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FOOD INTAKE OF OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* BY DAY AND BY NIGHT MEASURED WITH AN ELECTRONIC NEST BALANCE

MARCEL KERSTEN[1] & WILLEM VISSER

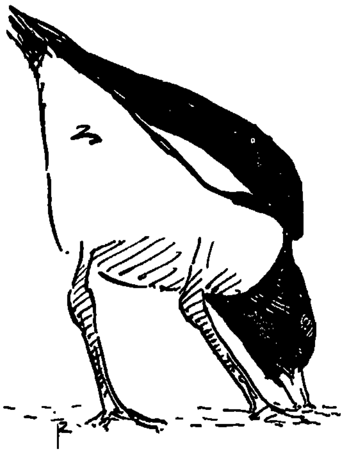
Kersten M. & W. Visser 1996. Food intake of Oystercatchers *Haematopus ostralegus* by day and by night measured with an electronic nest balance. Ardea 84A: 57-72.

We developed a model to calculate food intake by Oystercatchers from their weight gain between two incubation spells and correcting for the amount of excreta voided before the bird returned to its nest. The model predictions agreed well with estimated food consumption based on direct observations in the field, regardless of the type of prey consumed. The model was used to calculate food consumption of free-living Oystercatchers under circumstances when this could not be measured by direct observation; (1) when feeding downshore outside their territory and (2) while feeding during night-time low water periods.

The rate of food intake outside the territory did not differ from the rate within the territory and averaged 0.9 g min^{-1} fresh weight. Food intake rate in darkness did not differ from that during daylight ($p = 0.96$). The total amount of food consumed per low water period at night was higher in the ♂ and lower in the ♀ as compared to food consumed in daylight. The difference was probably induced by our activities which made the ♀ very reluctant to incubate during the daylight hours. The average amount of food consumed differed hardly between day and night-time low water periods.

Total food consumption over a 24 hour day was 162 ± 88 g for the ♂ and 196 ± 13 g for the ♀. Accounting for the weight loss of the ♂ over the observation period, the estimated energy expenditure is 535 and 565 kJ day^{-1} for ♂ and ♀, respectively. This is equivalent to 2.2 × *BMR* and strongly suggests that the incubation stage is a period when energy is conserved, rather than expended.

Although the amount of food consumed per low water period varied greatly from one tidal cycle to the other, the birds appeared to balance intake with expenditure on a 24 hour basis. In the discussion we address the possible repercussions for the birds when they fail to keep this balance in the short run.



Key words: Oystercatcher - *Haematopus ostrealegus* - energy requirements - food consumption - food intake rate - incubation - nest balance

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INTRODUCTION

Shorebirds, depending on intertidal mudflats for their food supply, live under a tidal regime. Although the feeding areas are exposed twice a day, some of this occurs at night. Many authors have reported that shorebirds are active during night-time low water periods and do feed (Evans 1976, Dugan 1981, Zwarts *et al.* 1990, McNeil *et al.* 1992), but quantitative data of night-time food intake are almost entirely restricted to captive birds (Hulscher 1976) or birds on semi-natural mudflats

(Leopold *et al.* 1989). In a long-term study on the energy requirements of Oystercatchers *Haematopus ostralegus* L. during the breeding season on the island of Schiermonnikoog in the Dutch Wadden Sea (53°26'N, 6°13'E) it was of paramount importance to measure food consumption during the night, since on average one third of the exposure time of the mudflats is in darkness during the breeding season at this latitude.

We developed a model to calculate food consumption from measured weight gain on a nest balance and a correction for simultaneous weight loss due to digestion and evacuation. We show that these estimates are reliable as the model predictions differ only slightly from measured food intake. We used this model to estimate the rate of food intake of Oystercatchers in situations when direct observations were not possible: (1) during night-time low water periods, (2) during feeding trips outside of the territory. The results are used to compute total food consumption per low water period and in the discussion we address the question at what time-scale Oystercatchers balance their energy budget.

METHODS

Body weight

The data was collected during the breeding seasons of 1986 to 1989 on the saltmarsh on the island of Schiermonnikoog (53°26'N, 6°13'E) in the Dutch Wadden Sea. All Oystercatchers breeding in the 13-ha study area depended on the tidal mudflats for their food supply. Each bird was marked with a unique combination of colour rings. Several nests (one in 1986, seven in 1987, five in 1988, one in 1989) were equipped with an electronic balance (Berkel, type DS-1) in order to measure the body weight of the incubating parent. Since the disturbance caused by installation of the balance may induce birds to abandon the clutch, balances were only installed after the clutch had been incubated for one week. Not a single nest was abandoned. The balance was connected to a portable computer which continuously evaluated whether there was a change in the weight of the nest. Every change was stored in memory and the body weight of a bird coming onto the nest or leaving it was later calculated by subtracting the weight of the empty nest from the total weight of bird plus nest (accuracy ± 1 g).

Table 1. Biomass (gram fresh weight) of prey taken by Oystercatchers. Size classes are arbitrary units in the molluscs (see methods); in worms two times the size class gives length (cm). Bivalves include large *Cerastoderma edule*, *Mya arenaria* and *Mytilus edulis.*

Size	bivalves	*Macoma*	*Nereis*
1	–	0.178	0.035
2	–	0.287	0.139
3	0.350	0.396	0.309
4	0.511	0.505	0.547
5	1.066	0.614	0.850
6	1.943	0.723	1.220
7	3.227	–	1.655
8	5.009	–	2.156
9	7.383	–	2.721

Food intake

Registrations of body weight always spanned an entire low water period (6-8 hours) and were accompanied by continuous observation of both members of the pair. The activity of each bird was observed with telescopes from a hide on the edge of the saltmarsh and an observation tower on the mudflats. The duration in seconds of the following activities were stored in a GECCO event recorder (an electronic device, designed and manufactured by Kees Rappoldt): incubating, resting, foraging, locomotion and aggression. We also measured food intake by recording type and size of each prey item consumed. The vast majority of prey taken were either Ragworms *Nereis diversicolor* or small bivalves *Macoma balthica.* Larger bivalves were taken occasionally. These include: Cockle *Cerastoderma edule*, Sandgaper *Mya arenaria* and Mussel *Mytilus edulis.* The shells of bivalves were always opened and only the flesh was ingested. The size of flesh particles was scored in arbitrary size classes from 1 to 9, where size class 4 referred to an item roughly the size of the colour ring. The length of *Nereis* was scored in 2-cm classes with reference to the bill-length of the bird (on average 7 cm in ♂♂ and 8 cm in ♀♀, Hulscher 1985).

To convert prey size into biomass (fresh weight), we conducted a number of calibration sessions. The results of these are presented in Table 1. In large bivalves, fresh weight was determined by holding the flesh content of large *Mya* in front of a stuffed Oystercatcher. Two observers with telescopes at a distance of approximately 40 m identified size class. Subsequently, the flesh was weighed. The relation between fresh weight (Y in g) and size class (X) was: $Y = 0.00532 \times X^{3.293}$ ($R^2 = 0.69$, $n = 22$). This equation was used to estimate fresh weight of each size class. Fresh weight of *Nereis* (adhering water removed by blotting with tissue) was determined for each 2-cm size class (maximum length), except for the largest size class which was rare. The relation between fresh weight (g) and worm-length (cm) was given by the allometric regression equation: $Y = 0.00895 \times X^{1.978}$ ($R^2 = 0.99$, $n = 8$ size classes). We used this equation to estimate fresh weight of the largest size class. Fresh weight of *Macoma* was measured directly by scoring the particle sizes ingested by two captive Oystercatchers presented with *Macoma* of known length (Alting unpubl.). Only *Macoma* larger than 14 mm were taken, and the relation between fresh weight (g) and size class was linear: $Y = 0.069 + 0.109X$ ($R^2 = 0.999$, $n = 6$ size classes).

Nocturnal observations

Nocturnal observations were conducted with a light intensifier during the first week of July 1987 and the second half of May 1989 (the same pair was observed in both years). The green-and-black image produced by the light amplifier made it impossible to identify a bird on the basis of its colour rings. Consequently, continuous observations had to be restricted to birds which could be identified from other characteristics. Male and ♀ of the resident pair selected (Ens *et al.*1992) differed considerably in body weight, so the readings of the nest balance enabled us to tell which pair member was active at the time. Occasionally we lost track of the active bird; this often occurred when it got involved in aggressive encounters with neighbouring pairs or intruders. After such an aggressive interaction, our birds always retreated to a small patch of *Spartina townsendii* within their territory where we were able to pick them up again. Consequently, we were able to measure the time budget of the birds under observation, but we could not measure their food intake since the low resolution of the light intensifier made it impossible to determine the size of prey items taken. Night-time food intake had to be estimated using the model explained below.

Summer nights are rather short in the study area, lasting approximately six hours. Since the duration of a low water period for resident pairs is about seven hours, a small part of each night-time low water period always occurs in daylight. When we compare food intake rates, we restrict ourselves to feeding trips in either darkness or daylight. However, when we compare time budgets and total food consumption per low water period we are talking about the entire night-time low water period, most of which occurred in darkness. Daytime low water periods did not include any darkness.

The model

The weight gain measured between two incubation spells represents only a fraction of the food consumed in between. Some food may already have been digested and excreted before the bird returns to its nest. Therefore, the actual amount of food consumed F equals the sum of the measured weight gain ΔW plus the weight of excreta E evacuated before the bird returned to its nest:

$$F = \Delta W + E \qquad (1)$$

ΔW can be measured directly, but E has to be estimated in some way. The value of E depends on the time available for digestion and the rate with which it proceeds. In a recent study we have demonstrated that Oystercatchers process food at a

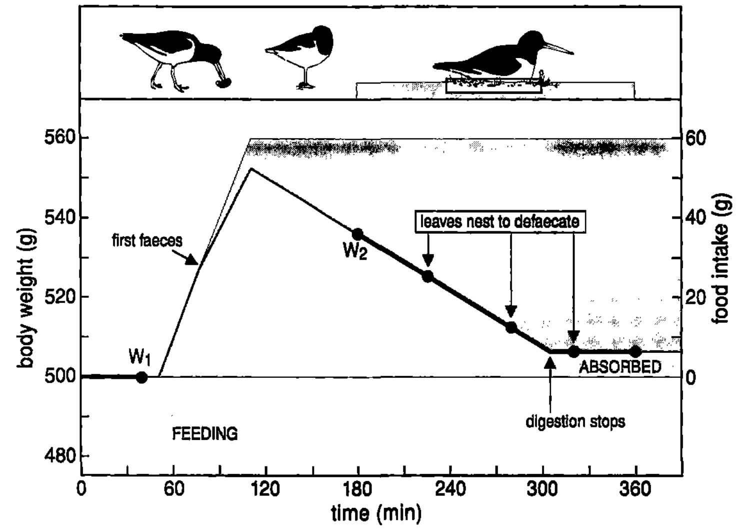

Fig. 1. Schematic reconstruction of body weight fluctuations caused by food intake and subsequent digestion in the Oystercatcher. Thick line: continuous registration of body weight when the bird was sitting on the nest. Dots indicate when the bird enters or leaves the nest. Thin line: reconstruction of body weight when the bird was off the nest. The total amount of food consumed is indicated on the right-hand axis, while the shaded area indicates how much food has been processed and excreted.

At the start of a low water period ($t = 0$) the focal bird was sitting on its nest and had no food left in its digestive tract since food was not available during the preceding six hours. After 40 minutes, its partner took over incubation and our bird left the nest weighing 500 g. Ten minutes later ($t = 50$) it started feeding for 60 minutes with an average intake rate of 1 g min^{-1} (fresh weight). The first faeces appeared 28.3 minutes after the first prey had been consumed ($t = 78.3$) and from this moment onwards excreta were produced at a rate of 0.233 g min^{-1}. After food intake stopped ($t = 110$), the bird did not immediately return to the nest which was still occupied by its partner. Since digestion continued, body weight decreased over this period. When our bird finally returned to the nest ($t = 180$) it weighed 536 g. However, digestion still continued and our bird had to leave the nest at regular intervals in order to defaecate (indicated by downward pointing arrows). Body weight stabilized at 507 g when all food was processed ($t = 306$).

constant rate of 0.233 g min^{-1}, which was independent of the amount of food consumed (Kersten & Visser 1996). It was shown that weight loss due to digestion can be conveniently described by a three-parameter model. These parameters are: (1) latency time (t_{lat} = 28.3 min), the time interval that elapses between the ingestion of the first food item and the production of the first faeces, (2) evacuation rate (ER = 0.233 g min^{-1}), the rate with which excreta are evacuated and (3) absorption coefficient (a = 11.3%), the proportion of food (fresh weight) which is not evacuated. The weight of excreta produced can now be estimated as:

$$E = ER \times (t - t_{lat}) \qquad (2)$$

where t is the time interval between the start of feeding and the moment that the bird returned to its nest. Since the values of the parameters are known, we can now calculate the amount of food consumed by substituting equation (2) into equation (1):

$$F = \Delta W + 0.233 \times (t - 28.3) \qquad (3)$$

We used equation (3) to estimate the food intake of incubating Oystercatchers on Schiermonnikoog. ΔW was measured with an electronic balance under the nest, while t was determined from continuous observation of the bird when it was away from the nest. Figure 1 gives a schematic illustration of the procedure.

Although the application of equation (3) is straightforward, there are two conditions to be met in order to give reliable results:

Conditions (a) $t \geq 28.3$ min
(b) $\Delta W > a \times F$

Condition (a) has never been violated in our observations, but it should be mentioned to ensure a sensible application of this method. It refers to the situation when a bird already returned to its nest shortly after it had started feeding, i.e. before the first faeces was produced. When $t <$ 28.3 min, the amount of excreta produced becomes negative (eq. 2) which is nonsense. Therefore, when $t < 28.3$ min, $E \equiv 0$ and the amount of food consumed should equal weight gain ($F = \Delta W$).

Condition (b) requires that digestion is still in progress when the bird returns to its nest. The amount of food consumed sets an upper limit to the time that digestion proceeds and the amount of excreta to evacuate. Since 11.3% of the food is absorbed (see above, Kersten and Visser 1996), the measured weight gain upon return to the nest should be larger than 0.113 times the estimated amount of food consumed. When the difference between ΔW and ($a \times F$) is small, say 1-2 g, the data are suspect and should be handled with great care. When condition (b) is violated, the calculated amount of food consumed represents the maximum amount that might have been ingested. In our study we were sometimes confronted with this situation and excluded these data from the analysis. Whether condition (b) is met can only be evaluated after food consumption has been calculated. This might be a little inconvenient but does not pose a problem.

RESULTS

Calibration

We compared the estimated food intake according to our model with the actually observed food intake between two incubation spells during daylight low water periods (Fig. 2). As expected, accounting for excretion greatly improved the accuracy of the estimated food intake. In general, estimated food intake compared well with observed food intake. The largest discrepancies were +55% and –57%, while two out of three estimates differed by less than 25%. The accuracy of the estimates improved when data of subsequent foraging trips were pooled, since deviations from the prediction tended to cancel each other out (Fig. 2C). The estimated sum of the food intake was remarkably similar to that actually observed. On average our model underestimated observed intake by 5%. This discrepancy is thought negligible given the unavoidable inaccuracies in the observed food intake. Therefore, we conclude that our model produced reliable estimates of the amount of food consumed between incubation spells and this was not affected by the kind of prey consumed.

Food intake rate outside the territory

Especially during the incubation period, Oystercatchers regularly left their territory to feed on mudflats further downshore, where food intake could not be measured by direct observation. We estimated food intake in these remote areas from our model. Food intake rate did not differ between birds feeding within or outside their territory (Fig. 3). Despite some scatter, the amount of food consumed increased linearly with the time spent feeding. Within the territory, the actual time spent feeding was, of course, directly measured by continuous observation, but this was impossible when birds left their territory. Occasional observations on these downshore feeding areas indicated that visiting birds which were known to have an active nest in the study area always behaved as if in a hurry and did not lose time to activities other than feeding. Therefore, we assumed

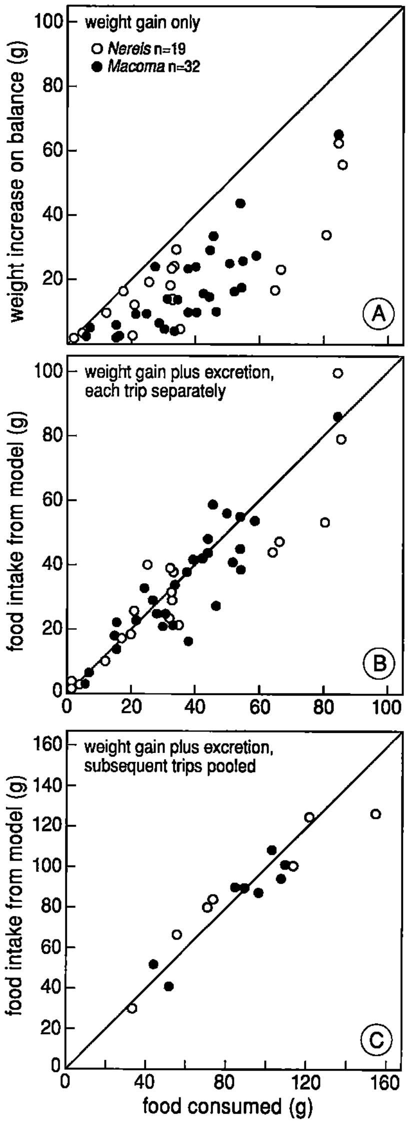

Fig. 2. Estimated food intake of Oystercatchers between two incubation spells in relation to their actual food intake as observed during continuous observation. (A) Estimated food intake equals the weight gain measured on the nest balance. (B) The outcomes of our model which accounts for weight gain plus excretion (see methods: eq. 3) when each foraging trip is represented separately. (C) As (B), but the data of subsequent trips during one low water period have been pooled. The shaded area indicates where estimated intake differed less than 25% from observed intake.

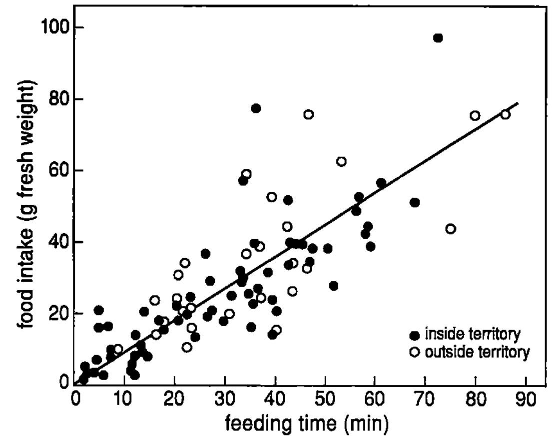

Fig. 3. Estimated food intake of adult Oystercatchers within and outside their territories in relation to the time spent feeding. The line represents the linear regression equation: $Y = 0.904X$ ($R^2 = 0.64$, $n = 92$).

that birds outside their territory were feeding for 100% of the time and only subtracted two times two minutes travel time from the total time that the bird was away. The average intake rate over all data was 0.9 g fresh weight per minute feeding.

Food intake rate at night

The amount of food consumed increased linearly with time spent feeding (Fig. 4), but the rate of food intake was significantly lower in 1989 than in 1987 ($F = 10.520$, $p = 0.003$). The rate of food intake did not differ between ♂ and ♀ ($F = 1.133$, $p = 0.295$). When the data for ♂ and ♀ were combined, the average intake rate was slightly higher at night than during the day (1.09 *versus* 0.93 g min^{-1}) in 1987 and slightly lower (0.53 *versus* 0.66 g min^{-1}) in 1989. Overall, there was no significant difference in intake rate between day and night ($F = 0.003$, $p = 0.959$).

Time budget during low water by day and by night

In 1987, we observed the birds for eight consecutive low water periods. This enabled us to compare the time budgets of this couple during

Table 2. The percentage of time devoted to various activities during day and night-time low water periods by both members of a pair of residents in 1987 (four night-time low water periods, average duration = 6.97 hours; four day-time low water periods, average duration = 7.19 hours).

activity	♂				♀			
	day		night		day		night	
	$\bar{x}$	*SD*	$\bar{x}$	*SD*	$\bar{x}$	*SD*	$\bar{x}$	*SD*
Foraging	7.9	4.1	20.2	11.3	28.0	4.6	16.0	6.2
Inactive	5.0	2.0	17.1	6.1	47.3	5.1	30.6	12.9
Incubating	81.0	4.8	52.5	19.6	6.8	6.2	41.2	20.8
Aggression	2.3	1.2	7.0	1.8	8.7	2.1	7.5	3.6
Walking	2.5	1.5	2.4	0.9	7.4	1.1	4.3	0.9
Flying	0.4	0.3	0.9	0.7	0.3	0.1	0.4	0.4

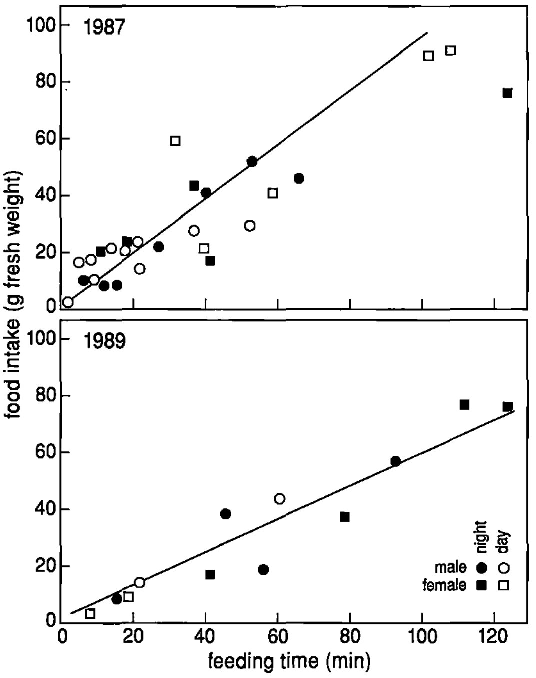

Fig. 4. Food intake between two incubation spells in relation to the time spent feeding by a ♂ and ♀ resident during day and night. Food intake rate did not differ between the sexes ($F = 1.133, p = 0.295$) or between day and night ($F = 0.003, p = 0.959$). Intake rate was significantly lower in 1989 (0.59 g min^{-1}) than in 1987 (0.98 g min^{-1}) ($F = 10.520, p = 0.003$).

daylight and by night. The differences were considerable, especially for the ♂ (Table 2). This was entirely due to the ♀ of this couple which was very reluctant to incubate the eggs when observers were close to the nest, especially during the day. She incubated on average only 6.8% of the time during day-time low water periods. Her mate had to compensate for this and incubated more than 80% of day-time low water periods. Consequently, the ♂ had less time available for other activities. As a result of this, it is the time budget during daylight low water periods which is at odds with the normal pattern of time allocation. The time budget during the night differed only marginally from the average time budget during the day of all other resident pairs (Table 3). The main difference was that the ♀ devoted relatively little time to foraging, but she collected most of her food during the day (Table 2) when she refused to incubate. In 1989, the ♂ devoted more time to aggression and spent less time inactive than did the other ♂♂ in the years before. All in all, the time budget of Oystercatchers during night-time low water periods appears very similar to the time budget during the day. This is in agreement with the results obtained on the German Wadden Sea island of Mellum where the activity of breeding Oystercatchers was studied using radio-telemetry (Exo 1993).

Table 3. The time budget (%) during the incubation stage of a resident male and female during night-time low water compared to the time budget of all other Oystercatchers with a resident territory during daytime low water periods (n = 13 by day in 1986-88, n = 4 nights in 1987 and n =3 nights in 1989). The percentage of time devoted to various activities during the night was tested against the corresponding values during the day with Mann-Whitney U-tests; - = not significant, * = $p < 0.05$, ** = $p < 0.01$.

	day 1986-88		night 1987			night 1989		
	$\bar{x}$	*SD*	$\bar{x}$	*SD*	*p*	$\bar{x}$	*SD*	*p*
♂♂								
foraging	23.2	9.1	20.2	11.3	-	22.8	10.0	-
inactive	19.4	11.4	17.1	6.1	-	7.7	5.3	*
incubation	44.0	15.3	52.5	19.6	-	52.5	13.6	-
agression	6.1	4.1	7.0	1.8	-	15.3	0.9	**
walking	4.0	1.3	2.4	0.9	*	1.5	1.2	*
flying	1.2	0.9	0.9	0.7	-	0.2	0.2	*
♀♀								
foraging	27.4	7.8	16.0	6.2	*	33.5	5.6	-
inactive	18.8	8.8	30.6	12.9	-	17.1	2.0	-
incubation	42.8	16.6	41.2	20.8	-	37.2	17.4	-
agression	4.9	3.1	7.5	3.6	-	6.4	2.7	-
walking	5.0	2.7	4.3	0.9	-	5.1	5.0	-
flying	1.1	0.9	0.4	0.4	-	0.7	0.5	-

Total food consumption per low water period

In 1987, the ♂ consumed on average more food during the night than during the day (Table 4), but the difference was not significant due to the enormous variation ($t = -0.486$, $p = 0.644$). In the ♀, this pattern was reversed; she consumed significantly more food during day-time low water periods ($t = 4.236$, $p < 0.005$). The difference between ♂ and ♀ was due to the different proportions of time allocated to foraging by day and by night (Table 2). In 1989, we have only measured food consumption during night-time low water periods. The amount of food consumed was very close to the average of day and night-time food consumption in 1987 for both ♂ (80.1 *versus* 79.8 g) and ♀ (107.0 *versus* 98.1 g). This suggests that the average amount of food consumed hardly differs between day and night-time low water periods.

Food consumption and body weight

The large variation in total food consumption per low water period provides an opportunity to

Table 4. Average amount of food consumed (gram fresh weight) by a male and female resident during day and night-time low water periods (day 1987: n = 4, night 1987: n = 4, night 1989: n = 3).

	day 1987		night 1987		night 1989	
	mean	*SD*	mean	*SD*	mean	*SD*
♂	70.0	59.5	89.6	54.7	80.1	24.6
♀	134.1	21.9	62.1	25.9	107.0	25.5

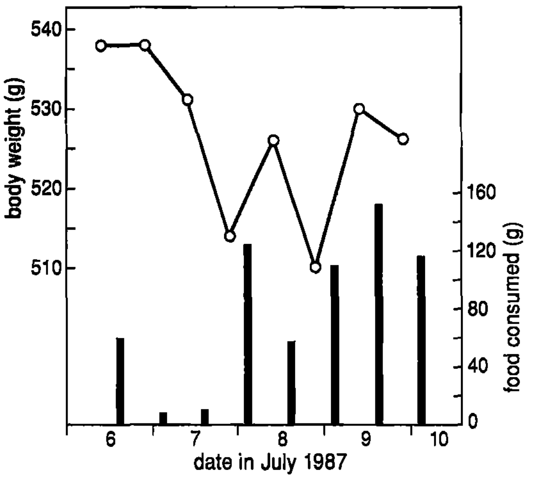

Fig. 5. Food consumption (bars, right-hand axis) of a male resident during eight consecutive low water periods and its digesta-free body weight (dots, left-hand axis) at the start of each low water period. The shaded areas indicate night-time low water periods.

evaluate how body weight is affected by food consumption. Crude body weight fluctuates wildly in the course of a low water period and depends mainly on how much food is still in the digestive tract. These fluctuations have little relevance for the question how much food is required to match energy expenditure and maintain body condition. The body weight of interest is the clean weight without digesta. Clean body weight is most likely to occur at the end of a high water period when the birds have not been able to eat for the past five or six hours. Since the maximum amount of food that Oystercatchers are able to store requires approximately five hours to process (Kersten & Visser 1996), it seems reasonable to assume that the initial body weight at the start of a low water period represents clean body weight. We always succeeded to measure clean body weight of the ♂, but for the ♀ we often failed. The only thing we can say about her clean body weight is that she weighed 556 g when measurements started on the 6th of July and still weighed 555 and 553 g on the 8th and 9th of July, respectively. This suggests that she maintained her body weight over the observation period. The data for the ♂ show a general agreement between body weight and the amount of food consumed during the preceding low water period (Fig. 5). Two low water periods with hardly any food intake resulted in a sharp decline of clean body weight. Although food consumption increased towards the end of our observations, his final body weight was still 12 g below the weight with which he started. In 1989, both birds were heavier than in 1987, but we observed only at night and cannot give a detailed account of the weight changes between one low water period and the next. Nevertheless, the ♂ weighed 549 g and maintained this weight over a three-day period. The clean body weight of the ♀ could only be determined once and was an impressive 583 g.

Average food consumption over a 24 hour day

Table 5. Food consumption per low water period (gram fresh weight) of a pair of resident Oystercatchers during four consecutive days in July 1987.

1987	♂			♀		
	day	night	sum	day	night	sum
6 July	59.2	8.0	67.2	110.6	84.5	195.1
7 July	10.9	124.9	135.8	120.3	80.6	200.9
8 July	57.1	109.4	166.5	155.2	54.7	209.9
9 July	152.6	116.1	278.7	150.2	28.7	178.9
average			162.1			196.2
SD			88.1			13.0

was 34 g less for the ♂ then for the ♀ (Table 5). Due to the enormous variation in the food consumption by the ♂, this difference was not statistically significant ($t = -0.766$, $p = 0.473$). Nevertheless, the female's food intake was sufficient to maintain a constant body weight, whereas this was not the case for the ♂.

DISCUSSION

Measuring food consumption with a nest balance

We developed a model to calculate food consumption of Oystercatchers from their weight gain between two incubation spells and the additional amount of excreta voided before the bird returned to its nest. The model parameters were previously determined in captive Oystercatchers eating Mussels *Mytilus edulis* (Kersten & Visser 1996). The input variables that have to be measured include the body weights of the bird upon departure from and arrival at the nest and the times when it starts feeding and when it returns to the nest. The only pre-condition is that measurements start when the bird has no digesta left in its digestive tract. The model predictions agreed well with estimated food consumption based on direct observations in the field, regardless of the type of prey consumed (*Macoma balthica* or *Nereis diversicolor*). Oystercatchers only consume the soft part of bivalves and the general composition of *Nereis*, the soft parts of *Macoma* and that of *Mytilus* as well is rather similar; they all comprise approximately 80% water and a very small percentage of inorganic matter (Zwarts 1991). Our results indicate that prey types with similar composition not only have a similar assimilation efficiency (Castro *et al.* 1989), but are also processed at a similar rate.

The model was used to calculate food consumption of free-living Oystercatchers under circumstances when this could not be measured by direct observation; downshore outside their territory and during night-time low water periods.

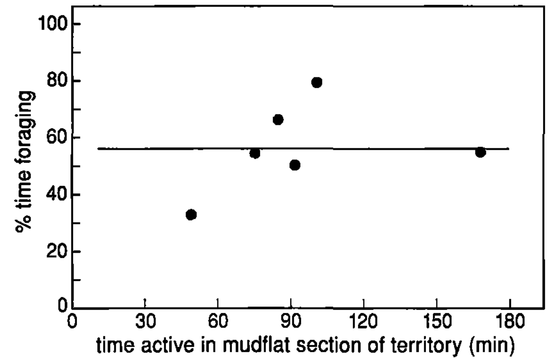

Fig. 6. Proportion of time spent foraging while the birds are active in the mudflat section of their territory. The data was collected during three night-time low water periods in 1989. Each dot represents one member of a pair of residents during an entire low water period.

Feeding outside the breeding territory

It came as a surprise that the rate of food intake outside the birds' own territories was comparable to the rate of food intake within the territory (Fig. 3). A higher rate of food intake in downshore areas was expected, but did not materialize. This raises the question why resident Oystercatchers leave their territory to feed elsewhere when the benefit is not a higher food intake or a shorter foraging time? It is possible that birds collect food elsewhere in order to conserve the food supply within the territory for later in the season when chicks are around which have to be fed from the food source that is left over. For two reasons this is not very likely. First, feeding elsewhere does not necessarily conserve food since intruders occasionally entered the territory to feed. Second, the growing season of the macrofauna in the substrate coincides with the Oystercatcher's breeding season. This results in a doubling of the biomass between March and June despite the consumption by the birds (Zwarts & Wanink 1993).

Another possible benefit of feeding elsewhere is related to the time spent in aggression while the birds are in their territory. The time budget of Oystercatchers incubating eggs is rather compressed, since half the time has to be allocated to the act of incubation itself. So, there is little time left for all other activities. From Table 2 it can be deduced that the ratio between time allocated to aggression and time allocated to foraging is about 1:3. However, foraging time includes a considerable fraction of time spent outside the territory, while aggression time is exclusively in the territory. This implies that the ratio between aggression and foraging while the bird is in its territory becomes less favourable. During our irregular observations in downshore feeding areas, we were often amazed by the observation of birds known to breed on the marsh foraging vigorously. This was in sharp contrast to the regular birds in these areas, non-breeders and many of them immature, who appeared to have all the time in the world. Occasionally, such a 'regular' approached a 'breeder' in an aggressive posture. The reaction of the 'breeder' was really impressive: without losing any time it took off, landed a hundred meters further on and continued to feed even before the landing was finished. We are pretty certain that in the same place but at another time these 'regulars' were no match for the established breeders. But now, while there were eggs on the marsh, they had no time to enter into ceremonial displays.

This option, to ignore your opponent, is not available to birds when they are in their territory. Given the overwhelming importance of a high quality resident territory for their reproductive prospects (Ens *et al.* 1992) the owners have to respond adequately to every intrusion: giving in today may well lead to bigger problems tomorrow. In 1989, we registered how long the birds were active in the mudflat section of their territory and what proportion of this time was devoted to either foraging or aggression. An impressive 43.5% of the active time on the mudflats was spent in aggression (Fig. 6). When half the time of a low water period has to be allocated to incubating and some 10% is lost to preening, flying and the transition between different activities, this leaves a maximum of 40% of the time available for foraging. At the average intrusion pressure, the time devoted to foraging is only ((1 – 0.435) x 0.40 =) 22.6% of the low water period. This is very close to the actual time spent foraging (Tables 2 & 3) and implies that there is no flexibility left in the time budget. When, by chance, the percentage of time allocated to incubating is higher than 50% or when there are more intrusions than normal, the birds are not able to meet their food requirements and draw upon their reserves which have to be restored later. This uncomfortable situation can be avoided by foraging outside the territory and thereby reducing the time that has to be allocated to aggression. There is, however, one condition to this solution. Resident territory owners can only afford this luxury when they are sure to expel every intruder that has entered the territory during their absence. This was never a problem during our observations.

Food consumption at night

The results of this investigation show that the rate of food intake, the time budget and the total amount of food consumed per low water period hardly differ between day and night-time low water periods. Hulscher (1996) reviewed the available evidence concerning nocturnal food intake in the Oystercatcher and concluded that there was no difference between day and night in those studies where food was available for several hours. This was based on observations of captive birds and birds feeding on semi-natural mudflats. Our data demonstrate that this applies to free-living birds as well.

Our measurements of night-time food intake were performed during moonlit nights. We have no data on food intake during a period of new moon since the situation on Schiermonnikoog is such that new moon always coincides with high water around midnight. Consequently, night-time low water periods in the complete absence of moonlight do not occur during the summer in our study area.

Food consumption and energy expenditure

The daily food consumption of the residents observed during eight consecutive low water periods in 1987 was 196 and 162 g fresh weight for ♂ and ♀, respectively. The ♀'s body weight remained constant over this period at 555 g, but the weight of the ♂ dropped from 538 to 526 g. We will use these data to estimate the daily energy expenditure of residents during the incubation stage. The ash-free dry weight of estuarine prey species is on average 16% of their fresh weight (Zwarts *et al.* 1996a) while their energy content averages 21.2 kJ g^{-1} AFDW (Zwarts & Wanink 1993). The assimilation efficiency of Oystercatchers is always close to 85% over a wide spectrum of diets with low ash contents (Kersten & Piersma 1987, Speakman 1987, Kersten & Visser 1996, Zwarts & Blomert 1996) and we assume this value holds for birds eating *Nereis* as well. The amount of energy assimilated per day amounts to (196 × 0.16 × 21.2 × 0.85 =) 565 kJ for the ♀ and (162 × 0.16 × 21.2 × 0.85 =) 467 kJ for the ♂. For the ♀, this value should be close to her daily energy expenditure, but for the ♂ expenditure was higher than income since he lost weight over the observation period. Therefore, we have to add something to correct for this weight loss of on average 3 g per day. Short-term weight loss usually consists of equal proportions of fat and wet protein (Davidson 1984, Meijer *et al.* 1994, Zwarts *et al.* 1996c) with an energy content of 40 and 5.1 kJ g^{-1}, respectively (Schmidt-Nielsen 1975). Using these values, the weight loss of the ♂ has an energy equivalent of (0.5 × 40 + 0.5 × 5.1 =) 22.6 kJ g^{-1}. Consequently, the daily energy expenditure of the ♂ is (467 + 3 × 22.6 =) 535 kJ day^{-1}. This differs only 5% from the female's 565 kJ day^{-1}.

This indicates that energy expenditure during the incubation stage is very low. The Basal Metabolic Rate (*BMR*) of Oystercatchers is 2.91 W, which amounts to 251 kJ day^{-1} (Kersten & Piersma 1987). Consequently, energy expenditure of our couple was only 2.2 × *BMR* and this is even less than the energy expenditure of captive Oystercatchers, which is on average 601 kJ day^{-1} (Kersten & Piersma 1987, Goede 1993). Consequently, the incubation stage is probably a period when energy is conserved, rather than expended. This appears in sharp contrast with the massive energy expenditure of incubating Turnstones *Arenaria interpres* in arctic Canada (Piersma & Morrison 1994). This was measured with the doubly labelled water technique and averaged 4.21 W or 4.25 × *BMR*. As the authors reported, daily energy expenditure of these birds decreased rapidly with increasing standard operative temperature from 4.3 W at -2°C to 3.0 W at +12°C (from Fig. 3B in Piersma & Morrison 1994). When extrapolated to the lower critical temperature of 22-23°C (Kersten & Piersma 1987), this leaves an energy expenditure at thermoneutrality of 2.02 W or 2.0 × *BMR*. In other words, the Turnstone transplanted to a benign climate would only require 2 × *BMR* during the incubation stage. We conclude that the low energy expenditure of our Oystercatchers is entirely due to the fact that they have no additional costs for thermoregulation since ambient temperature during the incubation period in our study area is above the lower critical temperature of 9-10°C (Kersten & Piersma 1987).

Food availability and food consumption

In both members of the pair that was observed during the night, the rate of food intake was about 40% lower in 1989 than in 1987 (Fig. 4). Since the time available for foraging is much restricted during the incubation stage, it seems reasonable to assume that the birds try to collect food at the maximum rate. This would imply that food availability in 1989 was reduced compared to 1987. Yet, the total amount of food consumed per low water period appeared to be similar in both years (Table 4). In addition, the digesta-free body weight of the birds was even higher in 1989 than in 1987. This suggests that the energy budget was still in balance, despite the reduced intake rate in 1989. Total food consumption could only have been maintained by relocating time devoted to other activities in 1987 to foraging in 1989. Not surprisingly, most of this reallocation comes from a decrease of the time spent inactive. In the ♂ this dropped from 17.1% to 7.7%; in the ♀ from 30.6% to 17.1% (Table 3). Although the birds were still able to cope with the situation in 1989, the buffer derived from time spent inactive was almost fully used up. Any further decline of food availability and a concomitant reduction of the

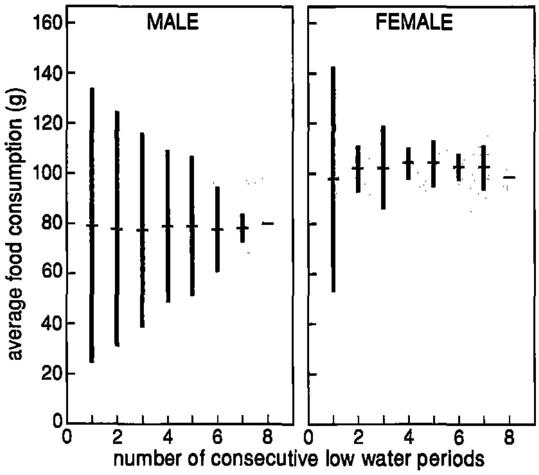

Fig. 7. Food consumption of a male and female resident averaged over an increasing number of consecutive low water periods. Vertical bars give the standard deviation and the shaded areas represent the expected standard deviation when food consumption does not depend on the amount of food consumed before. For instance, we have five measurements of the food consumption during four consecutive low water periods at our disposal. For each measurement we calculated the average amount of food consumed per low water period. The mean value of these five averages is plotted together with its standard deviation.

food intake rate may well lead to an emergency situation where it becomes very difficult, if not impossible, to maintain a balanced energy budget during the incubation stage.

Time scale at which food intake is regulated

One of the most striking outcomes of this investigation is that the amount of food consumed per low water period is so variable. For the ♂ this variation was to some extent induced by our activities, but even in the ♀ food consumption varied from 29 to 155 g per low water period. This variation can only persist when the birds are able to meet a large fraction of their daily food requirements in only one low water period. When we take 196 g fresh weight, the average daily food consumption of the ♀, as a first estimate of the food requirements of a bird with a constant body weight, it can be seen in Table 5 that on three occasions more than 75% of the amount required was collected in a single low water period. This raises the question at what time scale food consumption is regulated to balance energy expenditure. We used the data collected in 1987 to investigate how fast the variation in food consumption disappears when food consumption is averaged over an increasing number of consecutive low water periods (Fig. 7). In the ♀, variation in average food consumption decreased rapidly with the number of low water periods included. She appeared to regulate food consumption on a 24 hour basis. This was different for the ♂; the variation in his food consumption dropped under the random expectation only after it was averaged over six low water periods. This was caused by the fact that his food consumption was very meagre during the first part of our observation period when he spent almost all of his time incubating due to the female's abstinence. He compensated for this deficiency later, but by consequence low water periods with low and high food consumption were clustered in time. Despite this difference, the data for ♂ and ♀ are in a certain way consistent. The ♀ regulated her food consumption over a time scale of two low water periods and was able to maintain a constant body weight over the observation period. The ♂ hardly ate any food

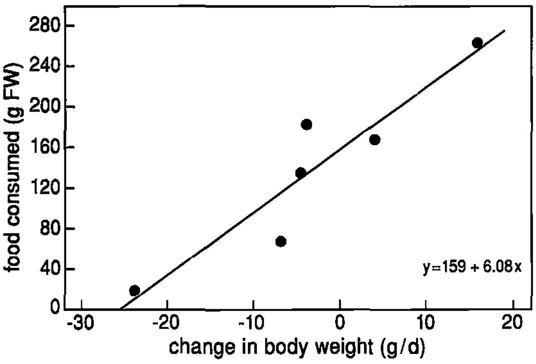

Fig. 8. Food consumption over two consecutive low water periods of a male resident in relation to fluctuations of its body weight. The linear regression equation explains 86% of the variance.

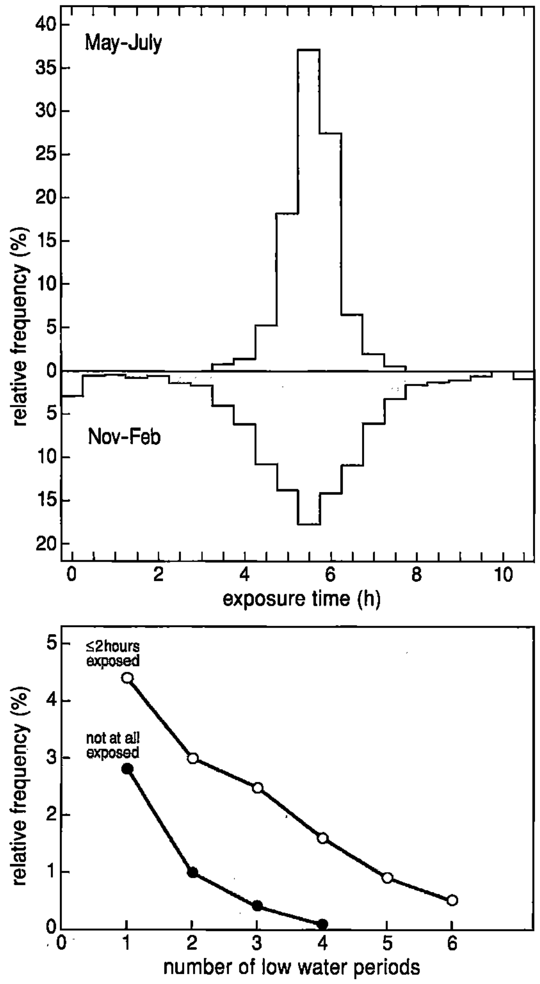

Fig. 9. (Top) Relative frequency of exposure times during low water at NAP-level in summer and winter. (Bottom) The incidence of short exposure times in winter, averaged over an increasing number of consecutive low water periods. Derived from data supplied by Leo Zwarts.

during two consecutive low water periods at the start of our observations. This resulted in a 24 g decrease of his digesta-free body weight. Despite increased food intake later on, the bird was not able to recover completely during the subsequent five low water periods. This suggests that it is important to match food consumption with energy expenditure on a 24 hour basis. Any deficiency accumulated over time takes a much longer time to compensate for. The effect of food consumption per 24 hours on the male's digesta-free body weight is shown in Fig. 8. The bird required 159 g of fresh food to maintain a stable body weight, while no food consumption at all resulted in a 26 g weight loss.

The reduction of the male's body weight over the observation period in 1987 was almost certainly induced by our activities and the female's response to these. Given the fact that Oystercatchers are able to collect the required amount of food in a remarkably short period of time (Table 2 and Kersten 1996), and that in summer the mudflats are predictably exposed for at least 5 hours twice a day, it does not seem likely that incubating Oystercatchers have any problem to match the demands on a 24 hour basis. This becomes entirely different in winter when some 250 000 Oystercatchers depend for their food supply on the intertidal mudflats in the Dutch Wadden Sea. Many of these birds feed around NAP-level where the average exposure time in winter, November until and including February, is 5.6 hours (L. Zwarts pers. comm.). However, exposure time is less predictable in winter and the birds regularly face a situation that the feeding area is available for less than two hours per tidal cycle (Fig. 9). On average more than twice per winter the feeding area is not exposed at all for two low water periods in a row. It is obvious that the birds have to draw upon their reserves under these conditions or resort to feeding in non-tidal areas. This emphasizes the adaptive value of the relatively large energy reserves carried around by birds feeding in these low-lying areas (Zwarts *et al.* 1996b). The real importance of these energy reserves may go well beyond that of a simple energy substitute. Partially depleted energy reserves may be restored quickly as soon as the situation has turned favourable again. However, if the deficit in the energy budget is retrieved from the more structural parts of the body, it may take a much longer time to recover from the effects. Such a prolonged revalidation period is suggested by our ♂ during the incubation stage, as he did not manage to recover completely from the ill-effects of only two low water periods with hardly any food intake during the next five low water periods.

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SAMENVATTING

De voedselopname van Scholeksters werd geschat op twee manieren (1) rechtstreekse waarnemingen aan voedselzoekende vogels, (2) registratie van de gewichtsverandering tussen het begin en het einde van een foerageerperiode bij broedende vogels, door een weegschaal onder het nest te plaatsen. In het laatste geval was het wèl nodig om aanvullende metingen te doen aan de hoeveelheid voedsel die intussen werd uitgescheiden. De twee typen metingen kwamen goed overeen. De automatische weegschaalregistraties konden daarom worden gebruikt om de voedselopname te schatten voor situaties waarbij rechtstreekse metingen niet mogelijk waren, bij voorbeeld als de vogels ver uit de kust en 's nachts foerageerden. Uit de gegevens bleek dat de opnamesnelheid in het territorium en ver uit de kust niet te verschilden, net zo min als die tussen overdag en 's nachts. Het ♂ at 's nachts meer dan overdag, bij het ♀ was dat andersom. Dit werd waarschijnlijk veroorzaakt door de verstoring die onze metingen gaven, omdat de gemiddelde comsumptie tijdens laagwaterperiodes overdag en 's nachts nauwelijk verschilden. De totale voedselconsumptie per etmaal werd geschat op 162 g nat vlees voor het ♂ en 196 g voor het ♀. Het ♀ bleef gelijk in gewicht, maar het ♂ verloor gewicht tijdens de waarnemingsperiode. Nadat daarvoor werd gecorrigeerd was de geschatte energie-uitgave per etmaal vrijwel gelijk: 535 kJ voor ♂ en 565 voor ♀. Dit was equivalent aan 2.2 × basaal metabolisme. De broedtijd was een goedkope periode. De voedselopname verschilde van de ene laagwaterperiode op de andere, maar over het etmaal gerekend was deze vrij constant.