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WHY OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* CANNOT MEET THEIR DAILY ENERGY REQUIREMENTS IN A SINGLE LOW WATER PERIOD

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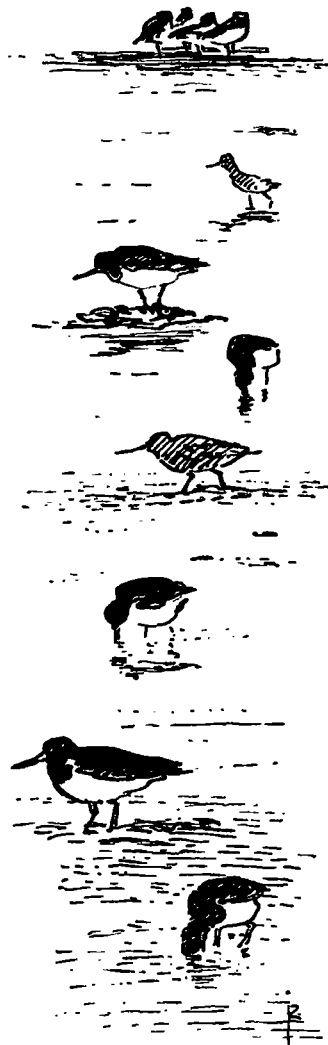
Captive Oystercatchers consume daily 25-40 g dry flesh or 550-850 kJ, of which they metabolize 450-700 kJ. Free-living Oystercatchers eat more than captive birds but, contrary to expectation, this is not due to greater activity costs but to a higher body weight. When body weights are equal, free-living and captive Oystercatchers consume the same amount of food. The intake rate of Oystercatchers generally varies between 1 and 3 mg dry flesh s^{-1} feeding, but if non-feeding times are included, the crude intake rate usually varies between 1 and 1.5 mg s^{-1}. Extremely high intake rates, above 4 mg s^{-1}, are only observed in birds feeding during a short bout after a long resting period. According to Kersten & Visser (1996a) such high intake rates cannot be sustained for long, because a maximum of 80 g wet flesh, equivalent to 12 g dry flesh, can be stored in the digestive tract and the processing rate does not exceed 4.4 mg wet flesh s^{-1} or 0.66 mg ash-free dry weight (AFDW) s^{-1}. Due to this digestive bottleneck, the birds are forced to spend much time on the feeding area each day. Since the exposure time of their intertidal feeding areas is usually 5-6 hours, Oystercatchers cannot meet their daily energy requirements in a single low water period, which would often suffice if intake rate was the limiting factor. For a given length of the feeding period, the bottleneck model predicts the maximum crude intake intake, called CIR_{max}, that can be achieved, i.e. the highest intake rate including the non-feeding time. When the birds are able to feed for less than three hours, the achieved crude intake rate usually remains far below this maximum, suggesting that the rate at which prey are found and eaten determines the intake rate. The consumption is also usually less than would be allowed by digestive constraint when the birds feed for twelve hours or longer, because the birds at thermoneutral conditions do not need more than 36 g a day. When the birds spend three to twelve hours on the feeding area, the average consumption is usually close to, or below the predicted maximum. However, in a few cases, the maximum was clearly exceeded. These studies do not invalidate the bottleneck model, because there is ample reason to believe that food consumption was overestimated. A detailed investigation of the many sources of error indicates that food consumption is more likely to be overestimated than underestimated in field studies.

Key words: Oystercatcher - *Haematopus ostralegus* - food consumption - food intake rate - processing rate - digestive constraint

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INTRODUCTION

The present-day consensus is that birds may fail to collect a sufficient amount of food in the time available, if they fail to choose correctly the prey species to take or the place to feed. Recently, Kersten & Visser (1996a) challenged this view by suggesting that Oystercatchers cannot process the food sufficiently fast during the time available for digestion, so that the digestion rate is often a more important constraint on consumption than the rate at which food is ingested. At first sight, this is a remarkable view as the time available for digestion will always exceed the time available for feeding. Thus, internal processing of the food may commence immediately after the first prey item has been ingested and continue long after the incoming tide prevents feeding. According to Kersten & Visser (1996a), food is processed at a constant rate, so that intake rates can only exceed this processing rate during periods when the digestive tract has not yet been filled to capacity.

The digestive bottleneck hypothesis has important implications, quite apart from challenging the traditional emphasis placed on maximization of intake rate in optimality models. It throws, for example, a different light on the occurrence of inactive birds during the time spent on the feeding area. These are not necessarily birds that are idling away their time, but could be birds whose digestive tract has been filled to capacity so that further feeding is impossible. Birds may not therefore always be able to fully exploit times of good feeding as, for example, when intake rate is high, and/or energy expenditure is low, and/or predation risk is low and/or risk of attracting parasites is low. If so, they may sometimes be forced to exploit less good feeding times as well. Evidently a bird that loses one hour of feeding time due to disturbance will suffer more if it has an empty gut than if its stomach is full because it loses irrecoverable processing time.

The bottleneck hypothesis dates back to Kenward & Sibly's (1977) work on Woodpigeons *Columba palumbus* eating vegetables and the work of Diamond *et al.* (1986) on hummingbirds feed-
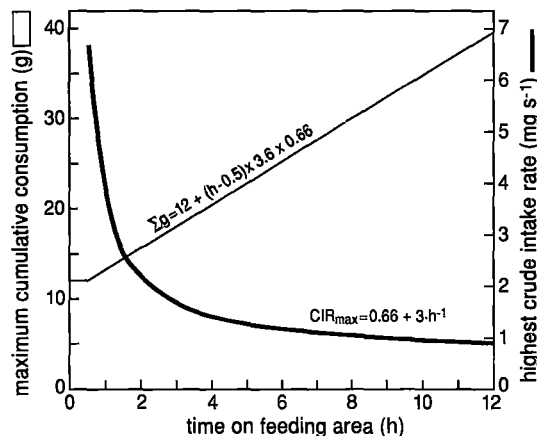

Fig. 1. Highest cumulative food consumption by Oystercatchers (g AFDW) as a function of the time spent on the feeding area (h), based upon the digestive constraint according to Kersten & Visser (1996a): (1) the storing capacity is 12 g AFDW, (2) defecation starts 0.5 hour after the start of feeding, (3) the processing rate is 0.66 mg s^{-1}. Thus, in a normal low water period of 5-6 hours, not more than 22.7 to 25.1 g can be consumed. From the predicted highest consumption, the highest crude intake rate (mg s^{-1} feeding, including non-feeding bouts; CIR_{max} (left axis)) can be calculated. In the first 0.5 hour, CIR_{max} equals the storage capacity (12 g) divided by the time spent feeding. Subsequently it decreases according to an inverse relationship that approaches the processing rate of 0.66 mg s^{-1} in the long term.

ing on nectar. The study of Zwarts & Dirksen (1990) on Whimbrel *Numenius phaeopus* eating crabs seems to be the only other case of this idea being applied to a carnivorous shorebird. As Kersten & Visser (1996a) derived their conclusions from only a limited number of experiments on captive Oystercatchers, before it is accepted as a fact in future Oystercatcher studies, it seems prudent to test the hypothesis and assess the potential for variability in the parameters.

If there is a digestive constraint, it follows that for a given length of the feeding period the total food intake cannot exceed the sum of the storage capacity and the amount of food that can be processed during that period ('broken stick' in Fig. 1). A necessary corollary is that maximal crude intake rates, or the intake rates calculated over a

period which includes the digestive pauses, will decrease with an increasing length of feeding period ('curved line' in Fig. 1). Since Oystercatchers start to defecate 30 min after the beginning of feeding (Kersten & Visser 1996a), the only limit to the intake rate during the first 30 min of feeding is the 80 g storage capacity for wet food, equivalent to 12 g dry flesh, i.e. ash-free dry weight (AFDW). Therefore, if Oystercatchers feed for 10 or 20 min, the highest possible intake rate will be 20 and 10 mg AFDW s^{-1}, respectively, and will decrease linearly to 6.67 mg s^{-1} if the birds feed for 30 min. If the feeding time is longer than 30 min, the intake rate further decreases with time but not any longer linearly because the birds start to defecate. There is thus an inverse relationship between the highest possible crude intake and the length of time spent on the feeding area (Fig. 1). When the birds feed for an infinitely long period, the crude intake rate cannot exceed the processing rate of 0.66 mg s^{-1}. However, when the feeding time is limited, the influence of the storage capacity increases as the feeding time h (hour) shortens, because the highest crude intake rate (CIR_{max}) can exactly be described by the equation:

$$CIR_{max} = 0.66 + 3h^{-1}.$$

The digestive constraint has one important consequence for the birds. If the daily requirement for food exceeds the maximum consumption that is predicted from the bottleneck hypothesis for a low-tide period, the birds will need to feed during both low-tide periods, irrespective of the intake rate that can potentially be achieved. In this paper, we will address two questions: (1) Do the many studies on food intake of Oystercatchers conform to the predictions of the bottleneck hypothesis, i.e. do the crude intake rates not exceed the curved line in Fig. 1? (2) Do birds rest more, or do they reduce their intake rate, if their consumption is restricted by the digestive bottleneck, or do they both?

To test the prediction of the bottleneck hypothesis, we use the data set on food intakes of Oystercatchers assembled from published and un-

published sources, of which a large part is summarized in Zwarts *et al.* (1996a). None of these studies was undertaken as an explicit test of the bottleneck hypothesis, but properly combining reported data on intake rate, feeding activity and time spent on the feeding area should yield figures that can be used for this purpose. The review shows that, except for a few cases, the prediction is met. In these anomalous cases, the intake rate exceeds the predicted maximum. This caused us to explore possible sources of error in the estimation of total food intake and whether they are most likely to overestimate, rather than to underestimate, intake rate. Furthermore, to evaluate whether the digestive bottleneck prevents free-living Oystercatchers from fulfilling their daily energy needs during a single tide, we need to know how much food an Oystercatcher in the wild needs per day. Several papers measured precisely the daily food consumption in caged birds and we convert these data into an estimate of the requirements of free-living Oystercatchers.

METHODS

Data

The data summarized in this paper have been taken from several sources, usually already published, but also unpublished theses, reports and data files. Zwarts *et al.* (1996a) give a full list of all sources. They also describe how these data were combined and how all measurements on prey size, prey weight, intake rate, time spent on the feeding time, and feeding activity were assembled into one data file, of which the essential measurements are given as an appendix; the intake rate were averaged per month of Oystercatchers feeding on a certain prey. In addition to these studies, their paper also includes long-term observations on individual birds studied in the Exe estuary (Ens & Goss-Custard 1984, Urfi *et al.* 1996), and the Dutch Wadden Sea (Blomert *et al.* 1983, Ens *et al.* 1996a & b, Kersten 1996).

Nearly all field studies give food consumption of Oystercatchers as AFDW. Hence we also use

this as the measure of food intake. Since, as discussed by Zwarts et al. (1996a), the energy content of marine invertebrates usually varies between 22 and 22.5 kJ g⁻¹ and Oystercatchers digest 85% of the ingested energy, the factor 19 can be used as a common multiplier to convert gross intake (mg AFDW) into metabolized energy (kJ) if necessary.

Definitions

Food consumption is measured as ash-free dry flesh (AFDW), gross energy (kJ) or metabolized energy (kJ). Intake rate is defined as food consumption per unit time of feeding, excluding the time spent resting and preening over the period the bird is on the feeding area. The feeding period is defined as the time spent on the feeding area, including any time not spent feeding. Feeding activity is the percentage of the time actually spent in feeding over the whole duration of the feeding period. Crude intake rate is the rate of food consumption over the entire feeding period, including all the non-feeding intervals. Finally, the highest possible crude intake rate, derived from the digestive bottleneck model and indicated by the curved line in Fig. 1, is called maximal crude intake rate (CIR_{max}).

RESULTS

Food consumption and feeding time

Figure 2A shows that the food consumption by captive birds lies, on average, just below the maximum predicted by the food processing model of Kersten & Visser (1996a). This is also true for field studies in which the consumption by individual, usually colour-banded, birds was measured over long periods (Fig. 2B). Most birds were observed over an entire low water period, but all observations longer than eight hours, and some of the shorter observation periods, refer to breeding birds or to non-breeding birds feeding in grasslands by day. Grassland-feeding birds foraged for less than half of the observation time, sometimes for even less than 20%, and therefore had very

low crude intake rates. Across all data, most crude intake rates fall below the predicted maximum, but a few do exceed this level. In contrast, there are several outlying points for the population averages, i.e. calculated for free-living birds feeding on a certain prey species (Fig. 2C). Some of these estimates are even three times higher than the predicted maximum consumption.

There are three possible explanations when the food intake exceeds the predicted maximum: (1) the bottleneck hypothesis is false; (2) the hypothesis is true, but the actual level of the digestive constraint is not constant but varies between conditions and (3) the food consumption is estimated incorrectly. If (3) is true, we would expect the frequency of excessively high food intakes to increase with the potential for errors being made. Our next step is therefore to assess the possible sources of error in the estimation of food intake and the most likely direction of these errors.

Food consumption in the field is often overestimated

To estimate the total food consumption over a feeding period it was necessary in most studies to measure the length of prey taken, their weight, the feeding rate (the number of prey taken per unit time feeding), the feeding activity (percentage of time spent feeding) and the duration of the feeding period. Since the estimation errors are multiplicative, even a few small errors in the component estimates may easily lead to a large overall error in the estimated total consumption.

Estimating prey size   When prey size is estimated from emptied prey found on the substrate surface, small prey may be overlooked more often than large ones. This error is possibly small when prey are collected on bare sand and mudflats, or from 'anvils', where each shell may be easily located. Small prey are possibly more easily being hammered under the surface, so one always needs to search with care. The error may be more serious on mussel beds (Ens 1982, Speakman 1984b, Cayford 1988). However, even if the sizes of prey found on the surface are representative of those eaten at the surface, the estimates may be biased
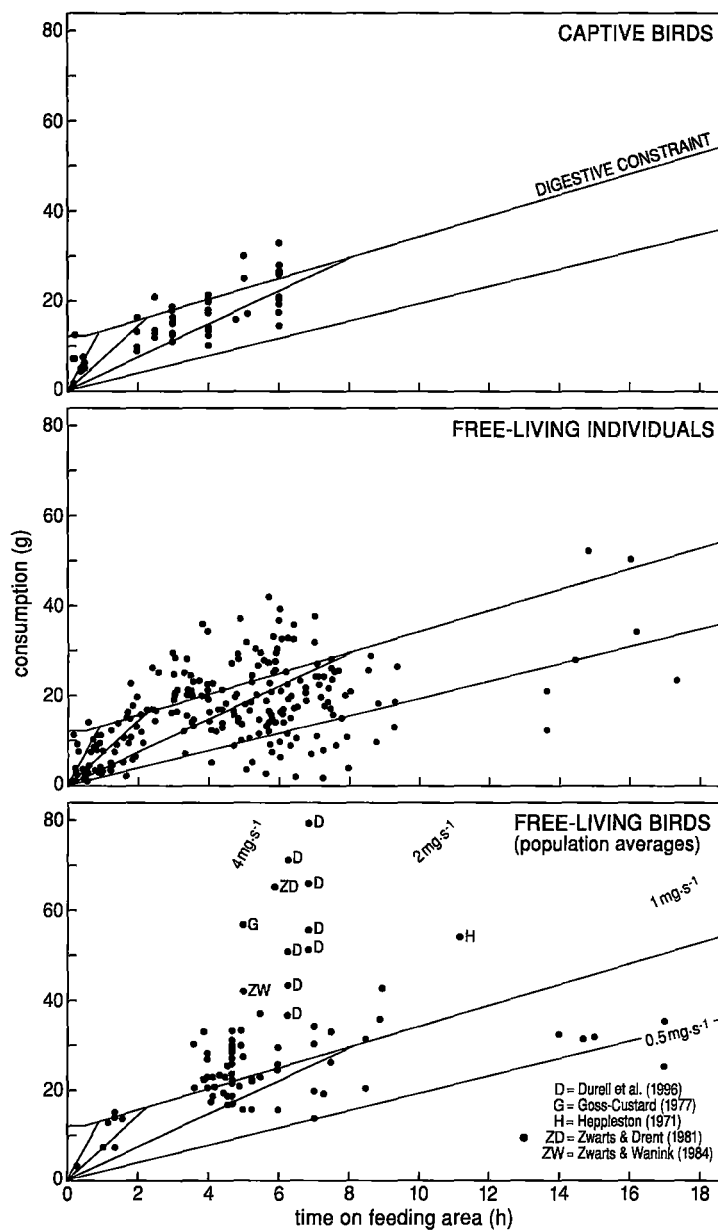
Fig. 2. Total food consumption (g AFDW) as a function of the time spent on the feeding area, given separately for (A) captive birds (*n* = 53), (B) free-living birds (long-term observations of individuals; *n* = 244) and (C) free-living birds (population averages; *n* = 83). The grey field indicates the predicted impossible consumption determined by the digestive bottleneck (Kersten & Visser 1996a). The solid lines give the consumption with the crude intake rate (during feeding and non-feeding periods combined) set at 0.5, 1, 2 or 4 mg s^{-1}. The sources of the data shown in panels A and C are listed in the appendix of Zwarts *et al.* (1996a). In addition, panel A gives the 34 measurements of Swennen *et al.* (1989) on captive birds. The data in B refer to the consumption of individual birds over a certain time, usually an entire low water period; sources: Blomert *et al.* (1983), Ens & Goss-Custard (1984), Ens *et al.* (1996a & b), Kersten (1996), Urfi *et al.* (1996) and Zwarts & Blomert (1996). Studies marked with a capital in panel C are discussed in the text.

if Oystercatchers eat certain size classes of bury-
ing bivalves *in situ*, and so beneath the surface.
Although this possible error has not yet been in-
vestigated, we might expect them to be errors of
overestimation for two reasons. First, prey *in situ*
are eaten in less time than lifted prey (Wanink &
Zwarts 1985, 1996, Hulscher *et al.* 1996), allowing
small prey eaten *in situ* still to be profitable.
Moreover, captive Oystercatchers lifted deep-liv-
ing prey more often than they lifted shallow prey
(Wanink & Zwarts 1985, Hulscher *et al.* 1996),
which would generally be smaller than those at
greater depths (Zwarts & Wanink 1993). Thus,
collecting samples of emptied prey at the surface
presumably causes large prey to be over-repre-
sented in the diet.

Converting prey size into prey weight Prey size is
usually converted to prey weight from allometric
relationships based on random samples of prey,
thus estimating the average weight of each size
class. Oystercatchers, however, do not take 'aver-
age' prey. They select thin-shelled Mussels *Myti-
lus edulis* when hammering; they search for bi-
valves that are slightly gaping when stabbing; and
when they probe for buried prey, they take those
living closest to the surface. Such accessible prey
are often in a relatively poor condition (Esselink
& Zwarts 1989, Zwarts & Wanink 1991, Goss-
Custard *et al.* 1993). The greatest overestimates
arising this way probably occur in Oystercatchers
feeding in winter on *Scrobicularia plana*. The
majority of these live out of reach of the bill and
the few that are still accessible are in very poor
body condition.

Prey not completely eaten It is usually assumed
that Oystercatchers clean a bivalve completely,
whereas some flesh often remains along the man-
tle edge and where the adductors are attached to
the valves. When in the laboratory, the bivalves
are briefly immersed in boiling water so that all
flesh can be easily removed from the shell, the
stub of the adductor muscle remains attached to
the shell, just as when Oystercatchers clean a
shell. However, it is not clear in how many stud-
ies the adductors are entirely cut free from the
valves instead. Obviously, the amount of flesh ex-

tracted in the laboratory is never below, but al-
ways exceeds the amount eaten by Oystercatch-
ers, although the differences may usually be
small. Occasionally, however, the error may be
large; for example, Oystercatchers left behind
11.7% of the AFDW of Cockles *Cerastoderma
edule* (Hulscher unpubl.); 7.6% of Mussels
(Speakman 1984a) and some 50% in Giant
Bloody Cockles *Anadara senilis* (Swennen 1990).
The only error is also serious when Oystercatch-
ers pull out the siphon of the Soft-bodied Clam
Mya arenaria and leave the rest of body behind;
an estimated 22% of the prey flesh can be lost in
this way (Zwarts & Wanink 1984).

It would be worthwhile in future studies to
measure the amount of flesh remaining in the ope-
ned shell, but there are two problems. Prey ope-
ned by Oystercatchers may be systematically cle-
aned by Oystercatchers or other waders, such as
Turnstones *Arenaria interpres* (Swennen 1990).
Secondly, part of the prey may be stolen by gull
and crow species (Zwarts & Drent 1981, Ens &
Goss-Custard 1984, Swennen 1990). As such prey
cannot be distinguished from prey eaten by Oys-
tercatchers, they will cause an overestimation of
the amount of flesh left behind if gulls and crows
are less adept than Oystercatchers at removing the
flesh from the valves.

Estimating time spent feeding The time spent
feeding is estimated in two ways, but both tend to
overestimate the percentage of time actually spent
feeding. When birds are observed for fixed inter-
vals of 5 or 10 minutes, birds should be chosen at
random, but observers will be inclined to start
with a feeding, and not a resting, bird. Inevitably
this overestimates the feeding activity when such
observations are used to estimate the time spent
feeding. For instance, the feeding activity of Oys-
tercatchers on leatherjackets *Tipula paludosa* in a
grassland from sunrise to sunset was estimated as
83.5% from birds observed for 15 min periods,
but 59.1% from group scans made every 15 min
(Veenstra 1977). Most studies overcome this diffi-
culty by determining feeding activity from regu-
lar scans of feeding and non-feeding birds, but
this method may also be biased because birds

may leave the feeding area to rest (Brown & O'-Connor 1974, Zwarts et al. 1990).

Estimating total time on the feeding area The estimate of the time spent on the feeding area by the average bird is too high when the feeding duration is based on the time birds are present on the feeding site, because individual birds may arrive later and/or leave earlier than the average (Ens & Goss-Custard 1984). The feeding time of individual birds was one hour less than the four to six hours estimated across all birds (Zwarts et al. 1996d). The difference is of course much larger during the breeding season when individual birds feed in bouts of only one hour and spend, in total, only 10 to 30% of the available low water period actually on the feeding area (Ens et al. 1996a).

Can high food intakes be explained as estimation errors?

To what extent can the extremely high crude intake rates in some studies plotted in Fig. 2C be attributed to these five types of error? The studies which estimated an extremely high consumption will be discussed in turn.

(1) Heppleston (1971) made all his measurements between 2.5 hours before and after dead low water. He warned that extrapolation to the entire exposure time would overestimate the total consumption, because the mussel bed was exposed for eleven hours and the birds hardly fed over the last few hours. However, as this was not quantified, it could not be taken into account.

(2) Goss-Custard (1977) feared that his consumption estimate was too high because his shell-collections may have been biased towards large Cockles. Nor did he take into account that Oystercatchers did not eat all the flesh from the Cockles.

(3) Zwarts & Wanink (1984) studied Oystercatchers feeding on small Mya in autumn. The birds used a mixture of three techniques: the birds either only grasped the siphon, or they ate the whole prey in situ or they lifted the prey to the surface. Although we know now (Hulscher et al. 1996, Wanink & Zwarts 1996) that larger prey are lifted more often than small ones, that study implicitly assumed that Mya found on the surface

were representative of all size classes taken, independent of the feeding technique used. Since the majority of prey were eaten in situ, the collection of prey lifted to the surface, probably caused the average size of Mya to be overestimated. Most clams in the mud were 16 to 30 mm long. The average length of the prey on offer was 22.8 mm, compared with 28.2 mm for the prey collected from the surface, a difference of 5.4 mm. Oystercatchers removed, in total, 80% of the prey over the months of observation. As Mya do not grow in autumn and winter, we would expect the size of the sampled prey to have gradually decreased over the season if Oystercatchers only took the larger prey. The extensive sampling programme showed, however, that the average size of the prey remained exactly the same, which implies that the frequency distribution of the prey taken did not differ from that on offer. Consequently, the prey weight was overestimated by 30%: the average prey taken was not 28.2 mm and 65.4 mg, but 22.8 mm and 50 mg. This error alone reduces the consumption over the five hours spent on the low water areas to 32 g. However, this is still 8 g above the maximum predicted by Kersten & Visser (1996a) suggesting a second estimation error was possibly made. The majority of Mya were eaten in situ. To estimate the amount of flesh remaining in the shell when the bird only took the siphon, the Oystercatchers were imitated by grasping the extended siphon with a pincer and pulling it from the shell. From this, it was estimated that 22% of the dry flesh remained behind. But perhaps Oystercatchers in the field left an even greater amount of flesh in the shell. If so, the estimated food consumption would no longer exceed the predicted maximum.

(4) Zwarts & Drent (1981) may have made three of the errors. First, they calculated from shell collections that Mussels of 50.5 mm long were taken. Although small prey were uncommon on their mussel bed, the average size of the prey taken would decrease by 5 mm if is assumed there was no size selection for prey size by Oystercatchers. If this is correct, the average AFDW of the prey taken would decrease from 981 to 687

mg, a reduction of 30%. Second, no correction was made for the flesh remaining in the shell, although it was clear that this was as much as 10-20%; juvenile Oystercatchers and several small wader species often took rather large bits of flesh left behind in the opened Mussels. Third, the activity counts were limited to the mussel bed itself, whereas birds sometimes roosted outside the counting site, causing the average feeding activity to be overestimated by some percent. There may have been a further error. Rather more measurements were made of the intake rate at the beginning and the end of the exposure time when the feeding rate was high. Correcting for this decreases the intake rate by a further 5%. Although each error in itself is not very large, in combination they result in a corrected estimate of the low water consumption being less than half of the original 61 g. However, this is still some g above the physiologically constrained highest consumption, perhaps because the Oystercatchers took prey in a poor condition.

(5) All eight estimates of the consumption of Oystercatchers in the Exe estuary feeding on Ragworms *Nereis diversicolor* (Durell *et al.* 1996) are above the digestive ceiling level. These authors collected droppings and measured the jaws of the worms to calibrate their size estimates. Since the majority of the large *Nereis* selected by Oystercatchers live in deep burrows out of reach of the bill, the birds usually feed on the rare worms that make grazing excursions to the surface and do not retreat fast enough into their burrow at the approach of a bird (Esselink & Zwarts 1989). Thus, it is conceivable that Oystercatchers do not take 'average' prey, but marginal ones with a low body weight. This is true even if Oystercatchers probe for worms down in their burrow, because within each size class, the heavy worms live in deeper burrows, so that only the relatively lightweight worms can be reached by a probing bird (Esselink & Zwarts 1989).

The studies discussed above, marked with capitals in Fig. 2C, have been omitted from further analysis. It is nonetheless possible that the same errors may also have been made in field studies recording a much lower consumption. However, if the average consumption in the field, without these outliers, is compared with consumption in controlled, experimental conditions, where most of sampling errors discussed above cannot be made, it is clear that the difference is not large (Fig. 2). From this we conclude that consumption may easily be overestimated in the field, but that the degree to which this occurs varies and is probably small in the majority of the studies.

Daily consumption

To investigate whether a digestive bottleneck forces Oystercatchers to feed during both low-tide periods, we must know how much food the birds need each day. These data are hard to get for free-living birds due to the difficulties in accurately measuring intake rate at night. There are two ways around this problem. First, we can exploit situations where the birds only feed by day. For intertidally-feeding birds, this occurs in the summer when the short night falls over the high water period. Blomert *et al.* (1983) selected such a day to measure the total consumption of a marked individual over 24 hours. Inland birds usually feed only during the daylight period and habitually roost communally at night, and a few studies have been made. Veenstra (1977) measured the feeding rate and feeding activity of inland Oystercatchers in March over the entire daylight feeding period, but since he did not measure prey weight, his data allow only a very crude estimate of the daily consumption to be made. Zwarts & Blomert (1996) observed some breeding pairs from sunrise until sunset in April, in the week before egg-laying, and measured prey fragments in the droppings to reconstruct prey weights. Second, it is possible to estimate nocturnal food consumption in nesting birds from weight changes recorded on an electronic balance placed under the nest (Kersten & Visser 1996b, Ens, Dirksen, Nieuwenhuis & Smit unpubl. and Exo & Scheiffarth unpubl.). The relation between weight change and consumption was calibrated by comparing weight changes to measured food consumption during the day.

Compared to these few field studies, many studies have measured daily consumption in captive birds (Table 1). With daily consumption expressed as AFDW, the variation is large. The average gross consumption is 32.3 g AFDW with a *SD* of 5.1 g, or 15.8% of the mean. This large variation is not due to daily variation in consumption, since the data in Table 1 for captive birds all refer to studies that averaged the consumption over longer periods, and in some cases over several individuals. We therefore first investigate to what extent this variation was due to differences in (1) energy content of the prey, (2) digestibility of the prey, (3) costs of thermoregulation, (4) weight changes, (5) body weight, (6) activity costs, (7) age and (8) season. This will then allow us to assess whether a difference in food consumption occurs between captive and free-living birds.

(1) Energy content of the prey The captive Oystercatchers were fed artificial food pellets, Cockles or Mussels. The four field studies refer to breeding birds feeding mainly on Cockles (Ens *et al.* unpubl.) and leatherjackets (Zwarts & Blomert 1996, Ens *et al.* unpubl.) and to a non-breeding bird feeding on *Scrobicularia* (Blomert *et al.* 1983). As different prey types contain different amounts of energy, this diversity of food types makes it likely that the variation in daily consumption would be less if it was expressed as gross energy intake. Hulscher (1974) found that three Oystercatchers alternately offered Cockles and Mussels, consumed, on average, per day 37.4 g AFDW if Cockles were taken, but 33.2 g, or 11% less, if their food was Mussels. The energy content of both prey was not measured, but other studies have found that the energy content of Mussels is 5-10% higher than that of Cockles (Chambers & Milne 1979, Merck 1983, Zwarts & Wanink 1993). The energy content of the food offered has been determined in 8 of the 13 studies and was estimated by us for the remaining ones (Table 1). The daily consumption of Oystercatchers averaged for all studies is 728 kJ (*SD* = 103); *SD* as percentage of the mean is 14.1% and thus marginally smaller than the variation in the daily AFDW consumption.

(2) Digestibility of the prey A further reduction in the variation may occur were the digestibility of the food to be known so that the daily metabolizable energy could be calculated. Digestibility in Oystercatchers feeding on Mussels was 85% of the energy (Speakman 1987, Kersten & Visser 1996a), whereas it varies between 65% and 89% in various types of food pellet (Kersten & Piersma 1987, Exo & Freimüth unpubl.). Even though a low digestibility might be expected for leatherjackets because this prey has a thick skin, 83 to 89% of the energy is actually metabolized (Zwarts & Blomert 1996). The metabolized energy consumption, averaged for all studies, amounts to 605 kJ per day on average (*SD* = 93; relative *SD* = 15.4%). Thus, in contrast to expectation, the variation in consumption did not decrease when expressed as net, rather than gross, energy.

(3) Thermoregulation The air temperature in most studies was above 10°C, the critical temperature below which the costs of thermoregulation increase (Kersten & Piersma 1987). However, two studies held birds at average temperatures of about 6°C. The extra amount of energy needed to meet these additional thermoregulation costs is estimated to be 30 kJ for each °C below 10°C, using the regression equation and conversion factors given by Kersten & Piersma (1987). The thermoregulation costs of waders along the shore are more effected by wind force than by temperature alone (Wiersma & Piersma 1994). The captive birds lived in sheltered cages, however, whereas the data for free-living birds were collected at air temperatures of > 15°C. Hence there is no need to estimate the extra costs due to wind flow.

(4) Gaining or losing body weight Another source of variation is whether birds were changing body weight. However, body weight remained constant in most of the experiments, the exceptions being indicated in Table 1. We assume that if Oystercatchers gain, or lose, 1 g fresh body weight per day, their net energy intake would be 20 kJ above, or below, the energy consumption required to keep their body weight constant. Oystercatchers are able to keep their body weight constant at a

daily gross consumption of 36 g and a net consumption of 670 kJ (see below). They lose 30 g a
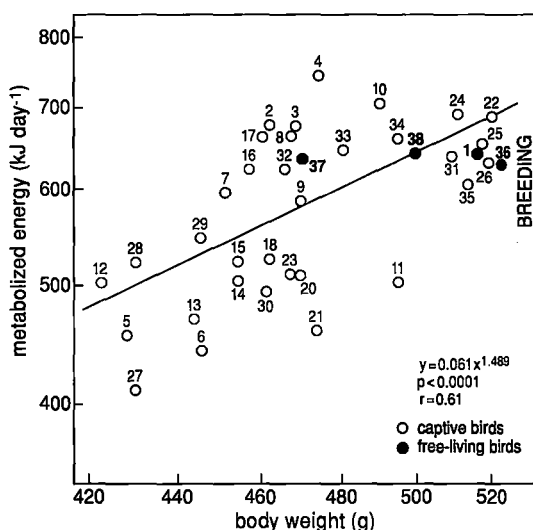
day if they take no food at all (Kersten & Visser 1996b). Hence, daily food consumption (C, AFDW) is a function of the daily change in body weight (ΔW, g):

$$C = 36 - 1.2\Delta W.$$

A slope of 1.2 g AFDW was found indeed in captive Oystercatchers by Kersten & Piersma (1987).

Fig. 3. The daily consumption (kJ metabolized energy) as a function of body weight in captive and free-living Oystercatchers according to several data sources given in Table 1. The digit codes in the figure correspond with the source numbers in Table 1. The grey field indicates the variation in daily energy expenditure of adult birds during the breeding season (Kersten 1996: Table 8). The daily consumption was measured at constant body weight and under thermoneutral conditions, and if this was not so, a correction was made (see text and Table 1).

Table 1. Daily consumption (g AFDW) and body weight (g) of Oystercatchers feeding on Cockles (*Cer*), Mussels (*Myt*), commercial food pellets (pel), *Scrobicularia* (*Scr*) or larvae of *Tipula* (*Tip*). Source numbers (used in Fig. 3) and sources are given in the first and last column. All birds were adults except one 1-year and four 3-year old birds (see column 'age'). All birds were held in captivity, but studies marked with F in column 'free' were free-living birds. All data were collected in thermoneutral conditions, except four and two birds held at an average air temperature of 6.5 and 6.3°C (see column '°C'). Body weight was constant in all studies over the periods concerned, but decreased in study 1 (18 g in 8 days), 23 (50 g in 26 days), 28 (19 g in 30 days), and increased in study 26 (38 g in 26 days), 27 (24 g in 28 days), 29 (13 g in 30 days) and 30 (34 g in 34 days); column 'BW$_c$' gives weight change (g day^{-1}). Change in body weight was unknown in field studies 36 and 38, but assumed to be constant. Average body weight (g, column 'BW') and month of observation are indicated. Body weight was not known for the days of observation in field study 36 and 38, but assumed to be equal to the average weight of the birds of the same sex, such as measured in other birds in the same time of the year and the same site. Columns 'g', 'kJ' and 'kJQ' give total daily consumption in terms of gross AFDW (g), gross energy (kJ) and metabolized energy (kJ), respectively. Kersten & Piersma (1987) found in pellets 22.8 kJ g^{-1} fresh weight being equivalent to 25.8 kJ g^{-1} AFDW, Goede (1993) 22.3-25.1 kJ g^{-1} AFDW for different kind of food pellets, Exo & Freimüth (unpubl.) 19.9 kJ in the pellets they used, Heppleston (1971) 22.56 kJ g^{-1} AFDW in Mussels, Merck (1983) 20.7 and 21.9 kJ g^{-1} AFDW in Cockles and Mussels, respectively, taken by the birds studied by Ens (unpubl.), Blomert & Zwarts (unpubl.) 24.5 kJ in leatherjackets in the same area where Ens collected his data (same month but later years), Zwarts (unpubl.) 22.2 kJ for *Scrobicularia* taken by the bird studied by Blomert *et al.* (1983), and Zwarts & Blomert (1996) 22.9 kJ for leatherjackets in April. It is assumed that in the remaining five studies the average energy content of Mussels was 23 kJ and of Cockles 22 kJ g^{-1} AFDW; column 'xkJ' gives the average energy content (kJ g^{-1} AFDW; printed in italics if estimated). Column 'Q' gives the digestibility and 'kJQ$_c$' the metabolized energy consumption (kJQ) corrected for weight change and thermoregulation costs (see text). Each measurement concerns an individual bird, except Kersten & Piersma (1987) and Goede (1993) whose measurements averaged 6 and 12 birds, respectively. Studies 32 to 34 concern the same six individuals being weighed each week. After a selection was made of weeks with a temperature > 10°C and constant body weights, the average consumption was calculated separately for three categories of body weight.

After correction for weight changes (20 kJ for each gram change of body weight) and costs of thermoregulation (30 kJ for each degree below 10°C), the maintenance metabolism in the birds amounts to, on average, 588 kJ day^{-1} ($SD = 85$). The coefficient of variation is 14.5%, and thus still quite large.

(5) The effect of body weight Body weight explains a significant part of the variation in daily energy intake. The correlation of the linear regression is +0.59 on a normal and +0.61 on a log-log scale (Fig. 3) with an exponent of 1.49 ($SE = 0.32$). The SD of the residuals from the regression line shown in Fig. 3 is 69, or still 11.7% of the av-

| no	prey	month	age	free	°C	BW_c	BW	g	xkJ	kJ	Q	kJQ	kJQ_c	source
1	Cer	6		F		-2.25	518	33.8	20.7	700	0.85	595	640	Ens *et al.* unpubl.
2	Cer	6					461	36.2	*22.0*	796	0.85	677	677	Hulscher 1974
3	Cer	6					468	36.2	*22.0*	796	0.85	677	677	Hulscher 1974
4	Cer	7					474	39.8	*22.0*	876	0.85	744	744	Hulscher 1974
5	Cer	6					426	24.4	*22.0*	536	0.85	456	456	Swennen *et al.* 1989
6	Cer	12			6.3		444	29.6	*22.0*	652	0.85	554	442	Swennen *et al.* 1989
7	Cer	12			6.3		450	37.8	*22.0*	832	0.85	707	595	Swennen *et al.* 1989
8	Cer	10					467	35.6	*22.0*	782	0.85	665	665	Swennen *et al.* 1989
9	Cer	6					469	31.4	*22.0*	691	0.85	587	587	Swennen *et al.* 1989
10	Cer	10					490	37.7	*22.0*	829	0.85	705	705	Swennen *et al.* 1989
11	Cer	6					495	26.9	*22.0*	593	0.85	504	504	Swennen *et al.* 1989
12	Myt	12	1				420	26.2	22.6	591	0.85	502	502	Heppleston 1971
13	Myt	7					442	24.0	*23.0*	552	0.85	469	469	Hulscher 1974
14	Myt	7					453	25.8	*23.0*	593	0.85	504	504	Hulscher 1974
15	Myt	7					453	26.8	*23.0*	616	0.85	524	524	Hulscher 1974
16	Myt	7					456	31.8	*23.0*	731	0.85	622	622	Hulscher 1974
17	Myt	7					459	33.9	*23.0*	780	0.85	663	663	Hulscher 1974
18	Myt	7					461	26.9	*23.0*	619	0.85	526	526	Hulscher 1974
19	Myt	8					467	34.0	*23.0*	782	0.85	665	665	Hulscher 1974
20	Myt	7					469	26.1	*23.0*	600	0.85	510	510	Hulscher 1974
21	Myt	7					473	23.5	*23.0*	541	0.85	459	459	Hulscher 1974
22	Myt	7					522	35.1	*23.0*	807	0.85	686	686	Hulscher unpubl.
23	Myt	3			6.5	-1.92	466	29.6	*23.0*	681	0.85	578	511	Koene 1978
24	Myt	3			6.5		512	40.7	*23.0*	937	0.85	796	690	Koene 1978
25	Myt	3			6.5		519	38.7	*23.0*	891	0.85	757	652	Koene 1978
26	Myt	3			6.5	1.46	521	39.1	*23.0*	899	0.85	764	629	Koene 1978
27	pel	8	3			0.86	428	32.4	19.9	644	0.67	432	415	Exo & Freimüth unpubl.
28	pel	7	3			-0.60	428	38.0	19.9	757	0.67	507	519	Exo & Freimüth unpubl.
29	pel	7	3			0.40	444	41.8	19.9	833	0.67	558	550	Exo & Freimüth unpubl.
30	pel	8	3			1.21	460	39.1	19.9	778	0.67	521	497	Exo & Freimüth unpubl.
31	pel	7					510	32.9	22.8	750	0.85	638	638	Goede 1993
32	pel	6					465	28.5	25.8	734	0.85	624	624	Kersten & Piersma 1987
33	pel	7					480	29.4	25.8	759	0.85	645	645	Kersten & Piersma 1987
34	pel	5					495	30.1	25.8	775	0.85	659	659	Kersten & Piersma 1987
35	pel	1					515	27.5	25.8	711	0.85	604	604	Kersten & Piersma 1987
36	Scr	7		F			525	33.3	22.2	739	0.85	628	628	Blomert *et al.* 1983
37	Tip	6		F			470	31.3	24.5	767	0.83	636	636	Ens *et al.* unpubl.
38	Tip	4		F			500	31.5	22.8	719	0.89	640	640	Zwarts & Blomert 1996
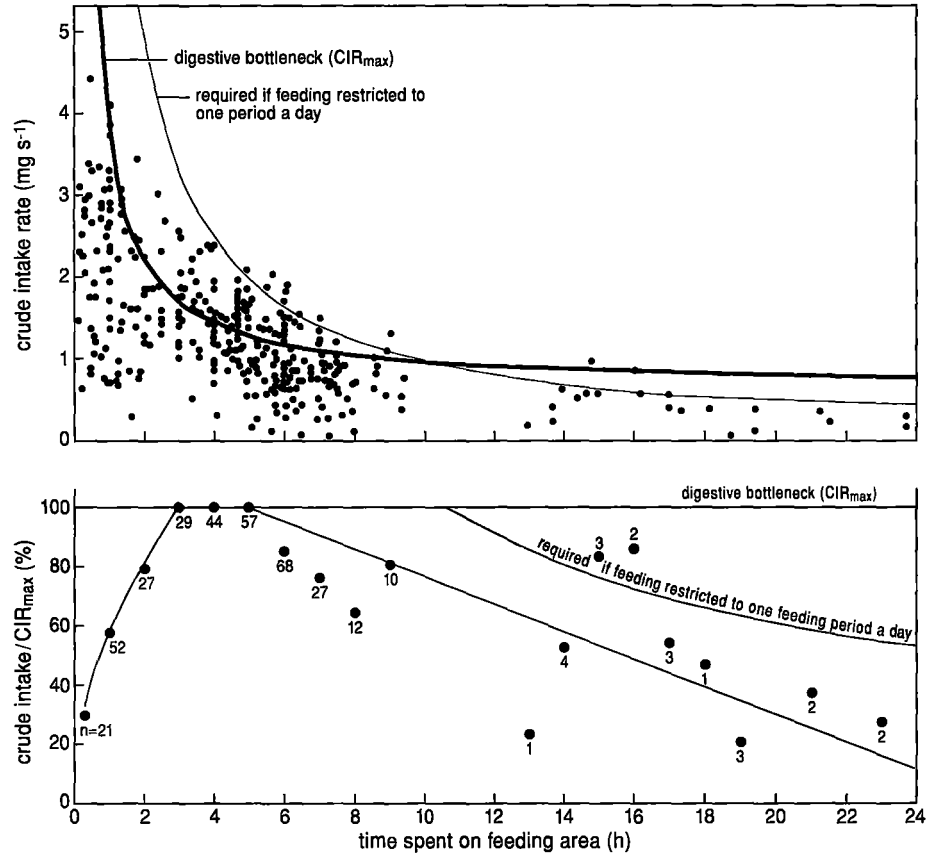
Fig. 4. (A) Crude intake rate (mg AFDW s^{-1}) as a function of the time spent on the feeding area. A selection was made of the studies summarized in Fig. 2A, B and C; $\Sigma n = 370$ studies. One curved line shows the highest possible crude intake rate such as determined by the digestive system (CIR_{max}; Fig. 1). The other line shows the intake rate required to keep their body weight constant, assuming that feeding is restricted to one feeding period a day. (B) Average deviation of the crude intake rate from CIR_{max} (set to 100%) or from the required crude intake rate at one daily feeding period (calculated from the data given in panel A); number of cases indicated.

erage consumption. The effect of the three remaining variables -activity costs, age and season- has been investigated after removing the effect of body weight by analysing the residuals.

(6) Activity costs The costs of feeding might vary between the studies, being higher for free-living birds (Blomert et al. 1983, Zwarts & Blomert 1996, Ens et al. unpubl.) than for captive birds. Within the captive birds, the feeding costs might differ too, being high if the birds had to feed on an artificial cockle bank (Swennen et al. 1989) or a mussel

bank (Koene 1978), and low if the birds were offered opened bivalves (Heppleston 1971, Hulscher 1974 & unpubl.) or pellets (Kersten & Piersma 1987, Goede 1993, Exo & Freimüth unpubl.). Although the energy expenditure has not been measured, the possible costs of feeding might be derived from an increase in the metabolized energy consumption. However, the daily consumption did not differ among the four categories of studies distinguished ($p = 0.81$), nor when free-living and captive birds were compared ($p = 0.89$).

(7) Age All studies dealt with adult birds, but Heppleston (1971) worked with a yearling and Exo & Freimüth (unpubl.) with two subadults three years old. The few data available suggest no reason to assume that the consumption is different for the age classes when birds of similar body weight were compared ($p = 0.87$).

(8) Season There is also no seasonal variation in the consumption at thermoneutrality ($p = 0.31$).

In conclusion, the daily consumption of Oystercatchers with constant body weight and living in thermoneutral conditions greatly depends on their body weight but not on whether they live in captivity or in the wild. Oystercatchers in the wild weigh 520 g during most months of the year. From Fig. 3, their daily net energy intake can be estimated at 672 kJ, which is equivalent to a gross consumption of 790 kJ or 36 g AFDW.

Crude intake rate and the digestive constraint

Although the amount of food consumed increases with the amount of time spent on the feeding area (Fig. 2), the rate at which food is taken nonetheless decreases. This is illustrated in Fig. 4A, where the crude intake rates are plotted against feeding time, using the data from Figs. 2A, B and C. The curved lines in Fig. 4A show CIR_{max} and the required crude intake rate, assuming that the birds need 36 g a day at thermoneutrality and take all this food during one feeding period a day. It is clear from Fig. 4 that, under these conditions, they cannot meet their daily energy requirements in less than 11 h.

The highest crude intake rate ever observed was 16 mg AFDW s⁻¹ and was measured in a hungry Oystercatcher, offered opened Mussels, that fed for 13 min (Hulscher unpubl.). This bird must have filled up its digestive tract completely during this short feeding bout. The three other studies with crude intake rates exceeding 5 mg s⁻¹ concerned birds foraging for less than 30 min. Even so, these extremely high intake rates still lie below CIR_{max}. But as Fig. 4A also shows, even though the observed crude intake rates decrease with the time spent on the feeding area, they do not all fall below CIR_{max}, perhaps because of er-

rors of estimation. In fact, the observed crude intake rates follow, on average, the CIR_{max} curve over the feeding time range of 3-5 hours. To show this, we turned all crude intake rates into deviations from predicted CIR_{max} and plotted the hourly average deviation from CIR_{max} against time (Fig. 4B).

Figure 4 shows that if the birds forage less than three hours, the CIR_{max} is so high, that the achieved crude intake rate usually remains far below this maximum. In other words, the rate at which prey are found and eaten determines the intake rate. The consumption is also usually less than CIR_{max} when the birds are able to feed for longer than elven hours, because they have time enough to consume the 36 g they need. However, when low water feeding areas are exposed only for 3-5 hours, the average crude intake rate is equal to CIR_{max} (Fig. 4B). On these occasions, the birds consume, on average, as much food as the digestive system allows.

Feeding activity and the digestive constraint
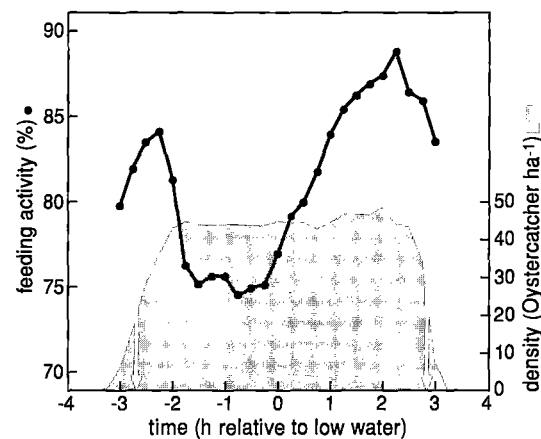
What do wild Oystercatchers do if the diges-

Fig. 5. Average feeding activity (% of Oystercatchers feeding) on a mussel bank over the low water period and the average total numbers (birds ha⁻¹) at which they occurred. Data of Zwarts & Drent (1981); a selection was made for the 220 low water periods that completely fell in the daylight period between July and November.

tive system sets a limit to their consumption? Do they feed at the low level of 0.66 mg s⁻¹, set by the processing rate, throughout the feeding period, or do they feed more quickly and stop feeding intermittently to resume feeding later on? The relationship between average intake rate and feeding activity over the entire feeding period in relation to the duration of the feeding period will be analysed in the next section, using the same data as shown in Fig. 4. However, to know what birds do as their digestive tract is filling, we need data on the change in intake rate and feeding activity within the feeding period. We therefore reanalysed the data of Zwarts & Drent (1981) who, over many days, counted the number of feeding and non-feeding Oystercatchers on a mussel bank each quarter of an hour. We restricted the analyses to counts made in late summer and autumn, since those from spring and early summer partly refer to breeding birds that visited the mussel banks during short bouts of only one hour.

Figure 5 shows that the Oystercatchers arrived on the mussel bed between 3 and 2 hours before low water and left between 2h 30′ and 3 hours after. The average Oystercatcher was present on the mussel bank between 2h 45′ before low water until 2h 52′ after low water, making a total of 5h 37′. On the digestive bottleneck hypothesis, the highest possible consumption over this time span would be 24.16 g (Fig. 1) and so CIR_{max} would be 1.20 mg s⁻¹, on average. The average feeding activity was 81%. Hence, the average intake rate must have been 1.49 mg s⁻¹ at the most. Can the dip in the feeding activity in the 1.5 hour before low water be explained by a digestive bottleneck? Were the birds to feed from the beginning of the exposure period at a rate of 1.49 mg s⁻¹, the digestive tract would not be full even after several hours of feeding. We know, however, that the feeding rate during the first 1.5 hour of the exposure period was twice as high as during the hours around low water (Zwarts & Drent 1981). Hence the intake rate would be 2.6 mg s⁻¹ during receding tide and 1.3 mg s⁻¹ around the moment of low water. At such a rate of consumption, a digestive pause would be necessary 1.5 hour after the start
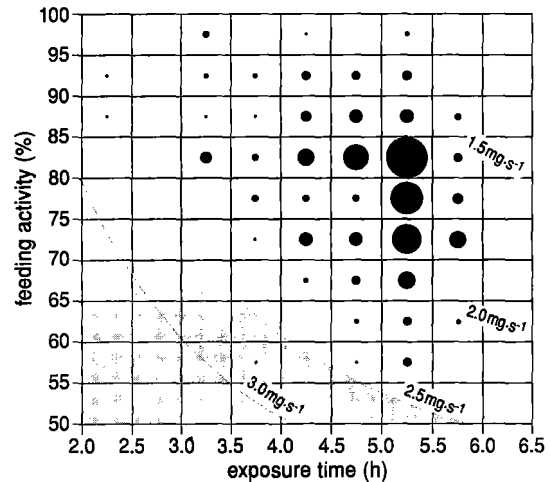

Fig. 6. Average feeding activity (%) during a low water period as a function of the duration of the exposure time of the mussel bank (i.e. water level below mean sea level). The surface of the circles indicates the number of low water periods, varying between 1 and 24 ($\sum n$ = 220). The curves show the expected relationship between feeding activity and exposure time, if the birds fed at a certain intake rate and the total consumption was as high as digestion allows. Data of Zwarts & Drent (1981).

of feeding. From this we conclude that the low feeding activity in the two hours before low water was indeed due to the digestion constraint and that the intake rate around low water must have been lower than 1.49 mg s⁻¹.

The Oystercatchers foraged, on average, 81% of the time they spent on the mussel bank, but the birds fed continuously when the feeding area was exposed for a short time and they were more often inactive when the exposure time was long. To what extent can this decrease in the feeding activity with the duration of the exposure time be explained by a digestive constraint? Figure 6 gives for four different intake rates the predicted relationships between feeding activity and exposure time. With an intake rate of 2 mg s⁻¹, a full digestive tract would force them to feed for not more than 77% of a four hours exposure period and 59% of a 6.5 h period. The circles show how often different combinations of exposure time and feeding activity occurred. It is obvious that the intake rate

must usually have been 1.5 to 2 mg s⁻¹, and thus in agreement with the estimate given above. The large scatter in the feeding activity may largely be explained by season. The birds fed more actively later in the season, apparently to compensate for the 30% decline in the condition of the Mussels, and thus for the probably lower intake rate.

Figures 5 and 6 show that the variation in the feeding activity during the course of the exposure period, as well as between different days, may also be explained by the digestive constraint. Both figures are based on population averages, but the intake rate, and possibly also the processing rate, may differ between individuals. It is thus of interest to analyse in more detail the consumption and time budget of individual birds over long periods. As an example, Fig. 7 shows the cumulative consumption in three individual birds observed over complete exposure periods of 4-6 hours duration. Hulscher (1976) allowed three captive birds to feed for exactly four hours on a cockle bed at a density of 13 to 450 large Cockles m⁻², whereas Blomert *et al.* (1983) observed free-living, colour-banded birds from their arrival on the feeding area until their departure to the high water roost.

The birds studied by Hulscher (1976) only reached a crude intake rate equal to CIR_{max} at the highest prey density on offer (Fig. 7A). On one day, bird WR fed continuously for three hours and consumed 17 g. Its digestive tract must have been filled completely, and indeed its consumption did slow down over the last hour of feeding. A week earlier, the bird had consumed as much, but rested halfway during the feeding period when the digestive tract was not yet full (Fig. 7A). This suggests that the strategy of Oystercatchers is not to fill their digestive tract as fast as possible when they begin feeding at the start of the feeding period, but to store the maximal amount of food at the end of the feeding period. The data on free-living birds studied by Blomert *et al.* (1983) suggest the same. Bird WW2023 (Fig. 7B) rested several times for 20 to 30 min even though its storage capacity had not yet been fully used, but after spending four hours on the feeding area, it
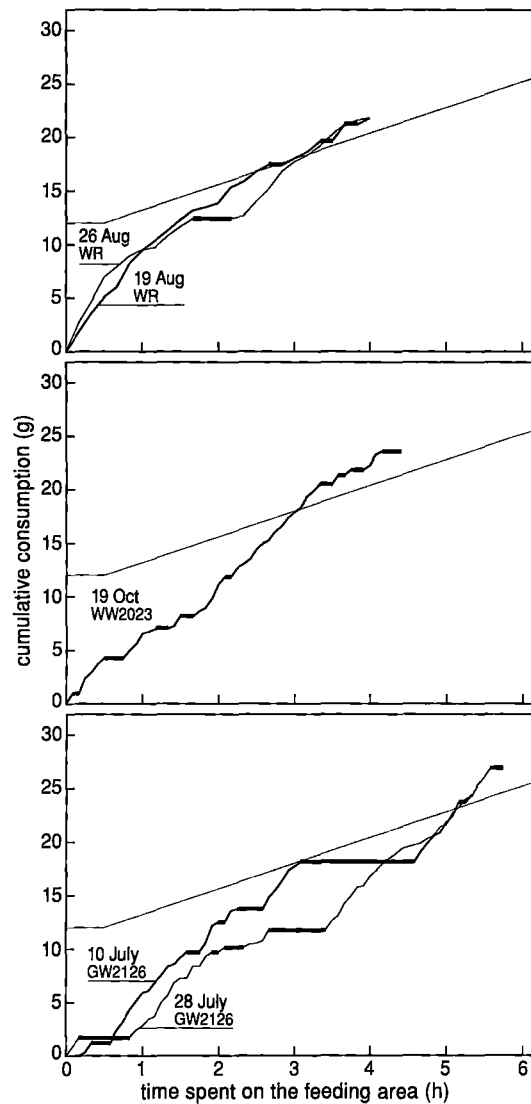

Fig. 7. Cumulative consumption (g) of three individual birds during the feeding period: (A) captive bird allowed to feed on a cockle bed in a temporary cage (Hulscher 1976), (B) and (C) two free-living, colour-banded birds feeding on *Mytilus* and *Scrobicularia*, respectively (Blomert *et al.* 1983) compared to the predicted maximal consumption determined by the digestive bottleneck (Kersten & Visser 1996a). Thick, horizontal lines indicate the resting periods > 5 min.
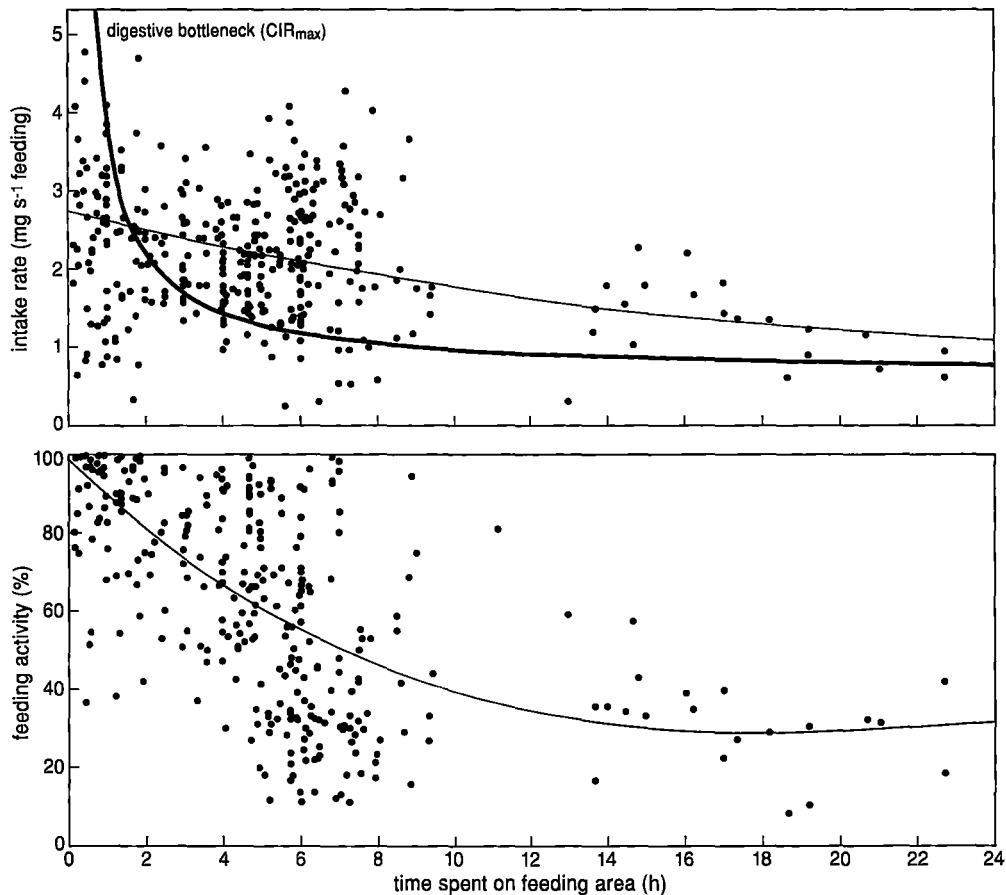
Fig. 8. (A) Intake rate (mg s⁻¹ feeding) and (B) feeding activity (%) as a function of the time spent on the feeding area. A selection was made of the studies summarized in Fig. 2A, B and C; $\Sigma n = 370$. The heavy line in panel A shows the highest possible intake rate if the birds feed as fast as digestion allows (CIR_{max}; Fig. 1) and for 100% of the time. Thin lines (based on polynomial regressions) give the average decrease of intake rate and feeding activity with time.

foraged for relatively less time, apparently due to the digestive bottleneck. The same pattern was observed even more evidently in bird GW2126 (Fig. 7C), which during one day rested for 100 min after it had filled its digestive tract completely and resumed feeding during the last 40 min. However, on the other day the bird rested at the beginning of the low water period, but ultimately reached the same result: the highest possible consumption set by the digestive constraint (Fig. 7C).

Figure 7 shows a selection of 5 days in which

the birds filled their digestive tract to the maximum possible. On not one day did any of the birds studied by Hulscher (1976) or Blomert et al. (1983) ever reach a consumption exceeding the digestive maximum. During the majority of the days, the consumption was 20 to 40% below this and, in some cases, it was even less. For instance, after GW2126 consumed 26.9 g (Fig. 7C) during an evening low water period it took during the next early morning low water period only 6.3 g, even though the duration of the exposure time would have allowed the bird to take three times as

much. There was no need for the bird to consume any more, because its intake over the 24 hours was sufficient to maintain its body weight (Fig. 3).

Do birds feed at a lower rate over long feeding periods?

The processing capacity is not being fully used if the actual intake rate remains below CIR_{max}. How often does this occur? Figure 8A plots intake rate against the time spent on the feeding area, using again the data from Figs. 2A, B and C. The intake rate is usually 1 to 3 mg s^{-1}. However, if the birds feed for less than two hours, the intake rate is more often 2 to 4 mg s^{-1}, whereas it is usually 1 to 2 mg s^{-1} if they remain for longer than six hours. Although the intake rate decreases when the birds spend more time on the feeding area, CIR_{max} decreases more. Hence the proportion of studies with an intake rate above CIR_{max} increases with the duration of the feeding period. If the intake rate exceeds the CIR_{max}, the birds have to interrupt feeding for digestive pauses. That is why the feeding activity decreases with the time spent on the feeding area (Fig. 8B). In conclusion, Oystercatchers have more digestive pauses, and also feed at a lower intake rate, if they can spread out their food consumption over long periods.

DISCUSSION

There is no difference in food consumption between wild and captive birds

We did not find a difference in food consumption between wild and captive birds. Since birds in the field fly, and possibly walk, more, than captive birds, some difference between cage and field metabolism had been expected, even for studies where the captive birds had to search and handle their own food. However, a theoretical calculation shows that the expected magnitude of this difference is actually quite small. Free-living Oystercatchers fly four times a day some 2 to 5 km between roost and feeding area and occasionally make short flights due to disturbance or interference. Assuming that (1) for an Oystercatcher weighing 520 g, the average energy expenditure is 7.8 W at thermoneutrality (Fig. 3; 672 kJ day^{-1} = 7.8 kJ s^{-1}), (2) captive birds never fly and free-living birds fly for 10-30 min a day (authors' unpubl. data), and (3) the flying costs are 36 W (Pennycuick 1989; given that the wingspan of an Oystercatcher is 83 cm (Welham 1994)), the energy budget of wild birds would only be about 3-8% above that measured in captive ones. As the three studies of free-living Oystercatchers refer to birds just before or during the breeding season that foraged close to their nest or on a tidal flat nearby, and flew even less than average (Zwarts & Blomert 1996, authors' unpubl. data), it is perhaps not surprising after all that their daily consumption did not differ from that of the captive birds. Also the estimates of the daily energy expenditure of adult breeding birds throughout the breeding season (Kersten 1996: Table 8) confirm that the life of breeding Oystercatchers is not expensive.

Food requirements and body weight

Daily consumption increases with body weight in Oystercatchers weighing between 420 and 520 g (Fig. 3). The body weight of wild Oystercatchers varies, however, over a greater range, between 500 in summer and 620 g in midwinter or just before migration (Dare 1977, Goss-Custard et al. 1982, Johnson 1985, Zwarts et al. 1996b). We therefore seek to identify the underlying cause of the relationship before deciding if we can safely extrapolate the regression line in Fig. 3 beyond the weight range of the captive birds to the generally higher weights of the free-living birds.

Oystercatchers with long wings (280 mm) weigh, on average, 12% more than birds with short wings (250 mm) (Zwarts et al. 1996c). Wing or bill lengths have not been measured in most studies summarized in Table 1 and Fig. 3. Therefore, it is not possible to standardize the body weights to birds of the same size. Were this correction possible, the scatter along the slope in Fig. 3 would possibly have been smaller and the slope less steep.
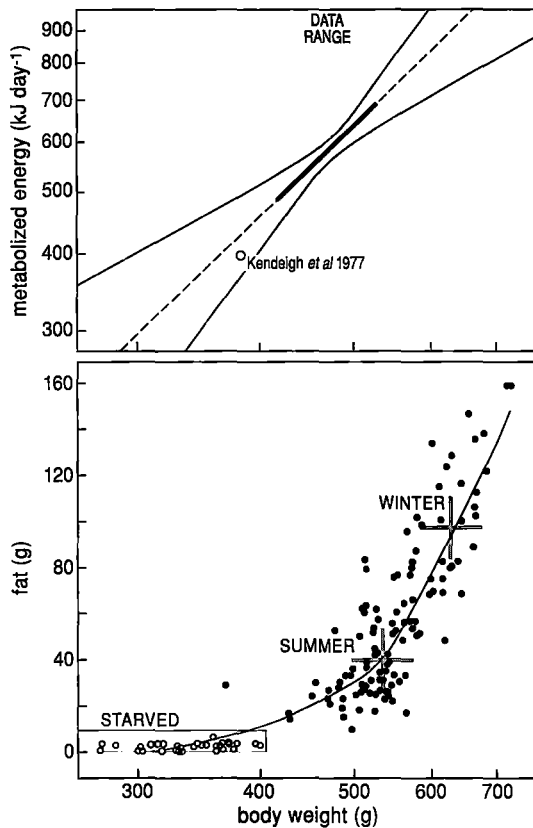
Fig. 9. (A) Net energy consumption (kJ day^{-1}; with 95% confidence interval) as a function of body weight in Oystercatchers, based upon the data from Fig. 3 (range shown), compared to the maintenance metabolism of an extremely lean Oystercatcher studied by Kendeigh et al. (1977). (B) Fat as a function of total body weight in birds starved in winter and living birds collected in all months of the year; crosses give the average fat and body weight in summer and winter birds; data from Zwarts et al. (1996b). The line was calculated with a running mean procedure ('lowess smoothing'; Norušis 1993).

Variation in energy requirements due to intraspecific variation in body weight, were expected to scale with the exponent 0.73, the exponent that applies across species (Kersten & Piersma 1987). However, we found the much higher exponent of 1.49. The exponent is about 1.35 if basal metabolic rate (BMR) is plotted against body weight in

an other wader, the Knot Calidris canutus (Piersma et al. 1995).

There are two explanations for this steep increase of metabolism with intraspecific variation in total body weight, as has also been found in other bird species (Bryant & Tatner 1991, Tinbergen & Dietz 1994 for parent birds provisioning their chicks). First, the much higher maintenance metabolism of heavy individuals must be due to a change in the metabolic machinery. Skin, feathers and the skeleton weigh the same for fat and lean birds of the same size, but since these parts of the body require less energy (Daan et al. 1990), the costs of living are relatively low in lean birds.

Second, if birds increase the weight of their body, they also increase the costs of living because walking and flying become much more expensive. Taylor et al. (1980) showed that the oxygen consumption increased in direct proportion to the added load for walking animals. In other words, the exponent is 1 if log(energy expenditure) is plotted against log(body weight). The costs of flying increase much more with body weight: the exponent against body weight is 1.52 (Pennycuick 1989). Thus, the exponent of the allometric relationship between body weight and maintenance metabolism depends on the activities of the birds, i.e. how much they fly. Per 24 hours, Oystercatchers rest during more than half of the time, they walk 30 to 40% and fly during 1 to 2%. Hence, the exponent of energy expenditure against body weight should be closer to 1 than to 1.52.

In conclusion, the steep increase of maintenance metabolism with body weight (exponent 1.49) may in a small part be attributed to the unmeasured variation in body size, but for the larger part to an increase of the costs of the basal metabolism and the costs of transport. Hence, although extrapolation of the regression line in Fig. 3 shows that a heavy Oystercatcher of 620 g would need 873 kJ per day, twice as much as an extremely lean bird of 394 g, this difference would be smaller if birds of similar body size could be compared. The only evidence that the regression line may be extrapolated downwards comes from

the study of Kendeigh et al. (1977) who gave the maintenance metabolism of an extremely lean Oystercatcher of 385 g. Their measurement falls within the extrapolated confidence interval (Fig. 9A). We badly need data on the energy consumption of extremely heavy birds at thermoneutrality and constant body weight to know whether the regression line in Fig. 9A may also be extrapolated upwards. Possibly, the increase of energy expenditure with body weight becomes less steep above a body weight of about 520 g because, from then on, an increase of the body weight is mainly due to fat deposition (Fig. 9B). However, even if fat deposition would not raise basal metabolic rate, the costs of transport will still continue to increase, so a higher body weight must enhance the costs of living.

How (in)flexible is the digestive constraint?

In our test of the bottleneck hypothesis, we found several estimates of food intake that exceeded the maximum predicted by the hypothesis, although the most extreme values could be explained as the result of errors of estimation. It is well known, however, that gut morphology is flexible depending on the types of food taken, as reviewed by Piersma et al. (1993). Although Oystercatchers take different prey species, their food always consists of soft flesh only. Hence no variation in the gut morphology, and thereby rate of food processing, in relation to their diet is to be expected. However, an enhanced rate of food processing in winter might be expected because more food has then to be processed to deal with the prevailing low temperatures, strong winds and increased body weight.

The size of the digestive tract determines the amount of the food, i.e. the volume, that can be stored, whereas the rate at which food can be processed is presumably constrained by the rate at which energy can be metabolized. A seasonal variation in the rate of digestion may therefore only be expected if the size of the digestive system varies during the season. If this does happen, the processing rate may increase with body weight, either because more food can be stored in

the larger gut and/or because the energy can be processed at a faster rate due to an increase in the length of the digestive tract. However, when a bird increases its body weight, it acquires more muscles and fat, but does not increase its structural size. An intraspecific comparison between the weight of the gut and the total body of some wader species (Piersma et al. 1993) shows that the exponent of the slope is usually less than 1. Furthermore, the seasonal variation in body weight in Oystercatchers is not as large as in migratory birds, even though a winter weight of 600 g is 20% above the body weight of inland Oystercatchers during the summer. Since Kersten & Visser (1996a) did their experiments in summer and their birds had a low body weight, the consumption in winter might exceed the digestive constraint these authors defined. However, our analysis of the crude intake rates (Fig. 4) revealed no seasonal variation. Hence we take the model of Kersten & Visser (1996a) as a general description of the constraint on the rate at which the food can be processed under a wide range of conditions, including extreme energy demands.

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SAMENVATTING

Scholeksters die in gevangenschap worden gehouden, nemen per dag 25 to 40 gram droog vlees op, of uitge-

drukt in energie 550 tot 850 kJ. Daarvan wordt 450 tot 700 kJ ook daadwerkelijk gemetaboliseerd. Vrijlevende Scholeksters eten meer dan vogels in gevangenschap, maar dat heeft niets te maken met een grotere activiteit, maar met een zwaarder lichaamsgewicht. Wanneer vrije en gevangen vogels even zwaar zijn, eten ze even veel. De opnamesnelheid van Scholeksters varieert tussen 1 en 3 mg per seconde voedselzoeken, maar als rustpauzes worden meegerekend, is het gewoonlijk niet meer dan 1 tot 1.5 mg per seconde. Opnamesnelheden boven de 4 mg per seconde worden alleen waargenomen bij vogels die heel kort voedselzoeken na een lange rustpauze. Volgens Kersten & Visser (1996a) kunnen Scholeksters zo'n hoge opnamesnelheid niet lang volhouden, omdat ze niet meer dan 80 gram nat (of 12 gram droog) vlees op kunnen slaan en de verwerkingssnelheid niet meer is dan 4.4 mg nat (of 0.66 mg droog) vlees per seconde. Als gevolg van deze bottleneck in de vertering moeten de vogels vele uren per dag op het voedselgebied doorbrengen. Aangezien in de Waddenzee de droogligtijd van hun voedselgebieden gewoonlijk vijf tot zes uren bedraagt, kunnen de vogels met één laagwaterperiode per dag hun energie-

behoefte niet dekken. Het bottleneck model voorspelt precies hoeveel voedsel de vogels in een bepaalde tijd kunnen opnemen en wat de hoogste opnamesnelheid kan zijn geweest, inclusief de verteringspauzes. In de praktijk zitten de vogels onder deze limiet als ze korter dan drie uur voedsel zoeken. Dit betekent dat opnamesnelheid wordt bepaald door de snelheid waarmee de vogels zelf voedsel kunnen zoeken. Als de vogels drie tot twaalf uur op het voedselgebied doorbrengen, zitten de vogels tegen de verteringslimiet aan. Daarentegen eten de vogels minder dan wat kan worden verteerd en opgeslagen als de verblijfstijden langer zijn dan twaalf uur. In het laatste geval hoeven de vogels niet tot het uiterste te gaan, omdat ze niet meer dan 36 gram droog vlees per dag nodig hebben om gelijk te blijven in gewicht. Er zijn een paar studies waarbij de consumptie duidelijk ligt boven de limiet die door de verwerkingssnelheid wordt gesteld. We verklaren dit met schattingsfouten. Een uitvoerige analyse van alle fouten die gemaakt kunnen worden bij het schatten van de consumptie in het veld, suggereert dat de opname eerder wordt overschat dan onderschat.