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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-speci c variation in bill length and shape as well as in foraging behaviou Pecking, or feeding on epifaunal intertidal invertebrates, is associated with a straight bill, while pro ing, feeding on infaunal prey, is facilitated by bill curvature. Here, we used high resolution microscop 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 fo aging behaviour between the sexes. Detection of infaunal prey can be facilitated by the presence Herbst corpuscles. These mechano-receptors are located in 'sensory pits' under the keratin laye the bill and are able to sense pressure gradients. They are postulated to be common among cal sandpipers, but comparative data are lacking. Using high resolution microscopy, we measured nu ber and size of sensory pits in Western Sandpipers, Least Sandpipers (*Calidris minutilla*) and Dunlin (*Calidris alpina*). The implications of these ndings to foraging adaptations and non-breeding site choice are discussed.

Keywords: bill micro-anatomy; Dunlin; foraging mode; Herbst corpuscles; Least Sandpiper; sensor 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 (Hu cher and Ens, 1992; Lauro and Nol, 1995; Mascitti and Kravetz, 2002; Durant et a

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

Shorebirds (Charadrii) show pronounced inter-sexual and inter-speci c variatio in bill length and shape as well as in foraging behaviour (Jehl and Murray, 198 Durell, 2000; van de Kam et al., 2004), and are a candidate group to study functior bill morphology. Certain aspects of gross bill morphology and micro-anatomy ar known to be adaptive to speci c modes of foraging. ‘Pecking’ is characterised b feeding on intertidal invertebrates at or near the sediment surface (epifaunal pre ‘Probing’, by contrast, consists of inserting the bill into the sediment, allowing the capture of invertebrates that live below the sediment surface (infaunal prey). Probi is observed more frequently in species with long and curved bills than in speci

METHODS

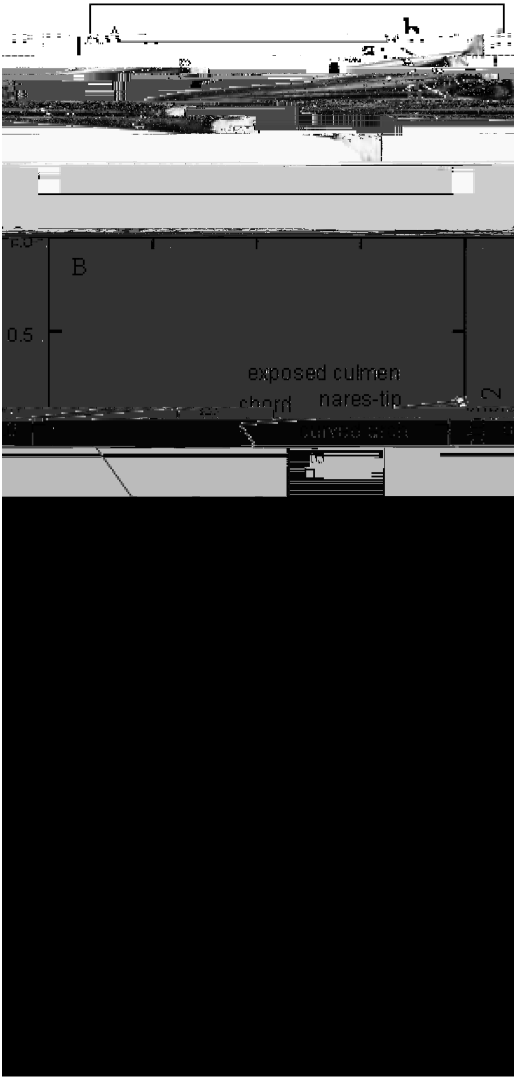

Figure 1. A. Five dimensions of Western Sandpiper bill shape (see Methods for details). B. Bil length and related variables constituted Factor 1, which explained 84% of the variance in bill sha Bill depth constituted Factor 2. C. Males (open circles) and females (lled circles) differed only with regard to Factor 1 (bill length), but not Factor 2 (bill depth).

RESULTS

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

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 t
maxilla and mandible for any of the three species.

DISCUSSION

In this study, we explored sex-speci c differences in bill morphology for Westerr
Sandpipers. As expected, gross bill morphology differed between male and fema
Western Sandpipers regarding bill length, which had been used to assign sex, wh
no difference was detected in bill depth or curvature. Therefore, the propensity
female Western Sandpipers to use the probing foraging mode more than ma
(Mathot and Elner, 2004; Nebel, 2005) cannot be attributed to a higher degree
bill curvature, despite curved bills being reportedly better adapted to probing tha

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

The ability to assess the availability and forage on infaunal prey may hav important implications to the underlying mechanism explaining the non-breedin distribution of calidrid sandpipers. The relative availability of epi- vs. infaunal prey has been hypothesised to change with latitude due to a general increase invertebrate burying depth (Elner and Seaman, 2003; Nebel, 2005) as a result either the differential distribution of epifaunal feeding crabs (Elner and Seama 2003) or higher sediment temperatures closer to the equator (Nebel, 2005; Ne and Thompson, 2005). Thus, longer-billed individuals would be at an advantage southern latitudes. Consistent with this notion is a latitudinal increase of bill lengt over the overwintering range in Western Sandpipers between sexes, as females h 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 aspect into the study of evolutionary ecology. Morphometric considerations can provid valuable insights to elucidating not only avian foraging decisions but also broad scale inter- and intra-species comparisons regarding distribution patterns and ni partitioning.

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