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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,thatkdi(hat)r known migradprimthatfarther

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

and age categories larger individuals will spend the

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 Sandpi-

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; $t_{40,11} = 3.3$, $P < 0.001$). 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

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 nonlinear 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

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