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THE EXPLOITATION OF INTERTIDAL FOOD RESOURCES IN INHACA BAY, MOZAMBIQUE, BY SHOREBIRDS AND HUMANS

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Abstract
The intertidal areas on Inhaca island provide important food resources for shorebirds as well as the local population. Average bird density is 2-6 individuals/ha during summer, decreasing to 0.3 in winter, which is one of the lowest records for the African coasts. Whimbrels Numenius phaeopus *and curlew sandpipers* Calidris ferruginea *are the most abundant species. Total littoral fauna consumption is low, estimated at 2.5 g ash-free dry weight/m²/year, of which only 18% is harvested by humans. Species preferences, numbers and weights are given for humans who collect invertebrates. The influence of human presence on bird behaviour is measured, using Minimal Approach Distances (MAD), foraging activity changes and people-bird abundance correlation. Larger birds have longer MADs and their foraging activity decreases earlier when approached by humans. The large, territorial whimbrel is most influenced by human presence and this interference competition is responsible for a 34% reduction of foraging time. Copyright © 1996 Published by Elsevier Science Limited*

Keywords: shorebirds, consumption, humans, disturbance, benthos.

INTRODUCTION

In recent years much work has been carried out on intertidal ecology, including studies on palearctic migrant waders in various staging areas around the world in relation to the available food supply. Much information is available regarding foraging strategies, available biomass of littoral fauna and related consumption, thermoregulation and other aspects of this fascinating phenomenon (Klaassen *et al.*, 1990; Zwarts *et al.*, 1990; Kalejta & Hockey, 1991; Wolff, 1991; Piersma *et al.*, 1993). However, most of this work has been done on isolated sites, often in specially protected areas with extremely high wader densities without any human interference.

Intertidal areas are important for coastal human communities as a source of proteins and minerals (Wynter, 1990). Moreover, the coastal areas of Mozambique have come under increasing pressure, as people moved from the inland to the coast during the civil war (1978-1992).

This paper focuses on consumption of littoral fauna by shorebirds and humans in Maputo Bay where bird densities are relatively low and where birds are obliged to survive in the presence of people collecting crabs, clams and other invertebrates. This situation is probably characteristic for African coastal areas in general. We analyse the joint exploitation of the intertidal area by birds and humans, estimate total consumption by both birds and humans and quantify the human influence of disturbance on bird foraging behaviour.

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Study area

Inhaca Island is located 35 km east of Maputo, southern Mozambique, at 26° 00′S and 33° 00′E (Fig. 1). Its general ecology is described in Macnae and Kalk (1962, 1969). The island is surrounded by the Indian Ocean in the east and by Maputo Bay in the west. The intertidal area of Maputo Bay is estimated at 234 km², equal to 22% of the total area, of which 52 km² is directly adjacent to Inhaca. Tides are semi-diurnal with a maximum spring tidal range of 3.9 m.

The mean annual rainfall is 800 mm (30 yearly data from broken series between 1955 and 1993, Inhaca Marine Biological Station), the mean monthly maximum temperature during the study period was 28.2°C (maximum in February: 30.3°C), whilst the mean monthly minimum temperature was 20.5°C (minimum in June: 16.3°C).

A large bay is situated in the southern part of the island, the Saco da Inhaca. The study area, with a total area of 66 ha (referred to hereafter as the Saco) is located in the northern part of this bay and is almost totally exposed at low tides: 94% of the flats emerge during spring tides and 78% during neap tides. A subtropical mangrove forest characterized by high species diversity (Macnae & Kalk, 1962; Guerreiro *et al.*, in press) fringes the area with large extensions in the northern and southern part of the Saco. A channel in the eastern part provides access to the open sea.

Six habitat types can be distinguished in the Saco (Fig. 1), namely: the mangrove fringe with short pencil roots of the white mangrove *Avicennia marina*; sandflats composed of sandy substrate always exposed during low tides; mudflats, a lower lying muddier area exposed only partially at low neap tides; two major sand banks with coarser sand, which are important roosting areas because of their exposure during high neap tides; and a channel fringed by two channel banks which are strewn with rocks and blocks of old coral. The littoral biomass is dominated by fiddler crabs *Uca annulipes* and *U. vocans* and other sand crabs *Macrophthalmus grandidieri*, *M. depressus* and *Dotilla fenestrata*. More details about the substrate characteristics, the littoral fauna and the crab distribution are given by Guerreiro *et al.* (in press).

METHODS

Birds

Data on bird presence and feeding were collected on a monthly basis from January to June 1994, in periods between 2 h before and 2 h after low tide. Each habitat type was mapped and divided into different observation zones (26 in total), separated by natural boundaries or other identifiable marks such as substrate differences, canals, presence of death shells, fishing poles and small paths. These zones could be easily observed from a distance. The number and distribution of the different bird species (nomenclature in Table 1 follows Urban *et al.*, 1986) was determined with the aid of 10 × 40 binoculars or a 25 × telescope. Mangroves served as cover and the small paths, frequently used by the local population, were used in order to minimize disturbance by the observer. Data were collected with reference to date, time, tidal depth and the number of birds per species per zone. The presence of people was recorded, indicating their activity: walking, fishing (using nets, lines or spears) or collecting invertebrates. These scans were done at least twice a month except for March when only one scan was made.

Intake by the birds was estimated using the formula described in Kersten and Piersma (1987) which relates bird body mass (M, in kg) to consumption (organic matter expressed as Ash-Free Dry Weight, AFDW). Basal Metabolic Rate (BMR in kJ/day) is estimated at $437M^{0.729}$. The energy requirements of waders in the tropics is assumed to equal 1.8 BMR. To correct for differences between ingestion and actual assimilation, assimilation efficiency is estimated at 80% (Klaassen *et al.*, 1990; Velasquez *et al.*, 1991). One gram of AFDW equals 21.1 kJ.

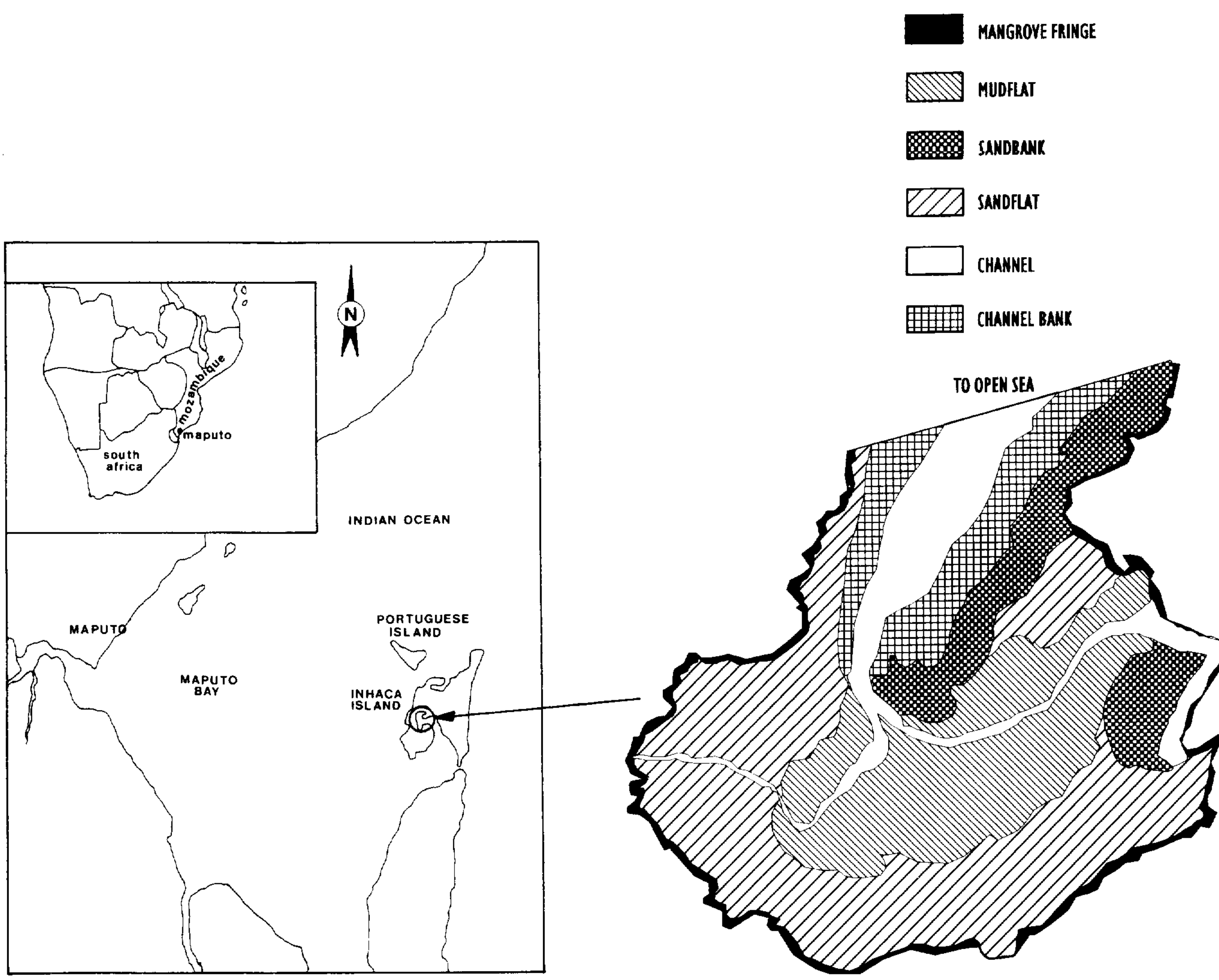

Fig. 1. Localization of the study area and main habitat types in the Saco.

Table 1. Average monthly number of birds (avg) and standard deviation (std) in the Saco between January and June 1994. Average weights (g) are based on Urban *et al.* (1986) and Maclean (1993). The assumed fraction of littoral fauna consumption (C) is given in the last column

			Weight (g)	January avg	January std	February avg	February std	March avg	April avg	April std	May avg	May std	June avg	June std	C
Bird															
	Grey heron	*Ardea cinerea*	1433	2.4	2.1	2	0	1	2.5	0.5	1	0	0.5	0.5	0.5
	Little egret	*Egretta garzetta*	447	7.8	2.9	2	1	10	10	3	7.7	1.7	6.5	0.5	0.5
	Cattle egret	*Bubulcus ibis*	345	0	0	0	0	0	16	2	0	0	0	0	0.5
	Green heron	*Butorides striatus*	214	8	3	6	1	4	7	2	6.3	2.6	10	0	1
	Hamerkop	*Scopus umbretta*	423	0	0	0	0	0	0	0	0.3	0.5	0	0	1
	Sacred ibis	*Threskiornis aethiopica*	1530	0	0	0	0	2	1.5	1.5	2.7	0.9	6.5	2.5	1
	Hadada ibis	*Bostrychia hagedash*	1262	0	0	0	0	0	1.5	1.5	0	0	0	0	1
	Greater flamingo	*Phoenicopterus ruber*	3052	8.5	6.3	0	0	0	16.5	14.5	10.3	14.6	23.5	8.5	1
	Lesser flamingo	*Phoeniconaias minor*	1760	0	0	0	0	0	0	0	0	0	2	2	0
	Black kite	*Milvus migrans*	642	0.5	0.9	1.5	1.5	2	0	0	0	0	0	0	0
	Blackbreasted snake eagle	*Circaetus pectoralis*	1962	0	0	0	0	0	0.5	0.5	0	0	0	0	0
	Osprey	*Pandion haliaetus*	1528	0.6	0.5	1	0	0	0	0	0	0	0	0	0
	Ringed plover	*Charadrius hiaticula tundrae*	63	9.8	6.1	16	4	19	0.5	0.5	0	0	0	0	1
	White-fronted plover	*Charadrius marginatus*	48	1	1.1	0.5	0.5	0	2.5	2.5	0	0	2.5	1.5	1
	Grey plover	*Pluvialis squatarola*	224	43	5.2	31	12	50	53.5	7.5	2	0.8	0	0	1
	Turnstone	*Arenaria interpres interpres*	133	3.8	4.8	1.5	1.5	10	17	8	0	0	0	0	1
	Terek sandpiper	*Xenus cinerus*	84	14.1	22.5	3.5	3.5	31	12	12	0	0	0	0	1
	Common sandpiper	*Actitis hypoleucos*	51	4.5	4.3	3.5	1.5	1	38.5	2.5	0	0	0	0	1
	Common greenshank	*Tringa nebularia*	213	18.3	6.1	20.5	9.5	25	0	0	1.3	0.5	2	0	1
	Curlew sandpiper	*Calidris ferruginea*	77	59.9	22.6	94.5	18.5	139	35.5	31.5	5	0.8	0	0	1
	Sanderling	*Calidris alba*	145	0.1	0.3	0	0	0	0	0	0	0	0	0	1
	Bar-tailed godwit	*Limosa lapponica*	345	0	0	0	0	0	0	0	0	0	0.5	0.5	1
	Whimbrel	*Numenius phaeopus phaeopus*	395	66.5	10.2	101.5	10.5	66	10.5	0.5	11.3	0.5	15	2	1
	Water dikkop	*Burhinus vermiculatus*	307	0	0	0	0	0	0	0	0	0	0.5	0.5	1
	Greyheaded gull	*Larus cirrocephalus poiocephalus*	278	0.4	0.5	1.5	1.5	0	0	0	0	0	0	0	0.5
	Caspian tern	*Sterna caspia*	635	0.4	1	0	0	0	0.5	0.5	0	0	0	0	0
	Swift tern	*Sterna bergii*	343	0	0	0	0	0	1.5	1.5	0	0	0	0	0
	Lesser crested tern	*Sterna bengalensis*	204	0.3	0.7	0.5	0.5	0	0	0	0	0	0	0	0
	Little tern	*Sterna albifrons*	53	0	0	0	0	0	0.5	0.5	0	0	0	0	0
	Pied kingfisher	*Ceryle rudis*	84	1.5	1.3	1	1	0	3	2	1.3	1.2	3.5	1.5	0
	Malachite kingfisher	*Corythornis cristata*	15	0	0	0	0	0	0	0	1.7	0.9	1.5	1.5	0
	House crow	*Corvus splendens*	307	2.9	3.4	0	0	0	6.5	6.5	0	0	0	0	1
	Pied crow	*Corvus albus*	568	0	0	0	0	0	0	0	0	0	1.5	1.5	1
Charadrii				220.9	62	272.5	52.5	341	170	60	19.7	0.5	20.5	0.5	
Ardeidae				18.1	4.9	10	0	15	35.5	2.5	15.3	4	17	0	
Total birds				254	65.7	288	57	360	237.5	49.5	51	18.5	76	10	
Humans															
	Walking			6.6	5.4	9	3	30	21.5	19.5	2.7	1.3	27.5	3.5	
	Fishing			3.8	4.5	0	0	2	7.5	0.5	1.7	2.4	6	2	
	Collecting			12.4	9.2	4.5	1.5	13	0	0	12.3	0.5	0	0	
Total humans				22.8	9.7	13.5	4.5	45	29	19	16.7	3.9	33.5	5.5	
Number of samples (days)				8		2		1	2		3		2		

Human exploitation of littoral fauna

Exploitation of littoral organisms by the local population was measured at the end of the tidal exposure period. Forty-four individuals were interviewed regarding locality and duration of collecting and group size. They were asked to estimate how long they had spent searching for animals and for how long they would continue doing so. The collected animals were counted and identified, carapace length of individual crabs was measured and the total wet weight per species was measured using a portable electronic balance. Total biomass taken was calculated from the measured weights but a correction factor (1 + time continuing searching/total time searched) was applied to people who would continue searching after the questionnaire, to improve the estimate of daily total biomass consumption. Wet weight was transformed to ash-free dry weight using the biometric formulae (power functions, Croes & De Boer, unpublished) relating carapace width to WW, and AFDW for *Dotilla fenestrata*, *Uca* spp. and *Macrophthalmus* spp. For the other crustacea the average of the different formulae was used, which yielded a WW-AFDW conversion constant of 0.148 ($n = 294$), similar to the 0.15 calculated by Wolff *et al.* (1993) (see also Lappalainen & Kangas, 1975), which was used for the other invertebrates.

Disturbance

Disturbance (Cayford, 1993) between the local population and birds was determined using the scan data (as described above) to test the null hypothesis that human presence does not negatively influence bird numbers and distribution. Due to low bird abundance in winter, only data from the summer period are used for this analysis.

The minimal approach distance (MAD, Pierce *et al.*, 1993) was measured for each species while directly approaching birds. At every 10 m the behaviour of a randomly chosen bird during 1 min was registered on a portable micro-cassette recorder, distinguishing between foraging and non-foraging. After each registration, the observer approached the bird by 10 m for another observation, until the bird flew away, after which the MAD was measured. Foraging behaviour observations were only made for whimbrel, curlew sandpiper and common greenshank.

Statistical tests were used as described in Pollard (1977), Sokal and Rohlf (1981) and Wonnacott and Wonnacott (1990).

RESULTS

Bird behaviour and food consumption

The bird species observed in the Saco and their average number per month are given in Table 1. Waders and especially whimbrel, grey plover and curlew sandpiper were the most common in the area. During the study period migratory birds left the area and numbers of shorebirds declined rapidly in the first two weeks of April. The observations from January to April are referred to as the summer period, after April as the winter period. Significant differences in abundance per day between summer and winter period, were detected for whimbrel, grey plover, curlew sandpiper, ringed plover and osprey (AOV, $n = 18$, all $p < 0.005$) with higher abundance scores in summer. Sacred ibis and malachite kingfisher increased significantly in the winter period (AOV, $n = 18$, $p < 0.001$). Most other species showed expected fluctuations (wader species declining in winter) but these were not significant, probably due to the small number of scans and number of birds present. No difference could be detected between abundance during low spring and neap tides.

Some species were not foraging on littoral fauna, for example piscivorous terns, kingfishers and birds of prey. Species such as little egrets, grey heron and grey-headed gull were estimated to feed 50% on benthic fauna. Sacred ibis and green heron fed entirely on benthos. The proportion of littoral fauna to total diet composition was estimated from observations (Table 1). Although a subjective estimation, total ash-free dry weight consumption was insensitive to changes (within 10% of the

Table 2. Total AFDW consumption (g/day) in summer and winter periods and the % consumption by individual species

	Summer					Winter		
	Jan	Feb	Mar	Apr	avg	May	June	avg
Species	%	%	%	%	%	%	%	%
Little egret	2	1	3	3	2	5	2	4
Green heron	3	2	1	2	2	5	4	5
Sacred ibis	0	0	3	2	1	9	11	10
Greater flamingo	22	0	0	42	16	61	71	66
Grey plover	15	11	17	18	16	2	0	1
Common greenshank	6	7	8	0	5	1	1	1
Curlew sandpiper	9	16	22	6	13	2	0	1
Whimbrel	35	57	34	5	33	14	9	11
Other waders	5	4	10	11	8	0	1	1
Others non-waders	3	2	2	11	4	1	1	1
Total consumption g AFDW/day	4635	4326	4638	4643	4561	2003	3945	2974

estimated total consumption) if the fraction of daily consumption of benthic fauna by birds, excluding waders and greater flamingos, was changed to 0 or 100%. Total consumptions in AFDW for the most important species and for other categories are given in Table 2. It is clear that whimbrels and greater flamingos were the most important species with regard to food consumption. Mean total consumption by birds was 69 g AFDW/ha/day in the summer period and 45 g AFDW/ha/day in the winter period. Total annual consumption was estimated at 2.08 g AFDW/m^2.

Human exploitation

The number of people and their activity per month is given in Table 1. No significant changes in number or activity were found during the study period.

Twelve species of Crustacea and five Mollusca were collected in the Saco by the local population (Table 3). The blue swimming crab *Portunus pelagica* was the most important animal collected in terms of weight, whilst the moon shell *Polynices mamilla* was the most collected species. Carapace width, measured on a subsample of the animals collected (Table 3), indicated that people preferred larger specimens: the average carapace width of collected army crabs *Dotilla fenestrata*, long-eyed crabs *Macrophthalmus grandidieri*, the two fiddler crabs *Uca vocans* and *Uca annulipes*, and *Thalamita danae* was always higher than the average carapace width of the species (all significant at $p<0.02$, Mann-Whitney *U*-test) (Croes & De Boer, unpublished).

The total consumption of invertebrates per person is estimated at 119.4 g AFDW. Extrapolating this figure, consumption by the local population can be estimated at 13.5 g AFDW/ha/day in summer and 11.1 g AFDW/ha/day in winter, totalling 0.45 g AFDW/m^2/year.

Disturbance experiment

The distance at which birds flew up when approached (MAD), was different among waders (equal variances: AOV, $F_{3,32}=15.5$, $p<0.0001$). MAD of whimbrel was significantly greater than for grey plover, common greenshank or curlew sandpiper (Fig. 2) (minimum significant difference at $p=0.05$). Grey plover MAD was higher than for curlew sandpiper. MAD was smaller for whimbrels in summer compared to winter ($F_{1,12}=12.3$, $p<0.005$), probably due to a difference in age of the birds; younger, first-year birds remain in the Saco during winter, while adults migrate (own observations). Younger birds are more wary and MADs are higher.

The percentage of time spent foraging declined for all three species as observers approached (Fig. 3). Whimbrel were most sensitive, showing a larger MAD and a longer decrease in foraging activity than the other species. There is a positive association between average MAD and the distance at which birds' foraging behaviour started to decline when approached (compare Figs 2 and 3).

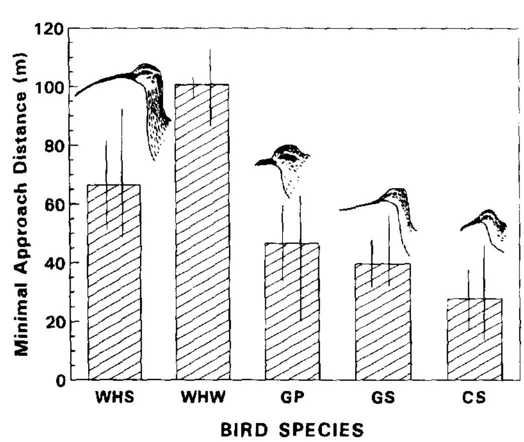

Fig. 2. Minimal Approach Distances, standard deviation (small error bar) and minimum-maximum values (large error bar) for waders: whimbrel in summer (WHS, $n=11$) and winter (WHW, $n=3$), grey plover (GP, $n=9$), common greenshank (GS, $n=7$) and curlew sandpiper (CS, $n=9$).

Bird response to human presence

Observing birds and humans per zone during summer, showed that 78% of total whimbrels foraged in zones without humans present compared to 60% when people were present ($F_{1,206}=11.25$, $p<0.001$). However, contrary to expectation, zones without humans had an average of 1.9 whimbrels compared to 2.5 for zones with humans present, though the standard deviations are high (both 4.6, $n=306$ and 94) and differences are therefore not significant. This higher whimbrel density in zones where humans where present could be caused by the fact that they both concentrate in areas with higher littoral biomass. Analysing just the zones with human presence, whimbrel numbers were higher when only a few people were present in the same observation zone compared to a high human presence ($r_s=-0{,}314$, $n=94$, $p<0.01$). Other species showed similar reactions but these could not be confirmed statistically.

In the summer period, 13 days' data were used to investigate negative correlation between people and bird numbers. The first indication of this is given by the fact that the highest bird numbers were recorded on 20 January, the day with the lowest number of people in the Saco. On the other hand, the highest human presence was recorded on 28 April coinciding with the lowest total bird numbers of one (but also with the period of

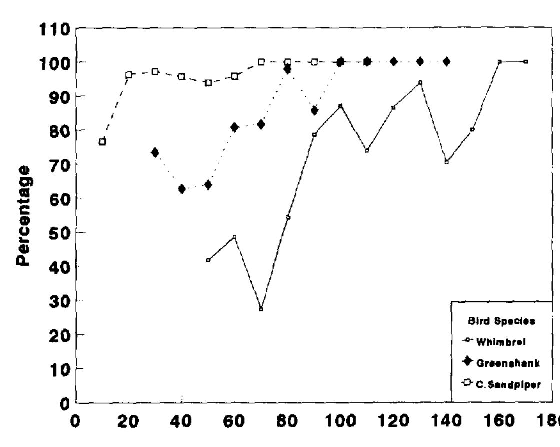

Fig. 3. The percentage of time foraging by whimbrel, common greenshank and curlew sandpiper in relation to human approach distance

Table 3. Species composition of animals collected by the local population based on 32 samples which were collected by 44 people. Total specimens collected (N1), total fresh weight per species, fresh weight-ash free dry weight conversion constant, total AFDW per species, species presence in Saco, and average total biomass taken (g AFDW/person) in the Saco. Total biomass values are corrected for searching time (see Methods). Carapace width and standard deviation are given of a subsample (size: N2)

		N1	Fresh weight (g)	Conversion constant	AFDW (g)	Saco	AFDW/person (g)	N2	Width (mm)	SD
Crustacea										
	Dotilla fenestrata	209	235.240	0.022	5.175	1	0.118	3	8.3	0.47
	Macrophthalmus grandidieri	45	1423.980	0.093	132.430	1	3.010	36	23.5	4.56
	Ocypode ceratophthalmus	6	81.060	0.148	11.997	0	0.000	7	17.1	11.42
	Ocypode kuhli	43	1734.700	0.148	256.736	0	0.000	14	25.3	10.94
	Uca annulipes	197	707.819	0.130	92.016	1	2.091	4	20.3	2.86
	Uca vocans	17	293.747	0.178	52.287	1	1.188	9	22.6	3.86
	Portunus pelagica	159	14,645.281	0.148	2167.502	1	49.261	111	83.4	23.44
	Scylla serrata	105	8770.263	0.148	1297.999	0.5	14.750	69	61.3	114.52
	Thalamita danae	120	4364.592	0.148	645.960	1	14.681	74	38.8	11.35
	Eurycarcinus natalensis	8	76.440	0.148	11.313	0	0.000	1	3.0	0.00
	Phymodius monticulosus	1	8.889	0.148	1.316	0	0.000	0		
	Calappa hepatica	25	770.708	0.148	114.065	1	2.592	25	55.4	8.22
Mollusca										
	Polynices mamilla	1400	9214.090	0.150	1382.114	1	31.412			
	Modiolus philippinarum	1	144.356	0.150	21.653	0	0.000			
	Cardium sp.	1	78.000	0.150	11.700	1	0.266			
	Tellina sp.	1	61.200	0.150	9.180	0	0.000			
	Volema paradissica	7	152.504	0.150	22.876	0	0.000			
Total			2345	42762.869	6236.317		119.369			

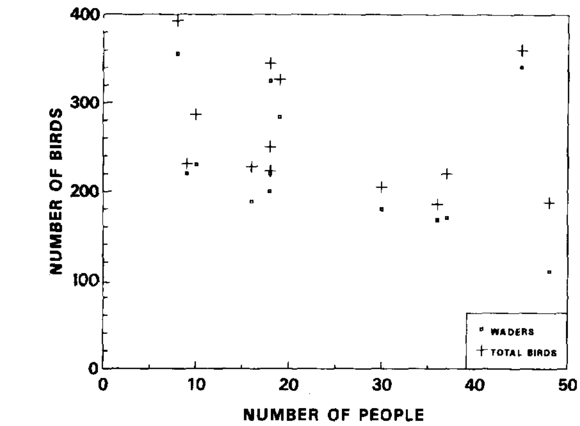

Fig. 4. The relation between the total number of people and birds counted per day ($n = 13$) in the summer period.

returning migrating birds). Negative correlations were found between the number of people and bird abundance, but only that for total waders was significant ($r_s = -0{,}492$, $n = 13$, $p < 0.05$, Fig. 4).

DISCUSSION

Palearctic migrant wader density during the summer period varied between 1.9 and 6.1 individuals/ha, which is low compared to other sites in tropical Africa (Wolff, 1991; Velasquez *et al.*, 1991). Outside the palearctic migration period, density decreased to 0.3 individuals/ha.

The human consumption of littoral fauna (0.45 g AFDW/m^2) is probably important at a household level, mainly as a supplementary food source, although some invertebrates are marketed (Wynter, 1990).

The annual littoral consumption by birds (2.08 g AFDW/m^2) is considerably greater but is still one of the lowest values recorded for wader consumption in Africa (Velasquez *et al.*, 1991; Wolff, 1991; Kalejta, 1992), highlighting the atypical character of other study areas which concentrate on protected areas known for high bird densities.

Competition between humans and birds can be distinguished as interference competition or exploitation competition (Begon *et al.*, 1990). The latter is probably small, because prey species of humans are in general larger and do not include polychaetes and small gastropods which are taken by the majority of the shorebirds. However, competition could occur with the smaller crustacea such as *Dotilla fenestrata*, *Uca* spp. and *Macrophthalmus* spp. Our observations confirm the joint exploitation of these species but more information is necessary.

Interference competition was studied by measuring MAD and foraging behaviour changes. Although based on relatively few data, body weight was strongly positively correlated ($R^2 = 98\%$) with average MAD for different species ($t = 9{,}04$, $p < 0.012$, Fig. 5(a)). The observed trend of heavier birds with larger MADs is consistent with the two hypotheses described by Holmes *et al.* (1993) (see also Ydenberg & Dill, 1986; Roberts & Evans, 1993; Smit & Visser, 1993). Smaller, inconspicuous birds have shorter MADs because of less risk of being detected or because of relatively higher energy costs for flying away. The negative correlation coefficients found between different birds and human presence in zones can likewise be related to species weight (Fig. 5(b)) with a significant linear relationship ($n = 9$, $t = -2.61$, $p < 0.05$, $R^2 = 0.49$).

The influence on whimbrel foraging behaviour by human presence starts at *c.* 90 m (Fig. 2). At the MAD (66.5 m), half of all whimbrels had flown and foraging declined to a minimum of around 30% of the total time (Fig. 3). Foraging time reduction is estimated at 36% (86 minus 50) between 90 and 66.5 m to human presence and 56% (86 minus 30) for birds closer than the MAD. Assuming a regular distribution of birds and humans within habitats, with densities per habitat equal to the observed values (de Boer, unpublished data), it is possible to estimate the average costs in terms of foraging reduction by human presence (see also Smit & Visser, 1993): for whimbrels a total reduction in foraging time of 34%, from 86% to 52%. This calculation can also be done for common greenshank and curlew sandpiper and yields foraging time reductions of respectively 8% and

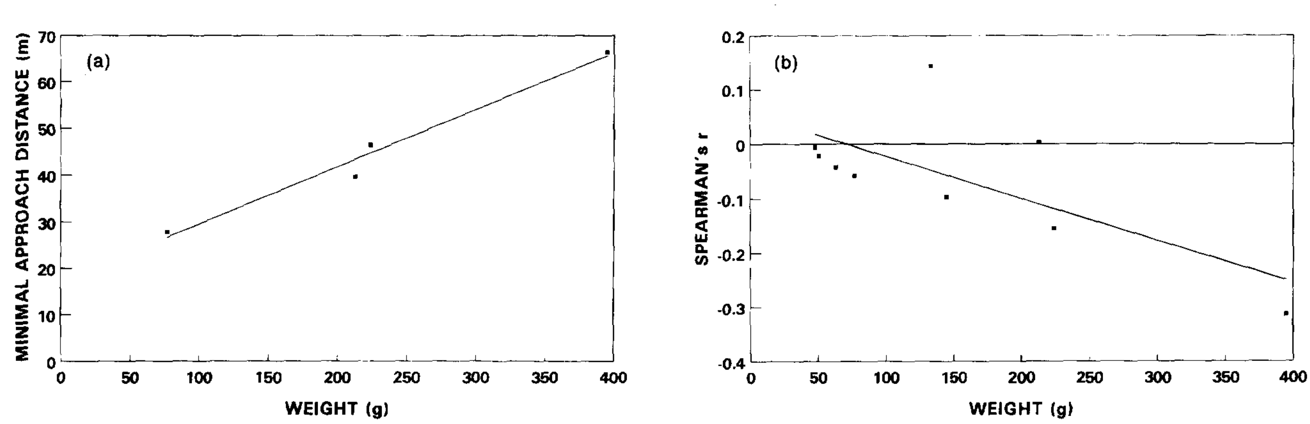

Fig. 5. (a) Linear relation between body weight and MAD of four wader species (whimbrel, grey plover, common greenshank, curlew sandpiper). (b) Spearman's rank correlation coefficient between human presence and bird numbers per zone, for wader species (including terek sandpiper, common sandpiper, white-fronted and ringed plover and turnstone), plotted against bird species weight.

2%. These values are rather crude and conservative estimates which do not take account of foraging efficiency and energetic costs of displacements. Whimbrels, especially territorial individuals, are more regularly distributed than the sandpipers which forage in flocks, and are therefore more affected by human presence than the smaller species.

The influence of human exploitation in the Saco is diverse, with direct and indirect influences. Daily biomass intake is only 18% of the total taken but a secondary consequence of human exploitation is the reduction of bird foraging. This effect is of the same magnitude as daily exploitation and equals a 34% reduction for whimbrel alone, estimated at 511 g AFDW/day in the summer period (Table 2). Although human exploitation of the intertidal fauna probably increases the availability of prey for birds on disturbed substrates (Wynberg & Branch, 1991, 1994; Pierce *et al.*, 1993; Brosnan & Crumrine, 1994; and own observations), no positive associations between birds and people were found.

People walking in the Saco disturb birds who fly to other areas. Human group size is important as well as their activity; larger groups who enter the Saco singing and beating their plastic jerrycans have probably a larger influence than single women searching for crabs. Foraging efficiency is negatively affected, because of reduced foraging time and increasing energetic cost related to disturbance. It is quite possible that disturbance during day time will result in a increase in (1) night time foraging, which can be as important as daytime foraging (Zwarts *et al.*, 1990; Turpie & Hockey, 1993), (2) foraging during high tides (Velasquez & Hockey, 1991) or (3) bird densities in undisturbed areas.

No negative correlation was found between bird numbers in general and humans over the study period, even for whimbrels with a relatively high MAD. This suggests habituation (Smit & Visser, 1993), the birds having adjusted their numbers to a certain level of human disturbance.

This work shows that the joint exploitation of the intertidal areas by both shorebirds and people is complex. The results indicate that the mere presence of people collecting invertebrates decreases the overall total consumption. However, more work is necessary, including night observations and control areas without human interference, to quantify the importance of this effect.

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REFERENCES

Begon, M., Harper, J. L. & Townsend, C. R. (1990). *Ecology, populations and communities, second edition.* Blackwell Scientific Publications, Cambridge.

Brosnan, D. M. & Crumrine, L. L. (1994). Effects of human trampling on marine rocky shore communities. *J. Exp. Mar. Biol. Ecol.*, **177**, 9–92.

Cayford, J. (1993). Wader disturbance: a theoretical overview. *Wader Study Group Bull.* **68**, 3–5.

Guerreiro, J., Freitas, S., Paula, J., Macia Jr, A. & Pereira, P. (in press). Macrobenthic communities of mangroves in an eastern African ecosystem (Inhaca Island, Mozambique). *J. Mar. Ecol.*

Holmes, T. L., Knight, R. L., Stegall, L. & Graig, G. R. (1993). Responses of wintering grassland raptors to human disturbance. *Wildl. Soc. Bull.*, **21**, 461–8.

Kalejta, B. (1992). Time budget and predatory impact of waders at the Berg River Estuary, South Africa. *Ardea*, **80**, 327–42.

Kalejta, B. & Hockey, P. A. R. (1991). Distribution, abundance and productivity of benthic invertebrates at the Berg River estuary, South Africa. *Estuar., Coastal & Shelf Sci.*, **33**, 175–91.

Kersten, M. & Piersma, T. (1987). High levels of energetic expenditure in shorebirds; metabolic adaptations to an energetically way of life. *Ardea*, **75**, 175–87.

Klaassen, M., Kersten, M. & Ens, B. J. (1990). Energetic requirements for maintenance and premigratory body mass gain of waders wintering in Africa. *Ardea*, **78**, 209–20.

Lappalainen, A. & Kangas, P. (1975). Littoral benthos of the Northern Baltic Sea II, interrelationships of wet, dry and ash-free dry weights of macrofauna in the Tvärminne area. *Int. Rev. Ges. Hydrobiol.*, **60**, 297–312.

Maclean, G. L. (1993). *Roberts' birds of Southern Africa*, 6th edn. Trustees of the John Voelcker Bird Book Fund, Cape Town.

Macnae, W. & Kalk, M. (1962). The ecology of the mangrove swamps at Inhaca Island, Moçambique. *J. Ecol.*, **50**, 19–34.

Macnae, W. & Kalk, M. (1969). *A natural history of Inhaca Island, Mozambique.* Witwatersrand University Press, Johannesburg.

Pierce, G. J., Spray, C. J. & Stuart, E. (1993). The effect of fishing on the distribution and behaviour of waterbirds in the Kukut area of Lake Songkla, Southern Thailand. *Biol. Conserv.*, **66**, 23–34.

Piersma, T., de Goeij, P. & Tulp, I. (1993). An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. *Neth. J. Sea Res.*, **31**, 503–12.

Pollard, J. H. (1977). *A handbook of numerical and statistical techniques, with examples mainly from the life sciences.* Cambridge University Press, Cambridge.

Roberts, G. & Evans, P. R. (1993). Responses of foraging sanderlings to human approaches. *Behaviour*, **126**, 29–43.

Smit, C. J. & Visser, G. J. M. (1993). Effects of disturbance on shorebirds: a summary of existing knowledge from the Dutch Wadden Sea and Delta area. *Wader Study Group Bull.* **68**, 6–19.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry.* Freeman & Company, New York.

Turpie, J. & Hockey, P. A. R. (1993). Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory grey plovers *Pluvialis squatarola* and whimbrels *Numenius phaeopus* in South Africa. *Ibis*, **135**, 156–65.

Urban, E. K., Fry, C. & Keith, S. (1986). *The birds of Africa.* Academic Press, London.

Velasquez, C. R. & Hockey, P. A. R. (1991). The importance of supratidal foraging habitats for waders of a south temperate estuary. *Ardea*, **80**, 243–53.

Velasquez, C. R., Kalejta, B. & Hockey, P. A. R. (1991). Seasonal abundance, habitat selection and energy consumption

of waterbirds at the Berg River Estuary, South Africa. *Ostrich*, **62**, 109–23.
Wolff, W. J. (1991). The interaction of benthic macrofauna and birds in tidal flat estuaries: a comparison of banc D'Arguin, Mauritania and some estuaries in the Netherlands. In *Proc. ECSA, Symp. Int. Symp. Ser, 19th*, ed. M. Elliot & J. P. Ducrotoy, pp. 299–306.
Wolff, W. J., Duiven, A. G., Duiven, P., Esselink, P., Gueye, A., Meijboom, A., Moerland, G. & Zegers, J. (1993). Biomass of macrobenthic tidal flat fauna of the Banc D'Arguin, Mauritania. *Hydrobiologia*, **258**, 151–63.
Wonnacott, T. H. & Wonnacott, R. J. (1990). *Introductory statistics*. John Wiley, New York.
Wynberg, R. P. & Branch, G. M. (1991). An assessment of bait-collecting for *Callianassa kraussi* stebbing in Langebaan Lagoon, Western Cape, and of associated avian predation. *S. Afr. J. Mar. Sci.*, **11**, 141–52.
Wynberg, R. P. & Branch, G. M. (1994). Disturbance associated with bait-collection for sandprawns (*Callianassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the biota of intertidal sandflats. *J. Mar. Res.*, **52**, 523–58.
Wynter, P. (1990). Property, women fishers and struggles for women's rights in Mozambique. *Sage*, **7**, 33–7.
Ydenberg, R. C. & Dill, L. M. (1986). The economics of fleeing from predators. *Adv. Stud. Behav.*, **16**, 229–49.
Zwarts, L., Blomert, A.-M., Ens, B. J., Hupkes, R. & van Spanje, T. M. (1990). Why do waders reach high feeding densities on the intertidal flats of the Banc D'Arguin, Mauritania? *Ardea*, **78**, 39–52.