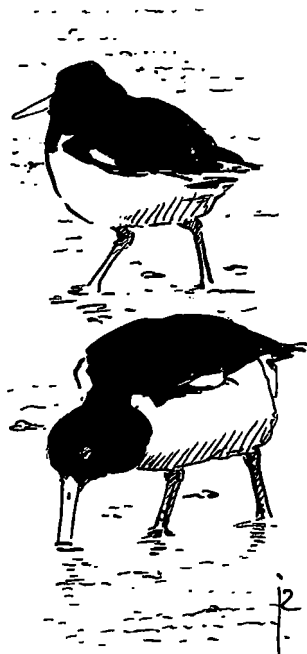


NOT ALL OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* SELECT THE MOST PROFITABLE COMMON COCKLES *CERASTODERMA EDULE*: A DIFFERENCE BETWEEN FEEDING METHODS

IAN JOHNSTONE¹ AND KEN NORRIS²

Johnstone I. & K. Norris 2000. Not all Oystercatchers *Haematopus ostralegus* select the most profitable Common Cockles *Cerastoderma edule*: a difference between feeding methods. *Ardea* 88(2): 137-153.



We use an optimality model to describe prey choice by wintering Oystercatchers *Haematopus ostralegus* using different feeding methods. Birds fed on Common Cockles *Cerastoderma edule*, which they opened by either exclusively hammering or stabbing. The model includes probabilistic time costs associated with successful and unsuccessful prey handling, changes in the energy content of prey, factors which affect prey availability and assumes that energy intake was maximised. Prey profitability increased with size for hammerers and stabbers. The model predicted that both should only consume cockles > 15mm throughout the winter. The decisions made by stabbers were consistent with this. Hammerers consumed cockles > 15mm during late winter, but during early winter, consumed more 0-15mm cockles than expected. This implies that selecting profitable prey entails an additional cost specific to hammerers. This cost could be the risk of bill damage. As a result, hammerers should only select the most profitable cockles when the benefit of maximising energy intake is greatest. This is most likely during late winter.

Key words: *Haematopus ostralegus* - feeding method - optimal diet

¹RSPB North Wales Office, Maes y Ffynnon, Penrhosgarnedd, Bangor, LL57 2DW, Wales, E-mail ian.johnstone@rspb.org.uk; ²School of Animal & Microbial Sciences, University of Reading, Whitenights, P.O. Box 228, RG6 6AJ Reading, England

INTRODUCTION

For many animals the time available for feeding is limited because of competition with other essential behaviours or because of environmental conditions. To maximise its fitness under these circumstances, an animal must make decisions concerning where, when and what to eat. As a result, a considerable body of work has been devoted to the decision rules a time-stressed foraging animal could use to maximise its fitness (see Stephens & Krebs 1986; Houston *et al.* 1988; Krebs & Kacelnik 1991 for reviews). Many models assume that a foraging animal would maximise its fitness by maximising its rate of energy intake.

For many wading birds, the opportunity to meet daily energy requirements is constrained by the tidal regime, competition with others and poor weather (e.g. O'Connor & Brown 1977; Goss-Custard 1980; Zwarts & Drent 1981; Goss-Custard & Verboven 1993; Kersten & Piersma 1987; Davidson & Evans 1983; Wiersma & Piersma 1994). To maximise their gross rate of energy intake in such situations, optimality theory predicts that birds should take the energetically most profitable prey. There are a number of studies, which show that wading birds do this (Goss-Custard 1977; Sutherland 1982; Wanink & Zwarts 1985; Meire & Ervynck 1986; Boates & Goss-Custard 1989; Cayford & Goss-Custard 1990; Zwarts & Blomert

1992). However, there is evidence that profitable prey is ignored on occasions (e.g. Hulscher 1982; Sutherland & Ens 1987; Cayford & Goss-Custard 1990; Ens *et al.* 1996a,b). Furthermore, birds are capable of increasing their energy intake rates when time limited, implying that they sometimes harvest energy below the maximum rate (Swennen *et al.* 1989). An explanation for these observations is that taking the most profitable prey entails additional costs. The magnitude of these costs could depend on the search speed, the size of prey selected and the method in which it is handled.

Oystercatchers *Haematopus ostralegus* feeding on Common Cockles *Cerastoderma edule* ('cockles' in the remainder of this article) open their prey by exclusively hammering a hole in the shell (hammerers), or stabbing their bill between the valves to sever the adductor muscles (stabbers) (Swennen *et al.* 1983). If birds, which feed by hammering, do experience different costs to stabbers, then we might expect prey choice to differ between feeding methods. Here we examine this by using an optimality model to predict prey size selection for an Oystercatcher attempting to maximise its intake rate using each feeding method, and comparing these predictions with observed behaviour.

The model

Cockles vary in size and energy content. We wished to determine which size classes should be selected by Oystercatchers in order to maximise their rate of energy intake. To do this we used a multiple prey version of Holling's disc equation (Charnov 1976). When there are i size classes of cockle, the rate of energy intake (gAFDM s^{-1} , where gAFDM = grams of ash-free dry mass) can be described as:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i Q_i}{1 + \sum \lambda_i h_i Q_i} \quad (1)$$

where E_i = energy content of a cockle of size i (gAFDM), h_i = handling time of a cockle of size i (s), l_i = encounter rate with cockles of size i (s^{-1}), and Q_i = probability that an Oystercatcher would

attempt to eat a cockle of size i after it is encountered. Charnov (1976) showed that to maximise energy intake, $Q_i = 1$ if $E/T < E_i/h_i$ and $Q_i = 0$ if $E/T > E_i/h_i$, so an Oystercatcher should take a cockle of size i if its profitability (E_i/h_i) is above E/T , and ignore it if its profitability is less than this value.

This model rests on a number of assumptions which are generally applicable to Oystercatchers feeding on bivalves (see Meire & Ervynck 1986), with the exception that prey are assumed to be recognised instantaneously and without error. Oystercatchers do waste time handling bivalves which they are unable to eat and abandon unopened (Meire & Ervynck 1986; Cayford & Goss-Custard 1990), so we used an extension of Equation (1) developed by Meire and Ervynck (1986) to include this additional time cost, which gives E/T as:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i P_i}{1 + \sum \lambda_i (h_i P_i + (1 - P_i) w_i)} \quad (2)$$

where w_i = time wasted handling a cockle of size i which the bird fails to open (s) and P_i = probability that a cockle of size i will be successfully opened after being attacked. All other symbols are as defined in Equation (1). The profitability (Z_i) of a cockle of size i can be defined as:

$$Z_i = \frac{E_i P_i}{h_i P_i + (1 - P_i) w_i} \quad (3)$$

and a cockle of size i should be taken by an Oystercatcher if $Z_i > E/T$, and ignored if $Z_i < E/T$. To estimate E/T using Equation (2) we estimated the encounter rate with cockles of size class i (l_i) as the reciprocal of the expected travel time between successive cockles, given by Ward (1993), and derived from Thompson (1983):

$$\lambda_i = 1/[(\sqrt{1/d_i}) / s] \quad (4)$$

where s = search speed of an Oystercatcher ($m s^{-1}$) and d_i = density of available cockles in size class i per m^2 . As Meire & Ervynck (1986) point

out, this function does not consider the width of the bird's search path. Furthermore, it assumes that a bird would encounter each cockle present in the sand (see also Ward 1993). However, since it seems reasonable to assume that the encounter rate with a particular size class of cockle buried in the sand should be an increasing function of its density, Equation (4) provides a measure of the relative encounter rate with each size class.

METHODS

We studied Oystercatchers wintering in the Burry Inlet (51°39'N, 4°10' W) South Wales, during the 1994/95 and 1995/96 winters. The invertebrate fauna of the sand flats is dominated by cockles, which support several thousand Oystercatchers each winter (see Davidson 1967; Horwood & Goss-Custard 1977), and a commercial cockle fishery (Hancock & Urquhart 1966; Franklin 1976). Study plots were established where Oystercatchers fed, and included a range of shore heights and sediment types (see Norris & Johnstone 1998).

Foraging observations

A vehicle located 100-200m from study plots or reference markers, was used as a hide for all observations. Cockle fishermen use vehicles on the cockle beds, so were regularly encountered by Oystercatchers. Observations were made at all times that birds foraged, using a x60 magnification telescope. Individuals opened cockles by either exclusively hammering or stabbing. Stabbers searched visually for cockles, whereas hammerers searched by sewing (locating buried cockles by touch with bill a movement resembling the action of a sewing machine), and probing (less frequent probes relying more on visual cues) on flood tides. During foraging observations a focal bird was located at random and followed for 269.3 ± 2.1 s on average for hammerers and 263.2 ± 7.7 s on average for stabbers (range; hammerers: 158.5 to 367s, $n = 220$; stabbers: 155.5 to 326.5s, $n = 31$). This is shorter than in other studies (see Mei-

re & Ervynck 1986; Cayford & Goss-Custard 1990; Zwarts *et al* 1996), but was necessary because focal birds frequently walked out of study plots. Nevertheless, the number of cockles taken by each bird was adequate (mean and range; hammerers: 11 3-26; stabbers: 6 2-13). Birds fed only on cockles.

A continuous sequence of behaviour was recorded from focal birds by one of us (IJ) using time-event logging software (Stirling Microsystems, University of Stirling), running on a Pison Organiser. Observations of each individual were assumed to be independent and the following summary data were extracted from each. (1) Feeding method: stabber or hammerer. (2) Searching method: visually for stabbers, sewing or probing for hammerers. (3) Sizes of cockle attacked, estimated as percentage of bill-length divided into discrete classes (0-10%, 10-20%, 20-30%, 30-40%, 40-50%). These were converted into size classes using the mean bill-length of a sample of Oystercatchers caught for banding on the site ($73.4\text{mm} \pm 4.79$, $n = 120$). Therefore, size-classes 1-5 were equivalent to 0-7, 7-15, 15-22, 22-29, and $> 29\text{mm}$. In some cases cockle size could not be seen because they were opened without being carried. In these cases the size class was recorded as unknown, and these cases are referred to as 'not carried' hereafter. (4) Handling time: the time between finding a cockle and the swallowing the last piece of flesh. (5) Waste handling time: the time between capturing a cockle and the rejection of the cockle having failed to open it. (6) Whether or not a particular cockle was successfully opened. (7) Length of each searching bout, for each searching method. (8) Other activities, which included preening, resting, displaying or fighting.

Searching speeds were calculated for stabbers, and hammerers. This was achieved by locating small posts in the sand every 10cm along the edge of several study plots, and measuring the distance covered and time taken by a bird searching for cockles while walking close and parallel to the line of canes.

Cockles

For each plot, we estimated the density of cockles in each size class in the sand once every two tidal cycles throughout the winter (a tidal cycle was the interval between successive spring tides: approximately two weeks). This enabled us to match bird observations to the prey densities that they encountered. Cockles were sampled using three randomly positioned 0.1m² quadrats in each plot (see Norris & Johnstone 1998). The number of cockles present in each size class were counted and averaged across the three samples. Some cockles were retained and frozen within 24 hours of being collected and the ash free dry mass AFDM, a measure of energy content, subsequently determined (see Norris & Johnstone 1998).

Prey remains

To quantify prey size selection independently of foraging observations, we collected prey remains from each plot during each cockle-sampling period and assigned them to size classes. Cockles opened by Oystercatchers using different feeding methods were readily identified. After hammering, prey remains consisted of an intact and shattered valve. Prey remains from stabbers consisted of two intact valves. For analysis, the mean size consumed during each tidal cycle was calculated as the product of the relative frequency of size i in the prey remains and its size class, measured as an integer value between 1 (0-7mm) and 5 (> 29mm cockles), summed across all size classes.

Availability of cockles

Oystercatchers that hammer open mussels select less robust thin-shelled individuals (Durell & Goss-Custard 1984; Meire & Ervynck 1986; Sutherland & Ens 1987; Cayford & Goss-Custard 1990; Ens & Altling 1996). To assess whether hammerers feeding on cockles showed a similar preference we measured the mass (a measure of robustness), to the nearest 0.1g, of a clean undamaged cockle valve minus the external ligament. To obtain a random sample of shell masses present in the sand we measured unpredated cockles of the same size classes as opened by hammerers.

Data analysis

Estimates of cockle size in relation to bill-length are prone to error. To quantify such error we conducted two trials during the winter (December 1994 and March 1995) (Appendix 1). To develop parameters for the optimality model we wished to generate statistical models, which described each parameter as a function of cockle size, feeding method, time after high water and season. Although the number of cockles attacked in each size class were corrected for observer error (see Appendix 1) bias in estimates of time costs h and w could not be. For example, if cockles were frequently assigned to smaller size-classes in error, then the handling times of these would be over estimated. To examine the effect of this, we estimated the actual mean size class of cockles estimated to be size class i as:

where s_i = weighted mean size class of cockle actually taken by birds which were estimated to

$$s_i = \frac{\sum_{j=1}^5 c_j P_j}{5}$$

be size class i , c_j = size class of cockles in integer values between 1 (0-7mm) and 5 (> 29mm), and p_j = probability that a cockle estimated to be size class i was actually size class j (calculated from observer error trials). We then modelled handling time (h) and waste handling times (w) as linear functions of this weighted mean size class. These linear models were then compared with similar models generated using the raw size class data. This analysis showed that there was no significant bias in handling costs as a result of observer error, so we used the size class observed in the field to generate statistical models of size-specific handling costs.

To generate statistical models which described the optimality model's parameters, we first constructed simple ANCOVAs which described each parameter in the optimality model as a function of cockle size and feeding method, assuming a common slope for each feeding method. We then additionally tested whether the rate of change in each parameter with cockle size was similar for birds

using each feeding method. For handling and waste handling times, we calculated a mean value for each size class taken by an individual bird during an observation session, and used these means in the ANCOVAs. We then tested whether a simple model containing cockle size class was sufficient, by additionally fitting terms which described the season (winter day; where 1st September = 1), and time after high water, in separate multiple regression models for each feeding method. Cockle size class was included in these models as an integer value, ranging from 1 (0-7mm) to 5 (> 29mm). These statistical models were then used as the basis for estimating intake rates using Equation (2).

RESULTS

Observed size selection

Of the Oystercatchers observed, 88% opened cockles by hammering. The frequencies of each size class consumed by Oystercatchers, based on the prey remains data, and the frequencies of the same size classes present in the sand are shown in Table. 1. Birds using both feeding methods showed significant selectivity (Stabbers: $\chi^2 = 175.4$, $df = 4$, $P < 0.001$; Hammerers: $\chi^2 = 3437.1$, $df = 4$, $P < 0.001$). Stabbers consumed mainly large cockles > 22mm, whereas hammerers consumed primarily intermediate sizes, ranging from 7-22mm. In hammerers, the mean size class consumed significantly increased over the winter (Fig. 1a). The mean size consumed estimated from the prey remains data was significantly smaller than the mean size class consumed during

observations ($P < 0.05$ in each tidal cycle where comparisons were possible). This was because small cockles were sometimes not carried prior to being opened and so their size was unknown. There was no doubt that these were cockles, since no alternative prey was present. As a result, 0-22mm cockles represented 86.5% of the prey remains, but only 41.3% of cockles in foraging observations. However, if cockles that were not carried were assumed to be 0-22mm in size the percentage was similar (i.e. 79.4%). However, both prey remains and foraging observations showed comparable increases in the mean size class consumed over time (Fig. 1a). In contrast, there was no evidence of an increase in mean size consumed by stabbers over the winter. Furthermore, there were fewer significant differences in the mean size of prey remains and foraging observations (two of four possible comparisons Fig. 1b).

Availability of cockles

The slopes of the relationship between cockle size-class and shell mass differed between cockles present in the sand and those that had been hammered open. Comparison of the regression slopes by ANCOVA indicated that hammerers opened shells with smaller masses for their size class than those present in the sand ($t = 10.63$, $P < 0.0001$), with the difference being most for larger size classes. This suggests that only a fraction of these were physically available to hammerers. To estimate this fraction we calculated the cumulative percentage of shell masses as a function of shell mass for a sample of cockles from the sand and a sample opened by hammerers. For hammered

Table 1. Frequency distributions of prey remains and cockles present in the sand for each size class, shown for hammerers ($n = 2790$ prey remains), and stabbers ($n = 271$ prey remains), averaged over the whole winter.

cockle size class	0-7 mm	7-15 mm	15-22 mm	22-29 mm	> 29 mm
Hammered %	0	52	38	9	1
Stabbed %	0	13	9	35	43
Present in sand %	1	42	25	26	6

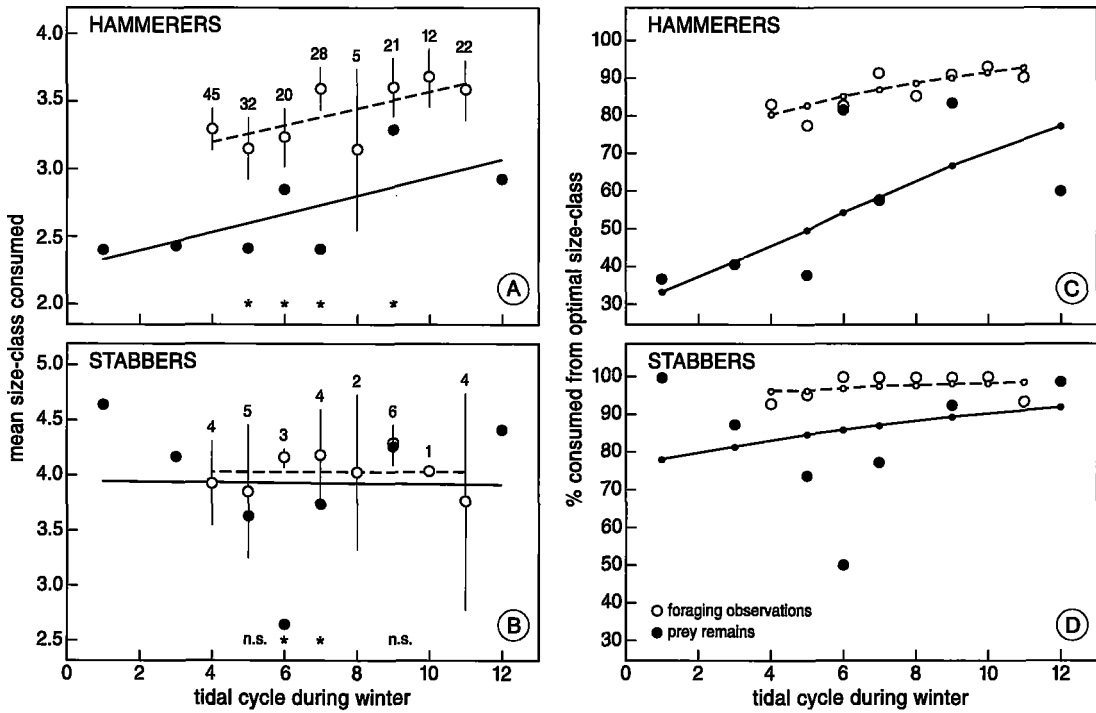


Fig. 1. Seasonal changes in the mean cockle size class consumed by hammerers (A) and stabbers (B) based on foraging observations. Tidal cycles were two-week periods between successive spring tides (5 September 1994 - 2 March 1995). Sizes classes: 1 = 0-7, 2 = 7-15, 3 = 15-22, 4 = 22-29, 5 = >29mm. Mean cockle size from bird observations \pm 95% confidence intervals plus sample size. Significance of differences between prey remains and foraging observations are indicated by '*' (significant) or 'n.s.'. For hammerers, seasonal trends are described by linear regression equations: bird observations $y = 2.99 + 0.062x$ ($r^2_{adj} = 7.6\%$, $n = 184$, $P < 0.001$), prey remains $y = 2.258 + 0.0682x$ ($r^2_{adj} = 39.9\%$, $n = 7$, $P = 0.076$). No significant seasonal trends for stabbers (bird observations $r^2_{adj} = 3.4\%$, $n = 30$, n.s., prey remains $r^2_{adj} = 24.5\%$, $n = 5$, n.s.).

The percentage of cockles consumed by (C) hammerers and (D) stabbers of the optimal size classes from bird observations and prey remains. For hammerers, the seasonal increase in the percentage is significant for both kinds of data (logistic regression: bird observations: $y = 1/(1 + e^{-(0.7844 + 0.1545 \cdot \text{tidal cycle})})$, $\chi^2 = 14.21$, $df = 1$, $P < 0.001$; prey remains $y = 1/(1 + e^{-(0.8777 + 0.1729 \cdot \text{tidal cycle})})$, $\chi^2 = 160.1$, $df = 1$, $P < 0.001$). Fitted values for foraging observations and prey remains generated using these models are shown with dashed lines. For stabbers, a significant increase in the percentage of cockles > 15mm in length in the prey remains (logistic regression: $y = 1/(1 + e^{-(1.16 + 0.1093 \cdot \text{tidal cycle})})$, $\chi^2 = 4.67$, $df = 1$, $P < 0.05$), no significant seasonal trend bird observations (logistic regression: $y = 1/(1 + e^{-(2.656 + 0.1422 \cdot \text{tidal cycle})})$, $\chi^2 = 0.296$, $df = 1$, n.s.).

cockles, this reached a plateau at a shell mass of c.2.5g. The percentage of unopened cockles with a shell mass of less than this in the 22-29 and > 29mm size classes was 77.3% and 2.4% respectively.

Model parameters

For cockles in the Burry Inlet energy content increased significantly with size, and for a given size class, declined throughout the winter, although the rate of the decline decelerated over (table 2). Handling times were an increasing line-

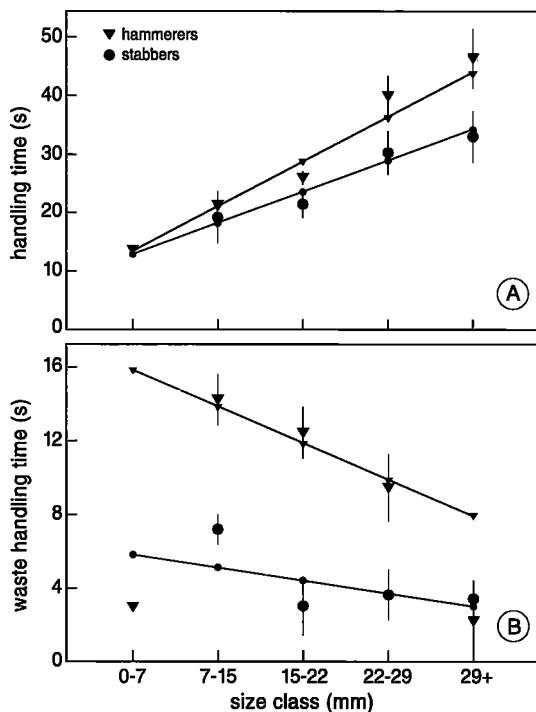


Fig. 2 Time costs of handling cockles of different size when (A) cockles were successfully opened (handling time), and (B) when cockles were subsequently rejected unopened (waste handling time) for hammerers and stabbers. For hammerers, these relationships are described by $y = 5.771 + 7.571x$ (handling times) and $y = 18.066 - 2.205x$ (waste handling times), each of which provided a significant fit (respectively $r^2_{adj} = 18.4\%$, $n = 275$, $P < 0.001$ and $r^2_{adj} = 2.2\%$, $n = 147$, $P = 0.039$). For stabbers, these relationships are described by $y = 7.412 + 5.331x$ (handling times) and $y = 6.588 - 0.709x$ (waste handling times). The first provided a significant fit ($r^2_{adj} = 11.9\%$, $n = 42$, $P = 0.013$), but the model of waste handling times was not significant ($r^2_{adj} = 2.1\%$, $n = 33$, n.s.).

ar function of cockle size class for both stabbers and hammerers (Fig. 2a), but were significantly shorter in stabbers for a given size class ($t = -2.27$, $df = 1$, $P = 0.019$). There was no evidence that the slopes of the regression lines differed between feeding methods ($t = -0.886$, $df = 1$, $P = 0.376$). The time wasted handling cockles which were

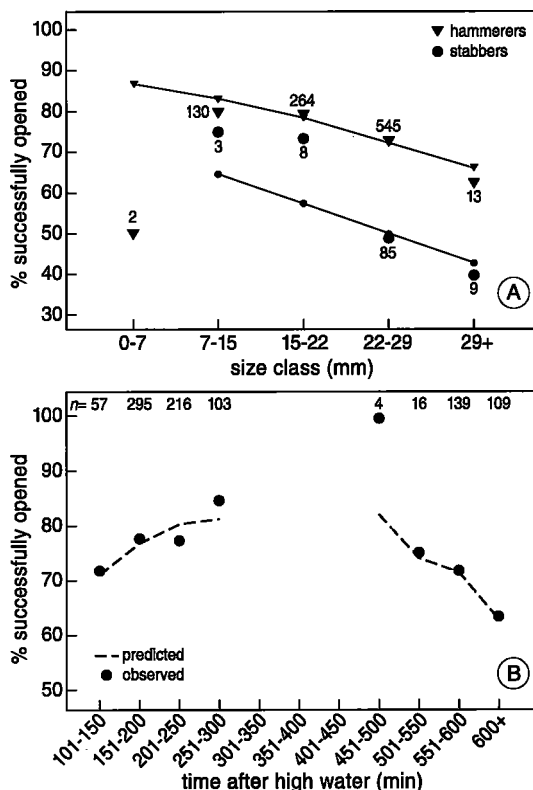


Fig. 3 Percentage of cockles successfully opened, attacked in relation to (A) size class and (B) time after high water. In (A) hammerers and stabbers are shown separately with sample sizes. The lines describe the predicted percentages from the logistic regression model shown in Table 3c. In (B) the observed percentages (solid circles) and predicted percentages (dashed line) generated by the logistic regression model shown in Table 3d are shown. Note that predicted values do not form a smooth curve due to differences in size classes attacked at different times after high water. Time after high water is shown as a series of 50-minute intervals. The number of cockles attacked during each time interval are shown.

subsequently rejected decreased with size in hammerers, but showed little variation in stabbers (Fig. 2b). Waste handling time was significantly shorter in stabbers ($t = -2.928$, $df = 1$, $P = 0.0039$), but the slopes of the regression lines did not differ significantly between feeding methods ($t = 0.745$, $df = 1$, $P = 0.457$).

Table 2. Statistical model describing energy content of prey (gAFDM). Predictor variables were fitted using a step-forward selection procedure. Size class was included in the model as \ln transformed values, 'day' = September day (1st September = 1) and 'exposure' refers to the time after high water the plot from which the cockle originated was exposed. Based on 837 cockles, the model accounted for 83.9% (R^2_{adj}) of the variance in $\ln(\text{gAFDM})$.

ANOVA of final model

Source of variance	<i>df</i>	<i>SSQ</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Regression	3	1073.237	357.755	1453.548	<0.0001
Residual	835	205.509	0.2461		

Variables included in model

Predictor variable	<i>b</i>	SE	<i>t</i>	<i>P</i>
Size class (\ln)	3.731	0.057	65.459	<0.0001
Day	-0.00635	0.00143	-4.435	<0.0001
Day ²	1.3499E-05	6.388E-06	2.113	0.0349

Variables not included in model

Predictor variable	<i>b</i>	<i>t</i>	<i>P</i>
Exposure	0.00416	0.294	0.769

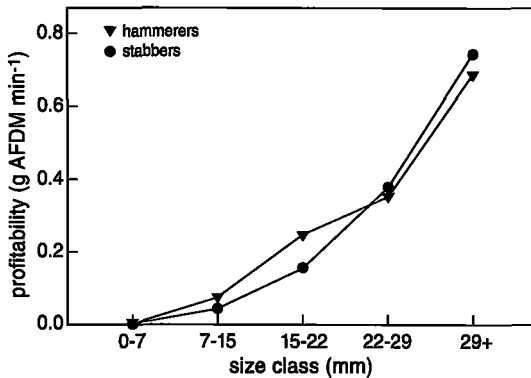


Fig. 4 Profitability (gAFDM min⁻¹) in relation to cockle size for hammerers and stabbers. Profitability was calculated using Equation (3), with handling costs as described in the text.

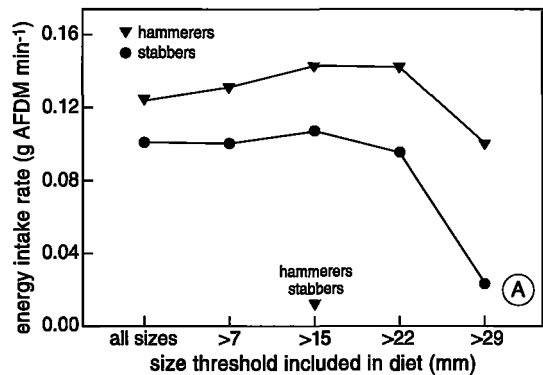


Fig. 5 (A) Predicted energy intake rates (gAFDM min⁻¹) for different size selection strategies for hammerers and stabbers. The selection strategy, which maximised intake rate, is shown for each feeding method. Only birds which experienced cockle densities > 0 for all size classes are shown. The percentage of birds predicted to consume only cockles > 15 mm at different times during the winter are shown in (B).

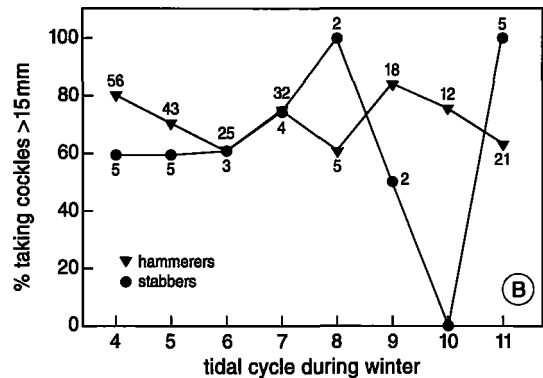


Table 3. Statistical models of time costs. Handling times (models A and B) were modelled using multiple regression analysis, assuming the response variable had a normal error distribution. The probability of successfully opening a cockle (models C and D) was modelled using logistic regression analysis, assuming the response variable had a binomial error distribution.

Handling time in hammerers

Variable	Coefficient, <i>b</i>	SE	<i>t</i>	<i>P</i>
x_1	7.625	0.975	7.818	0.0000
x_2	-0.050	0.024	-2.085	0.038
x_3	-0.169	0.044	-3.823	0.0002
x_4	2.149E-04	5.610E-05	3.83	0.0002
Constant	36.429	8.337	4.37	0.0000

where x_1 = size class (integer values: 1-5), x_2 = winter day (1 Sep = 1), x_3 = time after high water (mins), x_4 = time after high water squared. Overall fit of model: r^2_{adj} = 22%, n = 272, P < 0.0001.

Handling time in stabbers

Variable	Coefficient, <i>b</i>	SE	<i>t</i>	<i>P</i>
x_1	5.400	1.983	2.723	0.0095
x_2	-0.0989	0.0479	-2.064	0.046
Constant	19.518	9.81	1.99	0.054

where x_1 = size class (integer values: 1-5), x_2 = winter day (1 Sep = 1). Overall fit of model: r^2_{adj} = 18.4%, n = 41, P = 0.0064.

Probability of successfully opening cockle

Variable	Coefficient, <i>b</i>	SE	χ^2	<i>P</i>
x_1	-0.3052	0.1059	8.697	0.0032
x_2	-0.9772	0.2118	20.992	0.0000
Constant	1.7066	0.4198		

where x_1 = size class (integer values: 1-5), x_2 = feeding method (categorical variable: hammerer = 1, stabber = 2). The coefficient for x_2 shows the linear contrast between levels 1 and 2 of the categorical variable describing feeding method. The probability is significantly lower in stabbers. For both predictor variables, df = 1. Overall fit of model: χ^2 = 41.547, df = 2, P < 0.001.

Probability of successfully opening a cockle in hammerers

Variable	Coefficient, <i>b</i>	SE	χ^2	<i>P</i>
x_1	-0.238	0.1108	4.786	0.0287
x_2	0.4257	0.2157	3.906	0.048
x_3	-0.029	0.0129	5.072	0.0243
Constant	0.8042	0.8532		

where x_1 = size class (integer values: 1-5), x_2 = time after high water (min), x_3 = time after high water squared. Time after high water was expressed as an integer value which described time as a series of 50 min intervals (e.g. 3=101-150 min after high water). For all predictor variables, df = 1. Overall fit of model: χ^2 = 19.423, df = 3, P = 0.0002.

There was evidence that handling times in hammerers varied over the winter and during each daily tidal cycle, in addition to the effect of cockle size (Table 3a). Handling times decreased significantly over the winter, and were longest at the start and end of the daily tidal cycle. This was best described by a negative quadratic relationship. Handling times in stabbers also significantly decreased over the winter, in addition to the effects of cockle size (Table 3b). There was no evidence that waste handling times varied over the winter or during the daily tidal cycle, in either feeding method, in addition to the effect of size (additional variance explained when variables x_2 to x_4 in Table 3a added to a model of waste handling times already containing size class; hammerers: $F_{3,143} = 1.071$, n.s.; stabbers: $F_{3,29} = 1.167$, n.s.).

Hammerers attacked some 0-22mm cockles without lifting them from the sand, or after lifting them but not carrying them (see above). The handling times and waste handling times of these cockles were shorter than the corresponding time costs observed for cockles of similar size which were carried (Handling times: carried = 23.75 ± 0.79 s, $n = 239$ birds; not carried = 10.3 ± 0.49 s, $n = 152$ birds; Waste handling times: carried = 13.30 ± 1.04 s, $n = 119$ birds; not carried = 3.85 ± 0.26 s, $n = 126$ birds). Handling times were only 43.4% as long, and waste handling times only 29% as long, on average. The probability of successfully opening a cockle that had been attacked decreased with size in both stabbers and hammerers, and was significantly lower in stabbers (Fig. 3a; Table 3c). There was no evidence to suggest that the rate of change in the probability of success differed between feeding methods ($\chi^2 = 1.047$, $df = 1$, $P = 0.3062$). There was evidence that the probability of success varied with time after high water in hammerers, in addition to the effect of cockle size (Fig. 3b; Table 3d). The probability increased over time on the ebb tide, and decreased over time on the flood tide. There were no significant effects of season or time after high water on this probability in stabbers, in addition to the effects of cockle size ($\chi^2 = 1.719$, $df = 3$, $P >$

0.10). Among hammerers, 76.4% (1057/1383) of cockles not carried were successfully opened.

We calculated relative encounter rates using Equation (4). Densities were adjusted for hammerers by calculating the density of available 22-29 and > 29 mm cockles as the product of the density and the proportion of cockles with shell masses small enough to be opened by hammering (i.e. 0.773 and 0.024 respectively). Encounter rates with each size class were calculated assuming the cockle densities experienced by searching individuals were similar to those estimated during the closest cockle-sampling period. Searching speeds were measured for hammerers searching by probing and sewing, and for stabbers. Hammerers searched at a speed of 0.083 ± 0.0066 m s⁻¹ while sewing ($n = 11$) and at 0.218 ± 0.0296 m s⁻¹ while probing ($n = 40$). Stabbers searched at a similar speed to hammerers searching by probing, 0.19 ± 0.058 m s⁻¹ ($n = 36$).

Model predictions

We used Equation (3) to calculate the profitability of each size class to both hammerers and stabbers throughout the winter. Estimating the time costs for hammerers was complex, since parameters varied over the winter, through the tidal cycle and, for cockles < 22 mm in length, depended on whether or not the cockle was carried before being opened. To incorporate these components for size classes < 22 mm in length, we estimated the handling time (h) and waste handling time (w) of a cockle of size class i attacked by hammerers as:

$$h_i = h_c p_c + h_{nc} (1 - p_c) \quad (5a)$$

$$w_i = w_c p_c + w_{nc} (1 - p_c) \quad (5b)$$

where h_c = the handling and w_c = the waste handling time of a cockle of size i which was lifted and carried, h_{nc} = the handling and w_{nc} = the waste handling time of a cockle of size i which was not carried, and p_c = the probability that a cockle of size i would be lifted and carried. The handling and waste handling times of cockles lifted and carried were estimated from the statistical model

in Table 3a and Fig. 2b respectively, handling times and waste handling times of cockles not carried were estimated as 43.4% and 29% of the value of h_c respectively (see above), and the probability of a cockle being lifted and carried was calculated from the foraging observations (mean percentage: $49 \pm 3\%$). For size classes $> 22\text{mm}$ in length, we estimated time costs directly from the statistical models: handling times (Table 3a), and waste handling times (Fig. 2b). For cockles $< 22\text{mm}$ in length, we estimated the probability of successfully opening and consuming a cockle of size class i (P_i) after being attacked by a hammerer as:

$$P_i + p_{sc}p_c + p_{suc}(1 - p_c) \quad (6)$$

where p_{sc} = the probability of successfully opening a cockle of size class i that was carried (estimated from the logistic regression model in Table 3d), p_{suc} = the probability of successfully opening a cockle of size class i not carried (i.e. 0.764; see above), and p_c is as defined in Equation (5). For size classes $> 22\text{mm}$ in length, P_i was estimated directly from the logistic regression equation in Table 3d. For stabbers, handling times were estimated using the statistical model in Table 3b, waste handling times using the model in Fig. 2b, and the probability of success using the model in Table 3c.

Profitability increased with cockle size for birds using both feeding methods, and tended to be similar in stabbers and hammerers (Fig. 4). This was because although stabbers experienced lower time costs than hammerers when handling a cockle of a given size class (Figs. 2a and 2b), they also tended to be less successful at opening cockles they had attacked (Fig. 3). Furthermore, time costs for hammerers attacking cockles that were not carried were comparatively small.

To determine which size classes each feeding method should include in their diet to maximise their energy intake we used Equation (2), by calculating predicted energy intake rates for different selection strategies. That is, including only the most profitable size class in the diet, the two most

profitable size classes, etc (see also Meire & Ervynck 1986; Cayford & Goss-Custard 1990). For hammerers and stabbers energy intake was maximised if cockles $> 15\text{mm}$ were included in their diet (Fig. 5a). We tested whether the frequency of this predicted size selection strategy in the population showed any significant seasonal variation, since hammerers change their size selection over the winter. There was no significant seasonal change in the frequency of birds predicted to consume only cockles $> 15\text{mm}$, in stabbers or hammerers (logistic regression; hammerers: $\chi^2 = 0.649$, $df = 1$, n.s.; stabbers: $\chi^2 = 1.19$, $df = 1$, n.s.; Fig. 5b).

To test the model's predictions, we calculated the percentage of cockles consumed by each bird from the size classes the model predicted each should select. Over the winter, 48% of hammered prey remains were $> 15\text{mm}$ in length. There was a significant seasonal increase in the percentage of cockles consumed by hammerers from the most profitable size classes (i.e. $> 15\text{mm}$) (Fig. 1c), reaching a maximum of c. 80% during later winter (based on prey remains). Observations of hammerers showed a similar seasonal trend, although, overall, the percentage was higher because small cockles taken by hammerers tended to be missed during our foraging observations (Fig. 1c). In contrast, 87.1% (236/271) of the prey remains from stabbers were $> 15\text{mm}$ in length, and this percentage remained high throughout the winter (Fig. 1d), although there was a weak, but significant, trend for their percentage in the prey remains to increase slightly over the winter. There was no such significant trend in the foraging observation data (Fig. 1d). Therefore stabbers mainly consumed the most profitable size classes, whereas hammerers often consumed smaller less profitable cockles.

DISCUSSION

Sources of bias

The model predictions are critically dependent on the validity of the size-specific parameters for

which there were potential sources of bias. Firstly, estimates of prey size may be subject to observer error (Meire & Ervynck 1986; Goss-Custard *et al.* 1987; Cayford & Goss-Custard 1990), for which we were able to correct (Appendix 1). In addition, we found no evidence of observer error affecting estimates of handling and waste handling times in relation to cockle size (see also Norris & Johnstone 1998). Secondly, cockle size was estimated as a percentage of bill-length, and then converted into a size class based on the mean bill-length of birds from the site. This could affect results if bill lengths differ between feeding methods. There is some evidence for this on other sites, with hammerers having shorter bills than stabbers (Hulscher & Ens 1992). However, this would not effect the observed changes in diet over the winter. Thirdly, handling costs for each size class could be over-estimated if based solely on prey whose size was recorded, and therefore were carried during handling. Oystercatchers do open prey in the substrate or on the surface without being carried (e.g. Hulscher 1982; Wanink & Zwarts 1985), and these tend to have shorter handling costs. This bias was present in our data. However, we were able to incorporate these shorter handling costs by comparing prey remains and foraging observations to estimate the size of cockles which were handled but not seen. We conclude that our results are unlikely to be seriously biased.

Model parameters

Birds which hammered cockles >22mm selected those with shell mass less than average. Hammerers feeding on mussels avoid those with thick shells (Durell and Goss-Custard 1984; Meire & Ervynck 1986; Sutherland & Ens 1987; Cayford & Goss-Custard 1990), a preference related either to the lower profitability of thick shelled bivalves (Sutherland & Ens 1987; Meire 1993), or the risk of bill damage during hammering (Swennen & Duiven 1983; Swennen *et al.* 1983). An increase in handling time with prey size is well documented in Oystercatchers (see Meire & Ervynck 1986; Sutherland & Ens 1987; Cayford & Goss-Custard 1990; Zwarts *et al.* 1996). Handling time for both

hammerers and stabbers decreased through the winter, and in hammerers peaked when cockles were first available on the ebb tide, and just before cockles became unavailable on flood tides. One explanation for these patterns is substrate hardness. Overall, sediment hardness was negatively correlated with time after high water (Johnstone & Norris 2000). Furthermore, the concentration of birds along the advancing tide line could indicate an decrease in hardness just before being submerged. Such changes could explain why the probability of successfully hammering increases on the ebb, then declines on the flood tide. Over the winter, storms removed mud from some areas of the cockle beds, causing change in substrate hardness (Johnstone & Norris 2000). This might explain the decline in handling times in hammerers. A possible explanation for a decline in the handling times of stabbers is the decline in cockle condition over the winter, which will influence muscle strength. This could (1) cause cockles gape more making them vulnerable to attack and (2) affect a cockles ability to rapidly close its valves to thwart a stabbing attempt. The seasonal decrease in handling times for each feeding method could be due to the decline in flesh in each size class, which takes less time to extract and swallow (see also Ens *et al.* 1996b).

Waste handling times decreased significantly with increasing cockle size in hammerers. This contrasts with birds feeding on mussels, when waste handling times were found to increase with prey size (Meire & Ervynck 1986; Cayford & Goss-Custard 1990). A possible explanation for this is that hammerers feeding on larger cockles have to lift them from the substrate and subject it to a blow in order to determine whether it is vulnerable (i.e. its shell mass is small enough). Having established that it is not, they waste little time attempting to open it. Birds feeding on mussels frequently tap potential prey with their bill, which could establish its shell thickness, a behaviour that was not recorded as an attack. In contrast, a cockle lifted from the substrate and dealt a blow was recorded as being attacked by our study. Encounter rates were estimated as the reciprocal

of the expected travel time between successive cockles (Thompson 1983; Ward 1993). It could be argued that Charnov's model fails to predict a seasonal trend in size selection among hammerers because Equation (4) provides a poor estimate of true encounter rates. However, for hammerers searching by touch we have used the simple random search model developed by Hulscher (1976, 1982) to provide a quantitative estimate of encounter rates. This analysis generated similar predictions to those reported in the present paper: hammerers selected only cockles > 15mm in length throughout the winter (Norris & Johnstone 1998). Therefore, we consider the seasonal departure from the predicted size selection displayed by hammerers a real phenomenon, rather than an artefact of the way encounter rates were incorporated into the model.

Model predictions

The model predicted that both hammerers and stabbers should consume cockles > 15mm in length, and that the mean size consumed should remain constant throughout the winter. The decisions made by stabbers were consistent with these predictions, since 85% of cockles in the prey remains were > 15mm, and the mean size consumed did not change over the winter. In contrast, hammerers included smaller cockles than expected in their diet in early winter and increased the mean size class taken over the winter. During mid to late winter up to c.80% of cockles consumed were > 15mm in length. This suggests that selecting the most profitable prey has an additional cost, which differs between feeding methods.

What could this cost be? Parasites have been shown to reduce both host survival and fecundity (Hudson *et al.* 1992). Furthermore Goater *et al.* (1995) showed that helminth intensity in Oystercatchers on the Exe Estuary was highest in birds feeding on prey with the highest intensity of metacercaria infection. In the Burry Inlet, the intensity of helminth infection increased significantly with cockle size (Norris 1999). It might be expected that Oystercatchers should only risk eating larger cockles when the benefits of a high energy

intake outweighs the greater risk of infection, and this is most likely during late winter, when poor weather results in high daily energy expenditure. However, this does not explain why stabbers include large cockles in their diet throughout the winter. It is possible that exposure to parasites is one of a number of costs associated with eating large cockles, and only some of these differ between feeding methods. One such a cost could be an increased risk of bill damage when handling larger more profitable prey (Swennen & Duiven 1983; Swennen *et al.* 1983). This could include deformation through prolonged use close to its biomechanical limits, causing impaired foraging ability, or catastrophic failure followed by starvation. The observation that hammerers avoid attacking cockles > 22mm and with shell masses > 2.5g at all times supports the idea that hammering larger more robust cockles has different costs to stabbing. Furthermore, only hammerers would be expected to avoid larger more profitable cockles when energy demands are low, and this is what was observed. It would be interesting to compare the mechanical stresses under which the bill is put during hammering and stabbing as support for this.

A major assumption in our model of diet selection is that Oystercatchers maximise their gross instantaneous energy intake rate. However, a more appropriate currency for wintering Oystercatchers might be to maximise their net daily energy intake. This is because when deciding what to eat, birds must balance the energy gained by consuming prey with the energy costs incurred during searching and handling. When handling cockles, hammerers progressively escalate from light to heavy blows before succeeding or giving up (*pers. obs.*), suggesting birds try to minimise the effort required. The size specific energy costs of hammering and stabbing activities are currently unknown, but may be high and differ significantly. These costs might further explain the differences in prey size selection shown by Oystercatchers using different feeding methods.

ACKNOWLEDGEMENTS

We would like to thank Phil Coates and the fishery officers of the South Wales Sea Fisheries Committee, Tony Jenkins of the Countryside Council for Wales, and the National Trust, for their assistance throughout this project. John Goss-Custard provided enthusiasm, advice and technical support, and Richard Stillman, Bruno Ens and Patrick Triplet stimulating discussions and helpful advice. We would like to thank Wendy Grant and Paul Britten for data entry. This work was funded jointly by the European Commission (DG XIV), RSPB and ITE. Bruno Ens, John Goss-Custard and Bill Sutherland kindly provided comments on a previous draft of this paper. Sylvia's cafe provided buoyancy-enhancing breakfasts on cockle sampling days. Finally, we would like to thank the cockle gatherers of the Burry Inlet, without whose co-operation this work would not have been possible.

REFERENCES

- Boates J.S. & J.D. Goss-Custard 1989. Foraging behaviour of Oystercatchers *Haematopus ostralegus* during a diet switch from worms *Nereis diversicolor* to clams *Scrobicularia plana*. *Can. J. Zool.* 67: 2225-2231.
- Cayford J.T. & J.D. Goss-Custard 1990. Seasonal changes in the size selection of Mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*: an optimality approach. *Anim. Behav.* 40: 609-624.
- Charnov E.L. 1976. Optimal foraging: attack strategy of a mantid. *Am. Nat.* 110: 141-151.
- Davidson N.C. & P.R. Evans 1983. Mortality of Redshanks and Oystercatchers from starvation during severe weather. *Bird Study* 29: 183-188.
- Davidson P.E. 1967. A study of Oystercatchers (*Haematopus ostralegus* L.) in relation to the fishery for Cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. *Fishery Investigations Series II*, Volume XXV, no. 7.
- Durell S.E.A. le V. dit, & J.D. Goss-Custard 1984. Prey selection within a size-class of Mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*. *Anim. Behav.* 32: 1197-1203.
- Ens B.J. & D. Altig 1996. Prey selection of a captive Oystercatcher *Haematopus ostralegus* hammering Mussels *Mytilus edulis* from the ventral side. *Ardea* 84A: 215-219.
- Ens B.J., E.J. Bunschoke, R. Hoekstra, J.B. Hulscher, M. Kersten, M. & S.J. de Vlas 1996a. 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*. *Ardea* 84A: 73-89.
- Ens B.J., S. Dirksen, C.J. Smit & E.J. Bunschoke 1996b. Seasonal changes in size selection and intake rate of Oystercatchers, *Haematopus ostralegus*, feeding on the bivalves, *Mytilus edulis* and *Cerastoderma edule*. *Ardea* 84A: 159-176.
- Franklin A. 1976. The Burry Inlet Cockle fishery. In: Nelson-Smith A. & E.M. Bridges (eds) *Problems of a small estuary*: 3, 1/1. UCW Swansea, Swansea.
- Goater C.P., J.D. Goss-Custard & C.R. Kennedy 1995. Population dynamics of two species of intestinal helminth in Oystercatchers *Haematopus ostralegus*. *Can. J. Zool.* 73: 296-300.
- Goss-Custard J.D. & N. Verboven 1993. Disturbance and feeding shorebirds on the Exe estuary. *Wader Study Group Bull.* 68: 59-66.
- Goss-Custard J.D. 1977. Optimal foraging and the size selection of worms by Redshank, *Tringa totanus*, in the field. *Anim. Behav.* 25: 10-29.
- Goss-Custard J.D. 1980. Competition for food and interference among waders. *Ardea* 68: 31-52.
- Goss-Custard J.D. J.T. Cayford, J.S. Boates & S.E.A. le V. Durell dit 1987. Field tests of the accuracy of estimating prey size from bill length in Oystercatchers, *Haematopus ostralegus*, feeding on Mussels, *Mytilus edulis*. *Anim. Behav.* 35: 1078-1083.
- Hancock D.A. & A.E. Urquhart 1966. The fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. *Fishery Investigations Series II*, Vol. XXV, no. 3.
- Hudson P.J., D. Newborn & A.P. Dobson 1992. Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in Red Grouse. I Monitoring and parasite reduction experiments. *J. Anim. Ecol.* 61: 477-486.
- Horwood J.W. & J.D. Goss-Custard 1977. Predation by the Oystercatcher, *Haematopus ostralegus* (L.), in relation to the cockle, *Cerastoderma edule* (L.), fishery in the Burry Inlet, South Wales. *J. Appl. Ecol.* 14: 139-158.
- Houston A.I., C.W. Clarke, J.M. McNamara & M. Mangel 1988. Dynamic models in behavioural and evolutionary ecology. *Nature* 332: 29-34.
- Hulscher J.B. 1976. Localisation of cockles (*Cardium edule*) by an Oystercatcher (*Haematopus ostralegus*) in darkness and daylight. *Ardea* 64: 292-310.
- Hulscher J.B. 1982. The Oystercatcher (*Haematopus ostralegus*) as a predator of the bivalve (*Macoma balthica*) in the Dutch Wadden Sea. *Ardea* 70: 89-152.
- Hulscher J.B. & B.J. Ens 1992. Is the bill of the male Oystercatcher a better tool for attacking mussels than the bill of the female. *Neth. J. Zool.* 42: 85-100.

- Johnstone I. & K. Norris 2000. The influence of sediment type on the aggregative response of Oystercatchers, *Haematopus ostralegus*, searching for cockles, *Cerastoderma edule*. *Oikos* 89: 146-154.
- Kersten M. & T. Piersma 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* 75: 175-187.
- Krebs J.R. & A. Kacelnik 1991. Decision-making. In: Krebs J.R. & N.B. Davies (eds) *Behavioural Ecology: an evolutionary approach*: 105-136. Blackwell Scientific Publications, Oxford.
- Meire P. 1993. Wader populations and macrozoobenthos in a changing estuary: the Oosterschelde (The Netherlands). PhD-thesis, University of Gent, Gent.
- Meire P.M. & A. Eryvynck 1986. Are Oystercatchers (*Haematopus ostralegus*) selecting the most profitable Mussels (*Mytilus edulis*)? *Anim. Behav.* 34: 1427-1435.
- Norris K. 1999. A trade-off between energy intake and exposure to parasites in Oystercatchers feeding on a bivalve mollusc. *Proc. R. Soc., Lond. B* 266: 1703-1709.
- Norris K. & I. Johnstone 1998. The functional response of Oystercatchers (*Haematopus ostralegus*) searching for cockles (*Cerastoderma edule*) by touch. *J. Anim. Ecol.* 68: 329-346.
- O'Connor R.J. & R.A. Brown 1977. Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. *Oecologia* 27: 75-92.
- Stephens D.W. & J.R. Krebs 1986. *Foraging Theory*. Princeton University Press, Princeton.
- Sutherland W.J. 1982. Do Oystercatchers select the most profitable cockles? *Anim. Behav.* 30: 857-861.
- Sutherland W.J. & B.J. Ens 1987. Criteria determining selection of mussels by Oystercatchers. *Behaviour* 103: 187-202.
- Swennen C., L.L.M. de Bruijn, P. Duiven, M.F. Leopold & E.C.L. Martejn 1983. Difference in bill form of the Oystercatcher *Haematopus ostralegus*: a dynamic adaptation to specific foraging techniques. *Neth. J. Sea Res.* 17: 57-83.
- Swennen C. & P. Duiven 1983. Characteristics of Oystercatchers killed by cold-stress in the Dutch Wadden Sea area. *Ardea* 71: 155-159.
- Swennen C., M.F. Leopold & L.L.M. de Bruijn 1989. Time-stressed Oystercatchers, *Haematopus ostralegus*, can increase their intake rate. *Anim. Behav.* 38: 8-22.
- Thompson D.B.A. 1983. Prey assessment by plovers (*Charadriidae*): net rate of energy intake and vulnerability to kleptoparasitism. *Anim. Behav.* 31: 1226-1236.
- Wanink J. & L. Zwarts 1985. Does an optimally foraging Oystercatcher obey the functional response? *Oecologia* 67: 98-106.
- Ward D. 1993. African Black Oystercatchers (*Haematopus moquini*) feeding on wedge clams (*Donax serra*): the effects of non-random prey availability in the intertidal on the predictions of an optimal diet model. *Ethology, Ecology & Evolution* 5: 457-466.
- Wiersma P. & T. Piersma. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. *Condor* 96: 257-279.
- Zwarts L., B.J. Ens, J.D. Goss-Custard, J.B. Hulscher & S.E.A. le V. dit Durell 1996. Causes of variation in prey profitability and its consequences for the intake rate of the Oystercatcher *Haematopus ostralegus*. *Ardea* 84A: 229-268.
- Zwarts L. & A-M Blomert 1992. Why Knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Prog. Ser.* 83: 113-128.
- Zwarts L. & R.H. Drent 1981. Prey depletion and the regulation of predator density: Oystercatchers (*Haematopus ostralegus*) feeding on Mussels (*Mytilus edulis*). In: Jones N.V. & W.J. Wolff (eds) *Feeding and survival strategies of estuarine organisms*: 193-216. Plenum Press, New York.

SAMENVATTING

Sinds de opkomst van de optimale foerageertheorieën in de jaren zeventig wordt vaak aangenomen dat dieren die naar voedsel zoeken, hun overlevingskansen maximaliseren door tijdens dat voedsel zoeken te proberen zoveel mogelijk energie in zo kort mogelijke tijd op te nemen. Deze theorie heeft tot veel onderzoek geïnspireerd aan het gedrag van de makkelijk waar te nemen voedselzoekende Scholekster *Haematopus ostralegus*. Naast een groot aantal waarnemingen die overeenstemmen met dit simpele idee, zijn er ook waarnemingen dat Scholeksters niet altijd de meest profijtelijke prooien selecteren. Het ligt voor de hand dat in zulke gevallen niet alle kosten en baten simpelweg in termen van energie en tijd kunnen worden uitgedrukt. Er zijn dan mogelijk ook andersoortige kosten in het spel, zoals het risico van snavelbreuk of infectie met parasieten. Het ligt voor de hand dat die kosten samenhangen met de methode waarop de Scholeksters hun prooien openen: steken of hameren. Dit is de achtergrond van het hier beschreven onderzoek aan overwinterende Scholeksters in de Burry Inlet, een getijdengebied in Wales, en daar van Kkokkels *Cerastoderma edule* leven. De

auteurs beginnen met het beschrijven van een aangepast optimaal prooikeuzemodel, waarin bijvoorbeeld rekening wordt gehouden met het feit dat Scholeksters soms pas na enig hannesen met de prooi kunnen vaststellen of deze profijtelijk kan worden geopend. De stekende Scholeksters zochten op het oog naar Kokkels, terwijl de hameraars puur op de tast zochten (naaien) of een combinatie van beide zoekmanieren gebruikten (prikken). Uit experimenten bleek dat de auteurs in het veld de neiging hadden de grootte van de gegeten Kokkels een beetje te onderschatten, maar hiervoor kon worden gecorrigeerd en dit had daardoor geen gevolgen voor de schattingen van de parameters in het prooikeuzemodel. Stekers selecteerden vooral grote Kokkels, terwijl hameraars Kokkels van intermediaire grootte selecteerden. Daarbij moet worden aangetekend dat hameraars vooral de kleine Kokkels ter plekke consumerden, zodat de grootte niet kon worden geschat, met als gevolg dat er een duidelijk verschil is tussen grootte-selectie op basis van veldschattingen en prooi-restcollecties. Hameraars hadden meer tijd nodig dan stekers om een prooi te openen of om vast te stellen dat een prooi niet kon worden geopend. De kans om een aangepikte Kokkel te openen, nam zowel voor hameraars als voor stekers af met de grootte. Hameraars hadden het grootste succes rond het moment van laagwater wanneer het sediment goed is uitgedroogd. Hannestijd en

kans op succesvol openen hangen dus niet alleen af van kokkelgrootte en specialisatie, maar ook van het seizoen en het stadium in de getijcyclus. Voor zowel stekers als hameraars nam het prooi profijt sterk toe met de prooigrootte. Op basis van al deze metingen en verbanden konden de waarden in het prooikeuzemodel geschat worden. Volgens de berekeningen zouden zowel hameraars als stekers onder de meeste condities geen Kokkels moeten eten die kleiner zijn dan 15 mm. Het bleek dat stekers zich het gehele seizoen vrijwel volgens verwachting gedroegen. In tegenstelling tot stekers selecteerden de hameraars echter steeds grotere Kokkels in de loop van het seizoen, waardoor de grootte-selectie steeds beter in overeenstemming kwam met de voorspelling van het optimale prooikeuzemodel. In het begin van de winter aten de hameraars volgens de voorspellingen te veel kleine Kokkels. Het zou goed kunnen dat het risico van snavelbreuk hoger is voor hameraars dan voor stekers en dat er meer kracht nodig is om een grote Kokkel open te hameren. Dat zou kunnen verklaren waarom hameraars pas grote Kokkels, die gevaarlijk zijn voor de snavel maar profijtelijk vanwege de energie, gaan eten als hun energiebehoefte hoog is. (BJE)

Received: 24 March 1998, accepted 20 March 2000
Corresponding editor: Bruno J. Ens

Appendix 1. Correcting for observer bias and error in the estimation of cockle size during behavioural observations. A sample of cockles of known size ($n = 50$) were presented for one second at the bill of a life-sized model of an Oystercatcher, at distances of 100-200m from an observer. The size of each cockle was estimated as a percentage of bill-length, and subsequently converted into a size class (see methods). The cells of the table show the probability of a cockle estimated to be size i actually belonging to each size class. Trials were carried out with (a) observer distance = 100m and (b) observer distance = 200m. Data are based on the trial conducted during December 1994, using a sample of 50 cockles of known size, randomly presented for 1s to an observer at distances of 100 and 200m. The probability of a cockle of size class i being correctly estimated as size class i is shown in bold type. Probabilities can be used to estimate the actual number of cockles observed in size class i . For example, the number of cockles of size-class 3 (15-22mm) actually consumed by an Oystercatcher at a distance of 200m is given by: $(0.58 N_2) + (0.07 N_3)$ where, N_2 = number of cockles estimated to be size-class 2 (7-15mm), and N_3 = number of cockles estimated to be size-class 3 (15-22mm).

Observer distance = 100m

Estimated size class (size-range mm)	Actual size class (size range mm)			
	2 (7-15)	3 (15-22)	4 (22-29)	5 (>29mm)
1 (7-15)	0.4	0.57	0.03	0
2 (15-22)	0	0.19	0.81	0
3 (22-29)	0	0	0.94	0.06
4 (>29mm)	0	0	0.5	0.5

Observer distance = 200m

Estimated size class (size-range mm)	Actual size class (size range mm)			
	2 (7-15)	3 (15-22)	4 (22-29)	5 (>29mm)
1 (7-15)	0.37	0.58	0.05	0
2 (15-22)	0	0.07	0.93	0
3 (22-29)	0	0	0.77	0.23
4 (>29mm)	0	0	0.67	0.33