SEX, AGE, AND BODY SIZE DISTRIBUTIONS OF WESTERN SANDPIPERS DURING THE NONBREEDING SEASON WITH RESPECT TO LOCAL HABITAT

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C E , D a B a , Fa , 8888 D , B a , BC V 5A 1 6, C a a

A a . We documented the local density and sex, age-class, and body size distributions of Western Sandpipers (*C a*) among habitats at Bahía Santa María, northwestern Mexico, during the nonbr9 141.77531 587

Cresswell 1994, Whitfield 2003, Dekker and Ydenberg 2004). We therefore recorded predator encounter frequency and estimated distance to cover to rank the habitats with respect to relative level of predation danger.

METHODS

STUDY AREA

This research was conducted at Santa María (25 029N, 108 189W), about 90 km northwest of Culiacán City, northwestern Mexico. Santa María is the largest wetland on the Sinaloa coast, and is composed of 1350 km^2 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 wetland, just south of the village of La Reforma, covering an area of approximately 180 km^2 (15 km 3 12 km). 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 large areas ranging from completely open unvegetated flats to sparsely vegetated areas with spp. and *a* *a* spp. The mangrove–salt marsh flats (‘‘mangroves’’) were smaller open flats broken up by patches of mangroves. Mangroves were dominated by black mangrove (*A* *a* *a*) with some emergent vegetation, mainly *a* *a* spp. and *a* *a* spp. The cattail marshes were small beaches in freshwater areas, adjacent to extensive stands of cattails (*la* spp.) with other secondary vegetation, such as spp., *A* spp., and *Cl* spp. Brackish

In 2001 and 2002, we estimated distances from sandpiper capture sites to the nearest vegetation cover. We used these relative distances as an *a* index of the relative level of predation danger of each habitat (sensu Lank and Ydenberg 2003). In all three winters, the raptor encounter rate (raptors hr^{21}) was estimated for each habitat using a point-count method based on the number of raptors noted in 469 hours of fieldwork. The most common predators of Western Sandpipers were Peregrine Falcons (*Fa*) and Merlins (

habitat was more variable, and intermediate with regard to distance to vegetation (Fig. 1). Combining similar raptor encounter rates with differential distances to cover implies that, all else being equal, brackish flats are the safest and cattail marshes the most dangerous habitats for sandpiper (Table 2).

WESTERN SANDPIPER DENSITIES AND POPULATION STRUCTURE

Densities of Western Sandpipers ranged from 94 to 448 birds ha^{21} and differed among habitats (*F*

TABLE 2. Summary of habitat rankings with respect to environmental conditions and Western Sandpiper population structure, and inferred levels of overall suitability and interference competition in Bahía Santa María, northwestern Mexico, during the nonbreeding seasons of 1999–2001. NSD 5 no significant difference.

	Habitat type		
	Brackish flats	Mangroves	Cattail marshes
Environment			
Prey	High	Low	Low?
Predation danger	Low	Intermediate	High
Inferred overall ranking	Best	Intermediate	Worst
Population structure			
Bird density	High	Low	Low
Sex ratio	Male-biased	Male-biased	Even
Age ratio	Adult-biased	Adult-biased	Even
Body size	NSD	NSD	NSD
Body mass	Heavy	Heavy	Light
Mass change	Decreased	Decreased	Increased
Inferred interference	High	Intermediate	Low

9.5, P , 0.01). Adult mass decreased slightly in brackish flats and mangroves, while in cattail marshes mass increased over the winter period (Fig. 2). Controlling for seasonal variation, adult females in brackish flats and mangroves were heavier than those in cattail marshes ($F_{2,372}$ 5 11.4, P , 0.01; Fig. 3).

Adult males had longer exposed culmens than immature males (22.7 6 0.0 mm vs. 22.4 6 0.1 mm; $F_{1,1237}$ 5 13.1, P , 0.01), but exposed culmen length did not differ among habitats ($F_{2,1237}$ 5 2.0, P 5 0.13). Body mass did not differ throughout the winter with respect to male age class and habitat (day 3 age 3 habitat: $F_{2,1229}$ 5 1.0, P 5 0.35). Age classes differed in body mass among habitats (age 3 habitat: $F_{2,1231}$ 5 2.8, P 5 0.05). Adult males were heavier than immature males in brackish flats and cattail marshes, and body masses of immatures were more variable among habitats than those of adults (Fig. 3). Changes in body mass throughout the winter differed between

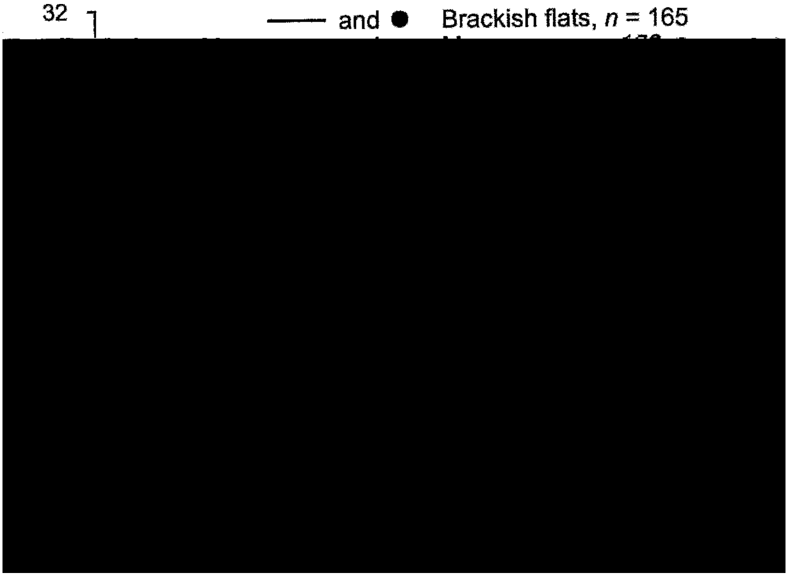

FIGURE 2. Body mass of adult female Western Sandpipers with respect to habitat type in Bahía Santa María, northwestern Mexico, during the nonbreeding seasons of 1999–2001.

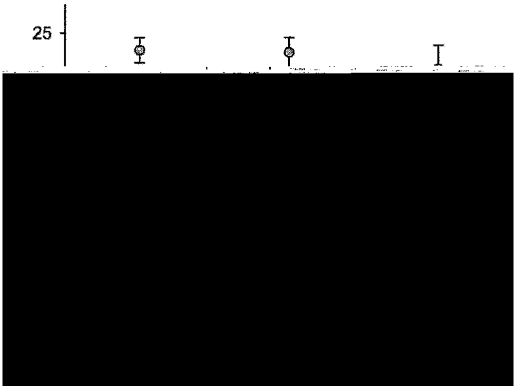

FIGURE 3. Body mass of Western Sandpipers with respect to sex and age class and habitat type in Bahía Santa María, northwestern Mexico, during the nonbreeding seasons of 1999–2001. Least-squares means (6 95% CI) are shown controlling for seasonal and annual variation, and interaction terms.

age classes (day 3 age: $F_{1,1231}$ 5 8.0, P , 0.01); immature males increased mass during the winter period, while we detected no weight change in adult males (Fig. 4a). Variation in body mass throughout the winter also differed with respect to habitat (day 3 habitat: $F_{2,1231}$ 5 7.0, P , 0.01); males maintained weight in brackish flats and mangroves, and increased weight in cattail marshes over the winter period (Fig. 4b). We summarize our results among habitats with respect to environmental variables and population structure in Table 2.

DISCUSSION

We documented prey density, predation danger, and Western Sandpiper population structure across three habitats at Santa María during the nonbreeding season. Brackish flats had the highest prey density and lowest level of predation danger, and we expected them to be favored over other habitats. Cattail marshes had lower prey densities and the highest level of predation danger, suggesting that they should be the least preferred habitat, all else being equal. Mangrove areas ranked as intermediate with regard to both prey densities and predation danger. Consistent with these rankings, brackish flats supported the highest densities of Western Sandpipers, which would further lower the per capita predation probability for these individuals, but also potentially increase competition for food. Indeed, we found that birds in brackish flats tended to lose weight as the season progressed. In contrast, in cattail marshes population densities were lowest and birds tended to gain weight over the winter.

There is considerable debate about the relative importance of food resources, predators, and competitors in determining local and latitudinal distributions of wintering shorebirds (Cresswell 1994, Warnock 1994, Nebel et al. 2002, Zharikov and Skilleter 2002, Whitfield 2003). At Santa María, Western Sandpiper density covaried positively with prey distribution among habitats, as generally predicted under ‘‘competition for resources’’ models (Parker and Sutherland 1986). In the absence of competition, all individuals should feed in the habitat with the most food per individual, and utilize the safest habitat. For shorebirds, safety is likely to be greater as density increases (Cresswell 1994, Whitfield 2003); thus, there is an additional negative selection against dispersing into sites with lower bird densities. Our observed patterns of population density thus present a prima facie case that density-dependent competition results in certain individuals using habitats with a lower ‘‘basic suitability’’ (sensu Fretwell and Lucas 1970) in terms of both resources and predation danger. At certain sites in brackish flats and mangroves, a small proportion of the population (5%–7%) defended territories for hours (Fernández Aceves 2005), a clear expression of competition for resources, which could cause subordinate individuals to move into less preferred sites.

The proportion of females and immatures was higher in less preferred habitats, suggesting asymmetry in competitive abilities, and possibly despotic displacement of these classes of birds (Marra and Holmes 2001). In Western Sandpipers, adults are more selective in their use of winter habitats during low tide than immatures (Warnock and Takekawa 1995), suggesting that adults may have excluded immatures from the most profitable habitat as a function of bird densities. However, there is no conclusive direct evidence supporting these competitive asymmetries between sexes and age classes in Western Sandpipers (O’Hara et al. 2005). Small sandpipers do not form stable dominance relationships, and adults do not necessarily win aggressive interactions with immatures more often than expected (Harrington and Groves 1977, Warnock 1994).

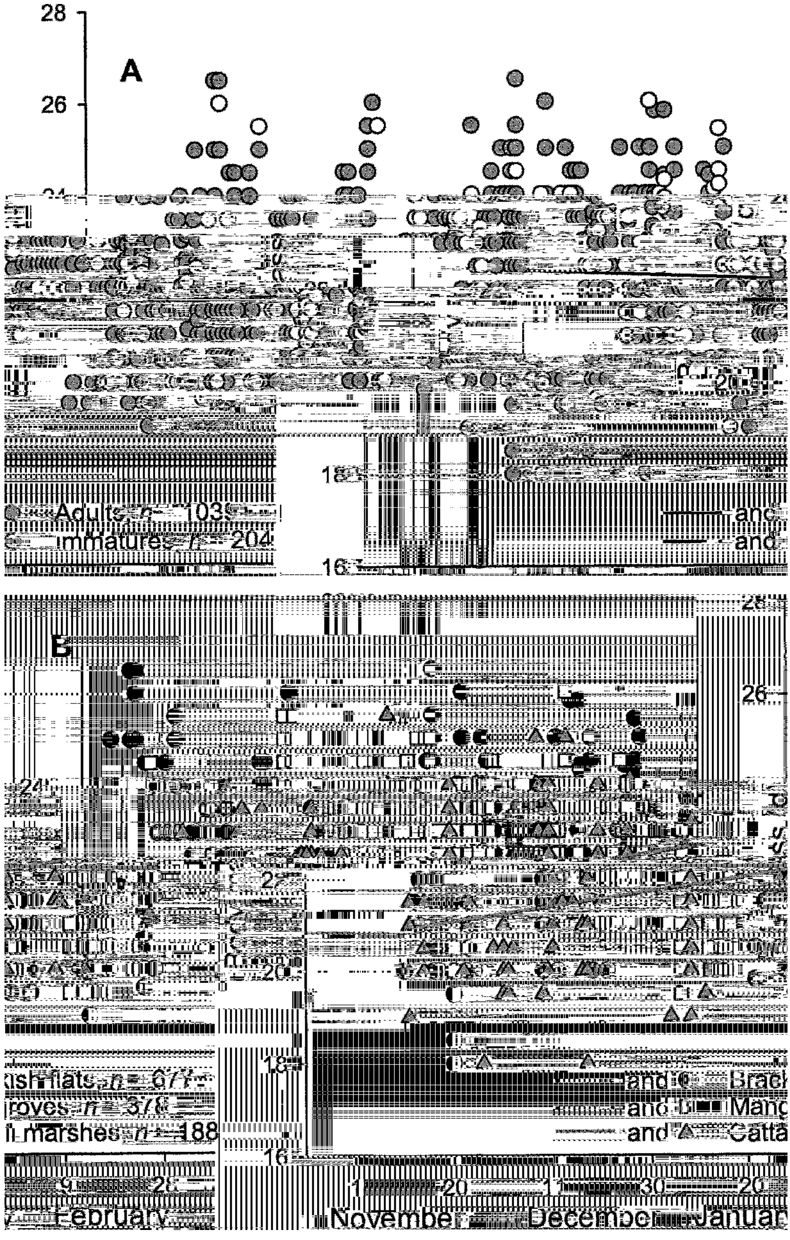

FIGURE 4. Body mass of male Western Sandpipers in Bahía Santa María, northwestern Mexico, during the nonbreeding seasons of 1999–2001, with respect to age classes (A) and habitat types (B).

An alternative possibility to competitive displacement from a globally preferred habitat is that birds with different morphologies, experience, or other attributes specialize in different habitats (Ydenberg et al. 2002, Zharikov and Skilleter 2002). In Western Sandpipers, the sexual dimorphism in bill length, which correlates with different foraging techniques, may result in a degree of sex-specific niche segregation and consequent resource partitioning (Mathot and Elner 2004). The longer bills of females provide them with a larger potential foraging niche, thus the use of cattail marshes may not be as unprofitable for females as for males. However, the ‘‘differential resource partitioning’’ hypothesis does not obviously account for age-class segregation. Also, although cattail marshes appear to be resource poor, this conclusion is based on a very small sample of substrate cores. It is possible that cattail marshes have higher prey densities than observed because of their finer-grained sediments and proximity to agricultural land.

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LITERATURE CITED

BISHOP, M. A., P. M. MEYERS, AND P. F. MCNELEY. 2000. A method to estimate migrant shorebird numbers on the Copper River Delta, Alaska. Journal of Field Ornithology 71:627–637.

BUENROSTRO, M. A., N. WARNOCK, AND H. DE LA CUEVA. 1999. Wintering Western Sandpipers *Ca* *a* at Estero Punta Banda, Baja California, México. Wader Study Group Bulletin 88:59–63.

BURNS, J. G., AND R. C. YDENBEitsN. W

O'HARA, P. D., D. B. LANK, AND F. S. DELGADO. 2002. Is the timing of moult altered by migra-