Foraging behaviour of non-breeding Western Sandpipers *Calidris mauri* as a function of sex, habitat and flocking

GUILLERMO FERNÁNDEZ[1]* & DAVID B. LANK[2]

[1]*Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apartado Postal 811, Mazatlán 82040, Sinaloa, México*

[2]*Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada*

Individuals within a population may vary considerably in the way they exploit available food resources. If the sexes differ in the size of their feeding apparatus, there can be differences in foraging behaviour and habitat use, hence one sex may be more susceptible to competition. We examined relationships between sexual dimorphism in bill size and foraging behaviour, and habitat and microhabitat use of non-breeding Western Sandpipers *Calidris mauri* at Bahía Santa María, northwestern Mexico. Western Sandpipers are sexually dimorphic, with females about 15% longer-billed than males. Males used a higher proportion of pecks, had a lower probing–pecking rate, walked at higher rates, foraged at sites with lower water content, and had greater variation in foraging technique than females. Moreover, males decreased their proportion of pecks and foraged at a higher rate than females when they changed from feeding alone to feeding in flocks, suggesting a greater safety advantage or susceptibility to conspecific interference when flock feeding. We compared behaviour and microhabitat usage in three habitats: brackish flats, mangroves, and cattail marshes. Sex-related differences in foraging behaviour and microhabitat use were consistent among habitats. Birds in brackish flats and mangroves used a higher proportion of pecks, foraged at lower rates and walked at higher rates, and foraged at deeper sites, with a lower proportion of water cover, than those in cattail marshes. Sex-related differences in foraging behaviour and microhabitat should reduce the level of competition between sexes, and may account for sex differences in Western Sandpiper distribution observed between habitats in Bahía Santa María.

Keywords: competition, interference, pecking rate, predation risk, sexual dimorphism.

Many wader species (Charadrii) are sexually dimorphic in bill length (Jönsson & Alerstam 1990), which correlates with sex differences in foraging behaviour, diet, and habitat use (Puttick 1981, Summers *et al.* 1990, Durell *et al.* 1993, Zharikov & Skilleter 2002). Waders have two main foraging techniques: tactile probing in the substrate, and visual pecking at or near the substrate surface (Pienkowski 1979). The sex with the longer bill generally uses more tactile probing and feeds on larger prey than the sex with the shorter bill (Durell 2000), but individuals switch between techniques in response to changes in prey availability and feeding habitat (Harrington 1982, Whitfield 1990).

Heterogeneity in the physical characteristics of foraging areas can also influence foraging behaviour. Increased water content makes substrates easier to penetrate and increases invertebrate activity, rendering prey more susceptible to wader predation (Mouritsen & Jensen 1992, Colwell & Landrum 1993). Conversely, standing water can decrease available foraging area if it is too deep in relation to tarsus length for birds to use (Baker 1979, Boettcher *et al.* 1995). Two general patterns have been formulated to describe the relationship between sandpiper foraging

*Corresponding author.
Email: gfernadez@ola.icmyl.unam.mx

behaviour and microhabitat characteristics (Gerritsen & van Heezik 1985): (1) long-billed individuals select softer substrates than short-billed counterparts and (2) individuals show a shift towards surface foraging on firmer substrates. Therefore, drier substrates and more structurally complex microhabitats may favour shorter bill size and pecking foraging behaviour (Whitfield 1990, Zharikov & Skilleter 2002).

The presence of other birds, usually conspecifics, may have a significant effect on foraging behaviour (Goss-Custard 1984, Puttick 1984). It is generally accepted that birds can reduce their risk of predation by associating with conspecifics (Lima & Dill 1990). As group size increases, however, competition for resources may also increase (Goss-Custard 1980). Theoretical (Stillman *et al.* 2000, Bednekoff & Lima 2004), field (Yates *et al.* 2000, Dominguez 2002), and experimental studies (Vahl *et al.* 2005) have shown that as a result of increased competition, individuals may exert greater foraging effort or change their foraging behaviour to obtain adequate resources. Goss-Custard (1970) proposed that in waders, interspecific differences in dispersion patterns result from interspecific differences in the costs of flocking due to feeding competition with conspecifics, combined with safety benefits. Thus, species which use foraging modes with less interference can feed in tighter, larger flocks. Overall, waders that locate their prey by probing tend to occur in compact flocks, whereas waders that use pecking tend to be more evenly dispersed, which has been interpreted as indicating that interference is higher for surface feeders (Goss-Custard 1970).

In this study, we examined the relationships between sexual dimorphism in bill size and the foraging behaviour, habitat and microhabitat use of Western Sandpipers *Calidris mauri* at Bahía Santa María, northwestern Mexico ('Santa María') during the non-breeding season. At Santa María, over 350 000 sandpipers spend the winter (Engilis *et al.* 1998), and they are widely distributed among a mosaic of habitats (Fernández & Lank 2006). Relative to other calidrid sandpipers, Western Sandpipers are highly sexually dimorphic; females are about 10% heavier and 15% longer-billed than males (Cartar 1984). Western Sandpipers are opportunistic feeders with short prey-handling times (Sutherland *et al.* 2000); males, however, tend to peck on the surface more than females, which more frequently probe (Mathot & Elner 2004, Nebel 2005). Although Western Sandpipers can be aggressive and defend feeding territories during the non-breeding season (Tripp &

Collazo 1997, Fernández Aceves 2005), they generally forage in loose flocks of varying individual membership with little obvious dominance structure (Warnock & Takekawa 1996).

At Santa María, we recognized three types of habitats used by Western Sandpipers: brackish flats, mangroves and cattail marshes (Fernández & Lank 2006). Habitats differ with respect to Western Sandpiper population structure, prey densities, and levels of predation risk. For small waders, feeding closer to cover entails a higher risk both of being attacked by an avian predator and of the attack being successful (Whitfield 2003a). Brackish flats were the most open, and thus potentially the safest; cattail marshes were most enclosed, and thus potentially most dangerous; and mangrove habitat was more variable, and intermediate with regard to distance to vegetation (Fernández & Lank 2006). Bird densities were highest in brackish flats, the richest and safest habitat, and males were overrepresented; in cattail marshes, which appeared to be the poorest and most dangerous habitat, bird densities were lower, and the female : male ratio was more even; and in mangroves, bird densities were similar to those in cattail marshes, but the sex ratio was similar to those in brackish flats (Fernández & Lank 2006). Western Sandpiper spacing behaviour also differed between habitat types. Birds in brackish flats foraged in smaller flocks than those in mangroves and cattail marshes, and in general, larger flocks were denser than smaller ones (Fernández Aceves 2005). These relationships suggest that brackish flats are higher quality habitat in terms of both food availability and safety, and should be favoured 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 & Lucas 1970).

If sexual dimorphism in bill size plays an important role in shaping foraging behaviour and microhabitat use by Western Sandpipers, a relationship between foraging technique and bill length should be observed between and within sexes (Elner & Seaman 2003). We predict that males, as the short-billed sex, should exhibit a higher proportion of surface foraging behaviour than females; they should prefer sites with lower water content; and that, as the more surface foragers, they should show greater shifts in foraging behaviour as flock size increases. The influence of habitat characteristics *per se* on foraging behaviour and microhabitat use should be similar for males and females, and thus the direction of differences in foraging behaviour between habitats should be similar for both sexes.

METHODS

Study area

This research was conducted at Santa María (25°02′N, 108°18′W), about 90 km northwest of Culiacán, Sinaloa, in northwestern Mexico. Santa María is the largest wetland on the Sinaloa coast, composed of 1350 km² of a diverse habitat mosaic, which includes an outer bay, intertidal mudflats, mangroves, brackish flats, emergent brackish marshes and freshwater marshes (Engilis *et al.* 1998). Study sites were located on the east side of the coastal wetland, just south of the village La Reforma, covering an area of approximately 180 km². The distance between study sites ranged from 0.3 km to 13 km. Three habitats were recognized: brackish flats, mangrove-salt marsh flats, and cattail marshes. Brackish flats were extensive areas (up to 3 km long) ranging from completely open unvegetated flats to sparsely vegetated areas with *Scirpus* and *Salicornia*. The mangrove-salt marsh flats (mangroves) were smaller (*c*. 0.6 km long) open flats broken up by mangroves. Mangrove forests were dominated by Black Mangrove *Avicennia germinans* with some emergent vegetation, mainly *Spartina* and *Salicornia*. The marsh areas include small beaches (*c*. 0.3 km long) in freshwater areas, adjacent to extensive stands of cattail marsh (*Typha*) with other secondary vegetation, such as *Scirpus*, *Atriplex* and *Chenopodium*. Brackish flats and mangroves were protected from water-level variation during daily tidal cycles, but were partly flooded twice a month during spring tides, with the highest tides in December. In cattail marshes, the water level was affected by the amount of rain and agricultural runoff during summer and winter, respectively.

Data collection

Observations of foraging behaviour were made at sites within each type of habitat in November–February of 1999–2000, and in December–February of 2000–2001 and 2001–2002. Foraging behaviour was scored during individual focal observations (Altmann 1974) using a 15–60× spotting scope. In each habitat, focal observations were carried out throughout the day (e.g. 07:00 to 15:00). Behavioural data were dictated into a tape recorder, timed with a stopwatch, and later transcribed. We preferentially observed birds that had previously been individually colour-banded (Fernández & Lank 2006). If no banded birds were present, focal birds were selected randomly by directing the spotting scope at a flock and selecting the individual in the centre of the field of view. We continued randomly selecting individuals by moving the scope in a zigzag pattern to reduce the probability of re-sampling the same individual. Banded birds were sexed based on bill measurements (female > 24.8 mm, male < 24.2 mm; Page & Fearis 1971). For unbanded birds, visual assignments were made based on relative bill size. When the accuracy of this technique was verified with banded birds, sex agreed with that based on measurements 90% of time (*n* = 234 birds).

Discrete foraging groups were defined as flocks. All birds that surrounded the focal individual were counted as a part of a flock. Although multi-species flocks occur in the study area, all data presented are for single species flocks. Birds were not considered part of the flock when their distance exceeded 3 m from the last individual counted in a particular direction. In our study, nearest neighbour distance was negatively correlated with flock size, suggesting that larger flocks were denser than smaller ones. Therefore, flock size can be used as an index of within-flock bird density. Foraging behaviour of Western Sandpipers was described using foraging technique, and foraging and walking rates. Foraging technique was categorized as pecking (single and multiple), with the bill just touching the substrate surface; or probing (single and multiple), when the bill was inserted into the substrate (Sutherland *et al.* 2000). The proportion of pecks was used as an index of foraging technique and was expressed as the number of pecks out of the total number of foraging attempts (i.e. pecks + probes). We studied the foraging and walking rates, defined as the number of foraging attempts and steps per unit of total time (/min), respectively. Western Sandpipers feed on a wide variety of small invertebrates that are handled very quickly (Sutherland *et al.* 2000) and the intake rate cannot be measured directly. Microhabitat was characterized in terms of water cover and water depth. Water cover was scored as the proportion of habitat that was covered with water within a 5-m radius circle around the focal bird. Water depth was scored using bird tarsus and the following ordinal scale: 0 = dry/mud; 1 = water just covering the toes; 2 = water at the half of tarsus level; and 3 = water above tarsus.

Statistical analysis

A single observer (G.F.) made 763 focal observations with a mean observation time of 1.9 min (range = 1–3 min),

of which 223 observations were of banded birds. Among 763 observations included in this analysis, 87 were made on territorial birds, which represented *c.* 5–7% of the population (Fernández Aceves 2005). 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 annual variation, foraging behaviour (foraging technique, foraging and walking rates) was not significantly different between banded and non-banded birds ($P > 0.20$), so we pooled all observations. To assess the effect of flocking on foraging behaviour, we compared birds foraging solitarily (singletons) versus those foraging in flocks; there were no changes with flock size between 2 and 80 birds ($P < 0.38$).

We analysed variation in foraging technique as the probability of pecking using a general linear model with events/trials syntax (where events = number of pecks and trials = total pecks + probes), binomial error structure, and a logit link function (Proc Genmod). We analyzed variation in foraging and walking rates using ANOVA, where data were log-transformed prior to analysis, producing approximately normally distributed data. Foraging technique, foraging rate and walking rate were analysed in relation to sex and habitat, 'flock effect' (single vs. flocks), and bill length, controlling for other variables as appropriate. Proportion of water cover was arcsine square-root transformed and analysed using an ANOVA, to determine the effects of sex and habitat, controlling for annual variation. Water depth was treated as an ordinal response variable and analysed using logistic regression models (Wald χ^2, two-tailed) with a cumulative logit link function, to determine the effects of sex and habitat, controlling for annual variation.

Of the focal observations on banded birds, 64% (147) were on 100 colour-banded individuals (44 females and 56 males). Individually colour-banded birds were observed on average 1.5 times (range = 1–5). We pooled all observations of individually colour-banded birds among habitats and years. First, we estimated the repeatability of foraging technique (Lessells & Boag 1987). Then, to avoid pseudoreplication in our analysis, for individuals with more than one focal observation, the average value for foraging technique was used in the 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 tests 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 sum of squares. We report least-squares means taking other factors and seasonal and annual variation into account. We made all pair-wise post-hoc comparisons using the Tukey–Kramer test. Least-squares means (± se) are presented unless otherwise stated. All statistical tests were performed using SAS® 8.2 (SAS Institute Inc. 2001).

RESULTS

The sexes differed in foraging behaviour, controlling for microhabitat use: males were about twice as likely to peck ($\chi^2_1 = 1355.47$, $P < 0.0001$), foraged at a lower rate ($F_{1,750} = 5.86$, $P = 0.01$), and walked at a higher rate ($F_{1,750} = 7.78$, $P = 0.005$) than females (Table 1).

Table 1. Summary of foraging behaviour and microhabitat use of Western Sandpipers with respect to sex and habitat at Bahía Santa María, northwestern Mexico, during the non-breeding seasons of 1999–2001. Least-squares means (± se), back-transformed after analysis, are reported controlling for sex (in habitat means), habitat (in sex means), annual variation and flock size. *Denotes significant differences with other habitats, $P < 0.05$.

|	Sex			Habitat type		
	Females	Males	P	Brackish flats	Mangroves	Cattail marshes
Number of observations	258	505		482 (114 ♀)	178 (84 ♀)	103 (60 ♀)
Foraging behaviour						
Proportion of pecks	0.18 ± 0.02	0.33 ± 0.01	< 0.01	0.27 ± 0.01	0.28 ± 0.02	0.21 ± 0.03*
Foraging rate (attempts/min)	74.7 ± 1.7	70.2 ± 1.5	0.01	64.8 ± 1.3	68.0 ± 2.0	84.7 ± 2.9*
Walking rate (steps/min)	74.5 ± 2.4	83.2 ± 2.2	0.005	83.2 ± 1.8	79.5 ± 2.8	73.9 ± 4.1*
Microhabitat use						
Proportion of water cover	0.89 ± 0.01	0.79 ± 0.01	< 0.01	0.80 ± 0.01	0.82 ± 0.01	0.90 ± 0.02*
Water depth index	2.64 ± 0.02	2.26 ± 0.02	< 0.01	2.55 ± 0.02	2.57 ± 0.03	2.22 ± 0.04*
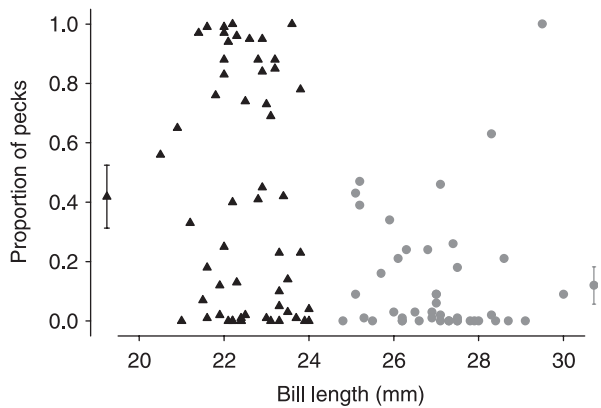
Figure 1. Distribution of the proportion of pecks in relation to bill length in Western Sandpipers at Bahía Santa María, northwestern Mexico, during the non-breeding seasons of 1999–2001. Each point represents a colour-banded individual. Circles represent females (*n* = 44) and triangles represent males (*n* = 56). On either side is the mean pecking rate (± 95% confidence intervals) for pooled males (left) and pooled females (right).

In both sexes, the proportion of pecks decreased with higher foraging rate (females: $F_{1,257} = 138.58$, $P < 0.001$, $r^2 = 0.35$; males: $F_{1,504} = 99.92$, $P < 0.001$, $r^2 = 0.16$) and increased with higher walking rate (females: $F_{1,257} = 91.40$, $P < 0.001$, $r^2 = 0.26$; males: $F_{1,504} = 144.85$, $P < 0.001$, $r^2 = 0.22$), and foraging rate decreased with higher walking rate (females: $F_{1,257} = 137.18$, $P < 0.001$, $r^2 = 0.34$; males: $F_{1,504} = 311.50$, $P < 0.001$, $r^2 = 0.38$). In the sample of colour-banded individuals, the proportion of pecks decreased as bill length increased ($\chi^2_1 = 16.65$, $P < 0.001$), which largely accounted for the differences between sexes (Fig. 1). Individual males showed a higher repeatability of foraging technique than females (0.43 vs. –0.28), and the distribution of proportion of pecks in males was bimodal, suggesting a tendency towards either peck or probe specialists (Fig. 1). However, within sexes, foraging technique was not correlated with bill length (both sexes $P > 0.27$).

Foraging behaviour differed between habitats (Table 1). Differences between females and males were consistent across habitats (all sex × habitat interaction terms: $P > 0.70$). Birds in brackish flats and mangroves used a higher proportion of pecks ($\chi^2_2 = 77.41$, $P < 0.001$), foraged at a lower rate ($F_{2,750} = 8.74$, $P < 0.001$), and walked at a higher rate ($F_{2,750} = 6.04$, $P = 0.002$) than those in cattail marshes. The microhabitat of foraging sites differed between sexes and between habitats (Table 1). Males foraged at shallower sites (Wald $\chi^2_1 = 124.68$, $P < 0.001$),
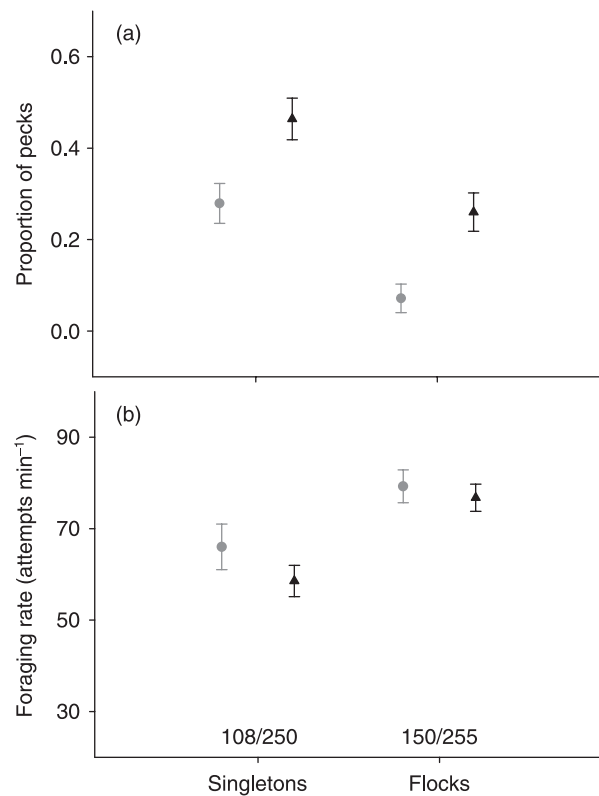

Figure 2. Proportion of pecks (a) and foraging rate (b) for singletons and flocks of female and male Western Sandpipers at Bahía Santa María, northwestern Mexico, during the non-breeding seasons of 1999–2001. Circles represent females and triangles represent males. Error bars indicate 95% confidence intervals. Sample sizes are given above the x axis (females/males).

with a lower proportion of water cover than females ($F_{1,756} = 43.96$, $P < 0.001$). Birds in cattail marshes foraged at shallower sites (Wald $\chi^2_2 = 59.99$, $P < 0.001$), with a higher proportion of water cover than those in brackish flats and mangroves ($F_{2,756} = 9.85$, $P < 0.001$).

Foraging behaviour changed when alone versus flocking, and the magnitude of this effect differed between sexes. Both sexes had a lower proportion of pecks ($\chi^2_2 = 90.41$, $P < 0.001$) and foraged at a higher rate ($F_{1,749} = 2.78$, $P = 0.04$) when they were feeding in flocks, but males changed their foraging technique and foraging rate more than did females (Fig. 2). There was no significant interaction between sex and flock effect on walking rate ($F_{1,749} = 0.40$, $P = 0.60$).

DISCUSSION

Based on bill length differences, we found, as expected, differences between sexes in foraging behaviour and

microhabitat use (Jönsson & Alerstam 1990). Males, which have shorter bills, use a greater proportion of surface foraging behaviours (pecking) than females and may search for prey more visually, producing higher walking rates and lower foraging rates. Conversely, females use a greater proportion of probing, suggesting that they rely more heavily on tactile cues and spend more time searching at each site, resulting in lower walking rates and higher rates of foraging. Surface foragers depend on the visible activity of prey, while tactile foragers depend on prey being near enough to the surface to be within range of the bill (Pienkowski 1979). These sex-related differences in foraging technique are similar to previous reports from migrant and non-breeding Western Sandpipers (Mathot & Elner 2004, Nebel 2005). In addition, we show that females foraged in sites with higher water content than males, where probing may be more effective (Gerritsen & van Heezik 1985).

Effects of sex and habitat

Sexual dimorphism can promote, and in evolutionary time result from, sex-specific niche segregation and consequent resource partitioning, reducing inter-sexual competition (Whitfield 1990, Durell 2000, Zharikov & Skilleter 2002). The sex-related differences in foraging behaviour and microhabitat use documented here suggest that the intensity of inter-sexual competition should be lower than the intensity of intra-sexual competition. In general, long-billed individuals are at an advantage when foraging on more deeply buried, and usually larger, prey; short-billed individuals are better adapted to foraging on surface prey (Jönsson & Alerstam 1990, Durell 2000). Whatever trade-offs occur, bill morphology will affect an individual's choice of most profitable foraging strategy. Elner and Seaman (2003) predicted that foraging specializations in Western Sandpipers are related to inter- and intra-sexual variation in bill length, and that plasticity of individual foraging tactics covers only part of the range found within the whole population. We found clear sex-related differences in the proportion of pecks and other behaviours, but within each sex, our behavioural samples from individually colour-banded birds did not show any correlation between bill length and foraging technique, despite reasonable power to have done so (Fig. 1). Furthermore, males showed greater foraging plasticity than females, with a bimodal distribution, suggesting some degree of foraging specialization that was not related to bill length

within sex. Variation in foraging technique within each sex may be at most weakly functionally related to bill length. Other wader studies have also reported that bill morphology does not account for all variation in diet and foraging technique (Eurasian Oystercatchers *Haematopus ostralegus*, Durell *et al.* 1993; Ruddy Turnstones *Arenaria interpres*, Whitfield 1990). Individual differences in foraging skills can arise from genetic, learning, and/or competitive differences (Durell 2000). Although foraging technique did not differ significantly between age classes, immature males tended to have a higher proportion of pecks than adult males (authors' unpubl. data).

Foraging behaviour can both influence habitat choice due to sex-related morphological differences (Puttick 1981, Summers *et al.* 1990, Zharikov & Skilleter 2002) and be affected by the availability of microhabitats (Harrington 1982, Gerritsen & van Heezik 1985, Mouritsen & Jensen 1992, Whitfield 1990). Although there were sex-related differences in foraging behaviour and microhabitat use in brackish flats and mangroves, both sexes foraged in deeper sites with a lower proportion of water cover (e.g. on the edges of tidal pools), used a higher proportion of pecks, foraged at a lower rate and walked at a higher rate than in cattail marshes. The habitat difference in foraging behaviour observed can be explained in part because sandpipers use foraging microhabitat with higher proportions of water cover at cattail marshes than those at brackish flats and mangroves (Gerritsen & van Heezik 1985). Thus sex-specific foraging behaviour and microhabitat use represent consistent preferences across habitats, despite differences in prey density and sandpiper sex ratio (Fernández & Lank 2006).

Effects of flocking

Birds might compensate for greater competition for food resources in larger groups by increasing their foraging effort or changing their foraging behaviour (Dominguez 2002, Bednekoff & Lima 2004). Goss-Custard (1970) argued that pecking-foraging waders tend to interfere more than probing-foraging waders during foraging. This logic may apply to male versus female Western Sandpipers. Males foraging in flocks decreased their proportion of pecks and foraged at a higher rate than did females. If this shift reflects foraging interference, when males change their foraging technique from pecking to probing as when flocking, it is likely that they lower their intake rate from that which they obtain in the absence of neighbours. All

else being equal, instead of changing their foraging technique, males might more profitably avoid nearest foraging neighbours to maintain their preferred foraging technique. The facts that males had similar nearest neighbour distance across habitats, whereas females had greater distances in brackish flats and mangroves than in cattail marshes, and males were more likely to be territorial than females, are consistent with this interpretation (Fernández Aceves 2005).

An alternative possibility is that reducing risk by associating with conspecifics may allow males to switch to a riskier, but more profitable, foraging technique. Probing is expected to facilitate the capture of larger prey (Durell 2000), but it also obstructs the field of vision more than pecking, and may reduce the ability to detect predators during feeding (Barbosa 1995). Several pieces of evidence argue against this risk-taking behaviour hypothesis. First, the risk hypothesis predicts differential changes as a function of habitat danger, but the sex-related differences in foraging technique and flock size were not affected by habitat type, as indicated by the lack of any statistical interaction between sex, habitat type, and flock size effects (Fernández Aceves 2005). Secondly, the sex-related differences in nearest neighbour distance among habitat types (see above) suggest that males forage in looser flocks to reduce competition and maintain their foraging technique. Finally, the higher propensity of males to use pecking technique than females, both during migration (Mathot & Elner 2004) and across different wintering sites (Nebel 2005, Mathot *et al.* 2007), suggests that this is their preferred foraging technique.

Negative effects of other foragers arise through changes in resources, which can either be depressed or depleted (Goss-Custard 1970, 1980), and through direct behavioural interactions between competitors (Goss-Custard 1980, Yates *et al.* 2000, Dominguez 2002). At the foraging sites, conspicuous social interactions among birds were unusual. The probable causes of competition in Western Sandpipers are prey depression produced when foraging birds induce prey to withdraw from the surface or the shallow water column, and/or that disturbance of the sediment makes prey harder to detect (Stillman *et al.* 2000, Yates *et al.* 2000). The differences in the flocking effects between sexes may explain in part the differential distribution by sex of Western Sandpiper in Santa María (Fernández & Lank 2006). Males were under-represented in cattail marshes, a relatively high-risk habitat. The most parsimonious explanation is that males, as consequence of their preferred foraging behaviour, are more susceptible to flocking effects and therefore avoid being in larger or tighter flocks, an anti-predator behaviour favoured in a higher-risk habitat, to maintain their intake rate.

Conclusions

Studies of temperate waders have suggested that differences in susceptibility to density-dependent competition during foraging can affect wader population size and structure during the non-breeding season (Goss-Custard 1980, Gill *et al.* 2001, Whitfield 2003b). In contrast, there has been much discussion about whether or not wader populations in tropical wintering habitats are regulated through competitive processes (Duffy *et al.* 1981, Myers & McCaffery 1984, Zharikov & Skilleter 2002). Our data provide evidence that sexes make use of different foraging behaviour, which results in differences in flock effects, and may account for differences in Western Sandpiper distribution observed between habitats. Habitat loss could be a major factor affecting these interconnected patterns of habitat distribution, because the effect of density-dependent competition is likely to increase (Goss-Custard *et al.* 1995). During the last two decades, the development of shrimp aquaculture has changed the coastal landscape in the Sinaloa region. Most of the shrimp farms have affected the hydrodynamics and connectivity of coastal wetlands, and they were built on brackish flats and emergent brackish marshes (Hernández-Cornejo & Ruiz-Luna 2000). Given the sex-related differences in local distribution and foraging behaviour in Western Sandpipers, development of the shrimp aquaculture may affect males more than females and increase the level of competition at the remaining habitat.

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 Phil Battley, Rob Butler, Dan Chamberlain, Sue Haig, Kim Mathot, Will Stein, Nils Warnock, Ron Ydenberg, Yuri Zharikov, and two anonymous reviewers. This paper is modified from one component of G.F.'s Ph.D. dissertation.

REFERENCES

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* **49**: 227–264.

Baker, M.C. 1979. Morphological correlates of habitat selection in a community of shorebirds (Charadriiformes). *Oikos* **33**: 121–126.

Barbosa, A. 1995. Foraging strategies and their influence on scanning and flocking behaviour of waders. *J. Avian Biol.* **26**: 182–186.

Bednekoff, P.A. & Lima, S.L. 2004. Risk allocation and competition in foraging groups: reversed effects of competition if group size varies under risk of predation. *Proc. R. Soc. Lond. B* **271**: 1491–1496.

Boettcher, R., Haig, S.M. & Bridges, W.C. 1995. Habitat-related factors affecting the distribution of nonbreeding American Avocets in coastal South Carolina. *Condor* **97**: 68–81.

Cartar, R.V. 1984. A morphometric comparison of Western and Semipalmated Sandpipers. *Wilson Bull.* **96**: 277–286.

Colwell, M.A. & Landrum, S.L. 1993. Nonrandom shorebird distribution and fine-scale variation in prey abundance. *Condor* **95**: 94–103.

Dominguez, J. 2002. Biotic and abiotic factors affecting the feeding behaviour of the Black-tailed Godwit. *Waterbirds* **25**: 393–400.

Duffy, D.C., Atkins, N. & Schneider, D.C. 1981. Do shorebirds compete on their wintering grounds? *Auk* **98**: 215–229.

Durell, S.E.A. Le V. dit 2000. Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biol. Rev.* **75**: 503–513.

Durell, S.E.A. Le V. dit, Goss-Custard, J.D. & Cladow, R.W.G. 1993. Sex-related differences in diet and feeding method in the Oystercatcher *Haematopus ostralegus*. *J. Anim. Ecol.* **62**: 205–215.

Elner, R.W. & Seaman, D.A. 2003. Calidrid conservation: unrequited needs. *Wader Study Group Bull.* **100**: 30–34.

Engilis, A. Jr, Oring, L.W., Carrera, E., Nelson, J.W. & Martinez-Lopez, A. 1998. Shorebird surveys in Ensenada Pabellones and Bahia Santa Maria, Sinaloa, Mexico: critical winter habitats for Pacific flyway shorebirds. *Wilson Bull.* **110**: 332–341.

Fernández Aceves, G.J. 2005. Ecological and social factors affecting the local habitat distribution of Western Sandpipers wintering at Bahía Santa María, northwest México. PhD Thesis, Simon Fraser University, Burnaby, British Columbia.

Fernández, G. & Lank, D.B. 2006. Sex, age, and body size distributions of Western Sandpipers during the nonbreeding season with respect to local habitat. *Condor* **108**: 547–557.

Fretwell, S.D. & Lucas, H.L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19**: 16–36.

Gerritsen, A.F.C. & van Heezik, Y.M. 1985. Substrate preference and substrate related foraging behaviour in three *Calidris* species. *Neth. J. Zool.* **35**: 671–692.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. 2001. The buffer effect and large-scale population in migratory birds. *Nature* **412**: 436–438.

Goss-Custard, J.D. 1970. Feeding dispersion in some overwintering wading birds. In Crook J.H. (ed.) *Social Behaviour in Birds and Mammals*: 3–35. London: Academic Press.

Goss-Custard, J.D. 1980. Competition for food and interference among waders. *Ardea* **68**: 31–52.

Goss-Custard, J.D. 1984. Intake rates and food supply in migrating and wintering shorebirds. In Burger, J. & Olla, B.L. (eds) *Shorebirds: Migration and Foraging Behavior*: 233–270. New York: Plenum Press.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A. Le V. dit, Urfi, A.J. & West, A.D. 1995. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. *Ibis* **137**: S56–S66.

Harrington, B.A. 1982. Morphometric variation and habitat use of Semipalmated Sandpipers during a migration stopover. *J. Field Ornithol.* **53**: 258–262.

Hernández-Cornejo, R. & Ruiz-Luna, A. 2000. Development of shrimp farming in the coastal zone of southern Sinaloa (Mexico): operating characteristics, environmental issues, and perspectives. *Ocean Coast. Manage.* **43**: 597–607.

Jönsson, P.E. & Alerstam, T. 1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. *Biol. J. Linnean Soc.* **41**: 301–314.

Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**: 116–121.

Lima, S.L. & Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.

Littell, R.C., Freund, R.J. & Spector, P.C. 1991. *SAS System for Linear Models*. Carey, North Carolina: SAS Institute Inc.

Mathot, K.J. & Elner, R.W. 2004. Evidence for sexual partitioning of foraging mode in Western Sandpipers (*Calidris mauri*) during migration. *Can. J. Zool.* **82**: 1035–1042.

Mathot, K.J., Smith, B.D. & Elner, R.W. 2007. Latitudinal clines in food distribution correlate with differential migration in the Western Sandpiper. *Ecology* **88**: 781–791.

Mouritsen, K.N. & Jensen, K.T. 1992. Choice of microhabitat in tactile foraging Dunlins *Calidris alpina*: the importance of sediment penetrability. *Mar. Ecol. Prog. Ser.* **85**: 1–8.

Myers, J.P. & McCaffery, B.J. 1984. Paracas revisited: do shorebirds compete on their wintering ground? *Auk* **101**: 197–199.

Nebel, S. 2005. Latitudinal clines in bill length and sex ratio in a migratory shorebird: a case of resource partitioning? *Acta Oecol.* **28**: 33–38.

Page, G. & Fearis, B. 1971. Sexing Western Sandpipers by bill length. *Bird-Banding* **42**: 297–298.

Pienkowski, M.W. 1979. Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. *Verh. Orn. Ges. Bayern* **23**: 105–124.

Puttick, G.M. 1981. Sex-related differences in foraging behaviour of Curlew Sandpipers. *Ornis Scand.* **12**: 13–17.

Puttick, G.M. 1984. Foraging and activity patterns in wintering shorebirds. In Burger, J. & Olla, B.L. (eds) *Shorebirds: Migration and Foraging Behavior*: 203–232. New York: Plenum Press.

SAS Institute. 2001. *SAS/SAT User's Guide*, Version 8.2. Carey, North Carolina: SAS Institute, Inc.

Stillman, R.A., Goss-Custard, J.D. & Alexander, M.J. 2000. Predator search and the strength of interference through prey depression. *Behav. Ecol.* **11**: 597–605.

Summers, R.W., Smith, S., Nicoll, M. & Atkinson, N.K. 1990. Tidal and sexual differences in the diet of Purple Sandpipers *Calidris maritima* in Scotland. *Bird Study* **37**: 187–194.

Sutherland, T.F., Shepherd, P.C.F. & Elner, R.W. 2000. Predation on meiofaunal and macrofaunal invertebrates by Western Sandpipers (*Calidris mauri*): evidence for dual foraging modes. *Mar. Biol.* **137**: 983–993.

Tripp, K.J. & Collazo, J.A. 1997. Non-breeding territoriality of Semipalmated Sandpipers. *Wilson Bull.* **109**: 630–642.

Vahl, W.K., van der Meer, J., Weissing, F.J., van Dullemen, D. & Piersma, T. 2005. The mechanism of interference competition: two experiments of foraging waders. *Behav. Ecol.* **16**: 845–855.

Warnock, S.E.G. & Takekawa, J.Y. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. *Ibis* **138**: 160–167.

Whitfield, D.P. 1990. Individual feeding specializations of wintering Turnstone *Arenaria interpres*. *J. Anim. Ecol.* **59**: 193–211.

Whitfield, D.P. 2003a. Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to Sparrowhawk *Accipiter nisus* predation. *J. Avian Biol.* **34**: 163–169.

Whitfield, D.P. 2003b. Predation by Eurasian Sparrowhawks produces density-dependent mortality of wintering Redshanks. *J. Anim. Ecol.* **72**: 27–35.

Yates, M.G., Stillman, R.A. & Goss-Custard, J.D. 2000. Contrasting interference functions and foraging dispersion in two species of shorebird (Charadrii). *J. Anim. Ecol.* **69**: 314–322.

Zharikov, Y. & Skilleter, G.A. 2002. Sex-specific intertidal habitat use in subtropically wintering Bar-tailed Godwits. *Can. J. Zool.* **80**: 1918–1929.