Increase of Feeding Time in Waders Preparing for Spring Migration from the Banc D'Arguin, Mauritania

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INCREASE OF FEEDING TIME IN WADERS PREPARING FOR SPRING MIGRATION FROM THE BANC D'ARGUIN, MAURITANIA

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ABSTRACT   In order to increase body mass during the 4-6 weeks before their departure from the Banc d'Arguin in spring, some waders, such as Dunlin, Knot, Bar-tailed Godwit, increased the total time they spent feeding. They fed more at night and fed throughout neap tides and at high temperatures, circumstances in which feeding activity was depressed in winter. In other species, however, such as the Little Stint, feeding time did not increase during the premigration period. In winter, feeding time and body mass in the 14 wader species studied were negatively associated, but this trend disappeared during the premigration period. Nocturnal feeding was particularly important in the smaller waders, but the larger waders also began to feed at night later in the season. It is suggested that only when pressed for time, waders will feed at times when the yield from feeding is low.

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INTRODUCTION

Before waders wintering on the Banc d'Arguin, Mauritania, can migrate to the northern breeding grounds, they have to increase their body mass to levels enabling them to reach the migratory stopover sites in Europe (Ens *et al.* 1990a, Piersma & Jukema 1990, Zwarts *et al.* 1990b). Since the energy intake and change in body mass in captive waders are well correlated (Klaassen *et al.* 1990), it can be assumed that the premigratory increase in body mass can only be achieved by an increase in the food intake. How do waders increase their daily consumption?

First, waders could obtain the extra energy intake within the same feeding time by a proportional increase in the rate at which food is taken per unit time while foraging. Swennen *et al.* (1989) showed experimentally that Oystercatchers *Haematopus ostralegus* were able to increase their intake rate when forced to do so by a reduction in feeding time. The same was suggested by field data from one Oystercatcher (Hulscher 1982). Such an increase need not necessarily imply the expenditure of greater 'effort'. Whimbrels *Numenius phaeopus*, for

instance, were able to increase the intake rate during the premigration period on the Banc d'Arguin in April because the availability of their main prey species increased (Zwarts 1990).

Second, wintering waders may already feed at a maximal rate in winter and have no other choice than to increase feeding time when they deposit body mass. Engelmoer *et al.* (1984) described the Banc d'Arguin as a site offering the wintering waders frugal feeding opportunities. The data collected since then show that the biomass of macrobenthic prey, although three times as high as previously estimated, is not high (Wolff & Smit 1990) and that most wader species eat surprisingly small prey items (Engelmoer *et al.* 1984, Zwarts *et al.* 1990a). Thus the opportunity to increase intake rate while foraging may be rather limited.

How much should the feeding time be expanded during the fattening up period, assuming intake rate remains at a similar level? The simplest prediction is that the extra energy intake would be achieved by a proportional increase in feeding time. In winter, the large wader species fed for 60-80% of the time the tidal flats were available by day (Engelmoer *et al.* 1984). Thus there would be the opportunity to

increase feeding time within this period. On the other hand, this would not be possible for the smaller species because they already fed for close to 100% of the time for which the intertidal feeding areas were exposed by day (Engelmoer *et al*. 1984).

The birds could increase feeding time in two other ways; by feeding over high tide when they normally rest and, secondly, by feeding more at night at low water. Both periods were little studied by Engelmoer *et al*. (1984). If waders usually choose to feed preferentially in periods of a high yield, such as low water by day, expanding the feeding time to include periods with a lower intake would mean that the length of the total feeding time would increase proportionally more than the increase in energy intake required.

This paper quantifies the duration of the feeding time of 14 wader species in winter and in the pre-migration period. It then compares the increases observed with the extra food intake required to raise body mass during the premigration period by the necessary amount (Klaassen *et al*. 1990, Zwarts *et al*. 1990b). Moreover, an attempt is made to answer questions concerning differences between the species, such as: why did large species feed in winter for a shorter time than small ones? Why did this trend disappear during the premigration period? Why did some species feed more at night than others?

METHODS

Counts

All field work was done in the Baie d'Aouatif between 14 February and 21 April 1986. Two study areas, A and B (Fig. 1), were pegged out around hides erected on scaffolding 5 m high and also on a dune (2 m). The same method of measuring feeding activity was used in both sites. Counts of feeding and non-feeding birds were made every 30 or 60 min during the entire low water period. The method is comparable to 'scan (or instantaneous) sampling' (e.g. Tyler 1979). The decision whether a wader was feeding or engaged in preening or aggression could be made in less than a second, but it took more time
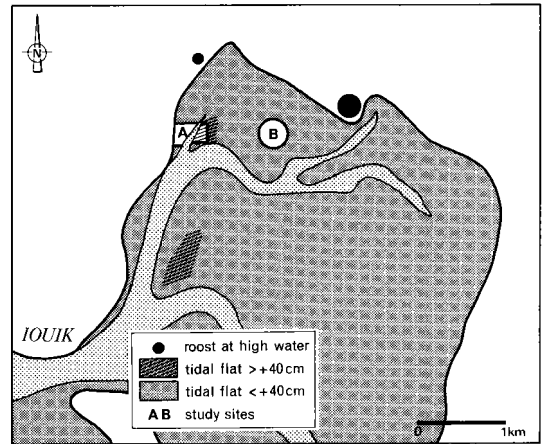
Fig. 1. The study area in the NW. part of the Baie d'Aouatif. Counting sites A and B are indicated, as well as two major tidal roosts. The waders occurred on the higher level parts of the tidal flats during the incoming and receding tides.

to discriminate between a resting bird and one that was merely looking around while feeding. Since most waders were active feeders, this was generally not difficult, but it took some time in species which waited either for emerging prey (e.g. Grey Plover *Pluvialis squatarola* and sometimes Whimbrel, Zwarts 1990) or for remnants left by other waders (e.g. Turnstone *Arenaria interpres*, Zwarts *et al*. 1990a).

At site A, activity counts were made during 64 daytime low water periods. Feeding and non-feeding birds were counted from the moment they left the high water roost until they returned with the incoming tide. Site A (5.44 ha) extended from the high to the low water marks. When time allowed, the data were supplemented by recording the activity of as many birds as possible outside this study site, again by sampling the whole intertidal flats from top to bottom of the shore.

At site B, feeding activity was measured by day and by night over 21 emersion periods. The hide was used once or twice a week over two consecutive low water periods. Once every other week, a complete daytime and adjacent night-time low water period were studied. In the intervening week, a low

water period that fell half in the light and half at night was watched and was followed by a period that fell half in the dark and half in the light. This observation schedule was chosen to rule out any tidal effect when day and night activity were being compared. An area of 6.88 ha was covered in daytime, compared with an area of 2.48 ha at night, due to the limited range (90 m) of the infra-red nightscope (magnification 10x).

Sexes could not be identified in most species, but the sex differences in bill lengths in Bar-tailed Godwits *Limosa lapponica* allowed the activity counts to be made separately for ♂♂ and ♀♀. Feeding activity was determined separately for waders in full winter plumage, full summer plumage and for two categories in-between in four common species: Dunlin *Calidris alpina*, Curlew Sandpiper *C. ferruginea*, Knot *C. canutus* and male Bar-tailed Godwit. Sex and plumage were not registered during the nocturnal observations.

Weather and tide

Weather data were obtained from our meteorological station near Iouik. Temperature was measured within a screen 150 cm above ground and varied from 12 to 36°C, increasing slowly from February to April (Wolff & Smit 1990). The daylength (morning evening civil twilight) was 12.5 h early February and 13.5 h at the end of April (Fig. 2).

Water level was measured continuously in a gully nearby. The tidal range varied from 2 m on spring tides to 1 m on neap tides (Wolff & Smit 1990). Waders did not feed at levels in the tidal zone 50 cm above mean sea level. The flights between roosts and feeding areas were recorded and took place over a short period when the water level was 43 cm on average above mean sea level. The length of the low water period varied during the lunar cycle (Fig. 2) from 7 h on spring tides to >12 h on extreme neap tides when part of the feeding area
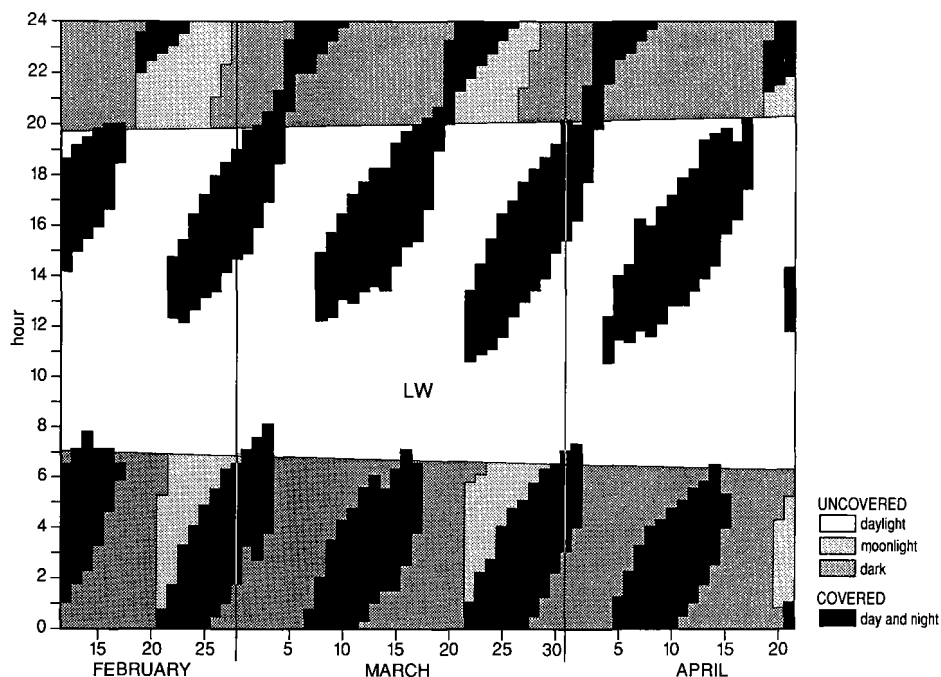
Fig. 2. The emersion period of the tidal flats situated at 43 cm above mean sea level in the period 12 February/22 April 1986. The daylight period is defined as the time between civil twilights. Nocturnal emersion periods with the full moon above the horizon are also indicated (see legend in figure).

was exposed throughout. One of these high-situated tidal flats fell in site A (Fig. 1).

Analysis

The term 'emersion period' refers to the time during which any part of the intertidal flats were exposed between the tide receded and advanced. The feeding activity in daytime, expressed as the percentage of waders feeding, was calculated for each count. Subsequently, these percentages were averaged over the entire low water period. But for the reasons given below, the first count on the receding tide and the last count on the incoming tide were excluded. All counts were used, however, to calculate the average time spent feeding per month (i.e. average % feeding * emersion period), after having taken into account the birds that were at the roost, and so not on the feeding areas, during the incoming and receding tides. The numbers at the roost were derived from the decrease and increase in numbers in the counting area.

The feeding activity appeared to be different in the two sites, being nearly always 100% at site B, but varying much more at site A. The average activity over all counts varied for the different species between 72% and 98% in area A and between 92% and 99% in area B. The same effect was apparent when counting areas within site A were compared. The reason for the difference is that non-feeding waders tended to congregate near the low water mark and site B was situated in the middle of the shore. The big flocks of waders preening and resting during the low water period always occurred outside site B along the creek. This did not apply to site A as it encompassed the entire tidal zone. For this reason, only the data from site A were used to describe the variation in feeding activity during daytime.

The feeding activity at night was calculated by comparing the numbers feeding in the 2.48 ha around the hide of site B at night and during the day. The amount of feeding done at night each month were calculated by multiplying the average proportion of birds feeding by day and the emersion period during the night, by the ratio between the numbers feeding at night and during the day in site B.

The statistical analyses were performed using SPSS (Norusis 1988).

RESULTS

Feeding activity within the tidal cycle

The flights between high water roost and the feeding areas were related to the water level and took place 160 min after high water on spring tides but only 60 min after high water on neap tides (Fig. 3). The same variation occurred during incoming tides. All species took part in the massive flights involved, but the three largest species, Oystercatchers, Whimbrels and Curlews *Numenius arquata*, arrived last on the feeding areas and left earliest.

The feeding flights of waders other than Oystercatchers, Whimbrels and Curlews as the tide receded were delayed, relative to water level, later in the season (Fig. 2), but the effect was very small and non-significant (13 min later in April than in February; averaged for 25 flights; $p = 0.43$).
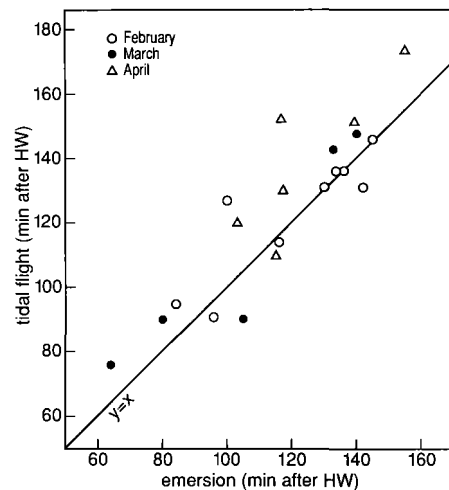
Fig. 3. The timing of the flights from the roost to the feeding area relative to the time of emersion of the feeding area (i.e. water level is 43 cm above mean sea level), both relative to the moment of high water. Three neap tides are not included when some waders remained on the high tidal flats throughout the high water period.
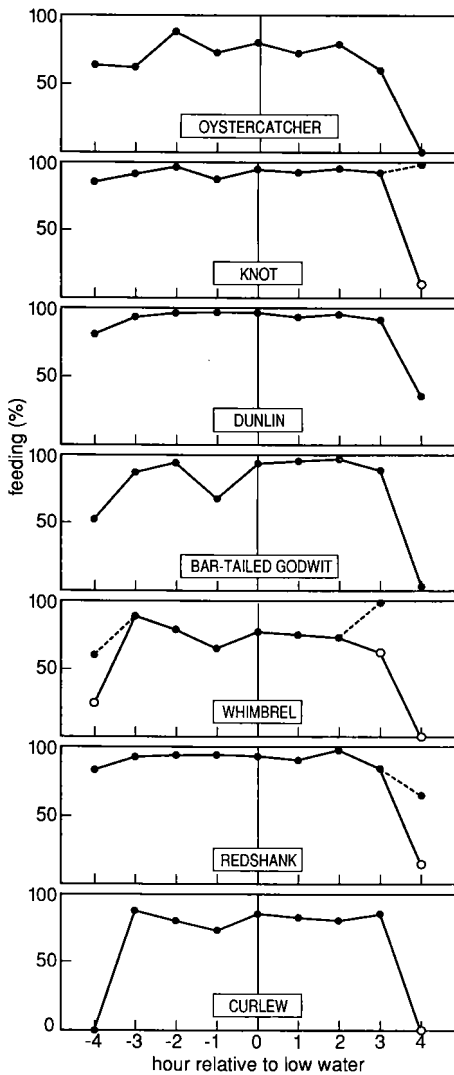
Fig. 4. Proportion of birds feeding during the low water period in February when the total emersion period was 8-9 h. Open dots show percentages feeding when the fraction of waders gathered at the roosts is taken into account.

There was no seasonal change in the timing of the flights on the incoming tide relative to the time of flooding of the feeding area ($n = 23, p = 0.45$).

Feeding activity was low just after the birds arrived on the tidal flats, but was high throughout the low water period and then decreased before the

birds left for the roost (Fig. 4). The activity counts on the feeding area may greatly overestimate the proportion of the population that is feeding if many birds were on the high tide roost at the beginning and end of the low water period (Fig. 4: Knot, Whimbrel, Redshank *Tringa totanus*). This will be taken into account in the estimation of the total feeding time.

Since no waders, with the exception of Whimbrels (Zwarts & Dirksen 1990), fed at high tide along the tidal edge, waders clearly did not increase the total time spent on the feeding area in daylight in the premigration period. The possibility that the feeding activity within the low water feeding period itself changed during the course of the season, and how this was achieved, is now considered.

Changes in feeding activity during the season

Feeding activity was invariably high in most species over the emersion period in the day, so there
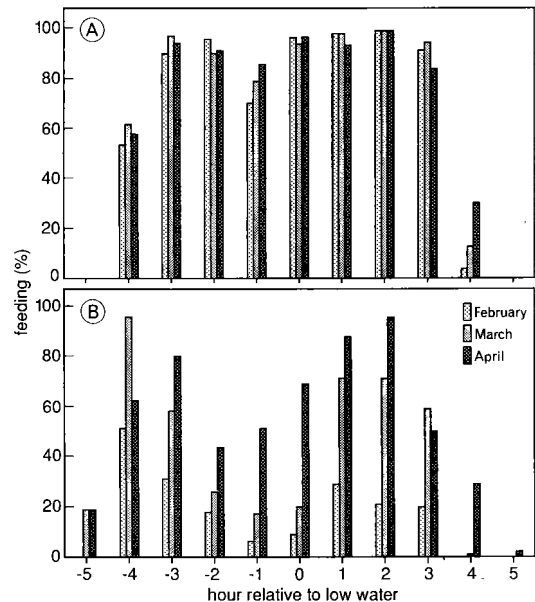

Fig. 5. The proportion of Bar-tailed Godwits feeding during the low water period by month. Panels A and B refer to emersion periods of 8-9 h and 11-12 h duration, respectively. The % feeding during the incoming and receding tide were corrected, where necessary, for waders being on the roost (see Fig. 4).

Table 1. Mean daytime feeding activity ($\% \pm SE$) in three months: February ($n = 12$ low water periods), March ($n = 31$) and April ($n = 17$). The feeding activity is calculated as the mean per low water period in counting site A during daylight. The results of the one-way analyses of variance are given ($R^2, p; n = 60$). The last column shows the mean number of birds per count ($\bar{x}$); 10-20 counts were done per low water period. The two-letter codes for the species names are used as abbreviations elsewhere in this paper. Body mass (in g) refers to winter masses in W. Africa (from Table 1 in Zwarts *et al.* 1990b), except for Oystercatchers which were obtained from Cramp & Simmons (1983): the mass of NW. European birds during moult in late summer were selected, because the masses of waders in moult matched the masses of species wintering in the tropics. Data on Greenshank were obtained from Summers & Waltner (1978), taking into account that wader masses in the W. Africa are 10% lower than in S. Africa; see Zwarts *et al.* 1990b).

species	code	mass	feeding activity by day (%)			R^2	p	$\bar{x}$
		(g)	Feb.	March	April			
Oystercatcher	Oy	525	61.9±5.8	72.5±3.6	76.7±7.2	0.049	0.236	38.1
Ringed Plover	RP	49	98.0±0.7	96.2±1.1	99.6±0.2	0.091	0.065	3.8
Kentish Plover	KP	38	96.1±2.1	97.1±1.1	98.0±1.1	0.013	0.700	3.0
Grey Plover	GP	187	94.1±1.1	93.5±1.0	93.7±1.0	0.002	0.943	6.0
Knot	Kn	119	85.5±4.6	93.4±1.0	95.5±0.9	0.162	0.006	32.5
Little Stint	LS	22	95.9±1.6	97.7±0.6	97.2±1.1	0.028	0.450	15.8
Curlew Sandpiper	CS	52	92.2±3.2	96.6±1.2	95.5±2.9	0.032	0.393	5.3
Dunlin	Du	42	89.2±3.3	93.7±0.9	94.9±0.6	0.091	0.054	117.1
Bar-tailed Godwit	BG	253	65.7±9.8	83.4±3.9	89.6±2.9	0.127	0.021	57.5
Whimbrel	Wh	414	79.5±3.3	85.4±2.4	84.3±3.8	0.032	0.426	2.9
Greenshank	Gr	188	95.1±1.9	93.0±1.7	95.8±2.4	0.021	0.558	2.1
Redshank	Re	108	92.9±1.4	93.3±0.7	93.7±2.2	0.002	0.939	7.4
Curlew	Cu	718	74.5±3.8	84.7±2.8	74.2±4.4	0.083	0.084	2.7
Turnstone	Tu	99	89.0±3.1	95.9±1.0	96.7±1.0	0.166	0.006	3.1

were generally no significant differences in feeding activity when the three months were compared (Table 1). However, in 10 of the 14 species, the lowest feeding activity was found in February, and activity was at a maximum in April in nine species. If all species are taken together, these trends are highly significant ($\chi^2 = 45.0$, $p < 0.001$; Friedman's two-way analysis of variance).
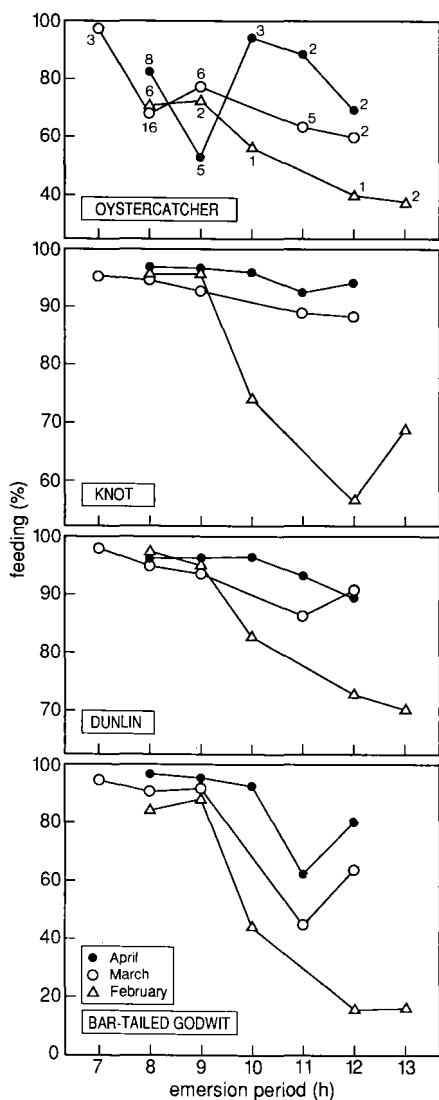
Feeding activity and emersion period

The waders fed almost continuously throughout the emersion period, although the larger species had a short pause just before low water (Fig. 4). As shown for the Bar-tailed Godwit in Fig. 5, the low water pause was much less pronounced during spring tides than neap tides, when the total feeding period was very long.

Average feeding activity decreased as the dura-

Table 2. Results of two-way analyses of variance to test the effect of emersion period (7 classes of 1 h between 7-13 h) and season (three months) on the feeding activity of 4 waders in site A. The same data are given as in Fig. 6 ($n = 60$, but for Dunlin $n = 64$). Letter codes indicating species see Table 1.

species code	source of variation					
	month		emersion		month • emersion	
	R^2	p	R^2	p	R^2	p
Oy	0.049	0.209	0.142	0.183	0.122	0.265
Kn	0.162	0.000	0.327	0.000	0.201	0.001
Du	0.092	0.000	0.550	0.000	0.131	0.001
BG	0.127	0.000	0.576	0.000	0.077	0.029

Fig. 6. Average low water feeding activity as a function of the duration of the emersion period, given separately for each of the three months. The number of low water periods per subcategory is shown in upper panel. Statistical analyses are given in Table 2.

the present emersion period or by that of the preceding one, but this cannot be resolved since the two are highly correlated (see Fig. 2). Knots and Dunlins did not feed for more than ca. 7 h per low water period in February, but continued to feed for longer, if possible, later in the season (Fig. 6). Bar-tailed Godwits did not feed for more than ca. 6 h in February, but only two h at neap tides. However, the feeding activity of Bar-tailed Godwits decreased over four successive neap tides in February (from 43% to 11%), so perhaps they were gradually feeding less because of 1) the cumulative effect of a series of very long emersion periods, and 2) the effect of temperature (see next section).
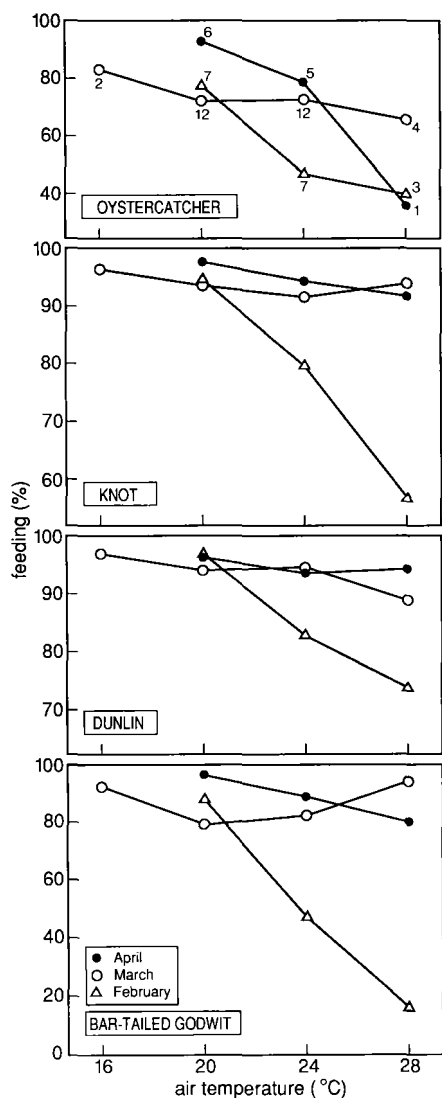
Feeding activity and temperature

The waders fed least actively at high temperatures in February. This effect of temperature was still present in March and April, but to a much lesser degree (Fig. 7, Table 3). Note that the effect was not affected by the duration of the emersion period. The average emersion period was similar for all the temperature categories, although the three low water periods with a high temperature in February were neap tides (cf. Fig. 6), so temperature depressed feeding activity independent of the effect of emersion period.

Table 3. Results of two-way analyses of variance to test the effect of temperature (4 classes: 16, 20, 24 and 28 ± 2°C) and season (three months) on the feeding activity of four waders in site A. One low-water period in March of 31 °C is pooled with the adjacent class. The same data are given in Fig. 7 ($n = 60$, but for Dunlin $n = 64$). Letter codes indicating species see Table 1.

species code	source of variation					
	month		temperature		month • temperature	
	R^2	p	R^2	p	R^2	p
Oy	0.067	0.080	0.170	0.183	0.152	0.026
Kn	0.182	0.013	0.134	0.000	0.229	0.001
Du	0.113	0.006	0.142	0.003	0.202	0.002
BG	0.132	0.000	0.044	0.305	0.234	0.002

tion of the feeding time available increased (Fig. 6, Table 2). This trend was particularly clear in February but was less marked in March and April. An interesting question is whether the level of feeding activity was determined by the duration of

Fig. 7. The average low water feeding activity as a function of the average temperature during the emersion period, given separately for each of the three months. The number of low water periods per subcategory is shown in upper panel. Statistical analyses are given in Table 3.

Feeding activity at night

The nocturnal feeding activity differed considerably between species, though the reliability with which the importance of night feeding could be accessed varied between species according to their

Table 4. Comparison of the feeding density by day and by night in February, March and April, given as the ratio between 'density by night' and 'density by day'. 82 counts were performed during the day and 60 at night. The number present in the counting site, averaged for all 142 counts, is given in the last column. Letter codes indicating species see Table 1.

species code	ratio night/day (density)				mean number
	Febr.	March	April	mean	
Oy	0	0.42	(20.74)	0.56	0.7
RP	0.46	0.98	0.02	0.28	1.9
KP	0	0	0	0.02	1.3
GP	0.06	0.77	0.69	0.69	2.6
Kn	0.02	1.46	1.51	1.39	22.1
LS	0.97	1.25	0.71	0.91	29.5
CS	0	0.02	0	0.01	2.8
Du	0.51	0.85	0.78	0.77	52.8
BG	0.61	1.01	1.40	1.22	23.1
Wh	0	0	0.16	0.06	0.2
Gr	0	0.45	0.32	0.29	0.2
Re	0.43	0.41	0.35	0.39	2.3
Cu	0	0.88	-	0.58	0.1
Tu	0	0	0	0	0.3

feeding density. The area counted at night measured only 2.5 ha, and the average number of birds present, day and night combined, varied from 53 for Dunlin to only 0.1 in Curlew (see Table 4). Feeding time at night increased during March and April, but three species were rarely, or never, seen feeding at night; these being Curlew Sandpiper, Turnstone and Kentish Plover *Charadrius alexandrinus*.

Only five species actually fed in the nocturnal counting site during February: the Ringed Plover *Charadrius hiaticula*, Little Stint *Calidris minuta*, Dunlin, Bar-tailed Godwit and Redshank. The 1-2 Oystercatchers present in daytime in February never fed there at night. This is in contrast to an *Anadara*-cockle bed where Oystercatchers continued to feed at night, at least when there was a full moon (Swennen 1990). During moonlit nights in February and March, Whimbrels fed on the beach, but rarely on the adjoining *Zostera* beds (Zwarts 1990, Zwarts & Dirksen 1990). However,

Table 5. Comparison of the feeding density during dark and moonlit nights in February, March and April 1986, given as the ratio between the 'density on dark nights' and 'density on moonlit nights'. Numbers of both types of low water periods are indicated. A moonlit night was defined as one in which the moon was above the horizon and full (8 succeeding nights; see Fig. 2). The remaining nocturnal emersion periods were defined as dark nights; clouds never obscured the moon. Letter codes indicating species see Table 1.

species code	ratio dark/moonlight (density)		
	Febr.	March	April
GP	0	0.12	0.83
Kn	-	0.58	0.90
LS	1.36	2.16	3.79
CS	-	0.17	-
Du	0.60	0.61	0.79
BG	0.66	0.58	1.11
Re	0.40	1.35	-
nights:			
moonlit	2	1	1
dark	1	5	4

they were mostly not present in the feeding territories at night and therefore probably roosted. In study area B, Whimbrels were also absent at night in February and March.

Assuming that waders fed less at night because their intake was reduced by the poorer visibility of prey, more waders would be expected to feed during bright nights than on dark nights, and this appeared to be so (Table 5). Comparison of Tables 4 and 5 shows that the increasing importance of nocturnal feeding as the season progressed (Table 4), was partly caused by more feeding occurring on dark nights (Table 5).

Not all waders depart in spring

Not all waders wintering on the Banc d'Arguin were preparing for the spring migration during March and April. In most species, juveniles did not lay down much extra body mass in spring, at least compared with adults (Kersten 1989, Ens *et al.* 1990a), because they remained on the Banc d'Arguin in summer (van Dijk *et al.* 1990), and retained winter plumage (Ens *et al.* 1990b). Such waders did not increase their feeding activity in April, and even in March, as much as did birds that were
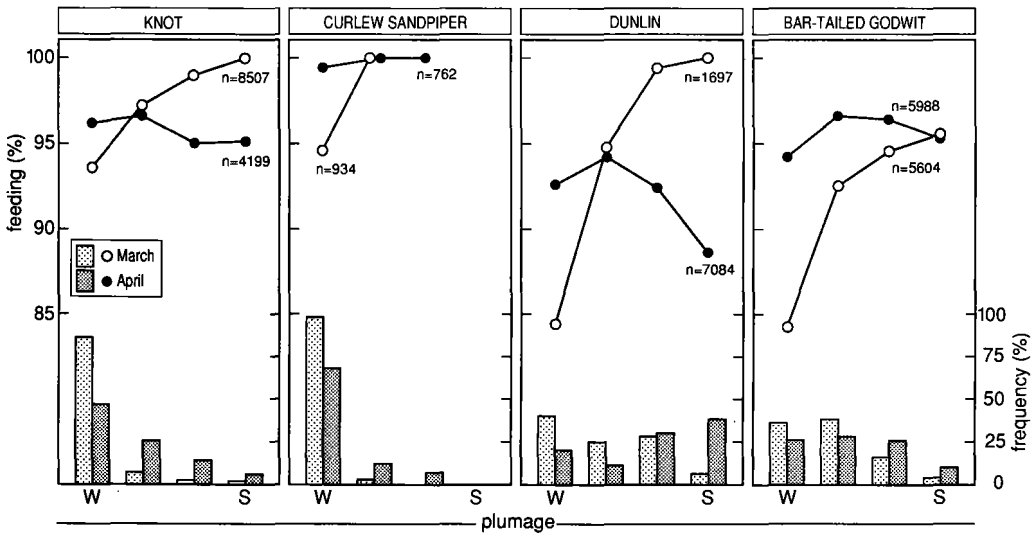
Fig. 8. The average feeding proportion of waders in winter (W) and summer plumage (S), and two classes in-between in March and April. The number of waders observed is shown. The frequency distribution of the plumage scores is given as histograms, separately for both months.

moulting into summer plumage (Fig. 8). But even so, some waders in full summer plumage in April did not fully utilize their time for feeding since they were 'ready to take off' (Zwarts *et al.* (1990b).

The Curlew was the only species that left the Banc d'Arguin before the end of March (Piersma *et al.* 1990). Activity counts in April were therefore on oversummering birds. Feeding activity in April was as low as in February (Table 1), so this figure was not used in the estimate of feeding time given below.

DISCUSSION

Feeding time in winter

In this section we analyse the time budgets of waders wintering on the Banc d'Arguin by using the activity counts for February. Since the body masses were still at their winter levels (Zwarts *et al.* 1990b), the daily energy expenditure was equivalent to the cost of wintering on the Banc d'Arguin.

There was a negative relation between the average body mass of a species and its feeding activity at low tides during the day ($r = -0.76$; body mass and feeding activity given in Table 1). Since the feeding activity counts refer to the entire emersion period (see Fig. 2) and few waders fed outside that time, the proportion feeding could be used to calculate the total time spent feeding in daylight. The 'night-day-ratio' (Table 4) could then be used to estimate the time spent feeding during the nocturnal low water periods. The total feeding time per 24 h could thus be estimated (Fig. 9).

The total daily feeding time in February varied from five h (Oystercatcher) to 17 h (Little Stint). The negative relationship between total feeding time and body mass (Fig. 9) was more pronounced for the whole 24 h period than for the daylight period alone because of the greater importance of nocturnal feeding in small waders. Of the three species having a body mass > 400 g, not one fed at night whereas seven of the eleven species with a lower body mass did do so.

The negative relation between average body
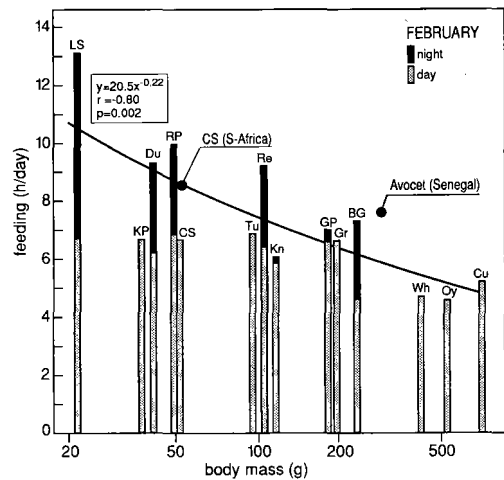
Fig. 9. The total feeding time per 24 h in February as a function of body mass, shown separately for day and night. The letter codes indicating the species are listed in Table 1. The daily feeding times are also shown for Curlew Sandpipers wintering in S. Africa (Puttick 1979) and Avocets *Recurvirostra avocetta* in Senegal. The latter was a non-tidal lagoon where birds only fed by day in December 1982 (Zwarts pers. obs.). The regression refers only to waders on the Banc d'Arguin.

mass and winter feeding activity has been described before for waders wintering in Great-Britain (Pienkowski 1977), on the Banc d'Arguin (Engelmoer *et al.* 1984) and in Australia (Dann 1987), but all these studies referred only to the daylight. A negative relation between feeding time and body mass was also found in woodland birds (Gibb 1954) and seabirds (Pearson 1968), and thus appears to be a common phenomenon.

Why do large waders feed less? The risk of starvation

Sutherland & Moss (1985) hypothesized that animals of the same size taking larger prey feed for less time than animals depending on small prey. Assuming that all animals encounter prey at random, they reasoned that animals eating larger prey have a higher probability of starvation and so must live in richer environments where they can be on average less active. On the other hand, animals taking small prey face a lower risk of starvation

and so can live in poor environments but therefore have to feed for more of the time.

Waders wintering in the tropics are able to survive a starvation period of some days (see Klaassen *et al*. 1990, Zwarts & Dirksen 1990). Assuming that prey capture is a random event, we have thus to know the risk that no prey are found during a total feeding period of about 20 h. The risk of death by starvation depends in this model on the average rate at which prey are taken. This rate is maximal for a small wader such as the Dunlin (20 prey min^{-1}) and minimal for a large species such as the Oystercatcher (0.066 prey min^{-1}). The decrease of capture rate with body mass (Fig. 7A in Zwarts *et al*. 1990a) might thus be interpreted in terms of the starvation hypothesis: large waders are less active since they take (relative to their body mass) larger prey (Fig. 7B in Zwarts *et al*. 1990a). Nevertheless we do not believe that the starvation hypothesis actually applies to waders on the Banc d'Arguin, since the risk that no prey are found within the starvation period is for all wader species infinitely small.

Why do large waders feed less? The importance of hidden feeding time

The time spent feeding per day or the daily feeding time is a function of daily food requirements and the rate at which the food is collected. The intake rate while foraging was determined in five larger wader species (Table 6) and can be estimated for the smaller waders in the following way.

Five wader species caged in the tropical conditions of W. Africa maintained constant body mass when their net rate of energy intake equalled 1.8 ∗ *BMR* (*SE* = 0.1) (calculated from Table 2 in Klaassen *et al* 1990; *BMR* according to Kersten & Piersma 1987, but as discussed by Klaassen *et al*. (1990) the *BMR* of waders wintering in the tropics is probably 0.7 times the *BMR* measurements of Kersten & Piersma (1987) which referred to waders wintering in the temperate zone). The energy costs for Whimbrels living in the field were similar to the costs in the cage because they remained still for 75% of the time and rarely flew, which is costly (Zwarts & Dirksen 1990). Since this time budget was similar to those of other wader species on the

Table 6. Intake rate (mg ash-free dry mass per s feeding) measured on the Banc d'Arguin and in NW. Europe in a sample of wader species. The predicted intake rates refer to waders wintering on the Banc d'Arguin and are based upon the allometric relation between mass and gross food intake (see text, and Zwarts *et al*. 1990a) divided by the total feeding time; winter masses taken from Table 1. The last two columns give the intake rate measured on the Banc d'Arguin and in NW. European areas. Letter codes indicating species see Table 1.

species code	intake rate (mg AFDM s^{-1} feeding)		
	prediction	found	
	BdA	BdA	NW. Europe
Cu	1.96	1.63[1]	1.6 - 2.5[4]
Oy	1.80	1.85[2]	1.4 - 3.0[5]
Wh	1.45	1.11[3]	
Kn	0.37		0.62[6]
Re	0.34		0.34[7]

[1]One individual Curlew feeding on *Zostera* taking a mixture of crabs (*Panopeus africanus* and *Uca tangeri*) and gobiid fish, observed during seven periods at five days (total feeding time 141 min; *SD* = 0.47; Zwarts pers. obs.). [2]Swennen (1990). [3]Zwarts & Dirksen (1990). [4]Zwarts & Wanink 1984, Ens *et al*. 1990b, Zwarts & Esselink 1989. [5]Zwarts & Drent 1981, Sutherland 1982b, Goss-Custard *et al*. 1984, Goss-Custard & Durell 1987a, 1987b, Swennen *et al*. (1989). [6]Knots feeding on *Macoma balthica* of 12.4-16.6 mm; August 1981; Dutch Wadden Sea (Blomert & Zwarts pers. obs.). [7]Goss-Custard 1970, 1977.

Banc d'Arguin (e.g. Oystercatcher: Swennen 1990), the cost of living for all species can be considered to be a similar multiple of *BMR*.

The gross daily food intake (g ash-free dry mass, or AFDM, per day) was estimated to be 47.6 $M^{0.723}$, assuming that 80% of the gross energy intake was metabolized and the energy content of the food was 21 kJ (Zwarts *et al*. 1990a), where *M* is body mass in kg (see Table 1). The average intake rate (mg s^{-1} feeding) was calculated by dividing the estimated daily consumption by the total feeding time (Fig. 10B). These values were similar to the real measurements made on the Banc d'Arguin
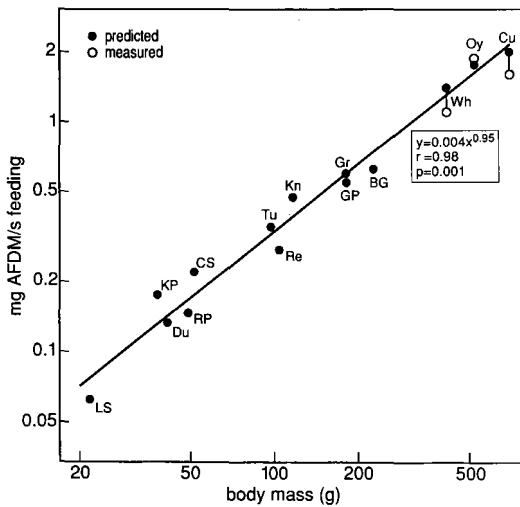
Fig. 10. The predicted average intake rate (mg s⁻¹) in February as a function of body mass, as derived from feeding period (see Fig. 9) and estimated daily consumption (see text). The feeding rate, measured in the three larger species, is indicated separately (see also Table 6). Two-letter codes indicating the species are listed in Table 1.

and elsewhere (Table 6). The allometric relation between M and intake rate (Fig. 10) has the exponent 0.95 (SE = 0.05). Exponents close to unity were also found by Bryant & Westerterp (1980) when they did the same calculations separately for seven groups of bird species (e.g. raptors, passerines, shorebirds).

If intake rate is indeed proportional to M, feeding time should scale with $M^{-0.25}$. The exponent was in fact -0.22 (SE = 0.06) in wintering waders (Fig. 9) and similar exponents, with an average value of -0.28, have also been found in wintering woodland birds (Gibb 1954 as analysed by Calder 1974). In breeding seabirds the feeding time (i.e. time spent at sea) also decreased with body mass (Pearson 1968), but here the exponent was -0.66.

The question remains as to why intake rate should be proportional to body mass rather than to metabolic requirements. A fixed portion of body mass in birds is allocated to the digestive tract which is probably why meal size is proportional to $M^{1.0}$ and not to $M^{0.75}$ (Calder 1984). The time need-

ed for rodents to digest a full digestive tract scales with $M^{0.25}$ (Daan & Slopsema 1978). The implication is that the maximal rate at which energy can be digested is proportional to $M^{0.75}$.

Waders continue to feed during food processing. Feeding Whimbrels, for instance, defecate each 2-20 min (own obs.) but, even so, the rate of ingestion was frequently greater than the rate of digestion: there was a digestive bottleneck when the birds stopped feeding to preen or rest for a period (Zwarts & Dirksen 1990). If these pauses are included in the feeding time, the resulting 'crude intake rate' is no longer proportional to M, since non-feeding pauses are more common in larger waders (Table 1, Fig. 4).

'Hidden feeding time' is not restricted just to the feeding period, since waders continue digestion after the end of the feeding period. The importance of this 'hidden feeding time' was shown by M. Kersten & W. Visser (pers. comm.) for Oystercatcher, a species known to dramatically increase its intake rate at the end of the feeding period (e.g. Zwarts & Drent 1981, Goss-Custard et al. 1984, Swennen et al. 1989). Waders lost mass at a rate of 1.5-2% h⁻¹ during the first four h at the roost, after which the loss was 0.5% h⁻¹ (Fig. 2 in Zwarts et al. 1990b). The initial high rates of loss were caused by defecation, so the fact that the initial loss was proportional to body mass implies that, relative to the metabolic requirements, food processing on the roost was more important in the larger species.

Summarizing, the negative relation between feeding time and body mass can be explained by the fact that the intake rate relative to the metabolic requirements increased with body mass. However, this effect was much reduced when the 'hidden feeding times' associated with digestive pauses were incorporated into the total feeding time.

Feeding time of waders at tropical and temperate latitudes in winter

Kersten & Piersma (1987) showed that the daily food consumption of captive waders held at an air temperature of 0°C were 1.5 times higher than compared at thermoneutrality, this being 10°C for a large wader, such as the Oystercatcher, and 20°C for a small wader, such as the Turnstone. Waders on the

Banc d'Arguin live under thermoneutral conditions (for air temperatures see Wolff & Smit 1990) and their average net energy requirements are 1.8 * BMR (see previous section). Waders wintering in NW. Europe experience low air temperatures, so their net energy requirements vary between 2.5 and 3 * BMR (Kersten & Piersma 1987, Drent & Piersma 1990). The feeding times of waders wintering in N. Europe would be expected to be 1.5 times as long as those on the Banc d'Arguin since the intake rates of the larger waders wintering on the Banc d'Arguin and in NW. Europe are similar (Table 6).

Waders wintering in NW. Europe feed for most of the daytime low water periods (e.g. Goss-Custard et al. 1977, Baker 1981), making the feeding time per day ca. 8 h. Some species may even continue to feed in fields at high water (Goss-Custard 1969, Heppleston 1971, Townshend 1981, Goss-Custard & Durell 1984). No studies on the duration of nocturnal feeding have yet been published. Wood (1983) concluded that Grey Plovers wintering in NE. England could not balance their energy demands if they only fed by day, and later showed that they did indeed remain on the feeding areas at night (Wood 1986). Our own unpublished data show that during winter similar numbers of feeding Curlews were present by day and by night on the intertidal mudflats of the Dutch Wadden Sea. This is in contrast to late summer when they rarely fed at night. Goss-Custard (1969), Heppleston (1971) and Pienkowski (1982) found similar seasonal variations in the relative numbers of waders present on the tidal flats at night.

Daylength (time between civil twilights) in NW. Europe amounts to 8-9 h during mid-winter and to 14 h at the end of March and September. The lower feeding activity in autumn and at the end of the winter compared to mid-winter (Goss-Custard et al. 1977, Pienkowski 1977, Baker 1981) may be caused by the higher temperatures reducing the costs of thermoregulation as well as by the longer daylength itself, assuming that food intake is lower at night.

To summarize, the estimates of the feeding times of waders on the Banc d'Arguin cannot yet be compared to similar estimates from the temperate zone. However it is likely that the northern birds feed for much longer because their daytime feeding periods exceed the total feeding time on the Banc d'Arguin yet they also feed at night.

Feeding time during the premigration period

On the Banc d'Arguin, the feeding activity of many waders over the low water period increased later in the season, in daytime (Table 1) as well as at night (Table 4). However, small waders could not extend their feeding time by much because they already fed for close to 100% of the time in winter.
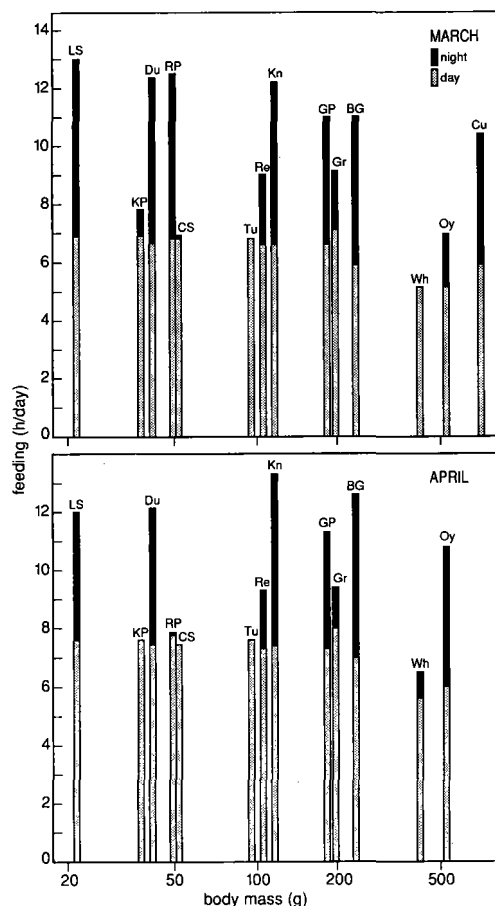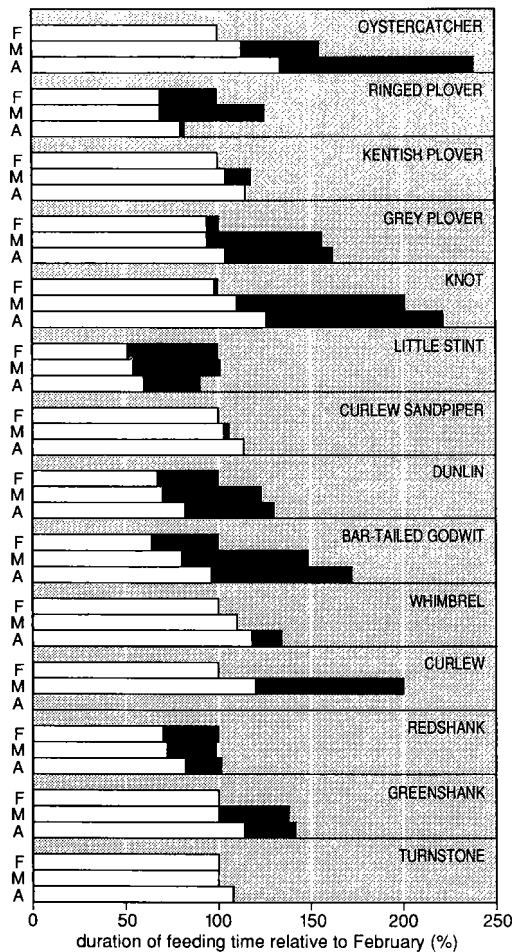

Fig. 11. Feeding time per 24 h as a function of body mass in March and April. Species are identified with two-letter codes given in Table 1. In contrast to February (Fig. 9), there is no significant relation between daily feeding time and body mass: March: $Y = 16.6 \cdot X^{-0.09}$ ($r = -0.33, p = 0.25$), April: $Y = 11.8 \cdot X^{0.00}$ ($r = 0.0, p = 0.99$).

Fig. 12. The change in feeding time in March and April relative to February. The total feeding time in February was set at 100 for each species. The feeding time by day (white) and by night (black) for the three different months are given as percentage of the total feeding time in February.

Since large waders could increase their feeding time, the negative relation between body mass and feeding time that occurred during winter disappeared during the premigration period (Figs. 9 & 11). In fact, the larger wader species increased their total feeding time by feeding more at night (Fig. 12).

This prompt two questions: 1) is there a correspondence between the timing of the body mass gain and the timing of the increased feeding time? 2) is the increase of the feeding time enough to explain the gain in body mass?

The timing of departure varied between species (Piersma *et al.* 1990) from the second half of March (Curlew) to the first half of May (e.g. Little Stint). The period preceding departure during which waders increased their body mass lasted at least four, and maximally six weeks (Zwarts *et al.* 1990b). Therefore April was the period during which all species gained mass, except for Curlew where only summering birds remained. The mass increase had already started by early March in some species, such as the Dunlin and Redshank, but for most species, too few were captured and weighed to indicate precisely the start of the premigratory hyperphagia period. However, it is likely it started in the Ringed Plover, Knot, Little Stint and Turnstone during the second half of March (see also Fig. 5 in Zwarts *et al.* 1990b). In line with this, the duration of the feeding time in March was clearly more than in February, though generally less than in April (Fig. 12).

The body mass increase of individual waders amounted to 1.0-1.2% per day and varied little between species (Zwarts *et al.* 1990b). Klaassen *et al.* (1990) showed that a mass increase of 1% per day corresponded to an increment in metabolism varying from 7% on average in Ringed Plover and Whimbrel to 16% on average in Knot and Turnstone (calculated from Table 2 in Klaassen *et al.* 1990). This variation could be attributed to the varying energy content of the reserve tissue that was laid down during the experiment, and clearly depended on the stage of premigratory fattening that had been reached. Only Knot weighing more than 120 g reached the later stages of fattening (67% of the reserve was fat; see Table 2 in Klaassen *et al.* 1990). Carcass analysis by Piersma & van Brederode (1990) provides an independent estimate of 60% as the fat content of reserve tissue (summarized in Fig. 13 in Zwarts *et al.* 1990b). The expectation is that in free-living waders a rise in maintenance metabolic rate of ca. 25% is necessary for each per cent gain in mass. Taking all this information together, we predict that the feeding time

for all species would increase by 25-30% in April compared to February, assuming that the food intake per unit foraging time remained the same. Was this so?

The most reliable estimate of time budget is for Dunlin, because it is the most common species. Its feeding time in March and April was 24 and 30% respectively above the February level (Fig. 12). These values are similar to the expected, but the majority of the other species were different to the Dunlin. Smaller species, such as the Little Stint and Curlew Sandpiper, showed no increase while the larger species, such as the Knot and Bar-tailed Godwit, showed a much larger increase. It is likely that part of this variation was due to errors in measurement, especially of the importance of nocturnal feeding in the rarer species (see Table 4). However, the difference between common species, such as the Little Stint on the one hand and Bar-tailed Godwit and Knot on the other must be real.

Little Stints and Curlew Sandpipers were apparently able to increase their intake rates so as to reach the higher energy requirements within the same period of time. Puttick (1979, 1980, 1984) showed that Curlew Sandpipers preparing to leave a S. African wintering area increased their feeding time by 43% by feeding more at high tide, an amount similar to the increase in the daily energy intake. Thus in contrast to the Curlew Sandpipers on the Banc d'Arguin, the increase of feeding time in S. Africa was sufficient to meet the enhanced energy requirements without increasing the rate of intake while foraging.

Optimal allocation of feeding time

In contrast to both Little Stints and Curlew Sandpipers, Knots on the Banc d'Arguin doubled the duration of their feeding time. This should have meant that the average daily intake decreased by ca. 35% to produce a daily consumption which was only 1.3 times the winter level, the increase expected to match the requirements for body mass gain. Did such a reduction take place and if so, why?

Feeding should be restricted to periods of a maximal yield, regardless whether birds minimize total feeding time or maximize daily intake. As-

suming that intake rates do differ between high and low tides and, for low water periods, between day and night, the time spent feeding at high tide and at night should depend, other things being equal, on the total consumption. This reasoning might explain whether waders should feed late in the season during periods of low prey digestibility (1), at high tide (2) and at night (3).

Digestibility (1) Klaassen *et al.* (1990) showed that, in captive waders fed with artificial food, digestibility decreased by 2.1% for each degree rise in the air temperature. Assuming, this phenomenon also applied to natural food, surely they should feed more, not less. The decreased prey digestibility might explain why waders fed less at high temperatures in winter (Fig. 7). We assume that waders accepted a lower rate of net energy intake later in the season and continued to feed at high temperatures. The overall result is that, in April, waders have to eat more to compensate for the lower rate of return. In the case of the Bar-tailed Godwit, the increase in gross intake in April would have to be
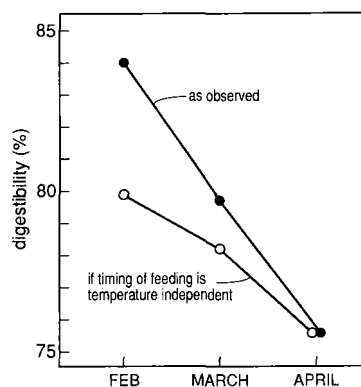
Fig. 13. The digestibility per month taking into account the effect of temperature (*T*, °C), on digestibility (*Q*) :*Q* = 125- 2.06 • *T*, according to Klaassen *et al.* (1990). The graph shows that digestibility would decrease because of the higher temperatures later in the season, assuming that feeding activity was not related to temperature. But as waders in February gave up feeding at high temperature (Fig. 7), whereas they did not do so later in the season, the difference becomes even larger, as shown here for the Bar-tailed Godwit.

more than 10% to counteract the depressed digest-ibility later in the season (Fig. 13). A great differ-ence in digestibility between winter and April is not to be expected in the small species, waders that did not stop feeding at high temperatures in winter (see Fig. 7).

There is another reason for assuming that the efficiency with which waders digested food might be greater in February than in April. Zwarts & Blo-mert (1990) showed that the digestibility of *Uca* taken by a Whimbrel decreased from 75% to 60% when the daily consumption increased, presum-ably because of the higher rate at which food was processed. However, the increased intake rate in April might be expected only to reduce prey di-gestibility in waders feeding on prey with a high inorganic content. Apart from Whimbrel, this would include Knots and Bar-tailed Godwits feed-ing on bivalves.

Our prediction was that the net energy intake in April should be 1.3 * the winter level. Assuming that the negative effect of temperature and the increased intake rate on digestibility were both ful-ly present, the gross food intake in April should have been raised to a maximum of 1.7 * the winter consumption, depending on the inorganic content of the prey. Thus this factor can explain only a part of the differences among species in the increase of feeding time from winter to April (Fig. 12).

High tide (2) Waders fed when the tidal flats were exposed. Relative to water level, there was little variation in the timing of the flights between roosts and tidal flats (Fig. 3). The feeding opportunities at high water were apparently so unfavourable that feeding was not worthwhile.

Night (3) Most species fed at night, at least later in the season (Fig. 12) when daily consumption had to be raised. The same was observed by M. Kersten (pers. comm.) in captive waders: nocturnal feeding only occurred if the daylight period was insuffi-cient for minimal energy requirements to be met (Fig. 14). Given the negative effect of ambient tem-perature on digestibility, the birds should always have fed during the cool nights and only fed during
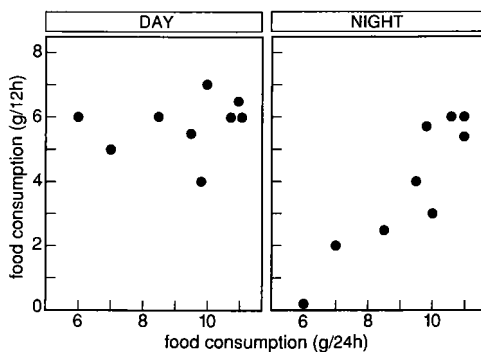
Fig. 14. Consumption by day and by night in captive Ringed Plovers as a function of total daily intake (M. Kersten pers. comm.). The experiment was run in Guinea-Bissau; birds were given ad libitum artificial food.
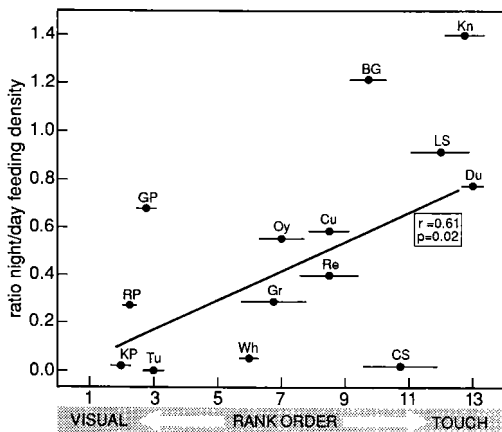
the hot days, when forced to do so by increased requirements. But in fact the opposite occurred. Why was this so?

One possibility is that waders in the field might have a much lower intake rate at night, though this is still unclear. Oystercatchers on the Banc d'Ar-guin took Giant Bloody Cockles *Anadara senilis* at the same rate during the day as on moonlit nights (Swennen 1990), although it is unknown whether the biomass intake rates differed, since Sutherland (1982a) found that Oystercatchers took smaller Edible Cockles *Cerastoderma edule* at night than by day. Though feeding success by day and night has been measured accurately in free-living and captive Oystercatchers, there is still no consensus, though the studies showed that the intake in dark-ness is lower or equal than the intake by day but never higher (Heppleston 1971, Hulscher 1976, Zwarts & Drent 1981, Hulscher 1982, Goss-Custard & Durell 1987b, Swennen *et al.* 1989). The intake rate of Whimbrels feeding on crabs on the Banc d'Arguin was only ca. 1/5 of the daylight rate during the winter (Zwarts & Dirksen 1990). According to our unpublished data, Curlews in the Wadden Sea fed on ragworms *Nereis diversicolor* at night at a strongly reduced rate.

Although several of these studies point to a reduction in intake rate at night, it is possible that

the feeding method of the bird affects the difference between daytime and night-time intake rates. The difference would be expected to be least in touch-feeding waders and greatest in visually hunting species (Vader 1964, Dugan 1981, Pienkowski 1977, 1982, 1983, Robert *et al.* 1989). To test this, we asked four experienced wader watchers to rank the 14 species wintering on the Banc d'Arguin along a continuum from 'typical touch feeder' to 'typical visual feeder'. The purpose of this was to score the probability that each species might switch profitably to tactile feeding at night when forced to do so (e.g. Hulscher 1976). As expected, the ratio between the numbers of birds feeding at night and during the day (Table 4) and the rank order were, in fact, highly correlated (Fig. 15). Two species did not fit in trend: the Curlew Sandpiper was rated as a touch-feeder yet rarely fed at night and nocturnal feeding was important in the visually hunting Grey Plover. Generally speaking the plovers, identified as visual hunters, fed less at night than the sandpiper species which were recorded as touch feeders.

The rather good fit in Fig. 15 is surprising, given the three factors that might have obscured the relationship: 1) Bird species differ in their capacity to

see at night (Martin 1985) and this is probably also true in waders, given the species differences in the rod/cone ratio (Robert & McNeil 1989). 2) Species differ in their ability to find prey by touch (Gerritsen & Meijboom 1986). 3) The feeding conditions might differ more between day and night in some wader species than in others. For waders hammering bivalves at the surface, it is very unlikely that prey availability differs between day and night. On the other hand, the feeding conditions might differ considerably for waders feeding on the small fraction of worms present at the surface, because some benthic prey may be more active at night than during the day (Vader 1964, Dugan 1981, Pienkowski 1983, Evans 1987).

The increase in feeding time during the premigration period (Fig. 12) cannot be interpreted without the intake rates by day and by night being known. If it is assumed that both rates were the same, the daily food intake of Knot in April would be double the daytime rate during the winter. But if the intake rate at night is 20% of the intake during the day, the total food consumption in April would be only 35% greater (cf. Fig. 12). Clearly, the next step is to measure intake rates by day and by night, during winter as well as premigration periods. This should clarify why some species increased their intake rates while others extended their feeding time and all species nevertheless achieved the same gain in body mass.

Fig. 15. The day-night ratio in the numbers of birds feeding (Table 4) as a function of average rank order (± *SE*) along a subjective axis describing feeding method, scored independently by four experienced wader watchers. Species are indicated with the two-letter codes given Table 1.

Conclusion

The costs of wintering on the Banc d'Arguin are likely to be 1.5 times as low as those for birds wintering in NW. Europe, because there are no thermoregulation costs in the tropics. There is no indication that the intake rates differed between the Banc d'Arguin and the temperate zone, but the daily feeding time in W. Africa was shorter than in NW. Europe. When species were compared, the daily feeding time during winter on the Banc d'Arguin decreased with body mass. However, this effect disappeared during the premigration period, because -in contrast to the small waders- the larger species increased their feeding time. We conclude that the increased energy requirements during the

premigration period were achieved in different ways. Large waders extended the feeding time, while small waders must have increased the intake rate. The next step in the research is to measure intake rates by day and night.

ACKNOWLEDGEMENTS

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SAMENVATTING

Steltlopers kunnen alleen in gewicht toenemen door de voedselopname te verhogen in de 4-6 weken voordat ze vertrekken van de Banc d'Arguin. Sommige soorten (b.v. Bonte Strandloper, Kanoet Strandloper en Rosse Grutto) bereiken dit door hun forageertijd te verlengen: ze forageren meer 's nachts en gaan door met forageren tijdens de lange droogligtijden met dood tij en wanneer het heel warm is. Onder zulke omstandigheden zijn ze in februari en maart meestal niet erg actief. De forageertijd van andere soorten (b.v. Kleine Strandloper) neemt niet toe in de loop van het seizoen, hetgeen inhoudt dat de vogels de opnamesnelheid moeten opvoeren. 's Winters bestaat er een negatief verband tussen de forageerduur per etmaal en het lichaamsgewicht, maar deze trend verdwijnt tijdens de opvetperiode in maart en april. Kleine steltlopers forageren 's nachts vaker dan grote soorten, maar tijdens de opvetperiode zijn ook grote steltlopers gedwongen om 's nachts voedsel te zoeken. De tijdbesteding wordt verklaard als een optimale tijdsbesteding.

RÉSUMÉ

La croissance pondérale des limicoles dans les 4 à 6 semaines précédant leur départ du Banc d'Arguin n'est possible que grâce à une augmentation de l'ingestion d'énergie. Quelques espèces (par exemple le Bécasseau variable, le Bécasseau maubèche et la Barge rousse) y arrivent en prolongeant le temps consacré à la recherche de nourriture: ils sont plus actifs la nuit et continuent de fouiller pendant les longues périodes de morte-eau quand la vasière s'assèche et de même quand il fait très chaud, c'est à dire des circonstances où ils sont d'habitude très paresseux en hiver. Par contre, chez d'autres espèces (par exemple chez le Bécasseau minute) le temps consacré à la recherche de nourriture n'est pas prolongé au cours de la saison, ce qui signifie qu'ils sont obligés d'augmenter la vitesse de l'ingestion. En hiver il y a un rapport négatif entre la durée de la recherche de nourriture sur vingt-quatre heures et le poids corporel, mais ce rapport disparaît quand ils constituent leurs réserves de graisse en mars et avril. Chez les limicoles plus petits la recherche de nourriture nocturne a plus d'importance que chez les espèces plus grandes, mais ces derniers se nourrissent davantage la nuit eux aussi quand ils constituent leurs réserves de graisse. L'emploi du temps est interprété en termes de problème d'optimalisation.