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Geographic Origins of Shorebirds Using an Alaskan Estuary During Migration

Sadie E.G. Ulman[1,4*], Steven L. Van Wilgenburg[2], John M. Morton[3,5], and Christopher K. Williams[1]

[1]Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE, 19716, U.S.A.

[2]Environment & Climate Change Canada, 115 Perimeter Road, Saskatoon, SK. S7N 0X4, CANADA

[3]Kenai National Wildlife Refuge, U.S. Fish and Wildlife Service, Soldotna, AK, 99669, U.S.A.

[4]Present address: Arctic National Wildlife Refuge, U.S. Fish and Wildlife Service, Fairbanks, AK, 99701, U.S.A.

[5]Present address: Alaska Wildlife Alliance, Anchorage, AK 99520

*Corresponding author; E-mail: sadie_ulman@fws.gov

Abstract.—Chickaloon Flats, Kenai National Wildlife Refuge, is an 11,000-ha tidal mudflat complex in upper Cook Inlet, Alaska. One-third (23 of 70) of Alaskan shorebird species use this protected coastal estuary stopover during migration. We conducted an isotopic approach to estimate probable breeding, staging and/or non-breeding origins of six shorebird species, some of high conservation concern, using Chickaloon during spring and fall migration of 2009 and 2010. We analyzed stable-hydrogen (δ^2H), carbon ($\delta^{13}C$), and nitrogen ($\delta^{15}N$) isotope ratios from feathers and performed a likelihood-based assignment to infer North and South American origins. Estimated molting distributions for Greater Yellowlegs (*Tringa melanoleuca*) occurred in southwest Alaska, and south-central Alaska for Short-billed Dowitcher (*Limnodromus griseus caurinus*). Lesser Yellowlegs (*Tringa flavipes*) likely molted in western Alaska and a latitudinal band across Canada and wintered throughout the contiguous United States. Least Sandpipers (*Calidris minutilla*) wintered from Oregon and south in North America but showed an isotopically similar possibility in Ecuador, Colombia, and Venezuela. Long-billed Dowitchers (*Limnodromus scolopaceus*) molted primaries across western United States and Canada. Pectoral Sandpipers (*Calidris melanotos*) likely molted near Rio de La Plata in southeastern South America. These results highlight the overall value of Chickaloon Flats as a stopover for long-distance shorebird migrants. *Received 29 Mar 2022, accepted 7 Aug 2023.*

Key words.—Alaska estuary, deuterium, Kenai National Wildlife Refuge, migratory stopovers, shorebird migration, stable isotope

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Determining the locations used by migratory birds throughout their annual cycle is increasingly important to developing conservation strategies (Hobson 1999; Hebert and Wassenaar 2005; Webster and Marra 2005). For long-distance migrants such as shorebirds, strategic stopovers rich in food are imperative for successful migration and subsequent nesting success (Castro and Myers 1993; Atkinson *et al.* 2005; Yerkes *et al.* 2008). Understanding movements within and among landscapes is crucial to better recognize and identify critical habitats needing protection (Alaska Shorebird Group 2019). Our knowledge of avian migratory movement patterns is incomplete, particularly with respect to discrete stopover sites. Therefore, identifying high-quality stopover sites along migration corridors aids local habitat conservation and management (Rocque *et al.* 2006; Hobson and Wassenaar 2008; Alaska Shorebird Group 2019).

The Kenai National Wildlife Refuge (Kenai NWR), located in south-central Alaska, is qualitatively known as an important migratory stopover and breeding grounds for many shorebird species. The geographic location and restrictive topography of the region create a corridor (Isleib 1979) where birds pass through during spring and fall migration. Of the 77 shorebird species recorded in Alaska, there are 37 common shorebird breeding species (Alaska Shorebird Group 2019). Almost two-thirds (23 of 37) of those species use Chickaloon Flats during spring and/or fall migration (Ulman 2012).

The use of intrinsic markers such as stable isotopes is a valuable tool to determine feather molt origins in shorebirds (Torres-Dowdall *et al.* 2009; Franks *et al.* 2012; Catry *et al.* 2016; Reed *et al.* 2018; Schmaltz *et al.* 2018). Metabolically inert tissues, such as feathers, maintain a signature corresponding

to what was eaten during the relatively short period of synthesis (Rubenstein and Hobson 2004; Hobson and Wassenaar 2008; Wunder 2012) and can be used to infer origins of feather molt (Hobson 1999; Caccamise *et al.* 2000; Rocque *et al.* 2006), but see Larson and Hobson (2009). This allows individuals to be sampled in one season (i.e., breeding) to estimate geographic origin of feather growth during another season (i.e., non-breeding). A combination of values from three stable isotopes (δ^2H, δ^{13}C, and δ^{15}N) can be used to infer feather molt origin on a broad geographic scale because predictable patterns of δ^2H occur in precipitation on a continental scale and δ^{13}C and δ^{15}N are used to determine if the feather was grown in a terrestrial versus marine environment. Assignment of geographic origin based on δ^2H can be compromised if birds forage on marine resources during feather growth, therefore, using δ^{13}C and δ^{15}N values to exclude samples with potential marine input improves the analyses (Yerkes *et. al* 2008; Ashley *et al.* 2010).

Our objective was to use stable isotope (δ^2H, δ^{13}C, and δ^{15}N) analyses to determine broad spatial scale breeding and non-breeding molting origin of migrating shorebirds using Chickaloon Flats as a stopover site during both spring and fall (Quimby 1972). We chose six species which were relatively abundant based on ground surveys of Chickaloon Flats during 2009–2010 (Ulman 2012): Greater Yellowlegs (*Tringa melanoleuca*), Lesser Yellowlegs (*Tringa flavipes*), Least Sandpiper (*Calidris minutilla*), Short-billed Dowitcher (*Limnodromus griseus caurinus*), Long-billed Dowitcher (*Limnodromus scolopaceus*), and Pectoral Sandpipers (*Calidris melanotos*). Four of these species are considered either of high (Lesser Yellowlegs, Short-billed Dowitcher, Pectoral Sandpiper) or moderate (Long-billed Dowitcher) conservation concern by the Alaska Shorebird Group (2019). Lesser Yellowlegs and Pectoral Sandpipers have shown a substantial decrease in population trend, while Short-billed Dowitcher has a moderate decrease or decrease suspected (Alaska Shorebird Group 2019), and all three species are on the North American Bird Conservation Initiative watch list (NABCI 2016).

METHODS

Study Area

Chickaloon Flats (60°53′57.10″N, 150° 4′44.05″W), located in upper Cook Inlet on the Kenai Peninsula (Fig. 1), is a relatively small, protected coastal estuary stopover site along the Pacific Flyway compared to other Alaskan estuaries. However, it represents 7% of the total estuarine intertidal area of Cook Inlet and Prince William Sound, the two water bodies that surround the peninsula. From a coastal migration perspective, Chickaloon Flats is strategically located on Turnagain Arm, the fjord that separates the peninsula and adjacent mainland. Tidal range in this area is 9.2 m, second greatest in the world behind the Bay of Fundy (11.7 m) (Mulherin *et al.* 2001). The area of vegetation within the mudflat is 6,894 ha (10,974 ha including mud) at high tide and entails about 1% of the 773,759 ha Kenai NWR. The estuary supports a diverse but low abundance of birds during migration and breeding periods.

Feather Sampling

During the spring and fall migration periods of 2009 and 2010 (25 April–9 June and June 30–August 1), we captured shorebirds primarily with drop nets (Doherty 2009) at various sites across the study area, primarily in tidally influenced areas with mud and low vegetation. We sampled the first primary feather from every individual. We aged birds as hatch-year (HY) vs. after hatch year (AHY) using species specific molt and plumage criteria (Pyle 2008). We used the tertials, scapulars, back feathers and central rectrices to differentiate Short-billed Dowitchers and Long-billed Dowitchers (Pyle 2008). We assumed primary feathers from adult Long-billed Dowitchers were grown at a molt-migration location (Putnam 2005; Barbaree *et al.* 2016). For all other species, we assumed that primary feathers from HY birds represent breeding origin and those from AHY birds represent non-breeding origins.

Stable Isotope Analyses

To clean the feathers, we followed a standard two-step method using both detergent and a 2:1 chloroform and methanol solution (Partitte and Kelly 2009). We sampled from the same location on each feather (Smith *et al.* 2009) and excluded the rachis (Wassenaar and Hobson 2006). Feather material was weighed (δ^{13}C and δ^{15}N: 1.1 ± 0.2 mg, δ^2H: 350 μg ± 10 μg) and enclosed in a tin (δ^{13}C and δ^{15}N; 5 x 9 mm) or silver (δ^2H; 5 x 3.5 mm) capsule (Costech Analytical Technologies Inc., Valencia, CA).

Carbon and nitrogen isotopic analyses were conducted at both the U.S. Environmental Protection Agency Atlantic Ecology Division Laboratory and Colorado Plateau Stable Isotope Laboratory. Analysis at the former laboratory was done using a Carlo-Erba NA 1500 Series II Elemental Analyzer (Carlo Erba Instruments, Milan, Italy) interfaced to a Micromass Optima Mass Spectrometer (Micromass, Manchester, U.K.). Samples were combusted (1020°C, chromic oxide catalyst)

Figure 1. Map of Chickaloon Flats, Kenai National Wildlife Refuge, Alaska (from Ulman *et al.* 2019). Estuarine intertidal zones of Cook Inlet and Prince William Sound derived from National Wetlands Inventory data (US Fish and Wildlife Service) and data from The National Map (USGS). Map displayed in the Alaska Albers Equal Area Conic projection (NAD83 datum).

sending CO_2 and N_2 to the mass spectrometer for the measurement of carbon and nitrogen isotope ratios, respectively. Two internal laboratory reference standards (dogfish muscle) were used for every 10 unknowns in sequence. The internal standard had a running average $\delta^{13}C$ and $\delta^{15}N$ measurement precision (standard deviation) of ± 0.17‰ and ± 0.16‰, respectively. Based on the assessment of the reproducibility of tissue sampled $\delta^{13}C$ and $\delta^{15}N$ measurements in this study, and propagating the measurement precision of the internal standard, reported tissue $\delta^{13}C$ and $\delta^{15}N$ measurements had measurement precisions of ± 1.00‰ and ± 0.41‰, respectively. Carbon and nitrogen stable isotope analysis at the Colorado Plateau Stable Isotope Laboratory was performed using a Carlo Erba NC2100 Elemental Analyzer (Carlo Erba Instruments, Milan, Italy) interfaced to a Thermo Electron Delta Plus Advantage stable isotope ratio mass spectrometer (Thermo Scientific, Waltham, MA). An internal laboratory standard (NIST 1547 - peach leaves) was used for every 10 unknowns in sequence. The internal standard has a running average $\delta^{13}C$ and $\delta^{15}N$ measurement precision (standard deviation) of ± 0.10‰ and ± 0.20‰, respectively. $\delta^{13}C$ values were normalized on the VPDB scale using IAEA-CH6 (−10.45‰) and IAEA-CH7 (−32.15‰). $\delta^{15}N$ values were normalized on the AIR scale using IAEA-N1 (0.43‰) and IAEA-N2 (20.41‰).

Hydrogen stable isotope analysis was performed only at the Colorado Plateau Stable Isotope Laboratory using a Thermal Conversion Elemental Analyzer (TC/EA) interfaced with a Thermo Electron Delta Plus XL stable isotope ratio mass spectrometer (Thermo Scientific, Waltham, MA). Stable-hydrogen isotope measurements were performed on H_2 from high temperature (1400°C) flash pyrolysis. Samples were analyzed using a comparative equilibrium approach with three calibrated keratin laboratory reference materials. The standards analyzed included: Spectrum Chemical keratin (δ^2H = −117.5‰), Bowhead Whale baleen (δ^2H = −108‰), and Cow hoof standard (δ^2H = −187‰), and resulted in accurate and precise (± SD) values of ± 2.2‰ (n = 18), ± 1.9‰ (n = 6), and ± 2.3‰ (n = 6), respectively. The control keratin reference standards yield a long-term SD of ± 3‰.

Statistical Analysis

Assignment of birds to terrestrial isoscapes based on δ2H can be compromised if birds forage on marine resources during feather growth (Yerkes *et al.* 2008; Ashley *et al.* 2010). Therefore, we used data reported in Yerkes *et al.* (2008), to develop a model to predict the likelihood that a given bird in our sample had derived resource for feather growth from a terrestrial versus marine environment based on the observed δ13C and δ15N values of feathers. We used the reported means, standard deviation and sample sizes of δ13C and δ15N in feathers from terrestrial versus marine environments reported in Yerkes *et al.* (2008) to simulate data with the same statistical properties. Specifically, for a given population, we generated random normal deviates using the means, standard deviations and sample sizes reported in Table 1 of Yerkes *et al.* (2008) as parameters for the simulations using the *rnorm* function in the R Statistical Computing Environment (R Core Team 2019). This resulted in a database consisting of 440 observations for δ13C and 369 observations for δ15N. We subsequently limited the data to only those rows with complete cases (i.e., data for both δ13C and δ^{15}N), leaving 369 observations. We then fit four competing general linear models to the data to model the probability that a feather was derived from a terrestrial (1) versus a marine (0) environment. Specifically, we used a binomial regression with a logit link to model terrestrial versus marine origins using models including δ^{13}C and δ^{15}N as main effects, a model with an additive effect of δ^{13}C and δ^{15}N, and a model including and interactive effect between δ^{13}C and δ^{15}N. We selected amongst competing models based on Akaike's Information Criterion (AIC), selecting the model with the lowest AIC value as the most parsimonious (Burnham and Anderson 2002). The most parsimonious model was the interactive model, which was separated from the next best model by > 4 AIC units. Thus, we predicted the probability that a sample came from a terrestrial environment using the equation:

$$\rho = \frac{1}{1+\exp(-(-33.4\ (SE\ 6.81)-1.82(SE\ 0.37)\cdot\delta^{13}C+1.30(SE\ 0.59)\cdot \delta^{15}N\ +0.08\ (SE\ 0.08)\cdot\delta^{13}C{:}\delta^{15}N))} \quad (1)$$

where p = the probability of the feather having been grown in a terrestrial environment given the observed δ^{13}C and δ^{15}N values measured in the feather. We subsequently only assigned birds to feather isoscapes based on δ^2H_f when there was ≥ 95% probability that the bird grew its feather in a terrestrial environment.

Calibration of Feather Isoscapes

We assigned feather samples to geographic origins using a spatially-explicit likelihood-based approach (Hobson *et al.* 2009; Wunder 2010; Van Wilgenburg *et al.* 2011). We began by first calibrating separate maps depicting predicted feather δ^2H for feathers grown at breeding or natal locations versus those grown over during the non-breeding period. To this end, we used bootstrap regression to compare δ^2H data from known-origin feathers of Lesser Scaup (*Aythya affinis*; Clark *et al.* 2006) against predicted δ^2H in precipitation from the amount weighted growing-season δ^2H (hereafter δ^2H_{GSD}) and the mean annual δ^2H (hereafter δ^2H_{MAD}) precipitation isoscapes of Bowen *et al.* (2005) for breeding season and non-breeding season assignments respectively. In each case, we conducted 1000 iterations in which n = 30 feathers were randomly selected and regressed against δ^2H in precipitation using general linear models. Our approach resulted in mean rescaling functions of δ^2H_f = –29.53 (SD = 14.35) + 0.94‰ (SD = 0.12) * δ^2H_{GSD} for feathers grown on the breeding grounds and δ^2H_f = –41.13 (SD = 16.69) + 0.72‰ (SD = 0.12) * δ^2H_{MAD} for feathers grown in the non-breeding period.

We applied the aforementioned mean rescaling functions to rescale the δ^2H_{GSD} and δ^2H_{MAD} isoscapes (Bowen *et al.* 2005) into predicted δ^2H_f isoscapes for feathers grown during the breeding and non-breeding periods respectively. In addition, we used the bootstrapping approach to derive spatially-explicit maps of predicted error (e_c) associated with the rescaled δ^2H_f isoscapes following Vander Zanden et al. (2014; hereafter: "error surface"). These error surfaces were created specifically to represent the error (measured in ‰) associated with a given cell ($_c$) or pixel of the raster surface given variation in between individuals growing their feathers at the same location and error in the rescaling equations. We obtained this error surface by taking the square root of the sum of the variation in parameter estimates of the rescaling functions ($\sigma^2_{rescale}$) and mean of the regression residuals ($\sigma^2_{individual}$). Variation in rescaling functions is given above, and $\sigma^2_{individual}$ was 12.40‰ and 13.47‰ for the rescaled breeding and non-breeding isoscapes, respectively.

Geographic Assignment of Origins

We first converted the long-term δ^2H_{GSD} and δ^2H_{MAD} isoscapes of Bowen *et al.* (2005) into δ^2H_f isoscapes for the breeding and non-breeding periods as explained above. We subsequently assessed the likelihood that a given cell of the calibrated feather isoscape represented the true origin for each feather sample (i.e., individual bird) using the following normal probability density function (hereafter PDF):

$$f(y^*|\mu_c, e_c) = \left(\frac{1}{2\pi e_c^2}\right)\exp\left[-\frac{(y^*-\mu_c)^2}{2e_c^2}\right] \quad (2)$$

where $f(y^*|\mu_c, e_c)$ represents the probability that a given cell ($_c$) is the potential origin for a sample individual (y^*), given the predicted δ^2H_f value from our calibrated isoscape for that cell (μ_c) and the predicted error for that cell (e_c).

RESULTS

We only assigned birds to feather isoscapes based on δ^2H_f when there was ≥ 95% probability that the bird grew its feather in a terrestrial environment given the observed δ^{13}C and δ^{15}N values measured in the

feather. The number of individuals in each species excluded from further analysis for not meeting these criteria are listed below.

Of 66 Greater Yellowlegs for which we had primary feather samples, one had a low probability ($P < 0.002$) of having grown its feather in a terrestrial environment based on the isotopic composition of its feather ($\delta^{13}C = -12.7‰$; $\delta^{15}N = 12.1‰$) and was therefore excluded from further analysis. The remaining 65 HY Greater Yellowlegs captured on Chickaloon Flats during the fall period originated in southwestern Alaska (Fig. 2a). HY Greater Yellowlegs were also isotopically consistent with regions of southern British Columbia and a latitudinal band of the boreal forest from southern Alberta through to Labrador (Fig. 2a); however, western Alaska is a more parsimonious origin for birds captured at Chickaloon Flats.

Of the 32 Lesser Yellowlegs captured, 26 were HY birds, all of which were included in analysis. The remaining six Lesser Yellowlegs captured were AHY birds. Of the six AHY birds, three were excluded from further analysis because they had < 95% likelihood ($P = 0.02–0.87$) of having grown their feathers in a terrestrial/aquatic environment. Analyses of δ^2H_f in the first primary feathers of migrating HY Lesser Yellowlegs showed they were isotopically consistent with western Alaska and a band of boreal forest spanning British Columbia and north and east through to Manitoba and northwestern Ontario (Fig. 2b). However, the greatest proportion almost certainly originated in western Alaska from approximately Homer to Kotzebue Sound (Fig. 2b). Of the three AHY Lesser Yellowlegs assigned to their molt origins based on δ^2H_f, two likely grew their feathers in the northwestern portion of their non-breeding range, while one molted in southeastern United States (Fig. 2c).

Of the 15 AHY Least Sandpipers, we captured 12 during fall and 3 during spring migration. All three of the Least Sandpipers captured in spring and one in fall were excluded from analysis. The remaining 11 fall migrant Least Sandpipers likely wintered throughout most of the nonbreeding range (Fig. 2d), from Oregon and south to Durango in North America. An isotopically similar region through Ecuador, Colombia and Venezuela also represents a likely origin for these birds

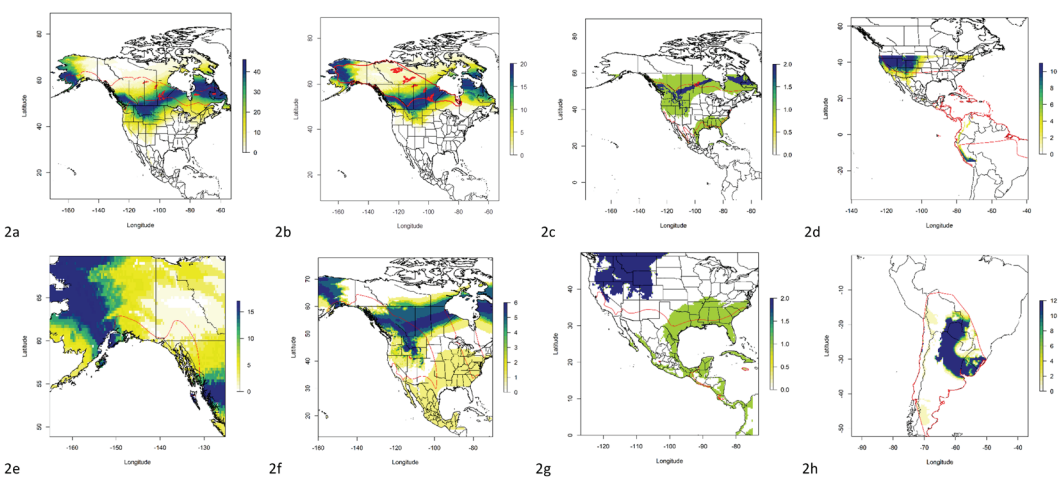

Figure 2. Probable origins of birds captured during migration on Chickaloon Flats, Kenai National Wildlife Refuge, Alaska, 2009-2010. Individuals were assigned geographic origins using a likelihood-based assignment based on deuterium (d^2H) values of primary feathers, unless indicated. Map represents the sum of origin assignments across all birds (HY=hatch year, AHY=after hatch year). The red border shows the biologically plausible origins, indicated by species-specific breeding or non-breeding ranges (Birdlife International 2016) as appropriate given the molt timing of the species in question. a) Greater Yellowlegs (*Tringa melanoleuca*; $n = 65$ HY); b) Lesser Yellowlegs (*Tringa flavipes*; $n = 26$ HY); c) Lesser Yellowlegs ($n = 3$ AHY); d) Least Sandpiper (*Calidris minutilla*; $n = 11$ AHY); e) Short-billed Dowitcher (*Limnodromus griseus caurinus*; $n = 26$ HY); f) Long-billed Dowitcher (*Limnodromus scolopaceus*; $n = 8$ AHY); g) Long-billed Dowitcher ($n = 3$ AHY, tertial feathers); h) Pectoral Sandpiper (*Calidris melanotos*; $n = 12$ AHY).

(Fig. 2d) and is consistent with South American observations through eBird (Sullivan *et al.* 2009) and the high-elevation Paramo ecosystem (Sevillano-Rios *et al.* 2020).

We sampled primary feathers from a total of 44 Short-billed Dowitchers, of which 18 were AHY birds captured in spring and 26 were HY birds captured in fall migration. All AHY birds were excluded from analysis as the likelihood of having grown in terrestrial/aquatic environment was $P < 0.17$. In contrast, all HY birds had feather $\delta^{13}C$ and $\delta^{15}N$ values that suggested they were grown in a terrestrial/aquatic environment (all $P > 0.99$). Stable hydrogen isotope analyses of primary flight feathers of all 26 HY birds indicated that migrant Short-billed Dowitchers likely originated from around the Kenai Peninsula and Kodiak Island in Alaska (Fig. 2e); however, they were also isotopically consistent with boreal regions of the Canadian prairie provinces though that region is an improbable origin given the location of Chickaloon Flats.

We captured 11 AHY Long-billed Dowitchers and sampled their primary feathers in spring ($n = 8$) and fall ($n = 3$), in addition to tertial feathers sampled during spring and fall migrations (two in each season). The tertial feather from one individual sampled during spring migration was excluded ($P < 0.07$). Stable hydrogen isotope analyses indicated that migrant Long-billed Dowitchers molted primaries at a variety of possible stopovers across western United States and Canada (Fig. 2f). Tertial feathers were isotopically consistent with molt in southern California, Arizona, or New Mexico in addition to Baja California, Sonora, Chihuahua in Mexico and coastal regions of the overwintering range (Fig. 2g).

We sampled primary feathers from 23 Pectoral Sandpipers during spring migration, and 11 were excluded. Assignment to molt origins of 12 Pectoral Sandpipers suggested that they likely molted near the Rio de La Plata estuary or in the Uruguay or Paraná rivers or their tributaries (Fig. 2h), consistent with shorebird density and census studies of these areas (Dias *et al.* 2014; Vizentin-Bugoni *et al.* 2015; Martínez-Curci and Isacch 2017).

DISCUSSION

Chickaloon Flats is an Alaskan estuary that supports a diversity of avian species with a range of migration pathways. Greater Yellowlegs captured at Chickaloon Flats likely bred in southwest Alaska, and Short-billed Dowitcher in southcentral Alaska. Lesser Yellowlegs were likely breeding in western Alaska and a latitudinal band across Canada, and their wintering grounds were estimated throughout the Lower 48 United States. Connors *et al.* (1979) found that shorebirds on Arctic coastal areas changed habitat use toward the end of breeding season and moved from upland tundra breeding sites to coastal littoral staging areas. A similar post-breeding shift in habitat use from vegetated to intertidal areas was observed on the Yukon-Kuskokwim Delta (Gill and Handel 1990). Chickaloon may provide similar important post-breeding coastal staging and foraging habitats before the southward migration, as illustrated by probable breeding origins for Greater and Lesser Yellowlegs and Short-billed Dowitcher (Figs. 2a, 2b, 2e).

Shorebirds from Chickaloon Flats used widespread non-breeding regions, which generally resemble those of highly productive coastal zones that hold major concentrations of shorebirds (Hötker *et al.* 1998; Butler *et al.* 2001). Most of these highly productive areas harboring major concentrations of birds are recognized as Western Hemisphere Shorebird Reserve Network sites. We estimated non-breeding distributions for Least Sandpipers, Long-billed Dowitchers, and Pectoral Sandpipers. Least Sandpipers likely wintered from Oregon and south to Durango in North America but showed an isotopically similar possibility of wintering in Ecuador, Colombia, and Venezuela in the Paramo ecosystem. Long-billed Dowitchers likely molted primaries at a variety of possible stopovers across western United States and Canada. Pectoral Sandpipers suggested they likely molted near the Rio de La Plata estuary or in the Uruguay or Paraná rivers or their tributaries.

Our study provided new information on the *L. g. caurinus* population of Short-billed Dowitchers. While they are a common and

widespread coastal migrant, little is known of their migratory biology, particularly on the North American west coast (Jehl *et al.* 2001). Of the three subspecies, each with separate breeding grounds and migration routes, the estimated global breeding population of *L. g. caurinus* is 75,000 (Andres *et al.* 2012). *L. g. caurinus* is a subspecies of high conservation concern owing to its relatively restricted boreal and subarctic breeding distribution, small population size, potential nonbreeding habitat threats, and declines in other populations (Alaska Shorebird Group 2019).

Interpretation of isotope assignment for Alaska breeding birds is not without its challenges, as the isocapes are similar between Alaska and eastern parts of North American (Meehan *et al.* 2004; Bowen *et al.* 2005) and there is longitudinal ambiguity in the isotope assignment. Additionally, a reminder that the probabilistic assignment depictions demonstrate that the pixels are consistent with what one would expect if birds molted in a location, not necessarily that the birds actually molted there. Another consideration is that we used the calibration equation for Lesser Scaup (Hobson *et al.* 2009) as that represents the most appropriate calibration equation available because there are no guild-specific equations available for shorebirds.

Long-distance migrant shorebirds rely on stopover sites to move between breeding and non-breeding grounds. Maintaining a network of stopover sites along shorebird flyways is important for shorebird conservation (Skagen and Knopf 1994a, 1994b; Farmer and Parent 1997; Xu *et al.* 2019), including a range of sizes from small (Skagen and Knopf 1993) to large (Connors *et al.* 1979; Isleib 1979). The importance of a stopover location within a migration flyway (Isleib 1979) can also be critical to migrating birds. Many of the Nearctic shorebirds breeding in western Alaska use a narrow migration corridor that follows the coast, which also presents topographic and climatic obstacles (Isleib 1979). Chickaloon Flats is in Upper Cook Inlet, nestled in Turnagain Arm, and may be more difficult for birds to access during northward migration because it is surrounded by the Kenai and Chugach Mountains. On the other hand, southeasterly winds from low pressure systems in the Gulf of Alaska during spring and fall are often funneled at high speeds through Turnagain Arm (Ager et al. 2010). Furthermore, Cook Inlet generally (Gill and Tibbitts 1999), and Chickaloon Flats specifically (Colwell 2010), provide high-latitude migratory birds with the last considerable area of predictable ice-free littoral habitat in the spring before reaching their breeding grounds. Stopover sites support behaviors beyond the well known re-fueling needs of migratory birds such as recovering, sleeping, waiting, information gathering, and social interactions (Linscott and Senner 2021). Chickaloon Flats likely provides all of these services, but future work is needed to assess the relative importance of these functions at this site

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