

Does an optimally foraging oystercatcher obey the functional response?

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Summary. (1) We describe an experimental test of the optimal diet model. An oystercatcher was offered bivalves *Scrobicularia plana* which were buried in the substrate at different depths. All prey were of equal length and thus of equal energy content. Since handling time increased with depth, deep-lying prey were less profitable.

(2) From the known increase of handling and search time with depth we were able to predict for each prey density which depth classes should be ignored by the bird so as to maximize its intake rate.

(3) The observed depth selection and intake rate were as predicted for the lower prey densities. At high prey densities the observed number of prey taken rose above the predicted intake rate. We suggest that the bird started to ignore closed bivalves with long handling times.

(4) The observed relationship between prey density and intake rate could not be described by Holling's type-2 functional response, because the handling time and the rate of discovery were density-related. A multi-species functional response is necessary to describe the intake rate of an optimally feeding predator.

The functional response, the predation rate of an individual predator related to differences in prey density, has been much studied during the last decades. In the simple one-prey situation, the intake rate of the predator often rises decelerating to a plateau (type-2 functional response; Holling 1959). The curve has been described by the disc equation:

$$\frac{N}{T} = \frac{aD}{1 + aDh} \quad (\text{Holling 1959}) \quad (1)$$

where N =number of prey taken, T =time predator and prey are exposed to one another, a =instantaneous rate of discovery, D =prey density and h =handling time.

Equation (1) can be simplified to:

$$\frac{N}{T} = \frac{\lambda}{1 + \lambda h} \quad (2)$$

where λ =encounter rate: the inverse of searching time per prey item ($\lambda=aD$).

This one-prey model is based on the assumption that a predator takes every prey it encounters. However, predators are usually faced with a number of prey types from

which they select their diet. When there are i prey types, Eq (2) can be rewritten as:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i P_i}{1 + \sum \lambda_i h_i P_i} \quad (\text{Charnov 1976}) \quad (3)$$

where E =energy intake, E_i =energy from one item of prey type i , P_i =probability the predator takes a prey item of type i after it is encountered, λ_i =encounter rate with prey type i and h_i =handling time of prey type i . It can be shown that to maximize the energy intake rate, $P_i=1$ if $E/T < E_i/h_i$ and $P_i=0$ if $E/T > E_i/h_i$ (Charnov 1976). So a predator should ignore a certain prey type when its profitability is below E/T and should take it if E_i/h_i is above that level. This prediction of the optimal diet model has now been confirmed in a lot of studies (see review by Krebs et al. 1983).

If the intake rate increases (because of rising prey density for instance), the model predicts exactly when a prey type should be dropped from the optimal set of prey types. This has been found in some studies (e.g. Davidson 1978; Pulliam 1980; Zwarts and Drent 1981). However, the functional response cannot yet be predicted quantitatively from the optimal set of prey types, since the encounter rate with the different prey types must also be known before Eq (3) can be solved. This paper describes an experiment in which E , h and λ for the different prey types were quantified. This allowed us to compare the observed behaviour of a predator to the decisions it has to make to maximize its intake rate at different prey densities, and to describe the functional response of a predator feeding on several prey types.

We selected the oystercatcher *Haematopus ostralegus* L. as the predator and the bivalve *Scrobicularia plana* (da Costa) as the prey. Oystercatchers locate buried bivalves like *Macoma balthica* L. and *S. plana* entirely by touch. The number of prey encountered can be estimated by a simple random search model (Hulscher 1976, 1982). The prey types were bivalves of the same size and thus of the same energy content, but they were buried in the substrate at different depths. Handling time increases when the prey are buried at greater depth (Hulscher unpublished) so varying prey depth also varies prey profitability. We selected a bird that showed the greatest increase in handling time for the less accessible prey so prey profitability could be manipulated most readily.

This paper attempts to answer the question whether the oystercatcher obeys the functional response as predicted by Eq (3) and thus ignores less profitable prey as predicted

by the optimal diet model. However, before the model can be tested, we have to show that the bird really searched at random for all prey densities.

Methods

The predator

We worked with an adult male oystercatcher (bill length 70 mm; weight 460 g) caught near the Dutch Wadden Sea in April 1981. Before we conducted our experiments which took during 30 July–18 August 1981, the oystercatcher had been foraging on *S. plana* and *Mya arenaria* L. in pilot studies conducted by Hulscher in the same experimental set-up as we used.

The prey

S. plana 35–36 mm long were dug out from the intertidal mudflats nearby. Their caloric value was 6.1 kJ (274 mg ash free dry weight; 22.2 J mg^{-1}). The prey were stored in fresh sea water at 4°C for a period of up to 5 days, during which time they remained in perfect condition.

The experimental set-up

We used two cages connected by a small passage that we could open or close from our hide. A hide was placed next to the cage in which we had constructed an artificial mudflat. The oystercatcher was allowed to enter this cage only during the experiments.

The mudflat consisted of three plastic boxes in a row, filled up with mud taken from the intertidal flats and sieved to remove potential prey. The surface area was 0.663 m^2 . The depth of the boxes was 12 cm, but by distributing at random 72 wooden blocks with a thickness of 1, 2, ..., 9 cm over the bottom, we made the depth of the mud-layer in the boxes irregular. The bivalves were placed on the bottom of the substrate in a vertical position. Prey depth was distance between the mud surface and the upper tip of the shell; since *S. plana* of length 35–36 mm have a height of 3 cm, when placed vertical, we created 10 classes of prey depth (0, 1, ..., 9 cm). A grid system numbered in relation to the side and back-side of the plastic containers allowed us to retrieve every buried prey afterwards.

The prey were buried in the substrate just before each experiment. All traces were erased from the surface to prevent the bird from using visual clues to locate the prey. The buried *S. plana* quickly started feeding in their normal way by scraping their syphon over the mud surface. We never noticed the oystercatcher responding to the moving syphons, thus reinforcing our opinion that the bird searched solely by touch. If necessary we added a little sea water to the mud surface so the bird could wash the flesh before eating as do oystercatchers in the field.

We offered ten different prey densities. At the start of the experiment the oystercatcher fed on an intermediate density (88 m^{-2}), after which we successively lowered the density to a level where the bird refused to search (Fig. 1). After that we increased the density progressively to the maximal value at the end of the experiment. This and not a random order was chosen to minimize the time the bird had to spend in adjusting its feeding behaviour to the changed prey densities.

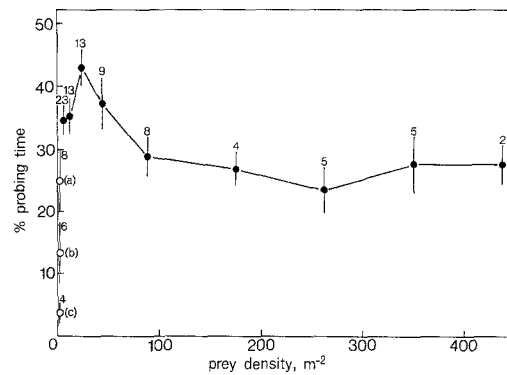


Fig. 1. Relationship between the time spent probing by the oystercatcher (as a percentage of available foraging time minus total handling time) and the density (D) of *Scrobicularia plana*. Means \pm S.E. (sample sizes indicated) are shown for all offered densities (\bullet). During three successive sessions at $D=2 \text{ m}^{-2}$ the bird found no prey at all and the amount of probing strongly decreased. Mean percentage probing time \pm S.E. (\circ) per 5 min observation time is given for a first session (40 min); b second session after 40 min (30 min); c third session after 19 h (20 min)

The bird was not able to learn the location of the profitable prey because we changed the depth distribution completely before any session, and in most sessions the bird was only allowed to take a few prey.

We controlled hunger level by allowing the bird the same amount of food each day; viz. 35 g (AFDW): this is the mean food requirement of an oystercatcher in captivity with a body weight of 460 g (Hulscher 1974). The extra food needed to make up this amount was given to the bird at the end of the daily experimental sessions in the form of opened mussels *Mytilus edulis* L. and *S. plana* in the non-experimental cage. Any remaining food was taken away every evening at 23.30 h. The experiments started each morning at 09.00 h, so the bird was deprived of food for 9.5 h. This is about 3 h longer than usually occurs in the field, so our captive bird was always motivated to feed.

The experimental sessions

The following were measured during a session:

(1) Available foraging time (duration of a session). The oystercatcher always entered the experimental cage immediately after the passage was opened. After it had eaten the allowed number of prey, the passage was opened again and the bird driven out.

(2) Searching time. Since we assumed searching was by touch, only the period in which the bill was beneath the mud surface and no handling could be observed was scored as searching time. This 'probing time' amounted to 30–40% of the total time minus handling time (Fig. 1), but was lower at the lowest prey density offered (2 prey per m^2). In this case the bird did not find a prey after probing for 15 min, so this density was not used in the analysis.

(3) Depth of located prey. We noted the co-ordinates of prey that were found so that after the experiment we could determine its depth.

(4) Handling time. As with oystercatchers feeding on *Macoma balthica* (Hulscher 1982) our bird handled prey in two ways: (a) opening the shell in situ, or (b) lifting the shell from the mud before opening. We always noted which method was used and measured total handling time

by stopwatch. We also measured the lifting time (time needed to pull the shell to the surface and to put it down); cutting time (time needed to remove the flesh from the shell), and eating time (time needed to wash and swallow the flesh).

(5) Number of prey taken. The number of prey the bird was allowed to take in one session depended on prey density: one prey at $D=2$ or 6 m^{-2} ; two prey at $D=12$ or 24 m^{-2} ; three prey at $D=44\text{ m}^{-2}$; five prey at $D=88\text{ m}^{-2}$ and ten prey (3–7%) from density 144 m^{-2} onwards. Because of the very low prey depletion, there was no need to correct for decreasing prey density during the course of a session (Rogers 1972). However, the fact that the number of prey the bird was allowed to take, increased with prey density, might have affected the decision making process of the oystercatcher. As shown by Lucas (1983) the bird might lower its selection criterion when the remaining time available for feeding decreases. Since not time itself was limited, but the number of prey allowed, time constraints are unlikely to have affected the optimal diet choice in these experiments.

The analysis would have been complicated if the bird had increased its handling or searching time during long sessions because of decreasing motivation (Holling 1966). However, this appeared not to happen: in 21 of the 24 sessions in which the bird took 5 or more prey, there were no significant trends in the handling time (Spearman rank correlation; $P>0.05$). A significant increase ($P<0.05$) occurred twice and a significant decrease ($P<0.05$) once. In the 12 sessions where the bird took 10 prey and searching time per prey item was measured, there were no significant trends in searching time ($P>0.05$) during the session.

After each session we checked the opened bivalves for remaining flesh, but fortunately our bird never performed partial predation.

Determining the effective touch area

In order to calculate the probability that a buried prey would be located by a randomly searching oystercatcher, we needed to know the cross-sectional area (touch area) of the bivalve and of the bill tip. We measured the touch area of 47 specimens (range 33–46 mm) by pressing the bivalve vertically into modelling clay and measuring the impress of the largest cross section which, for our prey size (35–36 mm), was 1 cm below the top of the bivalve. The touch area was 0.22 ± 0.01 (mean \pm S.E.) \times shell length squared. We used Hulscher's (1982) value of billtip touch area. The effective touch area was calculated as described by Hulscher (1982). The mean value for our prey size was 6.15 cm^2 .

The film sessions

For a quantification of the duration and the depth of the probes, we filmed the bird in five 3 min sessions with intervals of 5 min between. A 16 mm camera was used, with a speed of 16 frames per s.

Analysis

SPSS (Nie et al. 1975) was used for all statistical analyses.

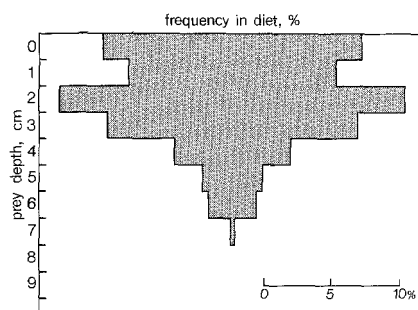


Fig. 2. Frequency distribution (%) of the selected depth classes in the oystercatcher's diet. Prey on offer were distributed equally over 10 depth classes. Combined data of all experiments were used ($n=305$)

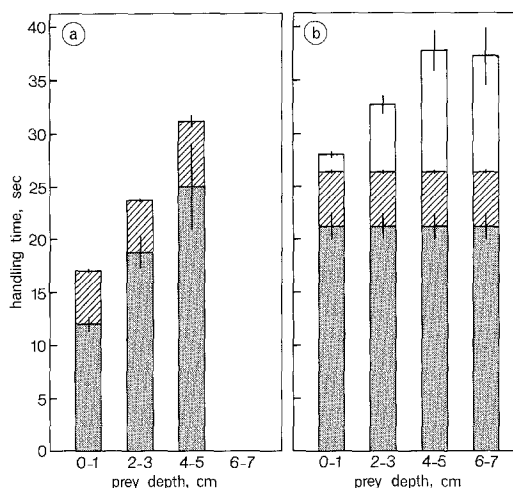


Fig. 3a and b. Duration of handling components (Mean \pm S.E.) as a function of prey depth, for **a** unlifted and **b** lifted bivalves. The distinguished components are: cutting (grey), eating (hatched) and lifting (white). See Table 1 for statistical analysis

Results

Depth selection

Prey out of the reach of the bird's bill (7 cm) were never taken (Fig. 2). So prey density was defined as the prey number present in the depth classes 0–7 cm. Though prey were distributed equally over the depth classes, the deeper prey were taken less than the shallow prey (Fig. 2).

Handling time

Handling time increased with prey depth (Fig. 3), so prey profitability decreased with depth.

The analysis of the different components of handling time, makes clear why the handling time is dependent on prey depth. For prey opened in situ, the oystercatcher spent 25 s cutting out the flesh and 6 s eating a prey at 4–5 cm, but only 12 and 5 s respectively for a prey taken from the upper 0–1 cm (Fig. 3a). If the prey was lifted to the surface, cutting and eating time were independent of the depth, but the lifting time increased with depth (Fig. 3b; Table 1).

It would be expected that all prey from the upper 5 cm would be handled in situ if the oystercatcher tried to mini-

Table 1. Results of five one-way analyses of variance to test the effect of depth on several components of the handling time, for unlifted prey ($n=113$; see Fig. 3a) and lifted prey ($n=186$; see Fig. 3b)

	Unlifted prey		Lifted prey	
	r^2	P	r^2	P
Lifting time	—	—	11.2	0.026
Cutting time	12.0	0.001	1.0	0.838
Eating time	7.3	0.001	6.5	0.061

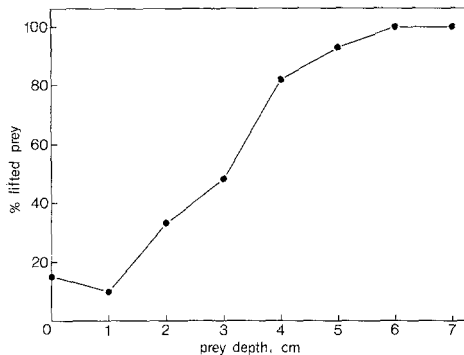


Fig. 4. Proportion of the prey being lifted (%), as function of prey depth

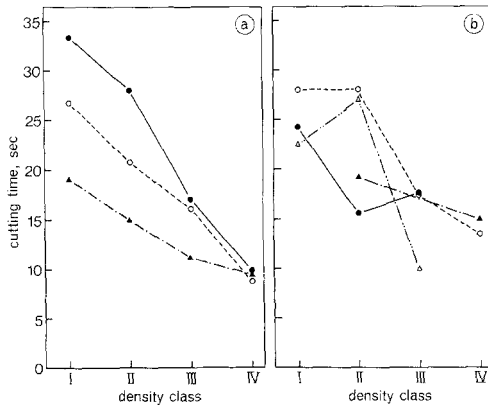


Fig. 5a and b. Relationship between cutting time per depth class and prey density, for **a** unlifted prey and **b** lifted prey. Four depth classes were distinguished: 0+1 cm (▲), 2+3 cm (○), 4+5 cm (●) and 6+7 cm (△); and also four density classes: $6+12+24 \text{ m}^{-2}$ (I), $44+88 \text{ m}^{-2}$ (II), $175+262 \text{ m}^{-2}$ (III) and $350+437 \text{ m}^{-2}$ (IV). See Table 2 for statistical analysis

mize the total handling time. All prey should be lifted at depth 6–7 cm, because the increase of handling time with depth is greater for unlifted than for lifted prey (Fig. 3), by which the extrapolated handling time for unlifted prey at 6–7 cm would surpass the observed handling time for the lifted prey at that depth. The bird behaved as expected for prey at depth 0 and 1 cm (in situ) and 6–7 cm (lifted), but for the intermediate depth classes an increasing proportion of the prey were lifted (Fig. 4).

Cutting time at each depth class decreased as prey density went up (Fig. 5; Table 2), perhaps because the oystercatcher rejected bivalves which were difficult to open when the prey density was high. It is possible that the bird was

Table 2. Results of eight two-way analyses of variance to test the effect of depth and density on several components of handling time, for unlifted prey (Fig. 5a), lifted prey (Fig. 5b) and for all prey (Fig. 6). A hierarchical approach was chosen in which the higher priority was assigned to depth

	Depth		Density		Depth \times density	
	r^2	P	r^2	P	r^2	P
Unlifted prey						
cutting time	12.0	0.001	15.4	0.001	2.0	0.550
eating time	7.3	0.001	0.4	0.858	1.1	0.911
Lifted prey						
cutting time	1.0	0.813	14.7	0.006	4.9	0.484
eating time	6.5	0.054	6.1	0.067	4.9	0.437
All prey						
lifting time	31.6	0.001	2.1	0.039	4.2	0.035
cutting time	12.2	0.001	13.9	0.001	1.9	0.549
eating time	6.4	0.001	1.7	0.145	3.0	0.289
handling time	22.0	0.001	12.7	0.001	3.0	0.102

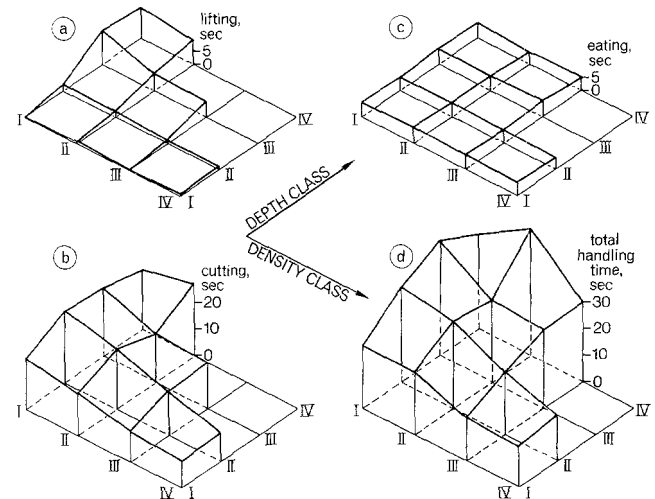


Fig. 6a–d. The components of handling time related to prey density and burying depth. Where handling time is not shown we have no observations. Four density classes were distinguished: $6+12+24 \text{ m}^{-2}$ I, $44+88 \text{ m}^{-2}$ II, $175+262 \text{ m}^{-2}$ III and $350+437 \text{ m}^{-2}$ IV; and also four depth classes: 0+1 cm I, 2+3 cm II, 4+5 cm III and 6+7 cm IV. See Table 2 for statistical analysis

able to decide in a fraction of a second whether an encountered bivalve was gaping enough to stab into the shell immediately.

Lifting and eating time increased for deep-lying prey and were nearly independent of prey density (Fig. 6; Table 2). This was the other way around for cutting time. From this we can conclude that the profitability of the prey was related to the depth as well as to whether or not the valves were gaping. The depth was known, but the gaping of the bivalves could not be determined. Hence, the predictions of intake rates could be based on the depth-related profitability only.

Predicted encounter rate

Hulscher (1976, 1982) successfully tested his hypothesis that oystercatchers, feeding on *Cerastoderma edule* or *M. bal-*

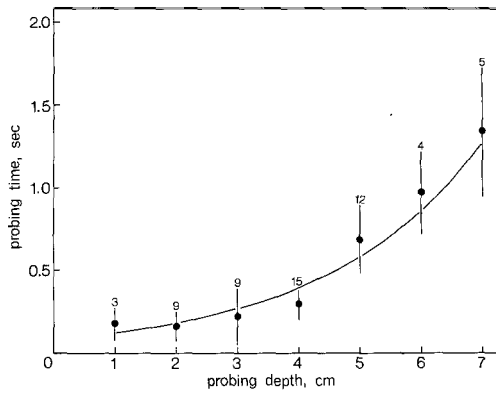


Fig. 7. Relationship between probing time and the depth of a probe. The values shown (means \pm 95% C.L.; sample sizes indicated) are based on film analysis (resolution 1/16 s) of searching behaviour at a prey density of 0 m^{-2} . $\ln(\text{probing time}) = 0.39(\text{probing depth}) - 2.49$ ($n = 7$; $r = 0.97$; $P < 0.005$)

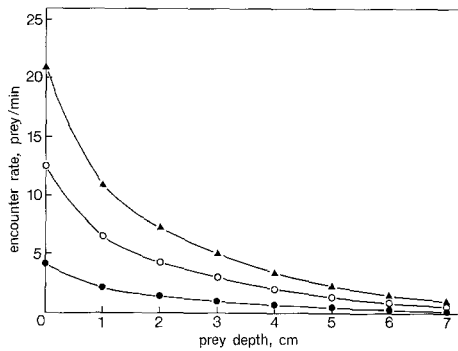


Fig. 8. Predicted encounter rate (λ) per depth class, for three different prey densities. $D = 437 \text{ m}^{-2}$ (Δ); $D = 262 \text{ m}^{-2}$ (\circ) and $D = 88 \text{ m}^{-2}$ (\bullet)

thica, probe the substrate at random, when they locate their prey by touch. He calculated the probability ($P\text{-loc}$) that a bird would hit a prey at one probe from the formula:

$$P\text{-loc} = Ds/10^4 \quad (4)$$

where D = prey density (m^{-2}) and s = mean effective touch area (cm^2).

To predict the encounter rate (λ) of the oystercatcher with prey from a certain depth class, we must divide $P\text{-loc}$ by the time it takes the bird to insert its bill to that depth into the substrate:

$$\lambda_i = P\text{-loc}_i / t_i \quad (5)$$

where λ_i = encounter rate with prey of depth class i (prey/min) and t_i = duration of a probe to a depth needed to locate a prey of depth class i (min). Since $P\text{-loc}$ is based on the cross section 1 cm below the top of the selected size class, we assume that the bird has to probe $i+1$ cm to locate a prey in depth class i . $P\text{-loc}_i$ depends on D_i only, because s is constant for all depth classes. D_i is known, so Eq (5) can be solved, for t_i has been measured using a film analyzer (Fig. 7). The logarithmic increase of probing time with probing depth determines the way the predicted encounter rate decreased for prey which were buried at greater depth (Fig. 8).

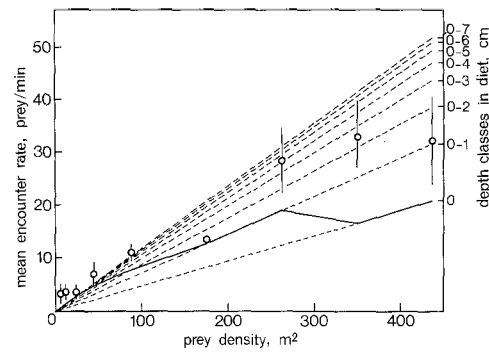


Fig. 9. Observed mean encounter rate (\circ) \pm 95% C.L. The broken lines represent values of λ ranging from no depth selection (upper line) to selection of depth class 0 cm only (lower line). The solid line gives the predicted λ for the bird selecting the optimal depth classes as calculated in Fig. 11

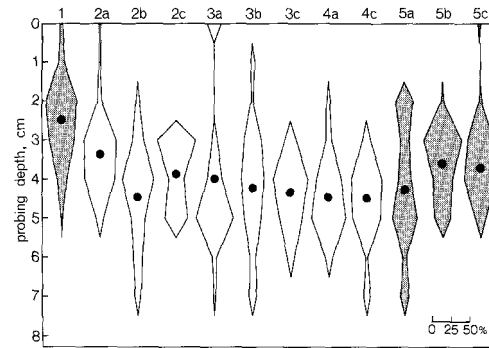


Fig. 10. Adaptation of the oystercatcher's probing depth to prey density. Mean probing depth (\bullet) and frequency distribution (%) are shown for five successive film sessions (3 min each; 5 min between the sessions) just after finishing the experiments at $D = 437 \text{ m}^{-2}$. Density during the film sessions 1 and 5 was 437 m^{-2} and at sessions 2, 3, 4 it was 0 m^{-2} . Samples of 20 probes were taken from the start *a*, the middle *b* and the end *c* of each film. For film 1 the values of *a*, *b* and *c* were combined and at 4b the bird made no probings at all

Observed encounter rate

We never saw the oystercatcher reject a prey it had discovered ('negative handling time'). That is why we used the observed searching time per prey taken to calculate the mean encounter rate. However, analysis of a high speed film showed that a prey can be located and refused too quickly to be noticed by an observer. We do not know how often we missed this kind of quick encounter, but it is certain that the observed encounter rate is an underestimation of the actual rate. Comparison of the predicted encounter rate for a random searching predator and the observed rate (Fig. 9) reveals that at low prey densities the oystercatcher took all prey it found, whereas at high densities less prey than expected were taken, perhaps because the observer did not see encounters where prey were rejected.

Another explanation for the lower-than-expected rate at high prey densities was suggested by the film analysis. The bird reduced its encounter rate with deep-lying prey by probing less deeply at high prey densities (Fig. 10). When the bird was allowed to feed for 15 min on a very high prey density, its mean probing depth at the end of this

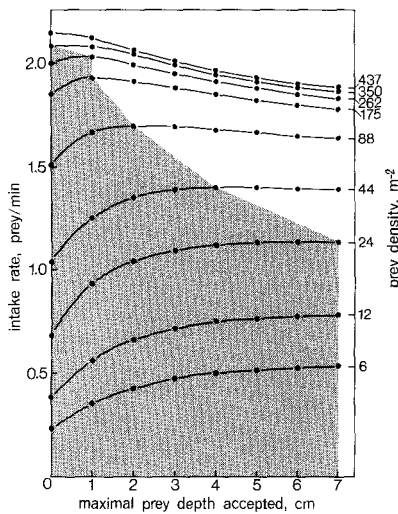


Fig. 11. The optimal set of depth classes predicted for all prey densities offered. The dots are solutions of Eq (3). The margin of the grey field connects values of maximal intake rate for the different prey densities. So, to maximize its intake rate, the oystercatcher should take all the depth classes within the grey field and reject deeper lying prey

session was 2.5 cm only, against 4.5 cm at the end of the next three sessions (3 min each) when prey density was zero. Probing depth decreased gradually during the three minutes after the bird was given the same high prey density as in the initial session.

We conclude that the oystercatcher took all prey it encountered at low prey densities, but when the prey density was high the bird became selective (1) by decreasing its probing depth and thus ignoring the deep-lying prey and (2) probably also by refusing a part of the prey that was encountered within the exploited layer of the substrate.

Predicted depth selection and intake rate

To solve Eq (3) we have to know λ_i , h_i and E_i . E_i has been set to 1, for all prey have the same energy value. The value of λ_i can only be estimated if it is known that the oystercatcher took all prey encountered. This was definitely the case for the lowest prey densities (Fig. 9). That is why we selected the observations on handling time for the three lowest densities to measure the effect of depth on handling time:

$$h_i(s) = 3.7 \text{ (cm)} + 24.9 \\ (n = 72; r = 0.37; P < 0.005).$$

We are now able to predict the hypothetical intake rate, assuming an optimal selection of the depth classes by the oystercatcher. The predicted intake rate for every possible selection level is presented in Fig. 11. The margin of the grey field in this figure connects the predicted maximal intake rates, and thus predicted depth selection for the different prey densities. According to these predictions the oystercatcher should take all attainable prey for densities 6 m^{-2} to 24 m^{-2} but it should successively drop the deep-lying prey from its diet at higher prey densities. Only depth class 0 cm should be taken from density 350 cm^{-2} onwards.

Observed depth selection and intake rate

Figure 12 shows the observed depth selection for four prey density classes. As predicted, the bird took all depth classes

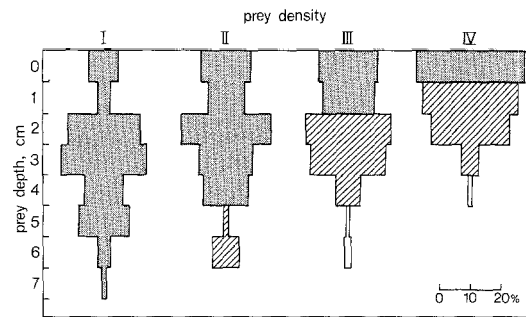


Fig. 12. Frequency distribution (%) of depth classes in the oystercatcher's diet at four density classes: $6 + 12 + 24 \text{ m}^{-2}$ I, $44 + 88 \text{ m}^{-2}$ II, $175 + 262 \text{ m}^{-2}$ III and $350 + 437 \text{ m}^{-2}$ IV. From Fig. 11 we have calculated which depth classes the bird should take to obtain the maximal intake rate (grey) and which classes it might add to the diet (hatched) before reducing its intake rate by more than 5% (white)

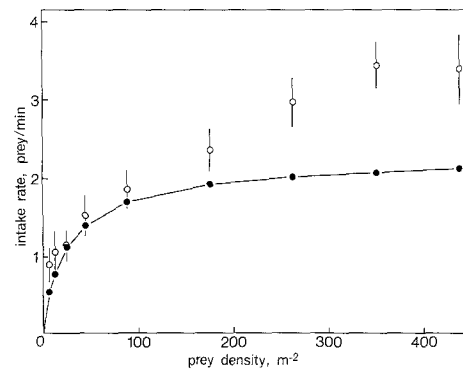


Fig. 13. Relationship between intake rate and prey density. Predicted values (●) are compared to the mean values observed $\pm 95\%$ C.L. (○).

at the low prey densities and ignored the deep-lying prey when the density was high. The bird did not show exactly the predicted change in rejection threshold. However, the deviation is small and as shown in Fig. 11a deviation of 2–3 cm from the predicted depth selection limit hardly reduces the intake rate. The bird added in fact only those depth classes to the optimal set by which the intake rate was reduced not more than 5%.

The predicted intake rate for the bird selecting exactly the optimal set of depth classes fits quite well with the observed values for the five lower prey densities (Fig. 13). However, from density 175 m^{-2} onwards, the number of prey taken by the oystercatcher rises above the predicted intake rate.

The predicted intake rate was based on the assumption that all prey must be taken from the optimal set of depth classes. However, by using a second selection criterion – ignore prey which are closed or not gaping enough, and so shorten the cutting time – the oystercatcher was able to reduce the handling time and so increase its intake rate at higher prey densities by as much as 50% of the expected value. A density-related selection of shells which could not be stabbed immediately has already been suggested by Hulscher (1976) for an oystercatcher feeding on cockles all buried at the same depth.

We suggest that at prey densities below 175 m^{-2} optimal depth selection is the only decision rule, but above

that density selection on depth as well as on 'easy' bivalves is optimized.

Discussion

Rate of discovery a

The disc equation of Holling (1959) is attractive because of its simplicity. The intake rate depends on two factors only, which should both be constant for all prey densities: the handling time and the rate of discovery a . Since a equals λD^{-1} (cf. Eq (2)), a will be density-independent only if the search time increases n^{-1} times when prey density increases n times. This was the case in the 'touch experiment' of Holling (1959) but in the 'sound experiment' described in the same paper, a decreased when density went up. Holling solved this problem by dividing the search time into two components, real search time and an identification time. Assuming that the rate of discovery based on real search time was constant, Holling could estimate the identification time, which was then added to the handling time.

The reasoning of Visser and Reinders (1981) is also based on the idea that a part of the search time in reality belongs to the handling time, they assume there is a waiting time after a prey is swallowed (an internal handling time) during which the predator is unable to eat a new prey.

In the case of our oystercatcher, it is unlikely that a recognition time or a waiting time after handling a prey, could explain the density-dependence of a . The recognition time must have been very short: prey which were located but refused were missed by us and could only be detected by film analysis. Also the waiting time cannot have been important. The bird was able to swallow prey after prey with very short intervals in between when we offered it opened bivalves, and we also saw no digestive pauses when the bird was eating prey containing much more flesh than the prey used in the experiments.

A decrease of a at higher prey densities could also be due to the predator spending less time in actively searching. For this reason, van Lenteren and Bakker (1976) stressed the importance of behavioural observations in the analysis of functional responses. Hassell et al. (1977) showed indeed the positive effect of the search effort on a .

We tried to minimize the effect of prey density on searching intensity by defining search time only as the time the bird is actively probing the substrate. In fact, percentage probing time is fairly constant over a large range of densities (Fig. 1), but we cannot rule out the possibility that the probing rate – and thus the relation between probe duration and probing depth (Fig. 7) – is related to prey density.

There are two other problems in estimating a : how to measure effective prey density and how to estimate the encounter rate. Measured prey density will be too high when part of the prey is unavailable to the predator (Murton 1971; Erichson et al. 1980; Myers et al. 1980; Zwarts and Wanink 1984; this study, Fig. 2). This will not affect the calculation of a if the available fraction is the same for all densities, but when the selection criterion is related to prey density (Figs. 9 and 12) the effective prey density has to be estimated separately for each prey density.

Furthermore, some of the available prey may be ignored, thus making it still more difficult to determine encounter rate. In this experiment, as in most other studies, the encounter rate is derived from the number of prey at-

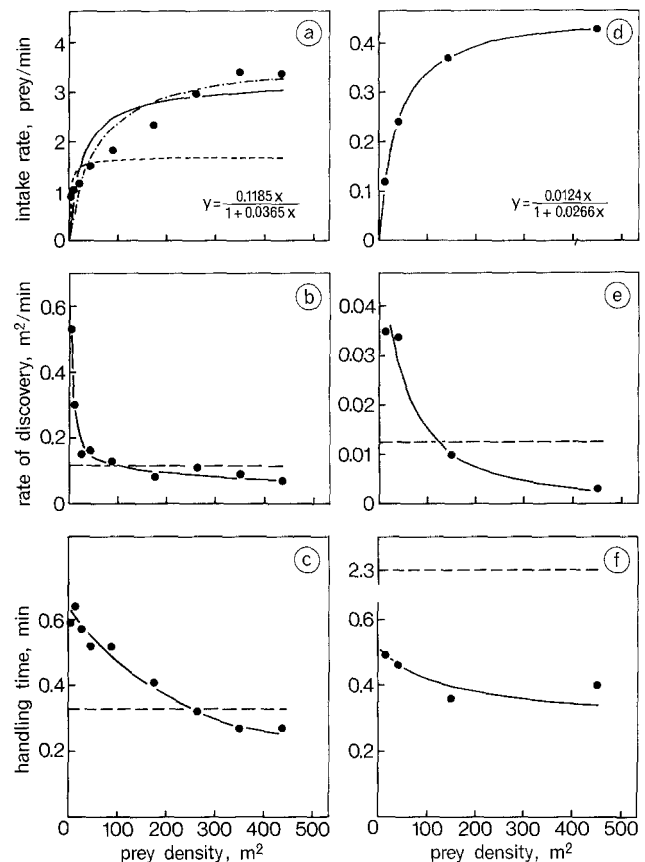


Fig. 14a–f. Functional response and its components (solid lines) for this study (a, b, c) and for Hulscher (1976) (d, e, f). The broken lines in b, c, e and f show the values as predicted from the disc equations. For (a) we have constructed two curves, using the measured values of a and h for the lowest (-----) and the highest (-----) prey density

tacked, but if some were ignored, encounter rate would be underestimated. This error becomes systematic and more serious if more prey are rejected at particular prey densities, as described by Hassell et al. (1976).

Optimal foraging theory predicts that the predator becomes more selective as prey density rises (MacArthur and Pianka 1966). Using the optimal foraging model of Charnov (1976) it is possible to predict for all prey densities the number of prey which should be ignored (Krebs et al. 1983; this study, Fig. 11).

Handling time h

The disc equation can only be solved if the handling time is independent of prey density (Holling 1959). Several studies have shown, however, that h decreased with increasing prey density (see review of Hassell et al. 1976). A common explanation of this might be a change in the feeding strategy of the predator. In cases where the predator eats the prey in several bites, it has been found that h decreases with higher prey density, because the prey is consumed completely at a low density whereas at high densities only the first, most profitable bites are taken (Haynes and Sisojevic 1966; Cook and Cockrell 1978; Giller 1980). Handling time also decreased in a predator which could act as a parasite too (Collins et al. 1981). Since an oviposition attack took less

Table 3. Handling times predicted from functional responses, and values observed. References: (1) and (2) Elliott 1983; (3) Green 1978; (4) Collins et al. 1981; (5) Feare et al. 1974, M.R. Berger and R. Veldhuis unpublished; (6) Hulscher 1976; (7) Sutherland 1982; (8) this study; (9) and (10) Holling 1959; (11) Davies 1977; (12) Tinbergen 1981; (13) Goss-Custard 1977a; (14) Goss-Custard 1977b

Ref.	Predator/Parasite *	Prey/Host *	h_{pred} (s)	h_{obs} (s)	Method
(1)	<i>Agriotypus armatus</i> *	<i>Silo pallipes</i> *	1,547	1,032 -1,368	Expt
(2)	<i>Agriotypus armatus</i> *	<i>Silo pallipes</i> *	979	1,032 -1,368	Field
(3)	<i>Alauda arvensis</i>	weed seeds	11.3	1 -2	Field
(4)	<i>Aphelinus basizonus</i> *	<i>Drepanosiphum platanoidis</i> *	829	456 -1,296	Expt
(5)	<i>Corvus frugilegus</i>	grain	9.0	0.5-0.9	Field
(6)	<i>Haematopus ostralegus</i>	<i>Cerastoderma edule</i>	139.5	21 -29	Both
(7)	<i>Haematopus ostralegus</i>	<i>Cerastoderma edule</i>	75.0	19 -29	Field
(8)	<i>Haematopus ostralegus</i>	<i>Scrobicularia plana</i>	19.6	16 -38	Expt
(9)	<i>Homo sapiens</i>	sandpaper discs	2.8	2.4-2.6	Expt
(10)	<i>Homo sapiens</i>	sandpaper discs	5.1	2.9-3.1	Expt
(11)	<i>Motacilla alba/flava</i>	Scatophagidae	1.7	<1 -10	Field
(12)	<i>Sturnus vulgaris</i>	<i>Tipula paludosa</i>	26.9	1.4-3.8	Field
(13)	<i>Tringa totanus</i>	<i>Nereis diversicolor</i>	12.0	0.4-6.0	Field
(14)	<i>Tringa totanus</i>	<i>Corophium volutator</i>	2.2	0.2-0.6	Field

time than the consumption of a prey, and the proportion of oviposition attacks went up with prey density, the mean handling time decreased.

Hulscher (1976) showed a decreasing handling time at high prey densities in an experiment where an oystercatcher fed on cockles of the same size and with a same availability (just below the surface) (Fig. 14f). Hulscher suggests that eating time was constant but that cutting time decreased with prey density. At a high density the oystercatcher started to select the cockles 'where the right information concerning the orientation of the cockle was known', this information is important for the feeding bird because the cutting time 'depends upon the extent to which the posterior adductor muscle was severed at the first jab' (Hulscher 1976, p. 307).

The oystercatcher in our experiment also became more selective when prey density went up. The bird reduced its handling time by ignoring deep-lying prey (shorter or no lifting time) and probably also by selecting prey it could stab into immediately (less cutting time).

Prey selection and functional response

A type-2 functional response is determined by the two constants a and h (Holling 1959), but as shown before (Fig. 14) a type-2 curve can occur where a and h are density-related. With the exceptions of Holling (1959) and Hulscher (1976), we could find no other papers where a and h were measured at all prey densities. We have found, however, several studies where the observed mean handling time could be compared to h as derived from the observed plateau-value of the functional response (Table 3). In most cases the measured h was too small to explain the asymptotic value of the feeding rate. The difference between predicted and observed handling times appeared to be greater in field studies than in the relatively simple experimental situations.

Krebs et al. (1983) suggested a model based on optimal diet theory to explain the limitation of feeding rate at the asymptote of the functional response. They constructed a family of functional responses for the different size classes of prey. If the predator takes only the largest (most profitable) prey, the curve will have a low asymptote since the

handling time of large prey is high. Adding smaller prey to the diet will increase the asymptotic value. Optimal foraging theory predicts an increase in selectivity when prey density rises, so the predator is expected to jump successively to lower feeding rate curves.

In our experiment the most profitable prey took the shortest time to handle, since the energy contents of all the prey were equal. We therefore expected the bird to jump to higher plateau-values when prey density increased. This was found indeed, but, as can be seen from Fig. 13, the oystercatcher managed to increase its intake rate at the higher prey densities even above the prediction based only on optimal depth selection. By selecting gaping shells the bird reduced the handling time and thus the asymptote of the intake rate curve went up even more.

Since we measured a and h for all offered prey densities, we could construct a family of functional responses based on real values for a and h . Fig. 14a shows the curves, extrapolated from the lowest and the highest density. In this way we get a better fit with the observed intake data than when the disc equation was used to predict the functional response.

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