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# PREY SELECTION OF A CAPTIVE OYSTERCATCHER *HAEMATOPUS OSTRALEGUS* HAMMERING MUSSELS *MYTILUS EDULIS* FROM THE VENTRAL SIDE

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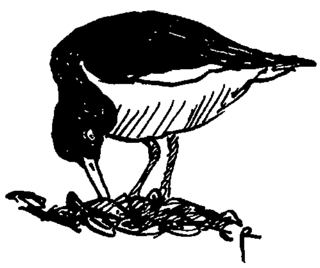
We studied prey choice of a captive Oystercatcher that hammered Mussels from the ventral side. The results replicate previous findings that ventral hammerers select Mussels of intermediate size, select against thick-shelled Mussels, abandon an increasing proportion of Mussels with increasing size and do not pick up Mussels covered with barnacles. Abandoned Mussels had thicker shells than Mussels that were successfully opened, but part of the selection against thick shells seemed to occur before the Mussels were picked up. Barnacles could not serve as cue for this. In fact, it remains unclear why ventrally hammering Oystercatchers ignore Mussels covered with barnacles.



Key words: Oystercatcher - *Haematopus ostralegus* - Mussel - *Mytilus edulis* - prey selection - optimal foraging

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## INTRODUCTION

Present-day ecology is not known for its tendency to replicate observations. Yet, there can be little doubt that successful independent replication provides powerful support for the conclusions of observations or experiments. This is one reason why we think it fit to publish our observations on prey selection in a captive Oystercatcher hammering Mussels from the ventral side, even though it involves observations on only one individual.

Oystercatchers can open Mussels in three different ways: stab the posterior adductor muscle, hammer a hole in the shell from the dorsal side or hammer a hole in the shell from the ventral side (Hulscher 1996, for a comprehensive description). When Ens (1982) tried to explain size selection in Oystercatchers hammering Mussels from the ventral side on the basis of an optimal prey choice model (Charnov 1976), he found that large Mussels were the most profitable, yet were selected against. One possibility for this was that the shells of large Mussels were often too thick to open, as was indeed amply confirmed in subsequent studies (Durell & Goss-Custard 1984, Meire & Ervynck 1986, Sutherland & Ens 1987, Cayford & Goss-Custard 1990). In a modification of the optimal prey choice model, Meire & Ervynck (1986) included the waste handling time taken to recognize Mussels with shells too thick to be opened. This model predicts the observed prey choice remarkably well for most of the year, if it is also assumed that Mussels covered with barnacles are inedible (Meire & Ervynck 1986, Cayford & Goss-Custard 1990).

Here, we report our observations on prey selection in an Oystercatcher hammering Mussels from the ventral side, kept in captivity under semi-natural conditions. The specific experimental set-up allowed us to collect Mussels that were picked up by the foraging bird but that it subsequently abandoned after a short period of handling. This proved that abandoned Mussels have relatively thick shells for their size, an implicit and untested assumption in the prey selection model proposed by Meire & Ervynck (1986). In fact, we took a whole array of measurements on the Mussels, which allowed us to test some hypotheses explaining why ventral hammering Oystercatchers do not pick up Mussels covered with barnacles. All hypotheses failed. In the discussion we therefore focus on alternative explanations.

## METHODS

In spring 1987 one Oystercatcher was kept under semi-natural conditions in a tidal outdoor cage on Texel (see Swennen *et al.* 1989 for a description of the cage). Due to technical malfunction we could not manipulate the tide in the entire cage, but only in the 1 m wide channel running through it. Along the sides of the channel we laid out Mussels collected on 26 and 30 March 1987 in the Mok on Texel. The total surface area of this mini mussel bed was 5 $m^2$ and it was alternatively six hours exposed and six hours covered with sea water. We allowed time for the Mussels, collected as clumps, to reconstruct themselves into a mussel bed and for the bird to get used to the experimental conditions. On 22 April the bird seemed habituated and we started observations They were ended on 30 April when the bird switched from hammering to stabbing for unknown reasons. Feeding behaviour was recorded on an electronic event-recorder (OS-3) by noting time spent searching, time spent handling (tearing the Mussel from the substrate, carrying it to an anvil, hammering, cutting and eating the flesh) and whether the Mussel was opened successfully or abandoned. The Oystercatcher invariably carried the Mussels out of the channel to the adjoining sandflats (measuring 49 $m^2$ in all) before opening them. By noting the exact location of each Mussel taken, we could later link the handling time to the measurements on shell characteristics. For each collected shell, we measured length, breadth, height, shell thickness, short and long diameter of the imprint of the posterior adductor muscle, whether the Mussel was covered with barnacles or showed growth deformations. Shell thickness was measured to the nearest 0.1 mm at the centre of the ventral surface. For a random sample from the Mussels on offer, taken on 1 April, we also measured the ash-free dry mass (AFDM in mg) using standard procedures; we measured the biomass of the posterior adductor muscle separately from the rest of the animal.

## RESULTS

As in other studies of ventral hammering Oystercatchers (Norton-Griffiths 1967, Ens 1982, Meire & Ervynck 1986, Sutherland & Ens 1987, Cayford & Goss-Custard 1990), the captive bird did not take very large and very small Mussels, but selected Mussels ranging in size from 25 to 45 mm length (Fig. 1). Profitability of a size class is calculated by dividing the biomass of that size class (Fig. 2A) by the time spent handling it (Fig. 2B). Profitability for successfully opened Mussels only increased with size (Fig. 2D). However, though small Mussels were always opened successfully,

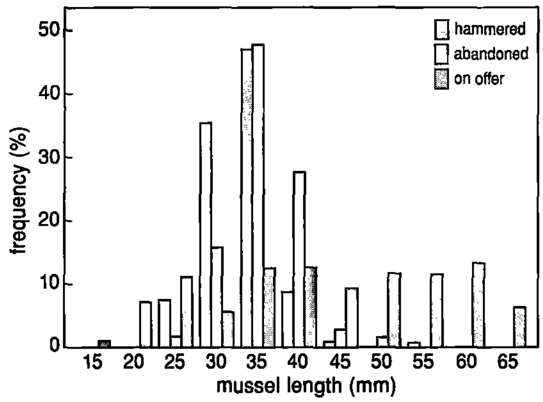
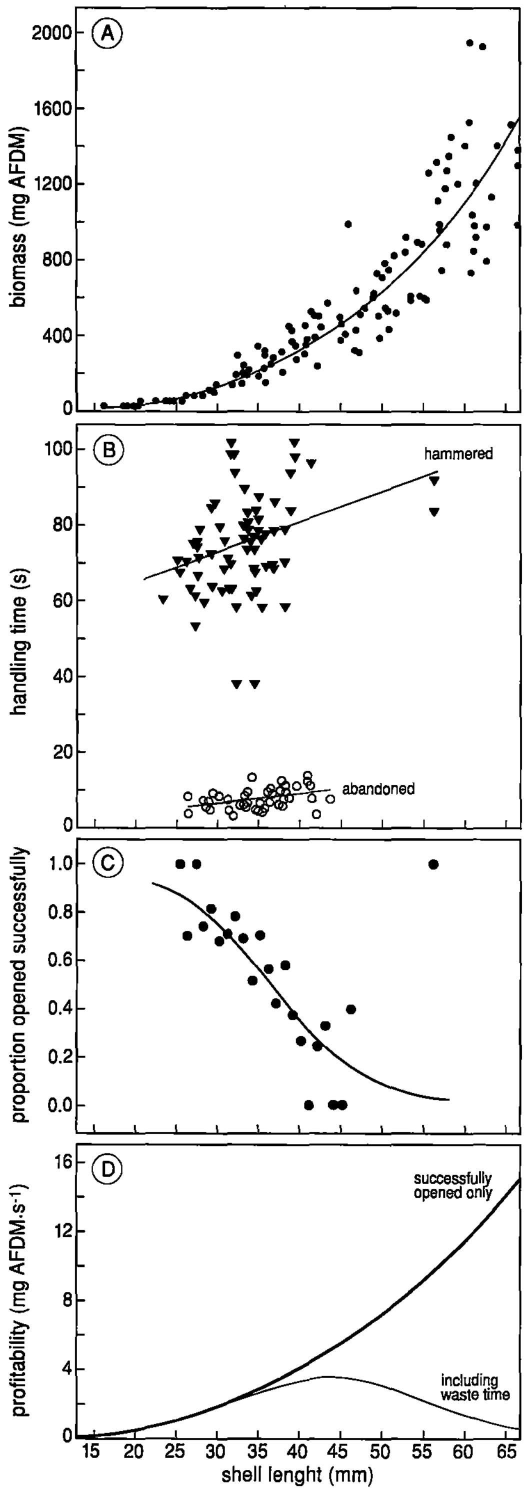



**Fig. 1.** Size distribution of Mussels on offer, Mussels that were abandoned after a few seconds of handling and Mussels that were successfully opened by the ventral hammerers in the tidal cage on Texel.




with increasing size the probability increased that the Mussel was rejected after a few seconds of handling (Fig. 2C). When this waste handling time was included in the calculation (see equation 1 in Meire & Ervynck 1986), profitabilities first increased but then dropped again for large sizes (Fig 2D).

The profitability calculation including waste handling time rests on two assumptions. First, Oystercatchers cannot open Mussels when the shell is too thick. Second, Oystercatchers need to hammer a particular Mussel to gauge its thickness, i.e. thickness cannot be judged from outward appearance. If true, the shell thickness of Mussels picked up (i.e. Mussels that were successfully opened as well as abandoned) should not differ from the shell thickness of Mussels on offer. An ANOVA with shell length as covariate indicated that the two groups differed significantly ($F_{1,549}$ = 48.8, $p < 0.001$): Mussels that were picked up had thinner shells compared to Mussels on offer (Fig. 3). However, when the shell thickness of abandoned Mussels was compared to that of successfully opened Mussels, there was again a significant difference ($F_{1,419}$ = 270.4, $p < 0.001$): hammered Mussels were thinner than abandoned Mussels (Fig. 3). Thus, the bird was able to select relatively thin Mussels during searching, but this selec-

**Fig. 2.** Calculation of profitability in relation to size of hammered Mussels in the experiment in the tidal cage on Texel. (A) Biomass (mg AFDM) in relation to length (mm) for the Mussels on offer: $\ln(mg) = -5.705 + 3.110 \times \ln(mm)$, $r = 0.97$, $n = 130$, $p < 0.0001$. (B) Handling time (s) of Mussels successfully opened ($s = 46.03 + 0.87 \times mm$, $r = 0.34$, $n = 115$, $p = 0.0002$) and of Mussels that were subsequently abandoned ($s = -1.55 + 0.26 \times mm$, $r = 0.41$, $n = 45$, $p < 0.01$). (C) Probability per 1 mm size class that a Mussel once selected and carried to an 'anvil' would be successfully opened; the curve was obtained using logistic regression: $P_{success}=1/(1 + \exp(-6.3126 + 0.1726 \times mm))$; both coefficients in this equation differed significantly from zero ($p < 0.0001$). (D) Profitability (mg AFDM consumed $s^{-1}$ handling) for successfully opened Mussels only and for all Mussels of a given size, i.e. when the time wasted on abandoned Mussels is included.

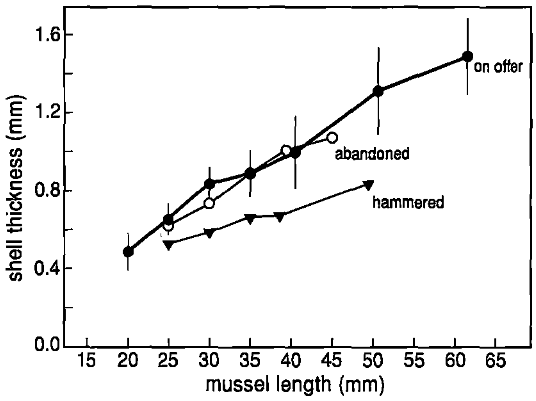



**Fig. 3.** Relationship between shell thickness and shell length for Mussels on offer in the experiment in the tidal cage on Texel, Mussels that were successfully opened and Mussels that were abandoned after a few seconds of handling. Bars indicating 1 *SD* are only drawn for Mussels on offer, but were of similar magnitude for the other groups. Linear regression yielded the following relationships between shell thickness (in mm) and shell length (in mm) for the three groups: (1) on offer: $Y = 0.030 + 0.0246X$, $r = 0.90$, $n = 130$, $p < 0.0001$, (2) hammered: $Y = 0.184 + 0.0132X$, $r = 0.36$, $n = 248$, $p < 0.0001$ and (3) abandoned: $Y = -0.074 + 0.0271X$, $r = 0.74$, $n = 174$, $p < 0.0001$.

tion procedure was apparently far from perfect and included many thick-shelled Mussels.

Did the bird select thin-shelled Mussels during searching by using barnacle cover as a cue? As in the studies of Durell & Goss-Custard (1984) and Meire & Ervynck (1986) our bird did not pick up Mussels covered with barnacles: 41% of Mussels on offer in the size range 40-50 mm were covered with barnacles, but for Mussels in this size range that were picked up this figure was only 2%. Smaller Mussels had no barnacles, while larger Mussels were usually covered with barnacles but were almost never picked up. To test if Mussels with barnacles had thicker shells we used the size range of 40-55 mm, as there were a sufficient number of Mussels with and without barnacles within this range. An ANOVA with length as covariate failed to find a significant difference between the two groups ($F_{1,34} = 0.002$, $p = 0.96$). This renders it unlikely that barnacles are a cue to shell thickness.

Why then, do hammering Oystercatchers select against Mussels covered with barnacles? Perhaps such Mussels have a lower biomass. To test this, we again compared Mussels with and without barnacles in the size range 40-55 mm through an ANOVA with length as covariate. There was no effect ($F_{1,34} = 0.74$, $p = 0.40$).

## DISCUSSION

Our results replicate previous findings that ventral hammerers select Mussels of intermediate size, select for thin-shelled Mussels, abandon an increasing proportion of Mussels with increasing size and do not pick up Mussels covered with barnacles. The apparent inability of the birds to accurately judge shell thickness from outward appearance explains why so many Mussels are abandoned and justifies the inclusion of the waste handling time in the calculation of profitability as proposed by Meire & Ervynck (1986).

Instead of simply assuming that thick shells cannot be opened, Meire (1996) explored the possibility that they can be opened but that it would be unprofitable to do so due to excessively long handling times. Meire (1996) used Norton-Griffiths' (1967) cracking machine to estimate handling time for a Mussel with a given length and thickness. This methodology should allow us to predict beforehand the proportion of Mussels for a given size class that will be abandoned. If our finding is correct that some of the selection against thick shells occurs before the Mussels are picked up, it follows that the predicted proportion abandoned should yield an overestimate.

Since barnacles do not correlate with shell thickness, they cannot be the cue for this pre-handling selection. As barnacle cover also does not correlate with low biomass of the Mussels, it is circular simply to declare Mussels with barnacles as inedible. Perhaps, Mussels covered with barnacles are not recognized as prey (P. Meire pers. comm.). Alternatively, coverage with barnacles may indicate that the particular Mussel has been living exposed for a long time and is more firmly attached to the substrate, i.e. a disproportionate force is needed to tear it loose. So far, only Norton-Griffiths (1967) has attempted to measure this force.

In conclusion it can be said that there has been considerable progress in our understanding of the prey selection of ventrally hammering Oystercatchers over the past decades, but that it is not yet complete. Further understanding requires more detailed investigations of the mechanics of prey detection and handling.

## ACKNOWLEDGEMENTS

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## SAMENVATTING

In dit artikel beschrijven we onderzoek naar de prooikeuze van een Scholekster in gevangenschap, die Mossels opende door de ventrale zijde kapot te hameren. Net als in vorige studies was gevonden, selecteerde de Scholekster Mossels van intermediaire grootte met relatief dunne schelpen, die niet begroeid waren met zeepokken. Ook nam de kans, dat een opgepakte Mossel uiteindelijk geweigerd werd, toe met de grootte. Zulke geweigerde Mossels bleken relatief dikke schelpen te hebben. Een deel van de selectie tegen de Mossels met een dikke schaal vond echter plaats voordat de Mossels werden opgepakt. Aangezien Mossels met en zonder zeepokken niet in dikte verschilden konden de Scholeksters hierbij niet afgaan op de begroeiïng met zeepokken. Al met al is het nog steeds niet duidelijk waarom ventraal hamerende Scholeksters geen met zeepokken begroeide Mossels selecteren.