

THE INFLUENCE OF WATER DEPTH AND SEDIMENT TYPE ON THE FORAGING BEHAVIOR OF WHIMBRELS

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Abstract.—Prey-size selection by Whimbrels (*Numenius phaeopus*) feeding on an intertidal polychaete was investigated to determine how different substrate conditions affect the foraging of Whimbrels feeding on an intertidal mudflat. Whimbrels preying almost exclusively on large polychaetes (*Perinereis gualpensis*) in an estuarine mudflat in Chile (Queule River estuary 39°20'S, 73°13'W) were studied. Birds were highly selective: the average prey size found on droppings was 53.6 ± 3.7 SE ($n = 914$) mm total body length, and 95% of them were larger than 40 mm. Whimbrels obtained their prey almost exclusively by deep probing because large worms were found mainly at depths below 3 cm in the substrate. Observations of feeding Whimbrels were made in five sediment conditions: (1) shallow water, sediment covered by a 2–10 cm water layer; (2) water film, sediment covered by a water film <2 cm deep; (3) wet sand with no water layer; (4) dry sand; and (5) mud. Foraging was significantly more successful in sandy areas than in muddy areas. This result corresponded with an observed lower density of large polychaetes (>40 mm) in the mud. Within sandy areas Whimbrels had the highest foraging success rate in wet sand. Wet sand was suspected to be optimal for visual detection of prey because, in water-covered sediments, water movement probably interfered with visual detection of prey. Whimbrels did not feed in dry sand, which suggested that prey were not detectable or were unavailable to the birds due to burrowing depth and increase in sediment compaction.

EFFECTO DE LA PROFUNDIDAD DEL AGUA Y DEL TIPO DE SEDIMENTO SOBRE LA CONDUCTA ALIMENTICIA DE *NUMENIUS PHAEOPUS*

Síntesis.—Se describe la depredación selectiva de poliquetos por parte de Zarapitos (*Numenius phaeopus*). Además se investiga cómo distintas condiciones del sustrato afectan el forrajeo de los Zarapitos que se alimentan casi exclusivamente del poliqueto *Perinereis gualpensis* en un intermareal cienagoso del estuario del Río Queule (39°20'S, 73°13'O), Chile. Se encontró que las aves fueron altamente selectivas: el tamaño promedio (longitud corporal total) de poliquetos encontrados en las heces fecales de Zarapitos fue de 53.6 ± 3.7 (E.S.) mm ($n = 914$), el 95% de los poliquetos depredados por las aves fueron mayores a 40 mm. Los Zarapitos capturaron poliquetos casi exclusivamente por picoteo profundo, ya que la mayoría de los poliquetos grandes se encuentran principalmente bajo los 3 cm de profundidad en el sustrato. Observaciones de conducta alimenticia de los Zarapitos fueron realizadas en cinco condiciones de sedimento: 1) sedimento cubierto por una columna de agua de 2 a 10 cm; 2) sedimento cubierto por una delgada película de agua <2 cm de profundidad; 3) arena húmeda sin película de agua; 4) arena seca; y 5) fango. La alimentación de los Zarapitos fue significativamente más exitosa en áreas con sedimento arenoso que áreas con sedimento fangoso, lo que se puede deber a la menor densidad de poliquetos grandes (>40 mm) observada en el fango. En arena húmeda, las aves obtuvieron la mayor tasa de éxito alimenticio en sedimento arenoso. Creemos que esto se debe a que la arena húmeda mantiene condiciones óptimas para la detección visual de los poliquetos. Los Zarapitos no se alimentaron en arena seca, lo cual puede deberse a que los poliquetos no son detectados o que no

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están al alcance de las aves debido a que se entierran a mayor profundidad, o que el sedimento seco presenta una mayor resistencia a ser penetrado.

Many shorebird species prey mainly on crustaceans and polychaetes that live in sandy or muddy substrata (Davidson et al. 1986). Bill length determines the depth to which birds can probe for prey and partly accounts for interspecific differences in prey size selection (Prater 1981). The dynamics of the physical conditions of the sediment and the pattern of prey availability during a tidal cycle can have a direct effect on the feeding behavior and distribution of shorebirds in intertidal soft-sediment habitats (Grant 1984). Receding tidal water has two important effects on feeding shorebirds. First, potential prey may follow the water table deeper into the substrate and become unavailable (Evans 1979, Goss-Custard 1984). Second, as the sediment dries it becomes more compact and foraging becomes energetically more demanding (Grant 1984).

Resistance to penetration varies widely among intertidal zone sediments. Soft sediments may also undergo substantial changes in resistance within each tidal cycle. Depth of interstitial water may affect prey availability and detectability during the tidal cycle over a given substratum (Grant 1984, Zwartz and Esselink 1989). Shorebirds with long, decurved bills (e.g., *Numenius* spp.) are particularly affected by compaction of sediment because a decurved bill is structurally weaker than a straight one (Burton 1974, 1986; Davidson et al. 1986).

The aims of this study are to describe prey-size selection by Whimbrels (*Numenius phaeopus*) and to assess how different foraging substrate conditions affect the foraging behavior of Whimbrels.

STUDY AREA AND METHODS

The study area, located in the Queule River estuary (39°20'S, 73°13'W), south central Chile, is a tongue-shaped intertidal sand-bank of about 3.5 ha. The sand-bank is composed of a central sandy area (97% sand: 2–0.063 mm, 3% mud: <0.063 mm) surrounded by a muddy area (79–87% sand; 13–21% mud) (Turner 1984). A polychaete worm, *Perinereis gualpensis*, is a common component of the macro-infauna (Turner 1984).

The density and size distribution of *P. gualpensis* in the study area was determined in November 1985. Ten randomly positioned cores of 7 cm diameter and 10 cm depth (Whimbrel bill length approximately 10 cm) were taken from wet sand (see below) and mud, respectively. Once the core was inserted into the sediment it was divided into upper 3-cm and lower 7-cm sections. Samples were washed through a 0.5 mm mesh sieve and the *P. gualpensis* retained were preserved in 10% formalin. Polychaetes were often broken during the sampling process; we measured the length from the base of the antennae to the base of the fifth parapodium and estimated total length by regression. The regression models were constructed using data from additional samples; cores were collected, sieved, and intact live *P. gualpensis* were placed on 70% ethanol. The following measurements were taken on each worm: total length, length

from the base of the antennae to the base of the fifth parapodium, jaw length, and dried mass. These measurements were employed to construct four regression models from which total length and biomass could be estimated.

To compare the size distribution of worms in the study area with those captured by Whimbrels, cores from sand and mud were pooled (20 cores). We decided to pool because it was impossible to determine from which area the worms had been taken, based on the stomach contents and droppings analyses alone. The densities of potential prey for Whimbrels were compared between sand and mud, however.

During the austral summer and spring of 1985, a total of 65 fresh droppings of Whimbrels was collected in the study area. Each dropping was washed on a 45 μm mesh screen, the chitinous jaws of *P. gualpensis* were separated and right-hand jaws measured. Four Whimbrel were shot (under license) in the study area, two while feeding and two while moving to a roosting area, and their stomach contents analyzed.

To assess the relationship between the size of worms taken by Whimbrels and the size distribution available in the sediment, an additional mudflat (located about 500 m from the study area) was also sampled (10 cores). The size distribution of worms found in the sediment was compared with the size distribution of worms found in the stomach of one Whimbrel shot while foraging in the area.

Observations of foraging Whimbrels were made during three consecutive days in January, March and November 1985 during the entire low tide period from a vantage point about 200 m from the study area using a 15–60 \times telescope. Foraging behavior was recorded throughout the tidal cycle using animals selected at random from those actively foraging. Individual birds were observed for 5-min periods, recording: (1) number of steps; (2) number of worms taken; (3) number of deep probes (i.e., when at least half of the bill was inserted into the sediment); and (4) sediment characteristics. A total of 1045 min of observations of Whimbrel foraging was made.

Traveling speed of feeding Whimbrels was calculated as number of steps per minute \times step length. Step length was measured directly on the substratum (mean = 12.5 \pm 0.3 [SE] cm, n = 238). Only step sequences with evidence of deep probing were used for this estimate.

Conditions of the foraging substrate were differentiated as: (1) sand covered by shallow water (2–10 cm); (2) sand covered by a water film (<2 cm); (3) wet sand; (4) dry sand (this category means the driest sand substrate found during the exposure, which still had a considerable amount of water); and (5) mud (always covered by a film of water). An index of sediment penetrability was obtained in sand and mud by dropping a glass rod (24 cm long, 5 cm diameter, and weighting 12.4 g) onto the sediment down a 1-m long aluminum tube of 20 mm diameter, and recording the depth to which the rod was buried. Two stakes were fixed in the study area, one located in the sand and another in mud. Measurements of penetrability and water content in wet and dry sand were made in the

same area at different tidal stages, thus representing real changes in substrate conditions during the tidal cycle. During the entire low tide, mud sediment was always covered with a film of water; therefore, penetrability and water content were measured only once. Water content of mud and wet sand (after 1 h of exposure) and dry sand (after 3.5 h of exposure) was determined by the difference in weight between the initial sample and after oven-drying (at 60 C for 48 h).

Means were compared using a one-way analysis of variance (ANOVA) (Sokal and Rohlf 1969) followed by multiple comparisons using the Tukey-Kramer procedure (Stoline 1981). When only two means were compared, we used a *t*-test. Frequency distributions of polychaetes were compared using a *G*-test (Sokal and Rohlf 1969). Variations about means are given as the standard error (SE).

RESULTS

Total length (T) (mm) of *Perinereis gualpensis* was highly correlated with the distance between the base of the antennae to the base of the fifth parapodium (P) ($T = 18.45 P - 9.01$, $r^2 = 0.96$, $n = 56$, $P < 0.005$), and the jaw length (J) ($T = 31.03 J - 4.8$, $r^2 = 0.98$, $n = 59$, $P < 0.005$) (Fig. 1). These equations were used to estimate total length. Dry mass (D) (g) of *P. gualpensis* was highly correlated to total length ($D = 0.0006 T^{2.703}$, $r^2 = 0.950$, $n = 56$, $P < 0.005$) and jaw length ($D = 3.179 J^{3.374}$, $r^2 = 0.952$, $n = 56$, $P < 0.005$) (Fig. 1).

The top 3 cm of substrate contained 82.4% of all *P. gualpensis*, although 100% of those >40 mm were found below 3 cm depth (Fig. 2A). There were no significant differences in the overall density of polychaetes between sand and mud (23.8 ± 7.3 , $n = 10$; 19.8 ± 5.3 , $n = 10$, respectively; $t_{18} = 1.39$, $P > 0.1$). The density of large worms (>40 mm) was significantly higher in sand than in mud (2.1 ± 1.3 , $n = 10$; 0.7 ± 0.5 , $n = 10$, respectively; $t_{18} = 3.22$, $P < 0.01$), however. Large *P. gualpensis* lived in vertically oriented burrows. The conspicuousness of the burrow entrance depended on the sediment texture, being much more obvious in sandy areas than in muddy sediments.

Analysis of droppings showed that Whimbrels preyed selectively on large worms. The average size consumed was 53.6 ± 3.7 mm ($n = 914$). Large worms comprised 95.2% by numbers of the diet. Sizes of polychaetes found in the stomachs were similar to those obtained from Whimbrel droppings (Fig. 2B) ($G_{[4]} = 6.1$, $P > 0.1$).

Results from the mudflat adjacent to the study area are shown in Figure 2C. The size distribution of polychaetes in both the sediment and stomach showed the occurrence of worms larger than those found in the study area. The mean prey size found in the stomach (66.0 ± 0.76 mm, $n = 98$) was greater than the mean prey size found in the study area (stomachs and droppings combined: 53.2 ± 0.22 mm, $n = 971$) ($t_{1067} = 16.2$, $P < 0.001$).

Analysis of stomach contents showed that Whimbrels preyed almost

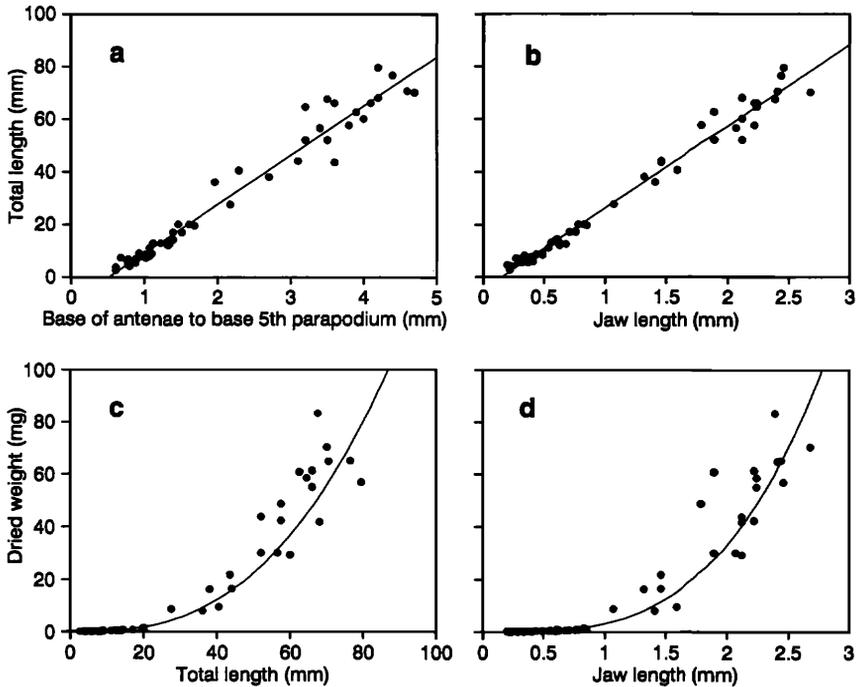


FIGURE 1. *Perinereis gualpensis*. Relationship between total length and (a) distance of antennae to base of fifth parapodia and (b) jaw length, and the relationship between dry mass with (c) total length and (d) jaw length. See text for equations.

exclusively on *P. gualpensis*. Remains of a crab (*Hemigrapsus crenulatus*) were found in one of the stomachs.

Between 22 and 39 Whimbrels fed daily on the study area during the period of observation. Whimbrels started feeding when the bank was still covered by a layer of water about 5 cm deep. They walked continuously and alternated surface pecking with deep probes. During deep probes the bill was inserted in the sediment up to the eyes and, at the same time, the bird rotated its head. The rotation of the head may have enabled the bird to detect the presence of vertically oriented worms, as suggested by Burton (1974) and Owens (1984). In most instances Whimbrels pulled out intact worms; and sometimes they washed the prey in small ponds before swallowing it.

The frequency of total probes made by Whimbrels was similar in shallow water and water film, and was significantly higher than in wet sand ($F_{[3,205]} = 5.6$, $P < 0.005$); the frequency of deep probes in mud was intermediate between these extremes (Table 1). The prey intake rate was significantly higher in sand (at any moisture condition) than in mud ($F_{[3,205]} = 29.1$, $P < 0.001$) (Table 1). There were significant differences in the proportion of successful probes when feeding on different substrates

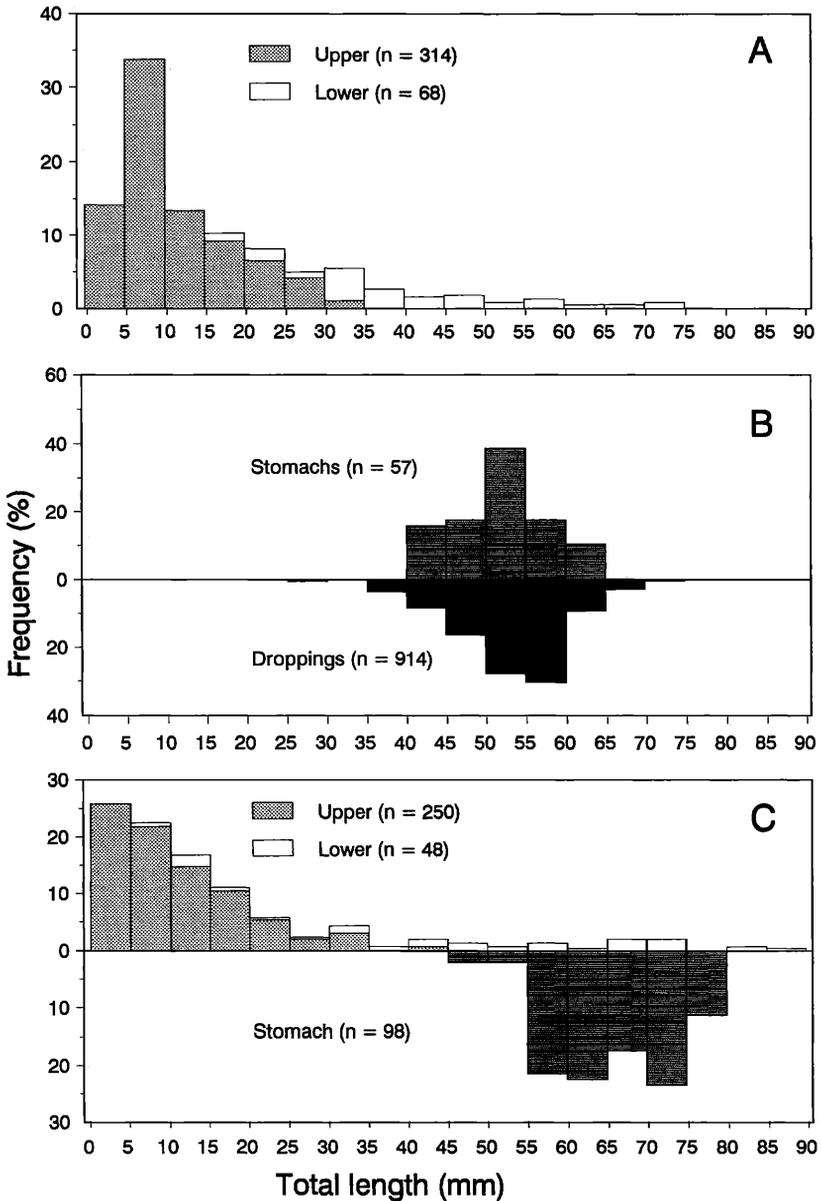


FIGURE 2. Size distribution of *Perinereis gualpensis* at the study area for (A) sediment samples and (B) Whimbrel stomachs and droppings. (C) Same for a mudflat adjacent to the study area. Sediment samples were subdivided in two strata: upper (0-3 cm) and lower (3-10 cm depth) layers. Sample sizes correspond to the number of worms measured.

TABLE 1. Foraging of Whimbrels under different sediment conditions. Data are means \pm SE. Letters following figures denote homogeneous groups (column wise) from ANOVA and Tukey-Kramer multiple comparisons.

Feeding conditions	Total probes (per 5 min)	Prey intake (prey per 5 min)	Successful probes (%)	Walking speed (m/min)	<i>n</i>
Shallow water (sand)	36.8 \pm 1.3 a	23.4 \pm 1.0 a	64.3 \pm 2.0 a	9.0 \pm 0.3 a	43
Water film (sand)	36.8 \pm 0.7 a	24.4 \pm 0.6 a	66.8 \pm 1.4 a	11.1 \pm 0.3 b	79
Wet sand	32.2 \pm 1.0 b	23.9 \pm 1.0 a	73.9 \pm 1.9 b	12.2 \pm 0.4 b	36
Muddy sand	33.4 \pm 1.0 ab	15.6 \pm 0.7 b	48.3 \pm 2.3 c	10.7 \pm 0.4 b	51

($F_{[3, 205]} = 29.3$, $P < 0.001$); these values were higher in wet sand, intermediate in shallow water and water film, and lower in mud (Table 1). Whimbrels walked significantly more slowly in shallow water than in other sediment conditions ($F_{[3, 186]} = 9.9$, $P < 0.001$) (Table 1).

The penetrabilities on three different sediment conditions were significantly different ($F_{[2, 97]} = 203$, $P < 0.001$): dry sand (1.4 ± 0.1 mm, $n = 10$) < wet sand (1.9 ± 0.1 mm, $n = 70$) < mud (3.91 ± 0.08 mm, $n = 20$). Water content was similarly different between the three sediment conditions ($F_{[2, 37]} = 59.2$, $P < 0.001$): dry sand ($19.7 \pm 0.4\%$, $n = 18$) < wet sand ($22.6 \pm 0.5\%$, $n = 18$) < mud ($31.0 \pm 0.4\%$, $n = 4$). Physical conditions of muddy areas remained almost unchanged throughout the tidal cycle. Whimbrels foraged mainly in wet sediments whereas dry areas were never used.

DISCUSSION

Whimbrels achieved a similar prey intake (number of prey per unit time) when foraging in sand under any condition of wetness. They reached the highest foraging success (% of probes successful) in wet sand (Table 1), perhaps because conditions are optimal for visual rather than tactile foraging. In support of this idea, we found that Whimbrels probe significantly more often when visual detection of prey may be reduced or affected by water movement (i.e., Whimbrels feeding on sand with shallow water or water film). In wet sand conditions, however, Whimbrels increased their walking speed and reduced the rate of deep probing, while maintaining their intake rate, suggesting that they were searching for prey visually. Esselink and Zwartz (1989) suggest that water movement within burrows of *Nereis diversicolor* is easily detected at the surface by waders, thus increasing their detectability. Evans (1986) found that visual foraging is more successful than tactile foraging in Dunlins (*Calidris alpina*).

The reduced foraging success of Whimbrels in shallow water and water film is probably due to effects of water movement. In both sediment conditions, the water movement at the surface may interfere with visual searching, especially during windy days, even though polychaetes may be

closer to the surface than in drier substrates. Both rain and wind are known to affect intake rate of visually hunting shorebirds by reducing prey detectability (Goss-Custard 1984). In shallow water, Whimbrels were observed walking significantly more slowly and orienting the bill perpendicular to the water surface, presumably to avoid refractive distortions.

In muddy sediment, Whimbrels forage less successfully than in any other sediment condition (Table 1). This result might be explained by the significantly lower density of large worms in muddy areas. The accumulation of fine sediment in the burrow entrance in muddy areas might also contribute to the reduction of prey detectability (pers. obs.) and Whimbrels therefore might have to rely almost entirely on tactile search. The total lack of feeding in dry sand suggests either that polychaetes are not available to the birds, as they burrow deeply to follow the water table, or that the energetic cost of deep probing in a hardened sediment makes these areas less profitable. Myers et al. (1980) found that the intake rate of captive Sanderlings (*Calidris alba*) feeding on isopods and sand crabs was significantly higher in wet and soft sand than in dry sand.

Even though the density of polychaetes in the sediment remains constant during the tidal cycle, their availability to birds varies as a direct consequence of sediment moisture. As a result, birds change both foraging technique, switching between tactile and visual search, and their local distribution, by moving away from dry areas to newly exposed ones. Though we did not quantify microhabitat preference by Whimbrels, we observed that birds spread more evenly and were more aggressive when foraging in sandy areas than in muddy areas. If Whimbrels rely more on visual search in sandy areas, then the increase in aggression and spacing may be a response to avoid interference during visual search (Goss-Custard 1980).

Prey size selection can be explained on the basis of availability and profitability of different prey sizes (Goss-Custard 1977). Droppings and stomach analyses showed that Whimbrels prey almost solely on large worms, even though small worms are far more abundant. Field observations and stomach analyses indicated that small worms are ignored (i.e., they are not captured and subsequently rejected). That prey selection is biased towards the larger worms available is clearly illustrated when comparing the study area (Fig. 2a, b) with the adjacent mudflat, where larger worms were available (Fig. 2c). This result strongly suggests that Whimbrels are using some reliable visual cue to determine prey size prior to a capture attempt. The only surface cue available is the width of the burrow entrance (cf. Zwarts and Esselink 1989). We suggest that Whimbrels search primarily for large burrow entrances, which are most evident in sandy substrata. The assessment of worm size using this cue is presumably crude, but remarkably few 'errors' are made, as evidenced by the very low frequency of worms <35 mm in length in the diet (Fig. 2). The high foraging success in wet sand, where burrow entrances are clearly visible and feeding is largely visual, supports this idea.

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