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 relation of wing shape or leg bone length with gender. Ultimately, greater predation risk due to habitat use, or large 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; Hedenström 1992; Witter and Cuthill 1993; Bednekoff and Houston 1994; Bednekoff 1996). Smaller fat reserves may improve take-off acceleration and flight maneuverability, both of which increase the ability to escape or elude an attack (e.g. Rudebeck 1950; Page

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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, 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 load 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 similar 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), here we examine the effects of gender on escape performance in birds.

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} (Pennycuick 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 res18.7 245T   0 TD dIo ,

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

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,

Fig. 5 Female least sandpipers (*filled circles*) escape with greater early stage speed and late stage angle than males (*unfilled circles*) (mean ± 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
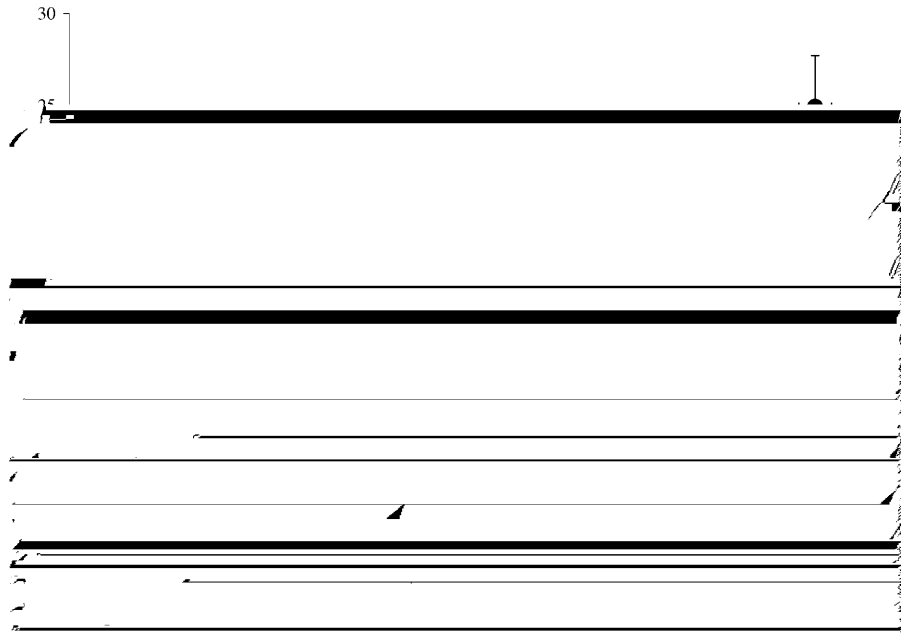
Table 2 Female late stage escape angle is greater than males, in least sandpipers (*n*=68) and western sandpipers (*n*=95), but the effects of wing loading, speed (covariate), year and hold time effects are less consistent. Factors in bold significantly affected angle. – indicates a negative effect on 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

	n	Speed		Angle	
		Early	Late	Early	Late

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

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.

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 (Pennycuick 1972; Tobalske and as 565 TD 0.h. Finallyler

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 warbers, 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 w (of wing w.3146 Tw [(yellowhamm

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(Pennycuick 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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