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The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*)

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Abstract High body mass caused by fat storage during migration is believed to increase a bird's risk of predation by decreasing its ability to escape predators. We demonstrate the negative effect of wing loading (mass/wing area) on escape speed and angle of two migrating species of shorebird. We also show significant differences in escape performance between the species and genders. To help explain these differences, we test two potential proximate causes, wing shape and leg bone length. Wing shape is correlated with differences in escape performance between the species, but we found no correlation of wing shape or leg bone length with gender. Ultimately, greater predation risk due to habitat use or larger body size, for the species and genders respectively, may have resulted in evolution of enhanced escape ability.

Keywords Avian migration · Escape · Mass-dependent predation risk · Take-off

Introduction

Many investigators have suggested that increased body mass due to fat storage reduces flight ability in birds and decreases the probability of escaping a predator's attack (Howland 1974; Lima 1986; Pennycuik 1989; Hedenström 1992; Witter and Cuthill 1993; Bednekoff and Houston 1994; Bednekoff 1996). Smaller fat reserves may improve take-off acceleration as well as flight maneuverability, both of which increase the ability to escape or elude an attack (e.g. Rudebeck 1950; Page

and Whitacre 1975; Cresswell 1993). Laboratory studies show that small diurnal changes in mass of wintering passerines do not cause detectable decreases in escape speed or angle, perhaps because the birds are somehow able to compensate for higher mass (Kullberg 1998; Kullberg et al. 1998; Veasey et al. 1998; van der Veen and Lindström 2000). However, large increases in mass during migration have been shown to decrease take-off speed (blackcaps, *Sylvia atricapilla*, Kullberg et al. 1996; sedge warblers, *Acrocephalus schoenobaenus*, Kullberg et al. 2000) and take-off angle (blackcaps, Kullberg et al. 1996; European robin, *Erithacus rubecula*, Lind et al. 1999). Sandpipers rely on fast escape flights from the ground to evade predators (Page and Whitacre 1975) and typically have large increases in mass during migration. As the issue of the effects of fuel reserves on escape performance is far from closed, the main goal of this study is to determine the effect of wing loading (mass/wing area) on the escape speed and angle of migrating least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*).

Shorebird migration is of particular interest to avian ecologists because of the large variability in migration strategies both between and within species. Predation risk is a major factor in many ecological situations, but has not been intensively studied in shorebird migration. We examine the differences in escape performance between two similarly sized sandpipers differing in foraging habits, with least sandpipers foraging in vegetated salt marshes more often than the mudflat feeding western sandpipers. Salt marshes may be more dangerous places to feed for least sandpipers because their ability to detect predators may be decreased by the visual obstruction of vegetation. Interestingly, Cramp (1983) notes that least sandpipers have a "remarkable rate of climb." The genders of these two species are also known to differ in migration timing (Butler et al. 1987; Butler and Kaiser 1995). Differential predation risk has been cited to explain gender differences in behavior of other taxa (e.g. guppies, *Poecilia reticulata*, Magurran and Nowak 1991), and here we examine the effects of gender on escape performance in birds.

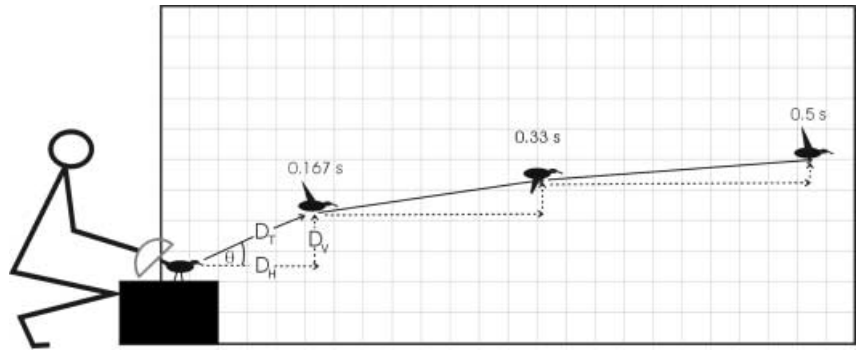
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Fig. 1 Camera view of a typical escape flight of a least sandpiper (*Calidris minutilla*), illustrating the three intervals at which total, vertical, and horizontal distances were measured (D_t total distance, D_v vertical distance, D_h horizontal distance, θ escape angle)



We investigate two potential proximate explanations for differences between species and genders. Wing shape and leg bone lengths could both influence escape ability (Swaddle and Lockwood 1998). Rounder wingtips maximize thrust from flapping and provide more lift at the wingtip, which aids take-off speed (Rayner 1993). Our investigation has been prompted by Cramp's (1983) description of the wing of least sandpipers as having a "more rounded tip than other small *Calidris*." Relatively long femora could allow a lengthened acceleration phase during a jump, which aids the initial phase of take-off (Swaddle and Lockwood 1998), but empirical data are scarce.

Methods

Escape flights

Western and least sandpipers were caught in mist-nets during their southward migration at Sidney Island, British Columbia, Canada (48°40'N, 123°20'W) in July and August of 1997 and 1998. Culmen length (with calipers to 0.1 mm), mass (with a Pesola spring balance to 0.1 g), and wing area [from digitalized photos taken of the right wing, standardized in a bent wing position on a custom board; area calculated using Scion Image (www.scioncorp.com)] were measured. Wing loading was calculated as the ratio of weight to wing area, expressed as $N\ m^{-2}$ (Pennycuik 1989). We use wing loading, rather than just body mass, to help account for the effects of body size (larger birds weigh more, but also have larger wings and muscles) and feather wear on flight performance. Gender was assigned based on culmen measurements [western sandpiper: <24.0 mm = male, >25.0 mm = female, 24.0–25.0 mm = unknown gender (Prater et al. 1977); least sandpiper: <17.5 mm = male, >18.7 mm = female, 17.5–18.7 mm = unknown gender (Page 1974)] and age (juvenile vs adult) was assigned by plumage characteristics (Cramp 1983; Paulson 1993). After banding and measurement, birds were held in cloth bags until released. The time between capture and release (hold time; range=7–247 min) was recorded to assess whether long holding periods affected escape flights (e.g. through dehydration or muscle stiffness).

To measure escape speed and angle, a bird was placed under a domed mesh cover on a 20-cm-high platform in front of a 110×245 cm board with a 10 cm grid (Fig. 1), positioned so that flights were in the lee of the wind. A person kneeling opposite the desired direction of flight lifted the cover. This person acted as a 'predator' model and elicited an alarmed response from the bird. We assume the birds were motivated to fly away as quickly as possible. Escape flights were videotaped with a RCA CC445 camcorder (at 30 frames/s) placed 10 m from the board.

Escape flights were played back on a video monitor, and horizontal and vertical displacement of the image were measured rela-

tive to the 10 cm grid. True distances flown were calculated from these measures, and then corrected for camera perspective (Burns 2001). Escape speed is total distance over time (number of frames \times 0.033 s/frame). Escape angle is the tangent of vertical distance over horizontal distance flown (Fig. 1). If birds did not fly parallel to the board, the angle away from parallel was determined by the releaser using fixed reference points on the ground, and incorporated into corrections.

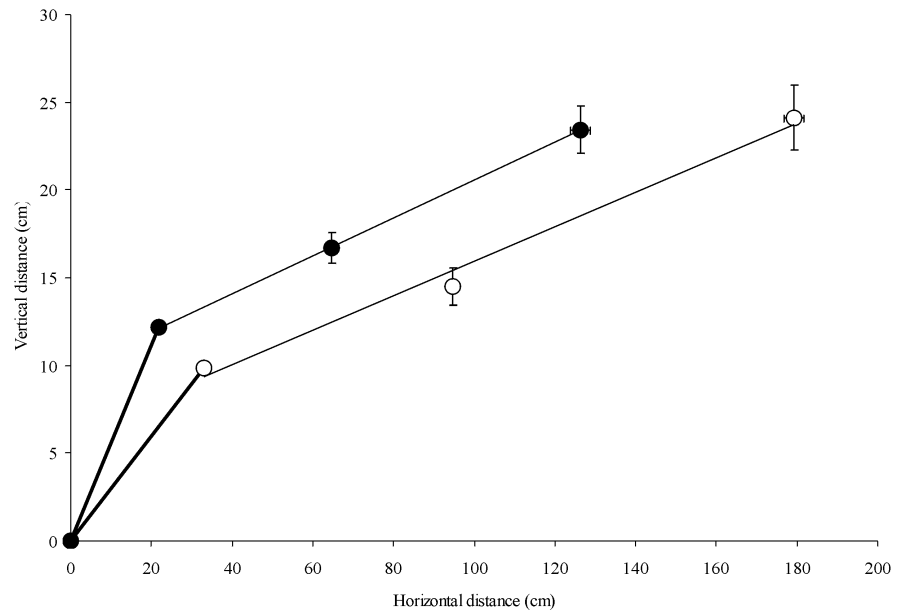
The video speed of 30 frames/s was too slow to determine instantaneous acceleration using numerical differential algorithms (Walker 1998; Nudds and Bryant 2000). Flights were therefore analyzed during three time intervals: between 1 and 5 frames, 6 and 10 frames, and 11 and 15 frames (Fig. 1). A repeated measures MANOVA examined interactions between intervals within species. There were significant interactions between factors (e.g. wing loading) and time interval, indicating that the effect of the factors differed between intervals. The analysis was repeated over the last two intervals and no interactions were found. One reason for this is that escape angle was much greater in the first interval than in the latter two intervals (Fig. 2). We therefore divided escape flights into 'early' (0–5 frames, or 0–0.167 s) and 'late' (6–15 frames, or 0.167–0.5 s) stages. Because speed and angle are not expected to be independent, we used ANCOVAs with angle and speed as covariates respectively, and wing loading, gender, year, and hold time as factors. Age was not a significant factor in any analysis and so was removed from the model. Outlier analysis was performed on the Studentized residuals of the ANCOVAs. Observations were considered outliers if Studentized residual values were outside the 0.025 alpha value for a t -distribution (least sandpiper, $t=1.995$; western sandpiper, $t=1.986$) (Myers 1990). Individuals with two or more observations of either early or late stage speed or angle that were considered as outliers, thus indicating they may not be part of the same population (due to illness, injury, or measurement error) were removed and the model refit.

Birds whose culmen length did not allow assignment of gender were removed from this analysis [least sandpiper $n=44$ (39%); western sandpiper $n=2$ (2%)]. Removal of these birds excludes the largest males and smallest females from the analysis. As this could bias the analysis of gender differences, we included all birds in 200 simulations of ANCOVAs with randomized gender assignment in analyses where gender was initially found to be a significant factor. Birds with culmen lengths just over the male threshold have a high probability of being male and the opposite for culmen lengths just below the female threshold. Thus, we assigned the probability of a bird being male based upon a normal distribution between the threshold culmen length values.

An additional series of ANCOVA analyses were conducted in an attempt to separate gender from body size effects on escape performance. We tested for the effect of culmen length (which is correlated with overall body size within a gender) on escape performance within each gender of each species separately. In these ANCOVAs we replaced gender with culmen length, but continued to include wing loading, speed/angle, year and hold time.

Non-significant interaction terms in the final ANCOVAs were removed with a backward stepwise procedure. Statistical analyses were made using JMPIN 3.2.1 (SAS Institute).

Fig. 2 Escape flights of least and western sandpipers (*Calidris mauri*) (mean \pm 95% confidence interval). Flights were analyzed in two stages (early = bold line). Unfilled circles represent least sandpipers ($n=112$), filled circles represent western sandpipers ($n=97$). Late stage line is the best fit for linear regression. Note the axes are not isometric and some error bars are obscured by data points



Wing shape

We used Lockwood et al.'s (1998) method of size-constrained components analysis to calculate wing shape. This method, related to principal components analysis, constrains the first component to size while the subsequent components describe shape. The lengths of the eight distal primary feathers are required for this method. The wing pictures used for wing area determination in the escape flight analysis were inappropriate for measuring primary lengths. Primary lengths were therefore measured (to 0.1 mm) from 26 least sandpiper and 26 western sandpiper museum specimens of migrating adults (equal number of each gender), as part of a larger interspecific study of wing shape. Values were log-transformed to meet the assumption of normality and standardized to equal unit variances.

Leg morphology

Maximum femur length, maximum tibiotarsus length, and maximum tarsometatarsus length were measured (to 0.1 mm) on seven least sandpiper and seven western sandpiper museum specimens as part of a larger interspecific study of leg morphology. We use size-constrained components analysis of leg morphology as per Swaddle and Lockwood (1998).

Results

Escape flights

We videotaped the escape flights of 314 sandpipers in 1997 and 1998. Twenty-seven flights could not be analyzed either because of video malfunction or unclear wing area pictures. Forty birds were removed from analysis because they flew in either a curved path relative to the board or flew to the ground and then took off again, and 31 more were removed because they flew downwards at some point in their flight. We found no effect of species, gender, or wing loading when comparing the birds removed from and those remaining in the analysis. Two least sandpipers and five western sandpipers were

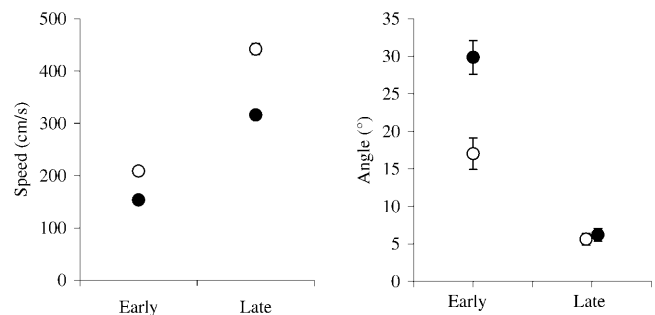


Fig. 3 Least sandpipers (unfilled circles, $n=112$) are faster than western sandpipers (filled circles, $n=97$) in both early and late stages of escape, but western sandpipers fly at a greater angle in the early stage of escape (mean \pm 95% confidence intervals). Note, some error bars are obscured by data points

removed because they were outliers, leaving a sample of 112 least sandpiper and 97 western sandpiper flights. For ANCOVA analyses, final sample sizes are 68 least sandpiper and 95 western sandpiper flights after removal of birds whose gender could not be determined.

Figure 2 compares escape flight profiles of the species. Least sandpipers were 38% faster than western sandpipers in the early stage ($t=11.98$, $P<0.0001$) and 40% faster in the late stage of escape ($t=15.96$, $P<0.0001$) (Fig. 3). During the early stage, western sandpipers escaped at greater angles than least sandpipers ($t=8.17$, $P<0.0001$), but there was no difference in angle in the late stage of escape ($t=1.05$, $P=0.30$) (Fig. 3).

The negative effect of migratory fuel on escape performance was apparent as wing loading was consistently the most important factor affecting escape flight speed within species (Table 1). All interaction terms were non-significant ($P>0.05$). Wing loading negatively affected early and late stage escape speed of both species. For example there was a decrease of 20% in late stage escape

Fig. 4 Late stage escape speed of least and western sandpipers is negatively affected by increased wing loading. Speed for each species is a residual (plus each species least square mean, to aid in comparison) of whole ANCOVA model with wing loading excluded

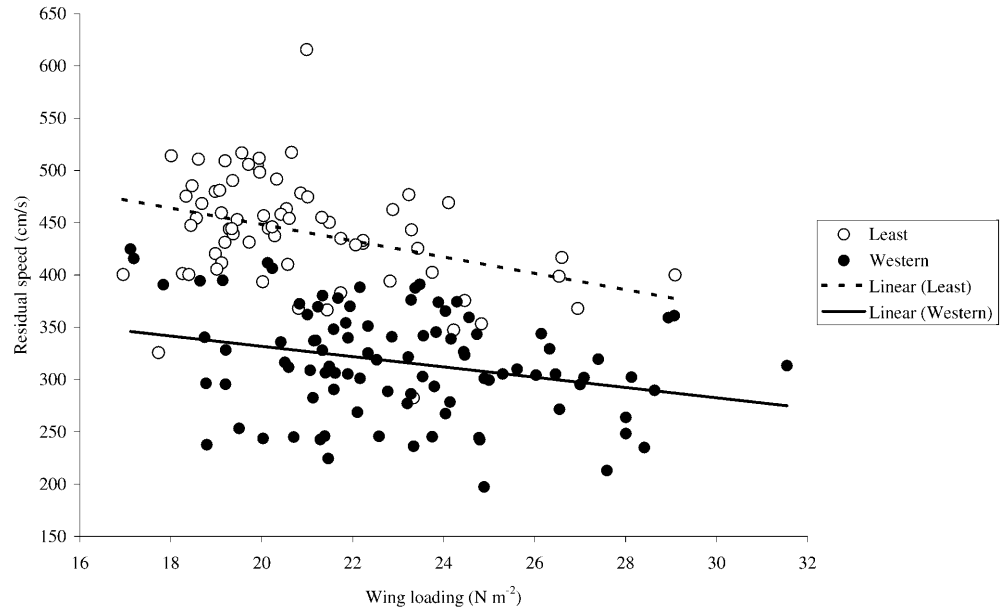


Table 1 Increased wing loading consistently decreases escape speed in least sandpipers ($n=68$) and western sandpipers ($n=95$), but the effects of gender, angle (covariate), year and hold time are

less consistent. Factors in bold significantly affected speed. – indicates a negative effect on escape speed when factor is increased

Factor	<i>df</i>	Speed						
		Early			Late			Direction
		<i>F</i> ratio	<i>P</i> value	Direction	<i>F</i> ratio	<i>P</i> value	Direction	
Least	Wing loading	1	7.75	0.0071	–	10.83	0.0016	–
	Gender	1	17.15	0.0001	f>m	3.52	0.0655	
	Angle	1	8.24	0.0056	–	15.19	0.0002	–
	Year	1	8.18	0.0058	97>98	3.33	0.0729	
	Hold time	1	3.43	0.0686		6.31	0.0146	–
Western	Wing loading	1	8.13	0.0054	–	8.84	0.0038	–
	Gender	1	0.87	0.3554		0.99	0.3219	
	Angle	1	4.00	0.0486	–	0.84	0.3630	
	Year	1	6.41	0.0131	97>98	0.40	0.5304	
	Hold time	1	3.33	0.0715		5.84	0.0177	–

speed of both least and western sandpipers over the range of wing loading observed (Fig. 4). Late stage escape angle was also affected in both species.

Females of both species showed greater flight performance than males in some aspects of escape (Tables 1, 2). Females flew at larger angles than males during the late stage of escape in both species [least square means: least sandpiper: female=6.0° ($n=43$), male=3.8° ($n=25$); western sandpiper: female=8.1° ($n=42$), male=5.7° ($n=53$)], and least sandpiper females were faster than males in the early stage of escape (least square means: female=223.0 cm/s, male=187.4 cm/s). Figure 5 compares the escape profiles of male and female least sandpipers.

Random assignment of gender to unassigned birds affected the least sandpiper analysis, but not the western sandpiper analysis. Gender differences remained significant for both least sandpiper early stage speed (median F

value from simulation=14.96, $P=0.0002$) and late stage angle (median F value from simulation=4.84, $P=0.0299$).

We were unable to detect a consistent effect of body size on escape performance within each gender (Table 3). Although body size (represented by culmen length) had a significant effect in 2 of 16 analyses, the direction of effect was different in each case. Overall, for the 6 analyses where P values were less than 0.15, culmen length had a negative effect on escape performance twice and a positive effect 4 times.

There was a trade-off between the covariates, speed and angle, in least sandpipers and the early stage of escape in western sandpipers (Tables 1, 2). The remaining factors had a lower overall effect on escape. Longer times between capture and release had a negative effect on late stage speed in both least and western sandpipers with 10% and 13% reductions over the range of hold

Fig. 5 Female least sandpipers (filled circles) escape with greater early stage speed and late stage angle than males (unfilled circles) (mean \pm 95% confidence intervals). *Bold line* represents early stage of escape. *Late stage line* is the best fit for linear regression. Note the axes are not isometric

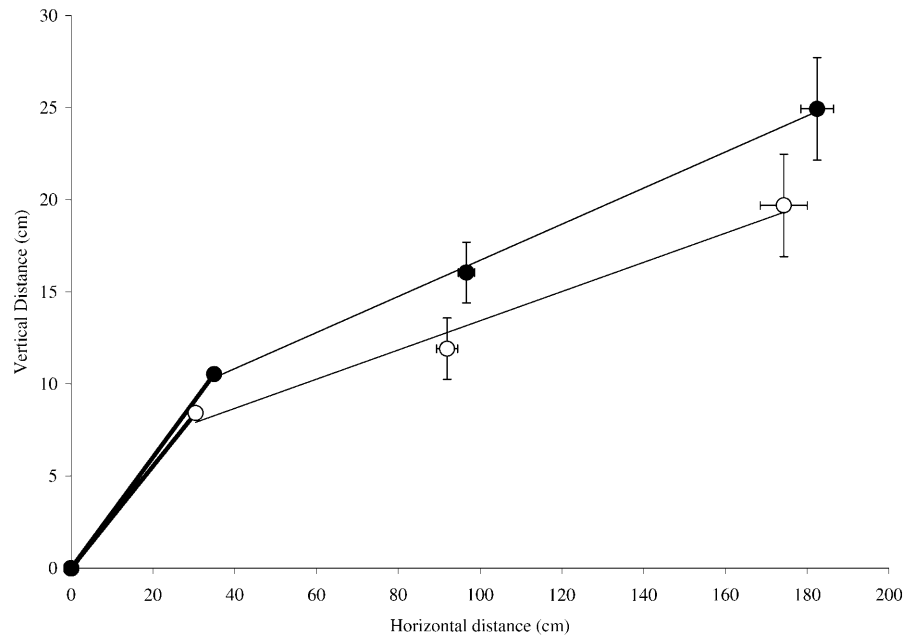


Table 2 Female late stage escape angle is greater than males, in least sandpipers ($n=68$) and western sandpipers ($n=95$), but the effects of wing loading, speed (covariate), year and hold time

effects are less consistent. Factors in bold significantly affected angle. – indicates a negative effect on escape angle when factor is increased

Factor		df	Angle					
			Early			Late		
			F ratio	P value	Direction	F ratio	P value	Direction
Least	Wing loading	1	2.08	0.1540		12.92	0.0006	–
	Gender	1	0.83	0.3649		5.55	0.0216	f>m
	Angle	1	8.24	0.0056	–	15.19	0.0002	–
	Year	1	0.19	0.6682		0.78	0.3809	
	Hold time	1	2.74	0.1026		0.05	0.8287	
Western	Wing loading	1	0.36	0.5475		5.02	0.0276	–
	Gender	1	1.67	0.1990		10.11	0.0020	f>m
	Angle	1	4.00	0.0486	–	0.84	0.3630	
	Year	1	2.47	0.1192		10.10	0.0020	97>98
	Hold time	1	3.58	0.0619		0.02	0.8866	

Table 3 Culmen length significantly effects 2 of 16 escape performance variables when the genders are analyzed separately, but in a different direction in the two cases. Values are *P* values for each ANCOVA. + indicates a positive effect of culmen on the escape variable, – indicates a negative effect. ANCOVAs included wing loading, speed/angle, year, and hold time

			Speed		Angle	
			Early	Late	Early	Late
Least	Female	44	0.7048	0.7434	0.0706	0.5825
	Male	24	0.3111	0.7823	0.0308 (+)	0.1037
Western	Female	42	0.5597	0.4536	0.1027	0.1571
	Male	53	0.0226 (–)	0.2231	0.0846	0.7432

times, respectively. Individuals of both species were faster during early stage escape in 1997 than in 1998 (Table 1; least sandpiper: least square means: 1997=220.9 cm/s, 1998=189.5 cm/s; western sandpiper: 1997=166.4 cm/s, 1998=147.3 cm/s) and there was also a year difference in late stage escape angle in western sandpipers (Table 2; least square means: 1997=8.5°, 1998=5.3°).

Wing shape and leg morphology

The species differ in wing shape and relative leg bone length. The first wing shape component was size (C1), and we interpreted the subsequent two components as wing pointedness (C2) and wing convexity (C3) (Table 4). Higher values indicate more tapered wing tips and a

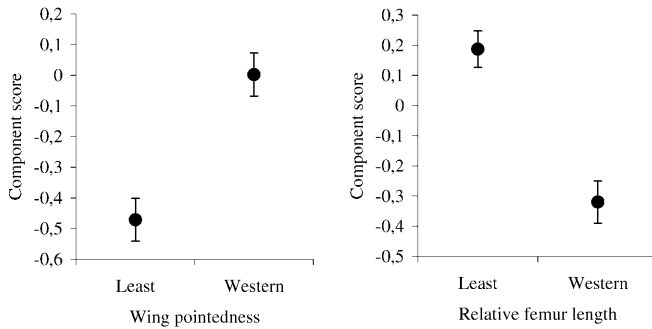


Fig. 6 Least sandpipers have less pointed wings and relatively longer femurs than western sandpipers, both of which may contribute to greater escape performance in least sandpipers (mean \pm 95% confidence intervals)

Table 4 Size-constrained components analysis of wing shape based upon primary feather length (P1-P8 refers to primaries 1 to 8, starting at the distal primary). C1 is constrained to representing size, C2 is interpreted as wing pointedness and C3 as wing convexity

Variable	Factor loading		
	C1	C2	C3
P1	0.337	0.465	-0.173
P2	0.343	0.400	-0.152
P3	0.352	0.238	-0.157
P4	0.353	0.139	0.007
P5	0.351	0.007	0.266
P6	0.355	-0.185	0.499
P7	0.361	-0.364	0.396
P8	0.375	-0.618	-0.667
% total variance explained	98.1	1.3	0.3
% shape variance explained		72.7	13.6

rounder trailing edge of the wing, respectively. The species did not differ in wing convexity ($t=1.81$, $P=0.08$), but least sandpipers ($n=26$) had significantly less pointed wingtips than western sandpipers ($n=26$) ($t=10.09$, $P<0.0001$) (Fig. 6). Thus, western sandpiper primary feathers are relatively shorter than least sandpiper feathers further they are from the distal edge of the wing. For instance, the second most distal primary feather was 0.4% shorter than the most distal primary in least sandpipers, but was 0.8% shorter in western sandpipers and the third most distal primary was 3.8% shorter than the second in least sandpipers, but was 5.9% shorter in western sandpipers.

We interpreted the first leg shape components as size (C1), and the next two as relatively long femora (C2) and relatively short tibia (C3) (Table 5). Least sandpipers ($n=7$) also had relatively longer femurs than western sandpipers ($n=7$) ($t=11.23$, $P<0.0001$) (Fig. 6), but they did not differ in relative tibia length ($t=-0.96$, $P=0.35$).

No differences were detected in wing shape between genders in either species (least sandpiper: pointedness – $t=0.41$, $P=0.68$; concavity – $t=1.24$, $P=0.23$; western sandpiper: pointedness – $t=0.36$, $P=0.72$; concavity – $t=1.09$, $P=0.29$). Sample sizes were too small to perform meaningful comparisons of leg morphology between genders.

Table 5 Size-constrained components analysis of hind limb morphology based upon the length of three leg bones. C1 is constrained to representing size, C2 is interpreted as relatively long femur and C3 as relatively short tibia

Variable	Factor loading		
	C1	C2	C3
Femur	0.533	0.822	0.199
Tibiotarsus	0.599	-0.201	-0.775
Metatarsus	0.597	-0.532	0.599
% total variance explained	97.6	2.2	0.3
% shape variance explained		89.3	10.7

Discussion

The data show that, as predicted by flight dynamic theory, escape speed slowed with increasing wing loading in both least sandpiper and western sandpiper. In addition, the data show that least sandpipers were significantly faster than western sandpipers, and had less pointed wingtips and relatively longer femurs. The species did not differ in wing convexity or tibia length. Finally, the data indicate the females exhibited significantly greater escape performance in some attributes (all differences were in the same direction), but there were no measurable differences in wing shape between genders in either species.

Species differences

Interspecific flight dynamic theory predicts that smaller birds should have greater surplus power output available for take-off than larger birds (Pennycuik 1972; Tobalske and Dial 2000). Least sandpipers (lean mass ~20 g, Cooper 1994) are slightly smaller than western sandpipers (lean mass ~22 g, Wilson 1994), but this small difference in size is unlikely to account for the large difference in escape speed between the species.

Ultimately, four major selective pressures affect flight ability and thus escape speed: foraging technique, sexual flight displays, migration, and predation risk (Marchetti et al. 1995). van der Veen and Lindström (2000) found a difference in escape speed and angle between two finch species, which they attributed to differences in escape tactics. Yellowhammers (*Emberiza citrinella*), which use an aerial flying escape, flew faster and at steeper angles, while the cover seeking greenfinches (*Carduelis chloris*) flew slower and at lower angles.

In this case, least and western sandpipers both use the same aerial escape tactic, but least sandpipers are 40% faster. Both species are ground foragers and have comparable sexual flight displays (Cooper 1994; Wilson 1994), leaving predation risk or migration as potential explanations for the difference in escape speed between species.

Predation risk could differentially affect these species if, for example, risk is higher in the foraging habitats of least sandpipers during migration. Least sandpipers for-

age in vegetated habitats such as salt marshes more often than western sandpipers (Cramp 1983; Cooper 1994; Wilson 1994). These sites could be more dangerous because the visual obstruction of vegetation allows predators to approach more closely without detection, or because group size is typically smaller (personal observation) which reduces risk dilution and group vigilance. If this is so, least sandpipers may have evolved greater escape ability over evolutionary time because they typically face greater danger than western sandpipers. This hypothesis remains unexplored.

Differences in migration strategy could also affect flight ability if one of the species is subject to greater selective pressure for aerodynamic characteristics that aid migration but hinder escape flights. For instance, longer migratory hops require greater fuel reserves, increasing the bird's mass and decreasing efficiency during the flight (Klaassen 1996). Pointed wingtips maximize the lift to drag ratio during long distance flight and are favored for migration (Rayner 1993). If western sandpipers take longer migratory hops than least sandpipers, and thus are under greater selection for pointed wings, the more pointed wing shape of western sandpipers is a result of a compromise of escape ability in exchange for efficient migration. Rounder wing tips, which aid rapid take-off from the ground (Rayner 1993; Swaddle and Lockwood 1998), are correlated with faster escape speed between least and western sandpipers (this study), between yellowhammers and greenfinches (van der Veen and Lindström 2000), and with lower relative mortality in a large selection of European passerines (Swaddle and Lockwood 1998).

Another proximate mechanism for the difference in escape flights between species is relative leg bone length. Relatively long femora are thought to increase the acceleration phase of take-off jumps (Swaddle and Lockwood 1998). Least sandpipers have relatively longer femora and are faster in the early stage of flight, where jumping would have the greatest effect, than western sandpipers. However, van der Veen and Lindström (2000) found an opposite correlation with escape speed between yellowhammers and greenfinches, and Swaddle and Lockwood (1998) found birds with long femora had a relatively greater mortality risk index. Longer femora could inhibit jumping and thus vertical distance gained in the early stage of flight, which could explain both yellowhammers and western sandpipers taking off at steeper angles than the species they were compared with. The two species compared here have more similar life histories and escape tactics than those studied by van der Veen and Lindström (2000), but the influence of relative leg bone length on take-off is complex and more direct empirical results are needed.

Wing loading

Previous studies on migrating birds have found a negative effect of fat load or wing loading on escape speed (black-

caps, Kullberg et al. 1996; sedge warblers, Kullberg et al. 2000) and angle (blackcaps, Kullberg et al. 1996; European robins, Lind et al. 1999). This study is the first to document this effect in shorebirds, a highly migratory family of birds that typically put on large amounts of fat during migration and rely on fast flight from the ground to evade predators. Escape speed in both western and least sandpipers was negatively correlated with wing loading at both early and late stages of escape. This increases the risk of predation of a bird with high wing loading because of an increase in the time it would take to reach cover or the refuge of a flying flock (Bednekoff 1996). Shorebirds can add pectoral muscle mass (muscle hypertrophy) while fattening for migration (Lindström et al. 2000), but any extra flight power from this muscle did not compensate completely for the increased wing loading in this study.

Wing loading is also correlated with late stage escape angle of both least sandpipers and western sandpipers, but not early stage escape angle. We interpret the effect of wing loading on early stage speed but not angle as follows: gaining height early in escape is critical and thus conserved at the expense of speed. This interpretation is supported by the steep early angle of western sandpipers, possibly a strategy to gain the same height as least sandpipers while being unable to reach the same speeds. Interestingly, studies on passerine birds have found the opposite relationship, with speed being conserved at the expense of angle (Witter et al. 1994; Lind et al. 1999).

Gender differences

No previous study has investigated the difference in escape performance between genders of birds. Females of both species exhibited greater escape performance in certain parameters, suggesting greater escape ability. Least sandpiper females were faster than males in the early stage of escape, and the magnitude of this difference was maintained into the late stage although the difference was no longer significant. In the late stage of escape, both least sandpiper and western sandpiper females have greater escape angles than males.

These gender differences could be due to greater evolutionary investment in escape ability by females. Research on other taxa, such as guppies, shows females invest more time in anti-predator behavior, which is consistent with females being at greater risk (Magurran and Nowak 1991). Foraging patterns can also expose genders differentially to predators (e.g. moths, Acharya 1995), but it is unknown whether the genders differ in foraging patterns in least sandpipers and western sandpipers.

We did not find any proximate causes for differences in escape performance between genders. In both species the female is larger than the male, and although this was partially taken into account in the wing loading factor of the analysis, it could be that within species larger birds have greater surplus power than smaller birds. However, this contradicts flight dynamic theory predictions

(Pennycuik 1972) and the limited empirical data available (Tobalske and Dial 2000). Our analyses of the effect of body size (using culmen length as a surrogate) on escape performance within gender found no consistent effect. Although these analyses had lower power due to smaller sample sizes, the inconsistency in the direction of the effect between analyses does not suggest culmen length is an important factor. A more detailed analysis of body size effects on escape performance within these species would require more structural size measurements, complemented with a principle components analysis to assign body size to individuals. Unfortunately, we do not have these data for our birds but this is a logical next step in this research. Whether it is due to body size or some other difference between the genders, females appear to have greater escape performance than males in these two species of sandpipers.

Although evidence is accumulating for decreases in escape ability with high fat loads or wing loading in migrating birds, there are no published tests of either behavioral adjustments or mortality costs in association with lower escape ability during migration. The behavioral costs of fat storage to wintering passerines has received quite a bit of attention (e.g. Lilliendahl 1998; Thomas 2000), but difficulties with following individual migrating birds may explain the dearth of studies in this area. More promising may be testing for differential mortality between migrating birds with high and low fat loads or wing loading, which could be conducted with carcass collection (e.g. Whitfield et al. 1999; Guglielmo and Burns 2001) to compare birds killed by predators with the surviving population.

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