

Picking out the plum jobs: feeding ecology of curlews *Numenius arquata* in a Baltic Sea wind flat

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ABSTRACT: On the German Baltic Sea coast most migrating shorebirds stage in wind flats that are characterized by irregular wind-induced fluctuations of water level. As it had been suggested that large shorebirds cannot fulfil their energetic requirements in wind flats due to the lack of prey organisms large enough to be profitable, we investigated the feeding ecology of curlews *Numenius arquata* at Hiddensee (July to November 1995). Most prey taken were the largest ragworms *Nereis diversicolor* present in the sediment (>85 segments), while 2 bivalves contributed 4.2% (*Cerastoderma lamarcki*) and 0.8% (*Mya arenaria*), respectively. Most curlews foraged in shallow water where we observed the maximum intake rate (3.5 prey min⁻¹) compared to exposed flats (2.0 prey min⁻¹). This is thought to be the result of highest surface activity and therefore best detectability and accessibility of ragworms in shallow water. Prolonged periods of low foraging activity in late morning and around noon as well as the aggregation at night roosts suggest that curlews do not have problems maintaining their energy budget in the study area. This is explained by their ability to find the few most profitable prey organisms available, even though these occur at low density.

KEY WORDS: Shorebirds · *Numenius arquata* · Feeding ecology · Wind flats · Baltic Sea · *Nereis diversicolor* · *Mya arenaria* · *Cerastoderma lamarcki*

INTRODUCTION

For many coastal shorebirds living along the East Atlantic Flyway in the non-breeding season, the Wadden Sea is an important staging area (Melfo et al. 1994). Extensive mudflats hold a large spectrum of macrobenthic invertebrates which serve as an excellent food supply for shorebirds and other coastal birds (Beukema et al. 1993, Zwarts & Wanink 1993). However, the foraging behaviour of birds is strongly constrained by the tides which make food resources inaccessible at high tide and determine activity and, therefore, availability of the macrozoobenthos (Vader 1964, Esselink & Zwarts 1989). In contrast, coastal habitats at the southern Baltic Sea coast are much less influenced by tides, as fluctuations of water level are mainly induced by wind direction and wind force as

well as atmospheric pressure (Brosin 1965). As a result, sand flats show an irregular and unpredictable pattern of emersion and inundation. Due to the low salinity in the Baltic Sea, these so-called wind flats hold an invertebrate fauna much lower in diversity and in part with reduced body size compared to the North Sea (Remane 1940). Nevertheless, many shorebirds use these wind flats as stopover sites during migration (Kube & Struwe 1994), although feeding conditions are considered to be unfavourable for at least some of the species (Kube 1994). Especially large shorebirds such as curlew *Numenius arquata* and bar-tailed godwit *Limosa lapponica* are supposed to suffer from the small size and low profitability of their preferred prey (the ragworm *Nereis diversicolor*). In theory, this should cause birds to leave the site (godwit) or switch to inland foraging habitats (curlew) in order to match their energetic requirements (Kube 1994).

In contrast to this scenario, a wind flat area off the island of Hiddensee (NE Germany) was observed to hold numbers of curlews throughout the non-breed-

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ing season, which only exceptionally leave the site for other foraging habitats. This implies that the feeding conditions in the Hiddensee wind flat must be sufficient with regard to abundance and availability of prey for curlews. In order to test this hypothesis, data about the macrozoobenthos and the mode of its harvesting by curlews were needed. Besides sampling benthic invertebrates, we studied in which parts of the wind flat area curlews forage (scanning for foraging habitats), which and how many prey they take (examination of pellets/droppings and observation of feeding birds, respectively) and how they allocate their foraging time over the day (scanning for percentages of foraging birds). We aim to show how a shorebird usually living under and potentially adapted to tidal conditions organizes foraging in a non-tidal environment.

STUDY AREA AND METHODS

As part of the national park 'Vorpommersche Boddenlandschaft', the wind flat area 'Bessinsche Schaar' (54° 35' N, 13° 09' E) is situated in the shelter of the islands of Hiddensee and Rügen (Fig. 1). Extending over 180 ha, this sandy study area is smaller than the 2 other wind flats 10 and 15 km further south (Vierendehgrund, 1500 ha and Bock, 1500 ha). Together these 3 sites are the most important wetlands for staging shorebirds on the German Baltic Sea coast (Kube 1994, Kube & Struwe 1994).

Within the studied wind flat, a 9 ha square ranging from 15 cm below to 10 cm above mean sea level was divided into 9 plots of 1 ha each and marked with posts (Fig. 1). More than 5 cm below mean sea level the sediment was covered with aquatic plants (*Ruppia maritima/cirrhusa*, *Potamogeton pectinatus*).

Macrozoobenthos. In July and October 1995, in each plot (in August and September 1995 in only 3 plots) 3 samples of macrozoobenthos, taken with a 10 × 10 cm corer reaching 20 cm deep, were sieved through a 0.5 mm mesh and frozen pending further treatment. Samples were searched for invertebrates under a stereomicroscope. Shell length of bivalves was measured to the nearest 0.5 mm, while ragworms were sorted according to the number of segments. In a sample of the ragworms we also measured relaxed body length for conversion from number of segments (SGM) to worm length (WL):

$$\log WL = 1.899 \log SGM - 1.860$$

$$(R^2 = 0.960, n = 366)$$

For size classes separately, 2201 ragworms were dried for 48 h at 60°C and combusted for 5 h at 550°C. Ash-free dry mass (AFDM) for bivalves was calculated

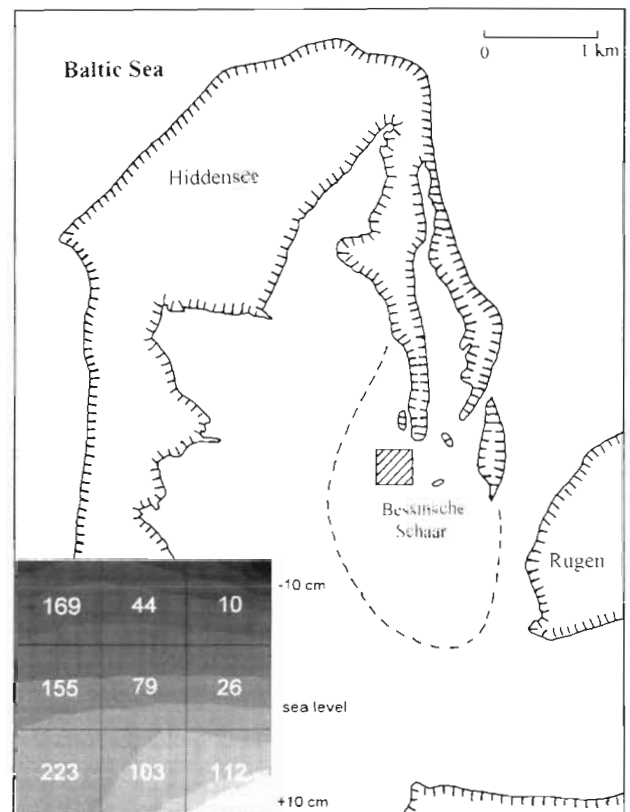


Fig. 1 Map of the study area. (---) Outline of wind flat area; (⊞) study plots. The shaded areas of the inset show the different height of the plots (measuring 100 × 100 m) in relation to mean sea level. In addition, the number of curlews counted during 534 scans from July to October 1995 is given for each plot

according to Zwarts 1991 (adopting formulae of *Cerastoderma edule* for *C. lamarcki*).

Feeding behaviour of curlews. Over the whole wind flat area (including parts outside the plots), we differentiated between 5 habitats: dry and wet sand (which could be distinguished by sediment colour), and shallow water 3 cm deep, up to 9 cm deep (water reaching the intertarsal joint of curlews) and up to 15 cm deep (water reaching belly). For male and female curlews foraging in these habitats we observed intake rates by counting swallowing movements during bouts lasting 1 to 7 min (July to November 1995). As bivalves were much easier to identify than ragworms, swallowing movements without determination of prey were considered to be ragworms.

We scanned all curlews foraging in the wind flat area to determine their distribution with regard to the habitats mentioned above, but for practical reasons lumped the 3 to 9 and 9 to 15 cm habitats for this purpose (354 scans, July to October 1993–95). Unfortunately, the size of exposed parts of the wind flat area in rela-

tion to the water level remained unknown, but all flats were inundated at 22 cm above mean sea level while almost all parts were exposed at about 25 cm below mean sea level. Additional information about choice of foraging habitat was obtained from the number of foraging curlews in the 9 plots counted every 30 min during observation periods of several hours (534 scans on 81 days) from July to October 1995.

As curlews spent most time in inundated habitats (see 'Results'), we could collect only 7 droppings and 8 pellets. These were scanned for prey remains such as ragworm jaws and hinges of bivalve shells, but prey lacking hard and indigestible body parts could not be recorded by this method (in this study only referring to *Arenicola marina*, which occurs in the study area at very low densities, see below). In order to convert the size of prey remains to body size, jaw length (JL, in mm; Zwarts & Esselink 1989) and hinge height (HH, in mm; Dekinga & Piersma 1993) were measured in a number of ragworms and bivalves, respectively. The resulting relationships

$$SL = 12.581 HH + 1.257 \quad (R^2 = 0.880, n = 95)$$

for *Mya arenaria*,

$$SL = 7.224 HH + 2.461 \quad (R^2 = 0.878, n = 88)$$

for *Cerastoderma lamarcki* and

$$SGM = 31.905 \ln JL + 86.018 \quad (R^2 = 0.977, n = 79)$$

for *Nereis diversicolor*

allowed us to calculate worm length (SGM, in number of segments) and shell length (SL, in mm), respectively. Ragworm jaws larger than those found in the longest worms examined from benthos samples were treated as a '>85 segments' size class.

A measure of the daily pattern of foraging activity was gained by counting numbers of foraging and non-foraging curlews every 15 or 30 min during several observation periods from 1993 to 1995 (scan sampling; Altmann 1974). For every hour of the day the average percentage of birds foraging (b_i) was calculated. Total foraging time (TFT) of an average curlew during daylight (45 min before sunrise until 45 min after sunset) was estimated as

$$TFT = \sum (a_i \times b_i)$$

with the number of minutes in 1 h (a_i). At dawn and dusk, a_i is actually less than 60 min because of darkness in part of the hour.

RESULTS

Occurrence of curlews at Hiddensee

Except during the breeding season (May to mid June), when only a few birds were present, curlews

stayed throughout the year at the wind flats around the island of Hiddensee. In 1994 and 1995, a flock of 60 to 80 birds was observed until late April and from mid July onwards in the 180 ha study area (Fig. 2). In July and August most birds present conducted their post-nuptial moult. Fluctuation in numbers occurred due to staging migrants and due to individuals foraging elsewhere and using the site as a night roost only occasionally. During the severe winter 1995/96 with ice-covered wind flats, curlews remained for about 6 wk into the cold spell (until early February) before leaving the region. The subsequent numbers during spring and summer 1996 were lower than those observed in the preceding years (Fig. 2).

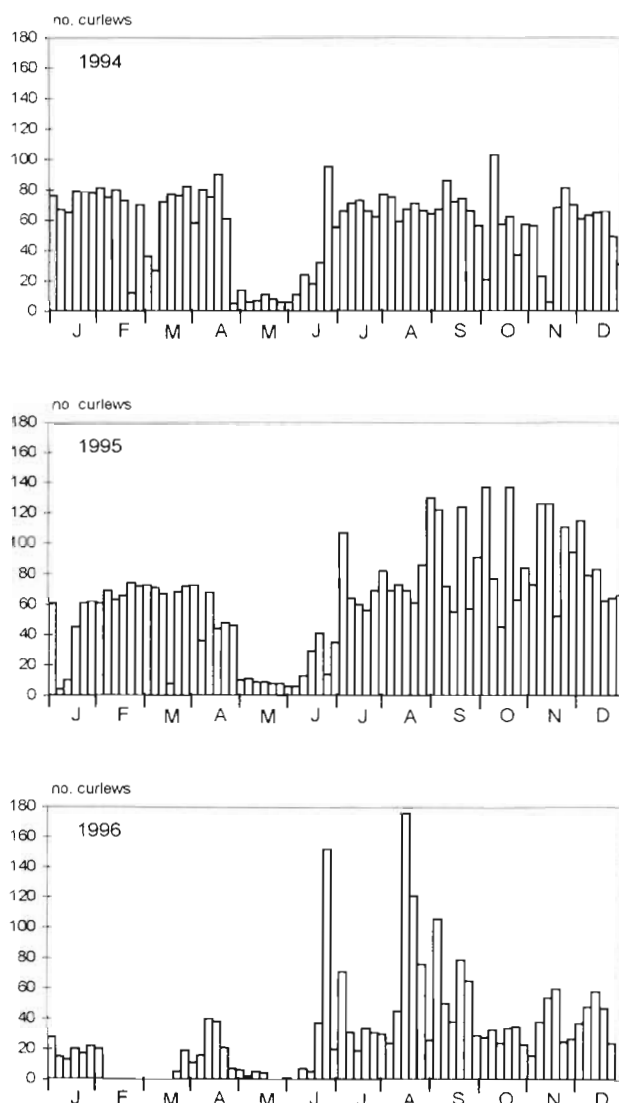


Fig. 2. *Numenius arquata*. Maximum counts of curlews per 5 d period at the wind flat area 'Bessinsche Schaar' (Hiddensee) in 1994, 1995 and 1996

Table 1. Abundance and biomass of potential prey species of curlew in a wind flat area at Hiddensee (July to October 1995). The density of *Arenicola marina* was estimated according to the number of casts visible in 10 × 10 m squares

	July			August			September			October		
	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
1995 abundance (ind. m⁻²)												
<i>Macoma balthica</i>	26	65	75	9	67	112	10	40	70	26	62	94
<i>Mya arenaria</i>	26	19	40	9	0	0	10	30	48	26	50	81
<i>Cerastoderma lamarcki</i>	26	4	20	9	0	0	10	0	0	26	8	27
<i>Nereis diversicolor</i>	26	2812	493	9	4267	1001	10	5710	2523	26	7854	1336
<i>Arenicola marina</i>							45	0.03	0.04			
1995 biomass (mg AFDM m⁻²)												
<i>Macoma balthica</i>	26	151	565	9	128	266	10	217	557	26	339	808
<i>Mya arenaria</i>	26	612	200	9	0	0	10	85	205	26	672	231
<i>Cerastoderma lamarcki</i>	26	67	341	9	0	0	10	0	0	26	8	37
<i>Nereis diversicolor</i>	26	6536	1840	9	6621	2051	10	11494	3909	26	10511	2736

Macrobenthic invertebrates in the wind flats

In addition to mudsnails *Hydrobia ventrosa* and *H. ulvae* (4600 to 38978 ind. m⁻²) and amphipods *Corophium volutator* (775 to 20500 ind. m⁻²), which are unsuitable as a prey for curlews, the most abundant invertebrate species in the wind flats was the burrowing ragworm *Nereis diversicolor* (Table 1). The increasing abundance in summer 1995 was mainly caused by reproduction while the number of worms of the largest size classes (>80 segments) remained constantly below 200 ind. m⁻². Lugworms *Arenicola marina* as a second polychaete species occurred in very low densities (Table 1) and were never found in the samples. The 3 bivalve species *Macoma balthica*, *Mya arenaria* and *Cerastoderma lamarcki* were found in low numbers, too (Table 1), and were mainly represented by small individuals (Fig. 3). Compared to the 1995 situation and following the severe winter 1995/96, ragworms occurred at very low densities in

summer 1996 (from May to October averages between 33 and 200 ind. m⁻² in 1 of the study plots; Dierschke 1997).

Prey of curlews

Both field observations and the contents of pellets and droppings revealed the dominance of ragworms in the diet of curlews at about 95% (ranging from 83.6 to 100% in the 8 pellets, 90.9% in total in the 7 droppings), while bivalves contributed about 5% (Table 2). Most of the 72 bivalve hinges found in pellets and droppings could be attributed to *Cerastoderma lamarcki* (84%) with *Mya arenaria* making up the remaining 16%. No indication of *Macoma balthica* as content of the diet was found. The scarce polychaete *Arenicola marina* could not be recorded due to the lack of indigestible body parts, but most likely was taken occasionally.

According to the size of jaws the smallest ragworms taken were in the size classes of 60 to 85 segments (worm length 37 to 79 mm), but 82% belonged to worms of more than 85 segments (Fig. 4). Thus, prey mainly consisted of the numerically very small fraction of large ragworms available in the sediment. The few *Mya arenaria* consumed also belonged to the largest size classes present in the wind flat area (at most 22 to 25 mm shell length; Fig. 3). Measuring 10 to 20 mm (Fig. 5), nearly all *Cerastoderma lamarcki* eaten by curlews were larger than the only 3 individuals found during sampling of invertebrates (2, 5 and 11 mm). The AFDM of the majority of bivalves taken ranged from 49 to 76 mg in *M. arenaria* and from 20 to 95 mg in *C. lamarcki* (September values according to Zwartz 1991), while almost all *Nereis diversicolor* eaten were above 18 mg AFDM.

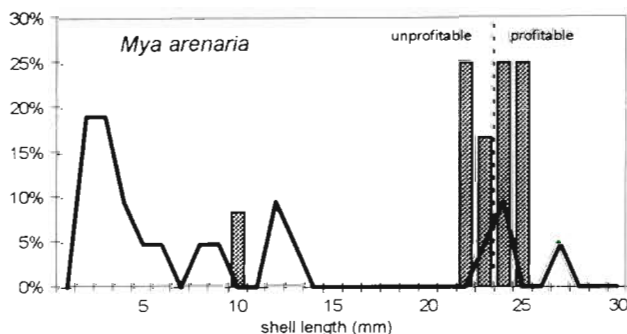


Fig. 3. *Mya arenaria*. Size distribution of clams in the wind flat area (continuous line, n = 21) and in the diet of curlews (columns, n = 12) at Hiddensee. The broken line indicates the lower size limit of profitable prey according to results from the Wadden Sea (Zwartz & Wanink 1984)

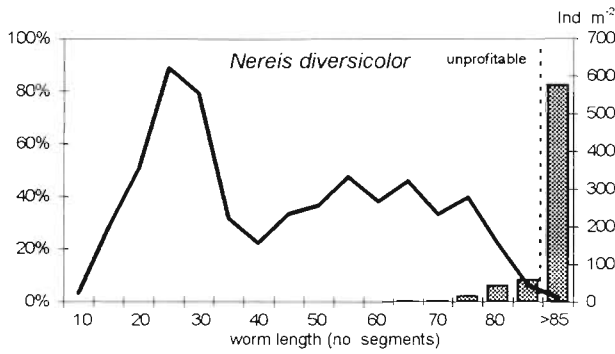


Fig. 4. *Nereis diversicolor*. Size distribution of ragworms in the wind flat area in August 1995 (continuous line, right axis) and in the diet of curlews (columns, left axis, n = 1355) at Hiddensee. The broken line indicates the lower size limit of profitable prey according to results from the Wadden Sea (Zwarts & Esselink 1989)

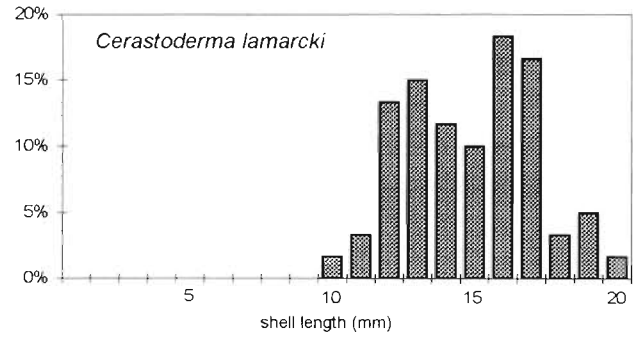


Fig. 5. *Cerastoderma lamarcki*. Size distribution of cockles in the diet of curlews at Hiddensee (n = 60). The only 3 individuals found during sampling measured 2, 5 and 11 mm, respectively

Rate of prey intake

On average, curlews ingested 3.4 prey items min^{-1} . The slight increase from 3.2 min^{-1} in July/August (SD 1.4, n = 111) to 3.6 min^{-1} in September/November (SD 1.8, n = 98) was not significant (2-tailed Mann-Whitney U-test: Z = 1.32, p = 0.186). Furthermore, no difference was found between males (mean 3.3 min^{-1} , SD 1.5, n = 90) and females (mean 3.6 min^{-1} , SD 1.8, n = 92; 2-tailed Mann-Whitney U-test: Z = 0.98, p = 0.326). However, intake rate differed significantly among the 5 habitats distinguished (Table 3; Kruskal-Wallis-test: H = 15.97, p = 0.003). This was the result of the difference between exposed and inundated habitats: intake rates in shallow water were 73% higher (3.5 min^{-1}) than on the exposed wind flats (2.0 min^{-1} ; 2-tailed Mann-Whitney U-test: Z = 3.50, p = 0.00047).

Table 2. Percentages of ragworms *Nereis diversicolor* and bivalves *Mya arenaria* and *Cerastoderma lamarcki* in the diet of curlews on the wind flat at Hiddensee. n: number of prey taken during feeding observations and the number of ragworm jaws and bivalve hinges

	n	Ragworms (%)	Bivalves (%)
Pellet no. 1	185	87.6	12.4
Pellet no. 2	216	91.2	8.8
Pellet no. 3	280	100.0	-
Pellet no. 4	125	100.0	-
Pellet no. 5	392	96.2	3.8
Pellet no. 6	101	99.0	1.0
Pellet no. 7	61	83.6	16.4
Pellet no. 8	23	100.0	-
7 droppings	44	90.9	9.1
All pellets and droppings	1427	95.0	5.0
Feeding observations	1105	94.2	5.8

Choice of foraging habitat

According to 354 scans (with 12232 birds), 84.4% of curlews foraged in shallow water (8.8% in water up to 3 cm deep, 75.6% in water 3 to 15 cm deep), even when most of the flats were exposed (Fig. 6). During the scans, only 0.7% of curlews were observed on dry wind flats, while 14.9% used the exposed but wet wind flats (Table 3). When not foraging on inundated flats, this happened mostly during falling water levels and on flats exposed very recently (Fig. 6). Within the sampling area, curlews preferred the plots with the deepest water and the furthest distance from the shore (Fig. 1). Densities of foraging curlews were neither related to total abundance and biomass of *Nereis diversicolor* in the squares (Spearman rank correlation; July/August: abundance $R_s = -0.20$ and biomass $R_s = -0.40$; September/October: abundance $R_s = 0.42$ and biomass $R_s = 0.37$, in all p > 0.05) nor to the abundance of ragworms with >75 segments (July/August: $R_s = -0.47$; September/October: $R_s = 0.45$, in both p >

Table 3. *Numenius arquata*. Intake rates of curlews in different habitats within the Hiddensee wind flat area and the distribution of foraging birds in these habitats (according to 354 scans with 12232 birds)

	Intake rate (prey min^{-1})			Habitat choice (%)
	n	Mean	SD	
Dry sand	8	2.01	1.83	0.7
Wet sand	7	2.00	0.81	14.9
Shallow water (1-3 cm)	34	3.10	1.42	8.8
Shallow water (3-9 cm)	82	3.37	1.55	75.6
Shallow water (9-15 cm)	74	3.77	1.73	

Time budgets

In summer, curlews showed high foraging activity during the first and last hours of daylight, but spent several hours resting during late morning and around noon (Fig. 7). This 'siesta' was less pronounced in October and nearly disappeared in winter (Fig. 7). However, total foraging time remained quite constant between 6.8 and 9.3 h and was much higher only prior to the homeward migration in April (11.6 h; Table 4). Due to the shorter length of the daylight period in winter, the percentage of daylight hours spent foraging was strongly correlated with daylength ($R_S = -0.836$, $n = 11$, $p = 0.0007$). All year round, curlews aggregated to night roosts within the wind flat area in the evening and dispersed again in the early morning (see decreasing foraging activity at dusk in Fig. 7). In contrast to some other shorebird species (oystercatcher *Haematopus ostralegus*, grey plover *Pluvialis squatarola*, dunlin *Calidris alpina*), no curlews

were seen to forage on the Hiddensee wind flat during nocturnal observations at full moon in August 1994 and 1995.

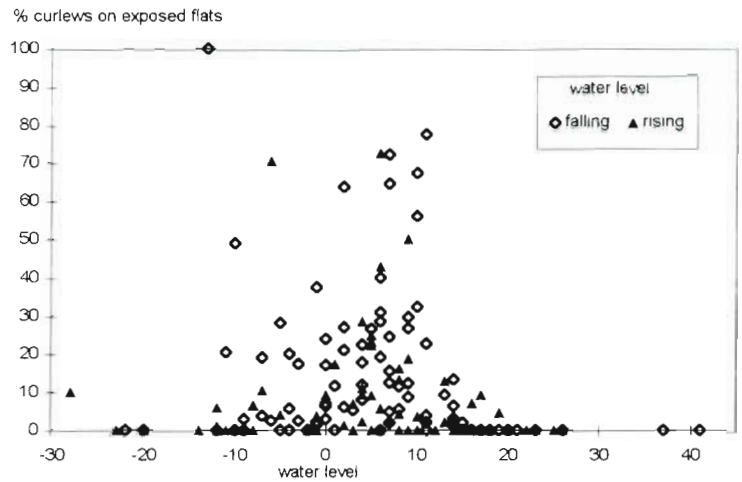


Fig. 6. *Numenius arquata*. Percentages of foraging curlews on exposed wind flats in relation to water level (0: mean sea level) and its change (90 scans during falling and 76 scans during rising water level)

Table 4. *Numenius arquata*. Total time and percentage of daylight period spent foraging by curlews on the Hiddensee wind flat. In addition, the daylength (45 min before sunrise until 45 min after sunset) is given for the median date of each period

Period	n scans	n birds	Daylength (min)	Total foraging time (min)	% daylight foraging
3–18 Jul 1994	42	2360	10 Jul: 1082	503	45.8
4–15 Aug 1993	62	3390	9 Aug: 1006	518	51.5
1–18 Aug 1995	103	5835	10 Aug: 1003	471	47.0
1–21 Sep 1993–95	68	4339	11 Sep: 871	521	59.8
2–9 Oct 1995	70	4179	5 Oct: 783	494	63.1
30 Oct–13 Nov 1995	81	5575	6 Nov: 639	474	74.2
18–30 Nov 1994	43	2660	24 Nov: 577	409	70.9
30 Nov–11 Dec 1995	81	5395	6 Dec: 549	468	85.2
21 Jan–2 Feb 1995	45	2148	27 Jan: 605	530	87.6
1–13 Mar 1995	83	5039	7 Mar: 762	558	73.2
21–30 Apr 1995	60	1572	25 Apr: 971	694	71.5

Table 5. *Numenius arquata*. Long-term average numbers of curlew during the day and in the evening (night roost) on different wind flats on the German Baltic Sea coast in August to October. The density is given as the numbers during the day in relation to the maximum extension of the wind flats during low water level

	Area (ha)	Day	Evening	Daytime density (birds ha ⁻¹)	Source
Oehe-Schleimünde	140	20–40	?	0.14–0.29	Erfurt & Dierschke (1992)
Wismar Bight	200	40–60	800–1500	0.20–0.30	Freitag (1987), J. Kube (pers. comm.)
Bock	1500	200–250	250–300	0.13–0.17	Graumann et al. (1980), Kube & Struwe (1994)
Vierendehgrund	1500	100–200	?	0.06–0.13	Vogelwarte Hiddensee (unpubl.)
Bessinsche Schaar	180	60–80	80–120	0.33–0.44	This study
Peenemünder Haken	200	30–80	?	0.15–0.40	B. Schirmeister (pers. comm.)
Struck	50	5–10	?	0.10–0.20	D. Sellin (pers. comm.)

DISCUSSION

In autumn, the average of 227 000 curlews present in 4500 km² of mudflat in the Wadden Sea (Meltofte et al. 1994) results in a density of 0.5 birds ha⁻¹, although many parts of the area hold more than 1 bird ha⁻¹. In contrast, much lower densities are observed on wind flats along the German Baltic Sea coast (at most 0.1 to 0.3 birds ha⁻¹; Table 5). However, in the study area at Hiddensee densities were only slightly lower than the overall abundance in the Wadden Sea (0.33 to 0.44 birds ha⁻¹; Table 5), and the effective density was even higher, as 84% of the foraging curlews used only stretches of shallow water. This choice of habitat is explained by the rate of prey intake which is twice as high in shallow water as compared to exposed flats. While no ragworms could be observed on the exposed wind flats, the high intake rate in shallow water is made possible by a high surface activity of ragworms, leading to improved detectability for predators (Dierschke 1997). Furthermore, in addition to other feeding mechanisms such as deposit feeding, ragworms as the main prey organism of curlews are known to filter feed in inundated habitats (Goerke 1971). This activity might enable curlews to detect ragworms due to air bubbles and water streams (Zwarts & Esselink 1989) and makes capture easier because worms are closer to the surface.

Within the wind flats, curlews not only preferred the most suitable habitat, but also took the most favourable prey. In contrast to the Wadden Sea (Zwarts & Wanink 1984, Zwarts & Esselink 1989), the Hiddensee wind flat contained only few prey organisms which are profitable with regard to the relation of costs and benefits. Our prey analyses showed that curlews are able to find the scarce individuals of *Nereis diversicolor* and *Mya arenaria* that are known to be profitable from studies in the Wadden Sea (Zwarts & Wanink 1984, Zwarts & Esselink 1989). Therefore, curlews are more skilful than ourselves as benthic ecologists, as we found only a few of these large individuals during our random sampling. The core sampling method may fail to estimate the abundance of invertebrates occurring at very

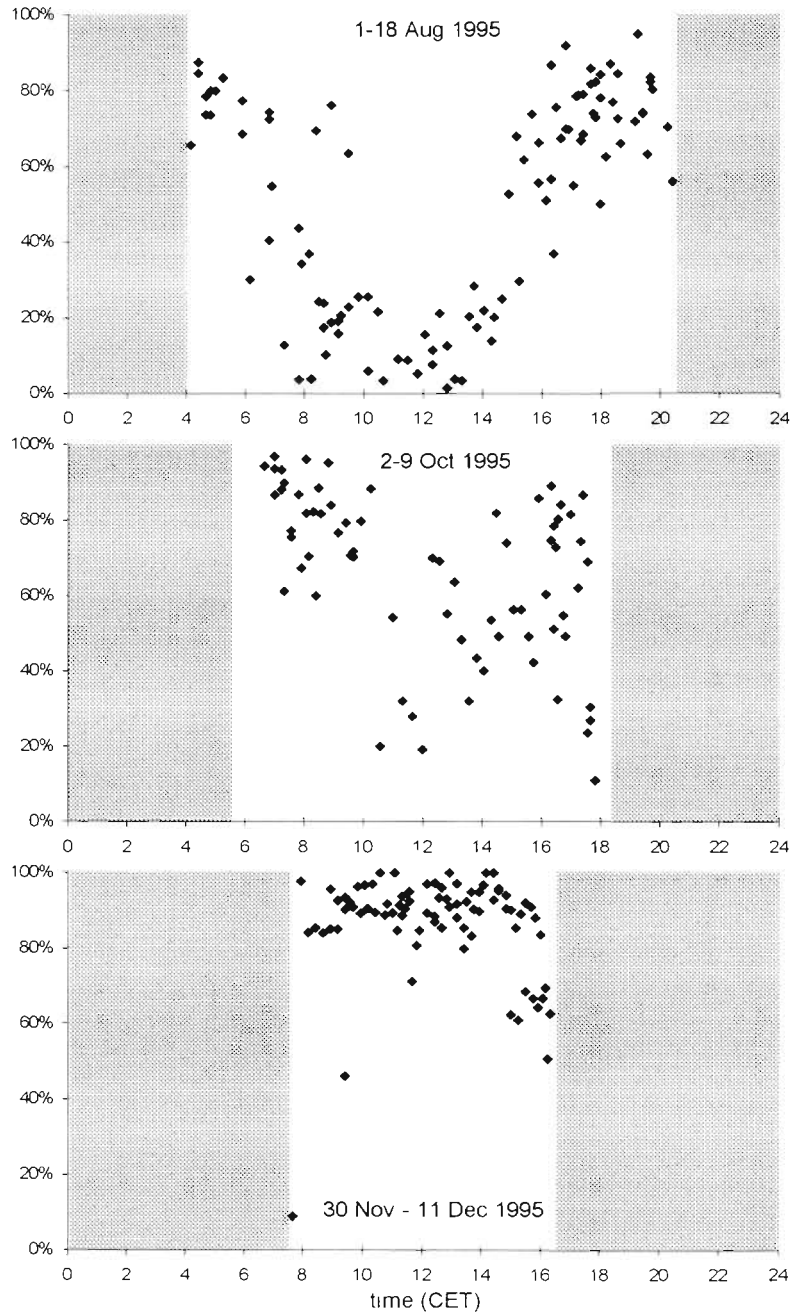


Fig. 7. Percentages of foraging birds among curlews present on the Hiddensee wind flat in August (103 scans), October (70 scans) and December (81 scans). Results of all scans are shown for the daylight period (45 min before sunrise until 45 min after sunset, periods of darkness are shaded). For additional information see Table 4.

low density (cf. Powilleit et al. 1995 for *Cerastoderma*). Furthermore, in a nearby habitat, burrows of *N. diversicolor* were found to be up to 25 cm deep (Zettler et al. 1994), thus slightly exceeding the maximum depth of our corer.

In addition to this highly selective and effective feeding strategy, prolonged phases of resting indicated that

curlews needed only a few hours of foraging during daylight to maintain their energy balance. Probably they do not even feed at night, since they aggregated to night roosts in the same way as described from other staging and stopover sites (Gloe 1972, Freitag 1987). Compared to smaller shorebird species, curlews spend only a small fraction of daylight hours or tidal cycles for foraging, even in tidal wetlands (Goss-Custard et al. 1977, Pienkowski 1981, Hötker 1995), but in addition may show nocturnal activity (Hötker 1995). However, nocturnal foraging is not necessary for curlews at Hiddensee as is indicated by a rough estimate of daily energy intake from July to October. Taking into account the intake of the smallest profitable ragworms (20 mg AFDM; with an energetic content of 23.79 kJ g⁻¹ AFDM; Bast & von Oertzen 1976) at a rate of 3.5 min⁻¹, curlews ingest 1649 to 1824 prey and 784 to 868 kJ during their daily foraging time of 471 to 521 min (Table 4). Even this consideration of only relatively small prey results in a gross intake comparable to 2.1 to 2.3 times the estimated basal metabolic rate (BMR) for a shorebird weighing 800 g (372 kJ d⁻¹ according to Kersten & Piersma 1987). However, as many prey items were larger, the estimated daily energy expenditure of about 3 times BMR (Kersten & Piersma 1987) can be assumed to be met.

Thus, in contrast to Kube's (1994) suggestion, the studied wind flat area at Hiddensee does not seem to be an unfavourable feeding habitat for curlews. Compared to tidal wetlands, they are available almost continuously. Curlews usually cease foraging at water levels of more than 30 cm above mean sea level, a relatively rare event (only on 12 d during the study period from July to November 1995). Even the unpredictability of water level fluctuations is less important for curlews, as they have access to water up to 15 cm deep due to their relatively long legs. Therefore, they are more flexible in habitat choice than other shorebird species. If they are forced to leave the study site, curlews have the possibility to switch to other wind flats nearby (with a different vertical situation compared to mean sea level) or to fields and meadows on the adjacent islands. However, the quite high curlew densities compared to other Baltic Sea wind flats (Table 5) may indicate unusually favourable conditions at Hiddensee. In contrast to at least some of the sites mentioned in Table 5, the studied wind flat area is relatively steep, situated deep in relation to mean water level and open to water bodies on 3 sides. This enables emigration and immigration processes which are the leading force in the establishment of benthic invertebrates at wind flats (Kube 1992). For the same reason, the bivalves *Mya arenaria* and *Cerastoderma lamarcki* occur at Hiddensee in contrast to other Baltic coastal sites (J. Kube pers. comm.).

The advantages of wind flats mentioned above are counterbalanced by the dependence more or less on 1 prey species. Long periods of low water levels leading to dried flats as well as periods of temperatures below 0.5°C combined with low salinity can induce mortality in populations of *Nereis diversicolor* (Hohendorf 1963, Arndt 1988, Kube 1992). After the Hiddensee wind flat was covered with ice for 4 mo in winter 1995/96, the abundance of ragworms was only 33 to 200 ind. m⁻² in summer 1996 (Dierschke 1997). As a possible result the number of curlews was also lower in 1996 than in the years before (30 to 40 birds; Fig. 2). However, even in this much more extreme situation curlews were able to find the few ragworms present (pers. obs.). Therefore, the reduced abundance of prey seems to be outweighed by the constant availability of suitable foraging habitats. As on the tidal flats of northwest European estuaries, curlews experience predictable prey availability on a day-to-day basis on the wind flats, where the almost continuous availability of shallow water habitats instead of the intermittent exposure produced by tides is characteristic. Consequently, foraging activity follows a diurnal instead of a tidal rhythm. Feeding is always possible in daylight, which can be regarded as advantageous for visual location of prey in shallow water. In conclusion it must be stressed that the wind flats at Hiddensee can hold certain numbers of curlews which almost exclusively use this habitat for feeding. Population size seems to be determined by the food supply, which is controlled by meteorological conditions (wind and winter temperature, see above).

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