Chapter 6: Optimal Foraging Theory: Constraints and Cognitive Processes

Barry Sinervo © 1997-2006

Optimal foraging theory

Chances are, when observing animals in the wild, you are most likely to see them foraging for food. If successful, their foraging efforts culminate in feeding. Animals search, sense, detect and feed. For humans, feeding is often associated with pleasure. Similar sensations may underlie the proximate drive that motivates feeding behavior of animals. However, the ultimate reason for feeding arises from the difference between life and death. At some point in an animal's life it may experience episodes of starvation and prolonged starvation can lead to death. If animals survive and die as a function of variation in their foraging strategies then natural selection has run its course. Animals that survive are able to contribute genes to the next generation, while the genes from animals that die are eliminated, and along with it unsuccessful foraging behaviors. Understanding the rules that shape the foraging behavior of animals has been a central focus of behavioral analysis for more than four decades (Pyke et al. 1977).

It seems reasonable to assume energy gain per unit of time might maximize the resource an animal has for survival and successful reproduction. For example, the common shrew, *Sorex araneus*, faces foraging decisions that keep it only a few hours away from death. Like all mammals, the shrew maintains a high and constant body temperature during activity. To keep itself warm, the shrew has a very active metabolism. Because the shrew's body is extremely small compared to larger mammals its surface area is very large relative to its body mass. If we compare the shrew to a rat, we would see that the shrew loses considerable heat to the environment. On a gram-per-gram basis the shrew's metabolism is much higher than mammals of larger size (Peters 1983; Calder 1984). Because of its high metabolism, the shrew satiates its voracious appetite with protein-rich insects, a high quality resource. The shrew must forage constantly, and barely has a moment to sleep because its small body size does not afford it the luxury of a thick layer of fat. The shrew has very few energy reserves onboard and only few hours without feeding (Barnard and Hurst 1987) can lead to death (Crowcroft 1957; Vogel 1976).

Even if food is abundant in the environment, and the shrew does not face life-or-death foraging decisions, it must have sufficient energy to reproduce. Natural selection will favor those individuals in a population

that have relatively high reproductive output. Thus, survival and reproduction must also be related to the efficiency of energy acquisition and energy storage. A reproductive female shrew has the added energetic outlay of nursing young. Reproductive females must maintain a positive energy balance for themselves and acquire enough excess energy to nurse their pups with energy-rich milk. The efficiency of the female shrew's foraging decisions may affect the size of her pups at weaning. In turn, the size at weaning might impact the probability of their survival to maturity. Life, death, birth, and successful reproduction in the shrew are measured in terms of calories taken in on a minute-by-minute basis.

Given the urgency of the "decisions" faced by shrews, the shrew may not even consider every insect it encounters as a worthwhile prey item. Imagine that a shrew is foraging for prey. During its forays in the rich humus of the forest floor, it encounters some small, but evenly dispersed species of grub with clockwork regularity. When it encounters one grub, should it eat the isolated prey? It takes some time to handle the prey and then more time to search for another. To calculate the value of that isolated prey item for the shrew we should take into account the value of the individual prey and the time it takes to find the prey. Should the shrew ignore the single isolated prey item or continue searching for a concentrated nest of termites that yields a much higher payoff. While the payoff from a termite nest is high, the nests are dispersed in the environment and locating them is a stroke of luck. The payoff from a large concentration of termites means the difference between making it through the long cold night versus the sure death it faces from feeding on the small grubs that are evenly distributed which it encounters on a regular basis. Yet these grubs are insufficient to sustain its needs. Animals make foraging decisions in the face of uncertainty. In this chapter, we address issues of foraging in the face of uncertainty. In other words, when does it pay to gamble? To understand gambling, we first need to understand the currency used by animals to make decisions, and the constraints on such decisions.

The theory of optimal foraging addresses the kinds of decisions faced by shrews, and indeed all animals. Regardless of whether foraging efficiency has an immediate impact on life or death, or whether it has a more cumulative or long-term effect on reproductive success, animals make decisions in the face of constraints. **Temporal constraints** are couched in terms of the time it takes to find and process food. **Energetic constraints** are couched in terms of the metabolic cost of each foraging activity (foraging, processing, etc.) per unit time. Animals must learn about the distribution of food in their environment if they are to make the appropriate choices. How much learning is possible for an animal? Is there a limit to learning and memory, and do such **cognitive constraints** limit the foraging efficiency of animals?

The first issue we must address before considering the more complex decisions faced by economically minded, but perhaps cognitively challenged animals is the choice of **currency**. What are the units of currency used by animals when conducting their day-to-day transactions with the environment? How do basic energy and temporal constraints dictate the form of currency that animals use? A simple currency can be expressed in terms of the value of an item, taking into account the cost of acquiring the item, and the time taken to acquire the item. Natural selection might shape decision rules such that animals maximize net energy gain (e.g., gross gain - costs) as a function of time:

$$\text{Profitability of Prey} = \frac{\text{Energy per prey item - Costs to acquire prey}}{\text{Time taken to acquire prey item}}$$

The Prey Size-Threshold: a Decision Rule that Maximizes Profit

Prey size is one of the most conspicuous features that a predator could use to discriminate prey quality. The quality of the prey expressed in terms of energy content rises in direct proportion to mass, and corresponds roughly to the cubic power of prey length. It is more profitable to eat large prey, provided the prey is not too large so that the predator runs into **processing constraints**. For most animals the rule "never swallow anything larger than your head" is a simple rule by which to live. However, snakes break this rule routinely. Consider the anaconda in the Amazon forest that is capable of swallowing a deer. Some animals find ways around processing constraints by evolving adaptations. Snakes can eat things that are bigger than their head because they have a hinged jaw with an extra bone that gives them great flexibility when swallowing. All snakes share this unique adaptation for foraging. Most other animals solve the problem by chewing their food.

How about the rule, "eat things you can open." The thickness of a shell may deter many predators. Most snakes can't eat a bird egg because eggs are very resistant to radially distributed crushing forces (i.e., eggs must sustain the weight of the adult female during incubation). However, egg-eating snakes have evolved special points on the bottom of the spine (Arnold 1983). They press the egg up against the point and voila, cracked egg. A force that is concentrated at a point source breaks the egg like the edge of bowl used by humans. Egg-eating snakes have evolved an additional adaptation. Difficulty in opening or subduing prey should rise with prey size. Indeed, egg-eating snakes may have difficulty with an ostrich egg. The **handling time**, or the time taken to catch, subdue, and consume prey, will increase with prey size and prey armor.

If it is generally desirable to acquire large prey up to a **maximum size threshold**, the crucial question becomes what is **minimum size threshold** for prey in the diet. A prey item that is encountered in the environment should be consumed if it is above the size threshold, but should be rejected if it is below this threshold. The point at which consuming the prey becomes profitable depends on the **search time** and **the handling time** of prey as a function of the size threshold. If the size threshold is too large, a predator will wander around and deem a large fraction of the prey to be unacceptable. Such finicky behavior increases the search time between encountering successive prey items. This additional search time will eat away at the predators overall profits from a long sequence of prey, because the predator is metabolically active for a longer period of time during search. The predator receives no reward until it accepts and eats an item. The smallest size of prey that a predator should attempt to eat to maximize energy gain per unit time is our first example of an **optimal decision rule**, subject of course to the **constraints** of prey armor and the time taken to find prey.

An Optimal Decision Rule for Crows Foraging on Clams

The common crow, *Corvus caurinus*, forages in the intertidal and provides a clear example of optimal decision rules for prey-size selectivity (Richardson and Verbeek 1986). Japanese little-necked clams of various sizes are found under the sand on a typical ocean beach along the northwest coast of North America. The location of clams is not obvious to a crow and it has to probe to find clams. A crow spends an average of 34.6 seconds locating and digging up a single clam.
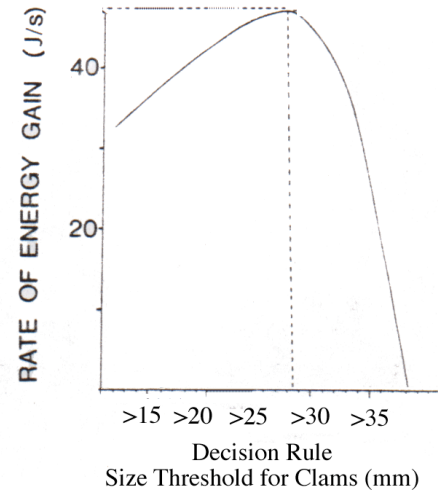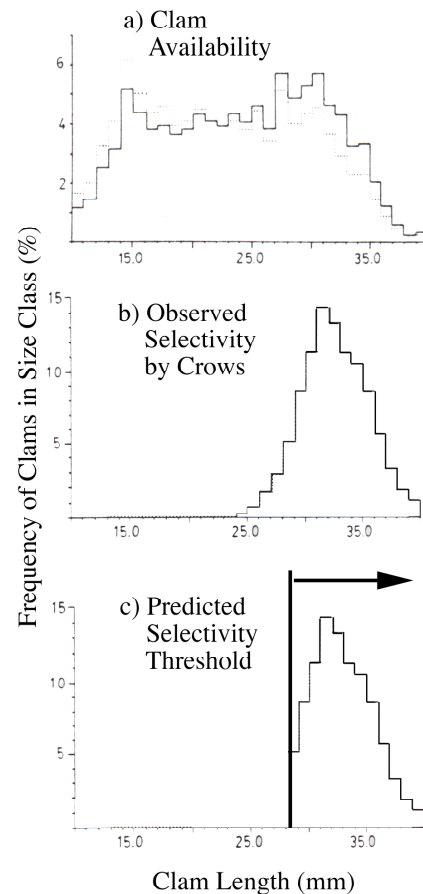

Figure 6.1. The rate of energy gain for crows, *Corvus caurinus*, foraging in the intertidal if they were to use different decision rules for the size threshold of clam that they are willing to open and eat. The greatest rate of energy gain or *optimal foraging strategy* would be achieved if crows ate every clam above 28.5 mm.

The crow has solved the problem of opening the clam with a short dive-bombing flight. The crow makes a short flight lasting 4.2 seconds and then drops the clam on a rock. If the clam does not break, the crow requires an additional 5.5 seconds for a second flight, and 2 more seconds for the second drop. It takes the crow an average of 1.7 flights to crack open a clam, thus the average clam requires 4.2 × 1 + 5.5 × 0.7 = 8.1 seconds of flight time. The probability that a clam breaks open is independent of clam size. The amount of time that a crow invests in searching for clams is 4.3 times greater than the amount of time the crow spends in cracking open the clam with its dive-bomb flights. However the cost of flight in crows is nearly 4 times more expensive than the cost of search and digging. Thus, the search costs and handling costs expressed in terms of energy are nearly equivalent, but the search costs are more than 4 times more expensive than the handling costs expressed in terms of time. Crows reject many clams that they dig up and leave them on the beach unopened. If the crow goes to the trouble of finding and digging up a clam and all this takes time and energy, why doesn't it eat all clams regardless of size, particularly since the search takes up the most time?

The answer to this question lies in the average net profitability of the clams as a function of size. We can compute the profitability of a single clam per unit of time once we discount all of the energy and time constraints of foraging by using the following equation:

$$\frac{Energy}{Time} = \frac{\text{Energy per clam as a function of size} - (\text{Search Costs} + \text{Handling Costs})}{(\text{Search Time} + \text{Handling Time})}$$

Figure. 6.2 a) Availability (frequency) of clams as a function of size on the beach at Mitlenatch Island, British Columbia. b) Frequency distribution of the clams that were eaten by the crows. c) Predicted size distribution of clams the crows should have chosen if they were foraging optimally and maximizing energy gain per unit time. The size-threshold is a truncation point or an absolute size below which the crows should not eat clams. Only a few clams were chosen below the size threshold and the majority of clams were chosen above the size threshold. The size-threshold is referred to as an *optimal decision rule*. From Richardson and Verbeek (1986)

a) Clam Availability

b) Observed Selectivity by Crows

c) Predicted Selectivity Threshold

Frequency of Clams in Size Class (%)

Clam Length (mm)

To compute a clam's net profitability, Richardson and Verbeek (1985) computed the amount of energy that the crow expends in each of the following tasks: walking and searching, flying, and handling. This reflects the amount of energy expended in foraging. The amount of energy increases with the size of the clam and the net profitability of a single clam increases with size.

However, the simple formula in equation 6.2 is for the profits from a single clam. A crow eats many clams during a single bout of foraging, thus we must calculate the average profitability from a long string of rejected and accepted clams (Figure 6.1). The greatest rate of energy gain is achieved if a crow accepts clams greater than 28.5 mm. Why does energy gain decline when the crow uses a larger cutoff value for acceptable clams? Shouldn't such finicky behavior mean that it eats only the best and largest clams? Rather than show a formula, let's consider a verbal argument. A crow that is too choosy will wander across the

mudflat rejecting too many small clams. A crow that is not choosy enough will waste a lot of time feeding on tiny clams that take too much time to crack open for the measly reward found inside. If crows were to accept clams below this size threshold of 28.5 mm, they would take too long to open the clams relative to the energy content of derived from small clams. Below the optimal size threshold the *energy per clam is* so low that the return is not worth the handling time of flying over to the drop rock to crack the clam open. Conversely, rejecting too many large clams and using a decision rule above 28.5 mm would lead to more time spent searching for suitably large clams. Large clams constitute a much smaller proportion of the available clams, than medium sized clams. Increased search time lowers the average yield from all clams eaten.

The best foraging strategy, or the **optimal decision rule** that crows should live by, is to accept all clams above 28.5 mm. It is always pays to attempt the largest clams because they are enormously profitable and do not require any extra energy to crack open. The size-threshold decision rule that was actually observed by Richardson and Verbeek (1985) was very close to 28.5 mm. How well does the model for the optimal foraging decision rule of clam selectivity fit the observed data? Only a few clams were chosen below this threshold, and nearly all clams were eaten above this size threshold. Crows appear to have an optimal decision rule for accepting and rejecting clams on the basis of size.

Oystercatchers and the Handling Constraints of Large Prey

Students of optimal foraging often seek generality by studying different species undertaking similar tasks. The foraging crows did not face any constraints of large prey size, however, the largest prey were relatively rare, forcing crows to feed on small clams to maximize profit. Meire and Ervynck (1986) carried out a similar analysis of Oystercatchers, *Haemotopus astralegus*, foraging in mussel beds as a test of optimal foraging theory. Oystercatchers forage on mussels with the added difficulty of cracking open the mussels with their bills rather than doing the fly-and-drop technique of crows. Oystercatchers appear to be quite size selective because large mussel have thicker shells. Even when they attempt to open the mussels with thin-walled shells, the oystercatchers have far lower success in opening large versus small mussel shells.

The increased handling time for the larger mussels enhances the relative profitability of small prey (see Side Box 6.1). If this difference in handling time were ignored and we used a model similar to the foraging crow, then oystercatchers should choose mussels greater than 55 mm in length. However, the enhanced profitability of the easy-to-open small mussels pushed the threshold value for the most profitability mussel down to a minimum size of 25 mm. Oystercatchers appear to use a decision rule that is very close to the size threshold predicted from an elaborate optimal foraging model that takes into account a number of constraints on foraging (see Side Box 6.1). Oystercatchers, like the crows, have developed an optimal rule for size selectivity feeding on mussels.

Figure. 6.3 a) Availability (frequency) of mussels, *Mytilus edulis*, as a function of size on Slikken van Vianen, a tidal flat in the Netherlands b) Frequency distribution of mussels that were observed as having been opened and eaten by oystercatchers (*Haemotopus astralegus*). c) Predicted size distribution of mussels the oystercatchers should have chosen if they were foraging optimally and maximizing energy gain per unit time. Only a few mussels were chosen below the optimal size-threshold and the majority of mussels were chosen above this point. See Side Box 6.1 for a complete description of constraints that Meire and Ervynck (1986) used in their optimal foraging model (from Meire and Ervynck, 1986).
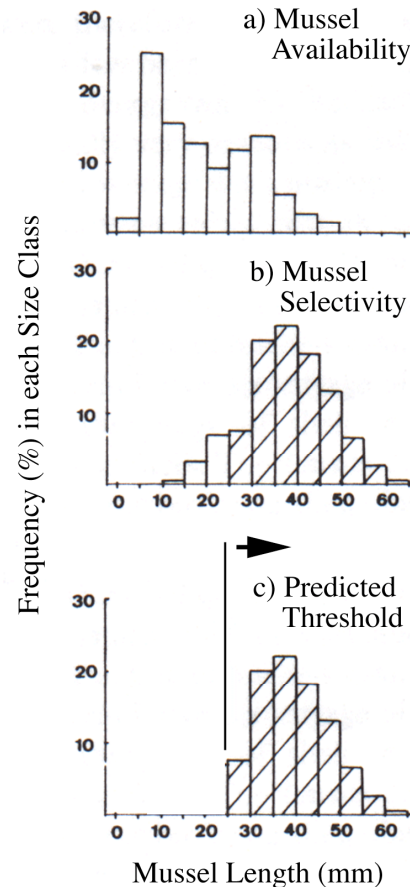
Comparable tests of size selectivity have been repeated in a variety of taxa feeding on the same resource or drastically different resources. Shore crabs, *Carcinus maenas*, prefer to eat mussels of a size that maximize rate of energy return per unit of time (Elner and Hughes 1978). The theory of selectivity also appears to hold for herbivores that show selectivity for quality of plant food. Herbivores that range in size from the Moose, *Alces alces*, to the Columbian ground squirrel, *Spermophilus columbianus*, appear to be energy maximizers. However, the requirement for a balanced diet restricts herbivores from feeding exclusively on the highest energy foods, which lack vital micronutrients. Herbivores supplement their dietary energy gains with the right mix of alternative foliage that supplies key micronutrients (Belovsky 1978; Belovsky 1984). In contrast, predators can often follow a simple rule of eating prey that are made of things that they can use in building their bodies. Predators need not be as picky about the composition of prey, but as we have seen, can be quite sensitive to handling constraints.

A Summary of the Model Building Process

Not all systems studied to date have shown such a perfect fit to the data. Indeed, when a lack of fit is observed, it may be the case that factors not considered may influence animals in nature. It is invariably assumed that animals maximize some currency, however, the maximization of this currency is subject to various constraints such as time and energy. Identifying the optimal decision rule that maximizes the currency while the animal labors under constraints is the primary goal of optimal foraging theory. Model building for Oystercatchers is detailed in Side Box 6.1 The model building process underlying optimal foraging theory entails the identification of three parameters (Krebs and Kacelnik 1991):

i) The foraging **currency** maximized by both crows and oystercatchers is energetic efficiency or net energy gain/unit of time. In the examples presented below, the currency may be quite different depending on the specific needs of animal. For example, a foraging parental starling is not just concerned with caring for its own needs, but must also tend to the needs of its developing chicks. Similarly, the foraging bee could be maximizing its own efficiency as a worker, but a more likely possibility is that the bee is maximizing efficiency for its colony.

ii) Foragers also work under energetic and time **constraints**. The time **constraints** may be fixed, as in the case of crows, which have a constant time to find the next item irrespective of prey size. Alternatively, the constraints such as handling time may vary with prey size, as in the case of oystercatchers (see Side Box 6.1). The energetic costs of foraging activities such as flight and walking vary enormously. Failure to identify all constraints, and the precise nature of the constraints will result in a model that has poor predictive power. Even in the case of a simple model for foraging, a suite of factors limits oystercatchers, which must all be considered to achieve a close fit between theory and observation (see Side Box 6.1). Finding the constraints may entail an iterative process; the complexity of an optimal foraging model is gradually increased and constraints are added until all salient ones have been identified and good fit is achieved.

iii) The appropriate **decision rule** must also be identified. A test of optimal foraging compares the observed size threshold with that predicted from the size distribution of prey in the environment and the constraints of foraging. The observed threshold size for acceptance of prey items for crows and oystercatchers appeared to match the predicted threshold size quite closely indicating a good fit with the model.

Richardson and Verbeek (1986) only considered a single model of optimal foraging. Animals labor under time and energy constraints that are independent of prey size and additional ecological constraint relates to the rarity of the largest, most-profitable prey. Meire and Ervynck (1986) considered three different models of optimal foraging that varied in the number of constraints built into the model. The simplest model only included the profitability as a function of prey length. A more complex model factored in the difficulty in opening prey of various size, and the attractiveness of prey (e.g., barnacles make mussels more difficult to open). The most complex model also factored in the availability of mussels on the beach. The simplest foraging model did not adequately predict the observed size threshold of acceptance, nor did the second model, but a more complex model that included the increased handling time and difficulty of cracking thick-walled mussels provided a surprisingly good fit to the observed size threshold. It is often the case that behaviorists first consider the simplest model before proceeding to a more complex explanation for the behavior of animals.

Finally, the crow and the oystercatcher faced the same basic search constraints. The size distribution of prey in the environment was a major factor governing whether or not a bird accepted or rejected a prey item. The size distribution of prey is an example of how ecology of the prey constrains the optimal foraging solution adopted by the birds. It is not necessarily the case that mussel availability remains constant throughout the year. Moreover, not all animals use the same foraging strategies, as there is more than one way to crack a nut. Crows drop clams while oystercatchers hammer them open. Individuals within a single species might likewise vary in their use of alternative feeding strategies.

Variation in feeding mechanisms within a population

Our models of crows and oystercatchers suggest that there is one unique decision rule that maximizes energy intake per unit of time. However, animals vary dramatically in the kinds of foraging behaviors that they use in nature. Differences in foraging techniques can have a dramatic effect on the optimization decision rules that various individuals use in a single population. Cayford and Goss-Custard (Cayford and Goss-Custard 1990) have observed oystercatchers foraging with three styles:

1. stabbers that use their bill to stab the vulnerable area between the valves,

2. dorsal hammerers that use their bill to hammer through the dorsal surface of mussels, and

3. ventral hammerers that opt for the opposite side.

Each foraging style has different handling times. Dorsal hammerers take the longest to break through the mussel followed by the ventral hammerers. The stabbers are the fastest at cracking mussels open with their bills. Given this efficient style, stabbers should feed on the largest mussels. Conversely, dorsal hammerers should feed on mussels that are intermediate in size. These gross expectations are borne out by natural history observations made by a number of researchers (Norton-Griffiths 1967; Ens 1982). Every factor considered by Meire and Ervynck (1986) to be constraints on foraging oystercatchers (see Side Box 6.1) were also found to differ for the individual oystercatchers that adopted one of the three feeding-styles (Cayford and Goss-Custard 1990).

Side Box 6.1. Constraints on Optimal Foraging

The mechanics of the optimal modeling process are well illustrated by Meire and Eryvnck's (1986) observations of foraging oystercatchers. The energy content of a mussel increases roughly to the cube of length (Dry Weight (mg) = 0.12 length$^{2.86}$) and large mussels have an enormous pay-off relative to small mussels. The following temporal, energetic, and ecological constraints set limits on decision rules adopted by oystercatchers.

a) Is the pay-off for large mussels offset by the increased handling time? The oystercatcher's handling time increases linearly with mussel length for both the mussels that they open (solid dots) or those that they abandon unopened (open dots).
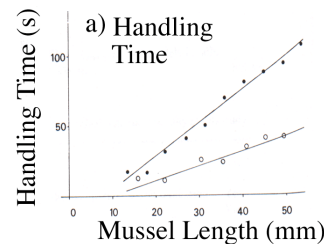
a) Handling Time

b) Model I: When we consider the increase in handling time for large mussels, profitability of Mussels still increases with Mussel Length (mm). Profitability = E/H, reflects energy gained per unit of handling time (Krebs 1978). Model I implies the largest mussels are always most profitable.

b) Profitability = E/H
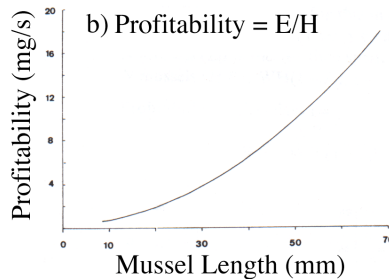
c) However, the probability that an oystercatcher successfully opens a mussel declines inversely with mussel size. An oystercatcher can open every mussel that is below 15 mm in length, but success declines rapidly as size increases and oystercatchers can't open mussels greater than 70 mm.

c) Success in Opening
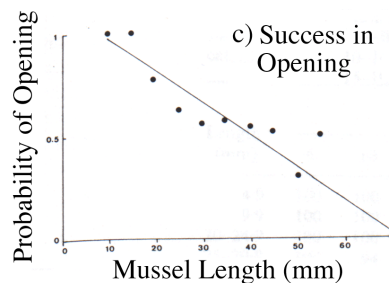
d) Model II: A more realistic model would adjust the profitability of a mussel by the size dependence of: energy content (E), probability of opening (P, from panel c) or failing to open the mussel (1-P), the handling time for opened mussels (H) and time wasted on unopened mussels (W):

$$P\mathit{rofit} = \frac{E \times P}{H \times P + W \times (1 - P)}.$$

Decision Rule: Size Threshold (mm)
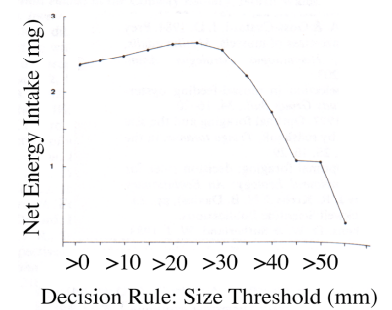
The optimal size (peak on the curve) predicted from this model is 52 mm, which is far greater than the observed 25 mm threshold.

e) In addition, mussels that are covered in barnacles are not as attractive to oystercatchers. The largest, oldest mussels have more barnacles.
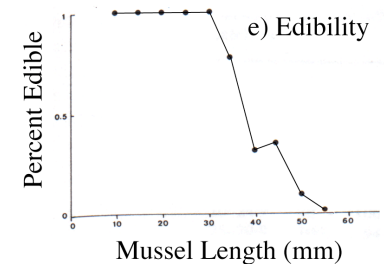
However, Model II is still inadequate as it is based on the profit from single individuals, not profit that an oystercatcher can extract from foraging sequentially on the mudflat for mussels that vary in size.

e) Edibility

f) Model III: As in seen in the example with finicky crows, if an oystercatcher rejects too many small mussels, travel time to the next suitable mussel is greatly increased. The increase in travel time causes a decrease in average profitability of being too finicky and feeding on large mussels. This shifts the curve for model II to the right. The resulting profit curve yields an optimal size-threshold for feeding of 25 mm (peak on the curve), which matches observed oystercatcher selectivity quite precisely (Fig. 6.3).

d) Energy Gain