A FIELD TEST OF THE ACCURACY OF ESTIMATING PREY SIZE-SELECTION IN OYSTERCATCHERS FROM RECOVERED MUSSEL SHELLS

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The extent of bias in the finding by an observer of mussel Mytilis edulis L. shells opened by Oystercatchers Haematopus ostralegus was studied. In a field test, an untrained observer searched for empty shells of different size which had been placed in one of three orientations on a mussel bed. Both the size and orientation of mussels affected the ease with which they were found. Small mussels were under-represented and large mussels over-represented in recovered samples for two of the three conditions studied. Shell recoveries would have over-estimated the average biomass of mussels eaten by Oystercatchers by as much as 61% in April when birds took very small mussels, but as little as 5% in November, when larger mussels

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INTRODUCTION

Many field studies of foraging in birds require the observer to make quantitative measures of the sizes of individual prey included in the diet. These measures are the basis for measuring intake rates (Goss-Custard *et al.* 1984), size selection (Ens 1982, Sutherland 1983), optimization (Goss-Custard 1977, Sutherland 1982, Thompson & Barnard 1984), prey depletion (Zwarts & Drent 1981), and interference (Ens & Goss-Custard 1984, Goss-Custard & Durell 1987).

In the majority of field studies it is not possible to measure prey sizes directly so an indirect approach is adopted. Several published studies have estimated prey size against bill length directly (Ens 1981, Goss-Custard *et al.* 1984, Thompson & Barnard 1984). Others have used shell recoveries to estimate prey size-selection in waders (*e.g.* Drinnan 1957, Sutherland 1982, Speakman 1984). In cases where shells are highly visible (*e.g.* cockles on the surface of sand, Sutherland 1982) there is no reason to doubt the validity of the results obtained from this technique. Recoveries of mussels from mussel beds are, however, likely to be biased towards the most visible shells, but the extent of this bias has not been measured. This paper describes the results of an experiment in which mussel shells of different size were placed in different orientations within a specified area of mussel bed, and subsequently recovered by an untrained observer.

METHODS

Prey

Mussels spanning the size range taken by Oystercatchers (10-60 mm) were collected on the Exe Estuary, South Devon. The flesh from each mussel was removed without breaking the hinge that joined the two halves together. Mussels were sorted into one of 5 size classes (10-20 mm, 21-30 mm, 31-40 mm, 41-50 mm and 51-60 mm) with a total of 20 mussels in each size class. Three complete series of 100 mussels were prepared in this way. All mussels were marked on the inside of the right valve with an indelible marker pen so that they could be distinguished from any other shells found during the experiment. A different coloured marker was used for each series.

Experimental procedure

Each complete series of shells was placed by an assistant in random sequence within an area of mussel bed measuring 7×7 m. For each series of 100 shells the presentation was as follows:

Condition 1. ("Carried Mussels") Each mussel was taken in turn and dropped onto the surface of the mussel bed from a height of approximately 20 cm.

<u>Condition 2. ("Buried Mussels")</u> Each mussel was pushed roughly into the surface of the mussel bed leaving approximately half the shell visible.

<u>Condition 3. ("In-situ Mussels")</u> Each mussel was placed ventral side down on the surface of the mussel bed.

Each condition was an attempt to simulate one of the three feeding techniques used by individual Oystercatchers (see Norton-Griffiths 1968, Goss-Custard & Sutherland 1984). Birds which stab their bill between the valves of mussels (stabbers) and those which hammer into the ventral side of mussels (ventral hammerers) carry a large proportion of their prey (condition 1); whereas dorsal hammerers direct blows at mussels in-situ (condition 3). Both stabbers and hammerers (dorsal & ventral), occasionally push mussels into the mud when removing the flesh, leaving them partly or completely buried (condition 2).

All 300 mussels were placed in the experimental area in my absence. When all the shells had been deposited, I entered the experimental area and systematically searched it for mussel shells. Each shell I found was placed in a separate polythene bag for storage and later allocated to one of the three conditions using the coloured markers. Eight shells located without a coloured mark were excluded from the analysis. The experimental plot was

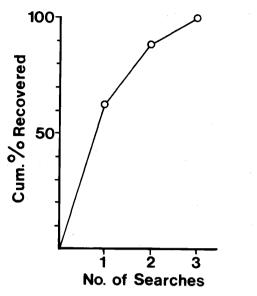


Figure 1. The proportion of total shell recoveries found in each successive search of the experimental plot.

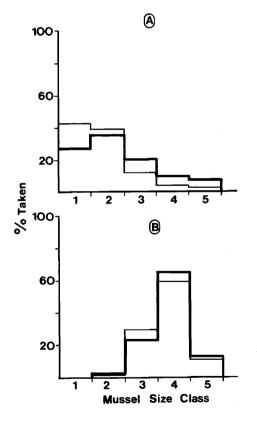


Figure 3. Comparison of the sizes of mussel taken* by stabbers on the Exe with the results which would have been obtained from the recovery of empty shells**.

A) April, B) November, (-) actually taken, (--) predicted from shell-recoveries. * based on observations of birds where mussel length was estimated against bill length and then corrected for my individual bias (see data for observer 2 in Goss-Custard *et al.* 1987). ** based on data for "carried" mussels in Figure 2. Sample sizes (n) are April 170, November 184.

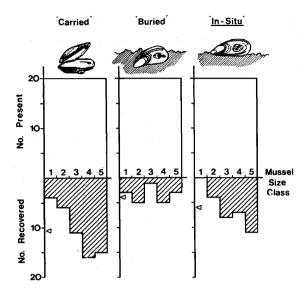


Figure 2. The number of mussel shells of different length recovered in each of the three conditions. Upper (open) histograms show the number of shells of each size class placed on the mussel bed. Lower (hatched) histograms show the number of each size class recovered. (<) is the expected number of recoveries in each size-class, based on the total number of recoveries in each condition. Size classes are 1-5 mm, 10-20 mm, 21-30 mm, 31-40 mm, 41-50 mm and 51-60 mm.

systematically searched three times in succession over a period of 115 minutes. The decision to give up searching was made when the trampling of the mussel bed made further efforts unprofitable.

RESULTS

The rate at which shells were found declined with successive searches of the experimental plot (Figure 1). As there was no time limit to the experiment the total number of recoveries was determined solely by my ability to discriminate empty shells from living mussels. A total of 99 mussels were recovered, giving an overall recovery success of 33%. Shells in the "carried" condition were easiest to find (52% recovered) and shells in the "buried" condition were most difficult to find (17% recovered) (Figure 2). Pooling the results for the three conditions, there was a significant overall difference between the proportion of mussels of each size-class recovered and that predicted from a random recovery of size-classes (x^2 =11.58, d.f.=4, P<0.01). The tendency to under-represent small mussels and over-represent large mussels in recoveries, was evident in the "carried" (x^2 =10.87, d.f.=4, P<0.05) conditions, but not in the "buried" condition (x^2 =3.27, d.f.=4, n.s.). There were no significant differences between the proportion of mussels of each size-class recovered in the three conditions with that expected (x^2 =11.75, d.f.=(n.s.).

The results clearly show that recoveries of mussel shells are biased, but is this bias great enough to really make any difference to estimates of size-selection or energy intake in Oystercatchers? I tested this by comparing the distribution of size-classes that I observed taken by stabbers on the Exe, with the results that would have been obtained had I collected a similar sample of empty shells (see Figure 3

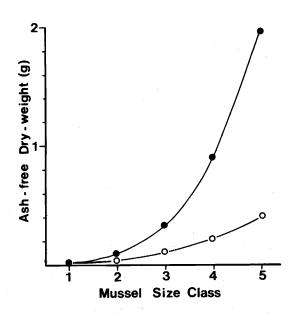


Figure 4. The biomass in each size-class for April(O) and November(O).

Values are derived from regression equations: April Log Y = -5.13 (± 0.05) + 2.72 (± 0.03) Log X, n=36, r²=0.89, p(0.001; November Log Y = -6.26 (± 0.05) + 3.76 (± 0.03) Log X, n=37, r²=0.93, p(0.001, where X is mussel length (mm) and Y is ash-free dry weight (g).

for details of methods). I chose November (when stabbers took predominantly large mussels) and April (when they switched to smaller prey) as the two months in which to make the comparisons, since these showed the extremes in the birds observed size selection (Cayford 1988). Shell-recoveries in November would have underestimated the proportion of medium (31-40 mm) mussels in the diet by 21% and over-estimated the proportion of larger (41-50 mm) mussels by 10% (Figure 3b). Because stabbers avoided the two smallest classes and took very few large mussels, shell recoveries gave a good approximation to the birds true selection. In April, the results from shell-recoveries were less reliable (Figure 3a). The smallest class (10-20 mm) was underestimated by 38% and the largest class (although rarely taken) overestimated by 133%. Because of the curvilinear relationship between mussel length and energy content, relatively small differences in the proportions of different size-classes taken can lead to serious errors in estimates of energy intake. I calculated the average biomass (ash-free dry weight) of mussels in each of the five size-classes from regression equations of log length vs log AFDW (see Figure 4). By combining the data in Figure 3 and Figure 4, I calculated the average biomass of mussels taken by the birds, and compared this with the value derived from the shell-recovery generated data (Table 1). Shell-recoveries would have overestimated the average biomass of mussels taken by stabbers in November by 5%. In April, the error was much greater, with a 61% over-estimate of mussel biomass.

DISCUSSION

The results of this simple experiment may have important consequences for the use of shell recoveries as indicators of prey selection and prey depletion in birds (particularly waders). Shell recoveries gave the equivalent of a 65% underestimate of the "total prey taken" as well as overestimating the proportion of large mussels and underestimating the proportion of small mussels "in the diet". An interesting feature of the results was the large between-condition differences in the recovery bias. Although the recovery success was higher for "carried" and in situ mussels, collecting "buried" mussels gave a more accurate approximation to the proportions of each size-class present.

Qualitative differences in the visual cues provided by shells in each conditions are the most likely reason for differences in the ease with which they were recovered. A large percentage of the "carried" mussels settled ventral side uppermost revealing the white inner nacrous layer, which was easily seen against the darker background of the mussel bed. By contrast, "in situ" mussels placed ventral side down were more cryptic and fewer were found.

Why should the recovery bias for "carried" and "in situ" mussels by size-dependant? Smaller mussels were certainly more likely to settle in the intersticies of mussel clumps, where they were hidden from view. The absence of a

Table 1. The effect of shell-recovery bias on calculating the average biomass (AFDW) of mussels taken by stabbers on the Exe during April and November.

Average biomass (g AFDW)

Method	of mussels taken*	
	April	November
Bill-length estimates corrected for my bias	0.059	0.847
Shell-recoveries uncorrected for my bias	0.095	0.886
Difference	+0.036	+0.039
Result	shell-recov. gave 61% overestimate	shell-recov. gave 5% overestimate

* Based on the average AFDW of each size-class (Figure 3) and the proportion of each class in the diet (Figure 4).

size-dependant bias for "buried" mussels suggests that in the two other conditions I may have concentrated my search on the larger mussels which were easier to find, since the majority of "buried" mussels were found by looking for disturbance to the substrate. rather than the mussel itself.

The extent of bias found in this experiment is likely to be less than that in a real field study using the same technique. First, as the observer, I had a priori knowledge of the number, approximate density and size-distribution of shells present; and secondly, the density of shells $(c. 6/m^2)$ was very much higher than that found naturally.

One alternative to shell recoveries is to estimate prey size directly against bill length. Goss-Custard et al. (1987) have tested the accuracy of this technique in free-living Oystercatchers eating mussels, and by the use of models. In their study, three of the four observers over-estimated the length of large mussels and under-estimated that of small mussels. The magnitude of bias differed significantly between observers and to a lesser degree between the "natural" and "model" tests. The main conclusion from the present study is that recoveries of mussel shells are also biased, but the effect of this is likely to be negligible during most months of the year, because Oystercatchers avoid the size-classes which are most prone to recovery bias (Cayford 1988). In spring, when Oystercatchers on the Exe took small mussels, estimates of energy intake based on shell-recoveries were subject to large errors. Because the extent of bias is likely to differ between individual observers, it is important that each observer measures, and corrects for, his/her own bias regardless of the technique used.

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