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VARIATION IN THE WING MORPHOLOGY OF WESTERN SANDPIPERS (*CALIDRIS MAURI*) IN RELATION TO SEX, AGE CLASS, AND ANNUAL CYCLE

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Abstract.—We analyzed differences in wing morphology between sexes and among age classes of Western Sandpipers (*Calidris mauri*) to assess possible relationships with differential migration, acrobatic aerial displays, and potential vulnerability to predation, using size-constrained component analysis. Data on wing morphology of all four sex and age classes were available from birds spending the nonbreeding season in northwestern Mexico, and data on females were available from throughout the annual cycle. During the nonbreeding season, females had longer and more pointed wings than males. Within each sex, adults had longer and more pointed wings than immature birds. Throughout the annual cycle, adult females tended to have longer and more pointed wings than immature females. The longer and more pointed wings of females are consistent with selection on flight efficiency for longer migration distances. The shorter and rounder wings of males are consistent with stronger selection for agility in flight during acrobatic aerial displays, but also with weaker selection for flight efficiency because of shorter migration distances. The rounder wings of immature birds are most consistent with stronger selection for take-off performance as an antipredator adaptation, at a cost of lower flight efficiency during long-distance migratory flight. Considering intraspecific sex and age class differences in wing morphology of species with differential migration complements interspecific comparisons assessing the relative importance of selective agents acting on this character. *Received 8 May 2006, accepted 14 September 2006.*

Key words: aerial displays, *Calidris mauri*, intraspecific variation, migration distance, vulnerability to predation, Western Sandpiper, wing morphology.

Variación en la Morfología del ala de *Calidris mauri* con Relación al Sexo, la Edad y el Ciclo Anual

Resumen.—Analizamos las diferencias en la morfología del ala entre sexos y clases de edad de *Calidris mauri* para evaluar su relación con la migración diferencial, los vuelos acrobáticos y el riesgo de depredación, utilizando un análisis de componentes de tamaño restringido. Recolectamos datos sobre la morfología del ala de ambos sexos y clases de edad durante la época no-reproductiva en el noroeste de México, y sólo de hembras a través del ciclo anual. Durante la época no-reproductiva, las hembras tuvieron alas más largas y puntiagudas que los machos. En cada sexo, los adultos tuvieron alas más largas y puntiagudas que los inmaduros. A través del año, las hembras adultas tendieron a tener alas más largas y puntiagudas que las

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hembras inmaduras. Las alas más largas y puntiagudas de las hembras concuerdan con la mayor eficiencia requerida para vuelos migratorios largos. Las alas más cortas y redondas de los machos concuerdan con la mayor agilidad requerida durante los vuelos acrobáticos, pero también pueden relacionarse en cierto grado con la eficiencia de vuelo porque su distancia de migración es más corta. Las alas más redondas de los inmaduros concuerdan con alas adaptadas para aumentar el desempeño durante el despegue y reducir el riesgo de depredación, a pesar del bajo desempeño durante vuelos migratorios largos. Considerar las diferencias intraespecíficas dadas por los sexos y la edad en la morfología del ala en especies con migración diferencial, complementa las comparaciones interespecíficas que evalúan la importancia relativa de los factores que determinan la morfología del ala.

Wings are subject to a suite of interacting and conflicting selective pressures. Migration (Mönkkönen 1995, Lockwood et al. 1998, Voelker 2001), sexual selection (Hedenström and Møller 1992), predation danger (Swaddle and Lockwood 1998), and foraging behavior (Marchetti et al. 1995) have all been implicated as factors influencing wing morphology. Every avian species is subject to at least some of these selective pressures. For instance, latitudinal migrants should lower the energetic cost of migration by evolving wings with higher aspect ratios, and longer and more pointed wings (Lockwood et al. 1998). If an ability to perform aerial displays is important, sexual selection should favor wings with lower aspect ratio; shorter and more rounded wings increase maneuverability and gliding ability (Hedenström and Møller 1992). Stronger selection for a quick and steeper take-off from the ground, important when escaping predators, would also favor shorter and more rounded wings (Swaddle and Lockwood 1998, 2003). Wing morphology should thus be a product of natural and sexual selection for an optimal balance between benefits and costs in multiple dimensions.

We studied intraspecific variation in the wing morphology of Western Sandpipers (*Calidris mauri*). Examining intraspecific differences between sexes and among age classes complements interspecific comparative studies for drawing inferences about the relative importance of different selective pressures (Alatalo et al. 1984, Mulvihill and Chandler 1990, Pérez-Tris and Tellería 2001, Peiró 2003), intrinsically controlling for phylogeny and many aspects of life history. Western Sandpipers have relatively small and rounded wings compared with other calidridine sandpipers that migrate longer distances (Burns 2003). This species breeds in a relatively restricted range in western Alaska and the Chukotskiy Peninsula (Wilson 1994). During the nonbreeding season, Western Sandpipers are found in coastal areas along the Pacific coast from California to Peru (Wilson 1994). Adults undergo flight-feather molt immediately after southward migration and arrival on the nonbreeding grounds, whereas immature birds do not molt their first set of flight feathers, grown on the breeding grounds, until their second summer (O'Hara et al. 2002). Immature Western Sandpipers also have a life-history difference as a function of migratory distance. Immature birds spending their nonbreeding season in northern Mexico migrate northward in their first spring, but those residing farther south (e.g., in Panama) remain on the nonbreeding grounds until their second spring (Fernández et al. 2004, O'Hara et al. 2005).

The combination of a restricted breeding range and a broad nonbreeding range means that some Western Sandpipers migrate much farther than others. Birds wintering in Panama travel ~18,000 km in a round trip, whereas birds wintering in Mexico may travel 12,000 km (O'Hara et al. 2005). Western Sandpipers are differential migrants. During the nonbreeding season, males spend the winter farther north than females, and immature birds are disproportionately represented on the northern and southern edges of the distribution (Nebel et al. 2002). The longer migration of females, particularly among immature birds, should favor more pointed wings. Within sex and age classes, individuals with disproportionately longer wings, compared with bill lengths, migrated farther south (O'Hara et al. 2006), which suggests an ecological relationship between morphology and migration distance.

In addition to migration distance, two other factors seem likely candidates to affect wing morphology. First, intraspecific studies of shorebirds indicate that smaller size is advantageous for males performing acrobatic aerial displays (Blomqvist et al. 1997), and comparative analyses suggest that this has selected for "reversed" size dimorphism in species with such displays (Jehl and Murray 1976; Figuerola 1999; Székely et al. 2000, 2004). Male Western Sandpipers use acrobatic aerial displays for mate attraction and territorial defense (Lanctot et al. 2000), which should favor more rounded wings in males than females. Second, throughout the range, females may have higher vulnerability to predation than males on the basis of both body size and foraging behavior. Females are larger and heavier (Jehl and Murray 1976) and, therefore, are expected on aerodynamic grounds to take off more slowly (Pennycuick 1972, Rayner 1988, Tobalske and Dial 2000; but see Burns and Ydenberg 2002). Females also use a more probing foraging mode, which obstructs their field of vision more than the pecking behavior favored by males (Mathot and Elner 2004) and may reduce their ability to detect predators during feeding (Guillemain et al. 2001). In several species of shorebirds, immature birds are more vulnerable than adults to attacks by predators (Kus et al. 1984, Cresswell 1994, Dierschke 1998, Whitfield 2003). Higher vulnerability to predation would strengthen selection for more rounded wings to enable faster take-offs, and greater flight agility in females and immature birds than in males and adults. Finally, in contrast to selection in some passerine species (Nyström 1991, Marchetti et al. 1995), we would not expect sex and age-class differences in foraging behavior to exert a large direct influence on wing morphology, because Western Sandpipers forage on the ground.

We analyzed wing morphology differences between sexes and among age classes of Western Sandpipers to assess possible relationships with differential migration, use of acrobatic aerial displays, and potential vulnerability to predation. We applied the method of size-constrained component analysis (Lockwood et al. 1998) to determine whether wing morphology differed significantly among the four sex and age classes of Western Sandpipers and to see whether differences were consistent between age classes at different periods of the annual cycle. The wing morphology indices introduced by Lockwood et al. (1998) were derived from an interspecific comparative study from a broad range of avian taxa and are now being applied to intraspecific studies (Peiró 2003, Swaddle and Lockwood 2003, Fiedler 2005). We discuss the importance of variation in wing morphology in terms of conflicting selection pressures in this species with differential migration by sex and age class.

METHODS

Study areas.—The wings of Western Sandpipers were measured at a range of sites throughout the annual cycle. Nonbreeding sandpipers were studied at Bahía Santa María (25°02′N, 108°18′W), the largest wetland on the Sinaloa coast, ~90 km northwest of Culiacán, Mexico (Engilis et al. 1998). Migratory Western Sandpipers on both northward and southward migrations were studied at the Fraser River Delta (49°05′N, 123°12′W) in southwestern British Columbia, the largest coastal estuary on Canada's Pacific coast (Butler et al. 1987). Breeding Western Sandpipers were studied at a 4-km^2 study site located 21 km east of Nome, Alaska (64°20′N, 164°56′W).

Data collection.—At Bahía Santa María (BSM; November–April, 1999–2000), we analyzed the wing morphology of 376 Western Sandpipers of assigned sex (females: 90 adults, 61 immature birds; males: 140 adults, 85 immature birds), based on bill measurements: female >24.8 mm, male < 24.2 mm (Page and Fearis 1971). In Nome (NOM; July 1999), we measured 16 females (8 adults and 8 immature birds). At the Fraser River Delta, we measured 19 females (13 adults and 6 immature birds) during northward migration (FRD-N; April–May 2003) and 28 females (13 adults and 15 immature birds) during southward migration (FRD-S; July–August 1999). Each bird was aged as an immature (<1 year old) or adult on the basis of plumage coloration and wear of primary feathers (Page et al. 1972, O'Hara et al. 2002). For each bird, we measured length of closed wing (flattened, ±0.5 mm) and the distances between the wingtip and the tip of each primary feather from the eight distalmost primaries, to the nearest half millimeter (Lockwood et al. 1998, Pérez-Tris and Tellería 2001). Measurements were taken of the right wing of birds that had previously been collected and frozen, except in BSM, where live birds were measured in the field. All measurements were taken by G.F.

Analysis of wing morphology.—We analyzed wing morphology using Lockwood et al.'s (1998) method of size-constrained component analysis. This method constrains the first component (C1) to be a measure of isometric size, in contrast to general principal component analysis, which typically includes some shape variation in the first component. Using Lockwood et al.'s (1998) method, the subsequent two components describe wing pointedness (C2) and wing convexity (C3). Wing convexity explained <14% of the shape variation and was not analyzed further here. Wingtip pointedness (hereafter "wing shape") is defined as a shift of the wingtip toward the leading edge of the wing in a more pointed wing, and away from the leading edge in a more rounded wing. This shape component corresponds with the wing pointedness examined in other studies of wing shape (Burns 2003), with positive values of C2 indicating more pointed wings, whereas negative values indicate more rounded wings. Size and wing-shape values from size-constrained component analysis do not have units.

We measured primary distances, which are less reliable and accurate measures of wing morphology than primary feather lengths (Lockwood et al. 1998) but were more practical to obtain during trapping and banding sessions at BSM. Values of distances between the wingtips were log-transformed [ln (ΔQ_i + 1)] to increase normality and were standardized to equal unit variances before analysis (Lockwood et al. 1998), but several primary distances may remain biased, because they are confined to be non-negative and must include zero. We evaluated the repeatability of primary distance measurements (Lessells and Boag 1987) on the basis of two repeated folded wing spreads of 262 Western Sandpipers during the nonbreeding season. Primary distances in this sample had relatively low repeatability (ΔQ_{1-8} = 0.4, 0.6, 0.5, 0.5, 0.5, 0.5, 0.4, and 0.4). The repeatability of wing size and shape, calculated from this sample only, was 0.4 and 0.3, respectively. Low repeatability values imply substantial measurement error, though the violations of normality may also play a role. Our wing morphology measurements are thus relatively noisy, which reduced our power to detect differences among groups.

To assess potential differences in wing size and shape during the nonbreeding season, we used analysis of covariance (ANCOVA) with age class and sex as factors, and the day of capture as a covariate to control for potential changes attributed to feather wear (Pienkowski and Minton 1973, O'Hara 2002). We expected a seasonal progression after initial feather production toward shorter and rounder wings, because the longest primaries experience the greatest friction (Pennycuick 1972). To assess potential differences in wing size and shape of females throughout the annual cycle, we used ANOVA with age class and site (BSM, FRD-N, NOM, and FRD-S), but not date, as factors. To reduce variability because of feather wear during the nonbreeding season, we only considered 64 females (36 adults and 28 immature birds) that were measured in November and December at BSM in these analyses. Western Sandpipers of different age classes grow wing feathers at different times: adults in early autumn at nonbreeding sites versus immature birds at midsummer on breeding sites, and feather wear may alter wing size and shape. To compare sizes and shape of equally aged feathers, we therefore compared the wing morphology of newly grown feathers from different age classes (immature birds from NOM vs. adults from BSM) and of feathers following one migration (immature birds from BSM vs. adults from NOM). If interaction terms were not significant, models were reduced to their most parsimonious form using Type III sum of squares ($\alpha = 0.05$), and we report least-squares means (±95% confidence interval [CI]) taking other factors into account. All statistical tests were performed using SAS, version 8.2 (SAS Institute, Cary, North Carolina).

Results

Both wing size and shape differed significantly by both sex and age class (size: sex $F = 13.87$, df = 1 and 371, $P < 0.01$; age class $F = 28.72$, df = 1 and 371, $P < 0.0001$; shape: sex $F = 14.60$, df = 1 and 371, $P < 0.01$; age class $F = 53.17$, df = 1 and 371, $P < 0.01$), controlling for seasonal variation, with no significant interactions (sex * age class: size, $F = 0.08$, df = 1 and 371, $P = 0.77$; shape, $F = 0.15$, df = 1 and 371, $P = 0.69$). Wings of females were longer and more pointed than those of males, and within each sex, adults had longer and more pointed wings than immature birds (Fig. 1).

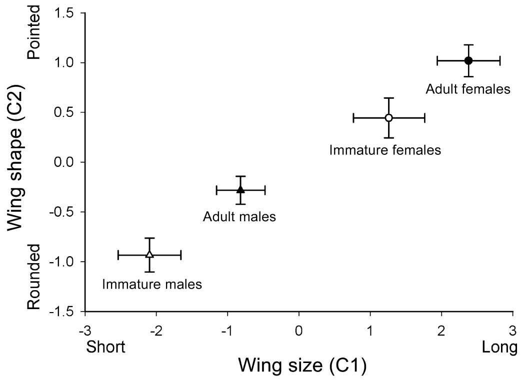

Fig. 1. Relation between wing size and wing shape by sex and age class in Western Sandpipers during the nonbreeding season in Bahía Santa María, northwestern Mexico. Least-square means (± 95% CI) are reported. Sample size: 90 adult females, 61 immature females, 140 adult males, and 85 immature males.

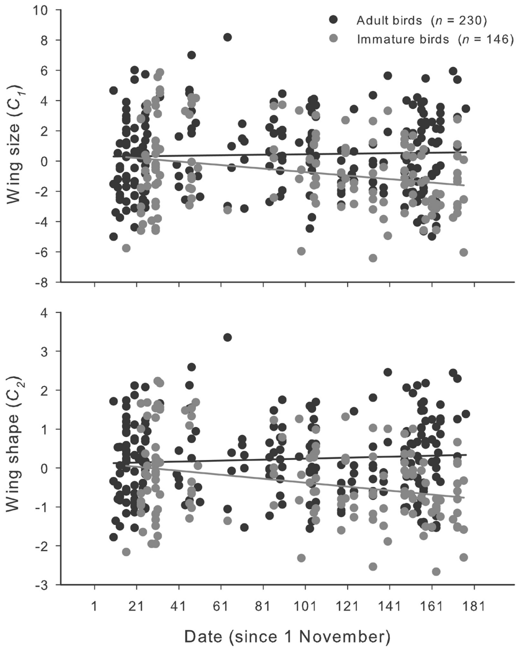

Fig. 2. Changes in wing size and wing shape of adult and immature Western Sandpipers, controlling for sex, throughout the nonbreeding season in Bahía Santa María, northwestern Mexico.

There was a strong positive relationship between wing size and wing shape ($r^2 = 0.94$, $F = 3{,}580.53$, df = 1 and 372, $P < 0.01$; Fig. 1). Interaction terms for wing size by age class ($F = 0.54$, df = 1 and 370, $P = 0.46$) or sex ($F = 1.42$, df = 1 and 370, $P = 0.23$) were not significant, indicating a common slope for all sex and age classes. Wing morphology varied differently between age classes, controlling for sex, throughout the nonbreeding season (size, day * age class: $F = 5.09$, df = 1 and 371, $P = 0.02$; shape, day * age class: $F = 9.45$, df = 1 and 371, $P = 0.002$). Wing size and degree of wing pointedness of immature birds (size: $t = -3.07$, $P < 0.01$, $r^2 = 0.06$; shape: $t = -3.42$, $P < 0.01$, $r^2 = 0.07$) decreased throughout the nonbreeding season, whereas we detected no change in adults (size: $t = 0.55$, $P = 0.58$, $r^2 < 0.01$; shape: $t = 1.09$, $P = 0.27$, $r^2 < 0.01$; Fig. 2).

Throughout the annual cycle, adult females had longer wings than immature females ($F = 4.07$, df = 1 and 122, $P = 0.04$), but wing size did not differ among seasonal periods ($F = 0.04$, df = 1 and 122, $P = 0.99$; Fig. 3). Although wing shape did not differ between age classes ($F = 1.92$, df = 1 and 122, $P = 0.16$) or among seasonal periods ($F = 0.02$, df = 1 and 122, $P = 0.99$), there was a general trend that adult females had more pointed wings throughout the annual cycle than immature females (Fig. 3). Among females, wing morphology did not differ between age classes in new feathers (adults BSM vs. immature birds NOM; size: $F = 1.17$, df = 1 and 43, $P = 0.19$; shape: $F = 1.67$, df = 1 and 43, $P = 0.20$) or between feathers with one migration (adults NOM vs. immature birds BSM; size: $F = 2.08$, df = 1 and 33, $P = 0.15$; shape: $F = 1.71$, df = 1 and 33, $P = 0.20$). However, the mean values were in the predicted direction of adult females having longer (new feathers: least-square mean ± SE, adults BSM: 0.24 ± 0.41 vs. immature birds NOM: –0.98 ± 0.83; one migration, adults NOM: 1.29 ± 0.99 vs. immature birds BSM: –0.31 ± 0.49) and more pointed wings (new feathers, adults BSM: 0.12 ± 0.19 vs. immature birds NOM: –0.42 ± 0.38; one migration, adults NOM: 0.53 ± 0.47 vs. immature birds BSM: –0.16 ± 0.23) than immature females.

Discussion

Inferences regarding the relative importance of multiple selective pressures on wing morphology of birds have been made primarily from interspecific comparisons. We are applying the comparative approach among sex and age classes within a species showing differential

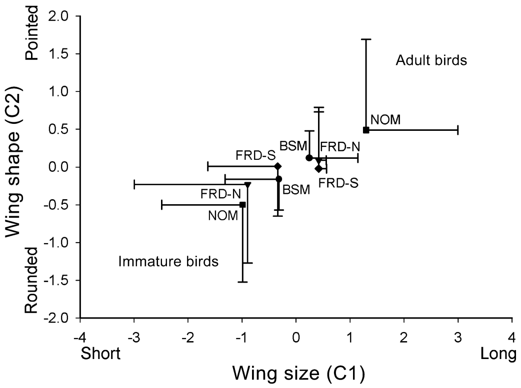

FIG. 3. Relation between wing size and wing shape by age class in female Western Sandpipers throughout the annual cycle. BSM = Bahía Santa María, FRD-N = Fraser River Delta northward migration, NOM = Nome, and FRD-S = FRD southward migration. Least-square means (± 95% CI) are reported. Sample size: NOM, 8 adults and 8 immature birds; FRD-N, 13 adults and 6 immature birds; FRD-S13, adults and 15 immature birds. For clarity, only positive and negative values of 95% CI are shown for adults and immature birds, respectively.

migration. Wing morphology differed by sex and age class during the nonbreeding season. We thus examined the consistency of patterns observed among classes, with predictions on the basis of selective factors expected to differ with respect to migration distances and nonbreeding distributions.

Wing size and shape.—Wing size and wing shape were strongly positively correlated among sex and age classes during the nonbreeding season, and a similar trend can be observed among females throughout the annual cycle. Given the tight relationship between the two variables, it will be difficult to distinguish between selection on wing shape versus selection on wing size *per se*. The conservative pattern of covariation in these traits we have found within and among classes of Western Sandpiper suggest that functional considerations keep this relationship tightly controlled. In comparative studies among migratory species (Mönkkönen 1995, Lockwood et al. 1998, Burns 2003), a positive relationship between size and shape is also implied, which suggests that smaller birds have more rounded wings.

As feathers wear, wing shape is expected to change toward being more rounded and shorter, because wear is greatest for the longest primaries, which move the farthest and encounter the greatest friction and turbulence (Pennycuick 1972). We documented this change throughout the nonbreeding season within immature birds but not adults. Adult feathers were newer and perhaps stronger, having been grown at the nonbreeding site following southward migration, whereas those of immature birds had been grown in Alaska before southward migration (O'Hara et al. 2002). We also did not find an expected trend toward more rounded wings during successive seasons following feather growth (Pienkowski and Minton 1973), which suggests that we were measuring different populations at different places and times of year.

Migration distance.—Interspecific studies have found that longer and more pointed wings are associated with longer migration distance (Mönkkönen 1995, Lockwood et al. 1998, Voelker 2001), as expected from selection for greater flight efficiency (Pennycuick 1972). Among calidrid sandpipers, more pointed wings occur in those species with longer migratory flight segments, and concomitantly higher fat loads, which were better predictors of wing shape than total migration distance (Burns 2003). Three polygynous species with ground displays and male-biased sexual size-dimorphism were excluded from Burns's (2003) analysis, which probably made potential flight-related associations easier to detect. Female Western Sandpipers have longer and more pointed wings than males, which is consistent with the predicted direction of differences favored by selection for flight efficiency on migration. The age class effects, however, produce mixed results. The rounder wings on immature versus adult males are consistent with their shorter average migration, but rounder wings for immature than for adult females is opposite to what would be expected as an adaptation for the sex and age class with the longest average migration (Nebel et al. 2002).

If the length of the longest leg of the migration journey were more important than total migration distance (Burns 2003), we might not expect major differences between sexes or among age classes. As far as we know, all classes of Western Sandpipers have a similar longest flight, that is, a nonstop segment southeastward from Alaska to the southern coast of British Columbia (Butler et al. 1996). Even with identical distances, however, flight performance could differ between age classes, because of seasonal differences in wind assistance and differences in body composition (Guglielmo and Williams 2003). Given that wing morphology differs, in fact, between age classes, either total migration distance is more important than the longest flight, or other factors are driving the differences.

Finally, within all sex and age classes, individuals with disproportionately longer wing chords compared to bill length migrate farther south (O'Hara et al. 2006). If our general relationship between wing length and pointedness holds, Western Sandpipers' migratory distance and wing morphologies are correlated within each sex and age class, as predicted by prioritizing selection for migratory flight efficiency. Selection for greater flight efficiency for longer-distance migrants thus accounts for most of the dyadic comparisons among the four sex and age classes, and for comparisons of individuals within classes.

Sexual selection for aerial displays.—The pattern of more rounded wings in male than in female Western Sandpipers is also consistent with sexual selection for acrobatic aerial displays by males (Lanctot et al. 2000). Effects of sexual selection on sexual dimorphism have been found in broad comparisons of Charadrii, with selection for acrobatic aerial displays being implicated as a general driver of smaller male body and wing size in some species, including Western Sandpipers (Jehl and Murray 1976, Figuerola 1999, Székely et al. 2000), and migration distance was not a significant predictor of size dimorphism in multivariate analyses (Székely et al. 2004). A study of Dunlin (*C. alpina*), which has patterns of male display and sexual dimorphism similar to Western Sandpipers, supported a mating advantage for smaller males (Blomqvist et al. 1997). These studies focus on smaller size rather than wing size or shape *per se*, but our general relationship between size and shape suggests that shape will change with size. In summary, both selection for acrobatic aerial displays and sexual differences in migration differences are consistent with the shorter, rounder wings of males we have observed. However, the age differences are more difficult to account for. The rounder wings of immature males could be interpreted as providing them with lower-performance wings that less-experienced birds might use during display, but this argument does account for the rounder wings of immature females.

Predation vulnerability.—The sex-related differences in wing morphology that we observed are not obviously consistent with the pattern predicted if females are more vulnerable to predation than males. Despite predictions based on body size and foraging behavior, an empirical study of take-offs indicated that females had steeper escape angles than males (Burns and Ydenberg 2002). Burns and Ydenberg (2002) suggest that females have compensated for a greater intrinsic vulnerability by making a larger evolutionary investment in antipredator capability (e.g., proportionally larger pectoral mass). The wing morphology patterns with respect to age class are better candidates for differences driven by danger of predation. Throughout the annual cycle and controlling for flight-feather molt and feather wear, adult females tended to have longer and more pointed wings than immature females. As indicated above, the rounder wings of immature birds are not well predicted by either selection for flight efficiency or sexual selection. Age-related variation is likely to reflect ontogenetic changes (Pérez-Tris and Tellería 2001), and studies in which the same individuals were measured before and after the first complete molt confirm age-related differences at the individual level (Leverton 1989, Harper 1999).

The more rounded wings of younger birds have been interpreted as favored by a greater need for evading predators (Alatalo et al. 1984, Pérez-Tris and Tellería 2001), by foraging in more dangerous habitats, or by other factors. In some shorebird species, younger shorebirds suffer higher mortality rates from predation than older birds (Kus et al. 1984, Cresswell 1994, Dierschke 1998, Whitfield 2003). The enhanced ability of individuals with more rounded wings to take off from the ground more steeply, and to maneuver with greater agility once in flight, should provide better escape performance (Lockwood et al. 1998, Swaddle and Lockwood 2003). However, during migration, no differences between adult and immature Western Sandpipers were detected in their escape performance (Burns and Ydenberg 2002). One possibility is that the more rounded wings of immature birds may have helped them achieve escape performance similar to that of adults despite other intrinsic handicaps, including their larger gut mass (Guglielmo and Williams 2003). A final consideration is that those immature birds making the longest migration will not, in fact, make another migratory flight with their feathers, because they remain on the nonbreeding grounds for ~18 months and grow new flight feathers before returning northward (O'Hara et al. 2002, 2005; Fernández et al. 2004). We conclude that selection for better escape performance is stronger on immature birds, which might benefit more than adults from having shorter and more rounded wings rather than wings better adapted for undertaking migratory movements.

Conclusion.—Western Sandpiper, a species with differential migration by sex and age class, has substantial intraspecific differences in wing morphology by sex and age classes. Multiple selection pressures operate to equilibrate the general phenotype at different states. We have drawn inferences about their relative importance from patterns in the data. In general, between and within sex and age classes, longer-distance migration is associated with longer and more pointed wings. The acrobatic displays of males also appear to contribute toward shorter and rounder wings. The rounder wings of immature birds compared with those of adults are most consistent with wings favoring antipredator adaptation at the cost of lower long-distance flight efficiency. The interplay among selection pressures on wing morphology in species with sex and age class differential migration merits further study. Intraspecific sex and age class differences can complement interspecific studies to better assess the tradeoffs birds make among selective factors affecting wing morphology.

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