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NOTE AND COMMENT

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Foraging behaviour of western sandpipers changes with sediment temperature: implications for their hemispheric distribution

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Abstract Migratory shorebirds need to replenish their energy reserves by foraging at stop-over sites en route. Adjusting their foraging behaviour to accommodate variation in local prey availability would therefore be advantageous. We test whether western sandpipers (*Calidris mauri*), a sexually dimorphic shorebird, adjust their foraging behaviour in response to local changes in prey availability, as inferred by changes in diurnal time and sediment temperature. Both males and females showed quantitative changes to foraging mode in relation to each of these variables. Probing, for example, which is used to exploit infaunal prey, was significantly more common at higher temperatures. The results presented here are consistent with the notion that western sandpipers can adjust their foraging behaviour in response to variation in prey availability. Further, we speculate that temperature-induced changes to prey location may contribute to the striking sexual segregation observed for this species during the non-breeding season.

Keywords *Calidris mauri* · Intertidal invertebrates · Migratory shorebirds · Prey burying depth · Sex-ratio cline

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Introduction

Shorebirds are capable of extreme long-distance migrations, covering thousands to tens of thousands of kilometres between breeding and non-breeding sites (Alerstam 1990; Piersma 1997). The energetic requirements of migration are substantial (Pennycuick 1989) and shorebirds must therefore continually replenish their energy reserves by feeding at intertidal stop-over sites en route. Energy up-take at these sites directly affects a migrant's chance of success (Alerstam and Lindström 1990; Zwarts et al. 1990), and foraging behaviour is therefore a factor that potentially limits the spatial and temporal boundaries of shorebird migration (Piersma 2002).

The western sandpiper (*Calidris mauri*) is a particularly well-studied shorebird (Nebel and Lank 2003). These long-distance migrants breed in western Alaska and eastern Siberia, and overwinter along the American Pacific coast between southern Canada and Peru and, to a lesser extent, in the Caribbean (Wilson 1994; Nebel et al. 2002). Western sandpipers feed on a wide variety of invertebrates typical of intertidal mudflats (Wilson 1994; Wolf 2001), which they mainly exploit by two distinct foraging modes: 'pecking' and 'probing' (Sutherland et al. 2000). The existence of dual foraging modes suggests that western sandpipers can exploit invertebrates located at different depths, and that they can potentially vary mode usage in response to vertical changes to prey location.

Sutherland et al. (2000) described 'pecking' as a single peck of the bill onto the sediment surface, and this mode is presumably used by sandpipers to capture invertebrate prey at or near the sediment surface. 'Probing', by contrast, consists of inserting the bill well into the sediment, and is presumably used to capture invertebrates that live below the sediment surface. If western sandpipers can vary mode usage in response to changes in prey location, then we predict that the proportion of probes will increase when the majority of prey tends to be located below the sediment surface (infaunal prey). Likewise, we predict a decrease in probe usage when prey tends to be located on the sediment surface (epifaunal prey).

Tracking changes in the spatial location of invertebrate prey while simultaneously observing changes to foraging mode of individual birds would be difficult. However, real-time changes in prey location can be inferred indirectly through proxies. Because invertebrate prey location is expected to vary with tidal, diurnal, seasonal and annual cycles (Sutherland et al. 2000), one could test for changes in foraging mode usage over these time scales. Changes to mode usage over diurnal time, for example, would suggest that western sandpipers do adjust their foraging mode in response to diurnal changes in prey location. Similarly, because invertebrate prey location is expected to vary with sediment temperature (e.g., Donn and Croker 1986; Zwarts and Wanink 1993; Somero 2002), one could test for changes in foraging mode in relation to this variable. A correlation here would suggest that western sandpipers do adjust their foraging mode in response to temperature-induced changes in prey location.

In this study we examine the foraging behaviour of male and female western sandpipers at one of their overwintering sites on the Pacific coast of Panama. We attempt to uncover the significance of their dual foraging modes, and predict that western sandpipers will show evidence of optimizing their energy up-take by altering their foraging mode in response to changes in prey location. We observe the foraging behaviour of our focal population directly but infer changes to prey location through proxy variables, namely diurnal time and sediment temperature.

Materials and methods

The foraging behaviour of individual western sandpipers was observed at Costa del Este, in the upper Bay of Panama (9.0°N, 79.3°W) in January and February 2002. Based on whether individual male and female birds inserted their bill to more than half of its length into the sediment, or fed directly off the sediment surface, foraging behaviour was scored as a ‘probe’ or a ‘peck’, respectively. Observations that were not clearly a peck or a probe under the above criterion were considered ambiguous and not included in subsequent analyses. Behavioural data collected on focal birds (average length of observation period: 57 s, range: 15–100 s) were transformed into a standardized score. This score is expressed as the proportion of probes, as in [number of probes/(number of pecks + number of probes)]. Score variance was subsequently normalized through arcsine transformation (Zar 1999) prior to being correlated with time and temperature. In each case correlations were assessed through General Linear Models (SYSTAT 2004). To test for a correlation between foraging score or sediment temperature (see below) and diurnal time we included both ‘time’ and ‘time-squared’ into the General Linear Model. This allowed us to detect hyperbolic, as opposed to linear, relationships that might exist between variables.

Sex was assigned to individual birds on the basis of bill dimorphism. Individuals with short (exposed culmen < 24.3 mm) and long (exposed culmen > 24.7 mm) bills are considered male and female, respectively (Page and Fearis 1971). Relative bill length, and thus sex, was assessed non-invasively using a spotting scope (Kowa 20–60×) from a 20–30 m distance, a technique that was deemed accurate following an a priori trial. Briefly, nine individuals of unknown sex were caught in mistnets and their bill length was measured directly. These birds where then colour-banded by a naive observer, released into a mesh enclosure and sexed again by the first author (S.N.) using the scope. In all but one of these cases ($n = 4$ males, $n = 5$ females) sex was assigned correctly.

Diurnal time of each behavioural observation was recorded to the nearest 30-min interval between 0700 and 1800 hours. Likewise, sediment temperature was recorded at 30-min intervals between 0700 and 1900 hours. Twelve temperature-recording probes (Yellow Springs Instruments, Ohio, USA) were inserted into the sediment, with four recorders each at three different depths (0, 10 and 30 mm). These depths reflect the approximate range of western sandpiper bills, which are about 25 mm long (Wilson 1994). The individual probes were positioned haphazardly in the upper intertidal zone in an area where western sandpipers had regularly been observed foraging.

Results

In total, 212 birds were observed. Of these, 59 were male and 153 were female, reflecting the female-biased sex ratio of western sandpiper populations wintering at southern latitudes (Nebel et al. 2002). The number of wintering western sandpipers in this study area varied between 3,000 and 50,000 birds, but averaged around 25,000. Focal individuals were typically part of a flock of about 40–400 western sandpipers.

Both females ($F_{2,150} = 7.39$, $P = 0.001$) and males ($F_{2,56} = 4.56$, $P = 0.015$) exhibited significant changes in their foraging score with diurnal time (Fig. 1a). Both sexes showed an initial increase in the use of probes with time of day, followed by a post-peak decline. Pooling all birds, including five individuals of unknown sex, did not alter the significance of this trend ($F_{2,214} = 9.23$, $P < 0.001$).

Both females ($F_{1,151} = 10.82$, $P = 0.001$) and males ($F_{1,57} = 7.26$, $P = 0.009$) significantly altered their foraging mode as a function of sediment temperature (Fig. 1b). Both sexes increased probe usage with increasing temperature, though the magnitude of change was greater for females. Again, pooling all birds irre-

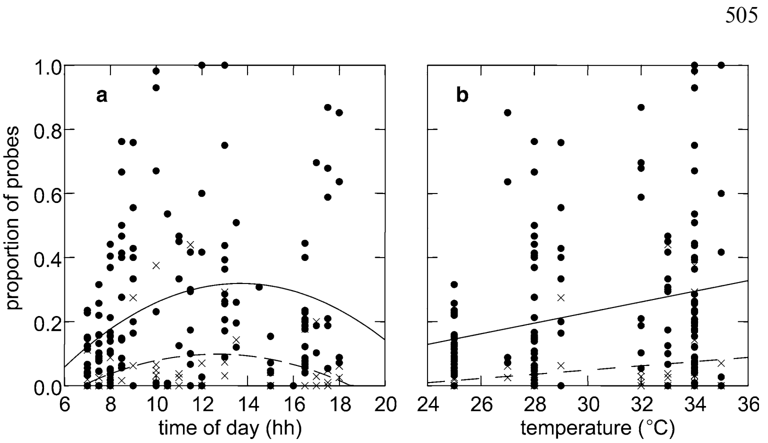

Fig. 1 Foraging behaviour of Western Sandpipers. **a** Foraging score (see Materials and methods) versus diurnal time. **b** Foraging score versus temperature of the sediment surface. Both females (*filled circle—solid line*, $n = 153$) and males (*crosses—stippled line*, $n = 59$) increased the proportion of probes as a function of diurnal time (hyperbolic model) and sediment temperature

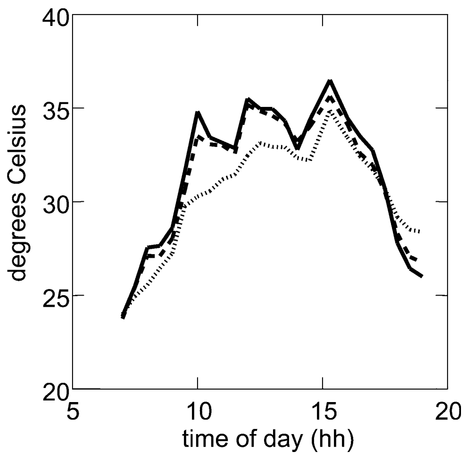

Fig. 2 Sediment temperature at Costa del Este, Upper Panama Bay, varied significantly with diurnal time and with sediment depth (*solid line* 0 mm, *broken line* 10 mm, *stippled line* 30 mm)

Table 1 Sediment temperature recordings at Costa del Este, Panama Bay

Depth (mm) at which temperature was recorded	Number of temperature readings	Mean temperature (°C) with standard deviation	Maximum temperature (°C) with range
0	270	31.5 (±3.73)	39.5 (17)
10	280	31.3 (±3.36)	38.0 (15)
30	282	30.6 (±2.85)	35.5 (12)

spective of sex did not alter the significance of this trend ($F_{1,215} = 13.24$, $P < 0.001$).

As would be expected, temperature co-varied significantly with diurnal time at all three sediment depths (0 mm: $F_{2,239} = 276.35$, $P < 0.001$; 10 mm: $F_{2,249} = 507.34$, $P < 0.001$; 30 mm: $F_{2,251} = 541.37$, $P < 0.001$; Fig. 2), and temperature was inversely correlated with sediment depth ($F_{1,746} = 9.84$, $P = 0.002$; Table 1, Fig. 2).

Interestingly, females were observed to probe significantly more than males across all observation periods ($F_{1,210} = 46.58$, $P < 0.001$), and also had a significantly higher variance in mode usage ($F_{1,120} = 38.14$, $P < 0.001$; Levene's Test, as implemented in the computer program JMPIN 4.0.4).

Discussion

Western sandpipers appeared to change their foraging behaviour throughout the day. The general trend was to initially increase probe usage, at the expense of pecks, until a peak was reached approximately midway through our 12-h observation period. The same trend was observed for both males and females (Fig. 1a), though the amplitude of change was greater for females. Moreover, western sandpipers also changed their foraging behaviour as a function of sediment temperature. The general trend was to increase probe usage, at the expense of pecks, with increasing sediment temperature. This trend was significant for both males and females (Fig. 1b), but again was more pronounced in females. Overall, these observations suggest that western sandpipers have the ability to quantitatively alter foraging mode usage in response to changes in environmental conditions. We propose that the observed changes to foraging mode are, in fact, a behavioural response to changes in invertebrate prey location.

While sediment temperature and diurnal time are tightly correlated (Fig. 2), we suggest that it is temperature, not time per se, that is affecting foraging behaviour. This suggestion stems from the demonstrated potential for sediment temperature to alter the spatial location of invertebrate prey, and hence the foraging behaviour of birds. Sediment temperature has been shown to affect the vertical zonation or burying depth of a wide range of intertidal invertebrates (Brown 1960; Wolcott 1973; Britton 1983; McMahon and Britton 1983; Donn and Croker 1986; Somero 2002). In a tropical environment like Panama, where the sediment surface becomes extremely hot, burying deeper could allow intertidal invertebrates to avoid desiccation (Brown 1960; Emson et al. 2002). No empirical data on the range of temperature-induced changes to invertebrate burying depth yet exist for the Bay of Panama but data from other studies (Donn and Croker 1986; Zwarts and Wanink 1993; Somero 2002), together with the general plausibility of this scenario (Sutherland et al.

2000), suggest that temperature-induced changes to prey location is a general mechanism that is applicable here. Temperature-induced changes to the spatial location of invertebrate prey thus provides a candidate explanation to our observation that western sandpipers probe significantly more at the hottest time of the day (Fig. 1a), or simply when it is hottest (Fig. 1b). Probing allows them to access the more deeply buried prey.

Temperature-correlated changes in shorebird foraging behaviour have been observed previously (Pienkowski 1981, 1983; Dominguez 2002), and have similarly been interpreted to reflect a temperature-induced change to the spatial location of prey or their detectability. These observations, together with our own, suggest that shorebird foraging behaviour is generally linked to temperature-induced changes to invertebrate prey location. If so, then inclusion of this parameter into arithmetic models predicting optimal foraging behaviour could improve their accuracy.

The association between changes in temperature and shorebird foraging behaviour at single sites is demonstrated by this study. However, the extent to which changes in temperature affect more general aspects of shorebird foraging ecology is not yet known. Western sandpipers are sexually dimorphic and show striking sexual segregation throughout their migratory range. Females, who have disproportionally longer bills than males (Cartar 1984), significantly outnumber males in the southern parts of their range. Males, by contrast, outnumber females in the northern part of their range (Nebel et al. 2002). Moreover, within both males and females, bill length increases towards southern latitudes (O'Hara 2002; Nebel 2005). A temperature-induced trend in prey burying depth across latitudes could potentially explain the observed latitudinal trends in sex ratio and bill length. Intertidal sediment temperature changes with ambient temperatures (Piccolo et al. 1993), which generally increase with proximity to the equator (Piersma et al. 2005). Invertebrates may therefore generally increase their burying depth towards lower latitudes. This would result in a latitudinal change in the relative availability of epi- versus in-faunal prey (Elner and Seaman 2003; Nebel 2005; Nebel et al. 2005). Birds with longer bills (females), or a greater tendency to probe (females; Fig. 1), would have an advantage at equatorial sites. This more general hypothesis remains untested but is consistent with the observed pattern.

In summary, we have shown that foraging behaviour of western sandpipers changes with sediment temperature on a tropical mudflat in Panama. We attribute the observed changes to the effect of temperature on burying depth of invertebrate prey. Through extension, we speculate that latitudinal variation in ambient temperatures may predispose birds of longer bill-length (females), or birds with a greater tendency to probe (females), to migrate to hotter (i.e., equatorial sites). This novel hypothesis potentially explains the conspicuous and large-scale latitudinal cline in sex ratio that is observed for this species.

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