



Range-wide patterns of migratory connectivity in the western sandpiper *Calidris mauri*

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Understanding the population dynamics of migratory animals and predicting the consequences of environmental change requires knowing how populations are spatially connected between different periods of the annual cycle. We used stable isotopes to examine patterns of migratory connectivity across the range of the western sandpiper *Calidris mauri*. First, we developed a winter isotope basemap from stable-hydrogen (δD), -carbon ($\delta^{13}\text{C}$), and -nitrogen ($\delta^{15}\text{N}$) isotopes of feathers grown in wintering areas. δD and $\delta^{15}\text{N}$ values from wintering individuals varied with the latitude and longitude of capture location, while $\delta^{13}\text{C}$ varied with longitude only. We then tested the ability of the basemap to assign known-origin individuals. Sixty percent of wintering individuals were correctly assigned to their region of origin out of seven possible regions. Finally, we estimated the winter origins of breeding and migrant individuals and compared the resulting empirical distribution against the distribution that would be expected based on patterns of winter relative abundance. For breeding birds, the distribution of winter origins differed from expected only among males in the Yukon-Kuskokwim (Y-K) Delta and Nome, Alaska. Males in the Y-K Delta originated overwhelmingly from western Mexico, while in Nome, there were fewer males from western North America and more from the Baja Peninsula than expected. An unexpectedly high proportion of migrants captured at a stopover site in the interior United States originated from eastern and southern wintering areas, while none originated from western North America. In general, we document substantial mixing between the breeding and wintering populations of both sexes, which will buffer the global population of western sandpipers from the effects of local habitat loss on both breeding and wintering grounds.

Understanding the population dynamics of migratory animals requires knowledge about the degree of migratory connectivity of populations across the annual cycle degree – that is, the degree to which individuals in a population co-occur in different seasons (Webster et al. 2002, Marra et al. 2006, Norris and Marra 2007). Stable isotope analysis of inert tissues such as feathers has been widely used to identify the geographic origins of migratory animals (Hobson and Wassenaar 1997, Clegg et al. 2003, Kelly et al. 2005, Bensch et al. 2006, Jones et al. 2008, Miller et al. 2011), but only a few studies have examined the degree of connectivity

across the entire range of a long-distance migratory species using this approach (Rubenstein et al. 2002, Boulet et al. 2006, Norris et al. 2006). Such range-wide information on connectivity is essential for making strong inferences about the causes of variation in population size of migratory animals (Taylor and Norris 2010) and for developing effective conservation strategies (Martin et al. 2007). Many studies using stable isotopes to infer geographic origins of migratory animals have relied upon geographic variation in isotopic ratios in the environment as a basemap, in conjunction with an assumed or estimated value describing the difference

in isotopic composition between the environment and the tissue of interest (i.e. a discrimination factor; Boulet et al. 2006, Dunn et al. 2006, Norris et al. 2006, Jones et al. 2008, Hobson et al. 2009, Miller et al. 2011). Developing a tissue-specific basemap (Lott and Smith 2006, Sellick et al. 2009) reduces much of the uncertainty associated with the former approach, especially when estimates of discrimination factors for the species, tissue, and isotopes of interest are not available. Using stable isotope ratios of multiple elements simultaneously can also increase accuracy of assignment of individuals to their correct place of origin (Kelly et al. 2005, Sellick et al. 2009).

In this study, we use stable-hydrogen (δD), -carbon ($\delta^{13}\text{C}$), and -nitrogen ($\delta^{15}\text{N}$) isotope ratios to develop an isotopic feather basemap of the wintering grounds of the western sandpiper *Calidris mauri* and examine patterns of migratory connectivity across the annual cycle. Geographical patterns in δD values of rainfall across the Americas are reflected in feathers, while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ feather values may vary according to diet (DeNiro and Epstein 1978, 1981, Hobson 1999). The western sandpiper is a small, long-distance migratory shorebird that breeds in western Alaska and far-eastern Siberia and spends the boreal winter (hereafter 'winter') predominantly on the Pacific coast of the Americas between California and Peru, and in smaller numbers on the Atlantic coast between South Carolina and Venezuela (Wilson 1994). During the winter, western sandpipers are latitudinally segregated by sex, body size, and age at first breeding. A higher proportion of females is found in the southern part of the wintering range, while males are predominant in the north (Nebel et al. 2002). Southern birds are larger overall and have disproportionately longer wings and bills (Nebel 2005, O'Hara et al. 2006). Northern-wintering juveniles are more likely to attempt breeding in their first summer, while southern-wintering juveniles are more likely to delay breeding until their second summer (O'Hara et al. 2005). Patterns in wintering distribution have led some to suggest that there may be genetic differentiation between northern and southern wintering populations (O'Hara et al. 2005).

Western sandpipers migrate along either the Pacific Coast (Pacific Flyway) or through the continental interior (Central Flyway; Senner and Martinez 1982, Butler et al. 1996). The Central Flyway is used mainly by southward migrants on route to wintering locations on the Atlantic coast; in spring, these same individuals are thought to return north via the Pacific Flyway (Senner and Martinez 1982). Migrants on the Pacific Flyway are thought to winter mainly along the Pacific coast of the U.S., Mexico, and Central and South America (Butler et al. 1996).

Juvenile western sandpipers grow their flight feathers on Arctic breeding grounds and retain these feathers for their first 11–15 months of life depending on their wintering latitude and age at first breeding (O'Hara et al. 2002). Adults predominantly grow flight feathers on their wintering grounds (Wilson 1994, O'Hara et al. 2002).

Our first objective was to examine whether δD , $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values of winter-grown feathers exhibited geographic patterns on the wintering grounds. Given documented geographic patterns in δD values of rainfall across North America and latitudinal variation in western sandpiper

food distribution (Mathot et al. 2007), we expected that we would detect geographic patterns in the stable isotope values of western sandpiper feathers grown on the wintering grounds. Our goal was then to create an isotopic basemap of the wintering range using winter-grown feathers, and test the ability of this basemap to assign known-origin individuals to their site of origin. Using this basemap, our final objective was to estimate the winter origins of western sandpiper individuals sampled on the breeding grounds and during migration. We used information on the origins of breeding and migrant individuals to address three questions about the migration patterns of western sandpipers: 1) do individuals from northern and southern areas of the wintering range migrate to different areas of the breeding range, suggesting that genetic differentiation between populations may drive observed latitudinal patterns in body size and age at first breeding? 2) Do individuals migrating south through the continental interior originate from the eastern coast of the Americas? 3) Do individuals migrating through southern British Columbia on both the northward and southward migrations originate from both western and eastern coasts?

Material and methods

Western sandpiper feather collection

We collected western sandpiper feathers at 18 wintering sites between November and February of 2008–2009; two migration stopover sites: one on the Pacific Flyway in British Columbia's Fraser Delta during the spring (April–May) and fall (July) migrations of 2008 and 2009, and one on the Central Flyway in Kansas during the fall (July–September) migration of 2007; and seven breeding sites during the summer (May–July) of 2008, 2009, and 2010 (Fig. 1, Supplementary material Appendix 1, Table A1). We captured sandpipers using mist nets (wintering and migration sites) or walk-in nest traps and bow nets (breeding sites), and then banded birds and recorded morphometric measurements. Sex was determined using culmen length measurement (Page and Fearis 1971), and birds were aged in the field as either adult (hatched at least two summers ago), young (hatched the previous summer), or local juveniles (chicks hatched locally in the current summer) by examining the edging colour of inner median coverts and the degree of flight feather wear (Prater et al. 1977, Franks et al. 2009). To avoid excessively impeding flight capacity of sandpipers, we chose to collect an inner primary feather. Western sandpipers generally shed and grow the first five inner primaries simultaneously, so we collected 1st primaries on each wing for stable isotope analysis.

Isotope analysis

We analyzed feathers at the Queen's Facility for Isotope Research in Kingston, Ontario, Canada. Feathers were washed in a 1:1 chloroform:methanol solution and allowed to equilibrate with the local atmosphere for 72 h. Samples for δD analysis (0.1–0.2 mg) were loaded into silver capsules and placed in an oven at 100°C for 24 h to remove surface water. Capsules were then crushed and loaded into a reduction

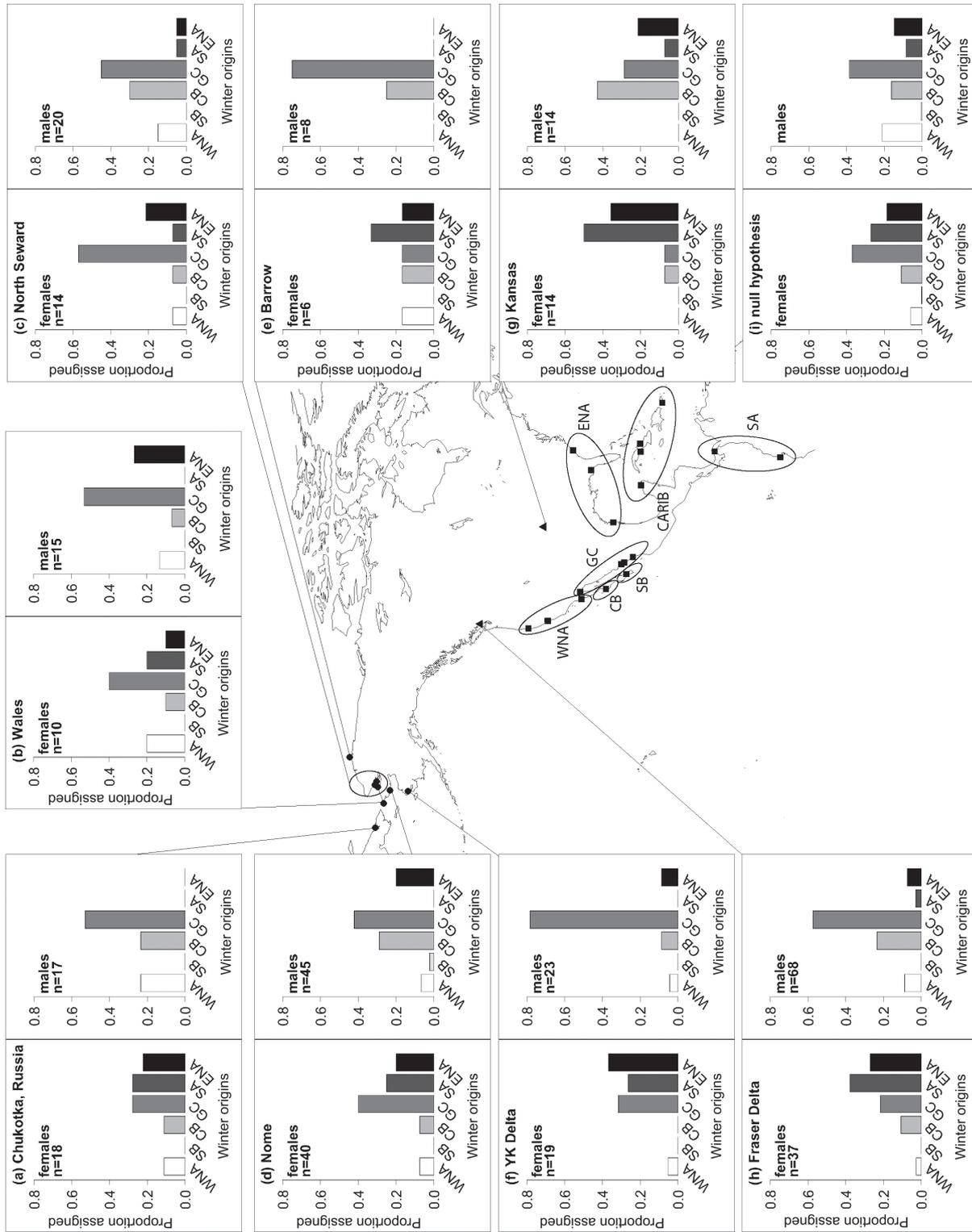


Figure 1. Map of all sites where feather samples were collected from western sandpipers (■ = winter, ▲ = migration, ● = breeding). Circled sites indicate regional groups (Supplementary material Appendix 1, Table A1). Inset graphs show the proportion of females and males from six breeding areas (a–f) and two migration sites (g–h) assigned to each winter region. An individual was assigned to the region with the greatest number of assignments out of 10000 simulations. In each simulation, an individual was assigned to the region with the highest probability of origin. The inset graph (i) shows the expected distribution of females and males from each wintering region based on patterns of relative winter abundance (the null hypothesis). Because very few breeding and migrant birds originated from the Caribbean, we grouped these assignments with those from eastern North America. WNA = western North America, SB = Southern Baja, CB = Central Baja, GC = Gulf of California, SA = South America, ENA = eastern North America, CARIB = Caribbean.

furnace (Finnigan TC/EA) at 1450°C and introduced on-line to an isotope ratio mass spectrometer (Delta^{plus} XP). Samples for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis (0.2–0.4 mg) were loaded into tin capsules, crushed, converted to gas in an oxidation/reduction furnace (Costech ECS 4010 elemental analyzer), and introduced on-line to an isotope ratio mass spectrometer (Delta^{plus} XP). Isotope analyses were conducted between October and December 2007, between October 2009 and January 2010, in August 2010, and in February 2011. Stable isotope ratios are reported in delta (δ) notation in per mil (‰) units, where $\delta X = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$. For hydrogen (δD), $R = {}^2\text{H}/{}^1\text{H}$ and R_{standard} is Vienna standard mean ocean water; for carbon ($\delta^{13}\text{C}$), $R = {}^{13}\text{C}/{}^{12}\text{C}$ and R_{standard} is PeeDee belemnite; for nitrogen ($\delta^{15}\text{N}$), $R = {}^{15}\text{N}/{}^{14}\text{N}$ and R_{standard} is air. For every 17 hydrogen samples, we ran three laboratory standards (mean \pm SD): brucite from the Univ. of Michigan ($-96 \pm 7\%$, $n = 209$), Georgia kaolinite clay ($-61 \pm 5\%$, $n = 268$), and an in-house feather standard from a captive blue-fronted amazon *Amazona aestiva* maintained on a constant diet ($-82 \pm 7\%$, $n = 122$). For every 50 carbon/nitrogen samples, we ran three out of the following four laboratory standards (mean \pm SD): domestic chicken *Gallus gallus* blood ($\delta^{13}\text{C} = -20.2 \pm 0.3\%$, $\delta^{15}\text{N} = 4.0 \pm 0.3\%$, $n = 56$), carbon standard ‘ucl’ ($\delta^{13}\text{C} = -25.6 \pm 0.3\%$, $n = 27$), carbon standard ‘q-c’ ($\delta^{13}\text{C} = -25.7 \pm 0.1\%$, $n = 9$), or silver nitrate ‘cil62’ ($\delta^{15}\text{N} = 16.8 \pm 0.2\%$, $n = 4$). Within each run, we also ran duplicates from the same individual and feather, which produced a difference (mean \pm SD) of $3.7 \pm 3.0\%$ ($n = 131$) for hydrogen samples, $0.30 \pm 0.33\%$ ($n = 71$) for carbon samples, and $0.38 \pm 0.44\%$ ($n = 71$) for nitrogen samples.

Data analysis

Interannual variation in isotope values

We tested for an effect of analysis year on isotope values by repeating δD measurements on a subset of the same feathers analyzed in 2007 and 2011 and found a significant difference ($t = -3.47$, $p = 0.03$, $n = 5$). However, the mean difference between years was only 6.8‰, which fell within the range of expected variation in δD based on repeated measurements of laboratory standards ($\text{SD} = 5\text{--}7\%$) and was generally smaller than the within-site variation observed in δD across sampling sites ($\text{SD} = 3\text{--}31\%$, Supplementary material Appendix 1, Table A2).

We also tested for an effect of sampling year on isotope values using winter-grown feathers collected from the same individuals recaptured in consecutive years (2008, 2009, 2010) at a breeding site in Nome, Alaska. In addition, we compared feathers collected in two different years at the same wintering site at three different locations in Mexico: Guerrero Negro in 2008–2009 and 2009–2010, Ensenada Pabellones in 2008–2009 and 2010–2011, and Bahía Santa María in 2008–2009 and 2010–2011. We examined interannual variation in adult feathers only (Age class identification below).

Geographic patterns in stable isotope values on the wintering grounds

To test whether stable isotope values would be useful for predicting the winter locations of sampled individuals, we

used linear mixed effects models to examine the relationship of each stable isotope (δD , $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$) with latitude and with longitude in wintering adult sandpiper feathers. We included site as a random effect to account for isotopic differences between sampling sites, and centered latitude and longitude around their respective means to reduce collinearity between linear and non-linear terms within models. We used an information-theoretic approach to evaluate the relative support for a null (intercept only), linear, or non-linear (quadratic and/or exponential) relationship of each isotope with latitude and longitude (Burnham and Anderson 2002, Table 1 for candidate model set). Non-linear relationships were included in the candidate model set after graphically visualizing the data. Site was included as a random intercept in all models. Models were ranked according to their ΔAIC_c score, calculated as the difference between a model's AIC_c value and that of the best-supported model in the candidate set. The support for each model given by the data was evaluated using Akaike weight ($\text{AIC}_c w$), which represents the probability of the model given the data in relation to all other models in the candidate set. Parameter likelihoods and weighted parameter estimates for each explanatory variable were calculated to assess an individual variable's relative importance within the candidate model set (Supplementary material Appendix 1, Table A3). All analyses were conducted in R ver. 2.14.0 (R Development Core Team). We used the package nlme to fit linear mixed effects models (Pinheiro et al. 2011). We specified no within-group correlations and used the maximum likelihood method to compare different fixed effect model structures. The package AICcmodavg was used to calculate AIC_c values, produce model selection results and calculate model averaged predicted response values (Mazerolle 2011).

Delineating winter regions

We divided the wintering grounds into seven regions (Fig. 1, Supplementary material Appendix 1, Table A1) based on prior knowledge of western sandpiper winter distribution patterns and what we believe to be geographically and biologically relevant regions, as well as the degree to which certain areas of the wintering range were isotopically distinct (e.g. Southern Baja, Central Baja). Assignments of known-origin birds to individual sampling sites was not possible using a maximum likelihood approach because some sites had sample sizes that were too small ($n < 4$). However, for individual sampling sites where sample size was large enough, we used a preliminary assignment test to examine how often known-origin wintering individuals were assigned to another sampling site in the same geographic area. We then grouped sites into regions where this was a frequent occurrence. Grouping sites regionally by pooling values across several sites increased sample size without substantially increasing variance (Supplementary material Appendix 1, Table A2).

Probability assignment tests

We used a maximum likelihood assignment approach to assign individuals to their most probable region of winter origin (Royle and Rubenstein 2004). To determine the likelihood that an individual originated from any one region based on its feather isotope values, we used a multivariate (δD , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) normal probability density function.

Table 1. The candidate linear mixed effects models used in the evaluation of the relationship between each stable isotope (δD , $\delta^{13}C$ and $\delta^{15}N$) and latitude and longitude of wintering adult western sandpiper feathers. All models include a random intercept of site. Sampled feathers are from 17 sites during the winter of 2008–2009. The number of parameters (K) includes a parameter for the intercept, the random effect of site, and the residual variance. Deviance is equal to $-2 \times \log$ -likelihood and was used to calculate AIC_c (Akaike's information criterion corrected for small sample size). Competing models were ranked according to ΔAIC_c and Akaike weight. Sample size $n = 109$ for all models.

Response	Model	K	Deviance	AIC_c	ΔAIC_c	$AIC_c w$
δD	latitude + latitude ²	5	904.4	915.0	0.0	0.57
	latitude	4	908.0	916.4	1.4	0.28
	NULL	3	911.4	917.6	2.7	0.15
$\delta^{13}C$	NULL	3	520.8	527.0	0.0	0.67
	latitude	4	520.6	529.0	2.0	0.25
	latitude + latitude ²	5	520.6	531.2	4.2	0.08
$\delta^{15}N$	latitude + latitude ²	5	508.9	519.5	0.0	0.89
	latitude	3	518.3	524.5	5.0	0.07
	NULL	4	517.3	525.6	6.1	0.04
δD	longitude	4	906.3	914.7	0.0	0.64
	longitude + longitude ²	5	906.3	916.9	2.2	0.21
	NULL	3	911.4	917.6	3.0	0.14
$\delta^{13}C$	longitude	4	516.3	524.7	0.0	0.59
	longitude + longitude ²	5	516.0	526.6	1.9	0.23
	NULL	3	520.8	527.0	2.4	0.18
$\delta^{15}N$	$e^{-\text{longitude}/5}$	4	508.1	516.5	0.0	0.61
	$e^{-\text{longitude}/10}$	4	509.5	517.9	1.4	0.30
	longitude + longitude ²	5	511.7	522.3	5.8	0.03
	$e^{-\text{longitude}}$	4	514.7	523.1	6.5	0.02
	longitude	4	515.1	523.5	7.0	0.02
	NULL	3	518.3	524.5	8.0	0.01

Assignment tests were conducted in R using the mvnml and mvtnorm packages (Genz et al. 2011, R Development Core Team). To account for analytical error in isotope measurements, we used a resampling simulation approach for the cross-validation of known-origin individuals and assignment of unknown-origin individuals (Wunder and Norris 2008, Miller et al. 2011). For each stable isotope observation per individual, we first randomly sampled 100 values from a normal distribution with a mean equal to the isotope value for that feather, and a standard deviation equal to the mean standard deviation of the lab standards for that isotope. This resampling procedure produced 100 new datasets of isotope values for all individuals. Secondly, we randomly chose one of these 100 datasets to define the parameters (mean, variance-covariance) of the multivariate probability density functions for the regions of winter origin. For each individual in every dataset, we determined its probability of being assigned to each region of winter origin, producing 100 assignment outcomes for each individual. Thirdly, we repeated step two a total of 100 times, each time using a new dataset from step one to define the parameters of the regional probability density functions. This produced 10 000 (100×100) assignment outcomes for each individual (Supplementary material Appendix 3, Table A5–7). Finally, we considered an individual to have originated from the region with the greatest number of assignments out of 10 000 simulations. We assessed confidence in the assignment by the number of times an individual was assigned to the region out of the total number of simulations.

To cross-validate our isotopic basemap of the wintering grounds, we evaluated the ability of the isotope data to correctly assign known-origin individuals back to their region of origin using the resampling simulation approach described above, but with an exclusion criterion. Specifically, if the

dataset being assigned in step two was the same as the dataset chosen to define the regional probability density functions, we calculated the parameters (mean, variance-covariance) of the probability density functions with the individual to be assigned omitted from the dataset. We then determined that individual's likelihood of coming from each of the candidate regions. We repeated this probability assignment for the remaining 99 datasets, but without using an exclusion criterion; in these remaining 99 cases, the dataset being assigned was different than the dataset chosen to define the regional probability density functions.

Age class identification

Previous work suggests that some individuals identified as adult by plumage characteristics have feathers with Arctic-type δD isotope values, indicating that these individuals may in fact be young birds (Franks et al. 2009). Because we were interested in the winter origins of adult birds, we needed to identify 'true' adults and remove young birds from all datasets, which we did using probability assignment of individuals to two possible regions of origin, Arctic or non-Arctic (Supplementary material Appendix 2). After removing juveniles and outliers from the datasets, 109, 243, and 137 'true' adults remained in the winter, breeding, and migration datasets, respectively.

Estimating migratory connectivity of breeding and migrant birds to wintering regions

Estimating the most likely origin of an individual based solely on stable isotope values assumes an equal prior probability of origin among all regions, which is unlikely since population density varies across space. To determine the most probable region of winter origin for breeding and migrant birds, we used a Bayesian approach that considers the likelihood of an individual's origin based on isotope data as well as prior

knowledge regarding the population's distribution (relative abundance) across possible regions of origin (Royle and Rubenstein 2004, Wunder et al. 2005, Norris et al. 2006). Bayes' rule states that: $f(w|y) = f(y|w) f(w)/f(y)$, where the posterior probability of origin, $f(w|y)$, is a function of the likelihood given by the isotope data, $f(y|w)$, multiplied by the prior probability of origin based on relative abundance, $f(w)$, and normalized by the sum of the likelihoods across all regions, $f(y)$. We estimated winter relative abundance by gathering population estimates for western sandpipers from local survey data, published atlases, and the literature (Spaans 1979, Morrison and Ross 1989, 2009, Fernández et al. 1998, Morrison et al. 1998, 2001, Page et al. 1999, Sociedad Ornitológica Puertorriqueña pers. comm.; Supplementary material Appendix 1, Table A4). Because male and female western sandpipers exhibit latitudinal segregation on the wintering grounds, we estimated the relative abundance of males and females in each winter region separately using the proportion of each sex captured in this study and in a study conducted by Nebel et al. (2002, Supplementary material Appendix 2).

We quantified migratory connectivity of western sandpipers using a Fisher's exact test with PROC FREQ for one-way tables in SAS (SAS Inst.). We compared the observed frequency distribution of winter origins for each breeding and migrant population against the null hypothesis – that is, the frequency distribution expected based on patterns of relative abundance for all western sandpipers and for each sex. Because very few birds originated from the Caribbean, we grouped these assignments with those from eastern North America. All data analyses were conducted in R (R Development Core Team), except where indicated.

Results

Interannual variation in isotope values

We found that, generally, there was no effect of sampling year on stable isotope values. There was no effect of year on the stable isotope values of feathers collected from recaptured birds on the breeding grounds in Nome, Alaska (paired t -test, δD : $t = 0.57$, $p = 0.58$; $\delta^{13}C$: $t = -0.98$, $p = 0.34$; $\delta^{15}N$: $t = 0.58$, $p = 0.57$; $n = 16$). When comparing feathers collected in two different years at three wintering sites in Mexico (Supplementary material Appendix 1, Table A2), neither isotope values from Ensenada Pabellones (unpaired Welch t -test for unequal variance, δD : $t = -1.78$, $p = 0.11$; $\delta^{13}C$: $t = -0.01$, $p = 0.99$; $\delta^{15}N$: $t = 0.84$, $p = 0.42$; $n = 17$) nor from Bahía Santa María (unpaired Welch t -test, δD : $t = -1.67$, $p = 0.11$; $\delta^{13}C$: $t = -0.69$, $p = 0.49$; $\delta^{15}N$: $t = 0.11$, $p = 0.91$; $n = 19$) differed significantly between years. Only $\delta^{15}N$ values at Guerrero Negro were significantly different between years and were higher in 2010–2011 compared with 2008–2009 (unpaired Welch t -test, δD : $t = -1.88$, $p = 0.08$; $\delta^{13}C$: $t = 1.60$, $p = 0.14$; $\delta^{15}N$: $t = -3.09$, $p < 0.01$; $n = 19$). In the second year of sampling (2010–2011) at Guerrero Negro, birds were captured 50 km from the previous year's location and on intertidal mudflats as opposed to in the salt ponds the

previous year. Low trophic level brine shrimp comprise a large proportion of available food resources in salt ponds (Franks unpubl.), while intertidal mudflats may encompass a wider spectrum of resources. This may potentially explain the lower $\delta^{15}N$ values observed at Guerrero Negro in 2008–2009. Because of the difference in the between-year sampling locations at Guerrero Negro and the fact that individuals show relatively high fidelity to specific wintering sites (Fernández et al. 2004), the comparison of interannual variation at Guerrero Negro may not be valid. Since δD , $\delta^{13}C$ and $\delta^{15}N$ values were not significantly different between years at any other site, all years of data were pooled.

Geographic patterns in stable isotope values on the wintering grounds

We found some support for a non-linear relationship between δD and latitude and a positive linear relationship between δD and longitude (Table 1, Fig. 2a, b). We found little evidence that $\delta^{13}C$ varied with latitude, as the null model received the most support (Table 1, Fig. 2c). However, we did find some evidence that $\delta^{13}C$ decreased linearly from west to east (Table 1, Fig. 2d). The data provided strong relative support for a quadratic relationship of $\delta^{15}N$ with latitude and some evidence of a negative exponential relationship of $\delta^{15}N$ with longitude (Table 1, Fig. 2e, f).

Cross-validation of an isotopic basemap of the wintering grounds

The wintering range was divided into seven regions: western North America, Central Baja, Southern Baja, the Gulf of California, eastern North America, the Caribbean, and South America. Sixty percent (65/109) of winter individuals were correctly assigned back to their region of origin. Of these, 82% (53/65) were assigned with greater than 70% confidence, while 97% (63/65) were assigned with greater than 50% confidence. The highest rates of correct assignment occurred on the Baja Peninsula (Fig. 3a, b), followed by western North America (Fig. 3c), South America (Fig. 3d), and eastern North America (Fig. 3e); only 39% of birds from the Gulf of California region of Mexico were assigned back to their site of origin (Fig. 3f), while just under 50% of birds from the Caribbean were assigned back to their site of origin (Fig. 3g).

Estimating migratory connectivity of breeding and migrant birds to wintering regions

Confidence in assignment of breeding birds to winter regions was $>70\%$ for 74% (180/243) of individuals and was $>50\%$ for 97% (236/243) of individuals. Many breeding sites were dominated by birds originating from the Gulf of California region of Mexico, as expected based on patterns of relative winter abundance (Fig. 1). Connectivity between breeding and wintering sites was fairly low, as individuals from all wintering areas were generally represented at all breeding sites (only a single individual came from the Southern Baja region of Mexico). The sample from the Yukon-Kuskokwim (Y-K) Delta had a distribution of winter origins

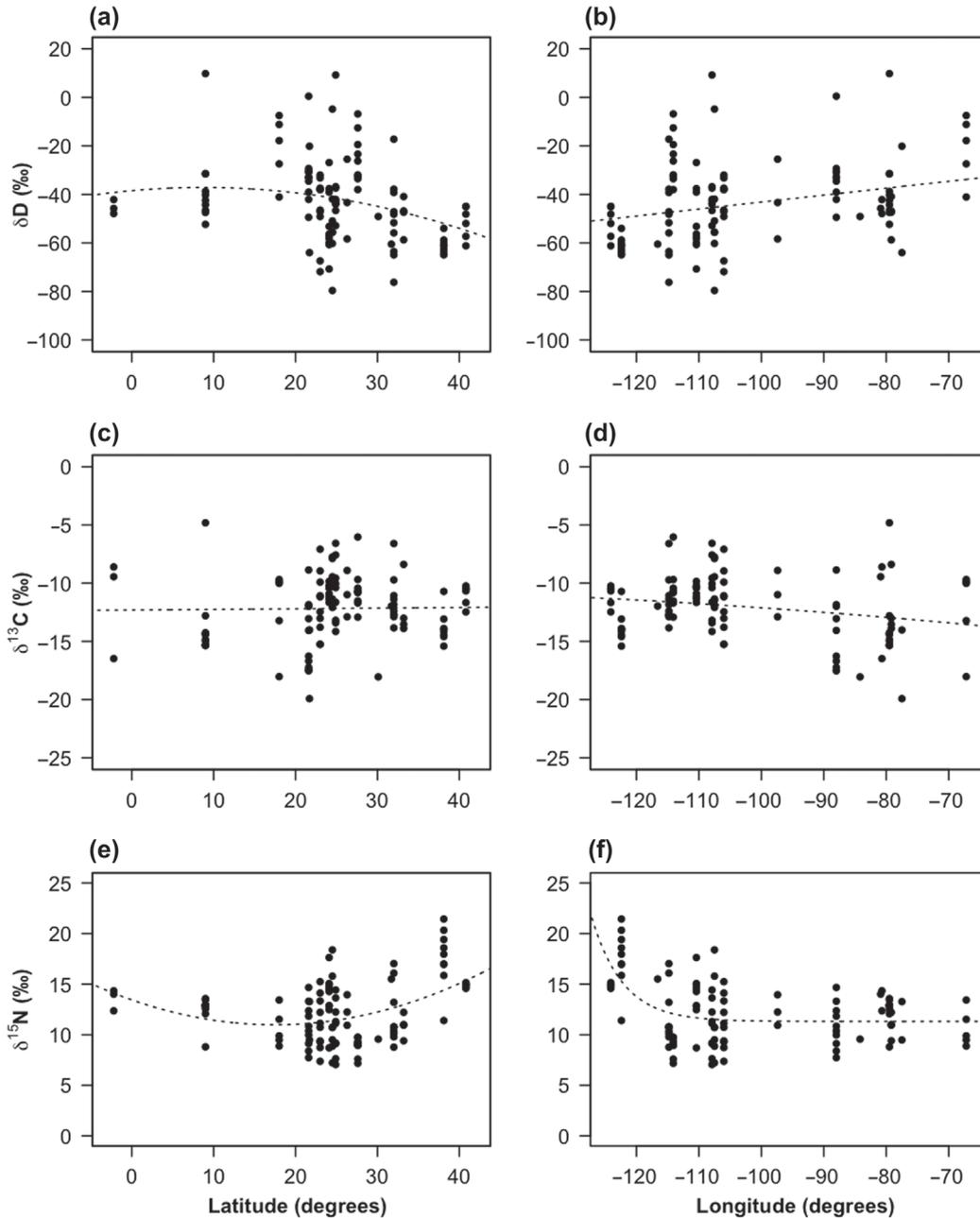


Figure 2. The relationship of each stable isotope (δD , $\delta^{13}C$ and $\delta^{15}N$) with latitude (a, c, e) and longitude (b, d, f) for western sandpiper feathers sampled on the wintering grounds. Data are adults only ($n = 109$). Dashed lines represent the model-averaged predicted response from the candidate set of linear mixed effects models (Table 1).

that was marginally significantly different from that expected based on patterns of relative abundance. At this site, relatively more birds originated from the Gulf of California than expected (Table 2). The distribution of female winter origins did not differ from expected at any breeding site. The distribution of male winter origins in Nome differed from that expected, with relatively fewer birds originating from western North America and more from Central Baja than expected (Table 2, Fig. 1d). In the Y-K Delta, males originated overwhelmingly from the Gulf of California region of Mexico, with relatively few from other locations on the wintering grounds (Table 2, Fig. 1f).

Confidence in assignment of migrant birds to winter regions was $> 70\%$ for 79% (108/137) of individuals and was $> 50\%$ for 99% (136/137) of individuals. The distribution of migrants in Kansas differed significantly from that expected, with relatively more individuals originating from eastern and southern wintering sites, as well as the Baja Peninsula (Table 2, Fig. 1g). No individuals in Kansas originated from western North America. The distribution of male migrant origins in the Fraser Delta also differed from that expected, with fewer birds originating from western and eastern North America and relatively more originating from western Mexico (Table 2, Fig. 1h).

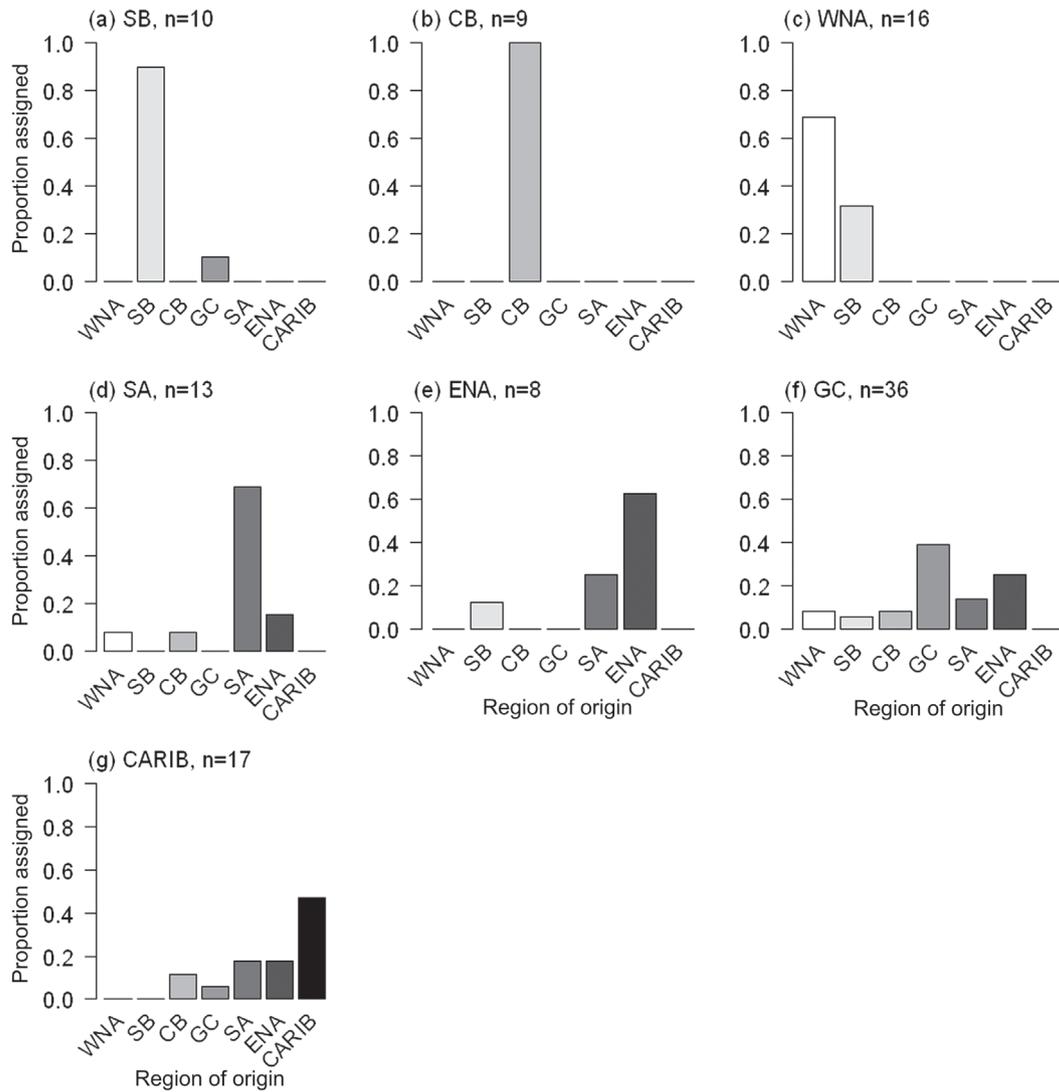


Figure 3. The proportion of winter adults assigned to each region from the cross-validation resampling simulation. An individual was assigned to the region with the greatest number of assignments out of 10 000 simulations. In each simulation, an individual was assigned to the region with the highest probability of origin. (a) SB = Southern Baja; (b) CB = Central Baja; (c) WNA = western North America; (d) SA = South America; (e) ENA = eastern North America; (f) GC = Gulf of California; (g) CARIB = Caribbean.

Table 2. Fisher's exact tests of the observed distribution of winter origins at each site compared to the expected distribution of winter origins based on patterns of relative abundance for pooled sexes, females, and males. Expected frequencies for pooled sexes were weighted by the sex ratio of the sample (i.e. we calculated an average expected frequency from the expected frequencies of males and females and their respective proportion at each site). Exact p values in bold with asterisks indicate sites where the observed distribution of winter origins is significantly different at a level of $\alpha < 0.05$ from that expected based on patterns of winter relative abundance, while p values in bold indicate marginally significant differences. Dashes (-) indicate where sample sizes were too small to conduct a χ^2 goodness of fit test.

	Pooled sexes			Females			Males		
	χ^2	exact p	n	χ^2	exact p	n	χ^2	exact p	n
Barrow	2.47	0.715	14	-	-	6	-	-	8
Nome	7.43	0.189	89	0.91	0.948	42	15.88	0.017*	44
North Seward	5.37	0.365	34	3.91	0.432	14	4.59	0.416	20
Russia	1.43	0.887	38	1.37	0.895	18	5.56	0.311	17
Wales	3.14	0.616	26	3.93	0.428	10	4.94	0.355	15
YK Delta	10.74	0.060	42	5.67	0.258	19	16.26	0.014*	23
Fraser Delta	9.14	0.101	107	6.08	0.271	37	18.72	0.008*	68
Kansas	13.55	0.027*	30	9.33	0.088	14	9.95	0.113	14

Discussion

Geographic patterns in stable isotope values on the wintering grounds

We found geographic patterns in δD , $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values among wintering western sandpipers.

δD – latitudinal patterns in δD feather values were similar to geographic gradients in δD precipitation values (Bowen et al. 2005) and to gradients in feather values of other species (Hobson and Wassenaar 1997, Kelly et al. 2002, Rubenstein et al. 2002, Norris et al. 2006), becoming more positive towards southern latitudes, although feather values began to decline again south of 10°N . Similarly, δD feather values increased from west to east, reflecting gradients in δD precipitation values (Bowen et al. 2005).

$\delta^{13}\text{C}$ – while $\delta^{13}\text{C}$ feather values showed no latitudinal pattern, they declined slightly from west to east. Stable-carbon isotope values for marine animals usually range from -20 to -10‰ , reflecting marine organic primary productivity (Hobson and Welch 1992, Kelly 2000). Many of the values we obtained were more positive ($> -10\text{‰}$), indicative of inorganic carbonates being digested and metabolized (Kyser unpubl.). Similarly high feather $\delta^{13}\text{C}$ values were found for red knots *Calidris canutus* wintering in South America (Atkinson et al. 2005), suggesting that sources of inorganic carbonates may not be unusual in shorebird diets. $\delta^{13}\text{C}$ values also become slightly enriched with increasing trophic level (DeNiro and Epstein 1978). The difference in feather $\delta^{13}\text{C}$ values between western and eastern coasts may indicate differences in the food resources used by western sandpipers. Western sandpiper diet includes low trophic level biofilm (a surface matrix of diatoms, microbes, organic detritus, and sediment in intertidal habitats) and meio- and macrofaunal marine invertebrates such as small crustaceans, bivalves, and polychaetes (Sutherland et al. 2000, Kuwae et al. 2008). Higher $\delta^{13}\text{C}$ values may reflect consumption of food resources rich in calcium carbonate and/or at higher trophic levels (e.g. crustaceans or polychaetes), while lower $\delta^{13}\text{C}$ values may reflect consumption of food resources based in marine primary productivity at lower trophic levels (e.g. biofilm). Alternatively, environmental variables such as temperature may influence baseline $\delta^{13}\text{C}$ values in a marine food web. A previous study examining the relationship between environmental variables and $\delta^{13}\text{C}$ in a phytoplankton-feeding bivalve mollusc found that $\delta^{13}\text{C}$ in muscle tissue increased with temperature (Barnes et al. 2009). However, temperature is unlikely to be the primary factor driving $\delta^{13}\text{C}$ values in western sandpiper feathers as sea surface temperatures increase with longitude across the wintering area, while $\delta^{13}\text{C}$ values decreased with longitude (NOAA Satellite and Information Service 2011, <www.osdpd.noaa.gov/ml/ocean/sst/contour.html>). It is also possible that baseline $\delta^{13}\text{C}$ of the marine food web may vary according to geographic variation in the $\delta^{13}\text{C}$ values of dissolved inorganic carbon, which differ between some ocean basins (Freeman 2001); however, we have no specific empirical data on how dissolved inorganic carbon may vary across the western sandpiper's wintering range, or to what extent any differences may be propagated into coastal habitats used by sandpipers.

$\delta^{15}\text{N}$ – we found that $\delta^{15}\text{N}$ values were higher at extreme northern and southern wintering latitudes, particularly in western North America. These geographic differences could be attributable to spatial variation in dietary and/or physiological processes producing different ratios of ^{15}N to ^{14}N . Higher $\delta^{15}\text{N}$ values are associated with lower protein quality in diet, higher protein content, or increased nutritional stress during feather growth (Martínez del Río et al. 2009). However, we have no knowledge as to how dietary protein or nutritional stress may vary across the wintering range of the western sandpiper which makes it difficult to infer whether any of these factors are related to variation in $\delta^{15}\text{N}$ values.

An alternative explanation is that variation in feather $\delta^{15}\text{N}$ values is related to geographic variation in baseline $\delta^{15}\text{N}$. Jennings and Warr (2003) found that spatial variation in $\delta^{15}\text{N}$ values of phytoplankton-feeding bivalve molluscs was strongly correlated with temperature and salinity gradients. Spatial variation in baseline $\delta^{15}\text{N}$ values was, in turn, highly correlated with $\delta^{15}\text{N}$ values of higher-level consumers. Several other studies have demonstrated that coastal waters subject to high wastewater-loading from sewage and other anthropogenic nitrogen inputs are characterized by enriched $\delta^{15}\text{N}$ values in sediments, macroalgae, and benthic invertebrates (McClelland et al. 1997, Costanzo et al. 2005, Savage 2005, Conlan et al. 2006). Several sites in our study with high $\delta^{15}\text{N}$ were near areas with extensive urbanization (San Francisco Bay and Panama) or sewage outflow (Humboldt); however, other sites with lower $\delta^{15}\text{N}$ values were also located near urban areas, agriculture, or industrial saltworks (Puerto Rico, Ensenada Pabellones, Guerrero Negro). While we cannot conclusively rule out anthropogenic nitrogen inputs as a factor driving variation in $\delta^{15}\text{N}$ values, it seems unlikely that they would vary spatially in such a way as to produce the observed geographic pattern in $\delta^{15}\text{N}$ values. Given that birds were sampled in habitats across a wide spectrum of hydrological regimes, it also seems unlikely that $\delta^{15}\text{N}$ values are driven by variation in some habitat-specific environmental variable such as salinity. While temperature seems a likely environmental variable to influence $\delta^{15}\text{N}$ values across a latitudinal gradient, the non-linear relationship of $\delta^{15}\text{N}$ with latitude suggests additional factors are driving variation in $\delta^{15}\text{N}$.

A third possible explanation for variation in feather $\delta^{15}\text{N}$ values is that there is geographic variation in the trophic level at which sandpipers are feeding across the wintering range. $\delta^{15}\text{N}$ values become enriched by approximately 3–4‰ with increasing trophic level (DeNiro and Epstein 1981). Wintering western sandpipers are latitudinally segregated according to bill length and their different food resources vary spatially across the wintering range (Nebel 2005). Mathot et al. (2007) found evidence for a latitudinal cline in the vertical distribution of marine intertidal invertebrates (higher trophic level) in sediments, while biofilm, a surface food source at a lower trophic level, was consistently distributed across the western sandpiper wintering range. Geographic variation in the distribution of different food resources coupled with the differential ability of birds of varying bill lengths to access these food types could lead to predictable spatial variation in the trophic level at which sandpipers are feeding across the wintering range.

Cross-validation of an isotopic basemap of the wintering grounds

We found that 58% of winter individuals were correctly assigned back to their region of origin with > 50% confidence. Under a null hypothesis of random assignment, we would have expected only 14% of individuals to be correctly assigned back to their region of origin. Other studies that have assessed the ability of stable-isotopes to correctly assign individuals to their area of origin have found a wide range of results depending on the species, isotopes, and sizes of regions used for assignment (Caccamise et al. 2000, Wunder et al. 2005, Kelly et al. 2008, Sellick et al. 2009, Torres-Dowdall et al. 2009). Rates of correct assignment varied between < 30% to > 90% of individuals depending on the study.

Evidence suggests that a lack of empirical data on where and when feather moult occurs may result in the misinterpretation of the origins and movements of migratory birds (Larson and Hobson 2009, Rocque et al. 2009). We found that the rate of correct assignment of western sandpipers to region of winter origin using stable isotope values of whole blood was both higher (80% correct) and more accurate (70% confidence) than when using feather stable isotope values, and that within-site variation of blood isotope values was lower than that of feathers (unpubl.). High variability in feather stable isotope values increases uncertainty in probability assignments because of isotopic overlap between regions of origin, and individual variation in the timing and location of feather moult is a likely contributing factor to the isotopic variability of feathers. Shorebirds have a high potential for complex moult patterns and only a few studies have investigated the frequency with which different patterns occur (Gratto-Trevor and Morrison 1981, Prater 1981, Atkinson et al. 2005, Jamieson 2009). The probability of moulting at a stopover site on migration (moult-migration) may be as high as 50% among some populations of western sandpipers (Franks unpubl.). It is possible that the relatively low proportion of individuals correctly assigned to their area of winter origin may be due to some individuals moulting at migratory stopover sites as opposed to at their wintering sites (Senner and Martinez 1982). Similarly, seasonal movements between wintering sites could also result in a low correct assignment rate if birds moult at a wintering site early in the season but are subsequently captured elsewhere. Shorebirds in Puerto Rico were hypothesized to disperse to other wintering sites in the Caribbean or South America as mudflats dried up towards the end of the wintering period (Rice et al. 2007). In creating an isotopic feather basemap of the western sandpiper wintering range, we could have selected only those individuals correctly assigned with high confidence to their region of origin. However, because we were interested in posing the question 'Where did a migrant or breeding bird spend the winter?', we chose to include all individuals in the creation of the basemap as this more accurately reflected the isotopic variation present for each population of wintering birds, rather than only representing those birds with a high probability of having moulted in the area where they were sampled.

Implications of migratory connectivity patterns

Observed latitudinal variation in the body size of western sandpipers from north to south across the wintering range and differences in the age at first breeding of juvenile western sandpipers wintering at northern versus southern latitudes have led to the hypothesis that there may be genetic differentiation between northern and southern wintering populations. A simple explanation for the maintenance of these patterns is if these populations migrate to different breeding areas (O'Hara et al. 2005). In general, western sandpiper breeding and wintering populations show a high degree of mixing and a consequently low level of migratory connectivity, with individuals from all major wintering areas represented at all breeding sites (Fig. 1). Our findings provide little support for the hypothesis that genetic population differentiation is a mechanism maintaining wintering distribution patterns of western sandpipers by body size and age at first breeding. Assortative mating between birds from the same wintering area and/or of similar size could, in theory, maintain genetic differentiation of wintering populations without geographic segregation on the breeding grounds; however, size-assortative mating does not appear to occur in western sandpipers (Sandercock 1998). Alternatively, patterns may arise from a non-genetic mechanism such as the trait-dependent migration of smaller birds to more northern and larger birds to more southern wintering areas, which in turn affects propensity to breed in an individual's first year. While the specific mechanisms influencing winter distribution patterns remain obscure, our findings suggest that environmental mechanisms are likely operating to maintain body size and life history differences.

Previous studies proposed that the Central Flyway through the continental interior is used by southward migrant western sandpipers on their way to wintering areas on the Atlantic and Caribbean coasts, while all migrants pass through the Fraser Delta in southern British Columbia on both the north- and southward migrations (Senner and Martinez 1982, Butler et al. 1996). The distribution of winter origins of migrant birds indicate that the Central Flyway is indeed strongly used by individuals wintering at southern and eastern wintering sites, but also, surprisingly, by many males wintering on the Baja Peninsula. Although present at all other breeding and migration sites, no birds from western North America were found on the Central Flyway. In contrast, the Fraser Delta on the Pacific Flyway is used by migrants from all wintering areas. The distribution of male migrants in the Fraser Delta differed from that expected under the null hypothesis with relatively more birds originating from western Mexico and fewer from other regions. This may potentially be attributed to when birds were captured during the migration period, if individuals from different wintering areas vary in their timing of migration. While we attempted to sample evenly over the duration of the north- and southward migration periods, the greatest numbers of birds were captured around the peak of the migration. Individuals from western Mexico may have been over-represented during this period, while those from other wintering sites may migrate slightly earlier or later. Alternatively, individuals from different wintering areas may vary in their use of the Fraser Delta

as a stopover site. While the Fraser Delta is a major stopover site for most western sandpipers on the north- and southward migration, it is possible that more birds from western Mexico stop at this site while birds from other wintering areas bypass it.

This study demonstrates that stable isotope analysis can be used to estimate the geographic origins of the western sandpiper, a shorebird species occurring at the interface between freshwater and marine ecosystems. However, inherent uncertainty in using stable isotopes to estimate migratory connectivity can have important consequences for modelling the population dynamics of the western sandpiper or any migratory species (Wunder and Norris 2008). It is therefore imperative that this uncertainty be quantified by modelling and incorporating potential sources of error in probability assignments, as we have done here. By obtaining a range of possible geographic origins for every individual, we allowed for uncertainty about connectivity patterns to be included in future population models, thus providing conservation managers with the ability to estimate the possible degree of change in population size that may occur as a consequence of habitat loss and/or conservation. However, even a small degree of uncertainty can influence whether models interpret population size to be increasing or declining, and detecting small population declines would therefore be difficult (Wunder and Norris 2008).

Although a moderate level of connectivity exists between the population breeding in the Y-K Delta and the overwintering population in western Mexico (many individuals from western Mexico occur together in the Y-K Delta), western sandpipers generally show substantial mixing between the breeding and wintering periods, suggesting that it is unlikely that genetic population differentiation maintains latitudinal patterns of body size and age at first breeding across the wintering range. Our findings suggest that sites in the western sandpiper migratory network are unlikely to become isolated and that the global population is likely to be somewhat buffered from the effects of habitat loss or changes in population dynamics at breeding or wintering sites (Taylor and Norris 2010).

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Supplementary material (Appendix J5573 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.