Oystercatchers use colour preference to achieve longer-term optimality

R. Nagarajan¹, J. D. Goss-Custard² and S. E. G. Lea^{1*}

¹*School of Psychology, Washington Singer Laboratories, Perry Road, University of Exeter, Exeter EX4 4QG, UK*

²*Centre for Ecology and Hydrology (CEH), Dorset, Winfrith Technology Centre, Winfrith, Dorchester, Dorset DT2 8ZD, UK*

The optimal diet model entails that foragers look beyond the individual prey encounter, to at least the level of intake rate across a bout of foraging, but optimization over a longer time remains controversial. In this paper, we show how oystercatchers increase their intake over the longer term using mussel colour as a cue. Wintering oystercatchers *Haematopus ostralegus* feed extensively on mussels *Mytilus edulis* in the estuaries of southern Britain. They show a marked preference for brown-shelled mussels over the commoner black-shelled morph, and we show that this enables them to maximize their rate of energy gain over a longer period than a single foraging bout. The brown and black mussels did not differ in ventral thickness and energy content, which are the main criteria for mussel selection and most important for short-term optimization. The brown mussels contained significantly less moisture, so by selecting them, oystercatchers could pack more mussel flesh into their limited oesophageal storage capacity. This enables them to increase their overall consumption during a feeding bout and increases their long-run energy gain rate, to an extent that is large enough to be significant for survival, especially during the short exposure of the mussel beds in winter.

Keywords: optimality; oystercatcher; colour preference; intake rate; mussel; polymorphism

1. INTRODUCTION

Optimal foraging models are successfully used to predict decision making in various animals. For example, rate-maximizing optimality models are successful in predicting prey-size selection by oystercatchers (*Haematopus ostralegus*) in the field (e.g. Zwarts & Drent 1981; Cayford & Goss-Custard 1990; Wanink & Zwarts 2001). Rate maximization, however, is an under-specified term. Over what period should a forager maximize energy capture rate—an individual prey encounter, a foraging bout, a day, a season, or a lifetime? The optimal diet model (Charnov 1976) implies that foragers look beyond the individual prey encounter, at least to the level of intake rate across a bout of feeding, although laboratory experiments suggest that there may be limits on their capacity to do so (Rachlin & Green 1972; Lea 1979). From the point of view of natural selection, however, the rate over quite long periods is most important.

Oystercatchers increase their intake rate by selecting the most profitable size of prey (Sutherland 1982; Meire & Ervynck 1986; Cayford & Goss-Custard 1990) and, perhaps, prey species (Ens *et al.* 1996a). Within a size class, they select the mussels with the thinnest shells, as this reduces handling time and energy expenditure—in addition, presumably, to reducing the risk of damaging their bill (Durell & Goss-Custard 1984; Meire & Ervynck 1986; Sutherland & Ens 1987; Cayford & Goss-Custard 1990). They select buried prey from shallow depths because the profitability of prey decreases with burying depth. They may adjust their search speed according to the detectability of the alternative prey on offer, and thus

regulate their searching efficiency (Ens *et al.* 1996b). With experience, oystercatchers reduce their handling time when eating clams by more rapidly opening the shell and cutting and removing the flesh from it (Wanink & Zwarts 1996). Cutting is always the most time-consuming component of prey handling, but relatively more so when a bird takes a less-preferred prey species. By rapidly improving their cutting technique for a specific prey, the birds increase the profitability with which they can be opened and the overall intake rate (Wanink & Zwarts 1996). There appears, therefore, to be a whole range of choices open to an oystercatcher when selecting which prey items it should take, and the birds' preferences are repeatedly explained in terms of rate maximization. The present paper shows how an apparently trivial preference observed in the field can only be explained in terms of rate maximization beyond the level of the foraging bout.

2. MATERIAL AND METHODS

(a) Study area

The Exe estuary and changes in its oystercatcher population are described, and the location of different mussel beds is shown in detail in Goss-Custard *et al.* (1982). For this study, data were collected from mussel bed 4, which is located on the western side of the estuary, between Starcross and Cockwood (50°37' N, 03°27' W), and is one of the beds that supports a substantial population of ventrally hammering oystercatchers, is free from human disturbance and is easy to access.

(b) Mussel collection and measurements

Once every two weeks, towards the end of the low tidal cycle, a total of 50 fresh mussel shells opened by ventrally hammering oystercatchers were collected. Most of the oystercatchers arrive in September and remain until the following March, hence

* Author for correspondence (s.e.g.lea@exeter.ac.uk).

samples were collected from September 1996 to March 1997. Freshly opened mussel shells can be identified easily from the fresh flesh that remains inside the shell near the attachment of the adductor muscle (Durell & Goss-Custard 1984). For each opened mussel, an unopened mussel of the same length was collected from under nearby weed (oystercatchers select 85% of their mussels from under weed). These are referred to as 'comparator mussels'. The length of each mussel, from anterior tip (umbo) to posterior tip, was measured by using a vernier calliper that was accurate to 0.05 mm. The shell's ventral thickness at the mid-point of the edge of the ventral surface was measured using a Mitutoyo digimatic micrometer that was accurate to 0.001 mm. The colour of the mussel was noted either as brown or black and the shape of the ventral side was identified as either flat or curved; although those two judgements were necessarily subjective, typical differences are large (see Nagarajan 2000, photographs 6 and 7), so the great majority of shells could be classified without hesitation. All shells were retained until the end of the study, so that earlier and later judgements in the few more ambiguous cases could be checked for consistency. The total number of barnacles attached to the mussel on the ventral side that were bigger than 0.5 mm were counted and noted.

(c) *Mussel energy estimation*

The relationship between the mussel length and ash free dry mass (AFDM) was calculated once every two weeks by using the comparator mussels. The AFDM does not differ between fresh and deep-frozen mussels (Goss-Custard *et al.* 1993) and, hence, all the AFDM estimation was done on deep-frozen mussels. As Moreira & Pugh Thomas (1988) found with Baltic tellin *Macoma balthica*, AFDM can be underestimated due to the leakage of liquid cellular material during defrosting, so each mussel was defrosted in a crucible to avoid loss of this material. AFDM was estimated by using the procedures of Cayford & Goss-Custard (1990). The wet flesh weight, dry weight and ash weight were estimated for all the mussels. The ash weight was subtracted from the dry weight to give the AFDM of flesh. The dry flesh weight was subtracted from wet flesh weight to estimate water weight in the flesh.

(d) *Data analysis*

We used multiple regression equations to explore the differences between black and brown mussels. The appropriateness of assumptions such as linearity, homoscedasticity and normality was strictly checked when developing the regression models. As the oystercatchers prefer to open mussels from the right valve (Nagarajan *et al.* 2002), the thickness of the right and left valves were analysed separately. Mussel thickness varies with mussel length and also with season: mussel shells are structurally dynamic with both thinning and thickening occurring during winter (Nagarajan 2000). In order to control for seasonal effects in the multiple regression equations, the number of days elapsed since 1 August 1996 (referred to as 'day') was included in the analysis; as non-monotonic seasonal effects are common, linear, quadratic and, if necessary, cubic terms were used for this variable. Length was included as a linear term. The qualitative information on colour was used as a dichotomous variable (Tabachnick & Fidell 1996) in all the regression equations, coding black as 1 and the rarer brown condition as 2.

3. RESULTS

In the mussel population, 13.6% had brown shells. However, 34.4% of the mussels that the oystercatchers

consumed had brown shells, a significantly higher proportion ($\chi^2 = 64.7$, $p < 0.0001$). One possible explanation for this preference is that, at a given length, a brown mussel is thinner on the ventral side than a black mussel. Regression analysis on the right and left valves of comparator mussels confirmed that brown-coloured mussels were, on average, 0.04–0.05 mm thinner than equivalent black mussels in the population (table 1, set 1). It was also found that the difference between the thickness of black and brown mussels did not change as a function of mussel length or season.

The next question was: Did the oystercatchers use colour as a cue to select thin mussels, or was their apparent selection of brown shells just an incidental consequence of their selection for thin-shelled mussels? To test this hypothesis, mussel shells that had been attacked by oystercatchers and their comparator mussels were compared using a binary logistic regression model. In the binary logistic regression, the dependent variable was the condition of the mussel (opened and comparator), and the independent variables were the measured characteristics, namely, mussel ventral thickness, number of barnacles, mussel colour, ventral shape and mussel length (table 2). These variables were included because oystercatchers are known to prefer ventrally thin mussels, which had fewer barnacles, were brown-coloured and ventrally flat (Nagarajan 2000). The aim of this analysis was to discover which variables have independent effects on the oystercatchers' selection: if, for example, the oystercatchers actually ignored colour and the apparent preference for brown mussels derived simply from the fact that oystercatchers prefer thin-shelled mussels, and brown mussels have thinner shells, then there should be a significant effect of shell thickness but no significant additional effect of colour. Table 2 shows that the regression coefficients for shell length and ventral thickness were significantly greater than zero, as expected, but those for the number of barnacles on the ventral surface and the shape of the ventral surface were not. The coefficient for colour, however, was highly significant. This result shows that only ventral thickness and colour had independent effects on the selection of mussels of a given length. Therefore, oystercatchers did not in fact select brown-coloured mussels simply because they had thinner shells.

It appears, therefore, that the cost, for an oystercatcher of breaking into a brown-shelled mussel (as measured by shell thickness) was no different to the cost of breaking into a black mussel. Perhaps, though, the benefit was greater. To test this hypothesis, we calculated a multiple regression equation in which the AFDM of comparator mussels was regressed against shell colour along with mussel length and season, both of which are known to affect AFDM (Nagarajan 2000). A multiple regression equation, with season and mussel length taken into account, showed that AFDM is most unlikely to differ between the black and brown mussels, and that oystercatchers would obtain the same energetic returns from opening mussels of either colour.

As neither ventral thickness nor energy content accounted for the preference of oystercatchers for brown mussel shells, we explored the possible effect of all the other measured weight variables by using regression, that is, wet flesh (including water weight), water weight in the

Table 1. Regression equation models on comparator mussels to explore the effect of mussel colour on the ventral thickness and wet flesh (including water weight) and water weight of comparator mussels.

set	group	variables	coefficient $\pm$ s.e.	<i>p</i>	model (r^2)	model (<i>p</i>)
1	right ventral thickness (mm) $n = 545$	constant	0.103 ± 0.092	0.265	26.8%	< 0.0001
		colour	-0.05 ± 0.025	0.045		
		length	0.017 ± 0.0014	< 0.001		
		day	0.0048 ± 0.001	< 0.001		
		day ²	$-0.000\ 02 \pm 0.000\ 004$	< 0.001		
	left ventral thickness (mm) $n = 545$	constant	0.21 ± 0.091	0.818	29.9%	< 0.0001
		colour	-0.04 ± 0.024	0.112		
		length	0.019 ± 0.001	< 0.001		
		day	0.005 ± 0.0001	< 0.001		
		day ²	$-0.000\ 02 \pm 0.000\ 004$	< 0.001		
2	mussel wet flesh including water weight (g) ($\log_e$) $n = 543$	constant	-9.2535 ± 0.2537	< 0.0001	86.4%	< 0.001
		colour	$-0.061\ 76 \pm 0.003\ 95$	< 0.001		
		$\log_e$ length	$2.781\ 17 \pm 0.050\ 38$	< 0.0001		
		day	$0.012\ 85 \pm 0.003\ 95$	< 0.01		
		day ²	$-0.000\ 095 \pm 0.000\ 03$	< 0.01		
		day ³	$0.000\ 0002 \pm 0.000\ 000\ 08$	< 0.01		
	mussel water weight in wet flesh (g) ($\log_e$) $n = 543$	constant	-9.5195 ± 0.2684	< 0.0001	85.1%	< 0.001
		colour	$-0.065\ 69 \pm 0.019\ 57$	< 0.001		
		$\log_e$ length	2.7587 ± 0.0533	< 0.0001		
		day	$0.017\ 371 \pm 0.004\ 179$	< 0.0001		
		day ²	$-0.000\ 126 \pm 0.000\ 033$	< 0.0001		
		day ³	$0.000\ 0003 \pm 0.000\ 000\ 08$	< 0.001		

Table 2. Binary logistic regression equation to explore the factors that influence mussel selection by oystercatchers. (Dependent variable is status of mussel, coded 1, comparator mussel; 2, opened mussel.)

variable	coefficients	<i>p</i>
constant	1.51 ± 0.755	0.046
ventral thickness	-6.13 ± 0.494	0.000
colour (1, black; 2, brown)	1.13 ± 0.177	0.000
number of barnacles on the ventral surface	-0.006 ± 0.086	0.942
ventral shape (1, flat; 2, curved)	-0.265 ± 0.264	0.333
length	0.746 ± 0.151	0.000
log-likelihood = -600.197; $G = 285.6$; d.f. = 5; $p < 0.0005$		

flesh, dry flesh weight and ash weight. The analysis showed that the dry weight and ash weight of brown and black mussels did not differ. However, the wet weight (flesh with water) and water weight were less in brown than in black mussels (table 1, set 2). By selecting mussels with brown shells, therefore, oystercatchers consumed less water with a given amount of energy than they would do by taking black-shelled mussels. Could this be an advantage that might drive the observed colour preference?

The capacity of the oesophagus of oystercatchers is 80 g wet weight, which is equivalent to 12 g dry weight (Kersten & Visser 1996). After a prolonged feeding bout, oystercatchers must stop feeding when their intake rate exceeds their gut processing rate (Zwarts & Dirksen 1990), and the storage capacity of the oesophagus has been reached. The daily consumption of oystercatchers varies from 36 to 50 g of dry weight (Zwarts *et al.* 1996), which they obtain by feeding for three to four bouts, interrupted by 'digestive pauses'. The length of the bout depends, of course, on the quantitative relationship between the instantaneous intake rate and the gut processing rate; the bout is shorter when the intake rate is high than when it

is low because the storage capacity of the gut, including the oesophagus, is more rapidly reached. By selecting mussels with a lower water content, the birds might be able to obtain more energy in a bout of given duration and thus reduce overall foraging time per 24 h by a significant amount.

Table 3 compares the amount of water consumed by a bird that fed either on brown mussels or on black mussels for one foraging bout, during which it was able to consume 80 g wet flesh weight before its storage capacity was fully reached. By eating only the brown-coloured mussels, oystercatchers would be able to consume at least one extra mussel within the consumption limit of 80 g of wet flesh weight for one foraging bout. Oystercatchers could avoid ingesting between 7.8 and 10.9% excess water during a foraging bout, depending on the length classes of mussels that they were taking. By avoiding taking in excess water, the oystercatchers could pack more mussel flesh into the available oesophageal storage capacity and thus increase their overall consumption rate of energy over the feeding bout. The percentage increase in the consumption of energy associated with eating brown-coloured mussel was

Table 3. The mean difference in wet flesh weight, water weight and AFDM in 80 g of wet flesh between black- and brown-coloured mussels.

(The column 'diff.' shows the difference between the black- and brown-coloured mussels. Values are means $\pm$ s.d.)

size class (mm)	colour	wet flesh with water weight (g)	diff. (%)	water weight in the flesh (g)	diff. (%)	no. of mussels = 80 g wet flesh weight	AFDM in 80 g wet flesh (g)	diff. (%)
35–40	black	3.81 $\pm$ 0.07	7.1	3.33 $\pm$ 0.07	7.8	21.1	8.56	1.99
	brown	3.57 $\pm$ 0.19		3.09 $\pm$ 0.16		22.4	8.73	
40–45	black	5.19 $\pm$ 0.10	6.3	4.50 $\pm$ 0.09	7.2	15.4	9.92	5.72
	brown	4.82 $\pm$ 0.17		4.15 $\pm$ 0.15		16.6	9.43	
45–50	black	6.81 $\pm$ 0.08	4.7	5.93 $\pm$ 0.07	6.2	11.7	8.63	12.6
	brown	6.49 $\pm$ 0.21		5.56 $\pm$ 0.18		12.3	9.72	
50–55	black	8.69 $\pm$ 0.16	11.5	7.55 $\pm$ 0.15	10.9	9.2	8.71	17.7
	brown	7.69 $\pm$ 0.49		6.73 $\pm$ 0.48		10.5	10.3	

2.0, 5.7, 12.6 and 17.7% for 35–40, 40–45, 45–50 and 50–55 mm long mussels, respectively (table 2). However, the oystercatchers showed a preference of 34.4% towards brown-coloured mussels, while in the mussel population, only 13.6% were brown coloured. Hence, we have calculated the intake improvement for the actual proportion of brown-coloured mussels that was consumed in different size classes compared to eating at random. The intake improvement was 0.41% for the 35–40 mm size classes, 1.2% for 40–45 mm, 2.6% for 45–50 mm and 3.8% for 50–55 mm. Although oystercatchers could not increase their instantaneous rate of energy intake rate while foraging by preferentially taking brown-coloured mussels, they were able to consume more energy over the whole feeding bout because more of their storage capacity was occupied by energy-containing flesh than water. But as brown-coloured mussels were rare in the mussel population on the mussel bed, the oystercatchers would not have been able to search continuously for them. Rather, we suggest that they took them opportunistically whenever they encountered a suitable one, and consumed such mussels even though the shells may have been thicker than that of a black-coloured mussel of a similar size. If oystercatchers do use this strategy, they would be more likely to pick up and subsequently reject brown than black mussels (not an uncommon behaviour); it would be possible to test this by field observations, but this has not yet been attempted.

4. DISCUSSION

Durell & Goss-Custard (1984) found that the proportion of brown-coloured mussels gradually decreased with mussel length in mussels less than 40 mm long, and did not find any brown-coloured mussels more than 40 mm in size. Because length is quite strongly related to the age of the mussel (McGrorty & Goss-Custard 1991), the colour may be associated with age. However, in our sample, a considerable number of brown-coloured mussels was found in the larger size classes (40–60 mm); 16% for 40–45 mm, 12% for 45–50 mm, 6% for 50–55 mm and 3% for 55–60 mm. Hence, we suspect that shell colour is not associated with the age of the mussel. Rather, the steady decline in the proportion of brown-coloured mussels with increasing size class could be due to the oystercatchers' preferential predation on brown-coloured

mussels, such that most brown ones have been removed by the time they reach *ca.* 40 mm long.

Although this explanation might account for the absence of brown mussels amongst the large mussels of the Exe, it does not explain why the different shell colour forms arise in the first place. It is important to consider the origins of these differences, as they might be related to nutritionally relevant differences. One possibility is that different shell colours indicate the presence of two subspecies. However, there is no subspecific difference between the two colours of mussel: both are classified as *Mytilus edulis* (Tebble 1966), so the colour difference should presumably be regarded as a polymorphism. All colours, other than white, are laid down in the shell or its periostracum as pigments that are also present in the soft parts. Sunlight and warmth, a food-rich environment and areas rich in corals are the factors that produce the most colourful shells in molluscs. Warm-water shells are generally more brightly coloured than those from cold waters (Dance 1974), but there seems to be no known basis for suggesting that brown shell colour reflects anything that could make mussels nutritionally advantageous, other than the water-content difference that has been identified in the present study.

Several previous studies have investigated colour preferences in waders feeding on molluscs. For example, Sorensen & Lindberg (1991) investigated the preferential predation by American black oystercatchers (*H. bachmani*) on transitional ecophenotypes of the limpet *Lottia pelta* (Rathke). They described three ecophenotypic forms (rock, *Eggregia* and *Mytilus*) of the limpet *L. pelta* and found that the *L. pelta* that changed substrata, occurred to a significantly higher extent in the oystercatchers' diet. When these ecophenotypes move among substrata, their shell colour changes to match the substratum, making the limpet more difficult to locate for visual predators. But sometimes when the limpets move to a new environment with different pigments, a transitional form will result because of the older portion of the shell. They speculated that this transitional shell often provides a strong contrast between the substratum and limpet, a 'bull's eye' effect that may make prey more obvious to visual predators. By contrast, Schneider (1982) observed the ruddy turnstone's (*Arenaria interpres*) predation on the polymorphic clams (*Donax variabilis*) at Sanibel Island in Florida, but there

was no significant difference between the morphs on predation by birds.

The oystercatchers' preference for brown-coloured mussels does not result in any increase in instantaneous net energy intake rate. It does, however, allow longer foraging bouts, and thus a higher prey capture rate across the day. It thus represents an adaptation, whether innate or learned, that allows the birds to achieve the maximum intake rate across a longer time horizon than has hitherto been thought possible. This argument is necessarily inferential, and to test it would require interventions to examine the oesophageal contents of oystercatchers feeding on different kinds of mussel, which would not be practicable under field conditions. However, other studies have shown that optimal foraging models that take into account digestion rate constraints can predict behaviour successfully (e.g. studies of dogwhelks *Nucella lapillus* foraging on mussels by Burrows & Hughes (1991a,b)).

In the model by Burrows & Hughes (1991b), it is assumed that physiological state variables can change the behaviour of animals (see also Houston & McNamara 1999). Although this is obviously reasonable, to include such variables in foraging models, we need to know how they influence both energy expenditure and the animal's ability to survive. It has already been shown that the oesophageal volume is a constraint for foraging oystercatchers (Zwarts & Dirksen 1990; Kersten & Visser 1996), and in this paper, we show one way by which oystercatchers can change their behaviour (by preferring brown-coloured mussels) to reduce the impact of this physiological constraint. As we have shown, the effect is large enough to have survival value in winter, which is an energetically expensive period and some oystercatchers die of starvation (Goss-Custard *et al.* 1996), especially when natural calamities, such as gales and floods, further reduce the time for which tidal areas are exposed (Goss-Custard & Durell 1983).

R.N. gratefully acknowledges the Commonwealth Commission, UK, and Ministry of Human Resources Development, Government of India, for funding. We thank Catriona Ryan and Ian Hocking for comments and Rachel Kirby for computer assistance.

REFERENCES

- Burrows, M. T. & Hughes, R. N. 1991a Optimal foraging decisions by dogwhelks, *Nucella-lapillus* (L): influences of mortality risk and rate-constrained digestion. *Funct. Ecol.* **5**, 461–475.
- Burrows, M. T. & Hughes, R. N. 1991b Variation in foraging behavior among individuals and populations of dogwhelks, *Nucella-lapillus*: natural constraints on energy intake. *J. Anim. Ecol.* **60**, 497–514.
- Cayford, J. T. & Goss-Custard, J. D. 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.
- Dance, S. P. (ed.) 1974 *The collector's encyclopaedia of shells*. New York: McGraw-Hill.
- Durell, S. E. A. le V. dit & Goss-Custard, J. D. 1984 Prey selection within a size-class of mussels, *Mytilus edulis* by oystercatchers *Haematopus ostralegus*. *Anim. Behav.* **32**, 1197–1203.
- Ens, B. J., Dirksen, S., Smit, C. J. & Bunscoke, A. J. 1996a 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.
- Ens, B. J., Bunscoke, E. J., Hoekstra, R., Hulscher, J. B., Kersten, M. & De Vlas, S. J. 1996b 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**, 73–90.
- Goss-Custard, J. D. & Durell, S. E. A. le V. dit. 1983 Individual and age differences in the feeding ecology of oystercatchers, *Haematopus ostralegus*, wintering on the Exe. *Ibis* **125**, 155–171.
- Goss-Custard, J. D., Durell, S. E. A. le V. dit, McGrorty, S. & Reading, C. J. 1982 Use of mussel *Mytilus edulis* beds by oystercatchers *Haematopus ostralegus* according to age and population size. *J. Anim. Ecol.* **51**, 543–554.
- Goss-Custard, J. D., West, A. D. & Durell, S. E. A. le V. dit. 1993 The availability and quality of the mussel (*Mytilus edulis*) prey of oystercatchers (*Haematopus ostralegus*). *Neth. J. Sea Res.* **31**, 419–439.
- Goss-Custard, J. D., Durell, S. E. A. le V. dit, Goater, C. P., Hulscher, J. B., Lambeck, R. H. D., Meininger, P. L. & Urff, J. 1996 How oystercatchers survive the winter. In *The oystercatchers from individuals to population* (ed. J. D. Goss-Custard), pp. 133–154. Oxford University Press.
- Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour: an approach based on state*. Cambridge University Press.
- Kersten, M. & Visser, W. 1996 The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. *Funct. Ecol.* **10**, 440–448.
- Lea, S. E. G. 1979 Foraging and reinforcement schedules in the pigeon: optimal and non-optimal aspects of choice. *Anim. Behav.* **27**, 875–886.
- McGrorty, S. & Goss-Custard, J. D. 1991 Population dynamics of the mussel *Mytilus edulis*: spatial variations in age-class densities of an intertidal estuarine population along environmental gradients. *Mar. Ecol. Prog. Ser.* **73**, 191–202.
- Meire, P. M. & Eryvynck, A. 1986 Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? *Anim. Behav.* **34**, 1427–1435.
- Moreira, H. M. & Pugh Thomas, M. 1988 The effect of deep freeze storage and subsequent thawing on *Macoma balthica* and its implication for energy related ecological studies. *J. Environ. Biol.* **9**, 417–428.
- Nagarajan, R., Lea, S. E. G & Goss-Custard, J. D. 2002 Mussel valve discrimination and strategies used in valve discrimination by oystercatchers *Haematopus ostralegus*. *Funct. Ecol.* **16**. (In the press.)
- Rachlin, H. & Green, L. 1972 Commitment choice and self-control. *J. Exp. Anal. Behav.* **17**, 15–22.
- Schneider, D. 1982 Predation by ruddy turnstones (*Arenaria interpres*) on a polymorphic clam (*Donax variabilis*) at Sanibel Island, Florida. *Bull. Mar. Sci.* **32**, 341–344.
- Sorensen, F. E. & Lindberg, D. R. 1991 Preferential predation by American black oystercatchers on transitional ecophenotypes of the limpet *Lottia pelta* (Rathke). *J. Exp. Mar. Biol. Ecol.* **154**, 123–136.
- Sutherland, W. J. 1982 Do oystercatchers select the most profitable cockles? *Anim. Behav.* **30**, 857–861.
- Sutherland, W. J. & Ens, B. J. 1987 The criteria determining the selection of mussels *Mytilus edulis* by oystercatchers, *Haematopus ostralegus*. *Behaviour* **103**, 187–202.
- Tabachnick, B. G. & Fidell, L. S. 1996 *Using multivariate statistics*. New York: HarperCollins.
- Tebble, N. 1966 *British bivalve seashells*. London: The British Museum (Natural History).
- Wanink, J. H. & Zwarts, L. 1996 Can food specialization by individual oystercatchers *Haematopus ostralegus* be explained

- by differences in prey specific handling efficiencies? *Ardea* **84A**, 177–198.
- Wanink, J. H. & Zwarts, L. 2001 Rate-maximizing optimality models predict when oystercatchers exploit a cohort of the bivalve *Scrobicularia plana* over a 7-year time span. *J. Anim. Ecol.* **70**, 150–158.
- Zwarts, L. & Dirksen, S. 1990 Digestive bottleneck limits the increase in food intake of Whimbrels preparing to migrate from the Banc d'Arguin, Mauritania. *Ardea* **78**, 257–278.
- Zwarts, L. & Drent, R. H. 1981 Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). In *Feeding and survival strategies of estuarine organisms* (ed. N. V. Jones & W. J. Wolff), London: Plenum.
- Zwarts, L., Cayford, J. T., Hulscher, J. B., Kersten, M., Meire, P. M. & Triplet, P. 1996 Prey size selection and intake rate. In *The oystercatchers from individuals to populations* (ed. J. D. Goss-Custard), pp. 30–55. Oxford University Press.