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Habitat choice and niche characteristics under poor food conditions. A study on migratory nearctic shorebirds in the intertidal flats of Brazil

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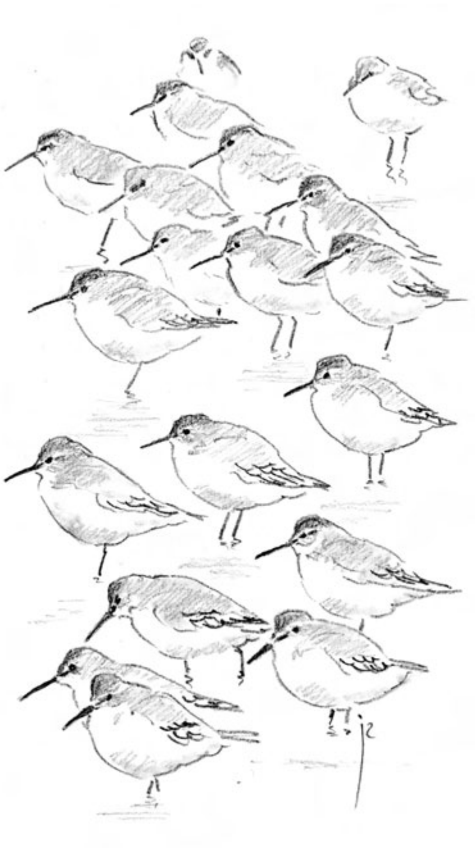

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The tidal flats of the Bragantinian Peninsula in the tropical part of Brazil harbour wintering and migratory nearctic shorebirds in very high densities, whereas the benthic food supply is very low. In 2001 and 2002 a study was conducted on the habitat choice and distribution of shorebirds to investigate the formation of niches and the spatial distribution under the constraint of a limited food supply. We showed that shorebird densities were not correlated with a range of abiotic variables or with prey density within sites, but that between sites birds tended to select sites with peak prey densities. Two foraging guilds were differentiated: Whimbrel *Numenius phaeopus*, Willet *Tringa semipalmata* and Short-billed Dowitcher *Limnodromus griseus* preferred to forage in the water or on wet sand at the water's edge; while Red Knot *Calidris canutus*, Grey Plover *Pluvialis squatarola,* Ruddy Turnstone *Arenaria interpres*, Semipalmated Sandpiper *Calidris pusilla* and Semipalmated Plover *Charadrius semipalmatus*, were found predominantly on dry substrate. Although the birds showed species-specific preferences for characteristics defining microhabitats, niches were broadly overlapping. The results of our study suggest that, in case of a very low food supply, individuals might not be able to react to competition by niche segregation but might be forced to feed in a broad range of available niches.

Key words: Brazil, guild, habitat choice, nearctic shorebirds, microhabitat characteristics, niche

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INTRODUCTION

The northeast coast of South America is recognized as important stopover and wintering area for shorebirds breeding in the low- and mid-Canadian Arctic (Morrison 1984, Morrison & Ross 1989). They migrate along the eastern coast of North and South America and they use few, but significant, stopover sites (Morrison 1984, Butler *et al.* 2001). South America's northeast coast is particularly important in spring, because many species bypass the Caribbean on their way north to their breeding grounds and face a long nonstop flight over the sea (Wunderle *et al.* 1989). Despite the documented ornithological significance of this region, only few studies investigated the shorebirds at this area, the structure of the community and the factors which influence the use of intertidal feeding areas (Spaans 1978, Spaans 1979, Rodrigues 2000).

Given recent information about a steady decline of global shorebird populations (BirdLife International 2000, Stroud *et al.* 2004), knowledge about bird numbers at stopover and wintering sites, and shorebird distribution in relation to food resources and habitat characteristics at these sites becomes increasingly important. This information will be useful in the future for a better understanding of the bird's habitat requirements at coastal sites around the world and for an informed management and conservation of crucial sites.

During preparation for spring migration, shorebirds have to gather enough food to build up sufficient fat reserves for migration. There is evidence that fat reserves accumulated before and during migration are important for survival and breeding once the nesting grounds have been reached (Morrison *et al.* 2007). Thus, birds are expected to stay at locations where they can forage most efficiently and experience the least competition from other predators. Generally, prey availability is assumed to be a major determinant of distributions of migratory and wintering shorebirds (O'Connor 1981, Evans & Dugan 1984) and much research is done on the relationship between shorebird densities and densities of their prey (Wolff 1969, Goss-Custard *et al.* 1977a,b, Smit & Wolff 1983, Meire & Kuyken 1984, Goss-Custard *et al.* 1991, Yates *et al.* 1993b, Kalejta & Hockey 1994). Abiotic factors, such as sediment conditions and tidal movements, are also considered to be important for the foraging success of the birds and, in turn, for their distribution (Pienkowski 1981, Quammen 1982, Pienkowski 1983, Burger 1984, Evans 1988, Zwarts 1988, Yates *et al.* 1993a, van Gils *et al.* 2003).

Beside these external factors, competition is thought to have an impact on the way individuals use their habitat. If shorebird densities and diversity are very high, competition between individuals is intensified and differentiation in prey choice or use of particular microhabitat characteristics is amplified (Recher 1966, Baker & Baker 1973, Burger *et al.* 1977, Lifjeld 1984, Davis & Smith 2001, Vahl *et al.* 2005).

In the first half of the years 2001 and 2002 we conducted a study on habitat choice and distribution of shorebirds at the tidal flats of the Bragantinian Peninsula in the tropical part of Brazil. This particular section of the coast harbours surprisingly high number of shorebirds, c. 3300–7500 individuals (Morrison & Ross 1989), given that at the same time the food supply is very limited (Kober & Bairlein 2006a). The aim of this study is to describe the spatial distribution and the niches used by shorebirds in this area, under the constraint of a limited food supply. We describe how shorebirds are distributed on tidal flats, between and within study sites and we determine the importance of prey availability and abiotic factors for the bird's distributions. We define preferences for microhabitat characteristics and niches among shorebirds. Our goal is to enhance understanding of niche dynamics of shorebird communities, particularly under the conditions of a limited food supply, and to provide information about foraging habitat requirements of shorebirds in the poorly studied northeast coast of South America.

METHODS

Study site

In 2001/2002 we conducted a study on shorebirds at the northeast coast of Brazil within MADAM ("Mangrove Dynamics and Management"), a cooperative project initiated by the University of Bremen in Germany and the Universidade Federal do Pará in Brazil. The study area was situated on the Bragantinian Peninsula about 150 km southeast of the Amazon delta (0°52'S, 46°39'W). The Bragantinian Peninsula has an Inner Tropical climate, with a wet season from January to May/June and a dry season from July to December. A mangrove belt borders the coast, forming with 1.38 million ha the world's second largest continuous mangrove region (Kjerfve *et al.* 1997). Small creeks, locally known as 'furos', cross the mangrove forest and widen out to extensive open intertidal flats at its edge, which cover approximately 8.5–9 km^2 in the vicinity of the Bragantinian Peninsula.

Data were collected between January and June in 2001 and 2002, thus the study period covered a part of the shorebirds' wintering period and the northward migration. Three sampling sites were chosen to represent all intertidal habitats available to birds (Fig. 1). The large open tidal flats of the Canelas sampling site were located between the Ilha de Canelas and the mainland. They were characterized by constant sediment relocations due to strong water currents. The Furo Grande sampling site was located within mangrove forest at the centre of the peninsula and stretched 200 m along the shore of the large mangrove channel Furo Grande. The Furo do Chato sampling site was at the mouth of the Furo do Chato, at the edge of the peninsula. It represented a transition area between open tidal flats and tidal flats bordering mangrove streams. Tidal flats further away from the beach were not accessible.

A total of 46 squared plots were marked with poles in 2001 (25 at Ilha de Canela, 6 at Furo Grande and 15 at Furo do Chato). Plot locations were chosen to cover the range of intertidal habitats found at the sites. Consequently, means of data obtained at the sites are not strictly representative and statistical comparisons between study sites are not valid. However, ranges and peak values provide estimates of site-specific values. In most cases plots covered 2500 m^2; only two plots had to be smaller because of limited space available (2000 m^2 and 750 m^2). In 2001, shorebirds used only Canelas in substantial numbers. Thus, in 2002, five plots were marked only at the Canelas site, each covering 2500 m^2. The following data were collected monthly at the plots.

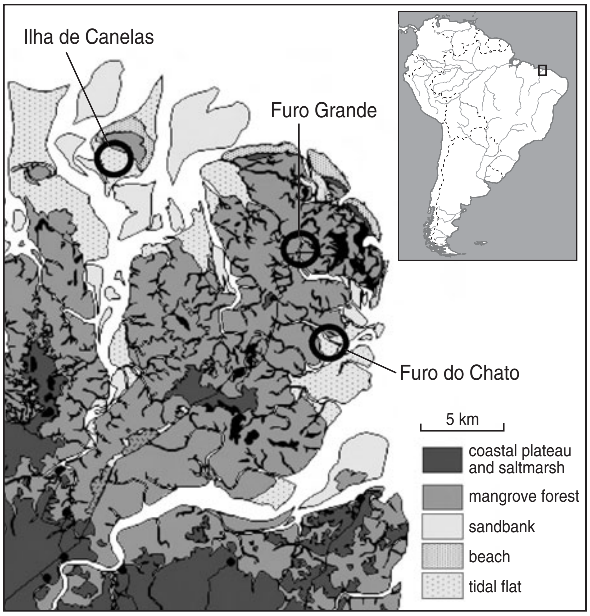


Figure 1. Study area on the Bragantinian Peninsula. Sampling sites are indicated with circles. The tidal flats (including the sandbanks) cover approximately 8.5–9 km^2.

Shorebirds. Low tide counts were conducted during midday low tides of four successive days each month. These were used to calculate a monthly mean low tide density (individuals/ha) for each plot. We recorded number of individuals for each bird species, distance to water (such as 'dry sand', 'waterline' if birds were clearly associated with the waterline and the wet sand close to the water, and 'in the water'). Because the shorebirds were not individually marked, it was not possible to distinguish between migrants who were passing though the area, migrants staying for the whole wintering season, and residents. However, because it can be assumed that most individuals in this area and during this time of the year are North American migrants, we will refer to them as migratory shorebirds.

To account for birds using the tidal flats during the falling tide, additional ebb tide counts were conducted once per month during one of the days when also a low tide count was done. This involved up to six consecutive counts, starting with the first count when the first plot could be used by the birds (defined as when all four poles were standing in water of lesser than 30 cm depth). Every hour this count was repeated until low tide was reached and the regular low tide count was carried out. The factor by which mean falling tide densities departed from the low tide densities of the same day was calculated. All four low tide counts of that month were adjusted by this factor (Kober 2004). The resulting adjusted bird densities – hereafter referred to as tide-calibrated bird densities – reflect mean bird densities of the time period of ebb-tide. Data collection during rising tide was impossible due to rapidity of the rising tide and the restricted time to leave the intertidal. However, the time period of rising tide appeared to be irrelevant for birds foraging, because they used this time mainly to return to their mangrove roosts with only short stops on the intertidal.

In 2002, foraging behaviour of shorebirds was investigated by focal observations at the Ilha de Canelas. A total of 617 individual birds were watched for three min each and the following data were collected: pecks from the sediment surface per min, probes in the sediment per min, prey consumed per min, prey handling time (s) (defined as the time period between the picking up of a prey item until it was finally swallowed), prey size estimated by comparison with bill size (mm), prey type, distance to water (dry sand, waterline, in the water), water depth estimated by comparison with leg length (mm), and probing depth (foraging depth) into the sediment estimated by comparison with bill length (mm). For the calibration of size estimations (% of bill length, % of leg length), observers were trained with paper bird models and alcohol fixed benthos organisms until the estimates were accurate. Size-spectra of 'worms' might be overestimated because they were stretched while they were pulled out of the sediment. Observed prey sizes and foraging depths were used to determine the available prey fraction, defined as the portion of all prey organisms which were reached by probing and of a size which could be handled and swallowed. In the few cases when individuals varied in the distance to water, the distance was taken where the bird spent most of the observation time.

Prey organisms. At each plot, three replicate benthic samples were taken with a corer of 15 cm diameter to a depth of 20 cm and divided into three slices (0–5, 5–10 and 10–20 cm). Within a few hours, samples were sieved through a 1-mm sieve, remains were sorted and extracted animals stored in 70% ethanol. Additional samples, obtained with a 0.5 mm sieve (Acheampong 2001), produced benthic densities and biomasses similar to those of our samples, thus we assume that sampling with 1-mm sieves was sufficient and did not disregard considerable prey fractions (Kober 2004). However, fast moving epibenthos is generally underrepresented with this method. Benthic organisms were identified to lowest taxonomic level possible and data were converted to densities. Sizes of intact individuals were determined using a graded microscope ocular. For

Brachyuran crabs carapace width, for bivalves shell width, for gastropods height of the shell, and for all other animals body length was recorded. 'Worms' were straightened without stretching. Prey identification and size measurements were made with a stereomicroscope (10x) and a microscope (10x/0.30, 20x/0.50 and 40x/0.75 oculars). To determine ash free dry masses (AFDM) of individual organisms (Higgins & Thiel 1988), additional benthic samples were taken from the Ilha de Canelas in March and April 2002. For each benthic taxon, the best nonlinear length–AFDM relation was calculated (Kober 2004). With the resulting functions all benthic samples were transformed into AFDM/m^2.

To obtain a measure of profitability of prey items for birds, the energetic value of a prey item was divided by the sum of handling and searching time (Pyke *et al.* 1977). While handling time was measured directly for each individual bird species and benthic group, searching time was calculated. An observed mean searching time was used to calculate searching times for individual bird species, and individual benthic groups and their densities, based on the assumption that searching time is inversely related to benthos density (for details see Appendix 1)

Abiotic variables. Each month, three core samples (2.5 cm diameter, 20 cm length) were pooled into one sediment sample, mixed until homogeneous, and 30–45 g dry weight was soaked for 24 hours in a solution of sodium hexametaphosphate (0.24 g/L) to dissolve agglomerated particles. Samples were wet-sieved with 6 sieves of mesh sizes of 1000, 710, 500, 315, 71 and 20 μm. The resulting 6 sediment fractions were dried (48 h, 60°C) and weighed. The proportional contribution of each fraction was used to define median grain sizes through a cumulative frequency curve on a phi (Φ) notation (Buchanan & Kain 1984). At each plot, the salinity of pore water was determined with a conductivity meter. Benthic burrow openings in the sediment surface, regardless of the responsible organism, were counted within 1 m^2 at each plot. Time of emergence of individual plots was determined by an observation over the complete tidal cycle at the Ilha de Canelas. At the other sampling sites, plots had very similar times of emergence.

Statistical Analyses

For the statistical analysis the programs STATISTICA (Version 5.1, StatSoft Inc.), Primer (Version 5.2.2 for Windows, Primer-E Ltd), and Excel (2000, Microsoft) were used. To test for monthly differences in abiotic variables, a Kruskal–Wallis ANOVA was conducted. Spearman rank correlation analyses were applied to shorebird numbers and microhabitat characteristics obtained during low tide counts at the plots. Only correlations with $r_s > |0.5|$ were considered, because lower r, even if significant, indicate only a weak relationship. For sediment depth and water depth, which were microhabitat characteristics obtained during focal observations, Mann–Whitney U tests were conducted to test for differential use of these characteristics between species. In case of multiple tests, such as the correlation analyses and the Mann–Whitney U tests, a sequential Bonferroni procedure was applied (Holm 1979). All microhabitat characteristics together were used in a Principal Components Analysis (PCA) to describe the bird's microhabitat use in relation to each other. It was based on arcsin-transformed proportions of birds found within a specific microhabitat (combinations from distance to water, water depth, foraging depth, pore water salinity, sediment grain size etc.) (Holmes *et al.* 1979). The resulting PCA-diagram was used to determine Euclidian distances between the species scores. A cluster analysis using group-average-linkage related bird species according to these distances, and a dendrogram was used for illustration. Guilds were defined as those groups that were separated by more than the mean Euclidian distance (Holmes *et al.* 1979).

Niche breadth was determined with Shannons formula (Mühlenberg 1993) for the following niche dimensions of the microhabitat: water depth, foraging depth, sediment conditions, study site and distance to waterline. To evaluate a multidimensional niche, niche breadths of the different niche dimensions were summed. The overlap of the niches between every pair of shorebird species and within every dimension was calculated with Pianka's formula (Pianka 1973):

$$O_{jk} = O_{kj} = \frac{\sum_{i}^{n} p_{ij}\, p_{ik}}{\sqrt{\sum_{i}^{n} {p_{ij}}^2 \sum_{i}^{n} {p_{ik}}^2}}$$

where p_{ij} and p_{ik} are the proportions of the i^{th} resource dimension used by the j^{th} and the k^{th} species respectively. Like other popular niche overlap measures, such as Schoener's (Schoener 1968) measure of niche overlap, O is a value between zero and one, reaching zero when niches are completely isolated from each other and becoming one when niches show a complete overlap. For each pair of species, a mean overlap is given for all niche dimensions investigated.

RESULTS

Shorebirds

Overall, 10 migratory shorebird species were observed in the study area: Grey Plover *Pluvialis squatarola*, Semipalmated Plover *Charadrius semipalmatus*, Marbled Godwit *Limosa fedoa*, Red Knot *Calidris canutus*, Ruddy Turnstone *Arenaria interpres*, Sanderling *Calidris alba*, Semipalmated Sandpiper *Calidris pusilla*, Short-billed Dowitcher *Limnodromus griseus*, Whimbrel *Numenius phaeopus* and Willet *Tringa semipalmata*. Although they were frequently observed in the study area, this was the first record of Marbled Godwits in Brazil (Kober *et al.* 2006).

Low tide shorebird densities ranged between 0–126 birds/ha. The mean density was highest in January with 21 birds/ha and it decreased steadily until it reached 1 bird/ha in June.

Tide-calibrated shorebird densities ranged between 0–703 birds/ha. At the Ilha de Canelas a median of 77.1 birds/ha were found, far lower values were observed at Furo Grande and Furo do Chato (25.6 birds/ha and 23.2 birds/ha) (Table 1). While most species occurred in high densities at the open intertidal of the Ilha de Canelas, Grey Plover and Semipalmated Plover, Whimbrel, Willet and Turnstone reached also reasonable densities at Furo Grande and only Sanderling and Semipalmated Sandpiper were found in high numbers at Furo do Chato (Table 1).

Prey occurrence and abiotic variables

Total benthic densities ranged between 0–677 individuals/m^2, benthic biomasses between 0–25.7 g AFDM/m^2. The benthic taxa contributing most to biomass were Callianassidae (Crustacea), *Tagelus plebeius* and *Protothaca pectorina* (both Mollusca) at the Ilha de Canelas; Callianassidae, Gammaridea and Idotheidae (all Crustacea) at Furo do Chato; and *Uca maracoani* (Crustacea), *Tagelus plebeius* and Mysidae (Crustacea) at Furo Grande. Mean benthic profitabilities per plot varied between bird species, because individual searching and handling times per prey type and individual harvestable prey fraction according to foraging behaviour were part of the calculation. For all species, the majority of plots offered a very low mean prey profitability with far less than 0.1 mg AFDM/s. However, most species had very high mean intake rates, at least occasionally (Table 1).

In 2001, the monthly mean of sediment grain sizes ranged between 2.88–2.92 Φ (SD 0.13–0.26). No significant monthly differences appeared ($H = 2.022$, $P = 0.85$, $n = 272$). Monthly mean salinity ranged between 9.3–24.8‰ (SD 2.5–5.3). With the onset of the wet season, average pore water salinity decreased, until a minimum was reached in April, before increasing again in May and June ($H = 132.487$, $P < 0.001$, $n = 215$). The time of emergence ranged between 3 h 39 min and 4 h 59 min, depending on plot location. Monthly means of burrow openings on the sediment surface ranged

Table 1. Median and maximum values of bird densities (individuals/ha) and mean and maximum prey profitabilities (g AFDM/s searching and handling time) per plot at the three sampling sites in 2001. Minimum bird densities and prey profitability were always zero.

	Ilha de Canelas		Furo Grande		Furo do Chato	
Species	Bird density	Profitability	Bird density	Profitability	Bird density	Profitability
Grey Plover	1.8 (12.0)	0.1 (46.1)	5.1 (25.0)	<0.1 (1.0)	1.6 (69.3)	<0.1 (29.2)
Semipalmated Plover	3.8 (40.4)	<0.1 (0.7)	3.3 (32.0)	<0.1 (0.4)	1.7 (35.2)	0.1 (0.2)
Marbled Godwit	0.5 (9.0)	<0.1 (0.2)	0	0.1 (0.3)	0	<0.1 (0.2)
Red Knot	12.8 (210.0)	<0.1 (54.5)	0	<0.1 (1.1)	0.8 (74.7)	<0.1 (3.9)
Ruddy Turnstone	4.6 (104.0)	0.1 (12.5)	1.9 (12.0)	<0.1 (3.1)	0.6 (37.3)	<0.1 (0.6)
Sanderling	1.3 (24.0)	<0.1 (3.1)	0	<0.1 (0.1)	2.2 (69.3)	<0.1 (3.1)
Short-billed Dowitcher	14.5 (277.3)	0.1 (28.2)	0.2 (6.4)	<0.1 (0.2)	0	0.1 (0.8)
Semipalmated Sandpiper	15.8 (378.0)	0.1 (1.4)	0	<0.1 (1.4)	8.2 (190.4)	<0.1 (0.2)
Whimbrel	5.6 (71.0)	0.2 (514.1)	4.0 (24.0)	<0.1 (30.8)	1.1 (40.0)	<0.1 (184.3)
Willet	4.8 (56.0)	<0.1 (166.9)	1.2 (13.3)	<0.1 (2.0)	< 0.01 (2.7)	<0.1 (59.8)
Total	77.1 (703.3)		25.6 (140.0)		23.2 (339.2)	

between 30–35 per m^2 (SD 29–45). A Spearman rank correlation analysis between burrow openings and total benthic densities revealed a significant but weak positive relationship ($r = 0.435$, $P < 0.001$, $n = 264$).

Bird distributions in relation to prey and abiotic variables

A total of 156 Spearman rank correlations between density of individual shorebird species and total harvestable benthic density, total harvestable benthic biomass and mean benthic profitability per plot and month detected no significant relationship.

Of 219 Spearman rank correlations, conducted between bird densities and sediment grain size, pore water salinity, density of burrow openings and time of emergence, four detected significant and strong correlations. In January, density of Semipalmated Sandpiper ($r_s = 0.581$, $P < 0.001$, $n = 42$) was correlated with the number of burrow openings in the sediment surface. The same species was correlated with time of emergence in February ($r_s = 0.694$, $P < 0.001$, $n = 25$). And in March, total bird density was correlated with sediment grain size Φ ($r = 0.581$, $P < 0.001$, $n = 46$) and so was density of Semipalmated Plover ($r_s = 0.518$, $P < 0.001$, $n = 46$).

Microhabitat characteristics and community structure

Usually, most species were found on dry sand; only Marbled Godwit and Short-billed Dowitcher were normally found on submerged areas, and the edge of the water was least important (Table 2). Each shorebird species had its individual range of water depths and probing depths (Fig. 2), e.g. Marbled Godwit probed up to more than 15 cm into the sediment while it foraged in water of up to 14 cm deep, while Semipalmated Plover and Sanderling probed only into the topmost centimetres of the sediment without any water coverage. In many cases, water depths and foraging depths

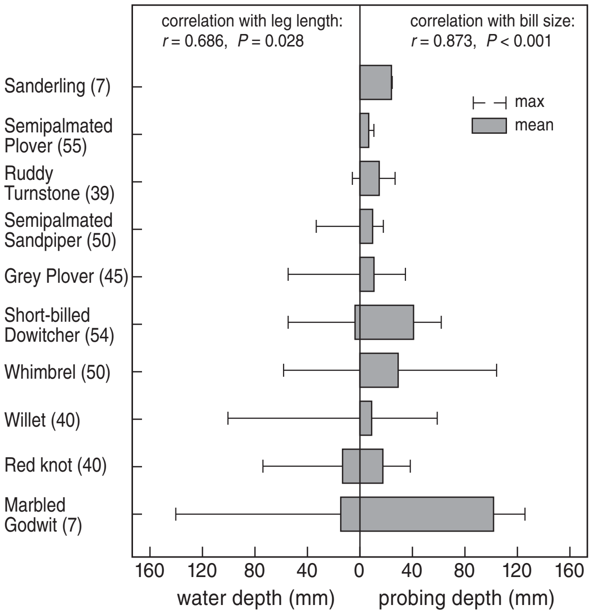
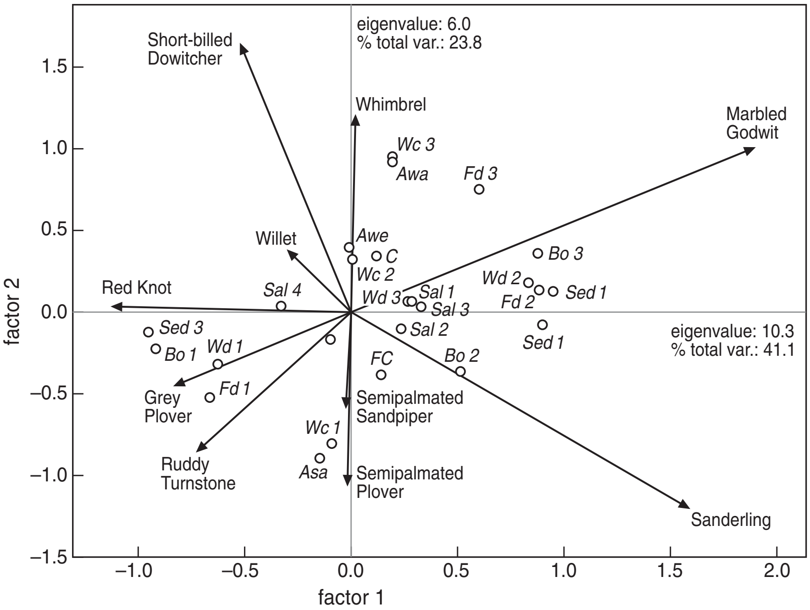


Figure 2. Observed water and foraging (or probing) depths of birds on the Bragantinian Peninsula in 2002. Foraging depth was calculated as the bill insert depth minus water depth. Samples size are given between brackets.

Table 2. Percentages of all birds observed on dry sand, at water's edge or in water. All data were obtained in 2001. Test statistics of χ^2-test for departure from homogeneous distributions are given in the last column ($df = 2$). Homogeneous distribution means here equal frequencies, since the availability of these habitats was considered to be high enough to support all individuals if necessary. Expected frequencies for Marbled Godwit were too low to allow for the χ^2-test.

Species	Dry sand	Water's edge	Water	Test for homogeneous frequencies		
	%	%	%	n	χ^2	P
Grey Plover	88	11	1	87	79.5	<0.001
Semipalmated Plover	87	12	1	159	142.8	<0.001
Marbled Godwit	12	19	69	10	-	
Red Knot	51	20	29	360	30	<0.001
Ruddy Turnstone	89	7	4	159	146.1	<0.001
Sanderling	89	7	4	27	25	<0.001
Semipalmated Sandpiper	67	27	6	524	170	<0.001
Short-billed Dowitcher	19	16	65	538	36	<0.001
Whimbrel	50	13	37	254	22.2	<0.001
Willet	30	33	37	130	0.4	0.55



category		range
sediment grain size (Φ)	*Sed 1* *Sed 2* *Sed 3*	2.5–3.0 3.1–3.5 >3.5
sampling site	*C* *FG* *FC*	Canelas Foro Grande Furo do Chato
water depth (mm)	*Wd 1* *Wd 2* *Wd 3*	0–65 65–130 130–195
foraging depth (mm)	*Fd1* *Fd 2* *Fd 3*	0–65 65–130 130–195
borrow openings per m^2	*Bo 1* *Bo 2* *Bo 3*	0–70 71–140 141–210
water coverage of the plots	*Wc 1* *Wc 2* *Wc 3*	0–33% 34–66% 67–100%
association with water	*Asa* *Awe* *Awa*	dry sand waters edge water
salinity (‰)	*Sal 1* *Sal 2* *Sal 3* *Sal 4*	0–10 10.1–20 20.1–30 30.1–40

Figure 3. PCA diagram illustrating the use of microhabitat characteristics by 10 shorebird species. The combined axes explain 65% of the variance.

proved to be significantly different between species pairs (Appendix 2 and Appendix 3, respectively). Mean water depths and foraging depths were positively correlated with bird morphology (Fig. 2).

A PCA was conducted on total range of measured microhabitat characteristics (Fig. 3). The diagram showed that the bird species were split into one large group of species on the left hand side of the diagram and two species (Marbled Godwit and Sanderling) on the right hand side. The environmental variables grouped around the centre of the diagram (e.g. the salinity categories, water depth categories and sampling sites) were used in a very similar way by all birds. The sediment categories are important for the spread of species along the first factor, showing that Marbled Godwit and Sanderling used medium and coarse sediments while the large group of remaining shorebirds were more frequently found on fine sediments. The association with water and, related to this, the degree of water coverage of the plots are the variables important for the spread of species along the second factor. Short-billed Dowitcher, Whimbrel and Marbled Godwit were found mostly in the water and on largely water covered plots; Willet and to a lesser extend Red Knot were associated with the water's edge and plots with medium water coverage; while Grey Plover, Semipalmated Sandpiper and particularly Ruddy Turnstone, Semipalmated Plover and Sanderling used dry sand and were found on plots with only little water coverage.

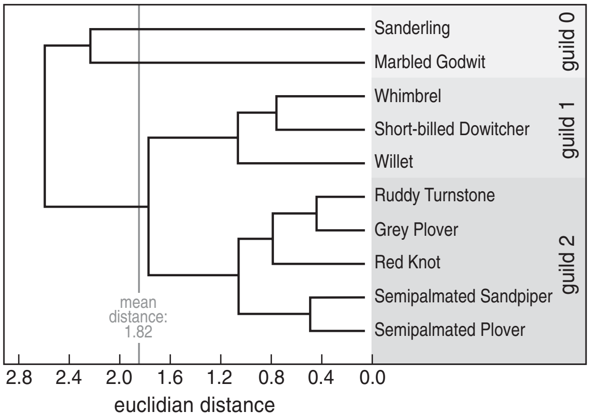


Figure 4. Dendrogram of the shorebird species' use of microhabitat characteristics. Cluster analysis was performed on Euclidian distances obtained from a PCA diagram.

Euclidian distances between species' positions within the PCA diagram were grouped by a cluster analysis into assemblages with similar habitat preferences (Fig. 4). Clusters were distinct, although the difference between guild 1 and guild 2 was not large enough to meet the set criterion. In contrast to the dendrogram where Sanderling and Marbled Godwit formed a separate cluster together, the PCA-diagram revealed that they cannot be combined in one guild. Sanderling was mostly found on dry areas with smaller sediment particle sizes, whereas most Marbled Godwit exploited submerged areas with medium to deep water by deep probing. The remaining shorebirds were grouped into guild 1, consisting of birds typically found on submerged areas using deep probes in or at the edge of water (Whimbrel, Willet and Short-billed Dowitcher), and guild 2, assembled of birds using shallow probes on dry and coarse sand (Red Knot, Grey Plover, Ruddy Turnstone, Semipalmated Sandpiper and Semipalmated Plover).

When niche breadths *NB* were investigated on basis of water depth, foraging depth, sediment grain sizes, foraging site and distance to the water, Sanderling occupied the most narrow niche (*NB* = 1.56) while Willet and Red Knot used the broadest niches (*NB* = 4.54; Table 3). The mean overlap of all niche dimensions was large between species, *O* ranging between 0.60–0.98. Marbled Godwit and Sanderling had the most distinct niches compared to other species. For Marbled Godwits deep probing and its ability to forage in reasonably deep water separated it from other species, while Sanderling differed through comparatively deep probing in the sediment away from the waterline. Niche overlap in single niche dimensions was large for the use of foraging site (mean *O* = 0.98) and water depth (mean *O* = 0.97), medium for sediment grain size (mean *O* = 0.87), while least overlap and largest niche separations were found for foraging depth (mean *O* = 0.66) and association with water (mean *O* = 0.75).

Table 3. Breadth of the multidimensional niche and mean overlap between niches within the niche dimensions water depth, foraging depth, sediment grain sizes, foraging site and distance to water.

	Grey Plover	Semipalmated Plover	Marbled Godwit	Red Knot	Ruddy Turnstone	Sanderling	Short-billed Dowitcher	Semipalmated Sandpiper	Whimbrel	Willet
Multidimensional niche	3.61	2.19	3.58	4.54	2.18	1.56	4.49	3.33	4.40	4.54
Semip. Plover	0.95									
Marbled Godwit	0.66	0.69								
Red Knot	0.89	0.88	0.69							
Ruddy Turnstone	0.93	0.91	0.60	0.93						
Sanderling	0.88	0.81	0.66	0.83	0.89					
Short-b. Dowitcher	0.75	0.74	0.77	0.87	0.77	0.73				
Semip. Sandpiper	0.97	0.95	0.72	0.91	0.93	0.91	0.78			
Whimbrel	0.90	0.92	0.81	0.91	0.88	0.83	0.88	0.92		
Willet	0.87	0.89	0.78	0.95	0.87	0.78	0.91	0.91	0.94	

DISCUSSION

As part of the northeast coast of South America, the Bragantinian peninsula is potentially an important site for migrant shorebirds. The shorebird densities we recorded in the study area provide evidence for its significance. Although the study area hosted in total fewer birds than neighbouring tidal flats (Morrison & Ross 1989), reported shorebird densities of 21 birds/ha were rather high compared to tropical tidal flats elsewhere (e.g. 15.5 birds/ha in Sierra Leone (Tye & Tye 1987) and 6.3 birds/ha in Guinea Bissau (Zwarts 1988), but 41.6 birds/ha in Mauritania (Altenburg *et al.* 1982)), indicating a relative high exploitation of the area on a worldwide scale.

Bird distributions in relation to prey occurrence and abiotic variables

Prior or during the energy demanding migration, shorebirds are generally assumed to use those sites and microhabitat characteristics which provide best foraging conditions (O'Connor 1981, Puttick 1984). As maximum food intake rate is reached in areas with high prey density (Holling 1959), shorebirds should favour areas with highest prey densities, or, more precisely, areas with highest prey profitability. When looking at shorebird distributions at the broad scale of site selection, the majority of shorebird species reached highest densities at study sites where maximum prey profitability was highest. Whimbrel, Willet and Grey Plover were found in higher densities at Furo Grande plots than expected by prey profitability alone. These species foraged on medium- and large sized mangrove crabs (*Uca* spec.), a species predominantly found at Furo Grande (Kober & Bairlein 2006b). Because *Uca* was presumably underrepresented in benthic samples obtained with corers (see Methods), prey profitability might have been underestimated at Furo Grande plots. In contrast, Semipalmated Sandpiper and Marbled Godwit occurred in lower densities at Furo Grande than would have been expected by prey profitability. Unconsidered factors, such as the presence of predators or interspecific interactions, could have been responsible.

Although potentially profitable sites appeared to be more frequently used, no correlation between bird densities and benthic densities, biomass and profitabilities was significant. Prey occurrence might therefore be influential for the choice of foraging site, but was not a good predictor for bird distributions on a smaller spatial scale. This effect of spatial scale, with strong correlations between shorebird- and prey occurrences on a large scale, but only weak or absent associations on a smaller scale, has been observed before (Colwell & Landrum 1993, Spruzen *et al.* 2008). Colwell & Landrum (1993) speculated that a decreased variation of physical variables and resulting invertebrate distributions in small-scale studies is responsible for this effect. The sites chosen in this study were indeed very different from each other, in benthic assemblages as well as in general habitat features (e.g. open tidal flats at Canelas in contrast to a site within the mangrove forest at Furo Grande), and within site habitat variability might indeed be much smaller.

Generally, there is literature describing significant spatial relationships between shorebirds and their prey (Bryant 1979, Colwell & Landrum 1993, Yates *et al.* 1993b), however, some studies fail to find a positive correlation. Goss-Custard (1970) speculates that mutual interference and random searching techniques of the shorebirds are responsible explanations, whereas Wilson (1990) assumes that birds are feeding only at sites exceeding a specific prey threshold density. Zou *et al.* (2008) speculate that depletion is the reason for a negative correlation between numbers of shorebirds and polychaete densities at the Leizhou peninsula, China, although they did not investigate their hypothesis in more detail. In this study, the sampling method could not assess large and mobile prey appropriately, hence detection of relationships for species feeding on *Uca spp*. might have been hampered. But we also failed to detect correlations for species with different prey items. So, although prey density and profitability might broadly affect shorebird distribution in the study area, we could not detect more specific prey availability factors affecting shorebird distributions.

Abiotic factors have been shown to have an impact on prey intake rates of shorebirds. Sediment grain size or substrate type influences foraging of shorebirds (Myers *et al.* 1980, Hicklin & Smith 1984, Zwarts 1988, Goss-Custard *et al.* 1991, Summers *et al.* 2002), either because penetrability of the sediment or detection of prey is affected (Quammen 1982). Pore water salinities might be influential for heat stressed birds in environments with high temperatures, because swallowing of adherent water with the prey might increase salt stress (Klaassen & Ens 1990). In this study only few significant and strong relationships between burrow openings in the sediment surface (a possible indicator of prey), time of emergence (an indicator of time available for foraging), and sediment grain size and bird densities were detected. We were therefore not able to identify abiotic variables which are generally strongly correlated with high bird densities.

Microhabitat characteristics and community structure

Although there was much overlap, microhabitat use often differed significantly between the focal species. It was determined by morphological characteristics: selected water depths were correlated with leg length, a relationship also described by Ntiamoa-Baidu *et al.* (1998), and foraging depth was correlated with bill size, with most birds probing as deeply as possible.

The PCA diagram identified two important gradients along which species distribute. The sediment grain size was responsible for a split between Marbled Godwit and Sanderling on medium and coarse sediments, and all other birds on more or less fine sediments; water coverage and association with water showed a gradual change from mostly large species on water covered areas, to medium sized and smaller species at the water's edge and on dry sand. Interestingly, water depth and foraging depth, even though often significantly different between species pairs, were not important for differentiation of microhabitat use. This emphasizes the need for a multidimensional approach for a realistic representation of niche dynamics, as proposed by Davies & Smith (2001), as individual niche dimensions are put in relation to each other. Granadeiro *et al.* (2007) conducted a similar analysis on bird feeding at the intertidal area of the Tagus estuary and their CCA ordination diagrams showed a similar importance of sediment characteristics (mud content) and surface water, together with exposure time and the extend of shell banks. However, the foraging guilds were very different. That is not surprising, given that a different number of dissimilar species and a different set of environmental variables were investigated. All the more remarkable is the analogous identification of sediment characteristics and water coverage as important environmental gradients for the differentiation of microhabitat use.

Two foraging guilds were described based on the use of microhabitat characteristics. The large shorebirds Whimbrel, Willet and Short-billed Dowitcher favoured submerged plots and preferred to forage in the water or on wet sand at the water's edge. Possibly, they took advantage of the soft wet sand for their deep probes (Colwell & Landrum 1993). In contrast, smaller birds, such as Red Knot, Grey Plover, Ruddy Turnstone, Semipalmated Sandpiper and Semipalmated Plover, were found predominantly on dry sand. They foraged partially with the guidance of visual cues (Kober 2004), which might be hampered by water cover. This is again in line with our observation and that of Granadeiro *et al.* (2007), that species assemblages were differentiated by their preference for particular sediment conditions. Jing *et al.* (2007) found that habitat preferences of shorebirds in China were related to their foraging techniques, such as visual or tactile foraging. This was not supported by our study where visual and tactile foraging individuals shared the same foraging guilds. Generally, the segregation into only two large foraging guilds emphasizes that there is no strong tendency for niche differentiation at the Bragantinian Peninsula.

Niches of the individual species were wide and broadly overlapping. Although a differential use of microhabitat characteristics was described (e.g. foraging sites, water depths), they were often of little value for niche differentiation due to the large niche overlap. A comparable study by Davis & Smith (2001) on the niche dynamics of shorebirds in Texas, USA, showed for the single niche dimension of water depth a mean niche overlap value of 0.49 (range 0.12–0.89, 95% ci 0.32–0.66, calculated with Schoener's measure for niche overlap). For comparison, we recalculated niche overlap for this study with the same formula and found for water depth a mean of 0.78 (range 0.56–1; 95% ci 0.73–0.82). Niche overlap for the dimension of water depth appears therefore was larger at the Bragantinian peninsula than in the Southern Great Plains in Texas. The discrepancy might be a result of the different set of species investigated (different morphological characteristics could limit the exploration of potential niches), but alternatively different prey availability could be responsible (although, unfortunately, we have no information about the invertebrate abundance at the study area in Texas). Since food availability was very low at the Bragantinian peninsula (Kober & Bairlein 2006a), shorebirds might be forced to explore wider niches with a larger overlap.

Niche width is thought to be a result of resource abundance. Abundant resources support specialisations, whereas scarce resources promote broad niches (Emlen 1966, MacArthur & Pianka 1966, Zwarts & Wanink 1993). The absence of a strong and clear niche partitioning at the Bragantinian Peninsula suggests that a limited food supply determined primarily the structure of the shorebird community. The significance of the limited prey availability is also supported by the finding that the birds differentiated between poor and rich foraging sites. It suggests that they maximize their prey intake, although this pattern disappears on a smaller scale within sites.

Competitive pressure of additive species, on the other hand, enhances niche differentiation (Cody 1974). Competition between individuals appears to be less influential at the Bragantinian peninsula, although bird densities were high when compared to other sites on a worldwide scale. In case of a very low food supply, individuals might not be able to react to competition by niche segregation but might be forced to feed opportunistically in every available niche.

Our study provided the first description of the shorebird community at the tidal flats of the Bragantinian peninsula at the northern coast of Brazil. The analysis presented in this paper suggests that resource availability has a strong impact on niche dynamics of a shorebird community.

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SAMENVATTING

Het tropische getijdengebied van het schiereiland Bragança in de staat Pará, Brazilië, ligt ongeveer 150 km ten zuidoosten van de Amazonedelta. Het schiereiland herbergt, ondanks de beperkte bodemfauna, grote dichtheden aan overwinterende en doortrekkende steltlopers. In 2001 en 2002 is een onderzoek uitgevoerd naar de habitatkeuze en de verspreiding van steltlopers over het gebied. De auteurs onderzochten wat het effect is van het beperkte voedselaanbod op de ruimtelijke verdeling en de nichevorming bij steltlopers. Ze vergeleken daartoe drie typen wadvlakten: een gebied met open wad (Ilha de Canelas), een besloten wad omgeven door mangrovebos (Furo Grande) en een deels open wadgebied aan de riviermonding van de Furo do Chato. De hoogste dichtheden aan steltlopers werden aangetroffen op het open wad van Ilha de Canelas waar de hoogste prooidichtheden aanwezig waren. In geen van de drie gebieden was er een verband tussen steltloperdichtheid en prooidichtheid of abiotische variabelen. Er konden twee foerageerstrategieën worden onderscheiden: Regenwulp *Numenius phaeopus*, Willet *Tringa semipalmata* en Kleine Grijze Snip *Limnodromus griseus* foerageerden bij voorkeur in water of op nat wad langs de waterlijn, terwijl Kanoet *Calidris canutus*, Zilverplevier *Pluvialis squatarola*, Steenloper *Arenaria interpres*, Grijze Strandloper *Calidris pusilla* en Amerikaanse Bontbekplevier *Charadrius semipalmatus* voornamelijk op droogliggend wad werden waargenomen. Hoewel de voorkeuren voor waterdiepte of sedimenttype soortspecifiek waren, was er een sterkere overlap in foerageerniches dan in vergelijkbare studies. Deze resultaten zijn een aanwijzing dat in een situatie waarin de voedseldichtheid laag is, steltlopers concurrentie niet uit de weg kunnen gaan door te zich te verdelen over verschillende niches, maar gedwongen zijn van een breder aanbod van niches gebruik te maken. (YIV)

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Appendix 1. Calculation of prey profitability

To obtain a measure of attractiveness of prey items the definition of profitability as proposed by Pyke et al. (1977) was adopted. They defined profitability as energetic value of a prey item divided by the sum of handling time and searching time.

$$P_i = \frac{E_i}{S_i + H_i}$$

i = number of prey types
E_i = energetic gain (gAFDW/prey item)
S_i = searching time (sec)
H_i = handling time (sec)

We aimed to define a theoretical mean profitability for each bird species at each plot. To obtain H_i for all benthic individuals found at the plots, a size-handling time relationship was described for each benthic group separately by a mean handling time or, when large differences occurred, with formulas calculated with the Nonlinear Estimation tool of Statistica. E_i was obtained as described in the methods. Since individual bird species needed different handling- and searching times, both were calculated for each species separately.

For the calculation of S_i it was assumed that prey items were evenly distributed and as a consequence, search time behaves inverse proportional to the density of organisms. Hence, random searching will take less time for organisms that are abundant than for rare items. For each bird species and month a mean search time ($\overline{S}$) per prey item could be calculated from the data as:

$$\overline{S} = \frac{T - H}{n}$$

$$\overline{S} = \frac{S_1 + S_2 + S_3 + ... + S_i}{i}$$

T = total time of focal observation
H = total handling time during focal observation
n = number of caught prey items

A factor (F_i) was calculated which accounts for the numerical relationship between the different prey items and reverses the proportions:

$$D_1 > D_2 > D_3 > \ldots > D_i$$

$$D_i = x_i \times D_1$$

$$F_i = \frac{1}{x_i}$$

D_i = density of individual prey types (individuals/m^2)
x_i = factor converting into

From this the proportional search time for each prey type could be calculated

$$\overline{S} = \frac{S_1 + (S_1 \times F_2) + (S_1 \times F_3) + ... + (S_1 \times F_i)}{i}$$

$$S_i = \frac{i \times \overline{S}}{\sum_1^i F}$$

$$S_i = (S_1 \times F_2)$$

Appendix 2. Results of Mann–Whitney U-tests between species on water depths used. Significant results according to the sequential Bonferroni procedure are indicated in bold.

	grpl $n = 46$	knot $n = 48$	mago $n = 9$	sand $n = 7$	sbdo $n = 56$	sppl $n = 55$	spsa $n = 61$	turn $n = 39$	whim $n = 54$
knot	$Z = 5.216$, **P <0.000**								
mago	$Z = 4.165$, **P <0.000**	$Z = 0.252$, $P = 0.801$							
sand	$Z = -0.557$, $P = 0.578$	$Z = -2.565$, $P = 0.010$	$Z = -2.257$, $P = 0.024$						
sbdo	$Z = 5.103$, **P <0.000**	$Z = -0.294$, $P = 0.768$	$Z = -0.601$, $P = 0.548$	$Z = 2.486$, $P = 0.013$					
sppl	$Z = -1.554$, $P = 0.120$	$Z = -6.348$, **P <0.000**	$Z = -5.707$, **P <0.000**	$Z = 0$, $P = 1$	$Z = -6.225$, **P <0.000**				
spsa	$Z = 2.976$, $P = 0.003$	$Z = -3.832$, **P <0.000**	$Z = -2.357$, $P = 0.018$	$Z = 1.580$, $P = 0.114$	$Z = -3.436$, **P = 0.001**	$Z = 4.203$, **P <0.000**			
turn	$Z = -0.469$, $P = 0.639$	$Z = -5.312$, **P <0.000**	$Z = -4.390$, **P <0.000**	$Z = 0.424$, $P = 0.672$	$Z = -5.169$, **P <0.000**	$Z = 1.188$, $P = 0.235$	$Z = -3.224$, **P = 0.001**		
whim	$Z = 1.859$, $P = 0.063$	$Z = -4.324$, **P <0.000**	$Z = -2.809$, $P = 0.005$	$Z = 0.476$, $P = 0.248$	$Z = -4.050$, **P <0.000**	$Z = 3.143$, **P = 0.002**	$Z = -1.125$, $P = 0.261$	$Z = 2.216$, $P = 0.027$	
will	$Z = 4.253$, **P <0.000**	$Z = -0.699$, $P = 0.485$	$Z = -0.836$, $P = 0.403$	$Z = 2.067$, $P = 0.039$	$Z = -0.457$, $P = 0.647$	$Z = 5.305$, **P <0.000**	$Z = 2.383$, $P = 0.017$	$Z = 4.314$, **P <0.000**	$Z = 3.014$, $P = 0.003$

Appendix 3. Results of Mann–Whitney U-tests between species on probing depths used. Significant results according to the sequential Bonferroni procedure are indicated in bold.

	grpl $n = 46$	knot $n = 48$	mago $n = 9$	sand $n = 7$	sbdo $n = 56$	sppl $n = 55$	spsa $n = 61$	turn $n = 39$	whim $n = 54$
knot	$Z = 1.357$, $P = 0.175$								
mago	$Z = 2.674$, P <0.008	$Z = 2.823$, $P = 0.005$							
sand	$Z = 0.766$, $P = 0.444$	$Z = 0.280$, $P = 0.780$	$Z = -1.985$, $P = 0.047$						
sbdo	$Z = 4.870$, **P <0.000**	$Z = 4.372$, **P <0.000**	$Z = -2.727$, $P = 0.006$	$Z = 2.119$, $P = 0.034$					
sppl	$Z = -2.126$, $P = 0.034$	$Z = -4.276$, **P <0.000**	$Z = -2.712$, $P = 0.007$	$Z = -3.103$, $P = 0.003$	$Z = -6.814$, **P <0.000**				
spsa	$Z = -2.077$, $P = 0.038$	$Z = -3.397$, **P <0.001**	$Z = -2.947$, $P = 0.003$	$Z = -2.775$, $P = 0.006$	$Z = -6.554$, **P <0.000**	$Z = 1.376$, $P = 0.169$			
turn	$Z = -0.912$, $P = 0.362$	$Z = -1.345$, $P = 0.179$	$Z = -2.611$, $P = 0.009$	$Z = -1.662$, $P = 0.097$	$Z = -5.015$, **P <0.000**	$Z = 1.922$, $P = 0.055$	$Z = 2.668$, $P = 0.008$		
whim	$Z = 2.813$, $P = 0.005$	$Z = 2.166$, $P = 0.030$	$Z = -2.742$, $P = 0.006$	$Z = 1.114$, $P = 0.265$	$Z = -0.084$, $P = 0.933$	$Z = 3.960$, **P <0.000**	$Z = 4.062$, **P <0.000**	$Z = 2.928$, $P = 0.003$	
will	$Z = -0.044$, $P = 0.965$	$Z = -0.837$, $P = 0.402$	$Z = -2.963$, $P = 0.003$	$Z = -0.418$, $P = 0.676$	$Z = -4.603$, **P <0.000**	$Z = 1.410$, $P = 0.159$	$Z = 1.372$, $P = 0.170$	$Z = 0.324$, $P = 0.746$	$Z = -2.950$, $P = 0.003$

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