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ORIGINAL ARTICLE

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Differential predator escape performance contributes to a latitudinal sex ratio cline in a migratory shorebird

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Abstract Sexual segregation outside the mating season is common in vertebrates, and has been attributed to sexual differences in predator escape performance in ungulates and fish, but not in birds. Here, we tested the hypothesis that sex- and latitude-specific predator escape performance underlies the differential nonbreeding distribution of western sandpipers (*Calidris mauri*), a migratory shorebird. Females overwinter further south along the American Pacific coast, creating a latitudinal cline in sex ratio. Escape performance is reduced with increasing body mass, and birds generally carry less fat further south. Western sandpipers with poor escape performance were therefore predicted to prefer southern sites to reduce the risk of mortality posed by predators. Data from four nonbreeding latitudes showed that wing loading, used as an index of escape performance, was overall higher for females, and that it decreased with latitude in both sexes. Within latitudes, wing loading was lower at smaller, and presumably more dangerous, sites. Flight response to a predatory attack was longer in the south. Mortality risk offers a novel and candidate explanation for differential distribution patterns in western sandpipers and possibly other avian migrants.

Keywords Differential migration · Mortality risk · Predation danger · Sex ratio cline · Western sandpiper

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Introduction

Males and females have to associate during mating, but in many vertebrates the sexes segregate for the rest of the annual cycle. Such sexual segregation is common in e.g., large herbivorous mammals (Mysterud 2000; Bonenfant et al. 2004), and in many avian species males and females migrate to different latitudes or habitats during the nonbreeding season (so-called 'differential migrants'; Cristol et al. 1999). Hypotheses to explain this phenomenon differ between taxa.

Ungulates typically show sexual segregation outside the rutting period. Three hypotheses are recognized as most likely (Bonenfant et al. 2004). (1) The 'forage selection' hypothesis states that due to body size dimorphism, males and females have differing nutritional requirements, forcing them to seek different habitats. (2) The 'predation risk' hypothesis assumes that females and offspring are more vulnerable to predators than are males, and therefore seek safer habitats, while (3) the 'activity budget' hypothesis states that sex-specific activity patterns lead to segregation. Bonenfant et al. (2004) find support for the latter two hypotheses.

Sexual segregation is also common in many fish species. For example, female guppies (*Poecilia reticulata*) are more vulnerable to predatory fish than males, but mitigate this danger by seeking safer places (Seghers 1973). Females also shoal more readily in response to predator stimuli, are more vigilant, and take fewer risks than males. The outcome of these interacting factors is that female mortality attributable to predators is lower than that of males (Magurran 1999). In the three-spined stickleback (*Gasterosteus aculeatus*), males and females differ in defensive morphology and hence in their vulnerability to different predators (Reimchen 1980; Reimchen and Nosil 2004). Each frequents habitats where their defences function most effectively.

Different hypotheses have been proposed for avian differential migrants (Berthold 1996). (1) According to the 'dominance' hypothesis, geographical segregation arises when individuals of the dominant sex are able to monopolise better nonbreeding areas (Gauthreaux 1978). (2) Another hypothesis suggests that individuals of the larger sex are better able to survive periods of fasting, allowing them to winter in colder and less predictable climates at higher latitudes (‘body size’ hypothesis, Ketterson and Nolan 1976). (3) Finally, the ‘arrival time’ hypothesis states that individuals benefiting more from earlier arrival on the breeding grounds will minimize migration distance (Ketterson and Nolan 1976; Myers 1981). Empirical evidence supporting these hypotheses remains equivocal (Cristol et al. 1999).

Though established as an important factor among ungulates and fish, predation risk does not figure in any of the three hypotheses raised to explain sexual segregation in avian migrants. We are aware of only a single avian study that suggests a link between sexual size dimorphism, predation danger, and segregation of males and females during the nonbreeding season. Erritzoe and Fuller (1999) recorded sex-ratio biases on a local scale among nonbreeding long-eared owls (*Asio otus*) in northern Europe. They hypothesized that females, due to their larger body size, are more vulnerable to predation by eagle owls (*Bubo bubo*) and goshawks (*Accipiter gentilis*), and therefore migrated to regions where predators occur at lower densities, resulting in local sex-biases.

Our goal in this paper is to develop and test predictions of the predation risk hypothesis as an explanation for the nonbreeding segregation of the sexes in a differential avian migrant, the western sandpiper (*Calidris mauri*). These birds breed in western Alaska and eastern Siberia, and spend the nonbreeding season over extensive stretches of the Pacific, Atlantic, and Caribbean coasts of the Americas (Wilson 1994). The species shows sexual segregation during the nonbreeding season. Sites at the northern end of the nonbreeding range in California and northern Mexico are occupied by 70–80% males, while the most-distant sites such as Ecuador and Columbia (both >9,000 km Great Circle distance from breeding areas) are comprised of 70–80% females (Nebel et al. 2002).

Hypothesis and predictions

‘Predation risk’ terminology and hypothesis statement

The predation risk hypothesis as developed for ungulates states that .... “anti-predator behavior shapes sexual segregation because females .... are more vulnerable to predation than ... males. Predictions are that females should choose safe sites, even at the expense of forage quality (Bonenfant et al. 2004, p. 883)”. The key ingredients of the hypothesis are: (a) that one sex is more vulnerable to predators; and (b) that some sites are safer than others; but (c) usage of these sites has a cost, so that (d) these sites are used by members of the more vulnerable sex. Due to their smaller body size, females and their dependent offspring are more vulnerable to predation than males, and lower forage quality is identified as the cost of using safer sites. Ungulates can gain safety from wolves and bears, their main predators, by either choosing sites with vegetation providing cover, or sites that facilitate quick escapes.

Vulnerability

In the context of predation risk for avian species, we define vulnerability as an individual’s ability to escape an attacking predator (see Lank and Ydenberg 2003). ‘Escape performance’ is reduced by extra body mass, as an increase in wing loading (mass/wing area) decreases take-off speed and manoeuvrability, traits crucial for escaping attacks by aerial predators such as merlins (*Falco columbarius*) and peregrines (*Falco peregrinus*) (Witter et al. 1994; Lind et al. 1999; Kullberg et al. 2000). A negative relationship between wing loading and escape performance has been demonstrated in western sandpipers (Burns and Ydenberg 2002); and we use wing loading as our measure of vulnerability.

Sites at higher latitudes have higher probabilities of cold spells than further south (Suter and van Eerden 1992; Lovvorn 1994; Tulp et al. 2002), and generally, birds at northern nonbreeding sites carry more fat than southern conspecifics (Ketterson and Nolan 1976; Nolan and Ketterson 1983; Davidson 1984). This is widely interpreted as a survival hedge against environmental unpredictability, rather than a response to lower ambient temperatures per se. Wing loading thus reflects a balance between reserves and vulnerability, with larger reserves decreasing the capacity to escape predatory attacks, but increasing the ability to survive threats such as inclement or cold weather. According to the predation risk hypothesis, individuals most vulnerable to predation undertake the longer migrations to southern nonbreeding sites in order to benefit from the lower wing loading at those sites. To test this prediction we used two measures to assess the vulnerability of individuals.

First, we measured the responsiveness of western sandpipers to raptor attacks. McGowan et al. (2002) argue that measures such as the proportion of a shorebird flock that flies and the distance flown in response to a disturbance reflect a balance between predation and starvation risks. Poorer escapers should be at greater risk of mortality, and hence must rely more on tactics such as long escape flights. (We discuss possible confounds below.)

Site danger

Our second method to assess escape ability relies on comparisons between foraging sites within latitudes. Sites vary in the danger (or ‘safety’) posed due to inherent characteristics of the site itself. For shorebirds, small sites are more dangerous than large sites, because the cover offered by vegetation and other visual obstructions can be used to advantage by aerial predators, and important predators such as falcons are more effective when stealth and surprise can be employed (Townshend 1984; Lissimore et al. 1999; Ydenberg et al. 2002; Whitfield 2003; Ydenberg et al. 2004). Dekker and Ydenberg (2004) offer direct evidence to support this assumption.

If individuals at southern latitudes are indeed those with poorest escape performance, we can predict that they should be less prone to occupy small sites. Thus, the reduction in wing loading necessary to make use of a small site worthwhile should be greater in the south than in the north. We compared wing loading of western sandpipers at paired small and large sites at each latitude.

Specific predictions

Applied to nonbreeding western sandpipers, the predation risk hypothesis for sexual segregation predicts that the sex with higher vulnerability will make greater use of locations where escape performance is less compromised by the requirement to carry reserves. The poorer escape ability of birds at these latitudes ought to be evident in their willingness to use small sites, and in the intensity of antipredator behavior employed, such as the duration of flights following raptor attacks.

This hypothesis for the southerly nonbreeding distribution of female western sandpipers makes the following predictions: (1) Nonbreeding females should have higher wing loading than nonbreeding males. (2) Wing loading should be higher at northern nonbreeding locations. (3) Within latitudes, wing loading should be lower on small sites. (4) The average difference in wing loading between small and large sites necessary to make use of a small site worthwhile should be greater in the south, as small sites place a greater premium on escape ability. Consequently, a site-size by latitude interaction should be observed. (5) Flight response to raptor attacks should be longer in south.

Finally, the hypothesis also requires that members of the more vulnerable sex frequent the sites that are more costly to use or get to. This requirement is met, as there is a strong positive relation between the proportion of females at a nonbreeding site and the distance from the centre of the (small) breeding range (Nebel et al. 2002).

Materials and methods

Study sites

Details of the study sites are provided in Table 1. Bodega Bay, Tomales Bay, and San Francisco Bay are pooled in the analyses due to the small sample size at each site. They are referred to as ‘California’ sites. Note that Bahía Santa María contains both large and small feeding areas and is referred to as ‘Mexico’. Sites larger than 500 km^2 were classified as ‘large’, and less extensive sites as ‘small’. Data reported here are restricted to the period November—early March, thus excluding recently-arrived southward migrants, and individuals preparing for northward migration.

Field measures

Birds were caught with mistnets, weighed and measured according to standard procedures, aged according to plumage characteristics (Prater et al. 1977), and sex-assigned based on the length of exposed culmen (Page and Fearis 1971). A digital picture was taken of the wing held in a standardized manner on a custom board (Burns and Ydenberg 2002). Wing area was calculated using Scion Image (www.scioncorp.com). Wing loading was calculated by dividing body mass by the area of a single wing.

Small shorebirds flock in response to raptor hunts, and show rapid, twisting, and highly synchronised flight manoeuvres (Bertochi et al. 1984; Buchanan et al. 1988; Buchanan 1996; Dekker 1998). Western sandpipers display a similar response, and in order to assess flight response to a predatory attack, ‘time in air/attack’ was measured each time such a response was observed, including cases when the predator itself causing the disturbance had not been sighted. This measure of flight response was obtained for each observation period. Likewise, the number of attacks in an observation period was divided by the duration of the observation period. This measure was then expressed as the number of attacks per hour. Observations were made by a single observer who focussed exclusively on observing raptor attacks and the resulting flight responses. Whether attacks are caused by single or multiple predators is not thought to affect the level of disturbance experienced by a flock of sandpipers, and each attack was treated as an independent event.

Statistical analysis

Data were analyzed using General Linear Models in the statistical package Systat version 11. We tested for

Table 1 Location and size of the study sites, and type and date of data collection

Site	Latitude, longitude	Size	Date of surveys	Type of data[a]
Tomales Bay, California, U.S.A	39.2°N, 123.0°W	‘small’	Nov.–Dec. 2000	WL, FR
Bodega Bay, California, U.S.A	38.2°N, 123.0°W	‘small’	Nov.–Dec. 2000	WL, FR
San Francisco Bay, California, U.S.A	37.5°N, 122.3°W	‘large’	Nov.–Dec. 2000, Feb. 2003	WL
Bull Island, South Carolina, U.S.A	32.8°N, 79.6°W	‘small’	Dec. 2001	FR
Bahía Santa María, Sinaloa, Mexico	24.0°N, 108.0°W	‘small’ & ‘large’	Jan.–Feb. 2000	WL, FR
Upper Bay of Panama, Republic of Panama	9.0°N, 79.2°W	‘large’	Jan.–Feb. 2002	WL, FR
Chitré, Herrera, Republic of Panama	8.0°N, 80.5°W	‘small’	Early Mar. 1998	WL, FR

[a] WL, wing loading; FR, flight response.

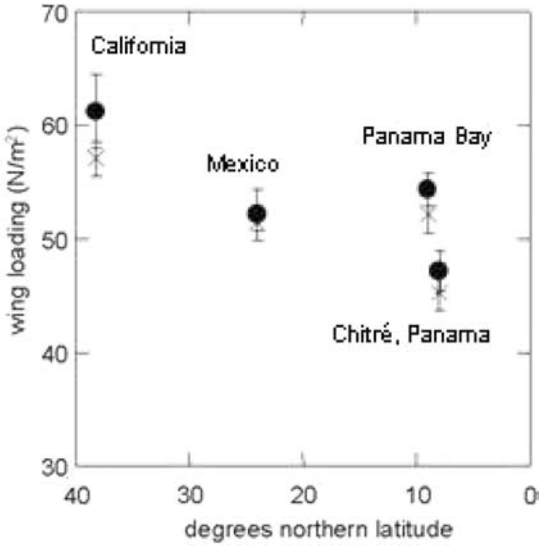

Fig. 1 Wing loading (mass/wing area ±95% CI) in Western Sandpipers was higher in females (●) than in males (*x*), and decreased from north to south. Numbers of females (*f*) and males (*m*) measured at each site were as follows: California: $f = 8$, $m = 40$; Mexico: $f = 19$, $m = 95$; Chitré, Panama: $f = 24$, $m = 21$; Panama Bay: $f = 31$, $m = 26$

a correlation between the dependant variable ('wing loading', 'flight response', and 'attacks/h') and latitude. Latitude was treated as a continuous ordinal variable, area size as categorial ('large' or 'small'). When analyzing the effect of latitude on wing loading, we accounted for the effect of sex, age, and site size. Interaction terms were considered significant at the $\alpha = 0.05$ level. We reported Type III sums of squares.

Results

A total of 276 western sandpipers were captured and measured at six locations within four sites distributed over the nonbreeding range. Age classes are pooled, as age had no significant effect on wing loading ($F_{1,271} = 1.79$, $p = 0.18$, $n = 273$, excluding three individuals of unknown age).

The first prediction was that females have higher wing loading than males. Results are displayed in Fig. 1, and show that at each latitude, females had higher wing loading than males (Table 2). The effect is significant, taking into account the effects of latitude, site size, and interactions.

Table 2 Wing loading changed significantly with latitude, sex, area size, and the area size × latitude interaction term[a]

Source	Sum-of-squares	*df*	*F*-ratio	*p*
Latitude	1936.11	1	111.33	**<0.001**
Sex	272.08	1	15.64	**<0.001**
Area size	881.49	1	50.69	**<0.001**
Area size × latitude	347.39	1	19.98	**<0.001**
Error	4504.37	259		

[a] Only individuals of known sex were included in the analysis.

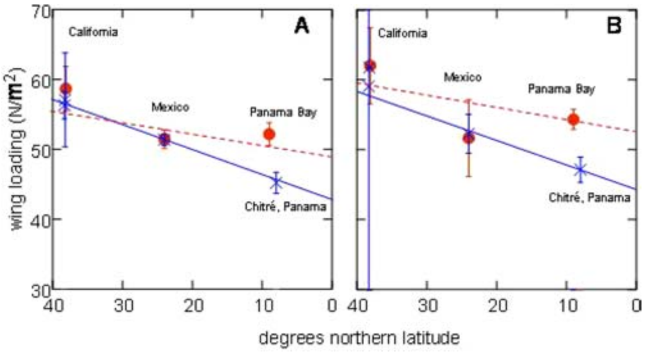

Fig. 2 Wing loading (±95% CI) of individuals caught at small site (*x* — solid line) declined steeply from north to south than in individuals caught at large sites (● — stippled line). This was observed in both males (**A**) and females (**B**). Linear regression lines are fitted through the graphs that allow visual comparison of the respective slopes

The figure shows that the second prediction is also upheld, as wing loading of both males and females diminished from north to south. This effect is also significant, taking into account the effects of sex, site size, and interactions (Table 2).

Wing loading was higher at large than at small areas (Table 2), supporting the third prediction. Figure 2 displays results with respect to the fourth prediction, and as predicted, there was a significant area size × latitude interaction, such that the difference in wing loading between large and small sites is greater at low latitude. This interaction also becomes apparent by visually comparing the slopes of the regression line between wing loading and latitude, which is much steeper at small than at large sites in both males (Fig. 2A) and females (Fig. 2B).

Finally, we predicted that flight response should be greater at southern latitudes. Indeed, flight response to a predatory attack increased from north to south ($F_{1,81} = 34.16$, $p < 0.001$; Fig. 3). The most frequently observed raptor was peregrine, followed by merlin. In a few cases, flocks were also seen responding to northern harrier (*Circus cyaneus*), turkey vulture (*Cathartes aura*), osprey (*Pandion haliaetus*), crested caracara (*Polyborus plancus*), and black hawk-eagle (*Spizaetus tyrannus*). Number of attacks per hour did not change with latitude ($F_{1,107} = 0.03$, $p > 0.05$; Fig. 4). An observation period was typically 1 h long. Total observation time (pooled over all observation periods), number of observation periods, and of attacks by site are provided in the legend of Fig. 4.

Discussion

We have presented evidence to support the hypothesis that the differential nonbreeding distribution of western sandpipers arises, at least partly, because females are more vulnerable to predation than males and hence migrate to more southerly sites, where their poorer escape performance is less compromised. Our data show that at each nonbreeding site, females have higher wing loading than males, that the wing loading of all birds is higher at northern sites,

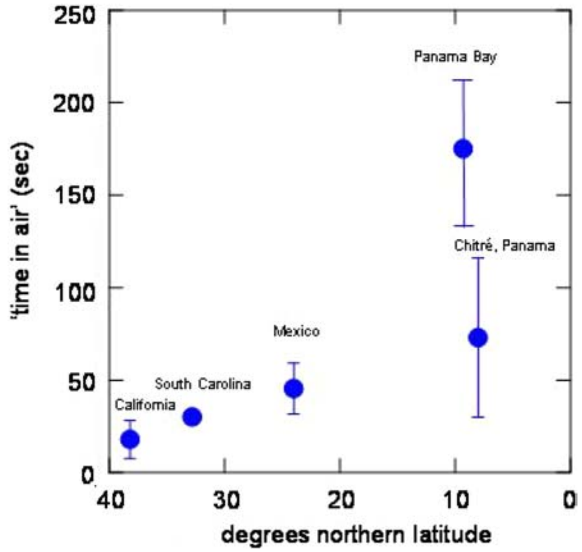

Fig. 3 Flight response to a predatory attack (expressed as 'time in air' ±95% CI) increased towards the south. Number of responses observed, total observation times (pooled over all observation periods), and number of observation periods at each site were as follows: California: $n = 9$, 13 h 24 min, $n = 22$; South Carolina: $n = 1$, 4 h 20 min, $n = 9$; Mexico: $n = 30$, 57 h 5 min, $n = 44$; Chitré, Panama: $n = 6$, 2 h 17 min; $n = 3$; Panama Bay: $n = 37$, 28 h 29 min, $n = 31$

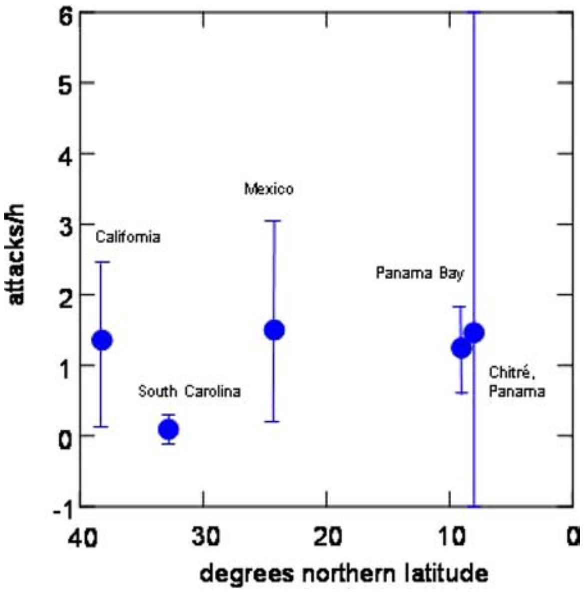

Fig. 4 Number of attacks per hour, as evidenced by observation of a predator, or by response shown by Western Sandpiper flock, did not change with latitude. Observation times are as in Fig. 3

and that individuals at small sites have lower wing loading than those at larger sites. Data collection took place in different years, which has the potential to confound our results. However, variation in wing loading within years at a given site was small compared to the differences we observed between sites (Fig. 1), providing further support for the expected effect of latitude-dependant environmental variability on wing loading. We also showed that a raptor attack evokes longer flight responses in the south, and that the large–small site wing loading difference is greater in the south. Together these findings support the predation risk hypothesis as a viable explanation for differential distribution patterns in western sandpipers.

Two assumptions of our hypothesis, however, require further scrutiny. We will first discuss the use of wing loading as an index of escape performance. Burns and Ydenberg (2002) showed that individual western sandpipers with higher wing loading had lower take-off performance at a migratory stop-over site, and other studies measuring take-off speeds of migrants have found comparable results (Witter et al. 1994; Lind et al. 1999; Kullberg et al. 2000). Yet, several studies on captive and nonbreeding birds have failed to detect this effect (Kullberg 1998; Kullberg et al. 1998; van der Veen and Linström 2000). The latter, however, report changes in body mass of only 7–8%, which may be too small to allow detection of an effect of body mass changes on escape performance. In contrast, average wing loading of western sandpipers increased by 20% between California and Chitré, Panama. Such an amount of extra reserves needed at northern sites is likely to compromise escape performance of an individual, though an explicit test is still needed.

The second assumption requiring scrutiny is that flight response reflects vulnerability. Ydenberg and Dill (1986) showed how the escape distance of an animal prey from an attacking predator can be viewed as a balance between costs (foregone opportunity) and benefits (increased survival). The resultant escape distance can vary between situations, or between individuals. McGowan et al. (2002) extend this logic, and argue that measures such as the proportion of a shorebird flock that flies and the distance flown in response to a disturbance reflect a balance between predation and starvation risks. Flight response to predatory attacks is known to vary with a number of factors, including the level of danger or disturbance (Ydenberg and Dill 1986; Lima and Dill 1990; Koolhaas et al. 1993), as well as environmental factors such as wind speed and air temperature that affect energetic requirements (McGowan et al. 2002). Escape flight characteristics could vary due to differences between locations, differences between individuals at those locations, or both.

We assumed that differences between latitudes in flight response of western sandpipers to raptor attacks arise because individuals at southern sites can depend less on escape performance to reduce danger, and so make greater investment in tactics such as long escape flights. But do any other factors change across latitudes? Data on the rate of predator-response flights indicate no change across latitudes (Fig. 4). Explaining the longer response flights of southern birds on the basis of environmental factors therefore requires that feeding is better there, or that requirements are lower. A latitudinal comparison in Palearctic migration systems suggests that tropical nonbreeding areas are poorer for feeding (Piersma et al. 2005), and while we suspect that this holds for Nearctic systems as well, we have no data on intake rates across latitudes. For the moment we can conclude that the pattern of longer escape flights at southern latitudes is consistent with the predation risk hypothesis, but we cannot exclude possible confounding factors.

Data provided here are consistent with the hypothesis that sex- and latitude-specific differences in escape performance contribute to the striking sex ratio cline in western sandpipers, which could potentially also explain similar sex ratio patterns in Dunlin (*Calidris alpina*) (Shepherd et al. 2001) and Least Sandpipers (*Calidris minutilla*) (Myers 1981; Nebel in press). However, other factors may contribute to these patterns as well. For example, resource partitioning is also known to contribute to the sex ratio cline in westerns sandpipers (Nebel 2005). Females have longer bills than males and use a probing foraging mode more, allowing them to feed on more deeply buried prey items. Prey burying depth is thought to increase with proximity to the equator, in response to higher ambient temperatures (Nebel and Thompson 2005). Individuals with longer bills would, therefore, be at an advantage at more southern sites. An increase in bill length within both males and females towards southern latitudes (O'Hara 2002; Nebel 2005) supports this hypothesis.

In the context of bird migration theory, predation has been shown to affect stop-over ecology of migrants (Lindström 1989; Dierschke 2003; Schmaljohann and Dierschke 2005), and small-scale site choice (Piersma et al. 1993; Whitfield 2003; Yasue et al. 2003; Ydenberg et al. 2004). Only recently has the importance of predation for the evolution for large-scale features such as the timing and routing of migration (Lank et al. 2003) begun to be recognized. A convincing demonstration of the predation risk hypothesis for differential nonbreeding distributions will require more challenging predictions in a variety of systems. This calls for conceptual advances to generate such predictions, and methodological advances to test them. For example, new techniques developed by Guglielmo and Burns (2001) and by Nebel et al. (2004) allow to determine the fat reserve and sex of avian carcasses. With a sample of carcasses (e.g., from raptor plucking posts), these techniques permit direct assessment of whether reduced escape performance of individuals with high wing loading results in higher mortality and whether a sex-bias exists in predator-induced mortality.

It remains to be empirically verified just how applicable the ideas developed here are to other groups of migrant birds. Nevertheless, we hold that a comprehensive understanding of migration will require much fuller exploration of the effects of predators to complement the extensive knowledge built-up over the past two decades about the role of energy management in shorebird migration.

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