# Prey choice and search speed

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# PREY CHOICE AND SEARCH SPEED: WHY SIMPLE OPTIMALITY FAILS TO EXPLAIN THE PREY CHOICE OF OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* FEEDING ON *NEREIS DIVERSICOLOR* AND *MACOMA BALTHICA*

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Oystercatchers breeding on the saltmarsh of Schiermonnikoog rely on two staple foods during the breeding season: the bivalve *Macoma balthica* and the worm *Nereis diversicolor*. Both prey are highly profitable, yet individual birds tend to specialize on either of the two prey species for prolonged periods of time, contradicting the simple or 'classic' optimal prey choice model. Although male Oystercatchers often specialize on *Macoma*, while ♀♀ often specialize on *Nereis*, none of the intensively studied individuals was so inefficient at handling either prey that this could have been the reason for excluding one of the prey from the diet. Furthermore, the two prey did not have different distributions in space, nor could short-term fluctuations in prey availability explain the specialization of individuals. It appears that Oystercatchers hunting for *Macoma* search at a slower speed and make more pecks per distance searched than do birds hunting for *Nereis*. This accords with the suggestion that, from the point of view of the Oystercatcher, buried *Macoma* are more cryptic than *Nereis* which emerge from their burrows to feed on the surrounding substrate. The incompatibility of searching for the two prey at the same time explains why the simple optimal prey choice model does not apply in this and probably many other cases. As argued by Gendron & Staddon (1983), the problem of search speed and the problem of prey choice cannot be treated independently.

Key words: Oystercatcher - *Haematopus ostralegus* - search speed - optimal foraging - prey choice - *Nereis diversicolor* - *Macoma balthica*

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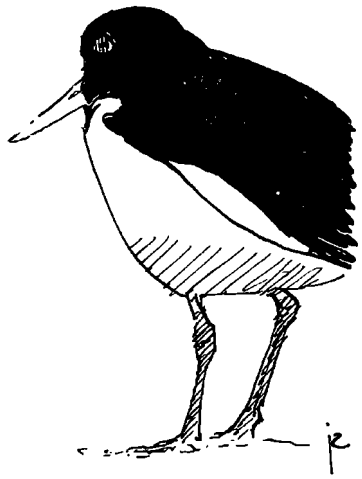

## INTRODUCTION

An important promise of optimal foraging theory is that it should allow us to anticipate the rate at which animals can harvest food in a given location from the densities of the various prey species present, without the need to make direct observations in the particular location. Indeed, the lawfulness in the feeding behaviour of the animals, established through field studies and experiments, may one day even allow predictions for areas presently not occupied by the animals or for prey species not yet encountered. An example of the latter is the prediction of the profitability to Oystercatchers of *Ensis directus*, a bivalve that was recently introduced in the Wadden Sea (Zwarts *et al.* 1996b).

Stephens & Krebs (1986) provide a thorough

description of the simple or 'classic' prey choice model (see the appendix for the precise equations). Prey of different species and sizes are ranked by their profitability, i.e. the rate of energy gain during handling. From the rate at which prey of a given class are encountered during searching it can then be calculated which classes should or should not be taken to achieve the maximum rate of energy gain during feeding. When prey with a profitability below the critical threshold are encountered, it is more efficient to continue searching than to handle and eat them. Because of its precise quantitative predictions, the model has proven a powerful research tool, which does not mean that it is necessarily true. In fact, on many occasions, the underlying assumptions haven proven to be rather simplistic. For instance, Ens (1982) calculated that, for Oystercatchers hammering Mussels from the ventral side, the largest size classes were the most profitable, yet these size classes were clearly selected against. Subsequent work showed that, within a size class of Mussels, the birds selected thin-shelled individuals (e.g. Durell & Goss-Custard 1984), and Meire & Ervynck (1986) successfully adapted the optimal prey model to include the time wasted failing to open thick-shelled Mussels. As this example illustrates, when the choice is between size categories within a prey species, it has generally been possible to modify or expand the original prey choice model to predict the observed effects. In contrast, understanding the choice between different prey species has proven more resistant. For instance, it is still a mystery why Redshank *Tringa totanus* ignore profitable worms when *Corophium* is abundant (Goss-Custard 1977).

A possible solution is provided by Gendron & Staddon (1983) who argued that there is a tradeoff between search rate and probability of detection, with more cryptic prey requiring lower search rates to achieve maximum intake rates (see appendix). Under these circumstances, profitable but cryptic prey may be 'ignored', because it does not pay to adjust the search speed to the cryptic species.

Inspired by this model this paper investigates the diet of Oystercatchers feeding on the Balthic Tellin *Macoma balthica* and the Ragworm *Nereis diversicolor* during the breeding season. Although both prey are profitable, individuals tend to specialize on either prey, suggesting that the simple prey choice model may not apply. Since we describe field observations, instead of carefully controlled experiments in the laboratory, we must put much effort into controlling for confounding factors like non-random distribution of the prey and short-term changes in prey availability. After we have taken these hurdles, we show that specialization may occur because searching for *Macoma* or *Nereis* are mutually exclusive behaviours. We then investigate the relationship between search speed and prey choice and assess the applicability of the model of Gendron & Staddon (1983) by evaluating the evidence that *Macoma* is the more cryptic prey species.

## METHODS

### Study area and study species

We observed individually marked Oystercatchers that breed on the saltmarsh of the island of Schiermonnikoog (53°29'N 06°13'E) in the Dutch Wadden Sea and feed in territories on the intertidal mudflats (Ens *et al.* 1992).

### Sampling the invertebrates

In 1986, prey abundance was assessed on 29-30 April, 26-27 May, 27 June-4 July and 12-13 August; for details, see Bunskoeke *et al.* (1996). We also sampled the depth distribution of *Nereis* on 30 April, 23 May, 7 June, 28 June and 20 August. We measured the maximal depth of the burrow of a total of 476 worms, using the procedures of Esselink & Zwarts (1989).

### Feeding observations

In all types of feeding observations we defined searching as mutually exclusive with handling the prey. Feeding included both searching and handling.

Focal animal records of foraging were made

during the spring and summer of 1985, 1986, 1987 and 1988, including 129 days during which an individual was observed throughout the entire low water period. The procedure is described by Bunskoeke *et al.* (1996). A table to transform the field estimates of prey size into biomass, expressed in mg ash-free dry mass (AFDM), can be found in Kersten & Brenninkmeijer (1995).

We also collected short observations on foraging method called 'T50' records hereafter. Using a stopwatch and counter, we recorded the time taken to make 50 paces, the time spent searching, the time spent handling, the number of pecks (including probes) and the number and species of each prey captured. Sometimes, the birds made 'multiple pecks' (Hulscher 1982) in which the bird walks slowly and moves the bill in the vertical position forward or sideways through the mud. Here, we counted as a peck each instance that the bird lifted its bill from the mud and reinserted elsewhere. Prey species, but not prey size, was recorded. If possible, we noted the prey the bird had been taking before the observation began, and, when no prey was taken during the observation, the prey taken after the observation had ended. A total of 642 records were collected on 22 different individuals in April, May and June of the years 1985 and 1986.

Finally, we collected 221 minutes of video recordings from 23 May to 18 July 1987 of Oystercatchers hunting for *Nereis* in their territories. From the video we measured the number of paces made while searching, the time spent in searching, the time spent handling the prey, the number of pecks made and the number of prey taken. For each prey we noted the species and, by reference to the length of the bill, the size and depth at which it was captured. For each peck, we noted the maximal depth of its penetration. To estimate worm length and probe depth, the full length of the bill was set to four units. The maximum depth was five units when the bird went into the mud up to his eyes. The maximum worm length observed was nine units. These field units were transformed to cms from the known length of the bill. A calibration experiment was performed in which the length of worms held next to a model Oystercatcher was estimated by a group of observers at a distance. These indicated that field length had to be transformed to obtain the live length, as measured on a *Nereis* crawling over a ruler in a thin film of seawater, using the equation:

$$L = 3.52 + 0.63E\ ,\ r = 0.77,\ n = 206,\ p < 0.0001$$

where $L$ is the live length in cm and $E$ the estimated field length in cm.

**Data analysis**

It was impossible to directly record the area searched per time unit (search rate) or the probability that the focal bird would detect a prey within the area searched (probability of detection). However, it seems reasonable to assume that search speed increases monotonically with search rate, i.e. if search speed increases, search rate increases too, although by an unspecified amount. Another reasonable assumption is that the number of prey encountered per unit distance searched increases monotonically with the number of prey encountered per unit area searched, i.e. possible variation in width of the search path was not so extreme that it offset the positive correlation between these two variables. We did not measure search speed directly, but pace rate can be transformed into search speed. Since for Oystercatchers pace length increases with walking speed (Grolle 1987, Speakman & Bryant 1993) we could not use average pace length. However, Speakman & Bryant (1993) regressed speed (in m $s^{-1}$) on pacing rate (in $s^{-1}$) after log transforming both variables:

$$\log_{10}(\textit{speed}) = -1.18 + 1.46 \log_{10}(\textit{pacing rate})$$

This equation allowed us not only to transform pace rate into search speed, but also to transform the total number of paces into the total distance searched for both the T50 records and the video records.

For our calculations we operationally defined prey profitability as the biomass consumption per

unit time spent handling and intake rate as the biomass consumption per unit time spent feeding.

Statistical analyses were performed using SPSS (Norušis 1986).

## RESULTS

### Prey detection

*Macoma* is a small bivalve that buries only to several cm depth in the mud. As a result, even the large specimens are rarely out of reach of the long bill of the Oystercatcher (Zwarts & Wanink 1993). How Oystercatchers locate *Macoma* has been studied in great detail by Hulscher (1982), who showed experimentally that the birds could use both sight and touch to detect the buried prey. Of these, touch is probably used predominantly.

Much less is known about Oystercatchers hunting *Nereis*. From our depth measurements, it is clear that the larger worms have the deeper burrows, so confirming Esselink & Zwarts (1989). However, even the smallest worms that are taken by Oystercatchers have burrows so deep that they could remain out of reach (Fig. 1). But if we compare the depth at which *Nereis* of a given size were captured with the maximum depth of their burrows, it is clear that the worms were captured while they were near the top (Fig. 1), probably to feed at the surface. Thus, the birds may have relied on sight to detect the worms.

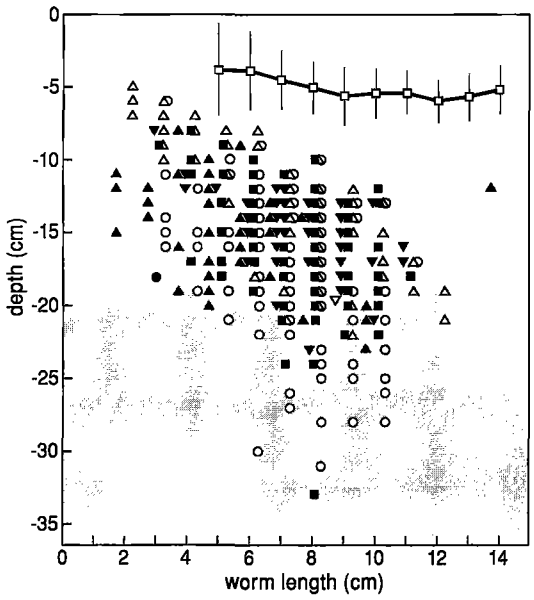


**Fig. 1.** Depth at which different sizes of *Nereis* (live length in cm) were captured (mean values with bars that represent 1 *SD*), compared to the maximum depth of the burrows of *Nereis* of similar size in spring 1987. Measurements on different dates are indicated with different symbols.

### Profitability

Since individual Oystercatchers may differ in the efficiency with which they handle prey (Hulscher 1982, Wanink & Zwarts 1996), we calculated the relationship between profitability and prey size separately for each individual (Fig. 2).

*Macoma* can be handled *in situ* or lifted (Hulscher 1996), but for our present purposes it was not important to make this distinction. Handling time increases with prey size such that there is no clear relationship between profitability and prey size (Fig. 2). This contrasts with Zwarts *et al.* (1996a & b) who conclude that profitability increases with size in *Macoma*; the difference may be due to the greater range of sizes reviewed in that study. The profitability of *Nereis* increases with the size of the worms. Despite large differences between birds, *Nereis* is clearly more profitable than *Macoma* over the range of sizes selected by the birds. However, the profitability of both prey greatly exceeds the intake rates, which averaged 2.9 mg AFDM $s^{-1}$ ($SD$ = 1.2, $n$ = 129) over an entire low water period and are depicted as a grey horizontal bar in Fig. 2.

This calculation ignores the effect on profitability of time wasted on handling prey that are not consumed, but rejected after capture, as happens with *Macoma* that are parasitized by the trematode *Parvatrema affinis* (Hulscher 1982). Although the time spent handling prey that are subsequently rejected is of the same order of magnitude as the time spent on prey that are consumed, the effect on profitability is small, since only a small proportion of prey are rejected (Table

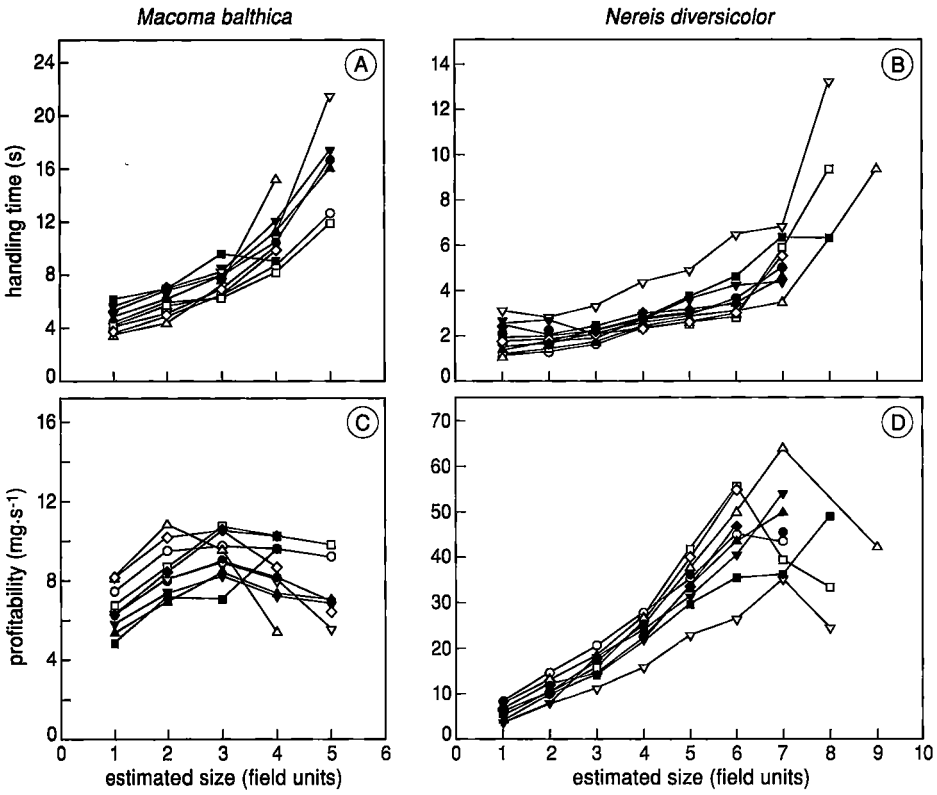


**Fig. 2.** Handling time in relation to prey size for (A) *Macoma* and (B) *Nereis*, and profitability (mg AFDM $s^{-1}$) in relation to prey size for (C) *Macoma* and (D) *Nereis*. Data are averaged per individual and also used in Table 1, where the relationship between biomass and field units is given. ♂♂ are represented by closed symbols and ♀♀ by open symbols, while the ♂ and ♀ of a pair have a symbol of the same shape. Observations that apply to only one prey are excluded. The grey bar indicates the average intake rate observed for individuals followed throughout an entire low water period plus or minus one *SD*.

1). Thus, the conclusion that both prey are highly profitable is unaltered.

## Prey choice

It is surprising that, as the profitabilities of both prey exceed the observed intake rates, individual Oystercatchers tend to specialize on either *Macoma* or *Nereis*. The capture of *Macoma* is nearly always followed by another capture of *Macoma*, while the capture of *Nereis* is nearly always followed by another capture of *Nereis* (Table 2). It is clear from the diet of individuals followed throughout an entire low water period that many Oystercatchers have an exclusive or nearly exclusive diet of either *Macoma* or *Nereis* over one tide (Fig. 3). We can think of four explanations of why individuals feeding on *Macoma* tend not to take *Nereis* and *vice versa*, despite the high profitability of both prey!

**(1) Individual specialization** Some individuals may be better adapted for feeding on *Macoma*, while others may be better adapted to *Nereis*. However, each of our study individuals in 1986 took both *Nereis* and *Macoma* (Table 3). Furthermore, none of the individuals was so inefficient at

**Table 1.** The effect of prey size (size = field units) and weight (mg AFDM) on handling time of consumed prey and prey that were rejected (s ± *SE*, *n*), rejection rate (%) and profitability of consumed *Nereis* and *Macoma* ($prof_1$; mg AFDM $s^{-1}$) and including rejected prey ($profit_2$). Conversion of field units into biomass according to Kersten & Brenninkmeijer (1995). For *Macoma* it was generally not possible to estimate the size of the rejected prey, so we calculated the rejection rate from the total number of *Macoma* rejected divided by the total number captured. Profitability including time that was wasted on rejected prey was calculated as follows: $B/(H+(P/(1-P))W)$ where $B$ is biomass (mg AFDM) of the prey, $H$ the handling time (s) of prey that were consumed, $P$ the probability of rejecting that prey and $W$ the time wasted (s) on prey that were rejected. For *Macoma* an average rejection rate of 8% and an average waste handling time of 6.0 s were assumed for all size classes. For *Nereis* the rejection rate and waste handling time of size class 9 were assumed similar to those of size class 8.

| size | weight | Handling time | | | Wasted handling | | | $Profit_1$ | rejected | $Profit_2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | mg | s | *SE* | *n* | s | *SE* | *n* | mg $s^{-1}$ | % | mg $s^{-1}$ |
| *Macoma* | | | | | | | | | | |
| ? | - | 7.8 | 5.5 | 94 | 6.0 | | 843 | - | - | - |
| 1 | 29 | 4.5 | 0.1 | 1119 | 6.0 | | 2 | 6.4 | 8.0 | 5.8 |
| 2 | 49 | 5.7 | 0.1 | 3702 | 6.0 | | 5 | 8.6 | 8.0 | 7.9 |
| 3 | 68 | 7.7 | 0.1 | 3519 | 6.0 | | 2 | 8.8 | 8.0 | 8.3 |
| 4 | 85 | 10.8 | 0.1 | 1076 | 6.0 | | 2 | 7.9 | 8.0 | 7.5 |
| 5 | 117 | 14.5 | 0.4 | 352 | 6.0 | | 1 | 8.1 | 8.0 | 7.8 |
| 6 | 127 | 21.3 | 2.5 | 14 | 6.0 | | 0 | 6.0 | 8.0 | 5.8 |
| *Nereis* | | | | | | | | | | |
| ? | - | 2.8 | 3.8 | 24 | 4.0 | 2.4 | 44 | - | 64.7 | - |
| 1 | 10 | 1.5 | 0.1 | 706 | 1.6 | 0.1 | 23 | 6.7 | 3.2 | 6.4 |
| 2 | 20 | 1.6 | 0.0 | 1451 | 1.7 | 0.1 | 74 | 12.5 | 4.9 | 11.9 |
| 3 | 35 | 2.1 | 0.1 | 1961 | 2.3 | 0.1 | 124 | 16.7 | 6.0 | 15.6 |
| 4 | 67 | 2.7 | 0.1 | 1802 | 2.3 | 0.1 | 121 | 24.8 | 6.3 | 23.5 |
| 5 | 111 | 3.3 | 0.1 | 1148 | 3.0 | 0.2 | 83 | 33.6 | 6.7 | 31.6 |
| 6 | 167 | 4.0 | 0.1 | 647 | 3.6 | 0.5 | 36 | 41.8 | 5.3 | 39.7 |
| 7 | 236 | 5.0 | 0.2 | 173 | 3.3 | 0.8 | 7 | 47.2 | 3.9 | 46.0 |
| 8 | 319 | 7.2 | 1.2 | 28 | 4.5 | 0.5 | 2 | 44.3 | 6.7 | 42.4 |
| 9 | 415 | 9.7 | 0.7 | 3 | - | - | 0 | 42.8 | - | 41.4 |

**Table 2.** Probability in % that the capture of prey species *x* was preceded by a capture of prey species *y* (data for the years 1986-1988; 100% = 45 744 prey).

| | previous prey | | | | | | *n* | % of total |
|---|---|---|---|---|---|---|---|---|
| | *Arenicola* | *Macoma* | *Mya* | *Mytilus* | *Nereis* | other | | |
| *Arenicola marina* | **47.3** | 11.5 | 3.1 | 0.1 | 36.3 | 2.9 | 821 | 1.8 |
| *Macoma balthica* | 0.5 | **94.9** | 1.2 | 0.4 | 1.9 | 1.2 | 19855 | 43.4 |
| *Mya arenaria* | 2.3 | 20.2 | **52.5** | 5.8 | 13.5 | 5.7 | 1123 | 2.5 |
| *Mytilus edulis* | 0.1 | 4.6 | 2.9 | **87.6** | 2.9 | 2.5 | 2151 | 4.7 |
| *Nereis diversicolor* | 1.4 | 1.9 | 0.8 | 0.3 | **92.8** | 2.8 | 19875 | 43.5 |
| other | 2.1 | 13.9 | 2.9 | 4.0 | 36.0 | **41.1** | 1619 | 3.5 |

**Table 3.** Prey choice of the ten individuals studied in detail in 1986. Number and biomass per prey are given as percentage relative to total number of prey consumed ($\Sigma n$) and total biomass ($\Sigma$g AFDM), respectively.

| | pair 1 | | pair 2 | | pair 3 | | pair 4 | | pair 5 | |
|---|---|---|---|---|---|---|---|---|---|---|
| individual | 200B1 | 022B1 | 021B6 | 001G6 | 102R6 | 101R6 | 200W2 | 101Y3 | 202R2 | RY |
| sex | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| bill length, mm | 68.0 | 79.0 | 72.5 | 76.2 | 65.3 | 77.2 | 71.2 | 81.4 | 72.4 | 84.8 |
| prey, $\Sigma n$ | 1479 | 2683 | 1578 | 1407 | 837 | 1571 | 1094 | 1599 | 889 | 1087 |
| *Macoma* | 63 | 21 | 54 | 17 | 83 | 67 | 20 | 18 | 58 | 81 |
| *Nereis* | 31 | 76 | 42 | 67 | 16 | 23 | 72 | 69 | 40 | 12 |
| *Mya* | 1 | 1 | 0 | 9 | 0 | 1 | 1 | 2 | 0 | 1 |
| *Arenicola* | 2 | 1 | 4 | 3 | 0 | 3 | 6 | 10 | 1 | 4 |
| *Mytilus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| other | 3 | 1 | 0 | 5 | 0 | 6 | 1 | 2 | 1 | 2 |
| biomass, $\Sigma$g | 96 | 141 | 106 | 94 | 60 | 108 | 56 | 95 | 51 | 61 |
| *Macoma* | 58 | 24 | 42 | 12 | 71 | 58 | 22 | 18 | 53 | 73 |
| *Nereis* | 27 | 69 | 57 | 59 | 24 | 34 | 62 | 61 | 41 | 13 |
| *Mya* | 7 | 1 | 0 | 15 | 2 | 3 | 0 | 3 | 0 | 11 |
| *Arenicola* | 7 | 5 | 2 | 13 | 0 | 4 | 15 | 18 | 6 | 3 |
| *Mytilus* | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| other | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |

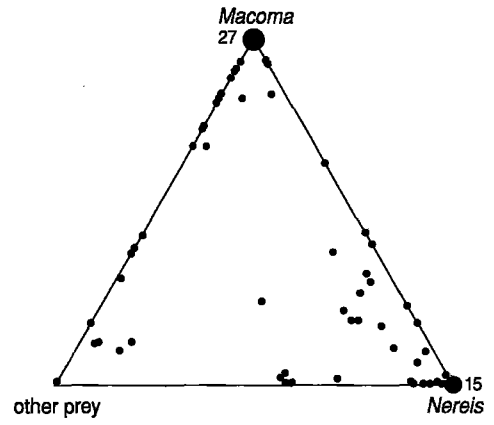


**Fig. 3.** Composition of the diet (expressed in % biomass consumed) of individual Oystercatchers followed throughout an entire low water period, plotted in a triangle with three corners: *Nereis*, *Macoma* and other prey. In this graph, the full length of the line from a corner perpendicular to the opposite side represents 100% of the prey 'in the corner'.

handling either prey as to exclude that prey from the diet (Fig. 2).

**(2) Distribution of the prey** Another possibility is that *Macoma* and *Nereis* are distributed such that areas with high densities of *Nereis* contain low densities of *Macoma* and *vice versa* (compare Ward 1993). If so, birds would only encounter one prey species at a time, possibly for long periods. This is not the case. Sample cores nearly always contain both prey and their numbers are not negatively correlated (Fig. 4). This picture is not changed if we exclude *Macoma* < 10 mm, which are never taken by Oystercatchers (Zwarts *et al.* 1996a). A similar correction is not needed for *Nereis*, since Zwarts & Esselink (1989) established that the majority of small *Nereis* pass through a 1 mm sieve. There is the possibility however, that during any one tide the density of *Nereis* actually available to Oystercatchers is negatively correlated with the density of available *Macoma*. While this possibility was not tested directly, indi-

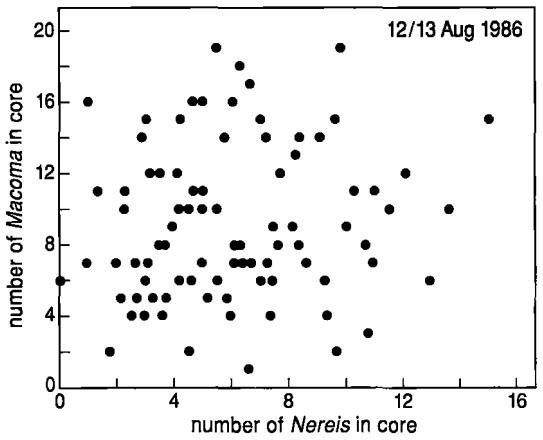


**Fig. 4.** Number of *Macoma* plotted against the number of *Nereis* found in the same sample. Each dot represents one sediment core of 0.0174 $m^2$ and all individual *Macoma* and *Nereis* that were retained by a 1 mm sieve are included.

rect evidence renders the suggestion unlikely (Hulsman *et al.* 1996). It regularly happens that the ♂ of a breeding pair feeds on *Macoma*, while the ♀ feeds on *Nereis* in the same territory. Hulsman *et al.* (1996) plotted all the prey captures and showed a substantial spatial overlap: ♂♂ took *Macoma* in areas where ♀♀ also took *Nereis*. This further suggests that an active selection for prey occurred.

**(3) Temporal changes in availability** Apart from variation in space, there may be changes in time. Most individuals change from a diet dominated by *Macoma* in early spring to one dominated by *Nereis* in late spring-early summer, but the timing of the switch differs between individuals (Bunskoeke *et al.* 1996). Furthermore, *Nereis* seem less active at the very beginning and very end of the exposure period (Esselink & Zwarts 1989), probably explaining why more *Macoma* are taken at these stages of the tide (de Vlas *et al.* 1996). Such temporal changes are at least partly responsible for the very high probability that a prey capture of either prey is followed by a capture of the same species in Table 2. To control for such temporal variability, we selected individual records of feeding behaviour during the middle of the tide and compared, for both prey, the probability of successive captures with the overall presence in the diet during that feeding period of the particular individual. This analysis confirmed that a bird that took a *Nereis* was still more likely to take another *Nereis*, while a bird that took a *Macoma* was more likely to take another *Macoma* (Fig. 5).

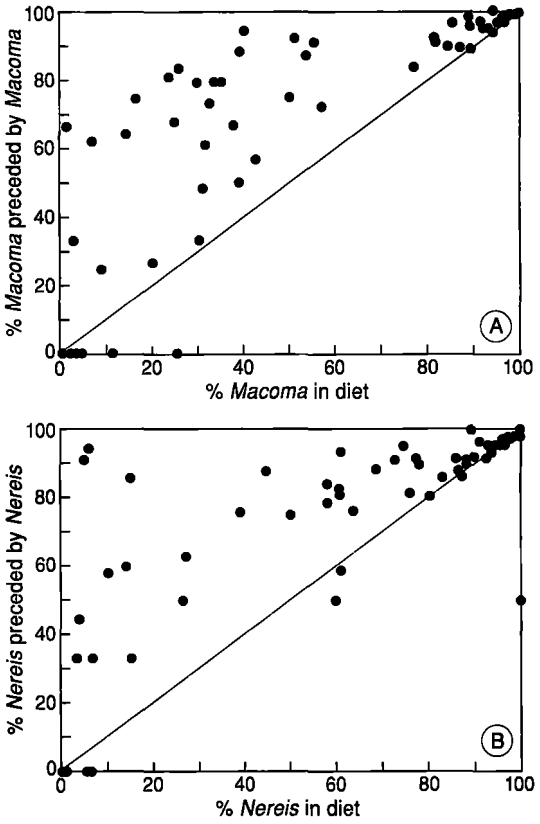


**Fig. 5.** Probability that a prey capture of a particular prey species was preceded by a capture of the same species, plotted against the overall frequency in the diet during the middle of the tide (i.e. excluding periods of decreased availability of *Nereis*) for (A) *Macoma* and (B) *Nereis*. Each dot represents data on one individual during one tide. Only records were included where more than five *Macoma* or more than five *Nereis* were captured respectively.

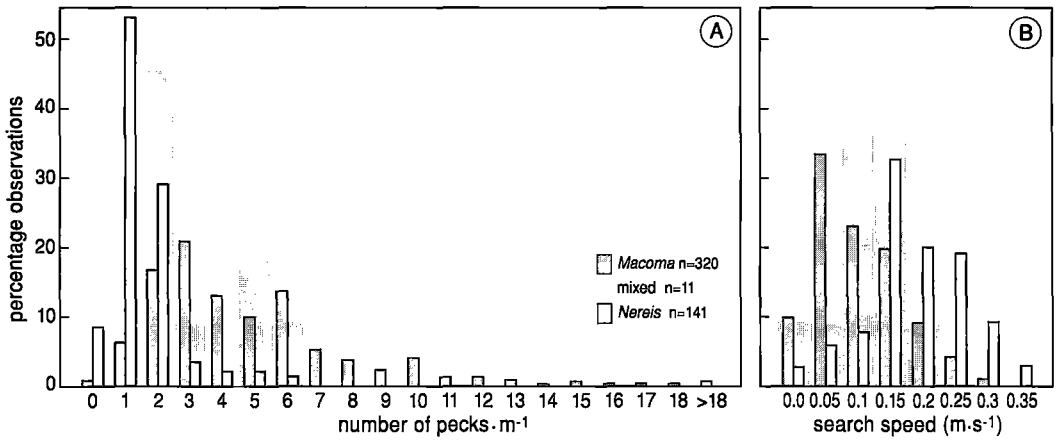


**Fig. 6.** Frequency distribution of (A) number of pecks $m^{-1}$ searched observed in the T50 records and (B) search speeds (calculated from pace rates, see methods). In both graphs, a distinction is made between records during which the focal bird caught one or more *Macoma* ($n$ = 320), one or more *Nereis* ($n$ = 141) or a mixture of both prey ($n$ = 11).

**(4) Search method** A fourth explanation is suggested by the obvious differences in searching behaviour. Individuals that feed on *Nereis* tend to search quickly, while individuals that feed on *Macoma* tend to search slowly (Fig. 6A). Individuals feeding on *Macoma* also peck at a high rate, while those feeding on *Nereis* take many fewer pecks per second of searching. This difference is even more dramatic when the numbers of pecks $m^{-1}$ searched are compared (Fig. 6B). These observations suggest that capturing either prey requires a specific hunting method and that hunting for one species is incompatible with hunting for the other. The rare cases (11 out of 461) in which both *Nereis* and *Macoma* were captured show intermediate values for search speed and the number of pecks $m^{-1}$ searched (Figs. 6A & B). This could be due to the existence of an intermediate hunting method which allows the capture of both prey. Alternatively, the birds may have switched between two distinct hunting methods during the observations.

## Search speed and encounter rate

Why should two prey that are both buried in the mud be localized in different ways? According to Gendron & Staddon (1983), the crucial parameter is search rate and its influence on the probability of detecting a cryptic prey item. Although we could not measure the area searched per time unit, the rate at which *Macoma* were captured declined from 5 $min^{-1}$ to almost 0 as search speed increased (Fig. 7A), while the rate at which *Nereis* were captured increased from almost 0 to 3 $min^{-1}$ (Fig. 7B). Remarkably, the rate at which pecks were made did not change with search speed (Fig. 7C). However, when expressed as number of prey taken and pecks made per m searched rather than per unit time, the number of *Macoma* captured (Fig. 7D) and the number of pecks $m^{-1}$ (Fig. 7F) declines steeply with search speed, while the number of *Nereis* captured fluctuates around 0.1 and even shows a significant positive trend (Fig. 7E). Although we could not measure the probability of detection, it seems reasonable to assume that, all else being equal, a greater number of prey captures $m^{-1}$ searched along with a reduced number of pecks made indicate a higher probability of detection.

A similar analysis can be applied to the video records. We excluded records that lasted less than 60 s, although the same general trends were apparent anyway. Since we only recorded individuals hunting *Nereis*, we could not analyse the effect

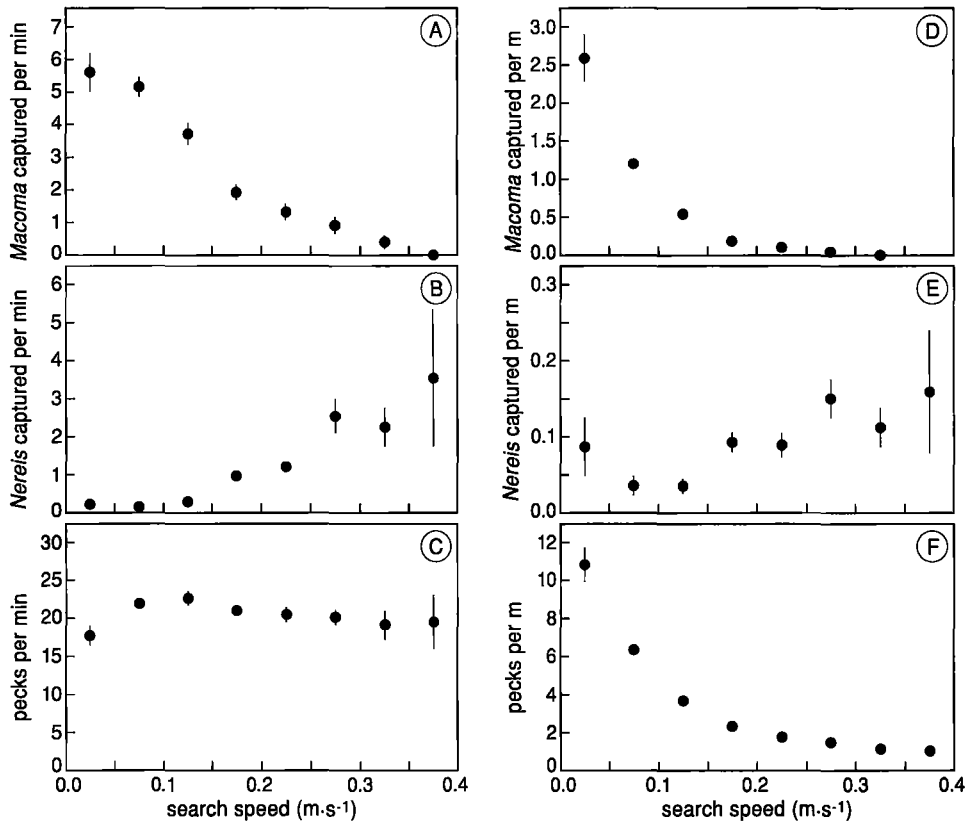


**Fig. 7.** The effect of search speed (m $s^{-1}$) on (A) the number of *Macoma* captured $min^{-1}$ ($r = -0.43, p < 0.0001$), (B) the number of *Nereis* captured $min^{-1}$ ($r = 0.41, p < 0.0001$), (C) the number of pecks $min^{-1}$ ($r = -0.05$, N.S.), (D) the number of *Macoma* captured $m^{-1}$ ($r = -0.61, p < 0.0001$), (E) the number of *Nereis* captured $m^{-1}$ ($r = 0.21, p < 0.0001$), (F) the number of pecks $m^{-1}$ ($r = -0.71, p < 0.0001$); based on the T50 records. Dots represent average values (sample sizes on which these average values are based are respectively 36, 120, 109, 159, 94, 50, 26 and 8, totalling 602 records), while bars represent 1 *SE*. T50 records without prey captures were included if either *Nereis* or *Macoma* was captured immediately before and after the actual observation, i.e. in the adjacent T50 records.

of search speed on *Macoma* captures. Apart from the 655 *Nereis*, 1 *Macoma* and 2 *Arenicola* taken, a remarkable number of 84 small prey were picked from the surface, these probably being the small crustacean *Corophium*. The rate at which these small surface prey were taken did not correlate with search speed ($r = -0.08, n = 44$, N.S.). As the video records comprise data on different individuals in different territories on different dates, which may potentially confound the patterns that we study, we only analysed data from three regularly observed birds. This allowed analyses of covariance with individual as factor and search speed as covariate. When the birds walked faster they caught more worms, independent of the individual (Fig. 8A). Peck rate was neither influenced by individual nor search speed (Fig. 8B). These findings compare well to the conclusions from the T50 records (Figs. 7B & C).

We might expect small *Nereis* to be more cryptic than large *Nereis*. If so, we would expect a positive correlation between search speed and mean length of worms taken; with increasing search speed small worms should increasingly of-

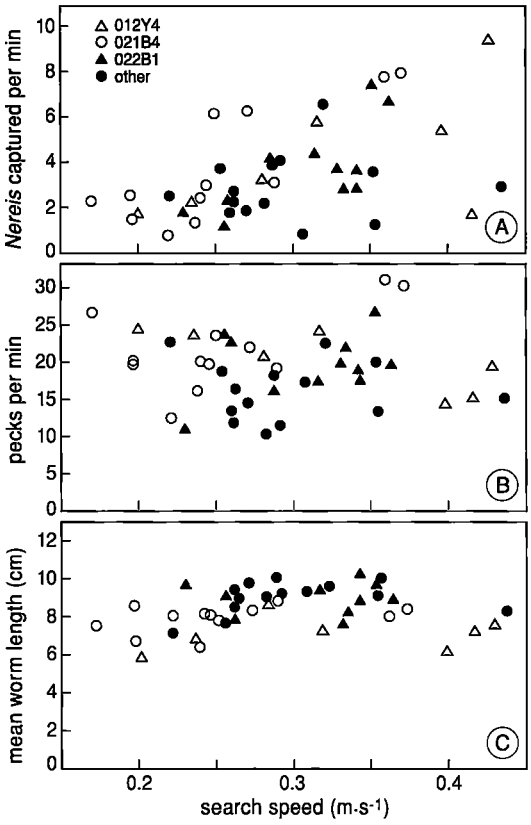


**Fig. 8.** The effect of search speed (m $s^{-1}$) on (A) the number of *Nereis* captured $min^{-1}$, (B) the number of pecks $min^{-1}$, (C) the mean length (cm) of the captured worms. Each dot represents one video record lasting at least 60 s and different symbols denote different individuals. Analysis of covariance with search speed as covariate and individual as factor yielded (A) a significant effect of speed on capture rate ($p < 0.001$), but no differences between individuals ($p = 0.16$), (B) no effect of either speed ($p = 0.96$) or individual ($p = 0.50$) on peck rate and (C) no effect of speed ($p = 0.32$) on the length of worms captured, but significant differences between individuals ($p < 0.001$).

ten be overlooked. However, there is no evidence for this (Fig. 8C). Nonetheless, individuals differed significantly in the average length of worms taken (Fig. 8C). The cause of these individual differences, which are not very large to begin with, is unclear. For example, among eight individuals that caught ten or more worms, there was no correlation between bill length and average length of worms taken. This was true irrespective of whether worm length was expressed in field units or cm live length, indicating that these differences are not an artefact of our procedure of length estimation and correction.

## DISCUSSION

### Prey choice and search speed

Our observation that one profitable prey species is apparently ignored, when the birds hunt the other species, contradicts the prediction of the simple optimal prey model that all sufficiently profitable prey should be taken. An important assumption in this model is that encounter rate, i.e. the number of prey encountered per time unit searching, is a fixed and invariable constraint (Stephens & Krebs 1986, see also the appendix). Since search speeds in Oystercatchers may vary by an order of magnitude (Fig. 6), this assumption is clearly violated in our study and explains why the model does not apply. Since there was also a close correlation between search speed and prey choice it seems that the problem of prey choice cannot be treated independently of the problem of prey specific searching behaviour, including the interactions between search speed and modes of prey detection. An integrative approach is needed.

Gendron & Staddon (1983) achieve this goal by assuming a negative relationship between the probability of detecting the prey and the rate of search (see appendix). For each prey, the probability of detection decreases with an increase in search rate, while, by definition, the more cryptic prey are less likely to be detected at a given search rate. If foraging predators make decisions so as to maximize the rate of energy gain, we would predict that the optimal search rate is slower when prey are more cryptic. We could not directly measure crypticity, and our expectation that small *Nereis* are more cryptic than large ones was not supported. However, more important is our expectation from the difference in search speed

that *Macoma* is more cryptic than *Nereis*. What is the evidence that this is indeed the case?

**Crypticity of *Macoma*** In spring and summer, virtually all *Macoma* exceeding 10 mm in size, the lower size threshold for Oystercatchers (Zwarts *et al.* 1996a) are buried at a depth of between 0 and 6 cm and thus within reach of the bill (Zwarts & Wanink 1993). When deposit-feeding, *Macoma* make star-like tracks with the inhalant siphon on the surface of the mud. Oystercatchers had a much higher success in cage experiments when these tracks were available than when they were experimentally removed (Hulscher 1982). Nonetheless, even without tracks Oystercatchers were able to achieve an adequate intake rate when prey densities were sufficiently high by detecting *Macoma* purely by touch, and this seems the predominant mode of detection in the field where the activity of other animals and the tide often destroys the tracks (Hulscher 1982). In conclusion, since *Macoma* is detected by touch it must count as a cryptic prey species.

**Crypticity of *Nereis*** In contrast, it is rather unlikely that Oystercatchers feed on cryptic buried *Nereis* by touch. This can be shown from a simple comparison of the observed pecking success with the success expected of a random vertical probe. If the surface of the bill tip is thought of as a rectangle with sides $x$ and $y$, while the horizontal cross-section of the burrow is thought of as a circle with radius $r$, we can calculate the effective touch area, i.e. the projection in a horizontal plane of the area of the prey that will be touched by a vertical needle, properly enlarged by the surface area of the bill tip. This effective touch area equals

$$\pi r^2 + 2ry + 2rx + xy$$

according to Habekotté (1987 in Zwarts & Blomert 1992). The largest *Nereis* measured by Esselink & Zwarts (1989) had a body width of 4 mm, so that a burrow diameter of 5 mm is likely to be a maximum estimate. Assuming the burrow is a perfect cylinder, this leads to a surface of 19.6 $mm^2$ of a horizontal cross-section across a maximum-sized burrow. Hulscher (1982) determined from imprints left on the mud that the tip of the Oystercatcher bill measures 1.4 x 11.0 mm. Thus, the maximum effective touch area is 97 $mm^2$. In June, the month during which most *Nereis* are taken by Oystercatchers, the density of *Nereis* of a sufficient size to be eaten by Oystercatchers was estimated at 280 worms per $m^2$ (Bunskoeke *et al.* 1996). From these values we calculate a probability of 0.03 of hitting a burrow with a random probe. This will only be equivalent to the probability of capturing a worm with a random probe if all worms are high up in their burrow, which is very unlikely (Esselink & Zwarts 1989). Thus, 0.03 is an absolute maximum estimate of capturing a *Nereis* with a randomly directed peck. Nonetheless, the observed pecking success was much higher; 0.14 ($SE$ = 0.02) for 94 T50 records with sufficiently high search speeds and 0.19 ($SE$ = 0.02) for 40 video records that lasted longer than 60 s. Due to the small $SE$ both values are significantly different from 0.03. Thus, we conclude that it is very unlikely that Oystercatchers detect *Nereis* by randomly probing the mud. In fact, we suggest that the birds hunt for worms that either give away their presence indirectly by body movements when feeding high up in their water filled burrows, or are protruding from their burrow to feed on the surrounding mud and therefore highly conspicuous. To further substantiate this suggestion we will first execute an indirect test and then solve an apparent contradiction.

The indirect test consists of a calculation to verify that we arrive at a reasonable width of the search path from the assumption that Oystercatchers hunt for *Nereis* protruding from their burrow. Field observations of Esselink & Zwarts (1989) indicate that *Nereis* spent 0.1% to 0.2% of the emersion period at the surface. At a density of 280 worms $m^{-2}$ this leads to an average of 0.28 to 0.56 worms $m^{-2}$ feeding on the surface. In the T50 records the number of pecks $m^{-1}$ searched ranges from 1 to 2 at high search speeds. If we assume that all failed pecks were due to successful escape

of the worm we arrive at a width of the search path between a high value of 7.1 m (3.6 on both sides) and a low value of 1.8 m (0.9 m on both sides). Even the low value seem rather high, given the size of the Oystercatcher. However, Esselink & Zwarts (1989) measured the activity of *Nereis* in September, whereas Oystercatchers primarily feed on *Nereis* in June (Bunskoeke *et al.* 1996). Feeding activity of *Nereis* is reportedly higher in spring than in autumn (Twisk 1986 in Esselink & Zwarts 1989). Furthermore, not all pecks may have been directed at *Nereis* actually at the surface, but also at worms high up in their burrow. The aquarium experiments of Esselink & Zwarts (1989) indicate that, over a tide, this would double the density of active worms, and therefore halve the estimated width of the search path. Thus, all arguments hint at a smaller and, and therefore reasonable, width of the search path.

The apparent contradiction is that if Oystercatchers hunt for *Nereis* protruding from their burrow it is surprising that the birds often insert their bill so deep into the mud when catching a worm (Fig. 1). A likely explanation is the anti-predator response of the worms when they retreat into their burrow. Thus, the bird has to grab the retreating worm before it is beyond reach. Some support for this comes from the observation that the number of worms captured $m^{-1}$ searched increased with search speed (Fig. 7E), as did the probability of a peck being successful (compare Fig. 7B to Fig. 7C and Fig. 8A to Fig. 8B). If the predator approaches at a higher speed, the prey has less time to escape.

**Conclusion** Summarizing, it seems likely that, from the point of view of the Oystercatcher, *Macoma* are more cryptic than *Nereis*, as we would expect from the model of Gendron & Staddon (1983). If the probability of detection is monotonically related to the number of prey captured $m^{-1}$ searched, the model of Gendron & Staddon (1983) yields the additional prediction that the number of a given prey species captured $m^{-1}$ should decline with increasing search speeds. However, instead, numbers increase (Fig. 7E). To explain this we suggest that a decrease in probability of detection is compensated by an increase in the probability of capture; when Oystercatchers approach at higher speeds, *Nereis* will have less time to retreat into their burrow. As we saw, the escape response of the worms may also explain why Oystercatchers probe so deep. Thus, the model of Gendron & Staddon (1983) may need to be modified before it can be fully applied to predators hunting prey that can perform escape behaviour; see appendix.

## Optimal search speed

If it is true that the probability of capturing a *Nereis* $m^{-1}$ searched does not decline with search speed, it is hard to understand why Oystercatchers do not always search at the maximal 'sustainable' speed. Speakman & Bryant (1993) estimate this speed at approximately 2 m $s^{-1}$. Starting from Fig. 7B, Hoekstra (1988) calculated that, in terms of energy, the increase in energy gain from catching more worms at high speeds more than offsets the estimated increase in energy expenditure from walking faster. On the basis of the unsubstantiated assumption that Oystercatchers come to a full stop when they peck and then need to accelerate again, Speakman & Bryant (1993) calculate how much observed search speed would be reduced below the maximal search speed for a given peck rate. Thus, it could be that Oystercatchers search at maximum speed, but that pecking inevitably slows them down. Although Speakman & Bryant (1993) observed Oystercatchers feeding at a wide range of prey encounter rates there was not a single instance where the birds appeared acceleration-limited in their prey-searching behaviour. Summarizing, it seems hard to escape the conclusion that the birds did not always search at the speed that maximized their intake rate of food, violating another simple optimality assumption.

## Is specialization due to incompatibility of searching special?

The incompatibility between searching for *Nereis* and searching for *Macoma* can explain specialization in the short term, but not in the long term, because there is nothing to prevent the birds

from switching between the two prey in response to temporal or spatial variation in harvestability. Specialization over a longer time scale therefore requires a brake on such switching behaviour. For Oystercatchers a well documented brake is the form of the bill tip, which adapts to the method in which prey are hunted and handled (Swennen *et al.* 1983, Hulscher 1985, Hulscher & Ens 1991, Durell *et al.* 1993).

Is our study special? We think not. Instead, it may be frequently the case that birds (or other animals) are forced to specialize, because of 'incompatible' hunting modes. For instance, Hulscher (1996) reports that search speeds also differ systematically among Oystercatchers feeding on other prey than *Macoma* or *Nereis*, while Goss-Custard (1977) reports that Redshank search more slowly when they hunt *Nereis* than when they hunt for the preferred and perhaps less cryptic *Corophium* and suggested this was involved in the prey selection mechanism. Zwarts & Wanink (1993) reviewed four other studies on waders, which reduced their search speed in response to prey becoming more cryptic. However, in all these four cases, the choice was not between different prey species, but between individual prey of a same species whose crypticity varied with their behaviour. For instance, Boates & Smith (1989) demonstrated that Semipalmated Sandpipers *Calidris pusilla* walked faster when pecking *Corophium volutator* from the substrate as the tide ebbed than later at low water when most *Corophium* were hiding inside their burrow. Similarly, Curlews *Numenius arquata* feeding on *Nereis* walk more slowly when they probe for the worms hiding inside their burrow than when hunting for the worms that are protruding from their burrow (Zwarts & Esselink 1989).

### Conclusion and suggestions

From the above we conclude that incompatibility of searching for different prey seems quite general and must be understood before we can hope to predict the rate at which birds can harvest food in a given location from the densities at which the various prey species are present. Even though our current observations suggest that the model of Gendron & Staddon (1983) may need to be modified before it can be applied to prey capable of escape behaviour, this does not detract from its power as a conceptual framework as it links the problem of prey choice to the problem of search speed. It certainly deserves more testing. We make two suggestions. The observational tests can be improved, if the detailed observations on the birds are accompanied by simultaneous detailed measurements on the local availability of the prey. Second, it may be possible to manipulate prey behaviour, and therefore crypticity, in the field. When Esselink & Zwarts (1989) poured a slurry of minced molluscs over the mud shortly after emersion, they observed a spectacular increase in the surface activity of *Nereis* scavenging on the pieces of meat.

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## APPENDIX

The aim of this appendix is to provide the minimum number of mathematical equations needed to specify the differences and similarities between the optimal prey choice model and the 'search rate' model of Gendron & Staddon (1983). Both models can be traced back to the disc equation of Holling (1959):

$$N = \frac{aDT}{1 + at_hD} \qquad (1)$$

where $N$ is the number of prey consumed during time period $T$ (s), $D$ is the prey density ($m^{-2}$), $a$ is the instantaneous area of discovery ($m^2$ $s^{-1}$) and $t_h$ the time (s) needed to handle and ingest one prey item after it has been captured. Since it applies to a single prey species, it must be generalized to a multi-prey 'functional response' before it can form the backbone of the optimal prey choice model and the search rate model.

Stephens & Krebs (1986) provide a thorough description of the simple or 'classic' prey choice model. Prey of different species and sizes are ranked by their profitability, i.e. the rate of energy gain during handling. From the rate at which prey of a given class are encountered during searching it can then be calculated which classes should or should not be taken to achieve the maximum rate of energy gain during feeding. For $i$ prey types:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i V_i}{1 + \sum \lambda_i h_i V_i} \qquad (2)$$

where $E$ is total energy intake (J) during observation time $T$ (s), $E_i$ is energy gain (J) from one item of prey type $i$, $\lambda_i$ is the encounter rate ($s^{-1}$) with prey type $i$ and $h_i$ is the handling time (s) of a prey of type $i$. Finally, $V_i$ is the decision variable to be optimized and represents the probability that the predator takes a prey item of type $i$ after it is encountered. When prey with a profitability below the critical threshold are encountered, it is more efficient to continue searching than to handle and eat them, i.e. $V_i = 1$ if $E/T < E_i/h_i$ and $V_i = 0$ if $E/T > E_i/h_i$ (Charnov 1976). To find the optimal $V_i$, i.e. the prey choice that maximizes intake rate of energy, it is necessary to treat the encounter rates $\lambda_i$ as fixed constants.

However, as Gendron & Staddon (1983) make clear, it is very likely that encounter rates are at least partly under the control of the foraging animal since we expect an animal to encounter more prey if it walks faster. Comparing equations (1) and (2) it is tempting to think of each encounter rate $\lambda_i$ ($s^{-1}$) as the product of the instantaneous area of discovery $a$ ($m^2$ $s^{-1}$) and $D_i$, the density ($m^{-2}$) of prey species $i$. According to Gendron & Staddon (1983) the world is not so simple and they effectively argue that $\lambda_i$ consists of $a_i D_i$ instead of $aD_i$. In other words, each prey species has it's own area of discovery $a_i$, which is the product of $S$, the area searched per unit time ($m^2$ $s^{-1}$), and $P_{di}$, the probability of detecting an encountered prey item of species $i$. Gendron & Staddon (1983) need this subdivision to implement the core assumption of their model that there is a trade-off between search rate $S$ and detection probability $P_{di}$ and that the exact form of that trade-off depends on the crypticity of the prey species. It suffices to show how they model this trade-off for a single prey species:

$$P_d = [\, 1 - ( S / M )^K \,]^{1/K} \qquad (3)$$

where $M$ is the maximum search rate ($m^2$ $s^{-1}$) and $K$ what might be called a 'conspicuousness index' providing an operational measure of crypticity. For small $K$ the detection probability $P_d$ drops off steeply with search rate $S$, while for large $K$ detection probability only declines when $S$ nears the maximum search rate $M$.

Unlike Getty & Pulliam (1991), who derive the rate at which a predator using pause-travel search detects prey from explicit quantitative assumptions on the process of prey detection and perceptual constraints of the predator, Gendron & Staddon (1983) consider equation (3) a qualitative, but heuristically useful speculation. They discuss that $a$ has been broken down into even more components by other authors, but argue that these components can be safely ignored for prey that are familiar, palatable and easy to capture. This last assumption may not apply in our study. Once detected, *Macoma* have no chance to escape. In contrast, *Nereis* can retreat into their burrow and an approaching Oystercatcher will be more successful in capturing a detected *Nereis* if approach is fast. Thus, instead of writing $\lambda_i = SP_{di}D_i$, we may need to write $\lambda_i = SP_{ci}P_{di}D_i$, where $P_{ci}$ is the probability of capturing a detected prey of species $i$. As should be clear, both $P_{ci}$ and $P_{di}$ are assumed to depend on search rate $S$. Substituting into equation (2) we see that the 'adapted' search rate model would be specified by the following equation:

$$\frac{E}{T} = \frac{\sum SP_{ci}(S)\, P_{di}(S)\, \mathrm{D}_i E_i V_i}{1 + \sum SP_{ci}(S)\, P_{di}(S)\, \mathrm{D}_i h_i V_i} \qquad (4)$$

where $S$ and $V_i$ represent the decision variables that the bird has to choose such that intake rate is maximized.

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## SAMENVATTING

Scholeksters die op de kwelder van Schiermonnikoog broeden zijn gedurende het broedseizoen afhankelijk van twee prooien: het Nonnetje *Macoma balthica*, een tweekleppige, en de Zeeduizendpoot *Nereis diversicolor*, een worm. Beide prooien zijn zeer profijtelijk in termen van biomassa-opname per tijdseenheid die nodig is de prooien voor consumptie te bewerken en in te slikken (Tabel 1, Fig. 2). Toch is het zo dat individuele Scholeksters zich gedurende het zoeken meestal specialiseren op één van de twee prooien en ogenschijnlijk 'doelbewust' de andere prooisoort links laten liggen (Tabel 2, Fig. 3). Dit is in strijd met het simpele, ook wel als 'klassiek' aangeduide, optimale prooikeuzemodel (Charnov 1976). Hoewel mannelijke Scholeksters vaker Nonnetjes aten en vrouwelijke Scholeksters meer geneigd waren zich op Zeeduizendpoten te specialiseren, at elk intensief bestudeerd individu op den duur beide prooien (Tabel 3) en was geen enkel dier dermate inefficiënt bij het bewerken van één van beide prooien dat het een reden kon zijn die prooisoort niet te selecteren (Fig. 2). Ook was het niet zo dat de twee prooisoorten een verschillende ruimtelijke verspreiding hadden (Fig. 4), of dat ze op verschillende momenten in het tij beschikbaar waren (Fig. 5). Het komt erop neer dat Scholeksters die naar Nonnetjes zoeken heel langzaam lopen en heel veel pikken maken per afgelegde meter, terwijl Scholeksters die naar Zeeduizendpoten zoeken juist heel snel lopen en heel weinig pikken maken per afgelegde meter (Fig. 6). Anders uitgezet: met een toenemende zoeksnelheid worden steeds minder Nonnetjes en steeds meer Zeeduizendpoten gevangen (Figs. 7 & 8). Dit past in het idee dat ingegraven Nonnetjes meer cryptische prooien zijn die op de tast gevonden moeten worden, terwijl Zeeduizendpoten die uit hun hol komen of bovenin hun hol actief zijn, juist opvallen en visueel worden bejaagd. De onverenigbaarheid van de twee zoekmethoden verklaart de hier waargenomen specialisatie. Waarschijnlijk is dit een voorbeeld van een algemeen verschijnsel dat verklaart waarom het simpele optimale prooikeuze model wel vaker faalt in de voorspelling van de in het veld waargenomen prooiselectie. Toch passen de gegevens maar ten dele in het inspirerende 'alternatieve' model van Gendron & Staddon (1983). Dit model veronderstelt dat met name bij cryptische prooien een hoge zoeksnelheid gepaard gaat met een verlaagde detectiekans, zodat bij een toenemende crypticiteit van de prooien de vangsnelheid wordt gemaximaliseerd door een steeds kleinere zoeksnelheid. Misschien moet hier aan worden toegevoegd dat een vergrote zoeksnelheid, naast een verkleinde detectiekans, wel weer een vergrote vangkans met zich meebrengt bij prooien zoals de Zeeduizendpoot, die zich, om predatie te voorkomen, snel kunnen terugtrekken. In ieder geval is duidelijk dat het probleem van de optimale prooikeuze en het probleem van de optimale zoeksnelheid niet onafhankelijk van elkaar kunnen worden bestudeerd.