Correcting the individual biases
made in collecting mussel shells opened by oystercatchers *'ex situ'*

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Accurate estimation of the sizes of prey consumed by avian predators from prey remains is subject to individual observer biases and may adversely affect prey biomass estimation and consequently other parameters related to bird foraging behaviour. Hence, a field experiment was carried out to measure the biases in collecting empty mussel shells left by oystercatchers that open mussels by hammering a hole on the ventral side *'ex situ'* (ventral hammerers). Two series of mussel shells, opened by ventral hammerers, spanning a size range of 11–50 mm in maximum length, were divided into seven different length classes, and distributed by one person over an experimental plot in one of two orientations, simulating the feeding techniques used by ventral hammerers. Another person then attempted to recover the shells and the percentage recovery of each length-class was used to correct the underestimates in prey-size selection that would otherwise occur arising from observer bias. By using the relationship derived from the regression of the calculated correction factors against mussel length, a more accurate estimate of the lengths of mussels taken by oystercatchers is possible.

It was found that mussel shells >30mm in length were over-represented and shells <31mm were under-represented in the shells that were recovered. Recovery success was significantly affected by shell size but not by shell orientation. If the biases had not been corrected using the derived regression equation, shell recovery would have given spurious estimates of the different sizes of mussels taken and, consequently, estimates of prey profitability and ingestion rates of oystercatchers.

INTRODUCTION

Inaccurate estimation of the sizes of prey consumed by predators may adversely affect prey biomass estimation as well as measurement of parameters related to foraging behaviour, such as prey size selection, ingestion rate, profitability of prey taken and feeding efficiency (Goss-Custard *et al.* 1987, Cayford 1988). The curvilinear relationship between prey length and prey biomass means that even small errors in prey-size estimation may result in large and significant errors in the corresponding estimated feeding parameters. In field studies of birds feeding, prey size has been estimated from a distance relative to some known measure such as bill length (Meire & Ervynck 1986, Goss-Custard *et al.* 1987, Boates & Goss-Custard 1989), head length (Boates & Goss-Custard 1989), coloured ring length (Sutherland & Ens 1987, Boates & Goss-Custard 1989) and quantity of flesh removed, and the depth to which the bill penetrated the flesh (Goss-Custard *et al.* 1984). The size of prey consumed may also be obtained by recovering the remains of prey left by birds in the feeding area. The sizes of mussels taken by oystercatchers have often been estimated by measuring the length of freshly opened empty shells left on mussel-beds (Durell & Goss-Custard 1984, Sutherland & Ens 1987). However, accuracy of prey-size estimation can be significantly influenced by individual observer biases. In particular, studies where prey size is measured against bill-length,

observer bias should always be measured, as otherwise major errors will occur in estimating prey biomass (Goss-Custard *et al.* 1987). Similarly, shell collection appears to be biased towards larger mussels in the case of oystercatchers that open mussels by stabbing in-between shell-valves (stabbers) and by hammering a hole on the dorsal side *'in situ'* (dorsal hammerers), but unbiased in the case of oystercatchers that open mussels by hammering a hole on the ventral side *'ex situ'* (ventral hammerers), probably due to their habit of carrying captured mussels to anvils before opening (Sutherland & Ens 1987). However, regardless of the feeding technique used by oystercatchers, the larger shells are more likely to be seen and found by an observer than smaller ones, and the orientation of shells on the mussel bed is also equally important and affects success in finding shells (Cayford 1988). Therefore, individual biases should be measured experimentally to avoid imprecise prey-size estimation leading to serious errors in estimating other bird foraging parameters (Cayford 1988, Nagarajan 2000).

In this study, observer biases in collecting empty mussel shells left by oystercatchers feeding on mussels by ventral hammering, were measured in an experimental plot established on an intertidal mussel bed on the Ythan estuary, Aberdeenshire, Scotland in January 2002. The experimental procedure followed was similar to that of Cayford (1988), with modifications.

METHODS

Preparation of mussel shells

Mussel shells opened by ventral hammerers collected on the study site covered a size range of 11–50 mm, which is the range most commonly taken by oystercatchers on the Ythan estuary (Fernando 2002). Maximum shell-length, from anterior tip to posterior tip, was measured using a vernier calliper to the nearest mm and assigned to size-classes: 11–20, 21–25, 26–30, 31–35, 36–40, 41–45 and 46–50 mm. Oystercatchers took very few mussels <20 mm in length during winter, and since only a small number of shells could be found in what would otherwise have constituted the two smallest size-classes (11–15 and 16–20 mm), these were amalgamated to form a wider (11–20 mm) size-class. Two series of mussel shells were prepared, each comprising 25 shells of each size-class except the largest (46–50 mm), which was represented by only 15 shells (n = 165). Using a different colour for each series, an inconspicuous spot was marked on the inner side of the unbroken valve of each shell.

Experimental procedure

A 7 m × 7 m experimental plot was marked out on an intertidal mussel bed near the mouth of the Ythan estuary that contained a high density of mussel shells left by oystercatchers including in shallow stagnant water area, representing the normal conditions for shell collection. In the absence of the observer, each series of shells was distributed by an assistant, within the experimental plot including patches of shallow water, in one of the two orientations described below, to simulate the normally observed orientations of mussel shells after predation by ventral hammerers.

Orientation I (Carried shells)

Ventral hammerers normally rip mussels from the bed and carry them a short distance to a piece of firm ground that they use as an 'anvil' to hammer a hole in the shell 'ex situ'. If the ground is not firm or the mussel falls over, they usually carry it to another anvil. A large proportion of these mussel shells that have been carried and opened are left oriented with the ventral side uppermost and with the white inner nacreous layer exposed. One series of shells was used to simulate this orientation by dropping each shell on to the surface of the bed from a height of about 20 cm (Cayford 1988), to prevent possible biases which could otherwise have arisen from the non-random placing of shells with either the lighter inner or darker outer side uppermost.

Orientation II (Buried shells)

Ventral hammerers often reposition the mussel several times while hammering and occasionally push the mussel into the mud or sand while hammering or removing the flesh. These shells are left by oystercatchers oriented upright with the anterior end downwards and partly or completely buried. The second series of shells represented the orientation of such buried shells. The anterior end of each shell was pushed into the mud, leaving only part of the shell visible.
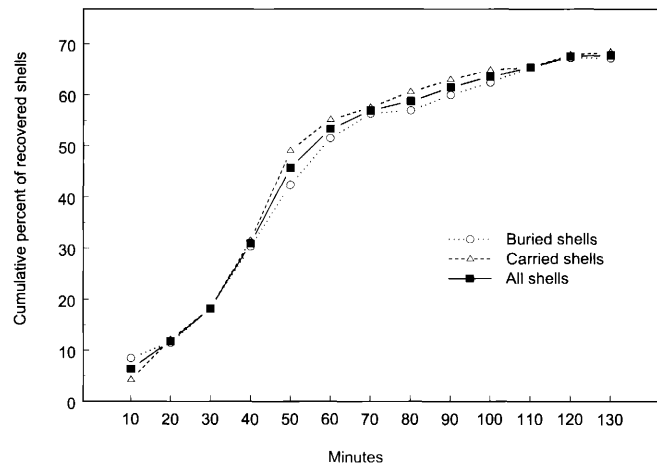

Fig. 1. Cumulative percent of recovered mussel shells in successive ten-minute searching periods.

Recovery of shells

After the shells were distributed, the marked ones were recovered by a different observer in thirteen consecutive ten-minute periods (a total of 130 minutes). Shells recovered in each ten-minute period were placed into a separate polythene bag. Recovered shells from each bag were sorted according to orientation, re-measured, and assigned to size-classes as before.

Data analysis

The percentage recovery of different size-classes of shells was estimated for both carried and buried shells and compared using paired t-tests. Pooling the data across the two treatments, variation in the recovery of different size-classes of mussels was examined using a one-way ANOVA followed by a Tukey test.

Correcting biases in shell collection

Data were first pooled across carried and buried shells and the percentage of shells recovered during the total search period (130 minutes), for each of the different size-classes was estimated. Correction factors were calculated by scaling up to 100% the recovered percentages of each individual size-class. For precise bias correction, a function was fitted between these correction factors and the mid-point of each length class. This was to avoid the inevitable errors that arise from using correction factors estimated from small sample sizes. In fitting the relationship, the correction factor estimated for shells of 46–50 mm in length was used for shells between 51 and 75 mm.

RESULTS

Out of 330 shells deposited, 224 (67.9%) were recovered over the 130-minute period. These consisted of 113 (68.5%) carried shells and 111 (67.3%) buried shells. The shell recovery rate (both carried and buried) was rapid during the first 40 minutes after which it started to decrease, levelling
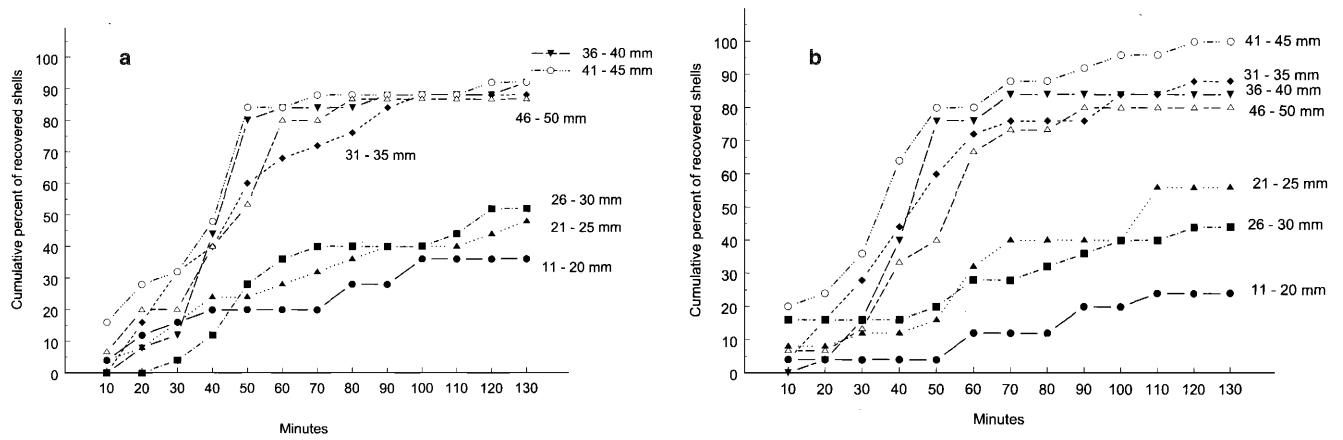
Fig. 2. Cumulative percent of recovered mussel shells of different size-classes in successive ten-minute searching periods (a) Carried shells (b) Buried shells.
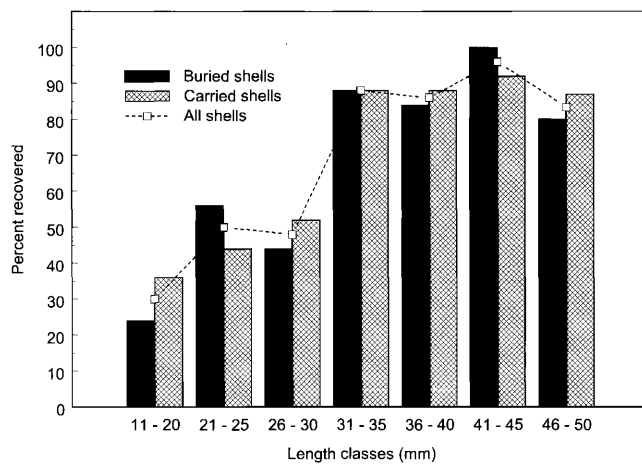

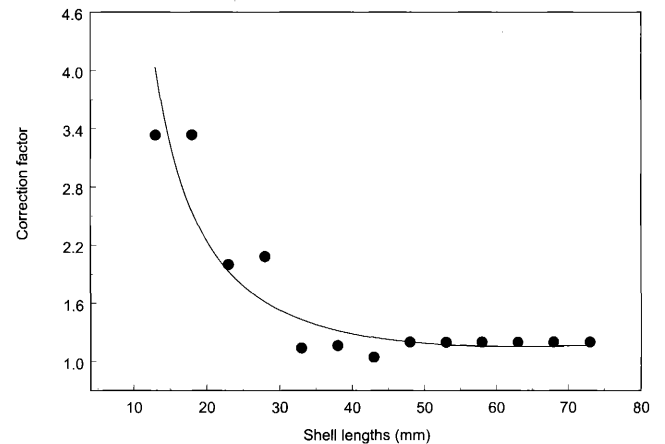**Fig. 3.** The percent of mussel shells recovered in the different length classes.

Fig. 4. The polynomial relationship between correction factors, estimated to correct individual biases in collecting mussel shells, and lengths of mussels (n = 13, see Table 1 for equation).

off after about 60 minutes (Fig. 1). The pattern was similar for both carried and buried shells.

A high proportion of 31–50 mm shells were recovered within the first 60 minutes; 78.9% of carried shells and 74.4 % of buried shells (Fig. 2). The recovery of carried shells <31 mm increased progressively until the end of the search. The recovery of buried shells <31 mm was very low within the first 50 minutes of search (13.3%), after which it started to increase progressively (Fig. 2b).

No significant differences were found in the percentage of shells recovered in the different size-classes between car-

ried and buried shells (Fig. 3). Overall, underestimation was 57.3% in the total recovery of 11–30 mm shells, and 11.1% of 31–50 mm shells. Hence, both carried and buried shells over 30 mm long were significantly over-represented, making up 71.4% of the recovered sample (ANOVA followed by Tukey test: $F_{6,7}$ = 18.34, $P < 0.001$).

The factors needed to correct biases in shell collection are significantly related to shell-length (Fig. 4). Hence, individual biases in collecting mussel shells can be corrected using the regression equation relating the correction factors to shell-length (Table 1).

Table 1. Equation derived, from regression of calculated correction factors in shell recovery and mussel shell length, to correct individual biases made in estimating mussel size.

Response variable	Predictor variable	Coefficient ±1SE	R^2	$F_{1, 12}$
Precise correction factor	Constant	$6.6354^{***}\pm0.8661$	92.3	36.01^{***}
	Shell length	$-0.29380^{**}\pm0.07490$		
	(Shell length)^2	$0.005084^{*}\pm0.001902$		
	(Shell length)^3	$-0.00002842^{ns}\pm0.000015$		

$^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$, ^{ns}non significant.

DISCUSSION

Our results demonstrate that recovery bias is size-dependent for both carried and buried shells. Overall, there was a notable increase in the percentage of shells recovered with a maximum length >30 mm. It seems that this is a threshold shell-length above which both carried and buried shells are particularly easy to detect. In contrast, Cayford (1988) found that only the recovery of carried shells was size-dependent and that buried shells gave a more accurate approximation of each size-class present. He explained this on the basis that it is easier to find large mussels lying on the surface over small ones, but finding buried mussels involves looking for signs of substrate disturbance rather than for the shell itself and this is independent of size. In field studies, visual cues such as bird footprints might be used by observers when collecting fresh prey remains left by birds, but these were not applicable to our experiment. Certainly the assistant had left footprints in the experimental plot. However, there were so many footprints in the study area and they were spread so evenly that they could not have been used, consciously or unconsciously, as visual cues.

No significant difference was found in recovery success between carried and buried shells in this study. Thus, shell orientation did not appear to affect recovery success. However, Cayford (1988) recovered a higher proportion of carried shells than buried shells and suggested that carried shells are more easily seen because of the contrasting white inner nacreous layer of the valves against a dark background. Although we recorded no significant difference in recovery success between carried and buried shells, we found that recovering smaller buried shells was very slow during the first 50 minutes of searching. This would suggest a tendency to search for smaller buried mussels during the later part of the survey, after the more easily found shells have been recovered. The experimental plot was small and this tendency to look for smaller buried mussels might not apply when collecting shells in larger plots. Therefore, although our experiment revealed no effect of orientation on shell recovery, this may not be the case when collecting shells in larger areas.

The amount of bias found in our experiment was much less than that found by Cayford (1988). This may reflect different field conditions during the two experiments. On the Ythan estuary, mussel beds are covered with brown or green macroalgae, but the experimental plot used had no macroalgae. If macroalgae were present, an influence on shell recovery would be expected but we did not test this. Furthermore, under natural conditions very small shells might have been hidden between mussel clumps, and would have been particularly difficult to find. It is important to note that the extent of bias is also likely to vary depending upon the observer and the observer's experience. Therefore, correction factors obtained by one observer for a particular study may not apply to another observer carrying out the same study or even the same observer carrying out the same study somewhere else.

In this study, although all errors may not have been corrected, the derived equation did improve the precision of the estimate of mussel size. This study also emphasises how individual biases can easily be corrected when using prey remains as an indicator of prey selection and energy consumption. This allows more accurate conclusions to be drawn, especially when comparing the predators' energy optimisation against different environmental conditions such as season, inter- or intra- specific interference, food depletion and physical barriers such as macroalgal mats.

CONCLUSION

Mussel shells >30 mm in length were over-represented and shells <31 mm were under-represented in those that were recovered. Recovery success was significantly affected by the size of the shells but not by their orientation.

ACKNOWLEDGEMENTS

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