

Disproportionate bill length dimorphism and niche differentiation in wintering western sandpipers (*Calidris mauri*)

R.W. Stein, G. Fernández, H. de la Cueva, and R.W. Elner

Abstract: Western sandpipers (*Calidris mauri* (Cabanis, 1857)) exhibit slight female-biased sexual size dimorphism (5%) but disproportionate bill length dimorphism (15.9%). We test two predictions of the niche differentiation hypothesis at two wintering sites in Mexico with uniform western sandpiper densities, and use sex ratio as an index of intersexual competition. First, to test whether bill length dimorphism is larger at sites where sex ratios are strongly male-biased, we develop a migrant-based null model to represent dimorphism (12%, based on the average of males and females) in the absence of competition. Relative to the null model, bill length dimorphism was significantly larger at the large site (Santa María: 13.4%) but not at the small site (Punta Banda: 12.7%). Second, we tested whether bill length dimorphism increases as sex ratio approaches 1:1. Although the sex-ratio difference between sites was only 5%, bill length dimorphism increased marginally in the predicted direction. Additional comparisons suggest a cline in bill length dimorphism that mirrors a latitudinal gradient in prey burial depth. While sexual size dimorphism in the western sandpiper likely derived from selection for different body size optima, intersexual competition for food on the wintering grounds appears to have promoted further divergence in bill length.

Résumé : Les bécasseaux d'Alaska (*Calidris mauri* (Cabanis, 1857)) possèdent un faible dimorphisme sexuel de la taille (5 %) qui favorise les femelles; en revanche, le dimorphisme des longueurs de bec (15,9 %) est disproportionné. Nous testons deux prédictions de l'hypothèse de la différenciation des niches à deux sites d'hivernage du Mexique à densités uniformes de bécasseaux et nous utilisons le rapport mâles:femelles comme indice de compétition entre les sexes. D'abord, pour vérifier si le dimorphisme sexuel des becs est plus important là où le rapport des sexes favorise fortement les mâles, nous mettons au point un modèle nul basé sur les migrateurs qui représente le dimorphisme en l'absence de compétition (12 % d'après les moyennes des mâles et des femelles). Par rapport au modèle nul, le dimorphisme des longueurs de becs est significativement plus important au site plus étendu (Santa María : 13,4 %), mais non au site plus restreint (Punta Banda: 12,7 %). Nous vérifions ensuite si le dimorphisme des longueurs de becs augmente lorsque le rapport des sexes s'approche de 1:1. Bien que la différence de rapport des sexes entre les sites soit seulement de 5 %, le dimorphisme des longueurs de becs augmente (marginale) dans le sens prédit. D'autres comparaisons laissent croire qu'il existe un gradient dans le dimorphisme des longueurs des becs qui reflète un gradient latitudinal des profondeurs d'enfouissement des proies. Alors que le dimorphisme sexuel de la taille chez les bécasseaux d'Alaska s'explique par une sélection d'optimums différents de taille du corps, la compétition entre les sexes pour la nourriture sur les sites d'hivernage semble avoir favorisé une divergence supplémentaire dans la longueur du bec.

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Introduction

Sexual size dimorphism (SSD) is widespread in animals, despite strong positive genetic correlations between the sexes for traits that determine body size (Lande 1980). SSD reflects different body size optima and arises as a consequence of sexual selection and (or) natural selection (Price

1984). Comparative phylogenetic analyses of SSD in the Charadriiformes (alcids, gulls, and shorebirds), an order that encompasses almost the entire range of SSD in birds, demonstrate that sexual selection has been an important driver of SSD (Székely et al. 2000, 2004). Once SSD has arisen, further divergence in bill morphology can occur in response to disruptive selection acting through intersexual competition

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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).

Bill length is a functionally selected trait in shorebirds (Scolopacidae) and bill length dimorphism is common in species that feed on invertebrates that occur in soft sediments (Jehl and Murray 1986). Consistent with the niche differentiation hypothesis, bill length tends to be more dimorphic than tarsometatarsus and wing-chord lengths in shorebirds (Jehl and Murray 1986), and pronounced bill length dimorphism is often associated with sex-dependent differences in foraging behaviour and resource use (Durell 2000). Thus, intersexual competition for food may have influenced shorebird bill length dimorphism routinely; however, it is unclear when and where in the life cycle disruptive selection has acted on bill length. There is no support for intersexual competition on the breeding grounds as a general process explaining bill length dimorphism in shorebirds (Székely et al. 2000, 2004); here, we consider this same mechanism from a wintering grounds perspective (Elner and Seaman 2003).

The western sandpiper (*Calidris mauri* (Cabanis, 1857)) is a differential migrant that breeds in western Alaska and eastern Siberia and tends to use large coastal stopover sites during migration (Warnock and Bishop 1998). The wintering grounds extend along the Pacific coast of the Americas, primarily between California and Peru (Wilson 1994). Males predominate at northern, and females at southern, wintering sites, respectively; this sex-bias is reflected in a latitudinal sex-ratio cline across the wintering grounds (Nebel et al. 2002). Intrasexual latitudinal clines in size are also evident across the wintering grounds: the smallest individuals of each sex occur at the northernmost and the largest at the southernmost wintering sites (O'Hara et al. 2006). The western sandpiper (22–35 g) exhibits slight female-biased SSD (6% for tarsus and 5% for wing chord) but disproportionate dimorphism for bill length (15%; Jehl and Murray 1986), which is implicated in foraging mode. Western sandpipers can feed on and within sediment, as well as in the water column (Sutherland et al. 2000; Rubega 2002). While surface feeding predominates in both sexes, females probe in sediments more than males (Mathot and Elner 2004; Mathot et al. 2007). The western sandpiper provides a good opportunity to test predictions of niche differentiation specific to the wintering grounds because the winter distributions of males and females overlap extensively (Wilson 1994) and intersexual competition is likely.

We test two predictions of the niche differentiation hypothesis to determine whether intersexual competition on the wintering grounds can explain disproportionate bill length dimorphism in western sandpipers. To do this, we develop a null model of bill length dimorphism (based on a large sample of migrants) that is taken to represent dimorphism in the absence of intersexual competition. First, we predict a higher level of bill length dimorphism at winter sites, relative to the null model, if there is morphological

subpopulation-structuring on the wintering grounds owing to intersexual competition for food. Second, using sex ratio as an index of intersexual competition at wintering sites, we further predict that bill length dimorphism should increase as the sex ratio approaches 1:1. To test these predictions we use linear models (LM) to contrast samples of sex-assigned wintering birds from Mexico against the null model of bill length dimorphism and, subsequently, evaluate between-site differences in bill length dimorphism in relation to the change in sex ratio.

Materials and methods

Data collection, compilation, and assessment

The present study is based entirely on pre-existing samples from research conducted from 1995 to 2003 (Fernández et al. 2003; Guglielmo and Williams 2003; Elner et al. 2005; Stein et al. 2005; Fernández and Lank 2006; Stein and Williams 2006). Bird-handling protocols for the research projects were approved by the Simon Fraser University Animal Care Committee (permit nos. 529B, 552B, and 671B), conformed to the guidelines of the Canadian Committee for Animal Care, and were in accordance with permits from Environment Canada and the Dirección General de Vida Silvestre – Mexico. None of the anatomically sexed migrants ($n = 380$) were sacrificed for the purpose of this study; these birds were originally collected for investigations into phenotypic flexibility of body composition (Guglielmo and Williams 2003), age-dependent differences in digestive physiology (Stein et al. 2005; Stein and Williams 2006), and functional morphology of a novel foraging mode (Elner et al. 2005). Migrants were studied at two adjacent coastal stopover sites in southwest British Columbia, Canada: Boundary Bay (49°03'N, 123°01'W) and Roberts Bank (49°05'N, 123°12'W). Adults and juveniles were collected at Boundary Bay during northward (20 April – 10 May) and southward (1 July – 30 August) migrations from 1995 to 2000, and at Roberts Bank during northward (20 April – 10 May) migration in 2003. Migrants were sampled across the entire stopover period, ensuring an inclusive sample from the range of wintering sites. Wintering western sandpipers were studied at two sites separated by 1600 km on the Pacific coast of Mexico: Estero de Punta Banda ("Punta Banda"; 31°52'N, 116°37'W), a small estuary on the northwest coast of Baja California, and Bahía Santa María ("Santa María"; 25°02'N, 108°18'W), a large wetland on the Sinaloa coast. Studies of wintering birds were conducted at Punta Banda from 1 October to 28 or 29 February of 1995–1996 and 1996–1997, and at Santa María from 1 November to 28 or 29 February of 1999–2000, 2000–2001, and 2001–2002.

These studies included a standard morphological examination at capture. Age (adult or juvenile) was assigned on the basis of plumage colour for migrants, and on the bases of plumage colour and primary feather wear for wintering birds (Page et al. 1972; O'Hara et al. 2002). Bill and tarsus lengths were measured with calipers calibrated to 0.05 mm and rounded to 0.1 mm. Exposed culmen (bill) length was measured from the tip of the bill to its base, as demarcated by a fleshy protuberance at the base of the ramphotheca. For migrants, tarsometatarsus (tarsus) was measured according to Prater et al. (1987) and includes both joint articulations

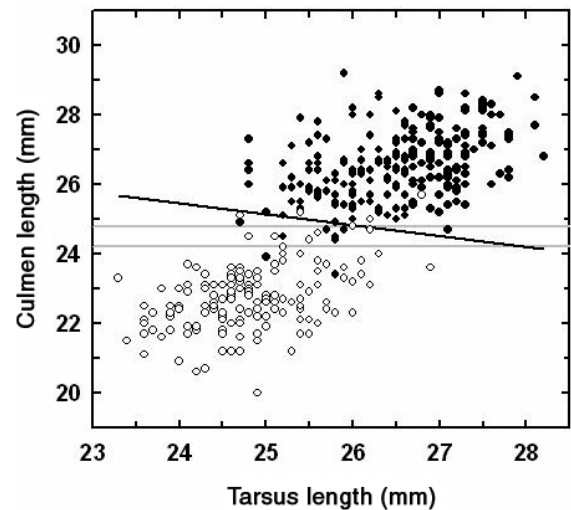
(maintained at 90° to the tarsus). For wintering birds, tarsus was measured according to Pyle et al. (1987) and excludes the joint articulations. For migrants, the sex of each individual was verified anatomically at dissection, when sternum length was also measured (from its posterior end to the point where it fuses with the ferculum) using calipers calibrated to 0.05 mm and rounded to 0.1 mm. For wintering birds, sex was assigned tentatively using the exposed culmen criterion of Page and Fearis (1971): males ≤ 24.2 mm, females ≥ 24.8 mm, and intermediate individuals were classified as unknowns.

Morphometric measurements were made by three individuals: R.W. Stein (RWS), C.G. Guglielmo (CGG), and G. Fernández (GF). The anatomically sexed migrants were measured by RWS and CGG, and here we assessed observer bias by first confirming that there were no differences in the way the measurements were made and then by testing for differences within each of the four age-by-sex categories. Only 1 of 12 comparisons, adult male sternum length ($t_{[113]} = 2.65$, $P = 0.014$), differed between observers. This difference was small (1.2% of the overall mean) and there were no consistent patterns in these tests, which were conducted on independent samples of birds, so we pooled measurements. Subsequent analyses verified that juveniles had completed structural growth: bill, tarsus, and sternum lengths were independent of age for males ($P = 0.13$ – 0.99) and females ($P = 0.06$ – 0.98), so we pooled age classes. Wintering birds were measured exclusively by GF and he used a different methodology for tarsus than RWS and CGG. Here, RWS and GF measured a common set of birds ($n = 56$) to assess observer bias. Their bill measurements were identical (mean = 26.8, SE = 0.1); however, because of the difference in measurement methodology, GF's tarsus (mean = 23.4, SE = 0.1) measurements were consistently smaller than RWS's (mean = 26.2, SE = 0.1). Thus, we generated a conversion equation from a regression based on repeated measurements of these 56 individuals (adjusted $r^2 = 0.84$) and adjusted GF's tarsus measurements so that they were comparable with RWS's.

Morphometric sex assignment and statistical analyses

To assign sex to individual western sandpipers on the basis of bill and tarsus lengths, we performed a discriminant analysis on the sample of anatomically sexed migrants (Fig. 1). We validated the accuracy of this sex-assignment criterion by reassigning sex to the anatomically sexed migrants and determining the percentage of misclassified individuals. As expected, an emphasis on females in the original sampling protocols caused the sex ratio of the migrant sample to be female-biased (58% females, $\chi^2_{[1]} = 9.47$, $P < 0.002$), so we set the prior probabilities (priors) of classification equal to the proportion of each sex in the sample, which was determined anatomically. Subsequently, 11 individuals (7 males and 4 females) were classified incorrectly (2.9%) and none were classified as unknowns. To facilitate comparison between migrants and wintering birds, we used this derived sex-assignment criterion to assign sex to the wintering birds. Here, we expected the sex ratio to be strongly male-biased (Nebel et al. 2002), so we used the exposed culmen criterion of Page and Fearis (1971) to estimate sex ratio (1378 males, 569 females, and 79 unknowns). After exclud-

Fig. 1. Morphometric differentiation of anatomically sexed male (○; $n = 160$) and female (●; $n = 220$) western sandpipers (*Calidris mauri*) by a derived bivariate discriminant function (solid black line; $Y = 0.903(\text{culmen}) + 0.286(\text{tarsus}) - 29.865$; accuracy >97%). If $Y < 0$, then there is a higher probability that the individual is male; if $Y > 0$, then there is a higher probability that the individual is female; if $Y = 0$, then there is an equal probability that the individual is male or female. The lower gray line (culmen = 24.2) is 93% accurate in classifying males and the upper gray line (culmen = 24.8) is 90% accurate in classifying females (Page and Fearis 1971).



ing the 79 unknowns, the apparent sex ratio was male-biased (71% males, $\chi^2_{[1]} = 336.15$, $P < 0.0001$). Again, we set the priors equal to the proportion of each sex. Although, under ideal circumstances, priors should be derived from an independent but representative sample, this was not possible here and we had to resolve the problem that the sample of migrants was female-biased, whereas the sample of wintering birds was male-biased. We also assigned sex using uninformative priors and this did not influence our results. To minimize bias in the sex ratios generated for the two winter sites from sex assignment, we generated priors from the apparent sex ratio of the entire sample of wintering birds and then assigned sex to all of the wintering birds as a single group, rather than conducting separate analyses for each site.

Western sandpipers exhibit female-biased SSD (Wilson 1994), as well as latitudinal clines in sex ratio (Nebel et al. 2002) and morphology (O'Hara et al. 2006) across the wintering grounds. This provides a predictive framework, so we use one-tailed tests to characterize dimorphism and for site comparisons. Sexual dimorphism is represented according to Storer's (1966) index: $\{(x - y) \times [(x + y) \times 0.5]^{-1}\} \times 100$, with x and y representing either the mean or the least-squares mean for females and males, respectively. We incorporate sexual dimorphism into LM explaining variation in bill length by modeling sex as a dummy variable (males = 0 and females = 1). We use tarsus as a covariate to control for structural size and assess heterogeneity of slope with the sex \times tarsus interaction term. We extend this approach to a series of comparisons made within a single LM that includes all of the migrants and wintering birds.

To test whether intersexual competition on the wintering

grounds is a factor influencing bill length dimorphism in western sandpipers, we contrast samples of sex-assigned wintering birds from Mexico against the null model of bill length dimorphism and, subsequently, evaluate site differences in bill length dimorphism in relation to sex ratio. To do this, we first constructed a two-factor LM to explain variation in bill length. The first factor was assigned sex. The second factor, "stage and site", consolidated stage and site into three groups: migrants, Punta Banda, and Santa María. After assessing all of the interaction terms between these factors and tarsus length, the size covariate, we further consolidated the two factors into one factor with six levels and used contrast statements to make specific preplanned comparisons within the LM. We extend this approach to test predictions from the niche differentiation hypothesis, which we evaluate with one-tailed tests. Statistical analyses were conducted in SAS release 6.03 (SAS Institute Inc. 1990).

Results

Migrants

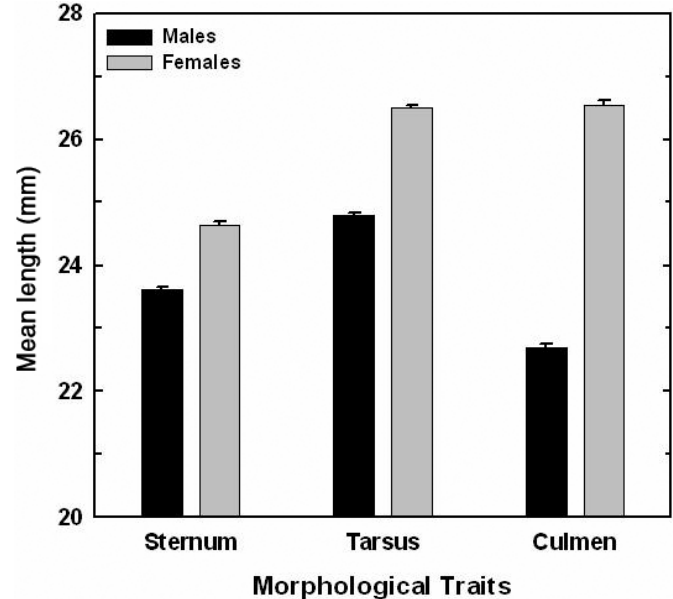
Anatomically sexed females had longer bill ($t_{[378]} = 37.52$, $P < 0.0001$), tarsus ($t_{[378]} = 22.75$, $P < 0.0001$), and sternum ($t_{[346]} = 14.18$, $P < 0.0001$) lengths than anatomically sexed males, and there was a marked asymmetry in dimorphism between bill (15.7%), tarsus (6.7%), and sternum (4.3%) lengths (Fig. 2). Once sex and tarsus lengths were entered into a LM explaining variation in bill length, the sex \times tarsus interaction term indicated a common slope ($F_{[1,376]} = 0.44$, $P = 0.51$) and sternum length did not explain a significant amount of residual variation ($F_{[1,344]} = 0.78$, $P = 0.37$). Size-corrected bill length dimorphism was 11.5% (from Table 2, model 1).

Similarly, sex-assigned females had longer bill ($t_{[378]} = 40.27$, $P < 0.0001$), tarsus ($t_{[378]} = 23.52$, $P < 0.0001$), and sternum ($t_{[346]} = 13.84$, $P < 0.0001$); females: mean = 24.62 mm, SE = 0.05; males: mean = 23.60 mm, SE = 0.05; dimorphism = 4.3%) lengths than sex-assigned males (Table 1). There were only minute changes in the mean trait values (mean change = -0.02 mm) after sex assignment; consequently, the asymmetry in dimorphism was practically identical for the anatomically sexed and sex-assigned groupings of migrants. Again, once sex and tarsus were entered into a LM explaining variation in bill length, the sex \times tarsus interaction term indicated a common slope ($F_{[1,376]} = 0.02$, $P = 0.88$) and sternum length did not explain a significant amount of residual variation ($F_{[1,344]} = 1.77$, $P = 0.18$). Size-corrected bill length dimorphism was 12.2% (from Table 2, model 2).

Wintering sites

Punta Banda (463 ha; Alfaro et al. 2000) and Santa María (41 383 ha; Fuente de León and Carrera 2005) support subpopulations of 4 000 (Buenorostro et al. 1999) and 350 000 (Engilis et al. 1998) overwintering western sandpipers, respectively. Despite the large difference in size, western sandpiper densities were surprisingly uniform at the two sites (Punta Banda: 8.64 birds/ha; Santa María: 8.46 birds/ha). Sex ratio was male-biased at both sites (Punta Banda: 77% males, $\chi^2_{[1]} = 58.58$, $P < 0.0001$; Santa María: 72% males, $\chi^2_{[1]} = 360.79$, $P < 0.0001$); at each site, sex-assigned

Fig. 2. Morphometric measurements (mean and SE) of anatomically sexed western sandpipers (*Calidris mauri*). The asymmetry in dimorphism demonstrates that males differ from females in size and shape.



females had longer bill (Punta Banda: $t_{[201]} = 21.65$, $P < 0.0001$; Santa María: $t_{[1821]} = 81.83$, $P < 0.0001$) and tarsus (Punta Banda: $t_{[201]} = 11.50$, $P < 0.0001$; Santa María: $t_{[1821]} = 43.94$, $P < 0.0001$) lengths than sex-assigned males (Table 1).

Sex ratio changed between sites in the direction predicted by the latitudinal cline; however, the change was small (5%, $\chi^2_{[1]} = 1.95$, $P = 0.16$). Bill lengths from Santa María, the southern site, were longer than those from Punta Banda as predicted (males: $t_{[1471]} = -4.04$, $P < 0.0001$; females: $t_{[551]} = -2.97$, $P < 0.01$). However, contrary to expectations, tarsus lengths from Santa María were consistently shorter than those from Punta Banda (males: $t_{[1471]} = 5.70$, $P < 0.0001$; females: $t_{[551]} = 4.19$, $P < 0.0001$).

Assessing bill length dimorphism

In the two-factor LM explaining variation in bill length that included all of the sex-assigned migrant and wintering western sandpipers, each interaction term indicated a common slope for tarsus across groups (tarsus \times "stage and site" \times sex: $F_{[4,2394]} = 0.50$, $P = 0.74$; tarsus \times "stage and site": $F_{[2,2394]} = 0.44$, $P = 0.65$; tarsus \times sex: $F_{[1,2398]} = 0.16$, $P = 0.68$). After removing these interaction terms, both factors were highly significant (sex: $F_{[1,2399]} = 1711.9$, $P < 0.0001$; "site and stage": $F_{[2,2399]} = 38.38$, $P < 0.0001$), and there was a significant "stage and site" \times sex interaction ($F_{[2,2399]} = 6.95$, $P < 0.001$), indicating at least one difference in bill length dimorphism among groups.

To determine whether it was a difference between males or between females that accounted for the difference in bill length dimorphism, we first tested for intrasexual differences in bill length and then tested for a difference in bill length dimorphism. Punta Banda males had shorter bills than migrant males (Fig. 3a; $F_{[1,2399]} = 15.25$, $P < 0.0001$); however, bill length was more uniform among females

Table 1. Morphometric measurements of sex-assigned migrant and wintering western sandpipers (*Calidris mauri*).

Parameter	Migrants	Punta Banda	Santa María
Sample size			
Female	223	47	506
Male	157	156	1317
Tarsus (mm)			
Female (mean, SE)	26.50, 0.04	26.64, 0.09	26.24, 0.02
Male (mean, SE)	24.76, 0.05	25.18, 0.05	24.89, 0.02
Dimorphism (%)	6.8	5.6	5.3
Bill (mm)			
Female (mean, SE)	26.55, 0.07	26.39, 0.14	26.86, 0.05
Male (mean, SE)	22.63, 0.07	22.47, 0.09	22.79, 0.03
Dimorphism (%)	15.9	16.0	16.4
Size-corrected bill (mm)			
Female (LS mean, SE)	25.89, 0.07	25.65, 0.14	26.36, 0.05
Male (LS mean, SE)	22.97, 0.07	22.58, 0.07	23.06, 0.03
Dimorphism (%)	12.0	12.7	13.4

Note: Dimorphism is represented according to Storer's (1966) index: $\{(x - y) \times [(x + y) \times 0.5]^{-1}\} \times 100$. Size-corrected bill lengths are least-squares means (LS means) from Table 2, model 3.

Table 2. Linear models explaining variation in bill length for anatomically sexed migrants (males: $n = 160$; females: $n = 220$) and for sex-assigned migrant (males: $n = 157$; females: $n = 223$) and wintering western sandpipers (*Calidris mauri*) from two sites in Mexico, Punta Banda (males: $n = 156$; females: $n = 47$) and Santa María (males: $n = 1317$; females: $n = 506$).

Models and parameters	Coefficient	SE	<i>P</i>	Partial r^2
1. Anatomically sexed migrants				
Intercept	7.83	1.57	<0.0001	82.9*
Sex	2.84	0.14	<0.0001	78.8
Tarsus	0.60	0.06	<0.0001	4.1
2. Sex-assigned migrants				
Intercept	9.45	1.55	<0.0001	84.2*
Sex	3.00	0.14	<0.0001	81.1
Tarsus	0.53	0.06	<0.0001	3.1
3. Sex-assigned migrant and wintering birds				
Punta Banda males	7.90 [†]	0.74	<0.0001	82.1*
Migrant males	0.40	0.10	<0.0001	0.1
Santa María males	0.49	0.08	<0.0001	0.2
Punta Banda females	3.07	0.15	<0.0001	2.7
Migrant females	3.32	0.10	<0.0001	8.3
Santa María females	3.78	0.09	<0.0001	13.9
Tarsus	0.58	0.03	<0.0001	57.0

Note: In models 1 and 2, sex (male = 0 and female = 1) was modelled as a dummy variable. In model 3, dummy variables were created to distinguish each of the six groups of sex-assigned migrant and wintering western sandpipers.

* r^2 for the full model.

[†]Intercept of the full model.

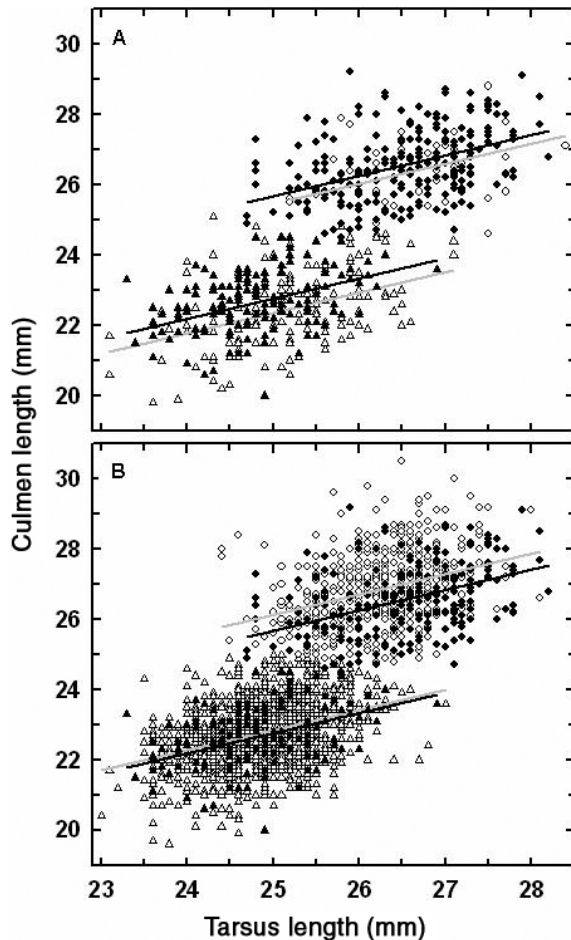
($F_{[1,2399]} = 2.85$, $P = 0.09$) and there was no difference in bill length dimorphism (Table 1, $F_{[1,2399]} = 0.78$, $P = 0.19$). In contrast, Santa María females had longer bills than migrant females (Fig. 3b; $F_{[1,2399]} = 41.89$, $P < 0.0001$), and bill length did not differ among males ($F_{[1,2399]} = 1.41$, $P = 0.24$). 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

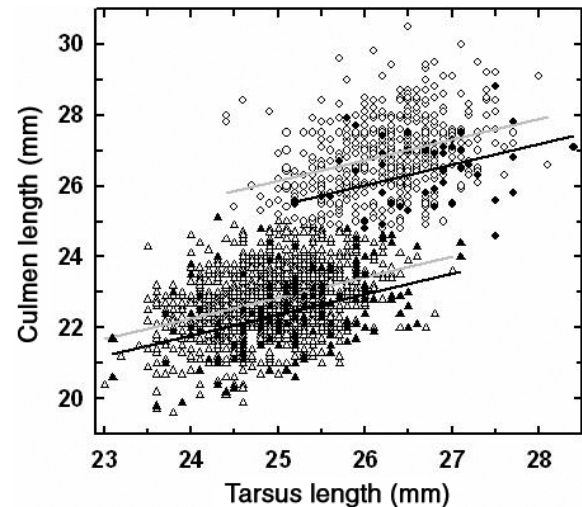
Fig. 3. For sex-assigned western sandpipers (*Calidris mauri*), sexual dimorphism of size-corrected culmen length is larger in wintering birds than in migrants. (A) Comparison between migrants and birds wintering at Punta Banda, a small estuary. (B) Comparison between migrants and birds wintering at Santa María, a large wetland complex. Migrants are represented by solid black lines (\blacktriangle , males ($n = 157$); \bullet , females ($n = 223$)) and wintering birds by solid gray lines (A — \triangle , males ($n = 47$); \circ , females ($n = 156$); B — \triangle , males ($n = 506$); \circ , females ($n = 1317$)).



Murray 1986) and our analyses further characterize an important morphological asymmetry in this species: bill length is more than twice as dimorphic as tarsus length and more than three times as dimorphic as sternum length. Based on principal component analyses conducted separately on the sexes, Guglielmo and Williams (2003) concluded that male western sandpipers are scaled-down versions of females; however, our analyses demonstrate that males differ from females in both size and shape. A shift in the relationship between tarsus length and bill length is manifested as sex-dependent morphological segregation, resulting in a short-billed and short-legged morph populated predominantly by males and a long-billed and long-legged morph populated predominantly by females (Fig. 1).

Disproportionate bill length dimorphism is consistent with niche differentiation, which results from disruptive selection associated with intersexual competition for food. We tested two predictions of this hypothesis, using sex ratio as an in-

Fig. 4. For sex-assigned wintering western sandpipers (*Calidris mauri*), sexual dimorphism of size-corrected culmen length increases as the sex ratio becomes more uniform. Black lines represent birds wintering at Punta Banda (\blacktriangle , males ($n = 47$); \bullet , females ($n = 156$)). Gray lines represent birds wintering at Santa María (\triangle , males ($n = 506$); \circ , females ($n = 1317$)).



dex of intersexual competition on the wintering grounds because western sandpiper densities were similar at the two winter sites. Both sites differed qualitatively from the null model of size-corrected bill length dimorphism (12.0%) in the direction predicted by the sex ratio, and bill length dimorphism was significantly larger at the large site (Santa María: 13.4%) but not at the small site (Punta Banda: 12.7%). If this is a general result and bill length dimorphism is only larger at large sites, then intersexual competition for food on the wintering grounds could still be an important process maintaining or driving bill length dimorphism because it is likely that the majority of western sandpipers overwinter at large sites. Although the between-site change in sex ratio was relatively small, there was a marginal increase in bill length dimorphism in the predicted direction. Both predictions received qualitative support; however, some of the results were either marginally significant or not significant by conventional standards. Nevertheless, these tests reveal consistent fine-scale differences in bill length dimorphism for winter subpopulations of western sandpipers that are associated with an index of intersexual competition for food; this provides evidence for an ecological mechanism that may be driving disproportionate dimorphism for bill morphology of western sandpipers and other sexually dimorphic shorebirds.

Latitudinal clines: pattern and process

Male and female western sandpipers are postulated to exhibit latitudinal clines in body size in association with migration distance (O'Hara et al. 2006). While our results for bill length are in accordance, tarsus length exhibited the opposite pattern in both sexes. This unexpected result contradicts Nebel (2005), who suggested that tarsus length does not vary across larger spatial scales (California to Panama); however, small sample sizes render Nebel's (2005) findings tenuous. If tarsus length is a good index of structural size, as

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 attributes are unlikely to apply to shorebirds, which use more open coastal habitats, we might expect equivalent operating rules. At southern wintering sites, interspecific competition with the semipalmated sandpiper (*Calidris pusilla* (L., 1766)), a shorter billed congener also adapted to surface feeding, may influence bill length optima of male western sandpipers (Cartar 1984), and this may account, in part, for the latitudinal cline in bill length in male western sandpipers reported by O'Hara et al. (2006).

Both male and female western sandpipers forage predominantly on the sediment surface (Mathot and Elnor 2004; Mathot et al. 2007), suggesting that intersexual competition for surficial food could be an important factor at winter sites. Recently, Mathot et al. (2007) reported a latitudinal cline in invertebrate burial depth across a substantial portion of the winter range of the western sandpiper, from epifaunal in the north to infaunal in the south. This is an important finding because on the wintering grounds females probe into the sediment more than males (10%–15% vs. 1%; Mathot et al. 2007), and infaunal invertebrates could provide an important ecological opportunity to escape competition for surface food. Consistent with this hypothesis, our data suggest a latitudinal cline in bill length dimorphism that mirrors the latitudinal cline in infaunal burial depth. Consequently, latitudinal variation in the tarsus and bill lengths of wintering subpopulations of western sandpiper may be structured by functional feeding considerations (Elnor and Seaman 2003), and intersexual competition for food on the wintering grounds may be the underlying evolutionary driver for disproportionate bill length dimorphism, such that competition results in disruptive survival or redistribution and promotes sex-dependent divergence in bill length and resource use. With only two wintering sites, a firm conclusion is premature but the notion warrants further study.

Bill length dimorphism: origin and maintenance

Sexual selection has been a potent driver of SSD in the Charadriiformes (Székely et al. 2000, 2004). Sexual selection favouring small males, associated with increased agility in aerial courtship displays (Blomqvist et al. 1997; Lanctot et al. 2000), could lead to parallel reductions in body size for males and females (Lande 1980). However, natural selection, associated with differences in migration distance (O'Hara et al. 2006) or energetic demands of reproduction, may have favoured different body size optima for males and females and resulted in small body size and female-biased SSD. Once SSD has been established, sex-dependent differences in bill length can be further accentuated by disruptive selection acting through intersexual competition for food; this leads to disproportionate bill length dimorphism and niche differentiation. Importantly, this scenario invokes interactions between processes occurring on the breeding grounds, such as selection for different body size optima for males and females, and processes occurring on the wintering grounds, such as intersexual competition for food.

In shorebirds, there is a correspondence between bill length dimorphism and intersexual differences in foraging mode (Durell 2000). Consequently, intersexual competition could be a driving factor in the evolution of shorebird bill length dimorphism (Cartar 1984; Székely et al. 2000; Sandercock 2001). The western sandpiper provides an important test case because the winter distributions of males and females overlap (Nebel et al. 2002) and intersexual competition is likely because both males and females are primarily surface feeders (Mathot and Elnor 2004; Mathot et al. 2007). The latitudinal cline in invertebrate burial depth offers an opportunity to escape intersexual competition for food resources on the sediment surface and could promote intersexual divergence in bill length for species exhibiting SSD (Mathot et al. 2007). Comparative phylogenetic analyses in shorebirds indicate that bill length dimorphism tends to be consistently larger than SSD; however, these analyses provide no support for niche differentiation on the breeding grounds as a mechanism explaining disproportionate bill length dimorphism (Székely et al. 2000, 2004). Rather, Székely et al. (2000) suggest that intra- and inter-specific competition throughout the year are probably more important than competition within a pair during the breeding season, and we provide supporting evidence for intersexual competition on the wintering grounds as a mechanism promoting disproportionate bill length dimorphism in western sandpipers.

Morphometrics can generate novel insights into sexual dimorphism and the ecological processes underpinning overwintering patterns in a calidrid sandpiper. It is likely that morphological variation across the winter distribution of western sandpipers relates to migration distance and also to site characteristics, such as predation danger, interspecific and intersexual competition for food, and (or) the distribution of food resources. The combination of large intersexual differences in feeding morphology and the markedly skewed sex ratios characteristic of wintering subpopulations of western sandpipers suggest that multiple ecological mechanisms resulting either in mortality or redistribution among wintering sites could be maintaining the extreme bill length dimorphism characteristic of this species. While the hypotheses

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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