

# Do sex and habitat differences in antipredator behavior of Western Sandpipers *Calidris mauri* reflect cumulative or compensatory processes?

Guillermo Fernández · David B. Lank

Received: 1 June 2009 / Revised: 9 December 2009 / Accepted: 9 February 2010 / Published online: 4 March 2010  
© Dt. Ornithologen-Gesellschaft e.V. 2010

**Abstract** Individuals manage their risk of predation in different ways in different situations. We studied the use of anti-predator behavior by Western Sandpipers (*Calidris mauri*) at Bahía Santa María, northwestern Mexico, foraging in three habitats that differed in presumed predation danger. Brackish flats are completely open, making them theoretically less dangerous for feeding sandpipers than mangroves and cattail marshes, which have closer visual horizons. Western Sandpipers are sexually dimorphic, with females about 15% longer-billed and 10% heavier than males. We previously showed that male and female sandpipers differed in their habitat choice and relative body mass in ways consistent with differential responses to predation danger (Fernández and Lank in *Condor* 108:547–557, 2006). Contrary to expectations, however, females were overrepresented in more dangerous habitats. Here, we examine differential usage across habitats and between the sexes of three anti-predator tactics—flock size, density within flocks, and vigilance rate—that may be used cumulatively to reinforce safety, or as trade-offs that compensate for levels of usage of each. We hypothesized, and found, that ordered differences occur among habitats, and that controlling for other factors, females were more

cautious than males. For the most part, the use of these three tactics appeared to be cumulative, rather than compensatory. However, with respect to habitat use, birds appeared to compensate for the higher probability of mortality intrinsic to the use of higher-danger habitats by increasing the use of vigilance, foraging in tighter flocks, and maintaining lighter body weights (females only). Thus, both cumulative and compensatory processes operate among anti-predator tactics to determine the net level of safety and trade-off against other factors.

**Keywords** Habitat quality · Local distribution · Predation danger · Sexual dimorphism · Shorebirds

## Introduction

Antipredator behaviors can have substantial effects on patterns of habitat use and population dynamics (Cresswell 1994a; Ydenberg et al. 2002, 2004; Whitfield 2003a; Taylor et al. 2007). General tactics for responding to predation danger include: choosing safer habitat, adopting a particular level of vigilance by adjusting the vigilance rate and (or) group size or density, and changes in body condition (Lima and Dill 1990; Lima 1998). Individuals that vary differ in their vulnerability to predation (“escape performance”, sensu Lank and Ydenberg 2003), e.g., as functions of sex, age, or size, may use different tactics to adjust their predation risk (Magurran and Nowak 1991; Burns and Ydenberg 2002; Childress and Lung 2003; Cresswell 2008). Different antipredator tactics may be used cumulatively to reinforce each other, or as trade-offs that compensate for each other (Lind and Cresswell 2006). A simple example of a trade-off is that individual vigilance rates typically decrease as flock sizes increase, implying

Communicated by F. Bairlein.

G. Fernández (✉)  
Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apartado Postal 811, C.P. 82040 Mazatlán, Sinaloa, Mexico  
e-mail: gfernandez@ola.icmyl.unam.mx

D. B. Lank  
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada

that a lower level of safety derived from individual vigilance is compensated for by some property of the flock. Whether this trade-off is worth making also depends on the effect of flock size, or nearest neighbor distance, has on foraging efficiency (e.g., Goss-Custard 1980). Antipredator behavior should be tailored by the individual to suit its specific needs and circumstance.

Shorebirds spend approximately 8–9 months on the nonbreeding grounds, where most annual mortality likely occurs (Piersma and Baker 2000; but see Sillett and Holmes 2002), and substantial fractions of local populations can be predated (Page and Whitacre 1975; Kus et al. 1984; Bijlsma 1990; Cresswell and Whitfield 1994). A large body of literature suggests that shorebirds are aware of predation danger during foraging and modify their behavior accordingly using a suite of antipredator tactics. The presence of raptors induces a short-term abandonment of territories and increases both the density within flocks and the ranging behavior of wintering shorebirds (Myers 1984; Whitfield 1988). Shorebirds rely on fast escape flights to evade predators (Page and Whitacre 1975), and initial escape performance of individuals is negatively correlated with wing loading (Burns and Ydenberg 2002). Shorebirds may thus decrease body mass to mitigate the danger posed by raptors (Piersma et al. 2003; Ydenberg et al. 2004, 2009; Fernández and Lank 2006).

Raptors hunt shorebirds primarily on the basis of their vulnerability rather than their abundance (Quinn and Cresswell 2004). Through habitat choice, shorebirds may trade-off predation danger and foraging opportunities in relation to their body condition (Hilton et al. 1999; Ydenberg et al. 2002; Yasué et al. 2003; Nebel and Ydenberg 2005; Pomeroy et al. 2006; Fernández and Lank 2006). For small shorebirds, feeding closer to visual cover for attacking avian predators entails a higher risk both of being attacked by an avian predator and of the attack being successful (Cresswell 1996; Whitfield 2003b; Dekker and Ydenberg 2004). Shorebirds thus treat sites close to vegetation cover with a greater degree of caution (Hilton et al. 1999; McGowan et al. 2002; Dekker and Ydenberg 2004; Fernández and Lank 2006; Beauchamp and Ruxton 2008).

In this study, we investigate the relative use of anti-predator behaviors of Western Sandpipers (*Calidris mauri*) wintering in a complex of coastal wetlands at Bahía Santa María (“Santa María”), located in northwestern Mexico. The Western Sandpiper, a mid- to long-distance migrant, is one of the commonest shorebird species in North America (Nebel et al. 2002). The main predators on sandpipers at Santa María were Peregrine Falcons (*Falco peregrinus*) and Merlins (*F. columbarius*) (Nebel et al. 2004). Sandpipers occasionally responded to encounters with Northern Harriers (*Circus cyaneus*).

The Western Sandpipers wintering in Santa María provided an opportunity to compare how sex and habitat differences affect antipredator tactics. Compared with other calidrids, the Western Sandpiper is highly sexually dimorphic; females are about 10% heavier and 15% longer-billed than males (Cartar 1984). Due to this morphological difference, females could be more vulnerable to predation because: (1) females have higher wing loading for a given body mass than males (Burns and Ydenberg 2002); (2) females have longer and more pointed wings than males (Fernández and Lank 2007), which impede rapid take-off from the ground relative to rounder wings (Swaddle and Lockwood 1998); and (3) females rely more on probing foraging behavior than males (Mathot and Elner 2004; Fernández and Lank 2008), which may decrease their ability relative to males to scan their environment while they forage (Barbosa 1995; Guillemain et al. 2001). During migration, Burns and Ydenberg (2002) found that females exhibited greater escape ability than males, which they interpreted as a compensation tactic for intrinsically greater vulnerability.

In a previous study (Fernández and Lank 2006), we unexpectedly found that females were over-represented in what appeared to be more dangerous habitat at Santa María. We recognized three habitats: brackish flats, mangroves, and cattail marshes, which differed in both Western Sandpiper and prey densities, and we inferred levels of predation risk based on average distances to vegetation. Brackish flats were the most open, cattail marshes were most enclosed, and mangrove habitat was intermediate with regard to distance to vegetation. The habitats had similar raptor encounter rates, and thus the differential distances to cover imply that, all else being equal, brackish flats are the safest and cattail marshes the most dangerous habitats for Western Sandpipers. Bird densities were highest in brackish flats, the richest and safest habitat; while in cattail marshes, which appeared to be the food poorest and most dangerous habitat, bird densities were lower. Patterns of wingloading changed throughout the season in ways suggesting that cattails were more dangerous habitats. These relationships suggest that brackish flats are higher quality habitat in terms of both food availability and safety, and should be favored over other habitats up to the point at which higher forager density causes sufficient interference to make the use of alternative habitats equally attractive (Fretwell and Lucas 1970). Females’ disproportionate use of cattail habitat was interpreted in this context.

In this study, we examine additional behavioral variables Western Sandpipers may use to adjust their probability of predation by avian predators: flock size, nearest-neighbor distances, and vigilance rates. We expected that females in cattail habitat would make more

use of these tactics, due to their greater vulnerability. Flock size in shorebirds (Cresswell 1994b; Barbosa 1997; Whitfield 2003b) and vigilance rate (Cresswell 1994b; Barbosa 1997; Pomeroy 2006; Sansom et al. 2008) increase as distance to vegetation cover decreases, presumably reflecting differences in predation danger. Individual vigilance decreases as a function of flock size (Cresswell 1994b; Barbosa 1997) and changes with foraging mode (Barbosa 1995). We therefore examined flock size and vigilance rate with respect to presumed differences in intrinsic vulnerability and habitat-specific levels of predation danger. We made the following predictions, which assume cumulative use of these tactics: (1) controlling for sex, wintering Western Sandpipers should form larger and/or tighter flocks, and have higher vigilance rates in more dangerous habitats, and (2) within habitats, females should form larger and/or tighter flocks, and exhibit higher vigilance rates, than males. Alternatively, some of these behavior patterns might trade-off and compensate for each other, rather than all covarying in the same direction. We tested these predictions by analyzing flock size, nearest neighbor distance, and vigilance behavior of Western Sandpipers using brackish flats, mangroves, and cattail marsh during the non-breeding season in Santa María.

## Methods

### Study area

This research was conducted at Bahía Santa María (25°02'N, 108°18'W), which includes 1,350 km<sup>2</sup> of a diverse wetland habitat mosaic, about 90 km northwest of Culiacán, Sinaloa, in northwestern Mexico. Fernández and Lank (2006) describe the three habitat types recognized in this study: brackish flats, mangrove–salt marsh flats, and cattail marshes, and the rationales for ranking them as safest, intermediate, and most dangerous with respect to avian predation (see above).

### Data collection

Fieldwork was carried out, from November to February of 1999–2000, and from December to February of 2000–2001 and 2001–2002. We trapped 1,818 Western Sandpipers during morning sessions (e.g., 0700–1100 hours) using mist nets accompanied by broadcasts of alarm calls, and 1,686 were individually color-banded. We measured body mass ( $\pm 0.5$  g) and bill length (exposed culmen,  $\pm 0.1$  mm), and assigned birds' sex following Page and Fearis (1971). Fifty-seven birds of unknown sex were excluded from analyses.

Vigilance behavior was recorded during individual focal observations (Altmann 1974) using a 15–60 $\times$  spotting scope. In each habitat, focal observations were carried out throughout the day (e.g., 0700–1500 hours). Behavioral data were dictated into a tape recorder, timed with a stopwatch, and later transcribed. We preferentially observed individually color-banded birds. If there were no banded birds in the area, focal birds were selected randomly by directing the spotting scope at a flock and selecting the individual in the center of the field of view. We continued randomly selecting individuals by moving the scope in a zigzag pattern to reduce the probability of resampling the same individual. To further reduce the probability of pseudoreplication, we sampled no more than five unbanded birds from the same flock. Unbanded birds were assigned a sex based on relative bill size. When this technique was used on banded birds, sex agreed with that based on measurements 90% of time ( $n = 234$  birds).

Discrete foraging groups were defined as flocks; all birds surrounding a focal individual were counted as a part of a flock and the nearest neighbor distance (m) was recorded for each focal bird. Although multi-species flocks occur in the study area, all data presented are for single species flocks. Birds were not considered part of the focal flock when their distance exceeded 3 m from the last individual counted in a particular direction. Scan rate (scans min<sup>-1</sup>) was used as a measure of vigilance behavior. A scan was defined as raising the head from the head-down foraging position such that the bill line was above the horizon.

### Statistical analysis

Habitat differences in the proportions of males were investigated with analysis of variance (ANOVA), weighted by the number of birds caught, controlling for annual variation. Proportions of males were arcsin-transformed prior to analysis. Since females are larger than males (Cartar 1984), body mass analyses were carried out separately by sex. Within each sex, habitat differences in body mass were investigated with ANOVA, controlling for age and seasonal and annual variation (Fernández and Lank 2006). Body mass and adjusted body mass (controlling for structural body size) were strongly positively correlated for both females ( $r^2 = 0.85$ ,  $F_{1,517} = 3,003.09$ ,  $P < 0.01$ ) and males ( $r^2 = 0.91$ ,  $F_{1,1242} = 13,729$ ,  $P < 0.01$ ), and we used the simpler index in our analyses.

A single observer (G.F.) made 776 focal observations with a mean observation time of 1.9 min (range 1–3). A total of 227 observations were of banded birds. Thirteen observations (four from banded birds) were removed from analysis because birds were not actively foraging during the focal observation. Age of bird was not included in

analyses because of small sample sizes; of 223 observations of banded birds, only 11 and 9% were made on immature females and immature males, respectively. Controlling for sex, habitat, and year, flock size and vigilance behaviors were not significantly different between banded and non-banded birds ( $P > 0.20$ ). To increase the power of our analysis, we pooled all observations between banded and non-banded birds. Sex and habitat differences in flock size were investigated with an ANOVA, controlling for seasonal and annual variation. The effects of sex and habitat on nearest neighbor distance and vigilance behavior, with flock size as covariate, were analyzed using an ANCOVA, controlling for seasonal and annual variation. Flock size, nearest neighbor distances, and vigilance rate were log-transformed prior to analysis to permit parametric analyses.

We considered statistical test results to be significant at  $P < 0.05$ , except for interaction terms, which we considered significant at  $P < 0.10$  since significance test for interaction terms have lower power than those for main effects (Littell et al. 1991). If interaction terms were not significant, models were reduced to their most parsimonious form using Type III SS, and we report least-squares means taking other factors and seasonal and annual variation into account. We made pair-wise post-hoc comparisons using the Tukey–Kramer test. Least-square means  $\pm$  SE are presented unless otherwise stated. All statistical tests were performed using SAS<sup>®</sup> 8.2 (SAS Institute 2001).

## Results

### Sex composition and body mass among habitats

Male Western Sandpipers predominated at Bahía Santa María, with a sex ratio of 0.72 among all birds captured. As expected from previous analyses, males were overrepresented in brackish flats, and sex ratios were most even in cattail marshes ( $F_{2,109} = 11.27$ ,  $P < 0.0001$ ) (Table 1), showing that females were biased towards using putatively more dangerous habitat. Females were significantly heavier in brackish flats and mangroves than in cattail marshes, with a range of mass difference among habitats of  $0.44\text{--}0.51 \pm 0.19$  g ( $F_{2,512} = 3.62$ ,  $P = 0.02$ ). The body masses of males did not differ among habitats ( $F_{2,1237} = 1.06$ ,  $P = 0.34$ ).

### Behavioral observations

Flock size differed significantly by sex and habitat type (sex  $\times$  habitat:  $F_{2,754} = 3.48$ ,  $P = 0.03$ ; Table 1). Birds in brackish flats and mangroves were in smaller groups than

those in cattail marshes. However, females were in smaller flocks than males within brackish flats, whereas in mangroves and cattail marshes, the sexes had similar flock sizes.

Nearest neighbor distance was negatively correlated with flock size; the nearest neighbor distance decreased as flock size increased (slope =  $-0.13 \pm 0.01$ ;  $r^2 = 0.54$ ;  $F_{1,762} = 912.03$ ,  $P < 0.0001$ ). Sexes had different nearest neighbor distances among habitats (sex  $\times$  habitat:  $F_{2,753} = 2.81$ ,  $P = 0.06$ ): males had similar nearest neighbor distances among habitats, whereas females had greater distances in brackish flats and mangroves than in cattail marshes (Table 1).

Vigilance rate was significantly different among habitats ( $F_{2,754} = 20.94$ ,  $P < 0.0001$ ). Birds in brackish flats had a lower rate than those in cattail marshes, while birds in mangroves had intermediate vigilance rates (Table 1). Controlling for habitat type, vigilance rates by sex were negatively correlated with flock size (flock  $\times$  sex:  $F_{1,754} = 4.52$ ,  $P = 0.03$ ). As flock size increased, the vigilance rate decreased in males (slope =  $-0.21 \pm 0.03$ ,  $t = -6.04$ ,  $P < 0.01$ ,  $n = 508$ ), but not in females (slope =  $-0.08 \pm 0.05$ ,  $t = -1.60$ ,  $P = 0.10$ ,  $n = 260$ ). Thus, females scanned at significantly higher rates than males for a given flock size (Fig. 1).

## Discussion

Birds employ a range of antipredator tactics. Different tactics may be used concurrently to cumulatively increase safety, or may be traded-off against each other to adjust the level of safety through compensation (Lind and Cresswell 2006). We predicted that cumulative effects, namely that flock size, tightness, and vigilance behavior of Western Sandpipers at Bahía Santa María would all show patterns consistent with our previous conclusions about the relative predation danger of habitat types and for each sex (Fernández and Lank 2006). We predicted that (1) sandpipers would differentially allocate effort towards antipredator behavior consistent with an a priori ordering of the three habitats with respect to predation danger based on distance to cover for approaching raptors, and supported by overall bird densities, patterns of body mass, and partially by sex ratios, and (2) that females, being more vulnerable, would bias their activity trade-offs more strongly towards components of anti-predator behavior, particularly so in more dangerous habitats.

For the most part, the changes in the use of tactics were largely in parallel directions among habitats and between sexes; we did not find trade-offs among the usage of different presumed anti-predator tactics. The patterns of vigilance, flock size, density of flocks, and body mass (females

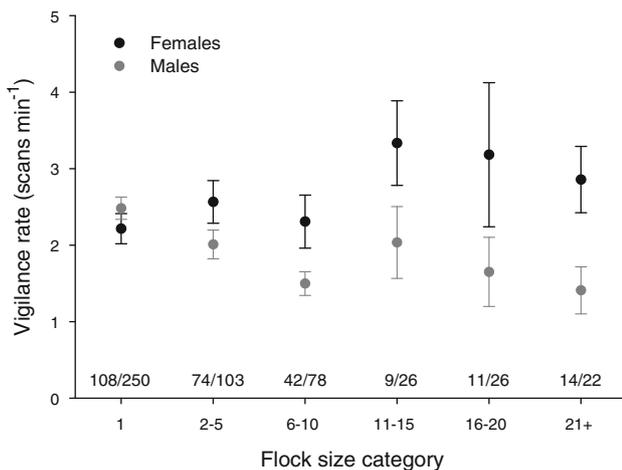
**Table 1** Summary of level of presumed predation danger, sex composition, and antipredator tactics of Western Sandpipers (*Calidris mauri*) with respect to habitat type during the non-breeding season in Bahía Santa María, northwestern Mexico

Parameter	Sex	Habitat type		
		Brackish flats (n)	Mangroves (n)	Cattail marshes (n)
Distance to cover (km) <sup>a</sup>		0.79 ± 0.08	0.47 ± 0.06	0.31 ± 0.30
Sex composition (proportion male)		0.78 ± 0.02 (865)*	0.64 ± 0.03 (578)	0.55 ± 0.04 (318)
Body mass (g)	Females	24.57 ± 0.12 (188)	24.50 ± 0.12 (200)	24.06 ± 0.14 (130)*
	Males	22.12 ± 0.06 (677)	22.08 ± 0.08 (378)	21.95 ± 0.09 (188)
Flock size (n)	Females	4.2 ± 0.7 (114)*	6.8 ± 0.9 (84)	9.5 ± 1.1 (60)*
	Males	5.6 ± 0.4 (368)	6.1 ± 0.8 (94)	9.9 ± 1.2 (43)*
Nearest neighbor distance (m)	Females	4.0 ± 0.3	3.2 ± 0.3	1.7 ± 0.3*
	Males	3.5 ± 0.1	3.5 ± 0.3	3.3 ± 0.4
Vigilance rate (scans min <sup>-1</sup> )		1.8 ± 0.1 (482)*	2.2 ± 0.1 (178)*	3.7 ± 0.2 (103)*

Least-squares means ± SE are reported controlling for habitat type and annual variation. Sample sizes for nearest neighbor distance are similar to those for flock size

\* Significant differences with other habitats,  $P < 0.05$  and  $P < 0.10$  for interaction term

<sup>a</sup> After Fernández and Lank 2006



**Fig. 1** The distribution of mean vigilance rate (±SE) according to flock size for Western Sandpipers (*Calidris mauri*) in relation to sex at Bahía Santa María, northwestern Mexico, during the non-breeding seasons of 1999–2001. Sample sizes are given above the x axis (females/males)

only) seen across habitats were consistent with the predicted ordering of perceived danger with respect to habitat openness, with sites closer to vegetation treated with a greater degree of caution (Hilton et al. 1999; McGowan et al. 2002; Dekker and Ydenberg 2004; Table 1). As predicted, in cattail marshes, the most closed habitat, birds foraged in larger and more cohesive flocks, had higher vigilance rates for a given flock size than birds in brackish flats, and females were lighter (Fernández and Lank 2006), showing more caution in a more dangerous habitat in multiple ways (Table 1; Cresswell 1994b; Barbosa 1997; Whitfield 2003b). In the brackish flats, the most open

habitat, Western Sandpipers showed the least allocation towards antipredator prioritization in general, consistent with a higher detectability of predators (habitat characteristics) and greater sandpiper density (collective detection and dilution effects; Fernández and Lank 2006). In mangroves, which were a mosaic of open areas with patchy vegetation, mean values of mass, flock size and coherence, and vigilance were intermediate between the other two habitats, although tending more towards values in completely open brackish flats.

Differences in behavior, body size, conspicuousness, and experience can make one sex or age class more vulnerable to predation (Magurran and Nowak 1991; Burns and Ydenberg 2002; Childress and Lung 2003; Nebel and Ydenberg 2005). Despite a prediction that females might be more vulnerable, Nebel et al. (2004) determined through DNA sexing of prey remains that there was no sex bias in avian predator-induced mortality of Western Sandpipers at Santa María. The differential behavior of males and females we document may account for the lack of large bias in mortality rates from this source.

Unexpectedly, we previously found that females were disproportionately present in the most dangerous habitat (Fernández and Lank 2006). This is the largest exception to our prediction that females would place a higher priority than males across all anti-predation tactics. Lind and Cresswell (2006) stressed that different components of anti-predator behavior might trade-off against one another, and thus studying single aspects could produce a misleading picture of the allocation to anti-predator effort as a whole. Fernández and Lank (2006) suggested that females might obtain higher feeding returns from cattail areas. We

can now interpret females' disproportionate usage of a putatively more dangerous habitat in the context of a richer trade-off among antipredator tactics. In apparent compensation, females had higher vigilance rates than males for a given flock size, formed more cohesive flocks in cattails, and maintained lower relative masses, particularly in the most dangerous habitat, patterns which did not occur in males.

What approach might we use to predict which tactics may be used by individuals cumulatively or as compensation in different states or situations? Identifying the specific functional significance of different behaviors with respect to predation danger and other factors may help focus thinking about when tactics will be used additively to reinforce, or as compensatory trade-offs to adjust, the level of safety. Table 2 presents the specific assumed functions for each of our five tactics, summarizes our findings with respect to sex differences, and presents inferences derived from them, focusing on females' perspectives. We can see that habitat choice and vigilance may at the simplest level trade-off against each other because both primarily address only the feeding rate/predation danger trade-off. Females disproportionately used a riskier habitat, but compensated with higher vigilance rates. Other behaviors may have primarily been used cumulatively because they at least partially address different components of safety and of foraging or social trade-offs. Considering the suite of tactics as a whole, as Lind and Cresswell (2006) stress, and focusing on females, we suggest the following integrated scenario.

Due to their longer beaks, females are better able than males to harvest invertebrates from cattail areas, where probing is more frequent (Mathot and Elner 2004; Fernández and Lank 2008). To compensate for the increased danger, they maintain themselves in tighter flocks, which increases foraging interference. Tighter flocks may be less costly to females than males, however, because foraging interference is lower when probing for invertebrates than when pecking at surface prey or mobile prey in the water column, favored by males, where evasion by prey may be of greater importance (Goss-Custard 1980). Females also devote greater time to vigilance at a given flock size than males, as predicted if they are intrinsically more vulnerable. Moreover, foraging and vigilance behaviors may be more mutually exclusive for females than males (Barbosa 1995; Cresswell et al. 2003). Shorebirds and dabbling ducks that forage deeply spent more time overtly vigilant during feeding sessions than when foraging with only the bill in the substrate or water surface (Barbosa 1995; Guillemain et al. 2001). Finally, females utilizing the more dangerous habitat are lighter than those elsewhere. This suggests either (1) that individuals in greater need of richer resources adopt a riskier approach (Clark 1994), or (2) that those females utilizing this habitat compensate by maintaining a higher level of escape performance (Lind et al. 1999; Burns and Ydenberg 2002; Ydenberg et al. 2002, 2004).

We conclude that multiple anti-predator tactics are, in this case, mostly used cumulatively. While some quantitative trade-off among these tactics may have occurred,

**Table 2** Summary of sex differences in antipredator tactics of Western Sandpipers during the non-breeding season in Bahía Santa María, northwestern Mexico

Anti-predator tactic	Principle functional significance	Sex difference: female perspective	Inference
Choice of habitat—danger level	Trade-off against foraging rate?	Higher proportion of females in more dangerous habitat	Females compensate for greater danger through sex specific feeding advantage
Body mass within sex	Affects escape ability and reflects stored reserve	Lower for females only in more dangerous habitat	Either (1) females with greater need, or (2) females maintain higher escape performance
Flock size	Affects safety through corporate dilution/detection rates, plus possible trade-off against foraging competition	Smaller for females in safer habitat	Feeding interference among females is greater than that of females when feeding in brackish flats, but not in cattail marshes
Density in flock	Affects level of foraging competition	Lower density for females in safer habitat	Females spread out more in safer habitat, presumably to lessen feeding interference
Vigilance rate	Predator detection, trade-off against foraging rate	Higher rate for females controlling for flock size	Females appear to be sacrificing foraging time for safety, indicating a higher intrinsic vulnerability

none were strong enough to produce negative relationships between components that we would have clearly recognized as compensatory. The strongest candidate for compensation came from a trade-off with respect to habitat choice, particularly for females. By controlling variables related to vigilance, flock size, nearest neighbor distance, and body weight, females in particular may increase the effectiveness of predator detection to compensate for costs incurred in for the use of higher-danger, but possibly higher foraging return, habitats (Fernández and Lank 2006).

## Zusammenfassung

Spiegeln Geschlechts- und Habitatunterschiede im Anti-Prädatoren-Verhalten von Bergstrandläufern *Calidris mauri* kumulative oder kompensierende Prozesse wider?

Individuen gehen mit ihrem Prädationsrisiko in verschiedenen Situationen unterschiedlich um. Wir haben den Gebrauch von Anti-Prädatoren-Verhalten bei Bergstrandläufern (*Calidris mauri*) in der Bucht Bahía Santa María in Nordwest-Mexiko untersucht. Die Strandläufer suchten in drei Habitaten, die sich in ihrem mutmaßlichen Prädationsrisiko unterschieden, nach Futter. Brackwasserflächen sind vollständig offen, was sie für futter-suchende Strandläufer theoretisch weniger gefährlich macht als Mangroven und Rohrkolben-Sumpfbereiche, wo die Vögel weniger weit sehen können. Bergstrandläufer sind sexuell dimorph; die Weibchen haben einen um etwa 15% längeren Schnabel und sind um 10% schwerer als die Männchen. Wir haben zuvor gezeigt, dass sich männliche und weibliche Strandläufer in ihrer Habitatwahl und ihrer relativen Körpermasse unterscheiden, und zwar in einer Art und Weise, die mit unterschiedlichen Reaktionen auf Prädationsgefahr in Einklang steht (Fernández and Lank 2006). Entgegen unserer Erwartungen waren Weibchen jedoch in gefährlicheren Habitaten überrepräsentiert. Hier untersuchen wir die unterschiedliche Anwendung dreier Anti-Prädatoren-Taktiken (Schwarmgröße, Dichte innerhalb der Schwärme und Sicherheitshäufigkeit) in verschiedenen Habitaten und bei den beiden Geschlechtern; diese Taktiken könnten additiv genutzt werden, um die Sicherheit zu verstärken, oder gegeneinander abgewogen werden. Wir nahmen an und fanden auch, dass es Unterschiede zwischen Habitaten gibt und dass, wenn man für andere Faktoren kontrolliert, die Weibchen vorsichtiger waren als die Männchen. Meist schien die Anwendung dieser drei Taktiken eher additiv als kompensierend zu sein. In Bezug auf die Habitatnutzung schienen die Vögel jedoch die höhere Mortalitätswahrscheinlichkeit, die der Nutzung gefährlicherer Habitate innewohnt, zu

kompensieren, indem sie wachsamer waren, in dichterem Schwärmen Futter suchten und geringere Körpermassen aufrechterhielten (nur die Weibchen). Daher wirken bei Anti-Prädatoren-Taktiken sowohl additive als auch kompensierende Prozesse, um den Nettograd an Sicherheit zu ermitteln und gegen andere Faktoren abzuwägen.

**Acknowledgments** Virgilio Antonio, Alfredo Castillo, and Miguel Guevara assisted with fieldwork. The Patolandia Hunting Club provided logistic support. We thank the family Cazares-Medina for their help during fieldwork, and Marco González, Xico Vega, family González-Bernal, and the Escuela de Biología-Universidad Autónoma de Sinaloa for support in Culiacán. Financial support was received from the Centre for Wildlife Ecology at Simon Fraser University, Canadian Wildlife Service-Latin America Program, and Patolandia Hunting Club. Additional financial support was provided by the National Science and Engineering Research Council of Canada, Pronatura A. C. Noroeste, American Wildlife Research Foundation, Lincoln Park Neotropic Fund, and Segal Travel Grant. Graduate scholarships from the Mexican National Council for Science and Technology (CONACYT, No. 90768), Government of Canada Award, and President's Ph.D. Research Stipend were awarded to G.F. Birds were banded under Mexican (DGVS: 3876, 3278, and 3592) and Canadian (#20383-D) bird-banding permits and procedures were approved by the Simon Fraser University Animal Care Facility Committee (No. 552-B). Earlier versions of the manuscript benefited by comments from Rob Butler, Sue Haig, Kim Mathot, Ron Ydenberg, Rob G. Bijlsma, and Nils Warnock. This paper is modified from one component of G.F.'s Ph.D. dissertation.

## References

- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–264
- Barbosa A (1995) Foraging strategies and their influence on scanning and flocking behaviour of waders. *J Avian Biol* 26:182–186
- Barbosa A (1997) The effects of predation risk on scanning and flocking behavior in dunlin. *J Field Ornithol* 68:607–612
- Beauchamp G, Ruxton GD (2008) Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks. *Anim Behav* 75:1837–1842
- Bijlsma RG (1990) Predation by large falcons on wintering waders on the Banc d'Arguin, Mauritania. *Ardea* 78:75–82
- Burns JG, Ydenberg RC (2002) The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). *Behav Ecol Sociobiol* 52:128–136
- Cartar RV (1984) A morphometric comparison of western and semipalmated sandpipers. *Wilson Bull* 96:277–286
- Childress MJ, Lung MA (2003) Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Anim Behav* 66:389–398
- Clark CW (1994) Antipredator behavior and the asset-protection principle. *Behav Ecol* 5:159–170
- Cresswell W (1994a) Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *J Anim Ecol* 63:589–600
- Cresswell W (1994b) Flocking is an effective anti-predation strategy in redshank, *Tringa totanus*. *Anim Behav* 47:433–442
- Cresswell W (1996) Surprise as a winter hunting strategy in sparrowhawks *Accipiter nisus*, peregrine falcon *Falco peregrinus* and merlins *F. columbarius*. *Ibis* 138:684–692

- Cresswell W (2008) Non-lethal effects of predation in birds. *Ibis* 150:3–17
- Cresswell W, Whitfield DP (1994) The effects of raptor predation on wintering wader populations at the Tynninghame estuary, south-east Scotland. *Ibis* 136:223–232
- Cresswell W, Quinn JL, Whittingham MJ, Butler S (2003) Good foragers can also be good at detecting predators. *Proc R Soc Lond B* 207:1069–1076
- Dekker D, Ydenberg RC (2004) Raptor predation on wintering dunlins in relation to the tidal cycle. *Condor* 106:415–419
- Fernández G, Lank DB (2006) Sex, age, and body size distributions of western sandpipers during the nonbreeding season with respect to local habitat. *Condor* 108:547–557
- Fernández G, Lank DB (2007) Variation in the wing morphology of western sandpipers (*Calidris mauri*) in relation to sex, age and annual cycle. *Auk* 124:1037–1046
- Fernández G, Lank DB (2008) Foraging behaviour of non-breeding western sandpipers (*Calidris mauri*) as a function of sex, habitat and flocking. *Ibis* 150:518–526
- Fretwell SD, Lucas HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor* 19:16–36
- Goss-Custard JD (1980) Competition for food and interference among waders. *Ardea* 68:31–52
- Guillemain M, Duncan P, Fritz H (2001) Switching to a feeding method that obstructs vision increases head-up vigilance in dabbling ducks. *J Avian Biol* 32:345–350
- Hilton GM, Ruxton GD, Cresswell W (1999) Choice of foraging areas with respect to predation risk in redshank: the effects of weather and predator activity. *Oikos* 87:295–302
- SAS Institute (2001) SAS/SAT user's guide, version 8.2. SAS Institute, Cary, NC
- Kus BE, Ashman P, Page GW, Stenzel LE (1984) Age related mortality in a wintering population of dunlin. *Auk* 101:69–73
- Lank DB, Ydenberg RC (2003) Death and danger at migratory stopovers: problems with “predation risk”. *J Avian Biol* 34:225–228
- Lima SL (1998) Stress and decision making under the risk of predation: recent developments from behavioural, reproductive and ecological perspectives. *Adv Study Behav* 27:215–290
- Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Lind J, Cresswell W (2006) Anti-predation behaviour during bird migration: the benefit of studying multiple behavioural dimensions. *J Ornithol* 147:310–316
- Lind J, Fransson T, Jacobsson S, Kullberg C (1999) Reduced take-off ability in robins due to migratory fuel load. *Behav Ecol Sociobiol* 46:65–70
- Littell RC, Freund RJ, Spector PC (1991) SAS system for linear models, 3rd edn. SAS Institute, Cary, NC
- Magurran AE, Nowak MA (1991) Another battle of the sexes: the consequences of sexual asymmetry in mating costs and predation risk in the guppy, *Poecilia reticulata*. *Proc R Soc Lond B* 246:31–38
- Mathot KJ, Elnor RW (2004) Evidence for sexual partitioning of foraging mode in western sandpipers (*Calidris mauri*) during migration. *Can J Zool* 82:1035–1042
- McGowan A, Cresswell W, Ruxton GD (2002) The effects of daily weather variation on foraging and responsiveness to disturbance in overwintering red knot *Calidris canutus*. *Ardea* 90:229–237
- Myers JP (1984) Spacing behaviour of nonbreeding shorebirds. In: Burger J, Olla BL (eds) Shorebirds: migrating and foraging behaviour. Plenum, New York, pp 271–321
- Nebel S, Ydenberg RC (2005) Differential predator escape performance contributes to a latitudinal sex ratio cline in a migratory shorebird. *Behav Ecol Sociobiol* 59:44–50
- Nebel S, Lank DB, O'Hara PD, Fernández G, Haase B, Delgado F, Estela FA, Evans Ogden LJ, Harrington B, Kus BE, Lyons J, Ortego B, Takekawa JY, Warnock N, Warnock SE (2002) Western sandpiper (*Calidris mauri*) during the nonbreeding season: spatial segregation on a hemispheric scale. *Auk* 119:922–928
- Nebel S, Cloutier A, Thompson GJ (2004) Molecular sexing of prey remains permits a test of sex-biased predation in a wintering population of western sandpipers. *Proc R Soc Lond B* 271(Suppl 5):S321–S323
- Page GW, Fearis B (1971) Sexing western sandpipers by bill length. *Bird-Banding* 42:297–298
- Page GW, Whitacre DF (1975) Raptor predation on wintering shorebirds. *Condor* 77:73–83
- Piersma T, Baker AJ (2000) Life history characteristics and the conservation of migratory shorebirds. In: Gosling LM, Sutherland WJ (eds) Behaviour and conservation. Cambridge University Press, Cambridge, pp 105–124
- Piersma T, Koolhaas A, Jukema J (2003) Seasonal body mass changes in Eurasian golden plovers staging in the Netherlands: decline in late autumn mass peak correlates with increase in raptor numbers. *Ibis* 145:565–571
- Pomeroy AC (2006) Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by western sandpipers, *Calidris mauri*. *Oikos* 112:629–637
- Pomeroy AC, Butler RW, Ydenberg RC (2006) Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. *Behav Ecol* 17:1041–1045
- Quinn JL, Cresswell W (2004) Predator hunting behaviour and prey vulnerability. *J Anim Ecol* 73:143–154
- Sansom A, Cresswell W, Minderman J, Lind J (2008) Vigilance benefits and competition costs in groups: do individual redshanks gain overall foraging benefit? *Anim Behav* 75:1869–1875
- Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J Anim Ecol* 71:296–308
- Swaddle JP, Lockwood R (1998) Morphological adaptations to predation risk in passerines. *J Avian Biol* 29:172–176
- Taylor CM, Lank DB, Pomeroy AC, Ydenberg RC (2007) Relationship between stopover site choice of migrating sandpipers, their population status, and environmental stressors. *Isr J Ecol Evol* 53:245–261
- Whitfield DP (1988) Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering turnstone *Arenaria interpres* and redshanks *Tringa totanus*. *Ibis* 130:284–287
- Whitfield DP (2003a) Predation by Eurasian sparrowhawks produces density-dependent mortality of wintering redshanks. *J Anim Ecol* 72:27–35
- Whitfield DP (2003b) Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *J Avian Biol* 34:163–169
- Yasué M, Quinn JL, Cresswell W (2003) Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding locations in redshanks. *Funct Ecol* 17:727–736
- Ydenberg RC, Dekker D, Kaiser G, Shepherd PCF, Evans Ogden LJ, Rickards K, Lank DB (2009) Winter body mass and over-ocean flocking as components of danger management by Pacific dunlins. *BMC Biol* (in press)
- Ydenberg RC, Butler RW, Lank DB, Guglielmo CG, Lemon M, Wolf N (2002) Trade-offs, condition dependence and stopover site selection by migrating sandpipers. *J Avian Biol* 33:47–55
- Ydenberg RC, Butler RW, Lank DB, Smith BD, Ireland J (2004) Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. *Proc R Soc Lond B* 271:1263–1269