

Territorial behavior of Western Sandpipers on their nonbreeding grounds: effect of sex and foraging interference

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ABSTRACT. Nonbreeding shorebirds often alternate social structure between anonymous flocks and territorial behavior in response to different environmental factors. To evaluate specific drivers for one species, we studied the spacing behavior of wintering Western Sandpipers (*Calidris mauri*) at Bahía Santa María, northwestern Mexico, using behavioral observations. The density, population structure, and territorial behavior of Western Sandpipers differed among three habitat types. Cattail marshes supported 110 birds per ha, 49% males, and no territorial birds. Mangrove flats supported 288 birds per ha, 58% males, and 5% territorial birds. Brackish flats supported 365 birds per ha, 76% males, and 7% territorial birds. Territories consisted of rectangular strips (5–9 m long, $N = 77$). Territory length was not related to either bird density or number of territorial birds by plot, but was positively related to nearest bird distance. Aggression rate was inversely related to territory length, suggesting that territory length is set by the costs of defense. Foraging rate was independent of territory length, and prey densities in territories did not differ from those in areas used by nonterritorial birds. Males were more likely to be territorial and had a higher aggression rate than females, suggesting that males, which forage more on surface prey, were more affected by foraging interference. Our results suggest that the territorial behavior of Western Sandpipers in our study was an opportunistic strategy to reduce foraging interference. The variation in spacing behavior we documented provides evidence that interference competition affects the social structure of Western Sandpipers during the nonbreeding season.

RESUMEN. Comportamiento territorial del Playerito Occidental durante la época no-reproductiva: efecto del sexo y la interferencia de forrajeo

Las aves playeras durante la época no-reproductiva alternan su estructura social entre parvadas compactas y comportamiento territorial en respuesta a diferentes factores ambientales. Para evaluar factores específicos en una especie, se estudio el comportamiento espacial del Playerito Occidental (*Calidris mauri*) invernante en Bahía Santa María, noroeste de México, utilizando observaciones de comportamiento. La densidad, estructura poblacional y comportamiento territorial del Playerito Occidental fue diferente en tres tipos de hábitat. Los tulares presentaron 110 aves por hectarea, 49% de machos, sin aves territoriales. Los manglares tuvieron 288 aves por hectarea, 58% de machos y 5% de aves territoriales. Las planicies lodosas presentaron 365 aves por hectarea, 76% de machos y 7% de aves territoriales. Los territorios fueron rectángulos (5–9 m largo, $N = 77$). La longitud del territorio no se relacionó con la densidad de aves o número de aves territoriales por cuadrante, pero estuvo inversamente relacionada con la distancia del individuo más cercano. La tasa de agresión estuvo inversamente relacionada con la longitud del territorio, sugiriendo que la longitud del territorio está determinada por los costos de defensa. La tasa de forrajeo fue independiente de la longitud del territorio y la densidad de presas no fue diferente entre territorios y sitios utilizados por aves no territoriales. La mayoría de las aves territoriales fueron machos y exhibieron una tasa de agresión mayor que las hembras, sugiriendo que los machos, que se alimentan de manera superficial, son más susceptibles a la competencia. Los resultados indican que la territorialidad del Playerito Occidental es una estrategia de oportunidad para reducir la competencia. La variación en el comportamiento espacial observada ofrece evidencia de que la competencia afecta la estructura social del Playerito Occidental durante la época no-reproductiva.

Key words: aggression, *Calidris mauri*, foraging, shorebirds, spacing distribution, territory size

During the nonbreeding season, the spacing behavior of shorebirds is flexible and variable,

ranging from individual territoriality to dense flocking (Myers 1984, Colwell 2000). For nonbreeding shorebirds, territoriality is the defense of a fixed location by an individual for a variable period of time, and is food-resource-related (Colwell 2000). Within species, individual

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differences in spacing behavior have been found to be correlated with body size and competitive abilities (Townsend 1985, Turpie 1995), predation danger (*sensu* Lank and Ydenberg 2003), with less territoriality and more flocking with higher environmental danger (Myers 1980, Whitfield 1988), and foraging mode, with territorial behavior more prevalent in species or individuals that use visual (pecking at or near the substrate surface) rather than tactile (probing in the substrate) cues to detect prey (Colwell 2000).

To be economically (or adaptively) defensible, a territory must yield net benefits greater than those available to individuals using the same space nonterritorially (Brown 1964, Myers et al. 1981). Because of the patchy distribution of resources, the sizes of territories defended by many species exhibit intraspecific variation. Two hypotheses have been proposed to explain variation in the size of shorebird territories (Myers et al. 1979a, 1981, Zharikov and Skilleter 2004). If individuals can assess the local food density, territory size may vary inversely with food density (the patch quality assessment hypothesis). Alternatively, individuals may defend as large an area as possible, but territory size may be limited by intruder pressure (the competition hypothesis). These hypotheses need not be mutually exclusive. Areas of higher prey density attract more competitors and thus become more costly to defend (Myers et al. 1979a, 1981). Therefore, territory size may be determined by a balance between resource benefits and the social costs of defense (McLean and Seastedt 1979, McNail 1987).

Although theoretical frameworks for understanding variation in territoriality are well established, determining their applicability to particular cases is necessary to substantiate inferences about the general adaptive significance of territorial behavior. We examined variation in the territorial behavior of Western Sandpipers (*Calidris mauri*) during the nonbreeding season at Bahía Santa María in northwestern Mexico (hereafter, Santa María). Western Sandpipers are highly sexually dimorphic, with females ~10% heavier and 15% longer billed than males (Cartar 1984). They are thought to be foraging generalists, feeding on virtually any invertebrate within the size range of 0.1–5.0 mm (Davis and Smith 1998, Sutherland et al. 2000) and on biofilm (Kuwaie et al. 2008, 2012). Males forage on drier substrates and tend to use a higher

proportion of pecks than females (Mathot and Elnor 2004, Nebel 2005, Mathot et al. 2007, Fernández and Lank 2008). Like other shorebirds, Western Sandpipers may defend small feeding territories on the wintering grounds (Recher and Recher 1969, Myers and McCaffery 1984, Tripp and Collazo 1997), but, in general, their nonbreeding population structure consists of broadly overlapping home ranges and little overt aggression (Warnock and Takekawa 1996).

At Santa María, >350,000 Western Sandpipers, ~10% of the global population (Bishop et al. 2000), spend the winter, widely distributed among a mosaic of habitats (Engilis et al. 1998). We recognized three habitat types—brackish flats, mangroves, and cattail marshes—used by sandpipers that differed with respect to prey and bird densities and level of danger from avian predators (Fernández and Lank 2006). We estimated the density of benthic prey density as an index of resource quality and inferred levels of predation danger based on average distances to vegetation. Distance to cover has been used to index environmental predation danger to foraging small shorebirds from raptors, their principle predators, because raptor success rates are highest when raptors are able to emerge from cover and surprise birds on the ground (Whitfield 2003, Dekker and Ydenberg 2004, Pomeroy et al. 2006). Brackish flats were the most open, cattail marshes the most enclosed, and mangrove habitat intermediate with regard to distance to vegetation. Brackish flats had the highest bird and prey densities and lowest predation danger, whereas cattail marshes had the lowest bird and prey densities and highest predation danger. Bird and prey densities and predation danger were similar in mangroves and cattail marshes. Given that bird densities broadly matched prey densities across habitats, Western Sandpipers may be distributed across habitats in an ideal free manner (Fretwell and Lucas 1970). The proportion of Western Sandpipers in brackish flats, their preferred habitat, may depend on the degree of interference between individuals (Fernández and Lank 2008).

If interference competition plays an important role in shaping Western Sandpiper local distribution, we predicted that territorial behavior would be more common in habitats with higher bird densities (brackish flats and mangroves). Further, we predicted that males, who more

often forage by surface pecking than females, would be more susceptible to interference than females, and thus gain more than females from being territorial. Based on differences between territorial and nonterritorial individuals in foraging and spacing behavior in other shorebird species (Myers et al. 1979a, Turpie 1995, Tripp and Collazo 1997), territorial birds should use a surface-pecking foraging strategy, be more dispersed, and have higher aggression and vigilance rates than nonterritorial birds. Additionally, we examined the effects of prey density and intruder density on territory size, and compared prey densities in territories with those in adjacent areas. If patchiness in prey distributions is driving territoriality in this system, we expected to find higher prey densities in territories.

METHODS

Our study was conducted at Bahía Santa María (25° 02' N, 108° 18' W), located 90 km northwest of Culiacan City in northwestern Mexico. Santa María is the largest wetland on the Sinaloa coast (1350 km²) and consists of a diverse mosaic of habitats, including an outer bay, intertidal mudflats, mangroves, brackish flats, emergent brackish marshes, and freshwater marshes (Engilis et al. 1998). Our study site was located on the east side of the wetland, just south of the village of La Reforma, covering an area of ~180 km². We captured and observed Western Sandpipers in three habitats: brackish flats, mangrove-salt marsh flats, and cattail marshes (Fernández and Lank 2006). Brackish flats were large areas (>3.0 km) ranging from completely open unvegetated flats to sparsely vegetated areas with *Scirpus* and *Salicornia*. Mangrove salt marsh flats (hereafter, mangroves) were smaller (<1.0 km) open flats interspersed by patches of mangroves. Mangroves were dominated by black mangrove (*Avicennia germinans*) with some emergent vegetation, mainly *Spartina* and *Salicornia*. Cattail marshes had small mudflats along the edges of the marshes (<0.5 km) in freshwater areas, adjacent to extensive stands of cattails (*Typha* spp.) with other secondary vegetation, such as *Scirpus*, *Atriplex*, and *Chenopodium*. Brackish flats and mangroves flooded twice a month during spring tides, with the highest tides in December.

Data collection. Observational data were collected from December to February 2000–

2001 and 2001–2002. Focal individual and scan sampling were used to collect behavioral data (Altmann 1974). Scan data were obtained using a 15–60× spotting scope at sampling plots (50 m × 50 m = 0.25 ha; $N = 62$) established randomly in each habitat. Boundaries of plots were defined using landmarks (e.g., water channels, mangrove trees, or salt marsh edges). Given the habitat configuration, plots in mangroves and cattail marshes were closer to vegetative cover (<200 m), whereas distances between plots and vegetation cover varied greatly in brackish flats (evenly sampled: close to cover, <200 m; intermediate, 200–900 m; and far from cover, >1000 m).

In each plot, all Western Sandpipers and territorial birds were counted at 20 min intervals for at least 4 h, and an average sandpiper density and the percentage of territorial birds per plot per day were calculated (Fernández and Lank 2006). Focal observations were used to determine the amount of time that selected individuals were engaged in distinct behaviors (see below) and were carried out in sampling plots. Randomly selected birds were observed for ~2 min from distances <30 m using a spotting scope. Data were dictated into a tape recorder, timed with a stopwatch, and later transcribed. We preferentially observed color-banded birds. However, 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 center of the field of view. We estimated the number of neighbors and nearest bird distance from the focal individual. Birds within 3 m of a focal bird were considered neighbors (Fernández and Lank 2008).

We trapped 1148 Western Sandpipers at over 86 locations in the wetland. We used two mist-nets (32 mm, 2.6 × 12 m, four shelves) accompanied by broadcasts of Western Sandpiper alarm calls to capture sandpipers during morning sessions (e.g., 07:00 to 11:00). At the time of capture, we measured body mass (± 0.5 g) and bill (exposed culmen, ± 0.1 mm). Birds were banded with a U.S. Geological Survey aluminum band and unique combinations of color bands. All morphological measurements were made by Fernández. Banded birds were sexed using bill length (Page and Fearis 1971; males < 24.2 mm, females > 24.8 mm), and the proportions caught were used to estimate local sex ratios. The mean (\pm SE) bill length of

captured females and males was 26.9 ± 0.03 mm ($N = 383$) and 22.7 ± 0.02 mm ($N = 765$), respectively. For unbanded birds, visual assignment of sex was made based on relative bill size. The accuracy of this technique was verified using banded birds, with 90% of 234 birds showing agreement with that based on measurements.

Behavior was classified into three main categories (Tripp and Collazo 1997, Davis and Smith 1998): foraging (pecking or probing), vigilance (bird visually scanning surroundings), and aggression (chasing, fighting, or threatening another individual with head and wings down and rump raised). These three categories were the most frequent behaviors during focal observations; other behaviors, such as body maintenance and sleeping, made up <8% of the total. During focal observations, a single observer (Fernández) tried to quantify all activities simultaneously to estimate the foraging (attempts per minute), walking (steps per minute), vigilance (scans per minute), and aggression (events per minute) rates. Western Sandpipers feed on a wide variety of small invertebrates that are handled very quickly (Sutherland et al. 2000) and intake rate cannot be measured directly. The proportion of pecks (pecks/total foraging attempts) was used as an index of foraging technique. 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 focal birds. Water depth was scored using 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 (Fernández and Lank 2008).

Western Sandpipers were considered territorial if they exhibited vigilance in response to potential intruders or aggressive displays (see above) associated with boundary disputes at particular locations during focal observations and scan sampling. In contrast, nonterritorial birds moved continuously while foraging and aggressive behavior was not associated with particular locations. Territory length was estimated based on the locations of other birds that elicited an aggressive stance or attack from the territorial birds (Myers et al. 1979a). Interactions between neighbors in the linear array were more common than those with intruders from nonterritorial areas. Due to physical characteristics of areas with territories (see Results section), we quantified

territory size in terms of the length of defended space between adjacent territorial birds or using landmarks as reference points, because length was more reliably measured than area, and the width of territories appeared fairly uniform within sites.

To estimate relative prey densities in territories and areas used by nonterritorial birds, sediment cores were collected from paired locations. Cores were extracted using a modified 60-cc syringe (2.6-cm inner diameter, with the apex sliced off and the edge beveled). Cores were collected in a randomly selected site within territories and areas used by nonterritorial bird (15 m apart) by inserting the syringe 3 cm into the sediment. Fifteen pairs of territorial and nonterritorial cores were collected in 2000, and 12 in 2001. Sediment cores were extruded in situ, inserted into appropriately labeled plastic bags, and placed in a freezer. After thawing, macrofaunal fractions were obtained by sieving each core through 0.5 mm mesh sieve following the method of Sutherland et al. (2000). Invertebrate taxa present were identified and counted to estimate potential prey density.

Statistical analyses. For analyses of bird and prey densities, the effect of habitat was analyzed using one-way analysis of variance (ANOVA). Sex- and habitat-type differences in standardized values of the inverse of territory length (m) were analyzed using a two-way ANOVA. Relationships between territory length and bird density, number of territorial birds, and nearest bird distance were analyzed with a general linear model (GLM). Habitat-type differences in the percentage of birds engaged in territorial behavior were analyzed using a one-way ANOVA. Habitat differences in the proportion of males were analyzed using a one-way ANOVA, weighted by the number of birds caught. We assumed that trapped samples were representative of the populations using each habitat. Sex ratios of Western Sandpipers captured in cattail marshes were even; sex ratios of sandpipers captured in mangroves and brackish flats were increasingly male-biased (Table 1). Prior to analyses, bird and prey densities, and nearest bird distance were log-transformed, and the proportion of males was arcsine square-root transformed. To account for potential annual differences, winter season (i.e., 2000–2001 and 2001–2002) was added as a covariate to models of bird and prey densities, territory length,

Table 1. Population structure and occurrence of territorial behavior of Western Sandpipers at Bahía Santa María, northwestern Mexico, during the nonbreeding seasons of 2000–2002. Bird densities and proportion of territorial birds were estimated using 50 m × 50 m plots (0.25 ha) established in each habitat.^a

	Brackish flats	Habitat type Mangroves	Cattail marshes
Number of plots	45	12	5
Bird density (birds per ha)	365 ± 40	288 ± 81	110 ± 102*
% Territorial birds	7.1 ± 1.0	4.9 ± 2.1	–
Proportion of males ^b	0.76 ± 0.03* (604)*	0.58 ± 0.04 (430)	0.49 ± 0.07 (114)
Territorial birds (No. of observations)	0.91 (58)	0.89 (19)	–

^aAn asterisk indicates significant differences with other habitats, $P < 0.05$.

^bBased on birds captured in mist-nets.

percentage of territorial birds, and habitat differences.

For comparison of territorial and nonterritorial birds, we included 575 focal observations, including 163 of banded birds, with a mean observation time of 1.90 min (SE = 0.01). Status (territorial and nonterritorial), sex, and habitat differences in foraging (foraging technique, and foraging and walking rates), spacing (number of neighbors and nearest bird distance), antipredator (vigilance rate), and aggressive behaviors were investigated with a mixed-model ANOVA. Differences between territorial and nonterritorial birds in microhabitat characteristics were also analyzed. Status, sex, and habitat differences in the proportion of water cover were analyzed using ANOVA. Water depth was treated as an ordinal response variable and analyzed using logistic regression models (Wald χ^2 , two-tailed) with a cumulative logit link function, to determine the effects of sex and habitat. Prior to analysis, proportion of pecking and water cover were arcsine square-root transformed, and number of neighbors, nearest bird distances, and foraging, walking, vigilance, and aggression rates were log-transformed to permit parametric analyses. Relationships between territory length, aggression, and foraging rates were analyzed with a GLM. Density of potential prey was analyzed using a two-way ANOVA to determine the effects of territorial and nonterritorial sites and habitat. For territories where sediment cores were taken, relationships between territory length, prey density, and aggression and foraging rates were analyzed with a GLM. Models of behavior budgets, water cover and depth, and prey density included winter season as a covariate.

We considered test results to be significant at $P < 0.05$, except for interaction terms, which we considered significant at $P < 0.10$ because 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 SS, and we reported least-squares means, taking the other factors and annual variation into account. We made all pairwise post hoc comparisons using the Tukey–Kramer test. Least-squares means and slopes (\pm SE) are presented unless otherwise stated. All statistical tests were performed using SAS 8.2 (SAS Institute 2002).

RESULTS

Territorial behavior. Territories were temporary feeding sites (10–60 min), rather than sites permanently occupied and defended throughout the day. Territorial behavior was observed in brackish flats and mangroves, but not in cattail marshes (Table 1). Because few banded territorial birds were observed (4%, $N = 77$), we were unable to determine if the same individuals repeatedly defended the same sites or to assess the duration of territory defense. When a predator approached, e.g., a Peregrine Falcon (*Falco peregrinus*) or Merlin (*F. columbarius*), territorial and nonterritorial birds formed flocks and avoided falcons by flying up. Even more transitory territorial behavior was observed in areas where the substrate was recently (<10 min) disturbed (e.g., footprints or airboat tracks); foraging sandpipers tended to concentrate at such sites for short periods of time

Table 2. Differences in behavioral activities between territorial and nonterritorial Western Sandpipers at Bahía Santa María, northwest Mexico, during the nonbreeding seasons of 2000–2002. Least-squares means (\pm SE) are reported, controlling for status, sex, habitat type, and winter season.

Variable	Nonterritorial	Territorial	F^a
Number of neighbors	4.6 \pm 0.3	0.8 \pm 0.9	55.3
Nearest bird distance (m)	3.5 \pm 0.1	5.7 \pm 0.3	48.5
Foraging mode (proportion of pecks/total foraging attempts)	0.17 \pm 0.01	0.45 \pm 0.03	50.6
Foraging rate (attempts per min)	72.4 \pm 1.3	49.7 \pm 3.1	49.6
Walking rate (steps per min)	73.2 \pm 1.8	102.4 \pm 4.3	38.4
Vigilance rate (scans per min)	1.98 \pm 0.01	3.19 \pm 0.21	32.7

^aFor all variables: $df = 1, 570$ and $P < 0.01$.

(<90 min) and site-based aggressive behavior was common.

Most territories were adjacent rectangles, end to end, in strips along deeper water channels, salt marsh edges, or patches of mud. Mean territory length ($N = 77$) was 7.80 ± 0.38 (SE) m. Territory length did not differ between sexes ($F_{1,72} = 0.3$, $P = 0.58$) or habitat types ($F_{1,72} = 0.8$, $P = 0.37$), and was not affected by sandpiper density ($F_{1,76} = 1.0$, $P = 0.33$) or number of territorial birds per ha ($F_{1,76} = 2.8$, $P = 0.10$). However, territory length was positively related to the nearest neighbor distance ($r^2 = 0.36$; $F_{1,76} = 42.4$, $P < 0.0001$).

Mean sandpiper densities varied from 110 to 365 birds per ha among habitats (Table 1). Densities were higher in brackish flats and mangroves than in cattail marsh ($F_{2,59} = 10.5$, $P = 0.0001$). The mean percentage of territorial birds in brackish flats (7.1%) and mangroves (4.9%) did not differ ($F_{1,56} = 2.8$, $P = 0.10$; Table 1). In cattail marshes, territorial behavior was not observed, and sandpipers always fed in flocks of a few to >50 individuals. Local sex ratios, from banding data, were more male-biased in brackish flats than in mangroves and cattail marshes ($F_{1,63} = 8.6$, $P = 0.0005$; Table 1). The sex composition of focal territorial birds further overrepresented males relative to local sex ratios (Fisher's exact tests; brackish flats, $P = 0.003$; mangroves, $P = 0.01$), but did not differ between the two habitats ($P = 0.77$).

Territorial versus nonterritorial behavior. Controlling for status, sex, habitat, and winter season, territorial birds had fewer neighbors and greater nearest bird distances, used a higher proportion of pecks, walked at higher rates (more steps per minute), foraged at lower rates, and were more vigilant

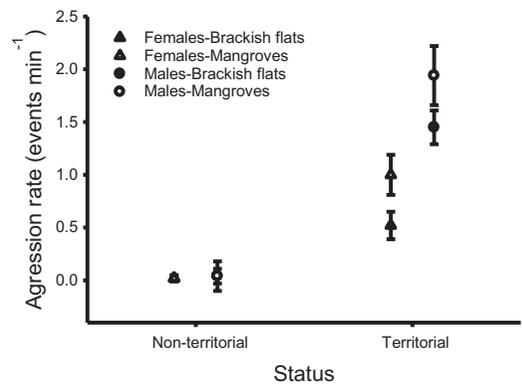


Fig. 1. Aggression rate of territorial and nonterritorial Western Sandpipers in relation to sex and habitat at Bahía Santa María, northwestern Mexico, during the nonbreeding seasons of 2000–2002. Least-squares means (\pm 95 CI) are reported controlling for status, sex, habitat, wintering season, and interaction terms: sex \times status and habitat \times status.

than nonterritorial birds (Table 2). We recorded 275 aggressive encounters during 575 focal samples. Social interactions were more common among territorial birds than nonterritorial birds. Aggressive encounters were observed in 87% ($N = 77$) of territorial birds compared with 6% ($N = 498$) of nonterritorial birds (Fisher's exact test, $P < 0.0001$). Among nonterritorial birds, aggressive interactions were simpler, mainly physically pushing other individuals to usurp a feeding site. Aggression levels were higher among territorial birds than nonterritorial birds (Fig. 1). However, aggression levels of territorial birds interacted significantly with sex (sex \times status; $F_{1,568} = 7.3$, $P = 0.007$) and habitat (habitat \times status; $F_{1,568} = 10.0$, $P = 0.001$). Territorial males had higher encounter rates

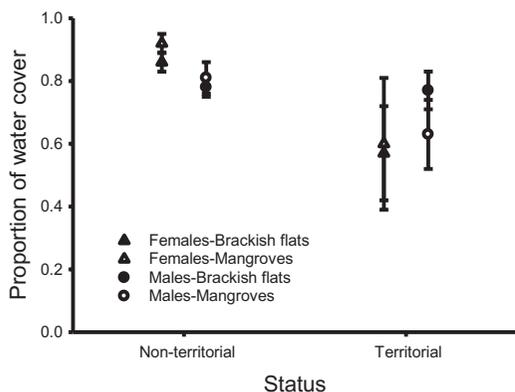


Fig. 2. Proportion of water cover of territories and areas used by nonterritorial Western Sandpipers in relation to sex and habitat at Bahía Santa María, northwestern Mexico, during the nonbreeding seasons of 2000–2002. Least-squares means (± 95 CI) are reported controlling for status, sex, habitat, wintering season, and interaction terms: sex \times status and habitat \times status.

than territorial females, especially in brackish flats (Fig. 1).

Microhabitat use also differed between territorial and nonterritorial Western Sandpipers. The proportion of water cover was lower in territories than at sites used by nonterritorial birds (Fig. 2), but the proportion of water cover in territories interacted significantly with sex (sex \times status; $F_{1,568} = 10.8$, $P = 0.001$) and habitat (habitat \times status; $F_{1,568} = 8.5$, $P = 0.003$), such that territorial males in brackish flats used sites with more water cover than territorial females and males in mangroves (Fig. 2). Water depth did not differ in areas used by territorial and nonterritorial sandpipers (Wald $\chi^2_1 = 1.1$, $P = 0.30$).

Territory size, prey abundance, and bird density. Aggression rate was inversely related to territory length ($r^2 = 0.15$, $F_{1,76} = 14.2$, $P = 0.0006$), but foraging rate was not ($P = 0.11$). Aggression rate was not significantly related to foraging rate ($P = 0.21$). Prey density in sediment cores was higher in brackish flats than in mangroves (least square means: 0.28 ± 0.02 vs. 0.08 ± 0.03 individuals per mL; $F_{1,53} = 10.3$, $P = 0.002$). However, controlling for habitat, prey densities in areas used by territorial and nonterritorial birds did not differ (least square means: 0.20 ± 0.02 vs. 0.16 ± 0.02

individuals per mL; $F_{1,53} = 0.6$, $P = 0.42$). Neither prey density ($P = 0.18$) nor foraging rate ($P = 0.13$) was related to territory length, and foraging rate was not related to prey density ($P = 0.95$). For territorial birds where prey was sampled, aggression rate was inversely related to territory length ($r^2 = 0.23$, $F_{1,26} = 7.7$, $P = 0.01$). Aggression rate was not related to either prey density ($P = 0.20$) or foraging rate ($P = 0.19$). Because aggression rate was the only variable explaining variation in territory size, partial correlations analysis was not used.

DISCUSSION

Different trade-offs between foraging costs (interference competition) and safety benefits (predation risk) may explain variation among habitats in the spacing behavior of Western Sandpipers at Santa María. In brackish flats and mangrove habitats, >90% of individuals foraged in dispersed mobile flocks, with 5–7% of sandpipers defending feeding territories for at least an hour. In cattail marshes, however, sandpipers always fed in flocks. In theory, interference competition should cause shorebirds to feed in smaller or more dispersed flocks (Goss-Custard 1970, Myers 1984). To further avoid interference, some individuals may defend exclusive feeding areas (Myers et al. 1979a, 1980). Conversely, the risk of predation is usually considered the primary selection pressure favoring flocking in shorebirds (Myers 1980, 1984, Whitfield 1988). Territorial behavior is less likely when predation danger is higher (Myers 1984, Whitfield 1988). The absence of sandpiper territoriality and use of flocking behavior in cattail marshes are consistent with the greater danger in habitats where low-flying raptors can surprise foraging sandpipers by emerging from cover (see Methods section). Antipredator tactics, such as flocking, may reduce predation risk and allow Western Sandpipers to use more dangerous habitats (Myers 1984, Whitfield 1988, Lank and Ydenberg 2003, Fernández and Lank 2010).

Fernández and Lank (2008) suggested that interference competition influenced the local distribution of Western Sandpipers at Santa María. Based on the extent to which sandpipers decreased the proportion of pecks in response to increasing flock size, foraging interference was stronger in brackish flats and mangroves than

cattail marshes. The occurrence of territorial behavior in these habitats is consistent with this interpretation because, in addition to encouraging flocking birds to spread out, defending exclusive feeding areas prevents or limits foraging interference. Based on field observations, Western Sandpipers defended territories on a scale of minutes, suggesting that territorial behavior at Santa María was opportunistic (*sensu* Colwell 2000). Observations of foraging birds at sites with recently disturbed sediment (e.g., footprints or airboat tracks) also support this idea. Observations suggest that sediment disturbance facilitates foraging due to an increase in the proportion of prey available at the substrate surface (Guillermo Fernández, personal observation). Territories occupied for a short period of time seem particularly likely to reduce the effect of foraging interference (Myers et al. 1979b).

As predicted, we found that territorial Western Sandpipers, because of their aggressiveness, used sites with lower densities of conspecifics, used a more surface-pecking foraging strategy, and were more vigilant than nonterritorial birds. In addition, territorial birds were more male-biased, especially in mangrove habitats, and aggression levels were higher among territorial males and territorial birds in mangroves. Fernández and Lank (2008) found that male Western Sandpipers decreased their proportion of pecks more than females when they changed from feeding alone to feeding in flocks, suggesting greater susceptibility to conspecific interference when flock feeding. This may explain why males were more likely to be territorial and aggressive than females, despite their smaller size. However, it is not clear why sandpipers were more aggressive in mangrove habitats. The area of mangrove habitat was smaller than for brackish flats in our study area, and within-habitat heterogeneity might influence availability of suitable foraging sites for sandpipers. Mangrove habitat consisted of a mosaic of open areas with patches of vegetation, including mangrove trees and salt marsh edges, which may have reduced the number of appropriate sites to establish territories, possibly requiring sandpipers to be more aggressive.

We found that territory size and nearest bird distance were positively correlated, and aggression rates decreased as territory length increased. In contrast, prey density and foraging rate were unrelated to territory length.

Although correlative, these results are consistent with the hypothesis that territory size was regulated by intraspecific intruder pressure (cost of defense). Similar results have been reported in studies of Sanderlings (*Calidris alba*), Black-bellied Plovers, and Semipalmated Sandpipers (*C. pusilla*; Myers et al. 1979a, Turpie 1995, Tripp and Collazo 1997). Conversely, territory size and intake rate were found to be negatively and positively correlated, respectively, with food density in Eastern Curlews (*Numenius madagascariensis*). Thus, territory size is governed by the density of available prey (Zharikov and Skilleter 2004). Differences between species in the importance of prey density versus intruder pressure in territorial behavior may be due to differences in winter spacing patterns. Among small sandpipers, most individuals are nonterritorial (80–98%, Tripp and Collazo 1997, Colwell 2000, this study). In Black-bellied Plovers, 35–75% of the population was found to be nonterritorial (Turpie 1995, Colwell 2000). In contrast, only 6% of an Eastern Curlew population was nonterritorial (Zharikov and Skilleter 2004). Therefore, the constant presence of nonterritorial birds may strengthen the relationship between intruder density and prey density and thereby exacerbate competition for preferred sites (Myers et al. 1979a).

Contrary to the patch quality hypothesis, we detected no difference in prey densities in areas used by territorial and nonterritorial Western Sandpipers. Territory holders often have nearly exclusive access to higher than average prey concentrations (Myers et al. 1979a, Turpie 1995, Tripp and Collazo 1997). To be profitable, defending a territory must yield net benefits greater than those available to individuals using the same space nonterritorially (Brown 1964, Myers et al. 1981). We were not able to identify the prey defended or estimate intake rate. However, in an environment with uniform prey abundance, territorial birds may create differential availability of prey by reducing the amount of prey depression by conspecifics, and thereby maintain their intake rate despite their lower foraging rate.

We conclude that interference competition partially shapes the spacing behavior of Western Sandpipers within and among habitat types at Santa María during the nonbreeding season. A facultative strategy such as nonbreeding territoriality offers shorebirds the flexibility to

cope with differences in bird density in areas with lower predation danger. Our observations suggest that territorial defense reduces the level of foraging interference. Duration of territory holding is likely a function of intruder densities rather than adjustments to fluctuations in resource availability, although transient temporary defense of disturbed sites also occurs.

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