

Sediment microtopography and shorebird foraging

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ABSTRACT: Short-billed dowitchers *Limnodromus griseus* were observed feeding on an intertidal sandflat in South Carolina, USA. The resulting probe marks were significantly more abundant on the crests than in the troughs of tidally-formed sand ripples. Penetrometry measurements indicated that ripple crests were significantly more penetrable than troughs. Crest-trough differences in prey distribution and other sediment parameters do not account for this selection of probing sites. Penetration of crests requires only 53 to 70 % of the force needed for troughs and thus requires reduced energy expenditure by the bird. Tactile-searching shorebirds apparently respond to microscale foraging cues as do visually-searching waders.

INTRODUCTION

Environmental factors such as wind, tide, daylength, and substratum all affect habitat use by shorebirds feeding in intertidal areas (Evans, 1976; Connors et al., 1981). Many of these influences are mediated through their effect on prey activity and availability. For example, infaunal prey may burrow more deeply at low tide making them inaccessible to probing birds (Evans, 1979). Because invertebrate activity rhythms (i.e. burrow ventilation, fecal cast production) are important cues for visually-searching waders, they have been the focus of shorebird foraging studies on small spatial scales.

On a larger spatial scale, studies of foraging site selection emphasize gross habitat differences such as grain size, tidal immersion, sediment water content, beach slope, and substratum penetrability (Burger et al., 1977; Myers et al., 1980; Connors et al., 1981; Quammen, 1982). These differences are presumably important in the selection of feeding sites by tactile feeders, but they have not been studied on the same spatial scale that has been applied to individual prey activity and the response by visual predators. Tactile searchers are also affected by prey activity due to large-scale environmental effects, e.g. prey seek refuge from extreme temperatures by burrowing deeper (Goss-Custard, 1969; Pienkowski, 1983b). In this instance feeding success is diminished due to a decreased probability of encounter. (Myers et al., 1980)

rather a lack of apparent cues given by prey. Overall influences such as temperature or tidal level may affect habitat selection and/or foraging success by tactile-searching waders, but they do not preclude the use of fine-scale substratum features when these birds probe for prey within a specific site. Given that visually-searching birds resolve their foraging environment on a scale of less than one square meter (Pienkowski, 1983a), I suggest that tactile-foraging birds also select probing sites on a fine scale rather than solely on gross habitat characteristics.

Observations in a South Carolina (USA) estuary indicated that tactile-searching, short-billed dowitchers *Limnodromus griseus* selectively probed on the crests of tidally-formed sand ripples rather than in the troughs. I hypothesized that this preference would be reflected by sediment penetrability. Abiotic and biotic features of sand ripples were thus measured to explain the birds' choice of microhabitat.

MATERIALS AND METHODS

Studies were carried out on Debidue Flat, a large sandflat in the pristine North Inlet Estuary near Georgetown, South Carolina, USA (33°19'N, 79°10'W). Sediments are well-sorted medium-fine sand (2.35 ϕ) (Grant, 1981a). Dowitchers are among the most abundant shorebirds overwintering in the estuary (Grant, 1981b). During a low tide (September

1980), numbers of dowitcher probe holes were counted on randomly selected ripple crests and adjacent troughs. A small metal rod was inserted into the holes to measure their depth. Sediment penetrability was measured in autumn 1982 with a Pocket Penetrometer (Soiltest, Inc., Evanston, Illinois, USA) on both ripple crests and troughs. This spring-loaded instrument is pushed into the sediment to 6 mm depth and compressive strength read directly. Water content of surface sediment was measured by weight loss after drying (Grant, 1981a). Additional information on sediments and fauna was taken from previous studies (Grant, 1981a, b, c).

RESULTS

Dowitchers fed in intertidal sand while continuously walking and using a series of 'jabs' (shallow and brief penetration) as is typical of their tactile feeding mode (Burton, 1972). Birds were observed after the flat was completely exposed, well above the water's edge. Tidally-formed sand ripples in the feeding area were 13 to 14 cm in wavelength and 3 cm in amplitude. No standing water occurred in ripple troughs. The number of probe marks on crests was significantly higher than in adjacent troughs (paired t-test, $p < 0.001$; Table 1, Fig. 1). Marks were absent in many areas of the flat, but where abundant occurred at a mean density of 85 ± 55 SD m^{-2} . The depth of holes made by bills was 0.5 to 1.0 cm, less than 20 % of average bill length (Stout, 1967). I created 1 cm holes in the sand with a metal rod and found that their depth did not change

during low tide. It is likely that dowitcher probe holes did not slump after they were formed. Probe marks generally followed the long axis (span) of the crest (Fig. 1). Footprints often followed the span but birds also walked transverse to the ripples. The width of the crests was 9 cm. Birds walking along the span would quickly enter a trough because current ripples are irregular and not linearly arranged (Fig. 1). Prey taken were too small to be observed during feeding.

If dowitchers probed randomly, the larger surface area of crests relative to troughs (maximum of 2:1) would create an apparent feeding selection for crests. When probe density per trough is multiplied by 2 to normalize surface area, site selection for crests is still significant, indicating a non-random effect. Semipalmated sandpipers *Calidris pusilla*, which spend most of their time pecking rather than probing (Ashmole, 1970), also fed on this flat but showed no preference for crests or troughs.

Because ripples were superimposed on large sandwaves, comparisons of ripple crest-trough penetrability were carried out in both the crest and trough of a sandwave. Ripple troughs were consistently less penetrable (i.e. harder) than crests; the results were highly significant (Wilcoxon rank sum test, $p < 0.001$, Table 1). This difference applied to ripples in both crest and trough of a sandwave (Table 1), however, the variance in penetrability measurements was significantly greater in the ripple troughs of sandwave troughs (F-test, $p < 0.05$; Table 1). The difference in variance within the sandwave crest was not significant ($p > 0.05$). Perkins (1958) also found more variability in the hardness of ripple troughs relative to crests.

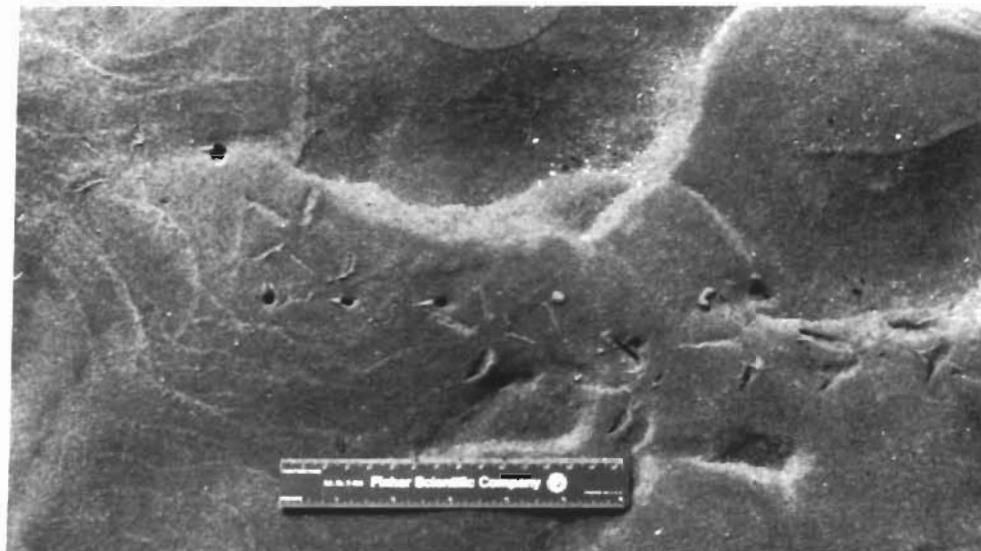


Fig. 1. Dowitcher *Limnodromus griseus*. Probe holes and foot prints on a ripple crest, Debidue Flat. Ruler is 15 cm long

Table 1. Dowitcher *Limnodromus griseus*. Foraging preference and sediment properties with respect to bedform topography on Debidue Flat. All values are means (\pm SD). Sandwaves were not present when dowitcher probes were counted. Smaller penetrability values indicate softer sediments

Parameter	Location					
	Ripple		Sandwave crest		Sandwave Trough	
	Crest	Trough	Ripple crest	Trough	Ripple crest	Trough
# Dowitcher probes n = 20 crest-trough pairs	4.0 (2.2)	1.2 (1.0)				
Penetrability (kg cm ⁻²) n = 15 for each mean			1.9 (0.3)	2.7 (0.4)	1.5 (0.2)	2.8 (0.8)
Water content (% weight) n = 6 for each mean	22.0 (0.5)	21.3 (0.8)				

DISCUSSION

In addition to penetrability, other factors could potentially explain preference for ripple crests. An obvious alternative is some other physical sediment variable which might differ between crest and trough. Sediment from ripple troughs may be slightly coarser (Harms, 1969; Grant, 1981a), but more extensive sampling by Hogue and Miller (1981) revealed no significant difference between crest and trough. Sorting and organic content are also extremely similar between crest and trough (Grant, 1981a; Hogue and Miller, 1981). Water content is related to penetrability, and as predicted by Perkins (1958) was greater in ripple crests, but this comparison is only marginally significant (Wilcoxon rank sum test, $p = 0.047$; Table 1).

Another possibility is a biotic variable such as prey distribution. The haustoriid amphipod *Acanthohaustorius millsii* is more abundant in ripple crests than troughs (Grant, 1981c). However, < 10 % of the *A. millsii* population occurs at 0 to 2 cm sediment depth; this species comprises only 10.4 % of the caloric intake by all shorebirds on Debidue Flat (Grant, 1981b). This prey is therefore unlikely to be the reason for selective probing by dowitchers. The polychaete *Paraonis fulgens* is the only species more abundant than amphipods, but is rare in uppermost sediment layers (Risk and Tunnicliffe, 1978), especially at low tide (Röder, 1971). Surface traces of other invertebrates such as hemichordates occur on Debidue Flat, but they are not more abundant on crests than in troughs.

A recent study by Hogue and Miller (1981) indicated that where fauna were more abundant in crests, highest densities appear to be beneath the crests rather than in the top 0 to 2 cm of sediment. On Debidue Flat, crest surface and subsurface samples did not differ significantly in crustacean density, however, samples were taken at 0 to 5 and 5 to 10 cm, respectively; this

scale could not resolve the finer vertical distribution which apparently occurs in crests. Smaller scale sampling in Grant (1981a) does confirm much lower amphipod numbers at 0 to 2 vs. 2 to 4 cm sediment depth. Dispersion patterns resulting from ripples can remain subsequent to ripple migration and may explain the observed periodicity of fauna in intertidal sand (Eckman, 1979; Hogue and Miller, 1981). This effect does not, however, produce a consistent crest-trough difference in faunal abundance. In essence, there is little evidence from studies on Debidue Flat or elsewhere to suggest that animals are more abundant in the upper centimeters of ripple crests compared to troughs. Moreover, though sediment penetrability may itself affect burrowing by prey organisms, Perkins (1958) found that the greater hardness of ripple troughs compared to crests was not reflected in differences in faunal distribution.

Recent experimental studies indicate that in harder sediments, both the depth of a single probe and the detection of buried prey by sanderlings decrease (Myers et al., 1980). In addition to capturing fewer prey, birds may expend additional energy probing harder sand. Penetration of crests requires only 53 to 70 % of the force needed for troughs (Table 1). To achieve the same depth of penetration as in softer sand, a bird must also probe repeatedly at the same site (Myers et al., 1980) because the grains are packed more tightly and the interstitial spaces are smaller in hard sands. In the field, ripple crests are sites of active sediment transport and thus the grains are less stably arranged. The larger pore volume in crests allows a higher water content and offers less resistance to penetration (Perkins, 1958). Although the differences in water content between crest and trough are small, minor changes in pore volume can produce major changes in the reaction of sand grains to a shearing force (Bagnold, 1966). Other habitats of active sediment transport such as the swash zone of sand beaches

display large changes in penetrability as waves recede (Myers et al., 1980).

While sediment penetrability may be important to tactile-searching waders, it has received little attention. Most studies of tactile feeders have centered on what affects the availability and activity of their prey, i.e. temperature, tidal exposure, darkness (Evans, 1976, 1979; Pienkowski, 1983b). However, a number of other factors related to substrate suitability may cause physical inhibition of foraging, i.e. compacted sediments, fluidized mud (Tjallingii, 1972; Evans, 1976; Myers et al., 1980). In recent field experiments, Quammen (1982) determined that sand may interfere with prey capture by waders because prey items cannot be distinguished from sediment grains. Direct inhibition of foraging such as substrate suitability or weather conditions may also act in concert with the less direct effect of prey availability. For example, strong wind conditions may both exclude birds from exposed tidal flats and cause a reduction in prey activity (Evans, 1976).

Sediment cues used by tactile feeders are difficult to ascertain, but are distinctly non-random in space (Myers et al., 1980). Resolution of foraging microhabitat by shorebirds is not solely dependent on biogenic cues such as worm traces. Small-scale abiogenic signals such as ripple topography are also recognized, and may be of widespread significance to tactile-searching waders.

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