

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

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 & Elnor 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 (Elnor & 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 ($P < 0.38$).

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 & Elnor 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. Elnor 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

Sexagiiibun addition,suggesomon musee8(ates of for) 17.8((ater)]TJ * 0.3063aging speciali8(andigher w)sw (dis are relatoc2

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 & Elnor 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.

SAS/SAT User's Guide

Behav. Ecol **11**

Calidris maritima

Bird Study **37**

Calidris mauri

Mar. Biol **137**

Wilson Bull **10**