DIFFERENTIAL MIGRATION IN WESTERN SANDPIPERS WITH RESPECT TO BODY SIZE AND WING LENGTH

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Abstract. We examined differential migration in the Western Sandpiper (*Calidris mauri*) with respect to body size and wing chord allometry within sex and age categories. Culmen and wing chord data were collected as indices of structural body size at three sites that vary latitudinally: Ecuador, Panama, and Mexico. Within all sex and age categories, larger individuals (i.e., those with longer culmens and wing chords) and those with a disproportionately longer wing chord relative to the culmen migrated farther south. Our results, coupled with known molting schedules, indicate that i) immature sandpipers that grow disproportionately longer primary feathers on breeding grounds migrate farther during their first southward migration, and ii) adults that fly farther grow disproportionately longer primary feathers on the nonbreeding grounds. Although no single-factor hypothesis accounts for all aspects of age, sex, and size of Western Sandpiper distributions, costs associated with flight during migration play a significant role in determining differential nonbreeding latitudinal distributions.

Key words: body size, Calidris mauri*, differential migration, latitudinal differences, nonbreeding distribution, Western Sandpiper, wing allometry.*

Migración Diferencial en *Calidris mauri* con Relación al Tamaño del Cuerpo y la Longitud del Ala

Resumen. Examinamos la migración diferencial en *Calidris mauri* con relación al tamaño corporal y las medidas de la cuerda alar para distintas categorías de sexo y de edad. Se colectaron datos de culmen y cuerda alar como indicadores del tamaño estructural en tres sitios ubicados a distinta latitud: Ecuador,

Panamá y México. Dentro de cada categoría de sexo y de edad, los individuos más grandes (con culmen y ala más largos) y con alas desproporcionadamente más largas con relación al culmen migraron más al sur. Nuestros resultados, considerados en conjunto con los patrones de muda, indican que i) los individuos inmaduros que desarrollan plumas primarias desproporcionadamente más largas en los sitios de reproducción llegan más al sur durante su primera migración hacia los sitios no-reproductivos y ii) los adultos que migran más al sur desarrollan plumas primarias desproporcionadamente más largas en los sitios no-reproductivos. Aunque ninguna de las hipótesis previamente propuestas para la migración diferencial explican todos los aspectos de las distribuciones por edad, sexo y tamaño en *C. mauri*, los costos asociados al vuelo durante la migración juegan un papel significativo en la determinación de la distribución latitudinal durante la época no-reproductiva.

Animal migration is an impressive phenomenon that is often difficult to investigate because of the scale over which processes that shape migration patterns occur. Within and among species of birds, morphologies or physiologies often vary with either migration distances or some proxy for migration distances, such as latitude of nonbreeding sites. Within species, migration patterns have often been addressed with respect to movements of groups of individuals categorized by sex and age (i.e., 'differential migration': for a review see Cristol et al. 1999), but latitudinal variation in body size during the nonbreeding season is probably the most commonly observed pattern in migratory birds (Ketterson and Nolan 1982, James et al. 1984, Prescott and Middleton 1990, Belthoff and Gauthreaux 1991, Prescott 1994, Katti and Price 2003). This variation has led to the development of hypotheses to explain migration patterns. Hypotheses typically focus on external factors that vary with migration distance and interact with morphological or physiological variation among individuals within species or sex and age classes, or within individuals themselves (e.g., conditional responses). External factors considered include climatic conditions (Prescott 1991, 1994, Newton and Dale 1996), social interactions (Gauthreaux 1982, Prescott 1991), predation (Lank et al. 2003, Lank and Ydenberg 2003, Ydenberg et al. 2004), and costs of flight associated with migration distance (Gudmundsson et al. 1991, O'Hara 2002). However, determining the importance of these external factors and how they interact with morphological attributes such as body size in the development of differential migration patterns can be difficult, because associating morphological attributes with migration patterns among sex and age categories often leads to overlapping and confounding predictions (Belthoff and Gauthreaux 1991, Prescott 1994). For example, in sexually dimorphic birds breeding in arctic or northern temperate areas, both tolerance of harsher and less predictable habitats and the ability to displace smaller individuals would be associated with the sex having the

FIGURE 1. Distances (in parentheses) from Nome, Alaska to the various nonbreeding sites where data were collected for this study (asterisks).

larger body size. Thus, larger individuals would be predicted to spend the boreal winter in northern nonbreeding areas by hypotheses based on both latitudinal variation in climatic conditions and despotic displacement. By considering morphological attributes such as body size within sex and age categories, we can reduce the number of overlapping predictions from competing hypotheses, especially if life history strategies vary with sex or age.

In this study, we present data on latitudinal distributions of structural body size and wing chord allometry (i.e., scaling relationships with body size) during the nonbreeding season within sex and age categories of arctic- and subarctic-breeding Western Sandpipers (*Calidris mauri*) spending the nonbreeding season at three sites ranging across 33° of latitude (Fig. 1). We believe this report represents one of only two studies comparing body size among nonbreeding populations of varying distance from the breeding area within sex and age categories of a single species (Prescott 1994), and the only study comparing wing allometry.

Western Sandpipers breed in western Alaska and the Chukotskiy Peninsula in Siberia, a concentrated area relative to the expansive nonbreeding region, which extends from Washington State to Peru along the west coast of the Americas and from New Jersey to Surinam along the east coast (Wilson 1994). During the nonbreeding season sex ratios vary latitudinally among populations, with male-biased northern populations and female-biased southern populations (Nebel et al. 2002). Also, the proportion of immature birds (individuals in their first year) is overrepresented at the northern and southern extremes and underrepresented in middle latitudes. Conventional hypotheses, based on climatic conditions and social interactions, predict that within sex

and age categories larger individuals will spend the nonbreeding season farther north. Here we test these hypotheses by comparing two indices of structural body size, culmen length and wing chord, within sex and age classes among three nonbreeding sites that vary by latitude (Mexico, Panama, and Ecuador).

We also present data on latitudinal distribution of wing chord allometry (i.e., wing chord relative to structural body size, represented by culmen length) as an index of wing morphology. Wing morphology coevolves with and is affected by migration behavior, through variation in flight energetics, migration routes, or performance associated with different wing forms. In Western Sandpipers, a latitudinal difference in the probability of first year birds migrating northward and attempting to breed versus spending the boreal summer on the nonbreeding grounds may be proximally or ultimately related to patterns of molt and feather wear (O'Hara et al. 2005). Immature Western Sandpipers do not replace wing feathers during their first nonbreeding season (O'Hara et al. 2002). Thus, in immature birds, wing shape may be more affected by migration distance between the breeding and nonbreeding grounds (resulting from wear during migration flights) than in adult birds, assuming flight feathers grown on the breeding grounds are structurally equivalent to adult feathers grown on the nonbreeding grounds. We explore the magnitude of this difference and its possible influence on migration patterns.

METHODS

We collected data from Western Sandpipers captured in mist nets at four nonbreeding sites in three countries (Fig. 1) from early November to late March during the boreal winters of 1995–1996, 1996–1997, and 1997–1998. In Mexico, we caught birds at Estero Punta Banda (31°52′N, 116°37′W), on the west coast of the Baja California peninsula, 13 km south of Ensenada. In Panama, we captured birds at Bahía de Parita, near Chitré, province of Herrera, Panama (8°0′N, 80°50′W). In southwestern Ecuador, we had two study sites, San Pablo (2°10′S, 80°45′W) and Punta Carnero-Ecuasal Lakes at Mar Bravo (2°15′S, 80°51′W). Typically, replacement of primary flight feathers by adults was completed at all sites by early November (O'Hara et al. 2002), and we excluded data from the few adults molting wing feathers after 1 November.

We measured exposed culmen to 0.1 mm using calipers and flattened wing chord to the nearest mm using a wing rule. We aged birds using banding histories (recaptured individuals) and plumage characteristics (Prater et al. 1977). All birds were sexed based on culmen length: females >24.8 mm, males <24.2 mm (Page and Fearis 1971). Birds of unassigned sex (approximately 4% of immatures [130 of 2897 birds] and 10% of adults [677 of 6584 birds]) were eliminated from the analyses described in the next section. Because one of our principal findings was that culmen length varied systematically with latitude, we also used a disjoint clustering technique to determine sex based on culmen length distributions within sites and age categories. This clustering

analysis (Proc FASTCLUS; SAS 1999) involves 'distances' computed between univariate measures (i.e., culmen lengths), assigning each observation to one of two clusters ('male' or 'female' in this case), and thus did not eliminate any individuals from our analyses. All analyses of body size patterns were done separately for females and males using both methods to classify individuals by sex.

Western Sandpipers aged 4–10 months were assigned the age category 'immature' based on presence of buff-edged inner medial covert feathers, in contrast to the white-tipped coverts of 'adults' (17 months or older; Page et al. 1972, Prater et al. 1977). However, as wing feathers became worn during the nonbreeding season, covert characteristics associated with age class disappeared, particularly in Ecuador. In cases where these plumage characteristics were unclear, we tended to classify individuals as adults. We used data on adults from all sites. Because age identification methodology differed in Ecuador, we only used data on immature birds from Mexico and Panama. For immature birds, wing chord measures were of primary flight feathers grown on the breeding grounds, i.e., their first set of flight feathers. In contrast, wing chord lengths for adults were taken from primaries grown immediately following southward migration. Because wing chords of immature birds were generally shorter than those of adults (due in part to feather wear during migration), possible identification of immature birds as adults in the Ecuador sample likely biases our results by reducing mean wing chord lengths estimated for adults spending the nonbreeding season in Ecuador.

STATISTICAL ANALYSES

We compared culmen and wing chord lengths and wing chord allometry among countries as indices of structural size (culmen and wing chord) and shape (wing chord allometry) for nonbreeding Western Sandpipers. We analyzed variation in culmen lengths among countries within each sex and age category with an ANOVA design (Proc MIXED; SAS 1999). Comparisons of wing chord length were performed using an ANCOVA (Proc MIXED; SAS 1999), with day of capture during the nonbreeding season as a covariate. We controlled for day of capture, calculated as number of days since 1 November, because primary feather wear occurs throughout the nonbreeding season as well as during migration (O'Hara 2002). Because culmen length did not vary with capture day ($P > 0.20$) or year ($P > 0.07$), we pooled data from all capture days and years. In all cases, F-values are reported and significance is determined with $\alpha = 0.05$. We made *post-hoc* comparisons among countries using LSMEANS statements in Proc MIXED (SAS 1999).

We analyzed for a shift in wing chord allometry among countries within sex and age classes by using wing chord-culmen residuals (hereafter referred to as 'wing chord residuals') in an ANCOVA design (Proc MIXED; SAS 1999), while controlling for wing feather wear by including day of capture as a covariate. Wing chord residuals were derived

between wing chord and culmen length. To control for nonlinear relationships between wing chord and culmen length, we tested for and included quadratic factors while deriving wing chord residuals. From our ANCOVA model using wing chord residuals, we predicted and compared estimated residual wing chord length on 1 November for each year of the study (i.e., directly following adult wing molt). *Post-hoc* pair-wise comparisons between countries were performed using ''estimate'' statements in Proc MIXED (SAS 1999), and differences are reported ± SE.

The above analyses were also conducted nonparametrically because distributions of either culmen or wing chord lengths may have been truncated due to our method of classifying sex. In Western Sandpipers, overlapping male and female distributions result in strongly bimodal abundance-length distributions for both culmen and wing chords. By separating these male and female distributions through classifying sex, we likely produced two skewed unimodal distributions because data in the region where the two distributions previously overlapped may have been truncated by the classification processes we used (i.e., eliminating data between 24.2 mm and 24.8 mm, or dividing the bimodal distribution based on cluster assignment). To confirm our results from parametric comparisons among sites (based on possibly skewed distributions), we used a nonparametric Kruskal-Wallis one-way ANOVA with Wilcoxon scores (Proc NPAR1WAY; SAS 1999). Wilcoxon scores for locations were based on culmen lengths, wing chord lengths, and wing chord residuals controlling for day of capture during the nonbreeding season.

RESULTS

Within sex, the mean exposed culmen of adults was longer at nonbreeding sites farther south (Fig. 2; female: $F_{2,2058} = 5.6$, $P = 0.004$; male: $F_{2,1485} = 15.3$, $P < 0.001$). In Mexico, both adult females and males had significantly shorter bills than those in Panama and Ecuador, and adult males in Panama had shorter bills than those in Ecuador (Fig. 2, Table 1). However, culmen lengths of adult females in Panama and Ecuador were similar. As for adults, longer billed immature female and male birds were found farther south (Fig. 3, Table 1; female: $F_{1,1015} = 14.6$, $P < 0.001$; male: $F_{1,649} = 19.2$, $P < 0.001$). Results from comparisons of wing chord lengths among sites, as an alternative index of structural body size, were consistent with the latitudinal trend in body size within sex and age categories suggested by the culmen analysis (immature females: $F_{1,1011} = 7.6$, $P = 0.006$; immature males: $F_{1,647} = 8.3$, $P = 0.004$; adult females: $F_{2,2057} = 8.9$, $P < 0.001$; adult males: $F_{2,1472} = 60.1$, $P = 0.01$). Wing chord length within adult females was more clearly latitudinal than culmen length, with individuals captured in Mexico having shorter wings than those captured in Panama, and those captured in Ecuador having the longest wings overall (mean adult female wing chord ± SE: Mexico, 99.0 ± 0.7 mm; Panama, 101.0 ± 0.3 mm; Ecuador, 102.1 ± 0.4 mm).
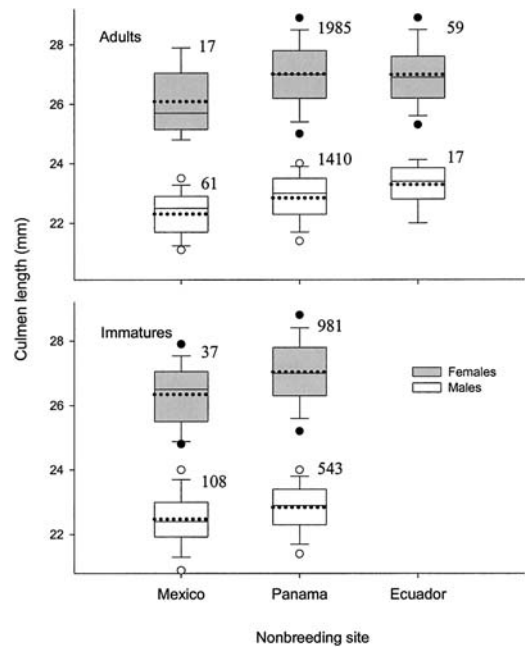

FIGURE 2. Exposed culmen lengths (mm) in male and female Western Sandpipers. The box and whiskers plots represent the distribution of culmen lengths for each sex and age class in each country, with 5% and 95% (circles), 10% and 90% (whiskers), and 25% and 75% (box) quartiles. Missing circles indicate that 5% =10% and 90% = 95% (i.e., low sample size). The mean is represented by a dotted line and the median by a solid line (a solid line with no dotted line indicates median = mean). Numbers represent sample sizes.

Within sex, adults farther south also had disproportionately longer wing chords (Fig. 3). Wing chords were reduced by flight feather wear ('wing chord losses'). In order to estimate wing chord at the beginning of the nonbreeding season (i.e., intercept at 1 November in the ANCOVA model) for each individual captured, we had to estimate site-specific rates of feather wear during the same nonbreeding season (i.e., control for day of capture). We found rates of wing chord loss varied among years (adult females: $F_{2,2009} = 20.9$, $P < 0.001$; adult males: $F_{2,1444} = 11.9$, $P < 0.001$), but there was no detectable variation among countries within years ($P > 0.6$). In adults, wing chord loss rates were significant for the first nonbreeding season only, with adult females losing approximately 5.4 mm and adult males losing 4.2 mm over a 200-day period (O'Hara 2002). Controlling for day of capture and year, we found that residual wing chords varied significantly among countries (females: $F_{2,2009} = 7.6$, $P < 0.001$; males: $F_{2,1444} = 10.4$, $P < 0.001$). Adult females in Mexico had significantly shorter residual wing chords (i.e., disproportionately shorter in relation to culmen length) than those in Panama (Fig. 3; difference =

TABLE 1.   Mean adult culmen length (mm) $\pm$ SE from least-squares regression analysis, with sample sizes in parentheses. *A posteriori* pair-wise comparisons between countries within sexes are indicated by superscript letters in the adult category—each letter indicates significantly different groupings ($P < 0.05$).

Country	Adults		Immatures	
	Females	Males	Females	Males
Mexico	26.09 ± 0.28 (17)[a]	22.31 ± 0.10 (61)[c]	26.34 ± 0.18 (37)	22.47 ± 0.08 (108)
Panama	27.01 ± 0.03 (1985)[b]	22.85 ± 0.02 (1410)[d]	27.03 ± 0.03 (981)	22.84 ± 0.03 (543)
Ecuador	26.99 ± 0.15 (59)[b]	23.29 ± 0.20 (17)[e]		

1.6 mm; $t_{15,1963} = 2.4$, $P = 0.02$), and those in Ecuador (Fig. 3; difference = 2.8 mm; $t_{15,39} = 3.7$, $P < 0.001$). Also, adult females in Panama had shorter residual wing chords than adult females in Ecuador (Fig. 3; difference = 1.3 mm; $t_{1963,39} = 3.0$, $P = 0.003$). Similar to females, adult males in Mexico had significantly shorter residual wing chords than those in Panama (Fig. 3; difference = 1.8 mm; $t_{40,1401} = 4.3$, $P < 0.001$), and those in Ecuador (Fig. 3; difference = 2.9 mm; $t_{40,11} = 3.3$, $P < 0.001$).
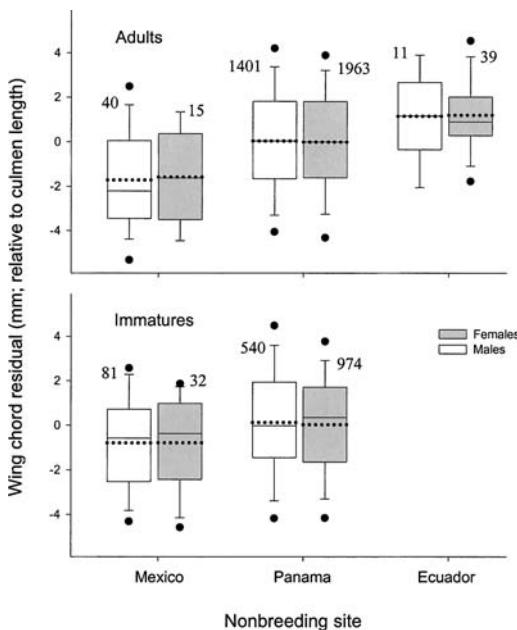

FIGURE 3.   Wing chord residuals (mm) from wing chord-culmen nonlinear regression controlling for year and day of capture, in male and female Western Sandpipers. The box and whiskers plots represent the distribution of wing chord residuals for each sex and age class in each country, with 5% and 95% (circles), 10% and 90% (whiskers), and 25% and 75% (box) quartiles. Missing circles indicate that 5% = 10% and 90% = 95% (i.e., low sample size). The mean is represented by a dotted line and the median by a solid line (a solid line with no dotted line indicates median = mean). Numbers represent sample sizes.

Although adult males in Panama had shorter mean residual wing chords than adult males in Ecuador, the difference was not significant (Fig. 3; difference = 1.1 mm; $t_{1401,11} = 1.4$, $P = 0.15$).

Immature birds of both sexes found farther south during the nonbreeding season also had disproportionately longer wing chords (Fig. 3). Rates of wing chord loss during the nonbreeding season varied among years for immature females ($F_{2,999} = 15.8$, $P < 0.001$), but not for immature males ($F_{1,616} = 1.4$, $P = 0.24$). There was no detectable variation in rates of wing chord loss within years between Panama and Mexico for immature females ($F_{1,998} = 0.75$, $P = 0.39$), but immature males in Panama may have had a higher rate of wing chord loss than those in Mexico ($F_{1,616} = 3.7$, $P = 0.05$). Controlling for day of capture and year, residual wing chords varied significantly between countries. Immature female birds in Mexico had shorter residual wing chords than those in Panama, but the difference was weakly significant (Fig. 3; $F_{1,999} = 4.0$, $P = 0.05$); differences in immature males were highly significant (Fig. 3; $F_{1,617} = 36.7$, $P < 0.001$). In general, immature females in both Mexico and Panama lost 5.8 mm of wing chord during a 200-day nonbreeding period, and immature males in Panama lost 2.3 mm. Loss rates for immature males in Mexico were not significant (<1 mm, $P > 0.5$). Controlling for this sex-dependent difference in rates of wing chord loss between countries during the nonbreeding season, we found that residual wing chords of immature males varied less between countries than those of immature females (female difference = 0.9 mm, male difference = 0.8 mm).

Classifying the sex of birds based on culmen distributions within sites and age classes using cluster techniques did not change our results appreciably, and truncating distributions by separating bimodal distributions into two unimodal distributions also did not affect our general results.

DISCUSSION

Many bird species partially segregate by sex and body size on the nonbreeding grounds (Cristol et al. 1999). In Western Sandpipers, females, the larger-bodied sex, are known to predominate farther south (Nebel et al. 2002). Here, we have shown that within all four sex and age classes, longer billed and longer winged Western Sandpipers spend the nonbreeding season farther south, at sites more distant from the breeding areas. Furthermore, within all sex and age

categories, there was an allometric shift in wing chord-culmen scaling with disproportionately longer wing chords relative to culmen length farther south. We assume that our comparisons from two or three sites represent samples from broad latitudinal clines; this assumption is supported by data from additional Western Sandpiper nonbreeding sites (Fernández et al. 2004). There is evidence for latitudinal body size variation at nonbreeding sites within sex and age categories in other species (James et al. 1984, Prescott 1994), but we are unaware of any other study that has documented a latitudinal cline in structural body size and clines in wing allometry within all four sex and age categories.

The wing chord-culmen scaling relationships among countries are not explained by a single non-linear allometry, as we used a nonlinear relationship between wing chord and culmen length to derive our wing chord residuals. Residual variation from this overall wing chord-culmen relationship is significantly different among sites, suggesting wing chords scale differently with culmen length among nonbreeding sites.

Latitudinal clines in bill size result directly from settlement patterns of individuals of various body sizes, or of different bill lengths that scale disproportionately to body size. The pattern within sex and age classes parallels that between the sexes, with longer billed, potentially larger bodied birds farther south. The most obvious hypothesis explaining disproportionately longer bill lengths for individuals wintering farther south is that there is a matching gradient in the relative availability of food of different types (Elner and Seaman 2003, Mathot and Elner 2004, Mathot 2005). We cannot directly address whether bill length scales linearly with structural size because wing chord, our other index of body size, also scales disproportionately among sites, at least with respect to bill length.

Generation of latitudinal clines in wing length could involve processes that differ between age classes. Immature birds grow flight feathers on breeding grounds, and do not replace them during their first nonbreeding season. Thus, the latitudinal distributions among immature birds during the nonbreeding season arise directly in association with wing size; within sex classes, immature birds with disproportionately longer wings fly farther south. In contrast, wing chords of adults measured in this study were grown on the nonbreeding grounds after (or possibly during) southward migration. Adults with disproportionately longer wings may fly farther south because of a genetic predisposition to longer migrations, or alternatively, adults spending the nonbreeding season farther south may grow longer primaries during their postmigratory molt as a response to their location. Further studies are required to differentiate between these alternative possibilities.

Several potential biases could have affected our wing chord results. Wing chords of immature birds should be affected by differences in primary feather wear among our sites at the beginning of the nonbreeding season because of differences in migration distances. Birds destined for nonbreeding sites in Panama fly approximately 5000 km farther each way than those spending the nonbreeding season in Mexico. In addition, primary feathers in immature birds may wear at a higher rate at more southerly sites during the nonbreeding season. Longer migration flights and higher rates of feather wear should produce disproportionately shorter wings in immature birds farther south. In contrast, we documented the opposite pattern here.

Second, apparent differences in residual wing chords of adults may have resulted from differences in the timing of molt among sites. If more southerly birds arrived and initiated molt later, there is a greater likelihood we measured wing chords that were incompletely grown on more southerly nonbreeding grounds. Alternatively, we may have measured newer flight feathers for birds captured on our more southerly nonbreeding grounds. It is unlikely we measured incompletely grown wing chords because we collected data from adults captured more than two months following the first arrivals of migrating individuals. Furthermore, a bias of this sort would have produced shorter wings at more southerly sites, opposite to the pattern observed. On the other hand, a bias resulting from measuring wing chords with newer flight feathers could have resulted in the pattern we documented here. However, rates of wing feather wear during the nonbreeding season are low and likely insufficient to account for the documented latitudinal differences in wing chord.

What may be the ecological significance of the patterns in bill size, wing size, and wing chord allometry we found? In addition to the distribution of food types mentioned above, the bill and wing size patterns may reflect selection on overall body size. Body size optima probably vary with climate, competitive interactions, or global distributions of predators. Our body size indicators are inconsistent with hypotheses based on Bergmann's rule, which states that larger bodied individuals are found farther north in harsher climates with less predictable food supplies, and with competitive interaction hypotheses that predict larger bodied individuals will displace smaller individuals from nonbreeding areas closer to the breeding grounds. However, if larger bodied individuals are more susceptible to avian predation (i.e., greater wing-loading), a higher predator density farther north may drive larger bodied birds to fly farther to more southerly nonbreeding areas (Nebel and Ydenberg 2005).

Body size may also interact directly with migration distance, with associated costs of flight, but the relationship with energetic expenditure during migration is not clear (Kvist et al. 2001). We suggest that wing morphology within sex and age classes is more likely to vary with migration distance, though our measures of wing chord are not necessarily indicative of wing shape. This is in contrast to Burns (2003), who compared adult wing shape and migration distance among calidrid sandpiper species, and concluded that relative fuel load is a better predictor of wing shape. However, Burns (2003) did not control for variation associated with migration distance within species, which may partly explain the lack of association between wing shape and migration distances among species found in his study.

Comparisons in other groups of species such as pipits (Voelker 2001) have demonstrated differences in wing allometry consistent with patterns we present here, with birds that fly greater distances having longer and presumably higher aspect ratio wings. An alternative explanation is that longer migrations result in greater wear of primary flight feathers (O'Hara 2002) and that longer primaries compensate for this additional wear, for both adult and immature birds. Longer winged individuals probably suffer smaller proportional changes in wing shape due to feather wear during migration.

Varying rates of change in wing shape could have important life history implications, especially in species that are sexually dimorphic. For example, our results showed that the difference in wing chord residuals among countries was more significant for males than females, which may indicate that selection in Western Sandpipers is stronger for males than females to attempt to breed in their first year. Breeding success for males probably depends on quality breeding territories, which are likely limited. Early experience on the breeding grounds probably facilitates the procurement and defense of territories that enhances future reproductive attempts in males. There is no evidence of a partial postjuvenile (Gratto and Morrison 1981) or supplementary (Prater et al. 1977) wing molt in immature Western Sandpipers (PDO'H, unpubl. data), which means that individuals opting to migrate northward in their first spring would have to do so using flight feathers already damaged from their first migration southward. Males may thus strongly favor nonbreeding grounds closer to the breeding grounds to mitigate changes in wing shape associated with three migrations (first southward and one return trip to the breeding grounds), shifting their distributions northward of areas that may otherwise be considered optimal.

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