



Do oystercatchers (*Haematopus ostralegus*) select the most profitable limpets (*Patella* spp.)?



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ABSTRACT

Eurasian oystercatchers (*Haematopus ostralegus*) feed on at least 15 different prey species in different habitats along the NW European coast. In each habitat, they specialise mostly on a single molluscan prey and within that prey type, they use various strategies to make foraging more profitable depending upon a number of internal and external factors. Oystercatchers resident on Lundy Island (SW England) feed mainly on limpets (*Patella* spp.). We found that the oystercatchers attacked both the common limpet, *Patella vulgata* and the black-footed limpet, *Patella depressa*, in any of four ways parallel striking, levering, hammering or pulling by weed. Oystercatchers took relatively deeper-shelled limpets in the 20–40 mm length class, but this tendency reversed in limpets >40 mm long. The oystercatchers showed a selective preference for smaller, deeper, irregular-bottomed limpets, and attacked them on the anterior region. The oystercatchers showed a strong preference for 20–30 mm long limpets (Jacob's preference index relative to other length classes $D = 0.85$) and increasing avoidance to larger length classes. But the calculated profitability for successfully opened limpets increased monotonically with the length, and the largest limpets had the highest profitability. Hence, the oystercatchers apparently did not select the most profitable limpets according to the simplest rate maximising optimal diet model; however we argue that this is because handling time varies as a function of substrate condition, so that a more complex model is needed.

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1. Introduction

Rate maximising foraging theory states that animals will make choices that maximise the net rate of energy intake while foraging on some component of their food supply. The simple form of the theory assumes that the animal has full knowledge of the potential intake rates available from different prey and in different feeding areas. It has been found that the density and distribution of different sizes of prey (Goss-Custard, 1977; Nagarajan et al., 2002a; Sutherland, 1982), the accessibility of prey (Goss-Custard, 1969; Nagarajan and Thiyagesan, 1996; Nagarajan et al., 2006, 2008) and season (Cayford and Goss-Custard, 1990; Ens et al., 1996) influence predators' decisions in selecting the areas and prey in ways that are consistent with this theory. Predators' preferences effectively rank prey according to their profitability, which in optimal diet models is defined as the intake rate while prey are being handled (energy value/handling time) (Krebs, 1978), and reject prey for which the profitability is below the current average intake rate

(Zwarts et al., 1996). Predators can switch prey depending upon the availability and activity of prey, to maximise the energy intake (Zwarts and Esselink, 1989).

Optimisation, however, is always relative to some set of constraints (Parker and Smith, 1990), and these constraints will be different for different species. For example, specialist foragers are expected to be more effective than generalists in any particular foraging situation, to the point where it is an open question whether specialists and generalists exploiting the same prey can coexist, at least on an evolutionary time-scale (e.g. Egas et al., 2004). Both specialists and generalists may be optimal foragers, but the assumption is that the constraints within which a specialist operates, when feeding on its preferred prey, are less severe. The evolutionary and cognitive challenges involved in foraging optimally are different, depending on whether the predator is a specialist or a generalist. A mechanism for guiding choice between prey items that leads to an optimal diet with one prey type may be unhelpful or counterproductive with another; a generalist must thus either use broader, less precise strategies than a specialist, or it must carry the overhead of having a number of mechanisms available and selecting the appropriate one for each type of prey.

It is therefore of interest to know how far species that are known to forage optimally, or nearly optimally, on one prey type also forage optimally on others. Eurasian oystercatchers (*Haematopus ostralegus*)

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feed on a wide variety of prey (Hulscher, 1996), but individual birds usually concentrate on one prey type for long periods (Goss-Custard and Durell, 1983); they might be described as serial specialists (LeRossignol et al., 2011; Nagarajan et al., 2002b,c), a strategy which ought to reduce the cognitive overhead involved in being a generalist. Extensive studies have been conducted to relate optimal foraging models to the behaviour of oystercatchers feeding on mussels (e.g. Goss-Custard, 1996; Meire, 1996; Meire and Ervynck, 1986), but less is known about their behaviour towards other prey types. A number of papers indicate that optimal diet models provide a good account of most though not all the variations in foraging behaviour towards cockles (e.g. Norris and Johnstone, 1998; Rutten et al., 2006; Sutherland, 1982), and behaviour when feeding on worms and insects (Zwarts and Blomert, 1996) is at least qualitatively consistent with optimality predictions. Less is known about their foraging strategies when feeding on limpets, although these are a common prey where oystercatchers feed on rocky shores around European coasts (Coleman et al., 1999; Feare, 1971; Harris, 1965). The present paper therefore examines whether optimal diet models provide a good account of oystercatchers' foraging on this kind of prey, in order to consider what kind of mechanism might provide for near-optimal foraging across a range of prey types.

The research was carried out on the shores of the island of Lundy, where there is a resident Eurasian oystercatcher population preying chiefly on limpets (Ghosh et al., 2003). Limpets are harder to harvest than other molluscan prey (Lowell, 1986; Tyler et al., 2014). Their behavioural adaptations show remarkable variation in relation to location, nature of the rock and tidal condition (Santini et al., 2004). Such behavioural adaptations should influence the predators' prey choices if they are to forage optimally. Here we extend the optimal foraging analysis to the behavioural strategies of oystercatchers that feed on limpets. We investigated different feeding techniques used to feed on limpets, the lengths and characteristics of limpets that make them vulnerable for oystercatchers to feed on, and the most profitable length classes of limpets for the oystercatchers. Such an analysis will enable us to ask whether there are general strategies that enable oystercatchers to forage optimally on a range of prey types, or whether each kind of prey requires a different set of specialist strategies. It will also give insight into a characteristic predator–prey system of rocky shores, a significant ecosystem in most parts of the world and one that is often affected by economic development especially tourism.

2. Materials and methods

2.1. Study area

Lundy Island (51°10'N, 4°40'W) is located in the Bristol Channel, approximately 17 km off the North Devon Coast, England (Fig. 1). The island is 3.5 km² in area, and the waters around it are a statutory Marine Nature Reserve. There are many types of habitat on the island, ranging from more sheltered shores to ones that are exposed to strong wave action and wind. The Landing and Lametry Bays, where the observations were made, are east facing, partly sheltered and bordered by an eroding slate cliff of approximately 30 m in height.

2.2. Oystercatcher observations

Observations were made by RN using a ×20–60-zoom telescope from a vantage point near the rocks where the birds fed during March and April months of 1997 and 1998. The Lundy population feed extensively on limpets (Ghosh et al., 2003). They do not feed continuously, resting for almost all the high tide period. Whenever we saw that birds were feeding at low tide, an individual focal bird was selected at random and was observed for at least 10 min. Consumption of a total of 257 limpets was observed. The total number of limpets consumed during the 10-minute period was recorded. The handling time was

measured as the time elapsing between the moment that the bird found a limpet and the moment when the bird resumed searching or changed its behaviour to something other than foraging. The length of the limpets attacked by oystercatchers was measured by comparison with bill length and later converted into millimetres by taking the mean length of the oystercatcher's bill to be 75 mm (Goss-Custard et al., 1987). Following the observations, observer bias was estimated by using testing with a model of an oystercatcher with a bill length of 75 mm. A total of 21 limpets of length ranging from 20 to 50 mm, representing in all the length classes of 20–30, 30–40 and 40–50 mm were placed beside the model bill and viewed from the same distances as used for the observations as described in Goss-Custard et al. (1987) and repeatedly validated since. From the test it was inferred that RN tended to underestimate the length of limpets across all lengths. All length estimates were corrected for this bias using the equation

$$\text{Original Length (mm)} = 17.7 + 0.883 \text{ Estimated Length (mm)}$$

$$\left(R^2_{(\text{adj.})} = 80.3\%, F_{(1,20)} = 86.77; P < 0.001 \right).$$

2.3. Limpet population and Ash Free Dry Mass determination

The limpet population on the “feeding” rocks was sampled at intervals of one metre. The samples were taken from the upper surfaces of the rocks, avoiding the sides of the rocks and gaps between the rocks where oystercatchers cannot reach the limpets. Sixty stratified random samples from quadrats measuring 30 × 30 cm were taken. All the limpets in different length classes (length from the anterior tip, umbo to the posterior tip) were measured using vernier callipers. The length classes were 20–30 mm, 30–40 mm, 40–50 mm and 50–60 mm. A sample of 121 limpets was collected from different length classes for Ash Free Dry Mass (AFDM) estimation. The collected limpets were immediately deep-frozen. The relationship between the limpet length and Ash Free Dry Mass (AFDM) was calculated by the method described by Nagarajan (2000).

2.3. Collecting limpets opened by oystercatchers

The characteristics of limpets attacked by oystercatchers and in the population were determined as follows. The shells of 102 limpets freshly opened by oystercatchers, identified from the fresh flesh that remained inside the shell near the attachment of the adductor muscle, were collected from various parts of the rocky shore. The number of limpet shells that could be collected was limited by the fact that collection had to be done before the incoming tide washing away loose shells, without disturbing the birds. The following measurements were made on each shell, as shown in Fig. 2.

Length: The length of the limpet from the anterior tip (umbo) to the posterior tip was measured to the nearest 0.05 mm using a vernier calliper.

Depth: The external depth of the shells from the apex to the bottom was measured using the vernier calliper. The depth classes used were 1–5 mm, 5–10 mm, 10–15 mm, 15–20 mm and 20–25 mm.

Width: The distance between the mid-lateral sides was measured in the same way as the length.

Shell thickness: The thickness of the edge of the shells on the anterior and posterior sides was measured by using a digital micrometer with an accuracy of 0.001 mm.

Attacking side: The damage caused by oystercatchers could be seen in some of the limpets and whenever possible its location was noted to test for any preference for attacking particular regions of the limpet shells. The region was noted viewing from above either as anterior region, posterior or mid-lateral region, and classified either as right side or left side.

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