Foraging Behaviour of Mussel Feeding European Oystercatcher (Haematopus ostralegus)

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Oystercatchers are characteristically large and heavily built, with black or brownish-black plumage, often with a prominent white wing-bar, or totally dark. The European race, Haematopus ostralegus ostralegus, 40-45cm long with a wingspan of 80-90mm, is among the largest of the western Palearctic waders, has red-pink legs and feet and scarlet-red eyes, with orbital rings. The bill is 65-75mm long, stout and laterally compressed for chiselling and breaking into the shells of lamellibranch and gastropod molluscs, which constitute the main prey species in Exe estuary, England. The sexes are alike. In Britain overwintering adult Oystercatchers forage predominantly on marine invertebrates especially hard and well-protected molluscs at low water, particularly mussels (Mytilus edulis), cockles (Cerastoderma edule) and Baltic tellin (Macoma balthica). Also the Oystercatchers feed on polychaete worms (Neris diversicolor and Arenicolor marina), Limpets (Patella sp.), dogwhelks (Nucella lapilus), periwinkles (Littorina sp.) and shorecrabs (Carcinus maenas). At high waters some Oystercatchers forage on grassland on soft-bodied terrestrial invertebrates, particularly earthworms (Lumbricidae) and the larvae of insects (Coleoptera, Diptera, Dermaptera) (Goss-Custard et al. 1996). Although Oystercatchers feed on a variety of organisms, they tend to specialize on a single prey species and within the species they optimize their foraging tactics. In addition, they increase their intake rate by adopting different strategies. In this talk, I review the foraging specialization and optimization of mussel feeding Oystercatchers.

Study Area

The river Exe in Devon, England forms a small, mainly muddy, sheltered estuary which is in the Southwest of England between Exmouth and Dawlish to the west (Fig 1). The estuary is protected from the sea by twin sand spits which reduce the entrance to a narrow channel (McGrorty, 1997). The main supply of freshwater comes from the rivers Exe and Clyst which enter from north. Boalch (1980) summarised the details and descriptions of geology, hydrography, sedimentology, fauna and flora of the Exe. I collected field data from mussel bed number 4, which is located on the western side of the Exe estuary, between Starcross and Cockward ($3^{\circ} 27' \text{ W}$, $50^{\circ} 37' \text{ N}$). This is one of the beds which support a good population of mussel feeding Oystercatchers. It is relatively free from anthropogenic disturbances and easily accessible for observation of birds.

Methods

Oystercatchers were observed from the hide through a 15x-60 magnification zoom telescope (Optolyth) mounted on a tripod by direct observations throughout the ebb tide period. A foraging Oystercatcher was selected at random for 10- minute focal animal sampling observation (Altman, 1974). Further, mussels were collected for different quantitative and qualitative measurements to identify the foraging specialization and optimization behaviour of Oystercatchers (Nagarajan 2000, Nagarajan et al. 2002a,b,c).

Results

I explored the foraging specialization and optimization of Oystercatchers across the winter and explained their foraging specialization, then showed how Oystercatchers specialized on different characters of mussel to increase their intake rate.

Foraging methods and selection

Oystercatchers open mussels in three ways, *viz.*, stabbing, dorsal hammering and ventral hammering (Hulscher, 1996).

Stabbing: Oystercatchers stab at the junction between the two valves. Mussels clump together by byssus threads that emerge from the ventral surface of the valves. The shells gape slightly under water and are closed only loosely when the shells are still moist. The stab is directed at the posterior adductor mussel which is then severed. As the tide receded and where no pools remain the substrate dries out, the bivalves close their valves. Many stabbers then turn to forcing apart the valves of the more firmly closed dry mussels.

Dorsal Hammering: Dorsal hammerers open the mussel *in-situ* from the above, breaking the shell at the dorsal posterior margin or at the side. The support provided by the attachment to other mussels in a clamp prevents the prey

from being driven far into the underground in slightly soft areas. It attacks the shell at the point at which the posterior adductor is attached to the shell and where erosion and so shell thinning often take place.

Ventral Hammering: Ventral hammerers normally clasp the mussel between the mandibles and tear it off from the bed by pulling upwards until the byssus threads break and then carry it to a firm hammering place, or "anvil". Then, the ventral surface is turned upwards and the hammer blows can be directed at in the mid-ventral region. The hammer blows from the strong bill causes a semicircular chip of the shell to be fractured from the ventral margin of one valve, at which point the bird inserts its bill, cuts the posterior and anterior adductor mussels and prizes the valve apart.

Prey Selection

Of the mussels opened by Oystercatchers, 70.8% mussels were between 35 and 55mm long. Oystercatchers selected ventrally thin-shelled mussels especially if the size was more than 35mm. The Oystercatchers also took mussels which had fewer barnacles on the ventral surface. Generally the Oystercatchers consumed ventrally flat mussels, especially in the smaller length classes, and this preference was particularly strong in the preferred size class 30-45mm. Hence, the opened mussels found to be ventrally thin, flat, brown coloured and to have few barnacles on the ventral surface. The binary logistic multiple regression equation model indicated that the ventral thickness and colour had independent effects on mussel selection (Nagarajan et al. 2002a).

Seasonal selection

The frequency distribution of the lengths of the mussels consumed by Oystercatchers and present on the mussel bed are evaluated for early 'winter' (September-November), mid-winter (December and January) and late winter (February and March). Most of the mussels eaten by the Oystercatchers were between 25 and 55mm in length in all three winter periods. The proportion of mussel frequency in the larger length categories declined over the winter. The observed data suggest that Oystercatchers selected smaller mussels as the winter progressed. The modal value declined from 40-45mm in early winter to 35-40mm in mid and late winter. Furthermore, according to Jacob's index, the most preferred length classes were 35-55mm in early winter but decreased to 20-40mm in the remaining periods of winter. The analysis of seasonal changes in the length frequency distributions of the mussels on the bed and of those opened by the Oystercatchers, it seems likely that, as the frequency of the initially preferred 35-55mm on the bed declined, the birds took a greater proportion of smaller mussels (Nagarajan 2000, Nagarajan et al. 2006 and 2008).

Morph selection

Although the brown coloured mussels were rare in the population, the Oystercatchers showed a strong preference towards them. The Oystercatchers strongly preferred brown coloured mussels, probably because the flesh of black-coloured mussels was much wetter than that of the brown-coloured mussels. By avoiding the ingestion of this extra water, the Oystercatchers increased their intake rate by 1.99% to 17.7% in different length classes of mussels. Over the course of winter, Oystercatchers took mussels with increasingly thick shells relative to those that were on offer, particularly in the most preferred length class of 40-50mm (Nagarajan et al., 2002c).

Valve selection

Of the opened mussels, 72% were opened on the right valve and the remaining 28% were opened on the left valve, none was attacked on both valves A chi-square test clearly showed that this preference for attacking on the right was not likely to have arisen by chance. This preference did not change either with mussel length or across the season. The right valve was generally thinner than the left, but the preference for right valve attack was greater than could be accounted for by this factor alone. The preference would be explained if Oystercatchers were able to detect the thinner valve in a mussel when the difference in the ventral thickness between the two valves was more than 0.036mm. If they were unable to discriminate the thickness difference, then they attacked the right side because 58% of mussels are thinner on this side. By following this strategy, Oystercatchers would need 15.5% less blows than if they attacked either valve at random. The improvement in the overall intake that could be achieved by valve thickness discrimination was 3.6% (Nagarajan et al., 2002c).

Layer selection

Mussel shell is made of three layers viz., outer peristracum, middle prismatic and inner nacreous, the prismatic layer contributed a major role to the thickness of the valves. The peristracum was the thinnest layer. The thickness of prismatic layer showed significant variation between opened and comparator mussels whereas the thickness of peristercum and nacreous layers did not differ between opened and comparator mussels. The independent effect of individual shell layer on the oystercatcher mussel selection choices was tested using binary logistic regression model. The model revealed that the Oystercatchers opened the mussels that had significantly thinner prismatic and nacreous layers. The regression co-efficients for the thickness of the prismatic layer was almost four times greater than that for the nacreous layer. Earlier I showed that the Oystercatchers prefer to attack medium sized mussels and

that preference for length selection changes across the seasons. Furthermore the mussel shells have been shown to be structurally dynamic with both shell thickening and thinning taking place across the season (Nagarajan et al. 2006 and 2008). Therefore, the length and season were included as regressors in the model but neither of these variables yielded significant co-efficients. These analyses indicated that the Oystercatchers preferentially opened the mussels which had thin prismatic layer, irrespective of length and season. The nacreous layer is the oldest and strongest layer but the prismatic layer act as shock absorber due to its crossed lamellar which has highest nominal fracture toughness. The thicker prismatic layer produces noncatastrophic failures of mussel shell. To crack a mussel successfully the nacreous layers of the mussels needs to be damaged and for making such damage the prismatic layer would be thin enough to allow the crack to the reach the nacreous layer. Hence, oystercatchers would have selected the mussels which had thin prismatic layer (André Le Rossignol et al. 2011).

Conclusion

The Oystercatchers are extreme specialist and from the intensive research on this species, it is clearly understood that they optimize in all possible ways while foraging on different areas in various prey species to increase their intake rate. They are capable of discriminating the minute differences among the habitats/seasons, between the prey species and within individual preys to achieve the maximum intake rate. For example, in this paper, I showed that the Oystercatchers selected medium sized mussels which did not yield any waste handing time. Within the medium sized mussels, they selected thin-shelled and preferred to attack the brown coloured morphs. The thin-shelled mussels were easy to crack. On the other hand, by preferring brown coloured morphs, they avoided ingestion of extra water, and increased the intake rate by 1.99% to 17.7% in different length classes of mussels. When they selected such mussels, they managed to discriminate the thickness difference down to the level of 0.036mm and attacked the thinnest valves. Within the thinnest valve, they managed to detect the mussels with thinner prismatic layer which allowed the maximum load of hammering by the Oystercatchers to crack the hard nacreous layer. Therefore, it is clear that Oystercatchers are capable to discriminating the minute differences and increase their survival rates.

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