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SHOREBIRDS OF THE BRAGANTINIAN PENINSULA II. DIET AND FORAGING STRATEGIES OF SHOREBIRDS AT A TROPICAL SITE IN NORTHERN BRAZIL

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Resumo. – Pássaros litorâneos da Península Bragantina II. Dieta e estratégias de alimentação dos pássaros litorâneos em um local tropical no norte do Brasil. – Sendo migratórios de longa distância, muitos passáros litorâneos têm que partilhar de uma variedade de hábitats que medem uma escala de regimes climáticos dentro de somente um ano. Embora suas adaptações para diferentes condições ambientais fossem o objeto de muitas publicações, poucas investigações ocorreram em ambientes tropicais. Como os pássaros lidam com o ajuste ecológico especial o qual encontram nos lugares tropicais aonde passam o inverno? Neste estudo nós focalizamos nas dietas e estratégias de alimentação dos passáros litorâneos na Península Bragantina no norte do Brasil durante 2001/2002. Todas as espécies tiveram grandes variedades de alimentos os quais se sobreporam, não houve nenhum agrupamento para uma relação evidente com a preferência alimentar. Certamente, um cálculo de dietas teoricamente ótimas mostrou que uma estratégia alimentar generalista foi mais vantajosa. As espécies maiores foram restringidas ligeiramente mais a grandes presas, ricas em biomassa, que foi vantajoso porque foi capturada e segurada facilmente. Como o estoque de alimento foi escasso e também variável temporariamente, nos supomos que uma estratégia generalísta e oportunista seria a mais ótima. As planícies de maré nos trópicos úmidos são sujeitas geralmente aos vários distúrbios ambientais tais como volumes sazonal de água doce; é provável que muitos têm estoques de alimentos de quantidade baixa e também variável como aqueles da Península Bragantina. A estratégia alimentar oportunísta empregada pelos pássaros em nosso local de estudo pôde conseqüentemente também ser uma estratégia apropriada em outras planícies de maré nos trópicos sujeitos para condições similares.

Abstract. – Being long-distance migrants, many shorebirds have to deal with a variety of habitats spanning a range of climatic regimes within only one year. Although their adaptations to differing environmental conditions are the object of many publications, few investigations have taken place in tropical environments. How do birds cope with the particular ecological setting they encounter on their tropical wintering grounds? In this study we focus on diets and foraging strategies of shorebirds at the Bragantinian Peninsula in northern Brazil during 2001/2002. All species had broad diets with overlapping spectra, no clear clustering according to dietary preference was evident. Indeed, a calculation of theoretical optimal diets showed that a generalistic foraging strategy was most profitable. Larger species were slightly more restricted to large, biomass rich prey, which was profitable because it was readily captured and handled. Since the food stock was scarce as well as temporally variable, we assume that a generalistic and opportunistic strategy would be most optimal. Tidal flats in the wet tropics are commonly subjected to various environmental disturbances such as seasonal volumes of freshwater inflow; it is likely that many have low as well variable food stocks as those of the Bragantinian Peninsula. The opportunistic foraging strategy employed by shorebirds at our study site might therefore also be an appropriate strategy at other tidal flats in the tropics subject to similar conditions. *Accepted 15 June 2006*.

Key words: Tropical habitat, shorebirds, foraging ecology, feeding strategy, opportunism, diet.

INTRODUCTION

Most shorebirds are long-distance migrants that have Arctic or temperate breeding sites and tropical or subtropical wintering- and migration stop-over sites. Consequently they are exposed to a variety of habitats within short time periods and need a remarkable adaptability to diverse environmental conditions. Even though many shorebirds spend over half of their life in tropical environments, there have been few studies of them in southern wintering habitats (Wolff & Smit 1990, Turpie & Hockey 1997, Ntiamoa-Baidu *et al.* 1998, Sitters *et al.* 2001).

Tropical tidal flats have specific properties when compared to their temperate counterparts, such as strong seasonal freshwater and sediment discharge from the rivers during wet seasons, nearby upwelling, and El-Niño/ Southern Oscillation (ENSO) events. Tropical intertidal benthos communities, the main food source for visiting shorebirds, are exposed to these frequent disturbances, and abundances and biomass are low (Reise 1991, Dittmann 2002). Additionally, the lack of seasonal temperature change does not force benthic taxa to reproduce synchronously, which leads to a pronounced temporal variability of the abundances of individual prey taxa (de Goeij *et al.* 2003). To our observations, benthic organisms react variably to changes in pore water salinity, hence the seasonal freshwater flushes during the wet season do not seem to be able to create a synchronized seasonal reproduction phase for the benthos community.

Historically, many studies of feeding strategies have focused on cost-benefit calculations, based on the implicit aim of fitness maximization (represented as maximized energy gain) per time unit. To achieve optimal foraging, shorebirds can 1) increase their feeding efficiency by specializing on particular biomass rich or abundant items, or they can 2) act as generalists with a smaller dependency on the presence of certain prey taxa (Begon *et al.* 1998). The degree of specialization is usually related to the productivity and stability of the environment (MacArthur & Pianka 1966, Cody 1974, Pyke *et al.* 1977).

In 2001/2002, we investigated a shorebird foraging site at the Bragantinian Peninsula on the northern coast of Brazil within a major wintering zone in South America (Morrison & Ross 1989). In another publication (Kober & Bairlein 2006), we describe this area in terms of its characteristics as a shorebird environment; the present study investigates how shorebirds cope with the constraints of tropical climates, and which foraging strategies might be employed in order to gain mass for migration.

METHODS

Study area and sampling site

The study was conducted at the Bragantinian Peninsula on the northern coast of Pará, Brazil (00°52.427S, 46°39.012W). This tropical region is characterized by a rainy season from January to May/June and a dry season from July to December. The coast is fringed by a dense mangrove forest, which is part of the worlds second largest continuous mangrove belt (Kjerfve *et al.* 1997).

Data were collected in January–June in 2001/2002 at an open intertidal site located between the island Ilha de Canelas and the mainland (Fig. 1). Sediment conditions and benthic assemblages were variable in time and space due to strong currents with heavy sedi-

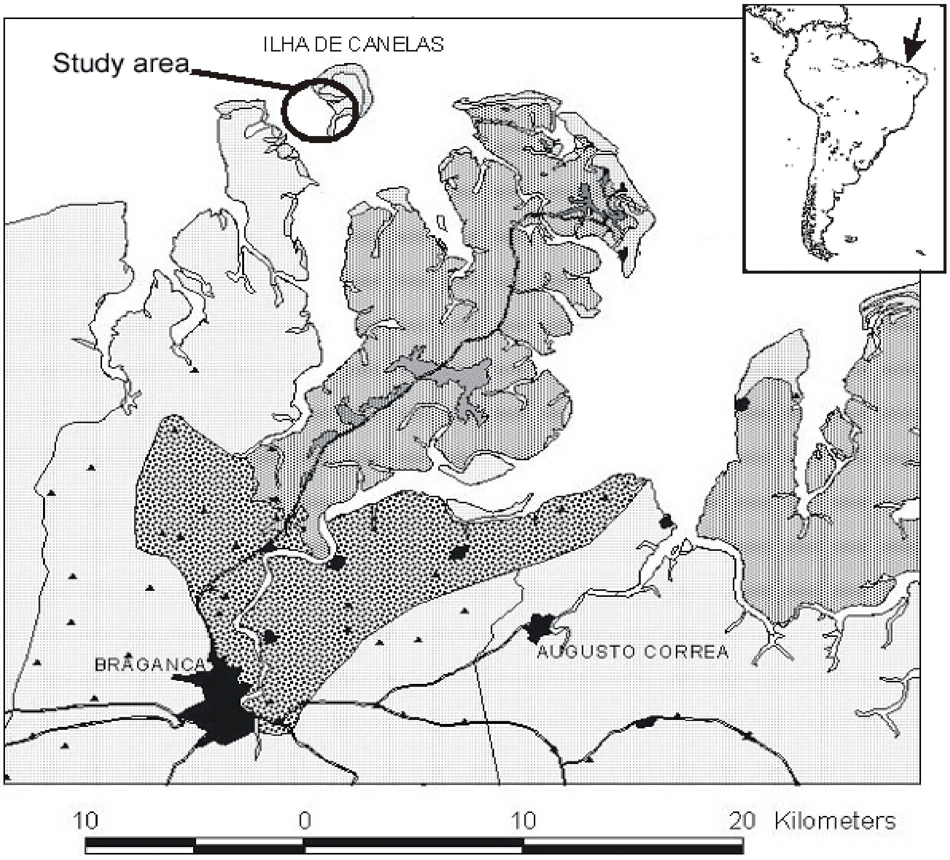

FIG. 1. Bragantinian Peninsula with the study area on Ilha de Canelas represented by a black circle.

ment loads, which led to a mosaic of patches with differing abiotic and biotic conditions. These characteristics were pronounced during the wet season, due to heavy rains and the high influx of freshwater to the tidal flats.

Sampling design

In 2001, a total of 25 squared plots (50 x 50 m) were marked with poles at their corners. To optimize data for correlation analysis and multivariate statistics, plots were not located randomly but covered the whole variety of distinguishable intertidal habitats. Although some plots were bordering each other, contingency tables showed that the benthic data obtained were independent from each other. In 2002, a further five plots (50 x 50 m) were marked at the same part of the mudflat which was investigated in 2001 in order to measure the temporal consistency of the results. The following data were taken on a monthly basis:

Abiotic variables. At each plot sediment samples were taken to determine sediment grain sizes and pore water salinity. For a more detailed description of the sampling methodology see Kober & Bairlein (2006).

Prey abundance. To determine the food supply available to the birds at each plot, sediment samples were taken to a depth of 20 cm with a corer of 15 cm diameter and benthic animals were separated with a 1-mm sieve. Additional samples processed with a 0.5-mm sieve (Acheampong 2001) produced benthic abundances and biomasses similar to those of our samples, thus sampling with 1-mm sieves is sufficient in this area and will not disregard considerable prey factions (Kober 2004). Each sample was divided into three horizons (0–5, 5–10 and 10–20 cm depth) and, for each layer, the benthic assemblage and the sizes of prey items were determined. With help of these size-measurements, the ash-free dry mass (AFDM) of the samples were calculated. For a more detailed description of the sampling methodology, see Kober & Bairlein (2006).

Avian abundance and foraging behavior. To determine bird densities in the study area, bird counts were conducted during the mid day low tides on four consecutive days, and a monthly mean low tide density of birds was calculated for each plot.

The detailed foraging behavior of the birds was investigated by focal observations conducted between February and June in 2002. Some 617 individual birds were observed, each for exactly 3-min, and the following data were recorded: pecks/probes per minute, prey consumed per minute, prey handling time (sec), prey type, prey size and probing depth, both estimated by comparison with the bill size (mm). Prey sizes determined during focal observations have certain drawbacks: Over-estimations of large organisms are a methodological problem, as well as the under-representation of small prey (Zwarts & Blomert 1992). Size-spectra of "worms" might be overestimated because they were stretched while they were pulled out of the sediment. We tried to avoid those problems by conducting a training for the observers on prey with known sizes, but the results showed, that they could not be prevented entirely. Prey sizes and probing depths were nevertheless used to determine the portion of all prey organisms which was in reach of the bill, and which could be handled by the birds (i.e., the harvestable prey fraction) (Kober & Bairlein 2006).

Observed diet. The prey ingested by the birds during focal observations in 2002 was differentiated into bivalves, crustaceans, snails and "worms". Where identification of prey was impossible due to either their small sizes or due to the speed of feeding, items were labeled as "unknown".

Faeces. More detailed information on prey taxa was provided by faeces collections, from which remaining parts of ingested prey taxa were identified (cirrae, mandibulae and shell fragments). Droppings were collected during focal observations whenever possible. Since observations suggested that most birds were feeding for a reasonable time at the same area, it was assumed that most droppings were representative of local prey organisms. Droppings were scraped off the surface and stored in 70% ethanol (Scheiffarth 2001). They were treated with ultrasound for 10 min to separate particles. After sedimentation, two fractions were obtained: supernatant and sediment. Floating parts within the supernatant were collected with a sieve (63 ìm), identified and counted in a cylindrical chamber with help of a microscope (Zeiss Axioskop 2 with 10 x/0.30, 20 x/0.50 and 40 x/0.75 oculars). The sediment was examined and larger prey remnants were counted and identified to provide qualitative data on the birds' diets.

Specific identification of remaining benthic parts was eased by the collection of a reference sample: benthic organisms were identified, measured (Stereomicroscope: Stemi 2000 from Zeiss with10x ocular, Microscope: see above), and subsequently left in warm water for 3–14 days. The more durable parts of animals were then described.

In comparison to temperate benthic assemblages, tropical tidal flats harbor a higher diversity of benthic taxa, which often cannot be accurately identified to species level due to incomplete taxonomic knowledge about the species in question. Furthermore, a significant proportion of the collected benthos, in particular soft-bodied species, cannot be detected within droppings due to a lack of body parts which endure digestion. Thus, data obtained by the analysis of the birds' faeces cannot provide quantitative information and records of prey identity are almost certainly incomplete.

Optimal diet. To assess whether prey species present in the birds' faeces corresponded to a diet which maximized intake rates, optimal diets as defined by Charnov (1976) were calculated, and compared with observed diets. To further determine the optimal diet for each bird species a measure of profitability was assigned to each prey species. Profitability was defined as the energetic value of a prey item divided by the sum of handling and searching time (Pyke *et al.* 1977).

Handling time for all benthic individuals found on the plots was determined by establishing a size-handling-time relationship for each individual benthic group. When a taxon covered a large size-range, size-dependent formulas were calculated with the nonlinear estimation tool of Statistica. Otherwise, a mean handling time was taken (Kober 2004). Since individual bird species required different handling and searching times for the same prey items, calculated profitabilities differed between bird species.

Searching time was assumed to be inversely related to the density of organisms. In other words, random searching took less time for organisms that were abundant than for rare items. Based on this assumption, a mean search time per prey item was calculated for each bird species and month (for calculation details see Kober 2004).

When profitabilities of individual prey items are known, an optimal diet can be calculated. If a predator, which already included the most profitable prey type into its diet, encounters a new and less profitable prey type, it has to decide whether to eat the prey or to carry on with searching for already included prey. Prey type *i* should only be included if its energy gain per handling time is equal or larger than the mean profitability of the already included items (Charnov 1976). For detailed descriptions of such calculations see Pyke *et al.* (1977). Since no size preferences for gastropods were available, they could not be included in the calculations for profitabilities or optimal diets.

Statistics

Statistical analyses were done with Statistica (Version 5.1 from StatSoft Inc.), Primer (Version 5.2.2 for Windows, Primer-E Ltd), and the Excel Add-In Biplot (Version 1.1 by Virginia Tech). To visualize any similarity between species assemblages, a Multi-dimensional Scaling plot (MDS-plots) was used. Since it expresses similarity in relative Euclidian distances, axe values are not relevant. Data were log-transformed to down weight the influence of abundant species before computing Bray-Curtis similarities. The plot reproduced well, its stress-values remained < 0.2 (Clarke & Gorley 1994). Beside this diagram, also a contingency table was used. For all tests, a significance level of $\alpha = 0.05$ was chosen.

RESULTS

A total of 11 abundant shorebird species were found in the study area, belonging to both Scolopacidae and Charadriidae (Table 1).

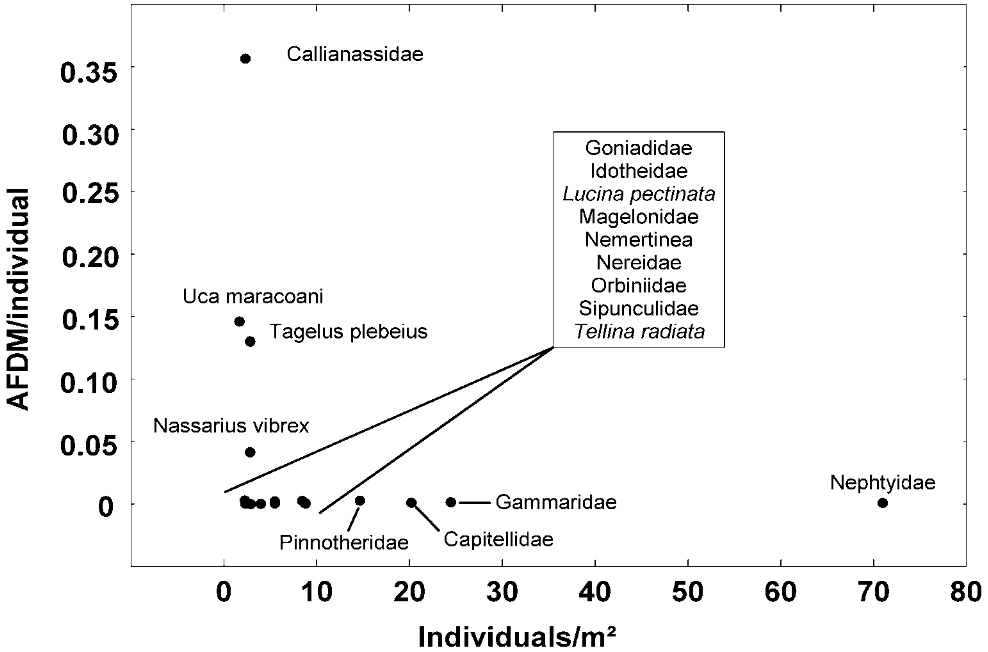

FIG. 2. Mean abundance vs mean biomass of benthic taxa in the study area in 2001. Only species with n > 30 individuals found were included.

Available prey

Most of the prey taxa available to the birds had very low individual biomasses, as well as very low densities (Fig. 2). Only a few mollusks or crustaceans showed high biomass values per item (Callianassidae, *Uca maracoani*, *Tagelus plebeius*, *Nassarius vibrex*), but these were found in very low densities. A few species (Nephtyidae, Gammaridae, Capitellidae, Pinnotheridae) occurred in high densities, but these only had low individual biomasses.

Observed prey

During focal observations in 2002, the percentage of prey organisms that could be identified averaged 41% and varied from only 21% [for Semipalmated Sandpiper (*Calidris pusilla*)] to 71% [for Semipalmated Plover (*Charadrius semipalmatus*)] (Table 1). Amongst identified prey, that of Marbled Godwit (*Limosa fedoa*) and all plovers was dominated by "worms", though the Grey Plover (*Pluvialis squatarola*) also fed on mussels and crustaceans. Identified prey of Willet (*Catoptrophorus semipalmatus*) were mostly crustaceans while that of the remaining sandpipers were bivalves supplemented mainly by worms. Identified prey of Red Knot (*Calidris canutus*) were almost entirely restricted to snails and bivalves (Table 1). Because there is often a large proportion of unidentified prey items, it has to be pointed out that the actual diets of the birds might depart considerably from those described above.

Based on the classification of prey items obtained during the focal observations, the birds' prey spectra were broad and overlapping. A MDS-plot illustrating the composition of identified prey showed that only gradual differences occurred; distinct special-

TABLE 1. Percentage prey composition for the birds during focal observations in 2002. N is the number of observed prey items. For the resident Spotted Sandpiper (*Actitis macularia*), data on prey items were not available.

Species	Prey					
	Bivalves	Snails	Crustaceans	Worms	Unknown	n
Collared Plover (*Charadrius collaris*)	4	0	2	42	52	163
Grey Plover (*Pluvialis squatarola*)	12	1	14	27	46	104
Semipalmated Plover (*Charadrius semipalmatus*)	1	0	0	70	29	269
Marbled Godwit (*Limosa fedoa*)	0	2	0	41	56	41
Red Knot (*Calidris canutus*)	13	19	0	1	68	96
Ruddy Turnstone (*Arenaria interpres*)	39	0	4	4	52	46
Sanderling (*Calidris alba*)	11	4	0	11	75	28
Short-billed Dowitcher (*Limnodromus griseus*)	13	4	0	9	74	152
Semipalmated Sandpiper (*Calidris pusilla*)	11	0	1	9	79	130
Whimbrel (*Numenius phaeopus*)	27	4	11	5	53	75
Willet (*Catoptrophorus semipalmatus*)	10	5	16	2	68	62

izations were not seen (Fig. 3). The further left a bird is located in the diagram, the larger is the proportion of worms found in its diet. Birds at the top include more crustaceans into their diet than birds at the bottom.

Droppings

Since observations of avian prey were not applicable to differentiate in detail between the dietary components of different bird species, a total of 68 droppings were collected to look for identifiable remaining parts of individual prey taxa. However, this analysis gave only qualitative results, not quantitative ones. The remains of four bivalve species, one gastropod, four crustacean species and six polychaete taxa were identified from the collected droppings (Table 3). Most bird species chose prey from all these benthic groups. Plovers fed on a larger variety of items than sandpipers (7–9 items and 5–6 items, respectively), including small polychaetes and crustaceans. However, the result is likely to be biased by the capability of a particular benthos species to endure the birds' digestion: some prey types may always leave hard, identifiable remains in the droppings while others may never or only occasionally do so.

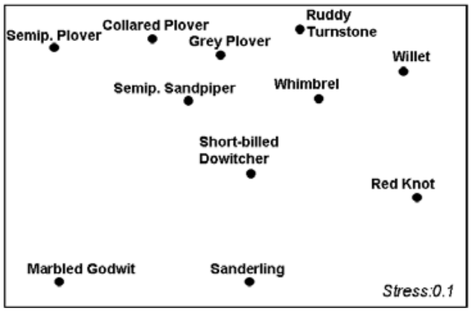

FIG. 3. Similarities of the birds diets. Shown is a MDS-plot on Bray-Curtis similarities of the diets as observed in 2002. Unidentified items were excluded from the analysis.

Prey size

Observed prey sizes indicate which size spectra the birds can handle. They ranged for bivalves between 1–63 mm (shell length), crustaceans between 3–61 mm (carapace width), and worms between 2–180 mm (length) (Table 2). For crustaceans and bivalves, prey size was significantly correlated with birds bill sizes ($r_s = 0.900$, $P < 0.001$ and $r_s = 714$, $P = 0.047$, respectively), "worms"

TABLE 2. Prey sizes (mm) observed during focal observations in 2002.

Species	Bivalves		Crustaceans		Worms	
	Mean ± DF (Max)	n	Mean ± DF (Max)	n	Mean ± DF (Max)	n
Collared Plover	6 ± 4 (10)	7	23 ± 20 (44)	3	27 ± 18 (116)	69
Grey Plover	17 ± 11 (36)	12	14 ± 11 (39)	15	41 ± 31 (180)	28
Semipalmated Plover	5 (5)	2	10 (10)	1	38 ± 26 (122)	189
Marbled Godwit					54 ± 29 (133)	17
Red Knot	27 ± 7 (40)	12			43 (43)	1
Ruddy Turnstone	23 ± 12 (59)	18	6 ± 2 (7)	2	33 ± 20 (47)	2
Sanderling	10 ± 4 (15)	3			26 ± 13 (38)	3
Short-billed Dowitcher	24 ± 18 (63)	19			32 ± 18 (68)	14
Semipalmated Sandpiper	6 ± 2 (10)	14	4 (4)	1	19 ± 15 (39)	12
Whimbrel	29 ± 12 (52)	20	39 ± 17 (61)	8	46 ± 8 (52)	4
Willet	18 ± 15 (44)	6	30 ± 14 (49)	10	11 (11)	1

only closely missed the 5% level ($r_s = 0.566$, $P = 0.055$).

Optimal diet

To identify which prey taxa individual bird species should ideally have consumed in order to forage with maximum profitability, an optimal diet was calculated for each bird species. Bivalves and crustaceans provided the highest biomasses per prey item, while polychaetes were insignificant in this respect (Fig. 2). Nevertheless, in some cases polychaetes were indeed profitable, due to their high densities, which resulted in shorter searching times. The optimal diet of some birds, like Red Knot, Sanderling (*Calidris alba*), Whimbrel (*Numenius phaeopus*) and Willet, was composed of only a few prey items. These specialists included particularly biomass rich prey in their diets, like large bivalves (often *Tellina radiata* and *Protothaca pectorina*) and crustaceans. Only the Sanderling was able to specialize on bivalves and polychaetes with low individual biomasses (Fig. 4, Table 3). Marbled Godwit, Ruddy Turnstone (*Arenaria interpres*) and Semipalmated Sandpiper had broad optimal diets. These generalists incorporated many types of bivalves, crustaceans and polychaetes with comparatively low individual biomasses. The remaining birds switched between these strategies, which is indicated by the large range of the mean number of prey taxa per month (Fig. 4, Table 3).

DISCUSSION

The tropical intertidal area of the Bragantinian Peninsula provides poor foraging grounds. Frequent sediment shifts combined with low sediment organic matter contents may have led to low as well as patchily distributed abundances and biomasses of benthic organisms (Kober & Bairlein 2006). As a consequence, prey handling times of the birds are short relative to searching times, and one would thus expect shorebirds to include a wide range of prey items (MacArthur & Pianka 1966, Pyke *et al.* 1977, Begon *et al.* 1998).

Theoretical optimal diets represent prey spectra, which should be eaten by the birds if they are optimizing their prey choice. These calculated diets, based on observed prey densities and foraging behavior, were in line with the above expectations (many bird species had broad optimal diets based on at least 5–15 prey taxa within one month). In the rare cases when bird species had optimal diets

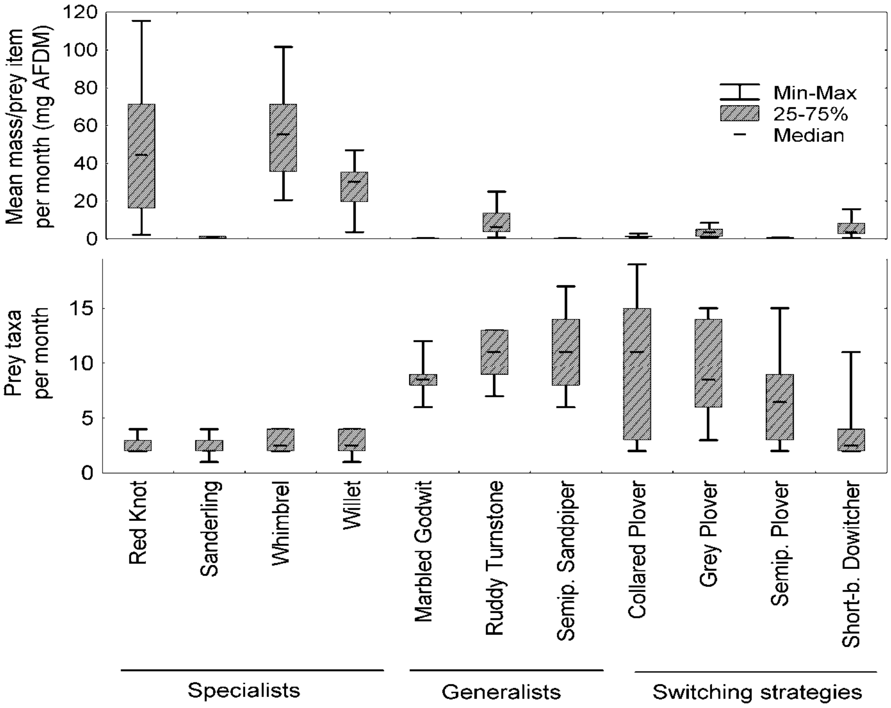

FIG. 4. Characteristics of optimal diets of birds with differing foraging strategies. Given are mean biomasses per prey item and per month at the top, and mean diet widths per month at the bottom.

with lesser than 5 items per month, these items were typically large and biomass rich. Large birds are more prone to narrower dietary spectra since they are more likely to include biomass-rich items in their diet in order to optimize their foraging patterns. Biomass-rich prey organisms, such as bivalves or crustaceans, are often less diverse than small prey species, which might lead to a lower food diversity for larger shorebirds (Recher 1966). Additionally, such benthic organisms are deeply burrowed in the sediment, making bill size a significant factor in a birds' abilities to reach these items – long-billed birds have an advantage over short-billed birds in this respect (Holmes & Pitelka 1968, Goss-Custard *et al.* 1977, Lifjeld 1984, Weber & Haig 1997). There are exceptions from this patterns, e.g., Sanderling is a comparatively small, yet relatively specialized species which fed in a highly profitable manner on small bivalves, while needing considerably longer handling times for other prey.

Optimal diets point out which strategies should ideally have been adopted in a tropical environment like that of the Bragantinian Peninsula. But did the birds indeed optimize their foraging as presumed? Visual observations showed that all species had broad diets which overlapped to a large degree; indeed, the shorebird community cannot be clearly divided into groups with particular feeding preferences. The MDS-diagram does reveal a weak gradual change from plovers with a large proportion of "worms" in their diet at one end of the spectrum, to medium and large sandpipers which also include crustaceans as well as mollusks at the other end. This is

TABLE 3. Prey items included into optimal diets (shading) and found in the faeces (numbers) during the entire study period. Given are the numbers of droppings which contained a particular prey item. Data were originally calculated/collected per month, thus items listed here do not necessarily occur simultaneously. Droppings of the Marbled Godwit and of the Whimbrel did not contain any identifiable parts. Since we had no AFDMs of gastropods, arthropods, unidentified bivalves, unidentified crustaceans and unidentified polychaetes, these groups were not included into calculations about optimal diets.

		Collared Plover	Grey Plover	Semip. Plover	Marbled Godwit	Red Knot	Ruddy Turnstone	Sanderling	Short-b. Dowitcher	Semip. Sandpiper	Whimbrell	Willet
Number of analysed droppings		21	40	23	0	11	10	4	18	17	1	20
Sipunculidae	Sipunculidae				▨							
Nemertinea	Nemertinea	▨	▨	▨	▨		▨		▨		▨	▨
Bivalves	Unidentified	1	3			1			1			
	Anomalocardia brasiliana		▨			▨	▨		▨		▨	▨
	Divaricella quadrisulacata	▨		▨						▨		
	Lucina pectinata	▨	▨	▨					▨	▨		▨
	Protothaca pectorina		▨ 4			▨ 1	▨		▨	▨	▨	▨ 1
	Tagelus plebeius	▨	▨ 3	▨		▨ 1	▨	▨	▨ 2	▨	▨	▨ 2
	Tellina spp.	▨ 2	▨ 7	▨ 2		▨ 1	▨ 2	▨ 1	▨ 2	▨ 1	▨	▨ 2
Gastropods	*Nassarius vibrex*					1	1					
Crustaceans	Unidentified	1	1	1		1			1	1		3
	Callianassidae	▨ 3	▨ 4	1			▨ 2	1	1	3		▨ 5
	Callinectes sp.	▨	▨									
	Decapoda	▨	▨			2						▨
	Eurytium limosum	▨								▨		
	Gammaridea	▨	▨				▨			▨		
	Hippolitidae	▨	▨				▨					
	Idotheidae	▨	▨				▨		1	▨		
	Mysidae	▨	▨	▨			▨					▨
	Pinnotheridae	▨ 1	▨ 1				▨			▨		
	Uca maracoani	▨	▨	▨			▨				▨	▨

TABLE 3. Continued.

		Collared Plover	Grey Plover	Semip. Plover	Marbled Godwit	Red Knot	Ruddy Turnstone	Sanderling	Short-b. Dowitcher	Semip. Sandpiper	Whimbrell	Willet
Polychaetes	Unidentified	3	2				1		1	1		1
	Capitellidae	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	
	Eulepethidae				🟨							
	Glyceridae	🟨		🟨	🟨		🟨		🟨	🟨		
	Goniadidae	🟨 1	🟨 1	🟨 2	🟨		🟨		🟨	🟨		
	Lumbrineridae	🟨		🟨 3			🟨			🟨		
	Magelonidae	🟨	🟨	🟨			🟨		🟨	🟨		
	Nephtyidae	🟨	🟨	🟨 2			🟨	🟨	🟨	🟨	🟨	
	Nereidae	🟨 3	🟨 2	🟨 5	🟨	🟨	🟨 1	🟨 1	🟨 1	🟨 2	🟨	1
	Onuphidae	🟨		🟨	🟨							
	Orbiniidae	🟨	🟨	🟨	🟨		🟨			🟨		
	Phyllodocidae		🟨	🟨	🟨		🟨			🟨		
	Pilargiidae (A)		🟨		🟨			🟨		1		
	Pilargiidae (B)	🟨	🟨	🟨	🟨		🟨			🟨		
	Saccocirridae	🟨			🟨							
	Spionidae	🟨 1	1	🟨	🟨			1				
	Terebellidae									1		
Arthropods	Unidentified	2	6	5		1	2		3	4		2
Total identified items in optimal diet		27	24	19	17	6	22	6	12	20	8	9
Total identified items in droppings		7	9	7	-	5	4	6	6	6	-	6

clearly consistent with the pattern proposed by the optimal foraging theory as explained above.

The faeces of all species contained on average six different prey taxa, but prey diversity was almost certainly greater because of the many items not leaving identifiable body parts. This is again pointing towards a pattern of limited dietary specialization. In agreement with the visual observations, pronounced specializations were not discovered, although sandpipers did seem to have a slightly more restricted diet when compared to plovers. This is in line with the prediction that long-billed birds, like many sandpipers, should be more specialized than short-billed birds, such as the plovers.

Unfortunately, neither direct observations, nor the analysis of faeces, provide a full assessment of the birds' dietary widths. The ability of focal observations to identify diets was limited by the often large proportion of unidentifiable prey organisms. Particular large proportions of unidentified prey were found for species with many bivalves in their fraction of identified prey [Sanderling, Short-billed Dowitcher (*Limnodromus griseus*), Semipalmated Sandpiper], sometimes supplemented by crustaceans (Willet, Knot). Minute bivalves are probably quickly swallowed and therefore hard to identify for the observers. An exception are Turnstones and Whimbrels, with a large proportion of identified bivalve prey organisms, but a small proportion of unidentified prey. A reason might be that they preferred large bivalves. Species with many worms in their identified prey had comparatively small proportions of unidentified prey [Semipalmated Plover, Collared Plover (*C. collaris*), Marbled Godwit]. Worms might be easier to identify from a distance.

The analysis of droppings had also some drawbacks. Many prey taxa did not provide body parts recognizable in droppings (e.g., Nemertinea). Of the polychaetes, only those were recognized in faeces which provide jaws (Goniadidae, Nephtyidae, Nereidae), specific aciculae (Pilargiidae, Spionidae) or uncini (Terebellidae). Crustaceans often had to be left unidentified since only the large Callianassidae had a carapace with an unmistakable light shading. Identification of bivalve shell fragments was often possible, e.g., *Tellina* which had an easily identifiable coloration. However, the weaknesses of both focal observations and analysis of droppings do not corrupt the observation of broad diets: if both would have provided more precise results, most likely these would have added even more prey taxa to the diets.

The prediction obtained from optimal diets that long-billed birds would feed on larger prey than short-billed birds when foraging optimally was also supported by focal observations: observed mean prey sizes and bill sizes of the birds were correlated with each other. Large birds with long bills are able to reach deeper burrowed prey, but also have wider throats and can swallow larger prey more easily. In addition, there are indications that large birds are more easily capable of digesting hard-shelled organisms because of their heavier gizzards (Piersma *et al.* 1993). The non-significance of the bill size-worm size correlation might arise because large worms sizes do not raise as much problems for handling, swallowing and digesting as hard shelled prey taxa. Consequently, even plovers with particularly short bills are able to take many long worms. However, observed prey sizes have to be treated with care, since sample sizes of some prey groups were extremely low. In some cases, sizes of bivalves appeared extraordinary large (e.g., Knots and Short-billed Dowitcher feeding on bivalves of 40 and 63 mm length, respectively); large sizes were possibly over-estimated while small organisms are under-represented, a methodological problem described also elsewhere (Zwarts & Blomert 1992). Finally, "worm" sizes are also problematic because worms might be stretched when pulled out of the sediment. Hence, the correlation between prey size and bird size can only be a rough estimation of the actual relationship.

In addition to the low prey abundances which force the birds to accept relatively broad dietary spectra, prey phenologies fluctuated strongly in the study area (Kober & Bairlein 2006). Within the time period of observations, trends in prey abundance were not synchronized as observed in temperate areas (Beukema 1974). Although total benthic abundance and biomass were stable and create the impression of an attractive food supply at some tropical tidal flats (as observed in West Africa, Wolff 1991), the strong fluctuations of individual taxa might prohibit specialized diets over longer time periods. In conclusion, it seems advantageous for birds to adopt a foraging strategy that is both generalistic and opportunistic in environments such as the Bragantinian Peninsula.

Early studies on the ecology of shorebirds on their wintering- and migration sites discussed the idea that shorebirds are limited through competition on tropical wintering sites (Recher 1966, Duffy *et al.* 1981). Recher (1966) proposed that due to high bird densities and uniform habitats on shorebird wintering grounds, morphological and behavioral segregation, including the specialization of diets, should be strong in order to minimize interspecific competition. At the tidal flats of the Bragantinian Peninsula, indeed high bird densities were observed (Kober & Bairlein 2006). However, based on the results of this study, we recommend to restrict this hypothesis to situations when food is abundant and stable enough to support birds, even when feeding on only a confined proportion of the food supply. We hypothesize that, in cases of poor foraging grounds, the ability to specialize on certain prey items is restricted, even though competition might be strong. Such poor and variable conditions, as observed at the tropical tidal flat of the Bragantinian Peninsula, are likely to occur at a number of tropical areas and it is possible, that the presence of generalistic versus specialized foraging behavior in migrating avian species is notably influenced by climatic conditions. Further research is needed to answer this question more thoroughly.

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REFERENCES

Acheampong, E. 2001. Distribution of macrozoobenthos abundance and biomass in intertidal soft sediments of North East Brazil. M.Sc. thesis, Univ. of Bremen, Bremen, Germany.

Begon, M. E., J. L. Harper, & C. R. Townsend. 1998. Ökologie. Spektrum Akademischer Verlag, Heidelberg, Germany.

Beukema, J. J. 1974. Seasonal changes in the biomass of the macrobenthos of tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. 8: 94–107.

Charnov, E. L. 1976. Optimal foraging: Attack strategy of a mantid. Am. Nat. 110: 141–151.

Clarke, K. R., & R. N. Gorley. 1994. Primer v5: User manual/Tutorial. Bourne Press Ltd, Bournemouth, UK.

Cody, M. L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, New Jersey.

de Goeij, P., M. Lavanleye, G. B. Pearson, & T. Piersma. 2003. Seasonal changes in the macrozoobenthos of a tropical mudflat. Royal Netherlands Institute for Sea Research (Nioz) and W. A. Department of Conservation and Land Management, Texel, Netherlands.

Dittmann, S. 2002. Benthic fauna in tropical tidal flats – a comparative perspective. Wet. Ecol. Manage. 10: 189–195.

Duffy, D. C., N. Atkins, & D. C. Schneider. 1981. Do shorebirds compete on their wintering grounds? Auk 98: 215–229.

Goss-Custard, J. D., R. E. Jones, & P. E. Newberry. 1977. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). J. Appl. Ecol. 14: 681–700.

Holmes, R. T., & F. A. Pitelka. 1968. Food overlap among coexisting sandpipers on northern alaskan tundra. Syst. Zool. 17: 305–318.

Kjerfve, B., L. D. Lacerda, & D. Diop. 1997. Mangrove ecosystem studies in Latin America and Africa. UNESCO, Paris, France.

Kober, K. 2004. Foraging ecology and habitat use of wading birds and shorebirds in the mangrove ecosystem of the Caeté Bay, Northeast Pará, Brazil. Ph.D. diss., Centre for Marine Tropical Ecology, Univ. of Bremen, Bremen, Germany.

Lifjeld, J. T. 1984. Prey selection in relation to body size and bill length of five species of waders feeding in the same habitat. Ornis Scand. 15: 217–226.

Kober, K., & F. Bairleins 2006. Shorebirds of the Bragantinian Peninsula I. Prey availability and shorebird consumption at a tropical site in northern Brazil. Ornitol. Neotrop. 17: 531–548.

MacArthur, R., & E. R. Pianka. 1966. On the optimal use of a patchy environment. Am. Nat. 100: 603–609.

Morrison, R. I. G., & R. K. Ross. 1989. Atlas of Nearctic shorebirds on the coast of South America. Canadian Wildlife Service, Ottawa, Ontario.

Ntiamoa-Baidu, Y., T. Piersma, P. Wiersma, M. Poot, P. Battley, & C. Gordon. 1998. Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. Ibis 140: 89–103.

Piersma, T., A. Koolhaas, & A. Dekinga. 1993. Interactions between stomach strength and diet choice in shorebirds. Auk 110: 552–564.

Pyke, G. H., H. R. Pulliman, & E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137–154.

Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47: 393–407.

Reise, K. 1991. Macrofauna in mud and sand of tropical and temperate tidal flats. Pp. 211–216 *in* Elliot, M., & J.-P. Ducrotoy (eds.). Estuarie and coasts: Spatial and temporal intercomparisons. Ohlson & Ohlson, Fredensborg, Denmark.

Scheiffarth, G. 2001. The diet of Bar-tailed Godwits *Limosa lapponica* in the Wadden Sea: Combining visual observations and faeces analysis. Ardea 89: 481–494.

Sitters, H. P., P. M. Gonzalez, T. Piersma, A. J. Baker, & D. J. Price. 2001. Day and night feeding habitat of Red Knots in Patagonia: Profitability versus safety? J. Field Ornithol. 72: 86–95.

Turpie, J. K., & P. A. R. Hockey. 1997. Adaptive variation in the foraging behaviour of Grey Plover *Pluvialis squatarola* and Whimbrel *Numenius phaeopus*. Ibis 139: 289–298.

Weber, L. M., & S. M. Haig. 1997. Shorebird diet and size selection of nereid polychaetes in South Carolina coastal diked wetlands. J. Field Ornithol. 68: 358–366.

Wolff, W. J., & C. J. Smit. 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. Ardea 78: 17–38.

Wolff, W. J. 1991. The interaction of benthic macrofauna and birds in tidal flat estuaries: A comparison of the Banc d'Arguin, Mauritania, and some estuaries in the Netherlands. Pp. 299–306 *in* Elliot, M., & J.-P. Ducrotoy (eds.). Estuaries and coasts: Spatial and temporal intercomparisons. Ohlson & Ohlson, Fredensborg, Denmark.

Zwarts, L., & A.-M. Blomert. 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. Mar. Ecol. Prog. Ser. 83: 113–128.