FORAGING BEHAVIOR

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PREFACE

Foraging behavior has always been a central concern of ecology. Understanding what animals eat is clearly an essential component of understanding many ecological issues including energy flow, competition and adaptation. Theoretical and empirical developments in the late 1960's and 1970's led to a new emphasis in the study of foraging behavior, the study of individual animals in both field and laboratory. This development, in turn, led to an explosion of interest in foraging. Part of the reason for this explosion is that when foraging is studied at the individual level, it is relevant to many disciplines. Behaviorists, including ethologists and psychologists, are interested in any attempt to understand behavior. Ecologists know that a better understanding of foraging will contribute to resolving a number of important ecological issues. Anthropologists and others are applying the ideas coming out of the study of foraging behavior to problems within their disciplines.

These developments led to a multidisciplinary symposium on foraging behavior, held as part of the 1978 Animal Behavior Society meetings in Seattle, Washington. Many ecologists, ethologists and psychologists participated or attended. The symposium was very successful, generating a high level of excitement. As a result, the participants decided to publish the proceedings of the symposium (Kamil & Sargent 1981).

The authors of chapters for that volume also decided to forego the usual royalties. These moneys were placed in a fund and used to finance a conference on foraging behavior which was held in June, 1984, in Providence, Rhode Island. Brown University, with Doug Morse in charge of local arrangements, provided an ideal setting for the conference. The conference was advertised, and an open call for papers published in various newsletters. As a result, almost 100 abstracts were submitted for consideration for inclusion on the program. In addition, three papers were invited, from James Gould, John Staddon and Robert May. The final program included 27

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FORAGING BEHAVIOR OF SOME WINTERING WADERS:
PREY-SELECTION AND HABITAT DISTRIBUTION

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During the non-breeding season, many species of waders (Charadriidae and Scolopacidae) depend on intertidal areas for feeding. Specific estuaries may be important either as refuelling sites for birds on migration, for wintering birds, for moulting birds or for any combination (Evans, Goss-Custard & Hale 1984).

These intertidal feeding areas can be divided into broad categories (macrohabitats) such as rocky shores, estuarine tidal flats, beaches, etc., each of which can be subdivided in several microhabitats. For many species, and for our purpose, estuarine tidal flats are the most important. On these flats several habitat types based on characteristics such as sediment, benthic macrofauna, presence of algae, and tidal elevation can be distinguished (Anderson 1972, Meire & Kuyken 1984a). Each wader species uses one or several habitat types. These habitat preferences have been investigated mainly for the new world species (Pitelka 1979) and to a lesser extent in Europe and Africa (Eddington, Morgan & Morgan 1973, Zwarts 1981).

Factors affecting habitat distribution in general have been reviewed recently by Partridge (1981). A very thorough analysis of habitat selection of some sunfish species has been carried out by Werner and coworkers (see Werner 1984 & Werner & Mittelbach 1981 for reviews). They have attempted to develop and test an approach for predicting habitat use by these fish, based on first principles of foraging theory. By calculating the expected energy return for each habitat based on an optimal diet model they could rank the different habitats. They found that the fish selected habitats according to their profitability. In further studies they also studied the effects of predation risk on habitat selection (Werner, Gilliam, Hall & Mittelbach 1983).

In this paper I explore whether or not the same approach is useful or possible for understanding and predicting the distribution of waders on tidal flats. This situation is more complex than in the fish studies since more factors affect the distribution (e.g., tidal conditions). However, understanding the relationship between habitat profitability and bird distribution is not only of fundamental interest but might have practical implications. Indeed tidal flats are threatened all over the world by

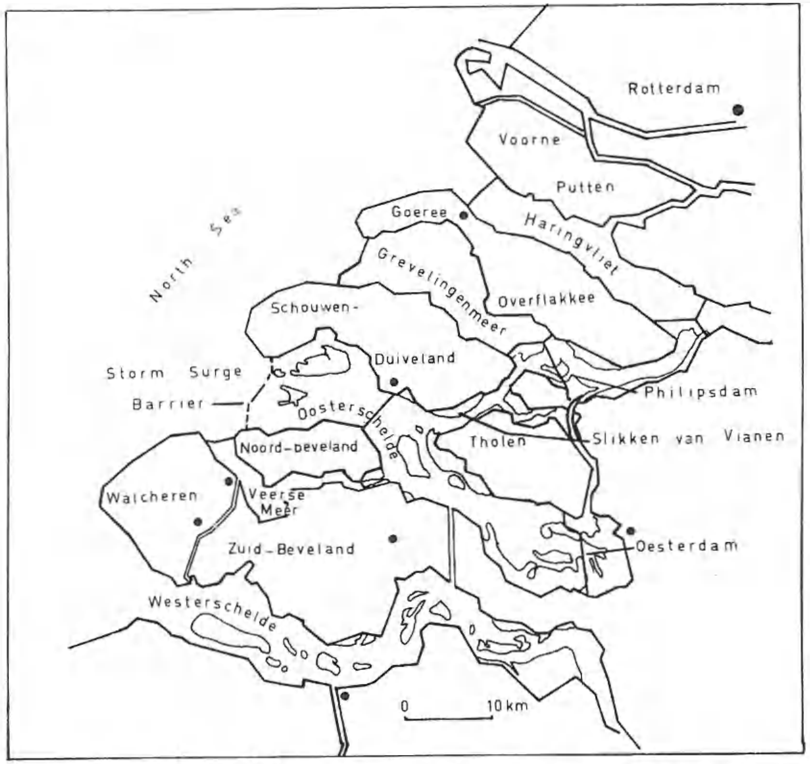

Figure 1. Map of the Delta area and location of the study site "Slikken van Vianen."

pollution, barrage building, recreation, etc. (Langslow 1981) and an adequate conservation policy needs predictions on the impact of these interventions. Therefore if this approach is successful, the use of optimal foraging models can become a tool in environmental management.

I will first briefly describe the distribution of waders on their feeding grounds and subsequently present a conceptual model in which several important variables are incorporated. The field evidence for optimal foraging theory (OFT) in waders is reviewed and this is incorporat-

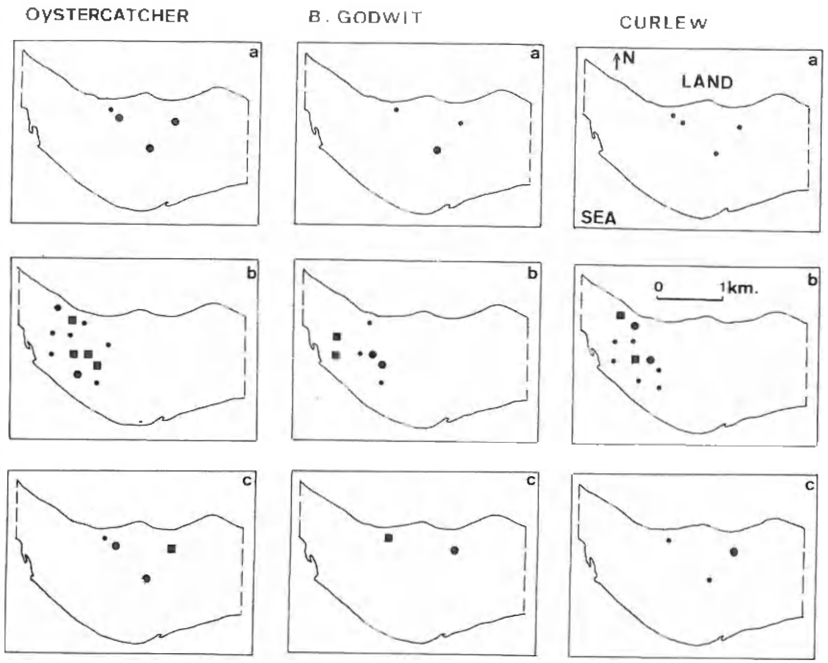

Figure 2. Habitat distribution of three wader species on the Slikken van Vianen. The density in the study-plots during autumn is given:

a. 4-3 hours before low water (L.W.);
b. during L.W.;
c. 3-4 hours after L.W.

For oystercatchers a small dot is 0.1 - 10, a large dot 10 - 20 and a square > 20 birds/hectare. For curlew and bar-tailed godwit a small dot is 0.1 - 5, a large dot 5 - 10 and a square > 10 birds/hectare.

ed in a model to predict habitat distribution. This is discussed in the light of the present results.

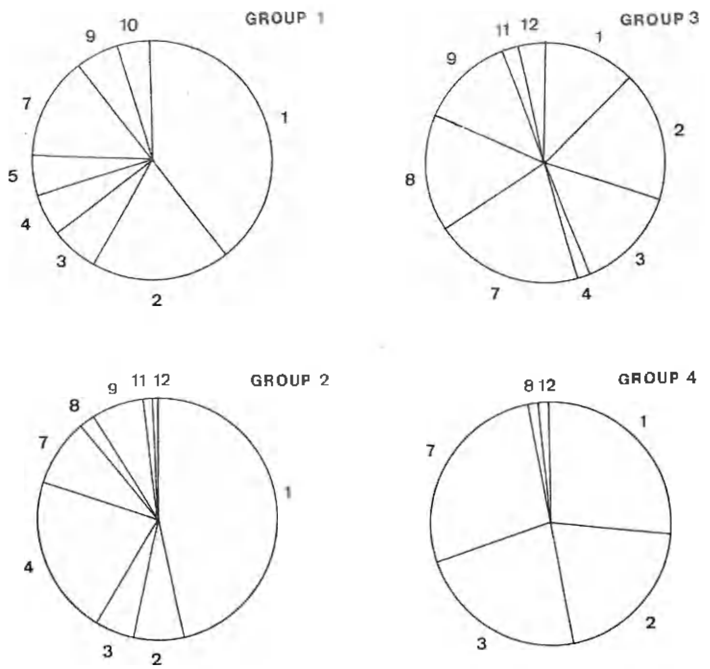

Figure 3. Average proportional composition of birds in 4 habitat types.

Group 1 = mussel beds
Group 2 = mudflats
Group 3 = high sand flats
Group 4 = low sand flats.

1. Haematopus ostralegus
2. Numenius arquata
3. Limosa lapponica
4. Tringa totanus
5. Tringa erythropus
6. Tringa nebularia
7. Calidris alpina
8. Pluvialis squatarola
9. Arenaria interpres
10. Larus argentatus
11. Larus ridibundus
12. Charadrius alexandrinus

THE SCENE

In our study area, the Slikken van Vianen (Fig. 1), several microhabitats (Burger 1984) can be distinguished (Meire & Kuyken 1984a) based on macrofauna and sediment characteristics. Wader use of a habitat is related to the number of birds in an area and the availability of the habitat as a feeding site. As this is continuously changing due to the tides, habitat distribution is a very dynamic process.

In general, and on the Slikken van Vianen in particular, all the birds roost in the salt marsh or on adjacent arable land during high tide. When the tide ebbs some birds immediately start to feed at the waterline. Their number rises gradually, and three hours after high tide, areas with low and high bird density can be distinguished (Fig. 2). This situation is very pronounced at low tide when some areas may accommodate hundreds of birds per hectare and other areas, previously having high densities, are almost completely abandoned. When the tide floods, the opposite migration takes place. In the course of a low water period several habitats may be used sequentially by a species. This also has been described by Burger, Howe, Hahn and Chase (1977) and Burger (1984). This distribution pattern also differs between species. In each community or microhabitat, the species composition is clearly different (Fig. 3). The density within a microhabitat is also variable and dependent on prey density. This pattern shows seasonal variations but this will be discussed in detail elsewhere (Meire in preparation).

A CONCEPTUAL MODEL

A conceptual model incorporating different factors which are influencing the observed distribution was described by Meire and Kuyken (1984b) and is in several respects similar to a framework of resource systems elaborated by Wiens (1984). It is argued that the density of a wader species in a prey-species community or microhabitat is not only dependent on the available prey density, but also on the total number of birds in the area, the availability of several microhabitats or communities, and the available feeding time. This last factor is very important since, together with the intake rate, it determines the overall intake of the birds. The overall intake, in turn, determines if birds will or will not stay in that area. When modelling this situation an optimal diet model could be used for calculating the intake rate. The evidence therefore will be discussed later. Obviously habitat selection by waders may be influenced by constraints other than foraging. Predation and distance from roosting sites are also important, but beyond the scope of this paper.

OPTIMAL PREY SELECTION IN WADERS

In this section I review some available evidence that wader foraging is indeed in accordance with OFT. In the OFT literature, a distinction has been made between prey choice and patch exploitation. In wader studies, most evidence has been gathered concerning prey choice. We will subsequently discuss prey choice in oystercatchers (Haematopus ostralegus L.), redshank (Tringa totanus L.), bartailed godwits (Limosa lapponica L.), and grey plovers (Pluvialis squatarola L.).

Oystercatchers Feeding on Mussels

Oystercatchers feeding on mussels (Mytilus edulis L.) have two essentially different methods for opening the shell. The first method is used against mussels which are slightly open and consists of stabbing the bill between the gaping valves and then prising them apart. The second method is used against tightly closed mussels and consists of hammering the shell with the bill until the shell breaks. The adductor muscle is then cut and the valves prised apart. The shell can be hammered either on the ventral or the dorsal side.

Hammerers

It is well documented that hammering oystercatchers select certain size-classes of mussels (Drinnan 1958, Norton Griffiths 1967, Goss-Custard, McGrorty, Reading & Durell 1980, Ens 1982, Meire & Ervynck in press). Only recently has this size selection been compared with the predictions of an OFT model. Ens (1982) concluded that the birds were taking smaller mussels than predicted by the optimal diet model. The active rejection of the large, most profitable mussels (which occurred often) was especially contrary to the expectation of the model. But as anticipated by Ens (1982), Durell & Goss-Custard (1984) and Meire and Ervynck (in press) have found that mussel selection involves more than size selection.

Meire and Ervynck (in press) analysed the selection of ventral hammerers in some detail at the Slikken van Vianen. A summary of the results is presented here. From the mussel population present, a limited size range was taken (10-60 mm but mainly between 30 and 45 mm) and there was no preference for the largest mussels (Fig. 4). There was also a strong selection for mussels with a thin shell. In Figure 5 the average shell thickness (measured at the ventral shell edge near the anterior adductor muscle) of the mussels present and taken by oystercatchers, is plotted. Clearly the larger the mussel was, the stronger the selection. Finally, oystercatchers are also selecting against mussels which are overgrown by barnacles (Balanus balanoides). Mussels are either clean of barnacles, have just a few, or are more than half covered. Although this last category was never found in samples of mussels taken by the birds, it could make

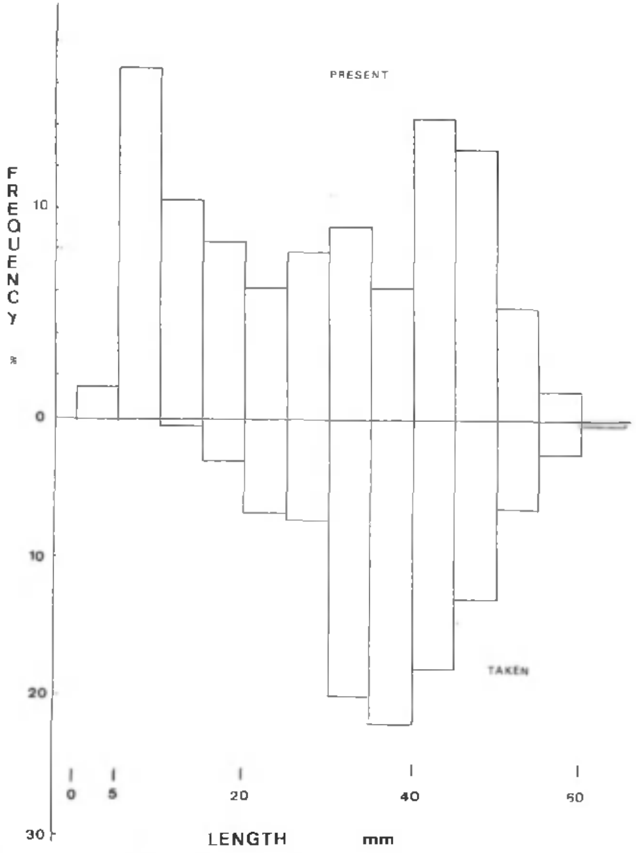

Figure 4. Frequency distribution of mussels present and taken by oystercatchers in a study plot.

up an important fraction of the mussels present in the bed (see also Durrell & Goss-Custard 1984). We assume that oystercatchers either cannot open these mussels (as the ventral side is overgrown), or else do not recognize them as mussels because in many cases only the barnacles are visible at the surface. To compare this selection pattern with the predictions of an optimal diet model (Charnov 1976), we first analysed length selection and afterwards selection for shell thickness. Based on the relationships between both handling time (H) and biomass (E) as a function of mussel length, the larger mussels are the most profitable (Fig. 6). However, an important number of large mussels taken were abandoned after some time (waste handling time WH) without opening them (the probability of opening a mussel once taken $P = 1.127 - 0.016$ shell length [in mm] $r^2 = 0.826$, $n = 11$, $p < 0.01$). This can be incorporated to estimate the profitability:

$$\frac{E}{H} = \frac{E \cdot P}{(H \cdot P) + WH\ (1-P)}, \qquad (1)$$

which is maximal for mussels of 55-60 mm (Fig. 6). This has to be incorporated in the diet model as well and this becomes:

$$\frac{E}{T} = \frac{\Sigma E_i \lambda_i P_i}{1 + \Sigma\lambda_i (H_i P_i + (1-P_i)\ WH_i)}, \qquad (2)$$

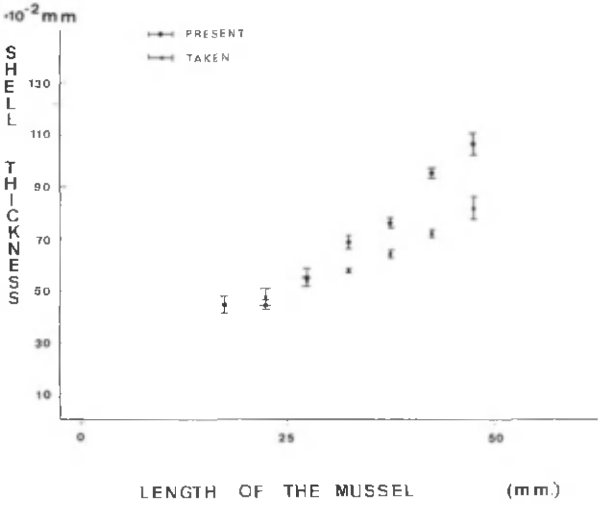

Figure 5. Average shell thickness (+ SE) of mussels present on the bed (·) and opened by oystercatchers (X).

Where λ_i is the encounter rate for class i. The assumptions behind this model (Krebs & McCleery 1984) are fulfilled.

Prey value is measured by a single dimension, ash free dry weight. Handling time is a fixed constraint. Handling and searching cannot be done at the same time. The prey should be recognized instantaneously and without errors. This is clearly wrong, but by incorporating the negative handling time into the model, errors are accounted for. It is assumed that the predators encounter the prey sequentially and randomly (no clumping of size classes within the bed was found) and the energetic costs per second of handling are similar for different prey.

Before we can calculate the optimal diet we must estimate the only unknown parameter of equation (2): the encounter rate (λ_i). Thompson (1983) used equation (3) to estimate λ_i:

$$\lambda_i = 1/100\ (\ \ (1/d_i)/S), \qquad (3)$$

where S is the search speed and d_i the density of size class i. S was estimated in the field to be 0.085 m/s and d_i is known from the sampling. The diet was calculated based on the total densities of mussels and on the density after subtracting the mussels which are too thick to be eaten or

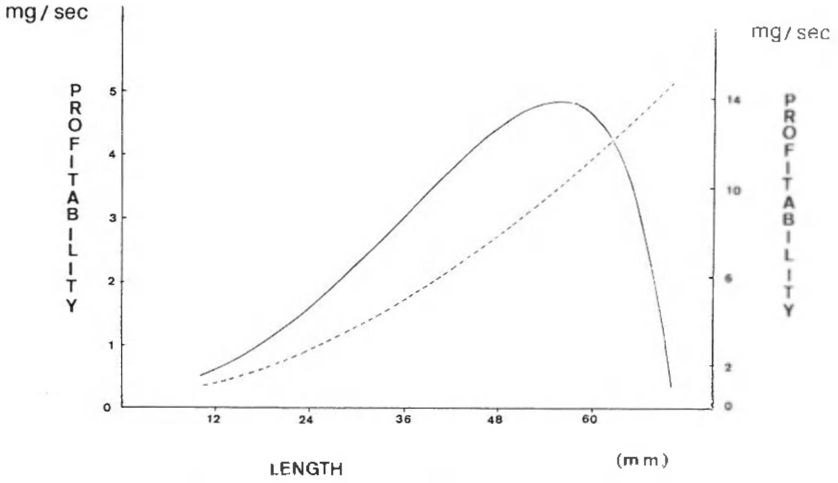

Figure 6. Profitability of mussels in function of mussel length. The full line gives the profitability after including the negative handlings. For explanation see text.

which are overgrown by barnacles. In Table 1 the percentage of the prey density available to oystercatchers is given and it is striking how few of the larger mussels are actually available. The results are given in Figure 7. There is a good agreement between the size range taken and that predicted, when we take into account the density of mussels really available to the oystercatchers. Comparison with the predictions of the model, based on the density of mussels present on the bed, (Fig. 7b) clearly indicates the importance of estimating the available prey population.

An experiment was carried out to test whether the selection for shell thickness is in accordance with the energy maximization hypothesis. In order to estimate the force necessary to open a shell, a copper model

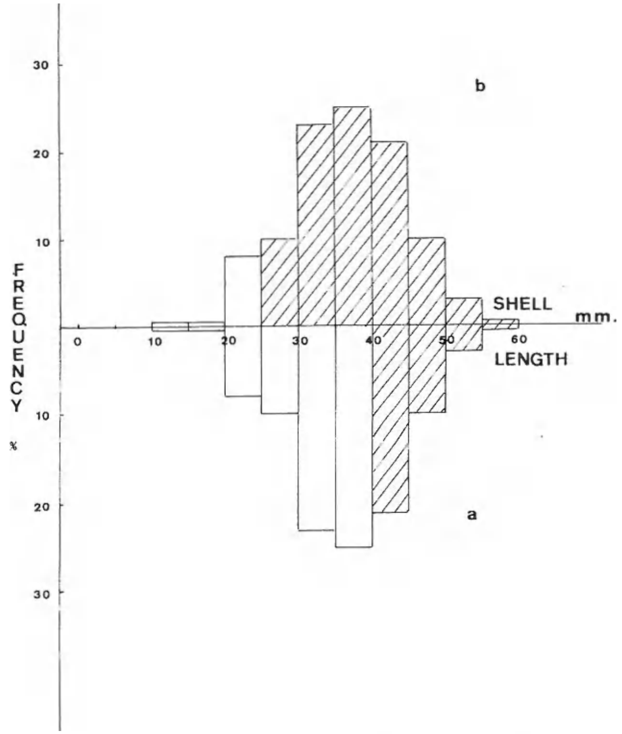

Figure 7. Frequency distributions of mussels taken by oystercatchers. The hatched part is the predicted diet based on the original densities (a) and available density (b).

TABLE 1. PERCENTAGE OF MUSSELS OF SEVERAL SIZE CLASSES AVAILABLE TO OYSTERCATCHERS

Size class (mm)	10-15	15-20	20-25	25-30	30-35
% available	100	100	100	100	100
size class (mm)	35-40	40-45	45-50	50-55	55-60
% available	73	31	36	12	1

oystercatcher bill was dropped from a standard height on a mussel until the mussel broke. An exponential relationship between force and shell thickness was found (Fig. 8). From the frequency distribution of mussels taken and present (for one length class), it is obvious that when the force necessary to open the shell starts to increase sharply, oystercatchers cease to take these mussels. Assuming that the number of blows of the copper bill is proportional to the handling time, we can estimate the handling time for thick shelled mussels (0.8 - 1.2 mm) based on the proportion between the numbers of blows for thin (0.4 - 0.8 mm) and thick (0.8 - 1.2 mm) mussels and the measured handling time of thin shelled mussels. The profitability of the mussels (of a size class) taken and rejected by

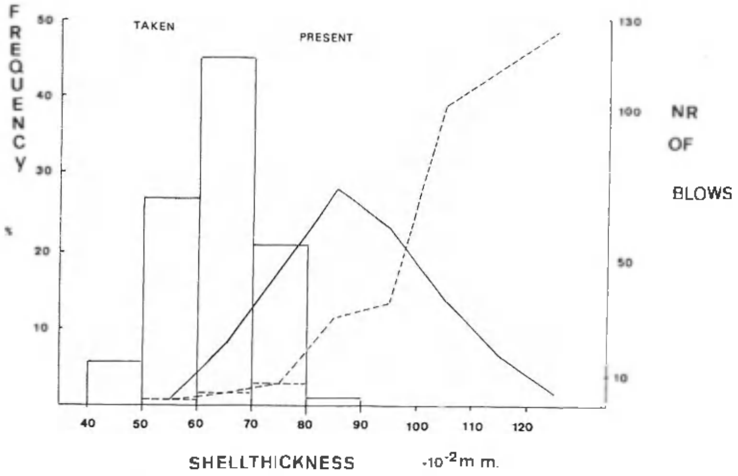

Figure 8. Frequency distribution of shell thickness of mussels of 35-40 mm taken by oystercatchers (histogram) and present (full line). The broken line gives the number of blows which where necessary to open a mussel (for explanation see text).

oystercatchers can now be estimated. As the profitability of the thicker ones is much lower than the average intake (0.3 mg/s versus 2 mg/s) we may conclude that the exclusion of the thick-shelled mussels from the diet is in accordance with the energy maximization principle.

This could explain why oystercatchers take smaller prey than those which seem to yield the highest E/H. There are, however, many possible explanations in addition to those considered here. Handling time may be more costly for larger prey, the risk of kleptoparasitism may increase with size, and long-handling times may increase the risk of predation of the bird.

Stabbers

Oystercatchers that stab their prey are dependent nearly entirely on mussels covered by a few centimeters of water, since only these mussels gape slightly. Shell thickness and barnacle coverage are not important in this case. Normally, stabbers do not appear to select for any particular type of mussel shell (Durell & Goss-Custard 1984), so a selection for larger mussels can be expected. In Figure 9 the frequency distribution of mussels present and mussels taken by stabbing birds is given. No apparent selection is obvious. It is not possible to compare this with predictions, since we can not estimate the proportion of the population which gape (and are thus available to the birds) at any one time. However, Zwarts and Drent (1981) found that on their musselbeds, with three to four times more mussels, there was strong selection for the larger mussels. The predicted lower acceptance threshold was very close to the observed lower limit.

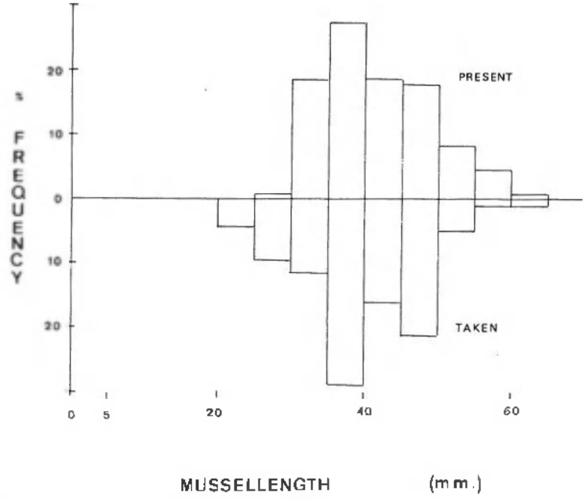

Figure 9. Frequency distribution of mussels present and taken by stabbing oystercatchers in a study plot.

Oystercatchers Feeding on Cockles

Another very important prey for oystercatchers is the edible cockle (*Cerastoderma edule*). The selection of cockles has been studied in detail by Sutherland (1982). He found a pronounced preference for the largest, most profitable cockles and could separate preference from availability by relating feeding rate and density for several size classes. The slope and correlation coefficient increased with size, showing the largest cockles are preferred, as predicted by the model.

Oystercatchers Feeding on Macoma Balthica

Oystercatchers feeding by touch on *Macoma balthica* also select for the larger ones. However, Hulscher (1982) showed that this is due to passive selection. The larger ones have a higher risk of being encountered. Prey smaller than 11 mm were actively rejected. This lower limit is near the expected acceptance threshold.

Bar-tailed Godwits

Bar-tailed godwits are euryphagous predators feeding on several species of Polychaetes, Molluscs and Crustacea. I studied the prey selection of godwits in several study plots on the Slikken van Vianen. Prey species were divided into several (broad) categories being:

A: *Arenicola marina*, the lugworm;
X: large worms, mainly *Nereis diversicolor* and *Nepthys hombergii*;
Y: small worms as *Heteromastus filiformis*, *Scoloplos armiger* and small individuals of the large worms;
M: molluscs, *Macoma balthica*;
O: small and unidentified prey.

It was found that as the density of the most profitable prey (A, M and X) decreased, the less profitable prey (Y and O) were added to the diet. The feeding rate of A, M and X was positively correlated with prey density but for Y and O no relation was found. (The details of this study will be published in detail elsewhere.)

Redshanks

Goss-Custard's studies of prey selection by redshank probably are the most cited examples of a field test of optimal foraging, so his results can be summarized very briefly. When feeding on *N. diversicolor* (Goss-Custard 1977a), redshanks selected for large worms, and took very few small ones when large ones were abundant. With a simulation model, incorporating all details of redshank foraging behavior, Goss-Custard found that the size selection shown by the birds actually resulted in the highest E/T. However, in many places redshanks are confronted with a choice between the ragworm and the small amphipod crustacean *Corophium volutator*. When both *Nereis* and *Corophium* were abundant, the birds showed a clear preference for the latter. With the same simulation model, Goss-Custard (1977b) found that this preference yielded two or three times less energy per unit time than the selection of *Nereis* would have yielded. Clearly, the birds were not maximizing rate of energy intake. Several explanations for this result have been suggested. There might be a difference in digestibility, birds might form a search image, etc. (Goss-Custard 1977b). None of these give a fully satisfactory explanation.

Grey Plovers

Grey plovers in intertidal areas feed mainly on Polychaete worms and to a lesser extent on Crustaceae. *A. marina*, *Notomastus latericerus*, *N. diversicolor* are the most important prey (Pienkowski 1982). Grey plovers forage by an apparently visual searching technique, which makes them entirely dependent on the activity patterns of their prey. Hence it is very difficult to estimate available prey densities. By observing the birds under different environmental conditions, which are known to influence the surface activity of the intertidal prey, Pienkowski (1983a) demonstrated that their selection behavior is consistent with the predictions of the optimal diet model. The rate of taking large prey increased with environmental conditions in which these prey became more active, or detectable, at the sand surface. As large prey became more available these were selected and feeding rate on small prey (also more available) fell (Pienkowski 1983a). Plovers appeared to select large prey, in suitable conditions, by not responding to cues of small prey at the start of each waiting period (Pienkowski 1983b).

The performance of the animals in these studies was tested either by calculating the optimal diet based on the available prey density, or by investigating the changes in diet where environmental factors are known to change the prey's availability, or by comparing the selection between different places. These studies do not provide unequivocal evidence for the optimal diet model.

In general, selection for size classes of one prey species gives good evidence for the E/T maximization hypothesis. When more prey species are involved we still find reasonable agreement with the predictions of the model in the studies of grey plover and bar-tailed godwit. However, the preference for *Corophium* by redshank is not consistent with the energy hypothesis.

However, in many species we find a preference for Crustaceae. Bar-tailed godwits were observed occasionally spending very long handling times on shrimps and crabs (which hence had a very low profitability). Curlew feed nearly exclusively on crabs in autumn. Sometimes oystercatchers take crabs as well. It is also known that waders in captivity do very well on a diet of shrimps (C. Swennen, personal communication). These observations make it likely that some factor other than energy might be important in Crustaceae. This should be studied in more detail.

Another point which makes the application of OFT models difficult is the problem of measuring the available prey density. This can only be done in very detailed studies (Hulscher 1982, Zwarts & Wannik 1984). Nonetheless, I believe that analysing prey selection within the framework of OFT is very useful and will especially focus our attention on important factors previously unknown or thought to be unimportant.

FORAGING BEHAVIOR AND HABITAT DISTRIBUTION

Based on the evidence and discussion presented in the previous section, it is assumed that the optimal diet model is at least a reasonable approximation of the foraging behavior of waders. I now incorporate this into a model which attempts to predict distribution across habitats. The overall intake (OI) of an animal is:

$$OI = TF \cdot IR \tag{5}$$

in which TF is the feeding time and IR the maximum intake rate possible in that area. IR can be calculated from the optimal diet model. The feeding time of an average individual can be estimated from data on numbers of birds present and feeding in an area:

$$TF = \frac{FD}{D} \cdot TT, \qquad (6)$$

where TF = feeding time; TT = total time available; FD = feeding density; and D = total density. However due to interference, IR decreases with bird density. Studies on oystercatchers revealed that the average intake rate declines with the density of feeding birds (Zwarts & Drent 1981, Goss-Custard 1980, Ens & Goss-Custard 1984). The mechanisms of interference have been reviewed by Goss-Custard (1980) and can be divided in two categories: reduction in feeding time and reduction in intake rate.

In oystercatchers it has been found that as the density of birds increases, the proportion of the population that is feeding decreases (Zwarts & Drent 1981, Zwarts 1981, Meire & Kuyken 1984a), or that the average individual is feeding for a shorter time. A reduction in intake rate can be caused either because birds have to alter their search patch, because they lose time in encounters, or because the available prey density is depressed (Goss-Custard 1970), or because they lose food by kleptoparasitism.

This can be incorporated in the model easily, by adding a term to equation (5):

$$OI = TF \cdot (IR - cst\ FD). \qquad (7)$$

It is assumed that there is a linear relationship between the intake rate achieved by an individual and the density, as found by Ens & Goss-Custard (1984), and that only the density of feeding birds is important (I never observed an interaction between resting and feeding birds). It is very important to stress that I talk of an "average" individual. Equation (7) can be rearranged to:

$$OI = TF \cdot (IR - cst\ [\frac{TF \cdot D}{TT}]) \qquad (8)$$

Since TT is constant for an area, and D remains nearly constant during one tidal cycle (certainly on preferred feeding areas), we have only one variable in the equation. This formulation is very similar to the model of Fretwell and Lucas (1970). However, one important difference is that in this model the distribution of the population depends not only on intake rate and number of birds but also on the energy need of the average individual. This alters the predictions somewhat.

Before elaborating this, we must analyse the relation between feeding density and total density. In Figure 10 the density of feeding birds which allows the highest overall intake/individual is plotted as a function of the total density. This density levels off to a plateau value because if, for instance, all 200 birds were to forage, the influence of interference would be very strong. But if only a proportion of the population were to feed at any one time, interference would be less important. The level of the plateau for a given IR is dependent on cst., the interference parameter. This relation is exactly what we find in the field. In Figure 11 the data of oystercatchers on one study plot (musselbed) are shown. Feeding density levels off at high bird densities because there are always some groups of resting birds on a musselbed. There is a continuous exchange of birds between these groups and the foraging groups.

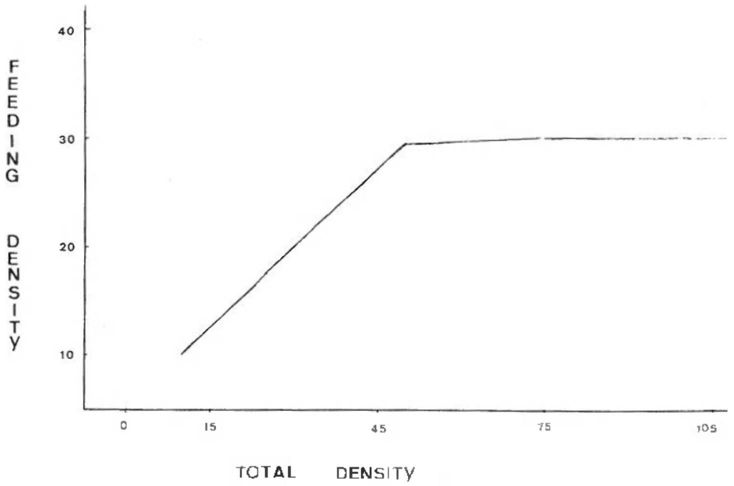

Figure 10. Density of feeding birds in function of the total density which allows each individual the highest intake rate. For explanation see text.

When energy need is low, a rather large number of individuals can stay in the best areas. When the energy demand increases (e.g., in winter), overall density will have to drop until the point where all the individuals can forage for all of the available time. In Figure 12a the total and feeding density of oystercatchers in a preferred study plot is plotted for July to December 1979. (On each observation day at least 10 times during one tidal cycle data were collected. Because density in these plots was quite stable during the whole exposure time, the average of these counts are presented.) The average temperature decreases from 16°C in July to 3°C in December. Therefore, the energy demand of the animals must increase. Subsequently, we see that the difference between FD and TD decreases from September to December. Some of the birds previously present have to go to other areas and there is indeed an increase in other plots (Fig. 12b; Meire & Kuyken 1984a). Dominance relationship and aggression may determine which individuals leave and which stay in the best areas. In other areas where the prey density is low, it may be that the obtainable energy becomes too low, and birds have to leave (Fig. 12c). This result could not be explained by prey depletion. The total number of oystercatchers in the study area increased from about 2000 in August to 5500 in December.

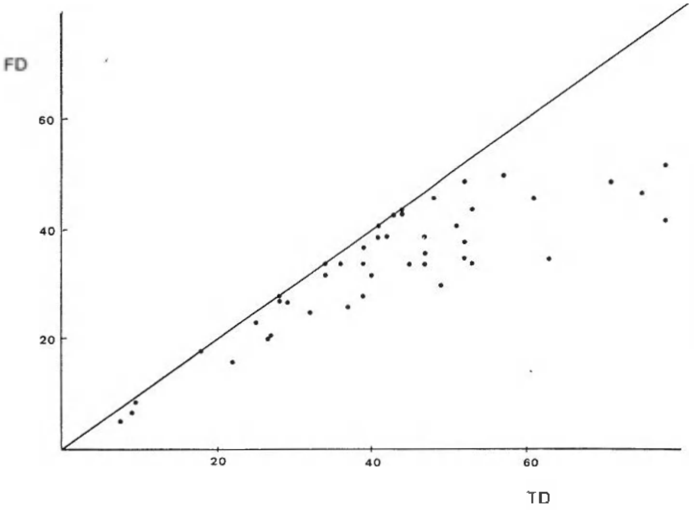

Figure 11. The feeding density plotted in function of the total density (birds/hectare) for one study plot.

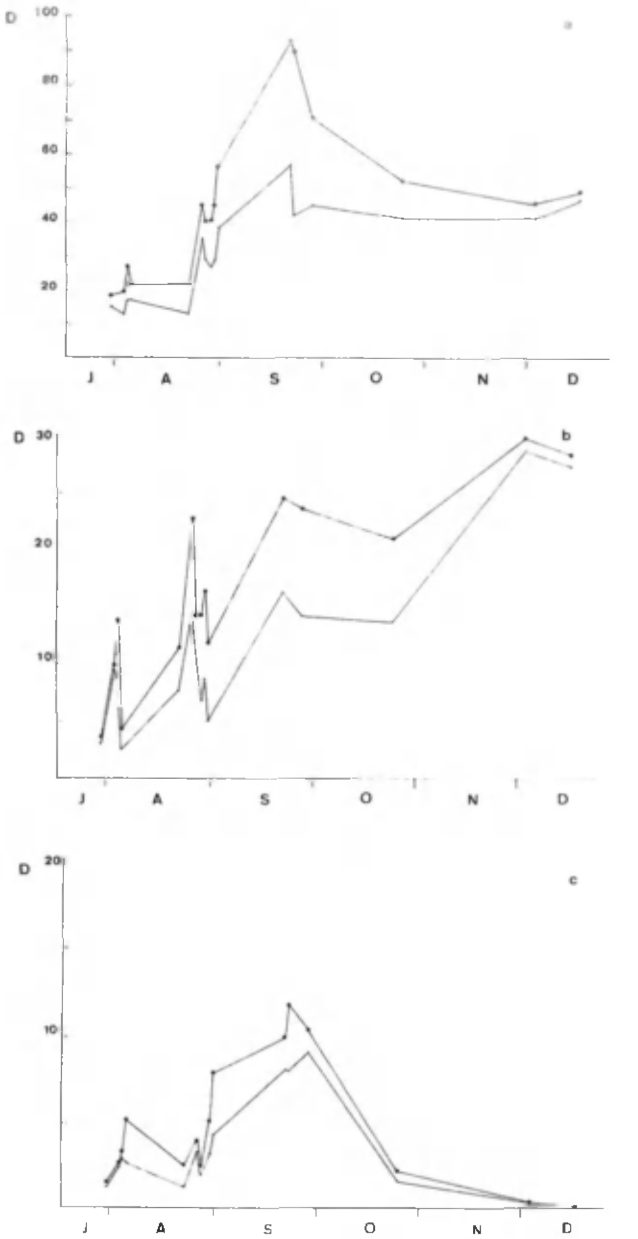

Figure 12. Total density (upper line) and feeding density (lower line) (birds/hectare) in three study plots for several days between July and December 1979 (for explanation see text).

The distribution depends on the number of birds in the whole area, their energy demand and the maximum IR of the different habitats or subareas. When the overall numbers are low, we expect an exponential relation between IR and TD, which becomes linear as the number of birds and the energy demand increases.

Discussion

When the tide ebbs and waders start foraging, they are confronted with a quickly changing environment in which they must make appropriate foraging decisions. These are influenced by the environment, by congeners and by the state of the animal. Many optimal foraging models assume that prey are selected so as to maximize energy intake. The results presented here only partly support this assumption. This should encourage us to undertake new studies to unravel underlying factors rather than just saying, "The animals are not optimal." One important problem, in many field studies of OFT, will be to estimate the available prey density. This should be related to the prey density (otherwise all the correlations between feeding rate and prey density are spurious!) but it is necessary to quantify it.

This becomes especially important when we want to understand carrying capacity, numerical and functional responses. It is necessary in order to know if an estuary is "full," the question conservationists are interested in. The huge difference between the mussel densities present on a bed and the density really available to oystercatchers underlines this point. Also when analysing the functional response, it is necessary to relate feeding rate to the available prey density and not to the prey density present.

Since all species are feeding on different prey types (length classes or species), and this is likely to depend on the abundance, it is also very hard to relate bird numbers to prey density. One can not simply add all prey species together to have a measure of prey density (100 small and 10 large prey or vice versa). Moreover the available fraction of the different species may differ. Therefore I think it is better to relate predator density to the average obtainable intake rate. This obviously is dependent on prey density, but it is the only sensible combined measure of prey density. The model presented is a preliminary step in this direction. Interference, likely to be an important factor in habitat distribution, is included as well, and we find that the relation between intake rate and bird density is dependent on the energy demand of the birds themselves. Although the few data presented do not contradict the model, much more evidence has to be collected to prove or disprove it. I have focused also on a very simple case in which the intake rate and hence the density remained constant. In intertidal areas, however, the IR can fluctuate during one tidal cycle. In this case birds visit several habitats sequentially. This has been described by Connors, Myer and Pitelka (1981). Several species of waders will also experience interference differently. The interference parameter cst. may itself be density dependent. In dunlins (*Calidris alpina*) or other social species the interference parameter may first be negative and becomes positive only at a certain density.

Although we cannot as yet describe habitat distribution as in the fish studies cited earlier, I believe this approach is very promising and can help us to understand why waders do what they do and hence use this for conservation.

SUMMARY

In intertidal areas, waders distribute themselves over several habitats during a low-water period. This is briefly illustrated and a conceptual model, in which the relevant factors for this distribution are incorporated is briefly discussed. The intake rate of the animals is a crucial variable and an optimal diet model is thought to be the appropriate function. To support this, studies on optimal prey selection in waders are reviewed. Although not all selection patterns can be explained by the diet model, I believe it can easily be used for our purpose. It is incorporated in a simple model to understand habitat distribution. I argue that next to prey density and number of birds, the energy need of the individuals influences distribution. Data are presented which are in accordance to this hypothesis.

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