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for food (Price 1984). The result is niche differentiation, which is characterized by disproportionate bill length dimorphism and sex-dependent differences in foraging behaviour and resource use. In the Charadriiformes, bill length dimorphism is only weakly associated with indices of sexual selection that explain SSD, suggesting that additional selection pressures have acted on bill length (Székely et al. 2004).





**Table 1.** Morphometric measurements of sex-assigned migrant and winter-

( $F_{[1,2399]} = 2.85$ ,  $P = 0.09$ ) and there was no difference in bill length dimorphism (Table 1,  $F_{[1,2399]} = 0.78$ ,  $P = 0.19$ ). In contrast, Santa María females had longer bills than migrant females (Fig. 3b;  $F_{[1,2399]} = 41.89$ ,  $P < 0.0001$ ), and bill length did not differ among males ( $F_{[1,2399]} = 1.41$ ,  $P = 0.24$ ). Bill length dimorphism (13.4%) was significantly larger at Santa María ( $F_{[1,2399]} = 13.0$ ,  $P = 0.0002$ ). Despite a relatively small change in sex ratio (5%), bill lengths of males (Fig. 4;  $F_{[1,2399]} = 40.90$ ,  $P < 0.0001$ ) and females

( $F_{[1,2399]} = 26.94$ ,  $P < 0.0001$ ) from Punta Banda were shorter than those from Santa María, and there was a marginal increase in bill length dimorphism ( $F_{[1,2399]} = 2.05$ ,  $P = 0.0764$ ) in the direction predicted by the sex ratio.

## Discussion

The western sandpiper represents an extreme case of bill length dimorphism among calidrid sandpipers (Jehl and

Murray 1986) and our analyses further characterize an important morphological asymmetry in this species: bill length

we suggest, then these results also contradict the notion of a latitudinal cline for body size (O'Hara et al. 2006); however, size was indexed by bill and wing-chord lengths, which may reflect variation in size and shape. One possible explanation for our opposing results for bill and tarsus lengths is that, in addition to migration distance, the morphological traits that determine size and shape might also vary in relation to factors associated with winter site size and (or) quality, such as predation danger, competition for food, and (or) the distribution of food resources (Pomeroy 2006). Consistent with this, intrasexual comparisons with the null model revealed contrasting site differences: at the small site, Punta Banda, males were relatively short-billed and at the large site, Santa María, females were relatively long-billed. This suggests that site size, or associated characteristics, may be important in determining tarsus length (structural size) and bill length optima at winter sites.

Some of the latitudinal variation in western sandpiper morphology could be attributable to a latitudinal differential in risk from falcons, such as the merlin (*Falco columbarius* L., 1758) and the peregrine falcon (*Falco peregrinus* Tunstall, 1771; Nebel and Ydenberg 2005). For forest passerines hunted by Eurasian sparrowhawk (*Accipiter nisus* L., 1758), Swaddle and Lockwood (1998) demonstrated that rounded wing tips and short femora, relative to tarsus, are associated with lower predation risk. While these specific shape attrib-

remain to be thoroughly tested, extending the analyses to other calidrid species could generate additional insights. For example, based on the hypothesized mechanisms in the present study, we predict a strong inverse relationship between bill length dimorphism and the degree of overlap between the sexes in overwintering distributions. Similarly, irrespective of the degree of overlap, bill length dimorphism should be maximal when the sex ratio is 1:1.

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