Functional association of bill morphology and foraging behaviour in calidrid sandpipers

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Abstract—Foraging behaviour in birds co-varies with bill morphology. Shorebirds exhibit pronounced inter- and intra-specific variation in bill length and shape as well as in foraging behaviour. Pecking, or feeding on epifaunal intertidal invertebrates, is associated with a straight bill, while probing, feeding on infaunal prey, is facilitated by bill curvature. Here, we used high resolution microscopy to study gross bill morphology of Western Sandpipers (*Calidris mauri*). We showed that bills of males and females differed with regard to length but not curvature or depth, despite clear differences in foraging behaviour between the sexes. Detection of infaunal prey can be facilitated by the presence of Herbst corpuscles. These mechano-receptors are located in 'sensory pits' under the keratin layer of the bill and are able to sense pressure gradients. They are postulated to be common among calidrid sandpipers, but comparative data are lacking. Using high resolution microscopy, we measured number and size of sensory pits in Western Sandpipers, Least Sandpipers (*Calidris minutilla*) and Dunlin (*Calidris alpina*). The implications of these findings to foraging adaptations and non-breeding site choice are discussed.

Keywords: bill micro-anatomy; Dunlin; foraging mode; Herbst corpuscles; Least Sandpiper; sensory pits; Western Sandpiper.

INTRODUCTION

Bill length and shape have important implications for foraging behaviour (Pierre, 1994; Zweers and Gerritsen, 1997; Barbosa and Moreno, 1999), diet choice (Hulscher and Ens, 1992; Lauro and Nol, 1995; Mascitti and Kravetz, 2002; Durant et al.,

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2003), and concomitantly, habitat selection in birds (Harrington, 1982; Gerritsen and Sevenster, 1985; Zharikov and Skilleter, 2002). Ultimately, differences in bill morphology between males and females can contribute to the evolution and maintenance of intraspecific foraging niche divergence (Suhonen and Kuitunen, 1991; Temeles et al., 2000; Temeles and Kress, 2003).

Shorebirds (Charadrii) show pronounced inter-sexual and inter-specific variation in bill length and shape as well as in foraging behaviour (Jehl and Murray, 1986; Durell, 2000; van de Kam et al., 2004), and are a candidate group to study functional bill morphology. Certain aspects of gross bill morphology and micro-anatomy are known to be adaptive to specific modes of foraging. 'Pecking' is characterised by feeding on intertidal invertebrates at or near the sediment surface (epifaunal prey). 'Probing', by contrast, consists of inserting the bill into the sediment, allowing the capture of invertebrates that live below the sediment surface (infaunal prey). Probing is observed more frequently in species with long and curved bills than in species with short and straight bills (Ferns and Siman, 1994; Barbosa and Moreno, 1999). The difference appears, at least partly, attributable to a probing curved bill being able to 'inspect' a greater volume of sediment than a straight bill of equal length (Zweers and Gerritsen, 1997).

Some species of sandpipers are known to use mechano-receptors to sense pressure gradients caused or reflected by invertebrate prey buried in the sediment (Gerritsen and Meiboom, 1986; Piersma et al., 1998). The receptors, called Herbst corpuscles, are located under the keratin layer of the bill and occur in high densities within small cavities ('sensory pits') (Gottschaldt, 1985). Data for 17 shorebird species showed that sensory pits are present in large numbers in species that probe for buried prey, as compared to species that hunt visually and have few or no sensory pits (Bolze, 1968). Calidrid sandpipers frequently use a probing foraging mode and sensory pits are, therefore, postulated to be common in this group (Gerritsen and Meiboom, 1986). However, with the exception of data on three calidrid species presented by Bolze (1968), comparative material is lacking.

Western Sandpipers (*Calidris mauri*) are small migratory shorebirds that breed in western Alaska and eastern Siberia and overwinter mainly along the American Pacific coast between southern Canada and Peru (Wilson, 1994; Nebel et al., 2002). They employ probing and pecking as their two main modes of foraging (Sutherland et al., 2000). However, females have a higher propensity to probe than males, both during migration (Mathot and Elner, 2004) and on the non-breeding grounds (Nebel, 2005). Whether this behavioural difference is associated with sex-specific morphological adaptations is not known. Here, we used high resolution microscopy to investigate sex-related differences in gross bill morphology in Western Sandpipers. Also, the technique allowed us to document the number and size of sensory pits in Western Sandpipers as well as two other small calidrids, Least Sandpipers (*Calidris minutilla*) and Dunlins (*Calidris alpina*).

METHODS

Study sites

Individuals that were inadvertent casualties of mist-netting were collected at Bodega Bay (38.2°N, 123.0°W; Least Sandpiper: n = 1), San Francisco Bay (37.5°N, 122.3°W; Western Sandpiper: n = 1), California, USA; and at Bahía Santa María, Sinaloa, Mexico (24.0°N, 108.0°W; Western Sandpiper: n = 11). On the Fraser River Delta, British Columbia, Canada (49.1°N, 123.0°W), specimens were collected by shotgun (Western Sandpiper: n = 16, Dunlin: n = 5) under the authority of Special Permit No. PK BC 92/13 issued by Environment Canada's Canadian Wildlife Service. The protocol was approved by the University of British Columbia Committee on Animal Care. Specimens were stored in a freezer within hours after collection.

Light microscopy

Observations of the bills were made with a Nikon SMZ-1500 stereomicroscope, fitted with an HR Plan Apo 1× objective. A combination of transmitted light from the base stand and epi-illumination from a fibre optic light ring was used to illuminate the specimens. Digital images were taken using a Nikon DXM-1200 high-resolution microscope camera, operating at a pixel resolution of 1280 × 1024. Additional image manipulations were performed using Adobe Photoshop, and Optimas® version 6.1 1 image analysis software (Media Cybernetics Inc., Silver Spring, MD, USA) was used for image analysis and measurements.

Measurements of bill morphology

Five standard measurements of Western Sandpiper gross bill morphology were taken (fig. 1A): exposed culmen length, the distance from the tip of the maxilla to the line of feathering on the dorsal surface of the maxilla (a); the distance from the maxilla tip to the ring at the dorsal end of the maxilla (b); the distance from the maxilla tip to the anterior margin of the nares (c); depth at nares (d); and arch surface length of the maxilla (e). Bill curvature was determined from the ratio of the arch surface length (e) to the length of the exposed culmen (a) (after Stiles, 1995). Individual Western Sandpipers with an exposed culmen length of <24.3 mm were classified as males, and >24.7 mm as females (Page and Fearis, 1971).
   To assess the number and size of sensory pits, the bill was soaked in water and the skin peeled off. The bill was then soaked in bleach to dissolve the remaining soft tissue and expose the pits. Individual differences in the occurrence of sensory pits in any given species of shorebird are reported to be minor (Bolze, 1968), they were therefore quantified only for a few individuals of each species. The number of sensory pits visible within the first 2 mm of the tip of the bill (maxilla and mandible) was counted.
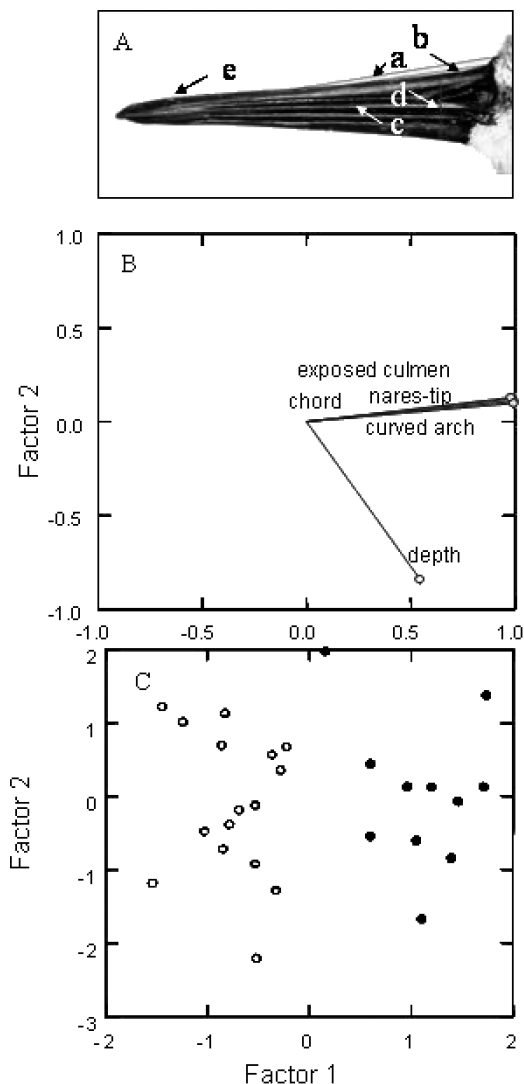
Figure 1. A. Five dimensions of Western Sandpiper bill shape (see Methods for details). B. Bill length and related variables constituted Factor 1, which explained 84% of the variance in bill shape. Bill depth constituted Factor 2. C. Males (open circles) and females (filled circles) differed only with regard to Factor 1 (bill length), but not Factor 2 (bill depth).

RESULTS

To test for differences in gross bill morphology between male and female Western Sandpipers, we performed a Principal Component Analysis on the five dimensions of bill morphology (fig. 1A). Factor 1 constituted measures of bill length, while Factor 2 constituted bill depth (fig. 1B). Factors 1 and 2 explained 84.1% and 15.2% of the total variance, respectively. To test whether factor scores differed

Table 1.
Bill morphology dimensions of female and male Western Sandpipers (sample size). Values indicate the mean in mm, with the standard deviation in brackets. The letters a-e refer to the measurement definitions given in Fig. 1a.

	Exposed culmen (a)	Chord (b)	Nares to tip (c)	Depth at nares (d)	Surface length (e)	Curvature
Female (11)	24.41 (1.14)	25.73 (1.11)	22.10 (1.18)	4.97 (0.33)	26.08 (1.09)	1.01 (0.001)
Male (17)	22.01 (1.01)	21.43 (1.01)	18.20 (0.80)	4.67 (0.31)	21.72 (1.02)	1.01 (0.001)
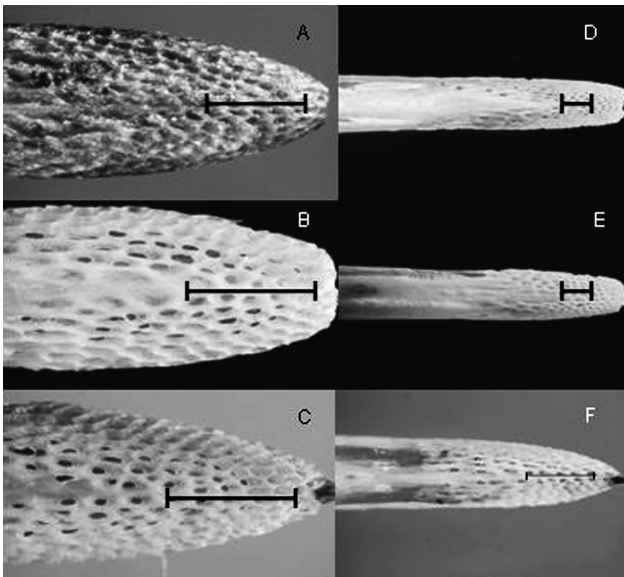
Figure 2. Sensory pits occurred in all three species in both upper and lower bill. The scale indicates 1 mm. A. Western Sandpiper female, lower bill, unbleached. B. Western Sandpiper female, upper bill, bleached. C. Western Sandpiper male, lower bill, bleached. D. Dunlin female, lower bill, bleached. E. Dunlin male, upper bill, bleached. F. Least Sandpiper male, upper bill, bleached.

between males and females, we performed a General Linear Model (GLM). Bills of male (n = 17) and female (n = 11) Western Sandpipers differed with regard to Factor 1 ($F_{1,25}$ = 113.76, P < 0.001), but not regarding Factor 2 ($F_{1,25}$ = 0.16, P > 0.05; Fig. 1C). Bill curvature did not differ between males and females (GLM: $F_{1,26}$ = 0.01, P > 0.05). Mean and standard deviations of all bill morphology dimensions are given in table 1.

Numbers of sensory pits in the first 2 mm of the bill tip were counted in a Western Sandpiper female (upper bill: n = 98), a Western Sandpiper male (lower bill: n = 88), a Dunlin female (lower bill: n = 85), a Dunlin male (upper bill: n = 56) and a Least Sandpiper male (lower bill: n = 52; fig. 2). In Western Sandpipers, sensory pits were ca. 22-27 μm long and ca. 6-9 μm wide, in Dunlin ca. 14-22 μm

long and ca. 6-10 μm wide, and in Least Sandpipers ca. 11-13 μm long and ca. 6-8 μm wide. No differences were detected in sensory pit dimensions between the maxilla and mandible for any of the three species.

DISCUSSION

In this study, we explored sex-specific differences in bill morphology for Western Sandpipers. As expected, gross bill morphology differed between male and female Western Sandpipers regarding bill length, which had been used to assign sex, while no difference was detected in bill depth or curvature. Therefore, the propensity of female Western Sandpipers to use the probing foraging mode more than males (Mathot and Elner, 2004; Nebel, 2005) cannot be attributed to a higher degree of bill curvature, despite curved bills being reportedly better adapted to probing than straight bills (Davidson et al., 1986; Ferns and Siman, 1994; Zweers and Gerritsen, 1997). However, optimal bill shape is subject to a trade-off between curvature and slenderness. While curvature may facilitate probing, a curved bill must possess a greater bone mass to maintain a resistance to bending comparable to that of an equivalent sized straight bill (Zweers and Gerritsen, 1997). In Western Sandpipers, the cost of greater bone mass required to stabilise a curved bill might outweigh the advantages of increased curvature. Also, straight bills are considered more versatile and better adapted for foraging in tundra habitats (Jönsson and Alerstam, 1990). Therefore selective pressures on the breeding grounds might also be influential in determining optimal bill shape.

Calidrid sandpipers can forage by both pecking and probing modes on intertidal invertebrates during migration and in the non-breeding season (Sutherland et al., 2000; Mathot and Elner, 2004; Nebel, 2005). Location of actively moving infaunal prey may be facilitated by using mechano-receptors that detect vibrations in wet sediment (Gerritsen and Meiboom, 1986). In comparison, Red Knots (*Calidris canutus*) are able to locate immobile, hard-shelled prey by detecting pressure gradients (Piersma et al., 1998). Western Sandpipers, Least Sandpipers and Dunlin feed on soft-bodied, mobile infaunal invertebrates as well as less-mobile bivalve molluscs (Cooper, 1994; Warnock and Gill, 1996; Sutherland et al., 2000). In all three of the latter species, high densities of sensory pits of oval shape were detected, consistent with observation made earlier on Dunlin (Bolze, 1968) and with the prediction that sensory pits are generally common in calidrid sandpipers (Gerritsen and Meiboom, 1986). In the Common Snipe (*Gallinago gallinago*), sensory pits are of polygonal shape, which allows the maximum concentration of sensory pits, and thereby Herbst corpuscles, on the surface of the bill. This is consistent with the finding that of all 17 shorebird species, the Common Snipe relies most on detecting prey by using the probing foraging mode (Bolze, 1968). While our results support the notion that localising prey by detecting vibrations and/or pressure gradients ('remote sensing') plays an important role in assessing availability of infaunal prey in calidrid sandpipers, the functional significance of the observed differences in

length, but not width, and number of sensory pits between the three species are uncertain. The morphological distinctions likely reflect inter-specific differences in infaunal foraging ability and behaviour, but comparative data on foraging behaviour across all three species are lacking. Nevertheless it should be possible to test this prediction empirically.

The ability to assess the availability and forage on infaunal prey may have important implications to the underlying mechanism explaining the non-breeding distribution of calidrid sandpipers. The relative availability of epi- vs. infaunal prey has been hypothesised to change with latitude due to a general increase in invertebrate burying depth (Elner and Seaman, 2003; Nebel, 2005) as a result of either the differential distribution of epifaunal feeding crabs (Elner and Seaman, 2003) or higher sediment temperatures closer to the equator (Nebel, 2005; Nebel and Thompson, 2005). Thus, longer-billed individuals would be at an advantage at southern latitudes. Consistent with this notion is a latitudinal increase of bill length over the overwintering range in Western Sandpipers between sexes, as females have longer bills than males and winter further south (Nebel et al*.,* 2002), as well as within sexes (O'Hara, 2002; Nebel, 2003).

Our study highlights the importance of incorporating morphological aspects into the study of evolutionary ecology. Morphometric considerations can provide valuable insights to elucidating not only avian foraging decisions but also broader scale inter- and intra-species comparisons regarding distribution patterns and niche partitioning.

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