the corresponding author upon request.

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