to habitat loss from climate change, the NGOM has been especially vulnerable to other natural and human mediated disasters, such as Hurricanes Katrina and Rita, and the Deepwater Horizon oil spill. The wetlands affected by these events are important habitats for 34 species of shorebirds, including 28 migratory species that spend all or part of their non-breeding season on the Gulf coast [2,3]. For many shorebird species, the wetlands and barrier islands of the NGOM represent important wintering and stopover habitats [2]. However, despite the variety of species using the NGOM, the migration ecology of shorebirds in these habitats has not been well studied.

At least 61% of North American breeding shorebird populations are declining [4], and of the migratory species using the NGOM, 17 are listed as shorebirds of conservation concern in the United States [5]. While shorebirds may be vulnerable at each stage of their annual cycle, evidence suggests that the migration period, in particular, may be severely limiting [6-9]. For example, precipitous population declines in the red knot (Calidris canutus rufa) and semipalmated sandpiper (C. pusilla) have been attributed, in part, to the collapse of the horseshoe crab (Limulus polyphemus) populations in the Delaware Bay. The Delaware Bay represents a major stopover site for thousands of shorebirds who rely on eggs from horseshoe crab spawning to fuel their long distance migrations to high arctic breeding grounds [8,10]. As with red knots using the Delaware Bay, some shorebird species may rely on northern Gulf habitats to provide the fuel necessary for spring migration to near-arctic breeding grounds.

Developing a better understanding of the ecology of shorebirds during migration through northern Gulf habitats is an important step towards predicting the potential population level effects of continued habitat loss on the NGOM.

The consequences of changes to migratory shorebird stopover habitats will depend on migration strategies within and among species. Shorebird migration strategies differ in how parameters of time, energy, and predation risk are used to decide location and duration of stopover [11,12]. If birds seek to maximize their overall

**Keywords:** Sandpipers, refueling rates, plasma metabolites, fuel stores, migratory fitness

**1 Introduction**

In the continental United States, the wetlands of the northern Gulf of Mexico (NGOM) are experiencing some of the highest global sea level rise rates [1]. In addition to habitat loss from climate change, the NGOM has been especially vulnerable to other natural and human mediated disasters, such as Hurricanes Katrina and Rita, and the Deepwater Horizon oil spill. The wetlands affected by these events are important habitats for 34 species of shorebirds, including 28 migratory species that spend all or part of their non-breeding season on the Gulf coast [2,3]. For many shorebird species, the wetlands and barrier islands of the NGOM represent important wintering and stopover habitats [2]. However, despite the variety of species using the NGOM, the migration ecology of shorebirds in these habitats has not been well studied.

At least 61% of North American breeding shorebird populations are declining [4], and of the migratory species using the NGOM, 17 are listed as shorebirds of conservation concern in the United States [5]. While shorebirds may be vulnerable at each stage of their annual cycle, evidence suggests that the migration period, in particular, may be severely limiting [6-9]. For example, precipitous population declines in the red knot (Calidris canutus rufa) and semipalmated sandpiper (C. pusilla) have been attributed, in part, to the collapse of the horseshoe crab (Limulus polyphemus) populations in the Delaware Bay. The Delaware Bay represents a major stopover site for thousands of shorebirds who rely on eggs from horseshoe crab spawning to fuel their long distance migrations to high arctic breeding grounds [8,10]. As with red knots using the Delaware Bay, some shorebird species may rely on northern Gulf habitats to provide the fuel necessary for spring migration to near-arctic breeding grounds.

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**Abstract:** Twenty-eight species of migratory shorebirds rely on the coastlines of the northern Gulf of Mexico (NGOM) to fuel migrations to near-arctic breeding grounds. Shorebird species vary in their migration ecology: some species use a “jump” strategy, migrating long distances without stopping, while others use “skip” and “hop” strategies, stopping to refuel at shorter intervals along their journey. We compared stopover duration, body condition (fat scores and size-adjusted mass), and refueling rates (plasma metabolite concentrations), in three Calidrid sandpiper species (Calidris pusilla, C. mauri, and C. alpina) that differ in migration strategy after leaving the NGOM during spring. Results indicate that, while birds refueled at similar rates, C. alpina, an intermediate distance jump migrant, reached higher fuel stores before departing on migration than the hop and skip migrants, C. pusilla and C. mauri. C. alpina also spent more time on the NGOM than the other two species. Results suggest that NGOM habitats may be particularly important for migration success in C. alpina. This knowledge will help us predict the potential population level consequences of habitat loss due to global change on NGOM shorebird populations and develop conservation plans to mitigate these impacts.

**Keywords:** Sandpipers, refueling rates, plasma metabolites, fuel stores, migratory fitness
migration speed (time minimization hypothesis), they should minimize time spent on migration by bypassing or stopping for only short periods of time at lower quality sites [12]. The competing energy-minimization hypothesis states that a bird will migrate to the next stopover site once its fat reserves allow it to make the journey safely, regardless of the intake rate (refueling rate) at current or future sites. Some species of shorebirds use a “jump” migration strategy, migrating long distances without stopping, whereas other species use a “hop” or “skip” strategy [13], stopping at shorter intervals in agricultural fields and natural wetlands during migration [14]. Migration theory suggests that such differences in migration strategy will result in variation in the requirements of migration physiology and stopover behavior [11,15,16]. On spring migration, shorebirds tend to exhibit time minimization behavior [17,18] in an effort to reach northern breeding grounds early and establish high quality breeding territories. Under time-minimization, birds preparing for long migratory flights demonstrate high fueling rates, attain large fuel stores prior to departure, and stay for longer periods (i.e., weeks) at stopover sites [16,19,20]. In comparison, even under time-minimization, high fueling rates and high fuel stores are not necessary in birds with a shorter distance to the next stopover. Therefore, birds using a “hop” or “skip” migration strategy, stay for shorter durations (hours-days) at stopover sites [20] and demonstrate higher selectivity for departure from stopover sites as soon as weather conditions, such as positive tailwinds, are favorable [21, 22].

Variation in migration strategy for shorebirds may occur not only among species, but within species, between sex and age classes. As early arrival on the breeding grounds can be related to successful territory acquisition [18,23], male shorebirds often migrate before females. Farmer and Wiens [18] observed a time minimization-only strategy in male pectoral sandpipers (C. melanotus) on spring migration, but a combination time/energy-minimization strategy for females, meaning that males migrated as soon as possible, whereas some females stayed at stopover sites longer and reached higher fuel stores. Patterns of habitat use while at stopover sites can also vary by sex and age class. Fernández and Lank [24] found female and juvenile western sandpipers (C. mauri) use resource-poor habitats more often than adult males during winter. Within-species variation in habitat use has been observed at both local [24-27] and latitudinal scales [28,29,30].

The goal of this study was to investigate variation in the migration ecology and behavior among and within three species of sandpipers that stopover on the NGOM: semipalmated sandpipers (C. pusilla), western sandpipers (C. mauri), and the Canadian arctic subspecies of dunlin (C. alpina). Populations of all three species use the central North American flyway en route to near-arctic breeding sites [31]. Using survey data during spring migration through the central United States, Skagen et al. [14] suggested that, after leaving the NGOM, C. pusilla use a hop migration strategy, making several short migratory flights on their northern migration, whereas C. alpina use an intermediate distance jump migration strategy, generally skipping over habitats in the central United States. C. mauri use a combination “hop/skip” strategy [14]. Therefore, we hypothesized that stopover duration, fuel stores, refueling rates, and response to favorable wind conditions in our target species would differ according to migration strategy. Specifically, given the need to attain large fuel stores in preparation for their longer journey [15], we predicted that stopover duration would be longest in our jump migrant, C. alpina, shortest in the hop migrant, C. pusilla, and intermediate in the hop/skip migrant, C. mauri. We predicted that fuel stores and refueling rates of jump migrants would increase more steeply over time than hop or skip migrants, i.e., we predicted a steeper positive slope of fuel stores and fueling rates over time for C. alpina, than for C. mauri and a steeper slope for C. mauri than for C. pusilla. We also predicted that refueling rates in the hop migrant C. pusilla would respond more strongly to positive wind effects than the species with longer distance flights.

As the key variable for these differences is distance to subsequent stopover site [20], we predicted that within species individuals would demonstrate the same migration strategy (hop, skip or jump), regardless of age or sex relative to the other species. However, due to variation in the selective pressures to reach breeding grounds, we also hypothesized that within species stopover duration and refueling performance by individuals would vary according to age and sex. Given the strong pressure to arrive on breeding grounds and establish territories, we predicted that male sandpipers of all species would migrate through the northern GOM earlier, depart with lower fuel stores, and stop over for shorter periods than females and juveniles. Finally, as juveniles often demonstrate lower foraging efficiency than adults, resulting in lower mass [32], we predicted mean fuel stores and refueling rates would be lower for birds completing their first spring migration (SY birds).
2 Methods

We studied spring shorebird migration at four study sites across the NGOM (Fig. 1). These sites represent habitat types commonly found on the NGOM coast including coastal mudflats, remnant wetlands, and barrier island tidal flats. Detailed descriptions of the sites are included in Coblentz et al. [33]. At these sites we investigated the **phenology** of migration for *C. pusilla*, *C. mauri*, and *C. alpina* by capturing and banding birds from 3 March – 29 April in 2011, 29 February – 28 May in 2012. We also investigated phenology by analyzing average counts for our target species retrieved from eBird database surveys (http://www.ebird.org) collected at Audubon Coastal Bird Survey Sites in LA, MS and AL (http://www.audubon.org/content/audubon-coastal-bird-survey) from March - May from 2011-2013. We investigated the relative age and sex ratios of birds captured across three periods of migration, defined as “Early” (28 February – 28 March), “Mid” (29 March – 28 April), and “Late” (29 April – 28 May) spring. In 2013, we measured variation in stopover duration by measuring **stopover site residence time** in birds captured at one study site, Dauphin Island, AL, between 1 March – 22 May.

We investigated the variation in **fuel stores** among and within species across all three years by measuring variation in size-adjusted body mass and subcutaneous fat scores. We measured variation in **refueling rates** through plasma metabolite levels of triglycerides (TRIG) and β-hydroxybutyrate (BOH). Because some metabolites increase during fat deposition, such as triglycerides, while others increase during fat catabolism (e.g., glycerol and β-hydroxybutyrate), metabolites can provide an instantaneous measure of physiological state and energetic condition of individuals just prior to capture, and therefore have been shown to be useful indicators of fattening rates in a variety of shorebird and passerine species [35-40]. As previous research suggests that of the fat catabolites, BOH is a better indicator than glycerol (GLYC) of fat catabolism in migrant birds [37,40,41,42], we focused on TRIG and BOH as our target metabolites, and measure of refueling rates for this study.

2.1 Data collection

Over a total of 71 trapping days shorebirds were captured, primarily at dawn and dusk, using 6 mist-nets placed in foraging areas for 3-5 hours during each period if weather conditions allowed. Total net hours during the springs of 2011-2012 were 78 hours at our Cameron site, 119 at Grand Isle, 88 hours at Ocean Springs, and 106 hours at Dauphin Island. Birds were passively captured in nets that were monitored constantly such that birds were retrieved from...
nents within 10 minutes. Captured birds were weighed (± 0.1 g) using a digital balance, measured (wing chord, tarsus length, and exposed culmen), and banded with a USGS numbered band. Each bird was classified as adult (ASY) or second year (SY) based on plumage characteristics [43]. **Fuel stores** were measured from fat scores, assessed on a scale from 0-5 [44], and body weight. Body weight was measured using an index of size-adjusted mass that adjusts body mass for size using the volumetric conversion of wing chord (size-adjusted mass = mass/(wing chord)^2)*10,000; [10,45,46].

**Residence Time.** - In 2013, we measured variation in stopover duration by measuring **stopover site residence time** in birds captured at one study site, Dauphin Island, AL, between 1 March – 22 May. Dauphin Island was selected for this intensive study as all 3 species were observed in large numbers at the site, and both foraging and roosting habitats for shorebirds were easily accessible. During the spring of 2013 trapped birds were banded with uniquely coded flags and unique color band combinations. All birds were released at their capture site after banding. We monitored residence time of shorebirds by resighting banded birds during twice daily surveys using binoculars and telescopes at the banding site (approx. 3.5 km²), and a known nearby roosting site (6.5 km²). Daily resighting effort was constant from 1 March through 24 May; however, analyses of stopover duration were limited to resighting data from 28 March – 24 May to account for differences in the migration phenology among species (i.e., *C. pusilla* do not arrive till late March, some *C. mauri* and *C. alpina* are overwintering). Birds captured and banded before 28 March were included in the resight analysis, with 28 March marked as their first banding date. In addition to these birds, each individual captured after 28 March was at the banding site for some undetermined amount of time prior to when it was captured, therefore stopover duration estimates in our study represent the length of stay from the beginning of the pre-migratory period (late March), and are conservative estimates of how much time shorebirds actually spent on the NGOM after capture.

**Blood sampling, plasma metabolite and molecular analyses.** - To assess **refueling rates** we collected blood samples (75 - 300 µl depending on the size of the bird) from the brachial vein using a 26-gauge needle and heparinized capillary tubes. Blood samples were stored on ice in a small cooler in the field and centrifuged within 2 h at 6000 rpm for 10 min. Separated plasma and red blood samples were stored in a -20°C freezer for 1–2 weeks and then stored at -80°C prior to analysis.

Lipid metabolites were assayed in 400-µl flat-bottom 96-well microplates (Greiner Bio-One, Monroe, NC) in a microplate spectrophotometer (Biotec 340EL) [37, 47]. Due to small plasma volumes, not all metabolites could be determined for all individuals. Following previous studies [37,38,48], we prioritized triglyceride assays. Total triglyceride (TRIG) and free glycerol (GLYC) were measured by endpoint assay (Sigma Diagnostics Trinder reagents A and B; [36]). True triglyceride concentration (mmol L⁻¹) was calculated by subtracting glycerol from total triglyceride. Inter-assay coefficients of variation (CV) based on chicken plasma pools were 7.4% for TRIG and 8.6% for GLYC (N = 18 assays over 3 years). β-hydroxybutyrate (BOH) was measured by kinetic endpoint assay (kit E0907979, R-7 Biopharm, [37]). The inter-assay CV for BOH was 12.9% (N = 18). All samples were run in duplicate or triplicate. Intra-assay CVs for TRIG, GLYC, and BOH 2011 were 6.2%, 4.4%, and 13.6%, respectively. Intra-assay CVs in 2012 were 3.6% for TRIG, 2.8% for GLYC, and 8.8% for BOH, in 2013 they were 5.4% for TRIG, 6.0% for GLYC, and 10.9% for BOH.

Molecular markers were used to confirm sex identification for all banded birds. We extracted DNA from red blood cells using a standardized protocol for the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) and sexed the birds by standard PCR methods, using primers 2550F/2718R [49]. The bands were separated by gel electrophoresis in 2% agarose gels, stained with ethidium bromide, and visually analyzed under UV light. We compared the lengths of the bands to a size marker (1-kb DNA ladder, Life Technologies).

**Wind effect** - To estimate the effect of wind on response variables, such that the effect is positive in tail winds and negative in head winds, we first calculated the expected ground speed (G) associated with ground wind speed and direction from the relationship:

\[ G = \sqrt{W \sin(\alpha)^2 + W \cos(\alpha)} \]

Where \( A \) is the airspeed of the birds (assumed to be 17 m/s following Green and Piersma [50]), \( W \) is the wind speed and \( \alpha \) is the angle between wind and track directions (with a track direction of 180°, and \( \alpha = 0° \) corresponding to tail winds and \( \alpha = 180° \) to head winds). The wind effect was then determined as ground speed minus airspeed ((G – A); cf. [51,52]). We acquired surface wind data recorded by the National Oceanic and Atmospheric Administration Buoy Center, Station CAPL1 in Cameron, La, Station GISL1 in Grand Isle, LA, Station DKCM6 in Pascagoula, MS, and Station DPIA1 in Dauphin Island, AL. Surface winds were used because shorebirds used these as cues to identify winds aloft [22, 53].
2.2 Statistical analyses

We investigated variation in phenology within and among species by using z statistics to test for differences in proportions between species, and between age and sex classes within species caught by period of spring. We assessed the drivers of variation in residence time among and within species using mark–recapture analysis implemented in program MARK [54] through the RMark package for R (version 2.1.11; Alaska Fisheries Science Center, NOAA, http://cran.r-project.org/web/packages/RMark/). We used the Cormack–Jolly–Seber (CJS) open-population model framework to analyze encounter histories of individual birds resighted at least one time between 28 March and 24 May by examining a set of candidate models explaining two modeled response parameters, \( \Phi \) (‘survival’ probability) and \( p \) (detection probability). In a model of residence time, survival probability is interpreted as the probability of remaining at the stopover site. To compare among species, our set of candidate models included constant response parameters (dot models) vs. allowing survival to vary by species, age (ASY vs. SY), sex, capture date, time since capture, size-adjusted mass, and time. We also modeled for interactions between these variables. To investigate variation in residence time within individual species we ran separate analyses by species, which allowed survival to vary by age, sex, age*sex, capture date, time since capture, and size-adjusted mass. We selected among models using Akaike’s information criterion adjusted for small sample sizes and lack of model fit (AICc) and the associated \( \Delta \)AICc and Akaike weights [55]. To test that our data met expectations based on the assumptions underlying the model, we evaluated the goodness-of-fit of our global model using the program RELEASE GOF provided in program MARK to calculate \( \hat{c} \) (variance inflation factor or lack of fit). We transformed the survival estimates into post-capture residence times according to Kaiser’s [56] formula for life expectancy, residence time = \(-1/\ln \Phi\). We report mean residence time ± 95% confidence intervals.

We assessed the drivers of variation within species in fat scores, size-adjusted mass, and plasma metabolites across periods of spring migration using multiple backward stepwise regression analyses. Size-adjusted mass and metabolite concentrations were log\(_{10} + 1\) transformed to normalize the data. We tested the independent effects of migration period, age (SY or ASY), sex, capture site, year, habitat type, time of day, time of day, bleed time (time between capture and bleeding), foraging area, and wind effect (corrected for Julian date), as well as the interaction effects of migration period*age*sex, and site*year.

It should be noted that predation pressure (the number of raptors observed during point count surveys at sites within one day of banding) was measured, but few raptors are observed during spring migration on the NGOM and predation pressure was not found to be a significant predictor of any response variables. The variables retained in the full models at \( P < 0.10 \) [37] were kept as covariates in an analysis of covariance (ANCOVA) to obtain marginal means for fat scores, size-adjusted mass, and plasma metabolites among migration periods by species classified by sex and age. Results of the reduced models, including significant covariates, were used to conduct pairwise post-hoc comparisons of variation between migration periods within species using the Tukey’s-HSD test. Values are presented as least-square means ± SE. Statistical analyses were conducted using R Software (version 3.1.0; R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/).

3 Results

A total of 505 individuals of the three target species were banded and sampled across 4 sites during spring migration 2011-2013: 177 C. pusilla, 121 C. mauri and 207 C. alpina (Table 1, Table S1). 358 were captured in the morning (71%) 147 in the evening (29%). Proportionally more C. pusilla were captured than the other two species during Late spring (C. mauri: \( z = 13.51, P < 0.001 \), C. alpina: \( z = 10.67, P < 0.001 \), Table 1). There was no proportional difference in the number of C. mauri and C. alpina captured during Early and Mid spring; however, more C. alpina were captured during late spring (\( z = 3.24, P = 0.001 \)). eBird database surveys (http://www.ebird.org) of our target species on the NGOM during spring migration reflect similar differences in phenology among species. The mean abundance for C. pusilla was less than 1 during both Early and Mid spring, and increased to 27.02 birds per survey during late spring. The highest abundance for C. mauri and C. alpina occurred during Early spring and dropped to 1.09 birds for C. mauri and 19.96 birds for C. alpina by Late spring (Table 1).

**Residence time -** During the spring of 2013, 76 C. pusilla, 34 C. mauri and 30 C. alpina were uniquely banded. Of these individuals 62% (87) were resighted more than once (37% (28) C. pusilla, 91% (31) C. mauri, 100% (30) C. alpina). We used encounter records for a 56 day period, 28 March to 24 May, to limit analyses to periods of time when all three species were present at our study site. Tests of goodness of fit of the CJS model found no evidence of overdispersion (\( \chi^2_{\text{res}} = 42.03, P = 0.99 \)). However, there was evidence of underdispersion of the data (\( \hat{c} = 0.22 \), or less
variation than expected by chance. As there is currently no clear procedure for dealing with underdispersion in these models [57] we did not adjust $\hat{c}$. In the best-fit model, variation in “survival” probability (the probability of not departing the site) was explained by species and capture date, and variation in detection probability was a function of species (Table S2).

Using estimates from our best-fit CJS model, *C. pusilla* exhibited shorter mean post-capture residence times (6.6 days) than *C. mauri* (9.3 days), and both species stayed for a shorter period than *C. alpina* (27.2 days, Table 2). Each individual was at the banding site for some undetermined amount of time prior to when it was captured, therefore residence time estimates in our study likely represent conservative estimates of how much time shorebirds actually spent at the study site after capture.

### 3.1 Semipalmated Sandpipers

**Phenology and residence time** - Of the 177 *C. pusilla* captured, none were captured during Early spring, and only 19.8% (35/177) were captured during Mid spring (Table 1). As most birds arrived in Late spring, no significant differences were observed between sexes and age classes in *C. pusilla* (Table 1). Using the best CJS model

| Migration Period | Sex | Age | Species | $C.\ pusilla$ | $C.\ mauri$ | $C.\ alpina$
|------------------|-----|-----|---------|-------------|------------|------------|
| Early (2/28-3/28)| Male| ASY | 0       | 31          | 31         |
|                  |     |     |         | (63.3%)     | (55.3%)    |
|                  | SY  | 0   | 14      | 35          |
|                  |     |     |         | (51.9%)     | (62.5%)    |
|                  | Female| ASY | 0       | 9           | 8          |
|                  |     |     |         | (47.4%)     | (29.7%)    |
|                  | SY  | 0   | 11      | 27          |
|                  |     |     |         | (42.3%)     | (40.9%)    |
| Capture totals: |     | 0   | 65      | 101         |
|                  |     |     |         | (53.7%)     | (48.8%)    |
| eBird abundance:|     |     | 0.32    | 19.8        |
|                  |     |     |         | 80.2        |
| Mid (3/29-4/28)  | Male| ASY | 10      | 15          |
|                  |     |     |         | (14.5%)     | (32.1%)    |
|                  |     | SY  | 8       | 10          |
|                  |     |     |         | (19.5%)     | (19.1%)    |
|                  | Female| ASY | 9       | 9           |
|                  |     |     |         | (24.3%)     | (40.7%)    |
|                  | SY  | 8   | 9       | 15          |
|                  |     |     |         | (26.7%)     | (28.8%)    |
| Capture totals: |     | 35  | 43      | 53          |
|                  |     |     |         | (19.8%)     | (25.6%)    |
| eBird abundance:|     |     | 0.87    | 2.17        |
|                  |     |     |         | 43.64       |
| Late (4/29-5/29) | Male| ASY | 59      | 3           |
|                  |     |     |         | (85.5%)     | (12.5%)    |
|                  |     | SY  | 33      | 3           |
|                  |     |     |         | (80.5%)     | (27.9%)    |
|                  | Female| ASY | 28      | 1           |
|                  |     |     |         | (75.7%)     | (29.6%)    |
|                  |     | SY  | 22      | 6           |
|                  |     |     |         | (73.3%)     | (30.3%)    |
| Capture totals: |     | 142 | 13      | 53          |
|                  |     |     |         | (80.2%)     | (25.6%)    |
| eBird abundance:|     |     | 27.02   | 1.09        |
|                  |     |     |         | 20.96       |
| Across spring Capture totals: | 177 |     |     | 207         |
| eBird abundance: |     | 9.41 | 4.41 | 62.27        |

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Table 1. Number and percentage of target shorebird species captured during spring 2011-2013 across species, age, and sex by migration period. Average weekly eBird (http://www.ebird.org) abundance data (average number of birds reported within specific date range and region) of target species from Audubon Coastal Shorebird Survey entries during the same periods and years are also presented.
to assess variation among species (Table S1) C. pusilla exhibited short post-capture residence times (6.5 days, Table 2). Analyses of within species models for C. pusilla show a stronger effect of sex than age or sex*age on stopover duration (Table S3a), with females staying on the NGOM longer than males on average (8.0 days vs. 3.8 days, Table 2). However, the AIC weight for the CJS model that varied by sex was not significantly greater than a model with no age/class variation for C. pusilla (Table S3a).

Fuel Load and Fat deposition - Neither fuel stores nor refueling rates were significantly influenced by migration period in C. pusilla (Table 3). Post-hoc tests indicate male C. pusilla had lower fat scores during Mid spring than females (Tukey’s HSD, p = 0.04, Fig. 2). Residual TRIG levels were slightly higher in SY C. pusilla across spring (Tukey’s HSD, p = 0.09 for Mid Spring, p = 0.06 for Late Spring, Fig. 2). Fat catabolism as measured by BOH levels did not change by migration period in C. pusilla. Residual TRIG levels in C. pusilla increased with increasing (+) wind effect (p = 0.01, Table 3).

3.2 Western Sandpipers

Phenology and residence time - More C. maui were captured during Early (53.7%) and Mid (35.5%) spring than during Late spring (10.7%, Table 1). While the highest proportion of males (both ASY and SY) were captured during the Early spring (Table 1), the only proportional differences observed within migration periods was between ASY males and SY females. More ASY males were banded during Early spring (z = 2.37, p = 0.02), and more SY females were banded during Late spring (z = 2.15, p = 0.03). There were no other differences between sex or ages classes by migration period (Table 1). The mean residence time for all C. maui in 2013 according to the best AIC model (Table S1) was 9.2 days (Table 2). Individual analyses of within species variation in residence time for C. maui shows the top two candidate models as models with survival varying by capture date, and survival varying by an age*capture date interaction (Table S3b). Using parameter estimates from this top model ASY C. maui were predicted to stay

Table 2. Estimated mean residence times (stopover duration) ± 95% confidence intervals by species, and by sex and age classes. Estimates are derived from the top candidate model for among species and within species comparisons (see Tables S1 and S2), results are omitted for within species comparisons where sex or age were not significant predictors of variation. Residence time estimates are calculated from mean values using Kaiser’s [56] formula for life expectancy, residence time = –1/ln Φ.

| Species | C. pusilla | C. maui | C. alpina |
|---------|------------|---------|-----------|
| Male    | 3.8        | 20.5    | 34.6      |
| Female  | 8.0        | 34.6    | 18.4-65.4 |
| ASY     | -          | 26.6    | 31.8      |
| SY      | -          | 21.7    | 23.1      |

Table 3. Variables retained in the multiple regression models for migration period comparisons following backwards stepwise regression at the p < 0.10 level for each species and metabolite. Variables for which p < 0.05 are indicated in bold. Abbreviations: SESA = Semipalmated Sandpiper, WESA = Western Sandpiper, DUNL = Dunlin, MP = migration period, Time = time of day of capture, Bleed = bleed time following capture, Size = size-adjusted mass. Wind = Residual wind effect corrected for Julian date. Invert = Residual mean weekly dried biomass in 2013 at Dauphin Island corrected for Julian Date. Direction for effect, if applicable, is indicated by (+) for positive effect and (-) for negative effect.

| Variable            | SESA (N=177) | WESA (N=121) | DUNL (N=217) |
|---------------------|--------------|--------------|--------------|
| Fat                 | Sex, Site, Year | MP, MP*Sex, Site, Site*Year | MP, Site, Year, Site*Year |
| Size-adjusted Mass  | ___          | MP, MP*Sex   | MP, Site, Year, Site*Year |
| Triglyceride        | Age, Wind (+), Bleed (-) | MP, Site, Year, Site*Year, Invert (+, 2013)) | MP, MP*Age, Site, Year, Site*Year, Time (+) |
| β-hydroxybutyrate   | Year (N = 131) | MP*Age, Wind (-), Year, Bleed(+)(N=85) | MP, Wind (-), Site, Time(-), Bleed(+)(n=142) |
Figure 2. Residual least-squared means ± S.E. for a) fat score, b) size-adjusted mass, c) plasma triglyceride concentrations, d) plasma \( \beta \)-hydroxybutyrate concentrations during 3 periods of migration by species, separated by age and sex classes. A, B, and C indicate within species differences among migration periods (p < 0.05). \( \alpha \), \( \beta \) indicated differences within species between age or sex classes (p < 0.05).
for longer (26.6 days) than SY birds (21.7 days, Table 3). Notably, very few ASY female C. mauri were captured during our study (29/121 for all three years, 3/34 in 2013), which may be influencing our results.

Fuel load and fat deposition - Migration period was a significant predictor of fat scores and size-adjusted mass in C. mauri (Table 3). Across age and sex classes fat scores and size adjusted mass were higher in Mid spring than Early (Tukey’s HSD, p = 0.003, and p = 0.09, respectively) or Late spring (Tukey’s HSD, p = 0.10, p = 0.001, Fig. 2). In Early spring the fat scores and size-adjusted mass of male C. mauri were significantly higher than females (Tukey’s HSD, p = 0.008, p = 0.02), but these differences were not observed during any other period of spring Fig. 2.

Migration period was also a significant predictor of residual TRIG levels across age and sex classes in C. mauri (Table 3, Fig. 2). TRIG levels were higher in Mid spring than in Early and Late spring (Tukey’s HSD, p = 0.03, and p = 0.02, respectively), but no difference was observed in TRIG levels between Early and Late migration periods (Tukey’s HSD, p = 0.45). Residual BOH did not differ by migration period alone in C. mauri; however, during Late spring SY birds had higher residual BOH levels than ASY birds (Tukey’s HSD, p = 0.05, Fig. 2). TRIG levels for C. mauri were not influenced by wind, however BOH levels for C. mauri decreased significantly with residual wind effects (p < 0.001, Table 3).

3.3 Dunlin

Phenology and residence time - More C. alpina were captured during Early (47.5%) spring than during Mid (27.7%) and Late spring (24.4%) (Table 1). The majority of males (both ASY and SY), and SY females were captured during the Early period (Table 1). Similar to C. mauri, fewer ASY females were captured than the other classes, and although not significant, more ASY females were captured during Late spring than ASY males (z = 1.9, p = 0.057). Proportionally more SY females were captured than ASY males during Late spring (z = 2.36, p = 0.02, Table 1). C. alpina exhibited the longest mean stopover duration of our three target species (27.2 days, Table 2). Analyses of within species models for C. alpina show a stronger effect of sex than age on stopover duration, however, the strongest model was one that held survival and resight probabilities constant (Table S3c). Parameter estimates derived from the three top CJS models show that in C. alpina females and ASY birds stayed longer on the NGOM than males and SY birds (Table 2).

Fuel Load and fat deposition - For C. alpina both fat scores and size-adjusted mass increased with migration period (Table 3, Fig. 2). Residual fat scores differed between all migration periods (Tukey’s HSD, Early → Mid: p = 0.006, Early → Late, p < 0.001, Mid → Late, p < 0.001, Fig.3). Residual size-adjusted mass differed between Early and Late periods (Tukey’s HSD, p = 0.05), but differences were not significant between the other periods (Early → Mid, p = 0.99, Mid → Late, p = 0.12, Fig 3).

All measures of refueling rates differed by migration period in C. alpina (Table 3). Residual TRIG levels were significantly higher in Late spring in comparison with Early spring (Tukey’s HSD, p = 0.004, Fig. 2). These differences appear to be driven by high TRIG levels in ASY birds during Late spring in comparison with both Early and Mid periods (Tukey’s HSD, p = 0.009, p = 0.05, respectively). Residual BOH levels were lower in Late spring in comparison with both Early and Mid spring (Tukey’s HSD, p < 0.001 and p = 0.003, Fig. 2).

Within migration periods, differences were observed between C. alpina age classes during Late spring in both plasma TRIG and BOH concentrations (p = 0.005 and p = 0.05, respectively), with both male and female ASY birds refueling at higher rates than SY birds (Fig 3). No differences were observed between the sexes. As observed in C. mauri, BOH levels were also influenced by wind, decreasing with increasing tail wind effect (p = 0.002, Table 3), but TRIG levels were not.

4 Discussion

Variation in migration ecology among species - Before departing the NGOM on spring migration, shorebirds exhibited stopover behavior consistent with behaviors predicted by optimal migration theory. Our results support the prediction that a hop migrant, C. pusilla, would not increase fuel stores, refueling rates, or stay for extended periods while migrating through the NGOM. Whereas C. mauri, a combination hop/skip migrant, and C. alpina, a jump migrant, demonstrated longer stopover durations, and significant increases in fuel stores and refueling rates across spring. Estimated mean residence time (stopover duration) for C. pusilla was shorter (6.5 days) than C. mauri (9.3 days), and both were much shorter than C. alpina (27.2 days). Consistent with a jump migration strategy and long stopover duration, the largest increase in fuel stores and refueling rates was observed in C. alpina, while less consistent increases in these measures were observed in C. mauri, and no differences were seen in C. pusilla. Our ability to draw broad conclusions about stopover durations is limited since our analyses of stopover duration occurred at only one study site, and did not differentiate...
between overwintering and migrating Dunlin and Western sandpipers. However, our measures of stopover duration are supported by our fuel store and refueling rate results, which were measured across the northern Gulf of Mexico.

The lack of detection of variation in fuel stores and refueling rates across spring in *C. pusilla* could be attributed to small sample sizes in all but one migration period. Additional support for *C. pusilla* behaving as a hop migrant upon departing the NGOM is found in the species’ response to wind. Optimal migration theory hypothesizes that species with multiple stopovers en route to breeding grounds will have more flexible migration strategies [58], varying with individual differences in body condition and with temporal variation in resources and weather [21,59,60]. *C. pusilla* was the only species for which we observed a positive effect of tail wind on plasma TRIG levels, suggesting that this species increases refueling rates when weather conditions are beneficial for migration. In their research of songbird migration, Covino et al. [61] observed that birds with high refueling rates chose a more northerly migration route, while those with lower refueling rates selected a more westerly direction (closer to next northerly migration route, while those with lower energy stores, in order to reach breeding grounds and establish breeding territories. Although their stopover durations were much longer than those of *C. pusilla*, female *C. alpina* stayed longer than males. These results may be driven by the extremely long mean minimum stopover duration (measure between banding date and day of last sighting) for the *C. alpina* ASY females (37.6 days, N=5). The mean minimum stopover duration for *C. alpina* ASY males was only 16.9 (N=6), indicating that although both adult males and females are stayed for relatively long periods on the NGOM, the adult males demonstrated a more time-minimized migration than adult females.

Our results for within species variation in migration ecology for *C. mauri* are more difficult to interpret. While we found no effect of sex on stopover duration or refueling rate patterns, fuel stores in this species varied by sex during early spring when males had higher fuel stores. Later in the season, fuel stores dropped off particularly in ASY males. These results may reflect that the majority of male *C. mauri* are departing the NGOM during mid-spring, and that the few *C. mauri* moving through during late spring are new arrivals, possibly in poorer condition, arriving from wintering grounds further south. Nebel et al. [30] documented segregation during the non-breeding season in *C. mauri*, according to both sex and age, with adult males wintering further north than adult females, and second year birds wintering either at the northern or southern edge of the non-breeding grounds. High capture rates of males during early spring and longer stopover durations observed in ASY birds (26.6 days vs. 21.7) suggest the *C. mauri* captured during early spring were likely birds overwintering on the NGOM. The variation in winter site
use by age and sex class observed by Nebel et al. [30] may also explain the very low capture rate for C. mauri ASY females during this study. An alternative hypothesis is that ASY females were foraging in different habitats than studied here. Franks et al. [61] found that at some non-breeding habitats female C. mauri occupy more freshwater-influenced habitats. As all of our study sites were located along the NGOM coastline, the C. mauri sampled in this study may better represent birds that preferentially forage in more saline environments. Therefore, results regarding C. mauri ASY females in this study should be interpreted cautiously.

Although we observed very few within-species differences in fuel stores and refueling rates, we did find higher plasma TRIG levels in ASY C. alpina during late spring than birds embarking on their first spring migration. As Franks et al. [61] observed in C. mauri, this could be the result of variation in foraging ecology among age classes, as SY C. alpina may also more readily forage in auxiliary terrestrial habitats than in high quality coastal habitats [62]. Alternatively, in several shorebird species juveniles or SY birds appear to be less efficient foragers than adults [63,64,65], which could result in lower plasma TRIG levels, especially during late spring when C. alpina are accelerating their refueling to prepare for their jump migration. The decreased refueling rates observed in SY birds in this study may indicate that SY C. alpina are facing difficulties reaching the high fuel loads and refueling rates necessary for long distance migration to near arctic breeding grounds in coastal NGOM sites. Additional research on inter-annual survival rates among age classes in C. alpina and between habitat types on the NGOM is an important next step to addressing population level questions in this species.

5 Conclusion

As processes of global change accelerate, the coastal areas of the NGOM are expected to experience increased levels of flooding and saltwater intrusion, leading to accelerated and dramatic land loss [66]. Using models of potential sea-level rise for the NGOM Galbraith et al. [67] predicted up to a 38% decline in tidal flats at Bolivar Flats, TX, by 2050. Bolivar Flats is a site categorized by the Western Hemisphere Shorebird Reserve Network (http://whsrm.org) as a site of hemispheric importance for shorebirds. This and other similar habitats across the NGOM host more than 5% of the total North American breeding population for 12 species of migratory shorebirds [3], suggesting predicted habitat loss and degradation on the NGOM poses a potential threat to the stability of these arctic breeding shorebird populations.

Understanding the importance of a non-breeding habitat to a particular species requires knowledge of the migration physiology of birds using that site. While their migration phenology and physiology varied somewhat within species by age and sex, our research shows that at our study sites on the NGOM, C. pusilla, C. mauri and C. alpina are behaving as hop, skip, and jump, migrants, physiologically, and perhaps, behaviorally. Warnock [20] suggests that stopover sites are particularly important for jump migrants, such as C. alpina. Recently listed on the 2015 list of Shorebirds of Conservation Concern [5], there are estimated to be only around 450,000 birds of the C. alpina hudsonia subspecies left [4]. Considering that at least 22% of this population uses the northern Gulf during the non-breeding season [3], understanding that this species, as a jump migrant, may be particularly vulnerable to habitat loss along the NGOM is important to the development of plans to monitor C. alpina population size and migration ecology as the wetlands of the NGOM continue to change.

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