

DO OYSTERCATCHERS SELECT THE MOST PROFITABLE COCKLES?

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Abstract. The profitability (energy content per second of handling time) of cockles, *Cerastoderma edule*, to oystercatchers, *Haematopus ostralegus*, increases with cockle size. In accordance with the predictions of optimal foraging theory, oystercatchers selected the more profitable (i.e. larger) cockles. The percentage abandoned at the different sites increased with the mean size taken, suggesting that attacks on large cockles were less likely to be successful. Oystercatchers use some visual cues to find prey during the day, but use only tactile cues at night. They take smaller prey at night, with a flesh content 25% less than those taken during the day.

A predator faces an array of prey differing in energy content and handling times. The profitability of a prey type can be expressed in terms of the energy gained per second spent handling the prey (MacArthur & Pianka 1966; Charnov 1976). A major assumption of optimal foraging theory is that predators can distinguish between prey of differing profitabilities and select the more profitable ones. In this paper I describe a test of this assumption.

Oystercatchers, *Haematopus ostralegus*, and cockles, *Cerastoderma edule*, provide an excellent opportunity for studying the factors affecting size selection. The cockles present in the mud can be easily sampled and measured (Boyden 1972), and the shells of predated cockles can be collected from the surface. Although oystercatchers feed on a wide range of prey items, individual birds in winter usually specialize on only one prey type (Goss-Custard et al. 1980); as the birds under study were cockle-specialists it was possible to ignore all other prey species.

Methods

Cockles Eaten

Twelve sites were marked out on the mudflats at Traeth Melynog, Anglesey (for details see Sutherland, in press a). Eleven of these sites were 100 m square but one was smaller (100 × 50 m) to ensure that conditions were uniform within the site. At low tide I collected samples of cockle shells attacked by oystercatchers. Cockles which have been opened by oystercatchers since the last high tide can be recognized because they have a characteristic position (valves separated by about 90° and the shell slightly submerged), they are surrounded by footprints where the bird has been struggling to prise open the valves,

and they contain shreds of torn adductor muscle. Shells of opened cockles were collected along a parallel series of transects, each 2 m apart. Collection was done either at low tide or after the oystercatchers had deserted a feeding site, whichever was the earlier. Checks failed to locate any more cockles, suggesting that there was no bias such as might occur if I noticed large ones more readily. All the collected cockles were measured. At one site the shells of those cockles that had been eaten at night were collected at dawn on those nights when dawn and low tide coincided.

Cockles Available and their Ash-free Dry Weight

The cockles were sampled from each site. Ten random 0.1-m² samples were taken from each site, or 20 samples in those sites with low cockle densities (below 100 cockles per m²). For each sample, a 0.1-m² core was inserted into the mud and the top 10 cm dug out — no cockles were ever found deeper than 5 cm. The sample was washed through a sieve of 7 × 7-mm mesh. In early December and early February 40 cockles, of as wide a size range as possible, were taken from each observation site; their lengths were measured and their ash-free dry weight determined (as in Sutherland, in press a).

Handling Times and Rate Taken

For each site, the number of cockles taken in 10 min was recorded and the handling time of each cockle noted (measured as the time elapsing between the moment that an oystercatcher found a cockle and the moment when the bird resumed searching or in some way changed its behaviour). For analysis, the cockles were divided into five size classes: 8–17.9 mm, 18.0–21.9 mm, 22.0–25.9 mm, 26.0–29.9 mm, and 30 + mm. For each site, the rate at which each size class was taken was calculated as the product of the feed-

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ing rate for that site (expressed in terms of search time) and the proportion of each size class taken.

Results

To estimate the profitability of a given-sized cockle it is necessary to know the energy content and handling time. The flesh content of cockles increases supraproportionately with length (Kristensen 1957; Hancock & Franklin 1972). A typical example of the change in ash-free dry weight with length is given in Fig. 1a. Figure 1b shows that mean handling time increased with mean length taken, where each point refers to a different observation site. I have assumed this relationship holds for different-sized cockles

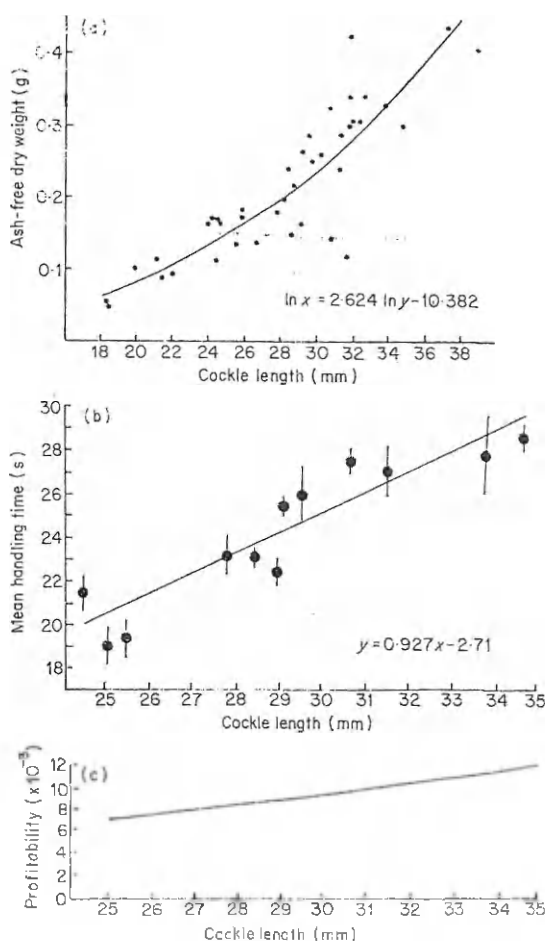


Fig. 1. Relationship between cockle length and (a) ash-free dry weight (all data from one site at Traeth Melynog), (b) handling time \pm SE (each point refers to one site), and (c) profitability, expressed as (a) divided by (b).

within a site. Dividing the energy content (estimated for each site) by the handling time (from Fig. 1b) gives an estimate of profitability of each size class for each site and shows that the largest cockles have the highest profitability (Fig. 1c). The flesh content of cockles varies between sites (Sutherland, in press a) and consequently there is a different relationship between profitability and size for each site. However in all 12 sites the ash-free dry weight increased far more steeply than handling time, so within the size range studied the largest cockles had the highest profitability. It is possible that extremely large cockles have exceedingly high handling times and thus that profitability does not increase consistently with size. There is no indication that this occurs (Fig. 1b) and so it is only likely to apply to cockles well over 35 mm—which in most sites were very scarce.

If oystercatchers behave according to the predictions of optimal foraging theory they should prefer the largest cockles because they are the most profitable. Comparing the sizes taken by oystercatchers with those present in the mud shows that oystercatchers do take a disproportionate number of large cockles (Fig. 2; see also Fig. 6). But this may be because large cockles are more available and so easier to find rather than because they are preferred.

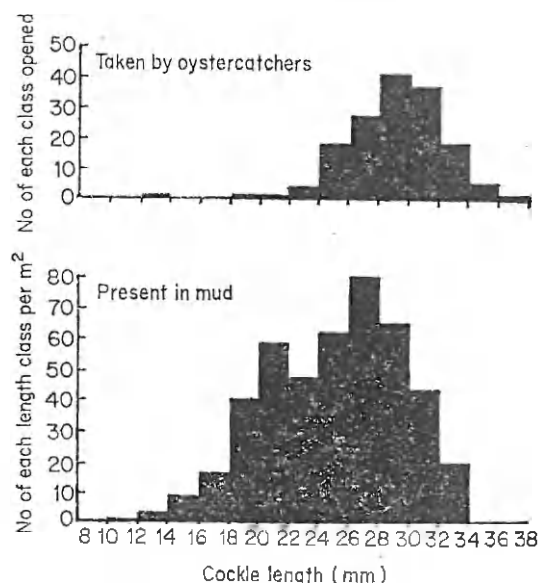


Fig. 2. The size of cockles taken by oystercatchers at one site and their density in the mud.

Preference can be separated from availability if the feeding rate on given cockle sizes is measured over a range of prey densities. If the predator shows a true preference then: (a) the most profitable prey should be taken whenever it is encountered: hence there should be a good correlation between the rate at which it is taken and its density in the mud; and (b) when choice is restricted, less profitable prey may also be taken — but whether this happens is unaffected by their own density (Charnov 1976). Hence a poor correlation is expected between the rate at which less profitable prey are taken and their density in the mud (Goss-Custard 1977a). Thus the correlation coefficient between rate taken and density in the mud (see Fig. 3) can be used as a measure of preference. The correlation

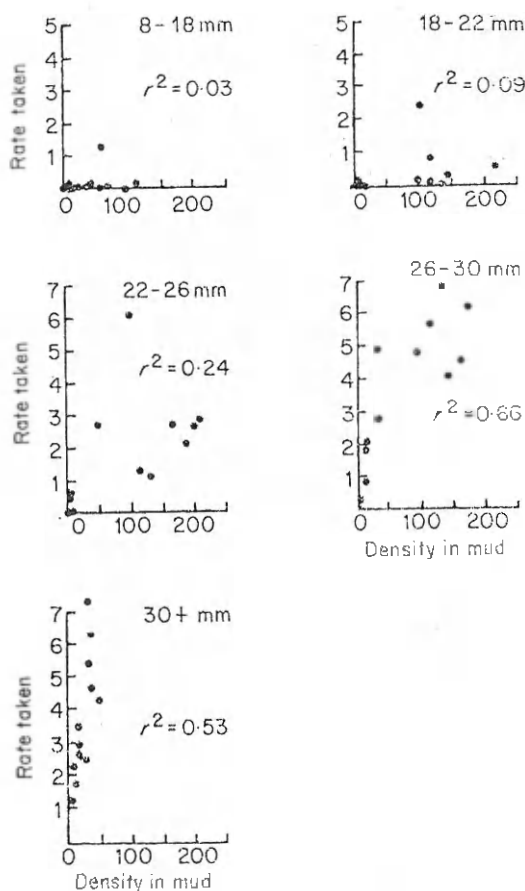


Fig. 3. The rate at which each of five cockle size classes is taken (per 10 min searching) in relation to its density in the mud (per m^2).

coefficient was found to increase with prey size (Fig. 4), showing that the largest cockles are preferred. The largest size class does not have the highest correlation coefficient, but the difference from the 26.0–29.9-mm class is not significant ($P > 0.1$). Larger cockles have a steep relationship between rate taken and density (Fig. 4), which confirms that a disproportionate number of large ones is being taken.

Some cockles were rejected once captured. Some of these appeared trapped on the end of the beak: the bird would then flick the beak to dislodge the cockle. The percentage abandoned after being extracted at the different sites varied between 0 and 9% and increased with the mean size taken (Fig. 5), suggesting that attacks on large cockles were less likely to be successful. As only a small proportion were abandoned, and these were never handled for more than three seconds, the influence on profitability should be negligible.

Night Feeding

Observations with an image intensifier showed that oystercatchers at Traeth Melynog feed as actively at night as during the day (Sutherland, in press b), but the feeding behaviour differs. During the day oystercatchers walk slowly forwards pecking intermittently at the ground, while at night they often use a sewing-machine-like action, a difference found also in captive oystercatchers by Hulscher (1976). This switch

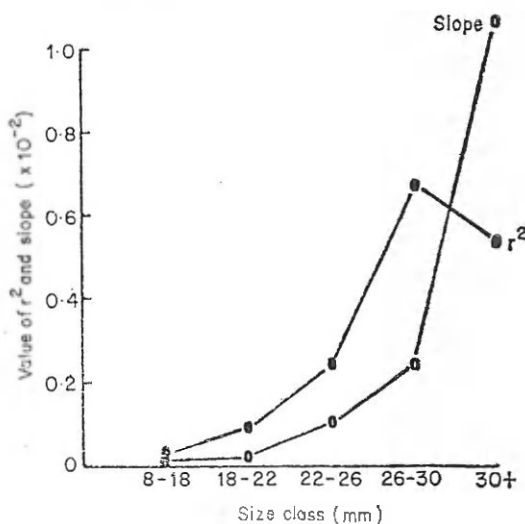


Fig. 4. The values of slope and r^2 for each of the graphs in Fig. 3 for each size class.

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in behaviour suggests that oystercatchers feed by touch at night yet use some visual cues during the day. Further indications of the latter are that birds sometimes reorientate themselves before pecking and take many paces between pecks.

Figure 6 shows that oystercatchers feeding at night take fewer large cockles than when feeding during the day. The means are significantly different ($P < 0.001$, Mann-Whitney U -test). Foraging by sight enables oystercatchers to find many of the large cockles (15% of the diet consisted of cockles larger than any found in the $20 \times 0.1\text{-m}^2$ samples). During the night the sewing-machine-like action must reduce the proportion of large cockles that are found.

The considerable increase in energy content with size makes the largest cockles highly profitable, and combining the data from Fig. 6 with the curve of energy content against cockle length shows that the cockles taken at night have on average an energy content 25% lower than that of cockles taken during the day. Moreover, as cockles are taken only half as fast as during the day (Sutherland, in press b), the biomass intake during the night is three-eighths of that during the day.

Discussion

All cockles are likely to have approximately the same nutrient composition, so maximizing energy intake will inevitably also maximize intake of protein, for example. Thus, although

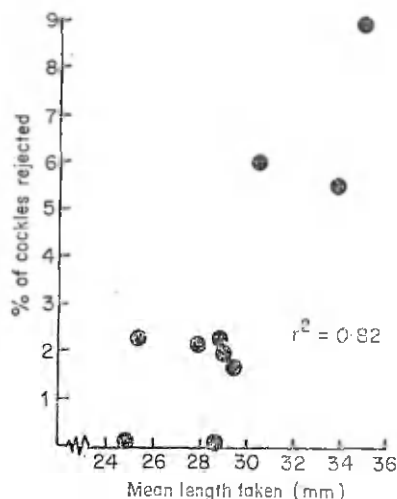


Fig. 5. The percentage of cockles extracted from the mud but then rejected in relation to mean size taken.

the results are expressed in terms of energy, it is clear that this is not necessarily the only consideration.

Optimal foraging theory assumes the ability to distinguish between prey of differing profitabilities, the predator then selecting the more profitable ones. As profitability of cockles at Traeth Melynog increased with size, large ones should have been preferred, and a disproportionate number was indeed taken. Furthermore, there was a strong correlation between the rate at which large cockles were taken and their density in the mud, suggesting that large ones are taken whenever encountered. The comparable correlations for smaller cockles were poorer, suggesting that other factors, such as the abundance of large cockles, were also important.

Field tests on redshanks, *Tringa totanus*, (Goss-Custard 1977a), pied wagtails, *Motacilla*

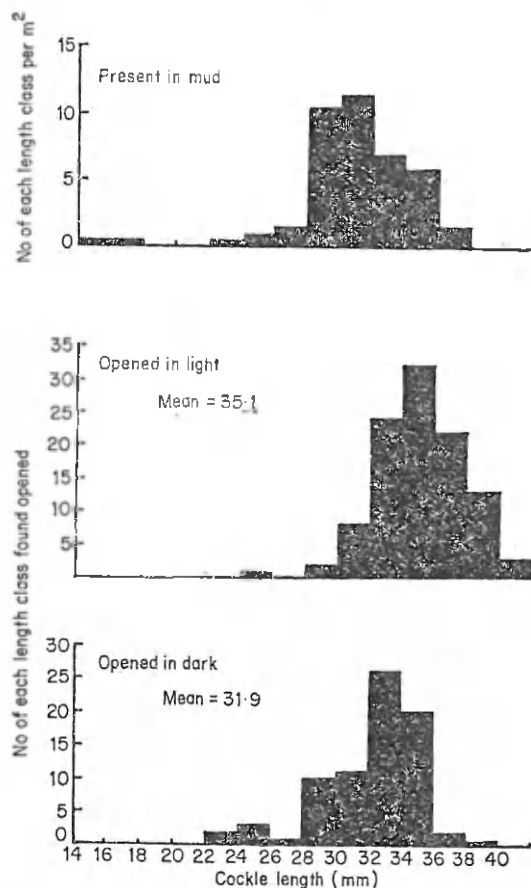


Fig. 6. The sizes of cockles taken during daylight and night, and those present in the mud (for one site only).

a, (Davies 1977) and chipping sparrows, *izella passerina*, (Pulliam 1980) showed that disproportionate number of the profitable prey as were taken. However, some highly profitable (in terms of energy intake) species of seeds are under-represented in the diet of chipping sparrows, and Pulliam (1980) attributed this to differences in chemical composition. Goss-stard (1977b) showed redshanks to prefer amphipod *Corophium volutator* to worms although worms provide a higher energy intake.

Optimal foraging theory predicts that for each prey type it is either worth attacking every one encountered or none of them (Charnov 1976). But in this study, as in other studies, the predators always took some of the less profitable prey (Davies 1977; Krebs et al. 1977; Goss-stard 1980). There are a number of possible explanations for this discrepancy. Predators may continually sample all prey sizes to confirm they have made the right decisions (Krebs et al. 1977). They may mistake some less profitable prey for profitable ones (Hughes 1979). Alternatively, the optimal solution may vary between days, or between patches, so that under some conditions they take all of a particular prey class encountered and under other conditions they take none. Averaging such data will make it appear that individual birds are following an intermediate solution.

These results, along with other studies, suggest that predators select the most profitable prey, but give no indication of the means of selection. Predators may either assess the profitability of each prey type and take the most profitable, or they may have evolved a crude rule—such as attack the largest prey—which will usually produce the optimal diet.

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