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An Introduction to Behavioural Ecology

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Chapter 3. Economic Decisions and the Individual

In this chapter we will describe in more detail how the idea of economic analysis of costs and benefits can be used to understand behaviour. Most of our examples will refer to foraging, but the same principles apply to other aspects of behaviour.

The economics of carrying a load

STARLINGS

Starlings feed their young mainly on leatherjackets (*Tipula larvae*) and other soil invertebrates. A busy parent at the height of the breeding season makes up to 400 round trips from its nest to feeding sites every day, ferrying a load of food to its insatiable nestlings on each trip (Fig. 3.1). In this section we are going to focus our microscope of economic analysis on one aspect of the parent starling's behaviour and ask: How many leatherjackets should the parent bring home on each trip? This may seem like

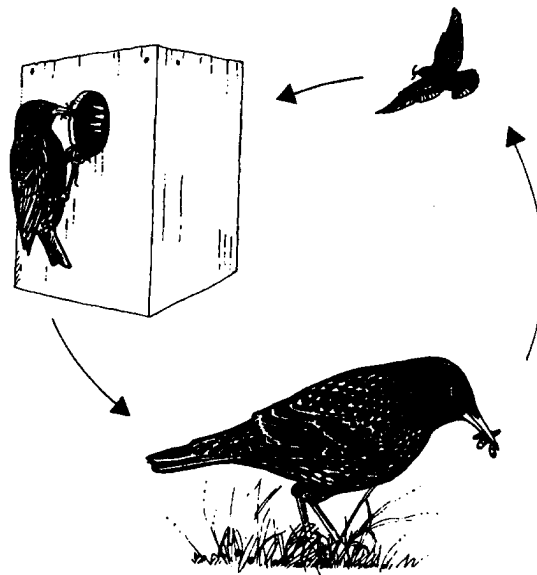


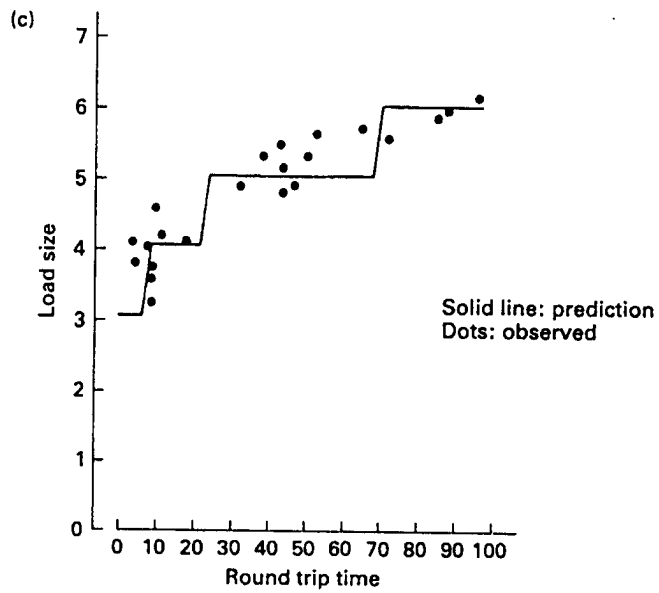
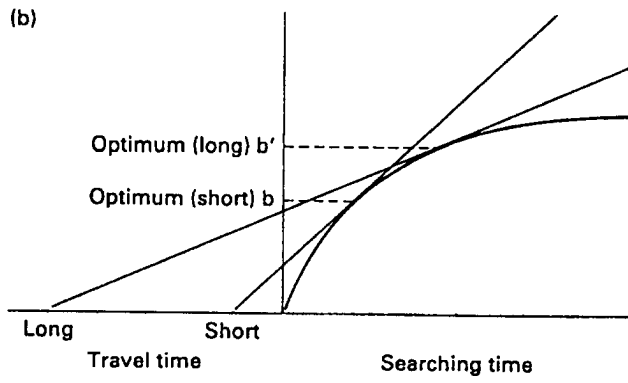
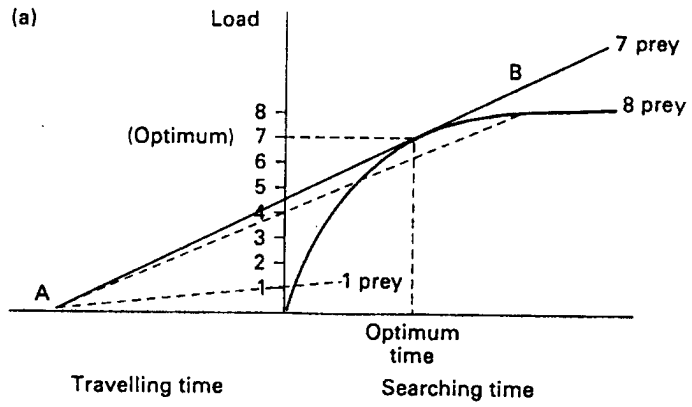
Fig. 3.1 Starlings fly from their nest to a feeding site, search for a beak-full of leatherjackets by probing in the grass, then take them home to the nestlings. The question examined in the first part of this chapter is how many items the parent should bring on each trip in order to maximize the rate of delivery of food to the nestlings.

an inconsequential question, but the size of load has a critical effect on the parent's overall rate of delivering food to the nest, which in turn determines whether or not the chicks survive to become healthy fledglings. As we saw in Chapter 1, the reproductive success of small birds is often limited by their ability to feed their young. There is therefore strong selective pressure on the parents to perform as effective food deliverers.

It is not hard to imagine why it would be a poor strategy to bring one leatherjacket on each trip, given that the parent is in fact capable of carrying several at a time: the amount of travelling back and forth for the parent would be unnecessarily high. It would be as if you did your week's shopping at the supermarket by making a separate trip for each individual item instead of collecting a whole bag full of groceries on one trip. Should the starling, therefore, bring back the biggest load it can carry on every trip? The answer is no, because of a crucial fact about starling foraging behaviour. A starling hunts for food by probing with its bill in a special way. It thrusts its closed bill into the turf of a meadow and then spreads its mandibles to part the vegetation and expose the leatherjackets just below the soil surface. The bird is very efficient at probing, but when it has a load of leatherjackets already in its bill it becomes less efficient. For this reason it is not necessarily the best thing for the starling to fully load its beak before flying home to unload and start again. A similar kind of problem faces many animals that carry a load back to their nest or some other central place such as a cache of food.

The starling's problem of load size can be summarized as a graph (Fig. 3.2a). The graph shows time along the horizontal axis and load (measured in leatherjackets) on the vertical axis. Consider a starling at the nest about to embark on a round trip. It has to fly to (and eventually from) the feeding site; the times of these two trips are added together and plotted on the graph as 'travelling time'. When it arrives at the part of the meadow where the leatherjackets are abundant it starts to load up with food. The first couple of leatherjackets are found quickly and easily, but because of the encumbrance of the prey in its beak, the bird takes longer and longer to find each successive prey. The result is a 'loading curve' (or 'gain curve' as it is sometimes called) that rises steeply at first but then flattens off. This is a curve of diminishing returns — the longer the starling has been foraging, the less likely it is to find another leatherjacket in the next few moments — and the starling's problem, as summarized in the graph, is when to give up on this curve. If it gives up too early it spends a lot of time travelling for a small load; if it struggles on too long it spends time in ineffective search which could be

Optimal load size in starlings: diminishing returns



better spent by going home to dump its load and starting again at the beginning of the loading curve. Somewhere in between these extremes is the starling's 'best' option. A reasonable hypothesis (but at the moment it is no more than this), is that for the starling 'best' means 'providing the maximum net rate of delivery of food to the chicks'. Any starling that is slightly better at producing chicks than its rivals will be at a selective advantage, so selection should in the long run favour behaviour that maximizes chick production.

The theoretical optimum can be shown graphically

The best load can be found by drawing the line AB in Fig. 3.2a. The slope of this line is (load/[travel-time + foraging-time]) or in other words rate of delivery of food; this can be seen by the fact that it forms the hypotenuse of a right angled triangle with a base measured in 'time' and a vertical corresponding to 'load'. Now, travel time and the loading curve are constraints – fixed properties of the environment (or more precisely of the interaction between the starling and its environment), so any line such as AB representing the starling's rate of delivery of food has to start at the beginning of the round trip travel time and touch the loading curve somewhere. Any other line you could draw with these constraints will have a shallower slope (that is, give a lower rate of delivery) than the line AB. A couple of examples are shown in Fig. 3.2a.

The model predicts smaller loads with shorter travel times

Figure 3.2b develops the argument a little further. Suppose that the starling now switches to feeding at a closer site with a short travel time, how should its load per trip change? Using the same method as before, we can now draw two lines (Fig. 3.2b):

Fig. 3.2 *Opposite.* (a) The starling's problem of load size. The horizontal axis shows 'time' and the vertical axis shows 'load'. The curve represents the cumulative number of leatherjackets found as a function of time spent searching. The line AB represents the starling's maximum rate of delivery of food to the nestlings. This rate is achieved by taking a load of 7 leatherjackets on each trip. Two other lines, corresponding to loads bigger (8) and smaller (1) than 7 are shown to make the point that these loads result in lower rates of delivery (shallower slopes). Note that although the cumulative load is shown here as a smooth curve, in reality it is a stepped line since each food item is a discrete package. (b) When the round trip travel time is increased from short to long the load size that maximizes delivery rate increases from b to b'. (c) When starlings were trained to collect mealworms from a feeder, they brought bigger loads from greater distances. Each dot is the mean of a large number of observations of loads brought from a particular distance. The predicted line goes up in steps because the bird is predicted to change its load size in steps of one worm (of course the mean loads do not have to be integers). The prediction shown here is one based on the model of Fig. 3.2b, but it also includes the refinement of taking into account the energetic costs to the parent of foraging and to the chicks of begging. From Kacelnik (1984).

when the travel time is shorter, the load that maximizes rate is smaller. One way to think of this is to imagine the starling at its moment of decision to go home. If it goes it loses the opportunity to continue foraging, if it stays it loses the opportunity to go home and start afresh. When it is far away the expected returns from going home are relatively low, since there is a long way to fly before the next chance to forage. It therefore pays to persist a little longer on the present trip, until current gains drop to a slightly lower level.

The predicted and observed relationships between load size and travel time are similar

Alex Kacelnik (1984) tested this prediction of the model of load size in the following way. He trained parent starlings in the field to collect mealworms for their young from a wooden tray onto which he could drop mealworms through a long piece of plastic pipe. Rather than letting the birds generate their own loading curve by diminishing search efficiency, Kacelnik generated the curve for them by dropping mealworms at successively longer and longer intervals. The trained bird would simply wait on the wooden tray for the next worm to arrive, until eventually it flew home with a beak-load for its chicks. The beauty of this experimental method is that Kacelnik knew the shape of the loading curve precisely and was hence able to present exactly the same loading curve at randomly varying distances (ranging from 8 to 600 m) from the nest on different days. The results were striking (Fig. 3.2c): not only did the load size increase with distance from the feeder to the nest, but there was a close quantitative correspondence between the observed load sizes and those predicted by the model of maximizing delivery rate.

Optimality models include assumptions about currencies and constraints

Let us briefly summarize what the results of the starling study show. We started off by considering load size from the point of view of costs and benefits. We formulated a specific hypothesis about how costs and benefits might influence load size in the form of a model (Fig. 3.2a), and then used the model to generate a quantitative prediction (Fig. 3.2b). In making the model we did three important things. First we expressed a general conviction that starlings are designed by natural selection to be good at their job of parenting. This is not something that we aimed to test, but it is our general background assumption to justify thinking in terms of maximizing pay-off in relation to costs and benefits. Second, we made a guess about the *currency* of costs and benefits; we suggested that for a parent starling the crucial feature of doing a good job is maximizing net rate of delivery of food to the nestlings (rather than, say, waking them up as little as possible which is what human parents of young babies might favour!). Third, we specified certain *constraints* on the starling's behaviour. Some of these constraints are to do with features of the environ-

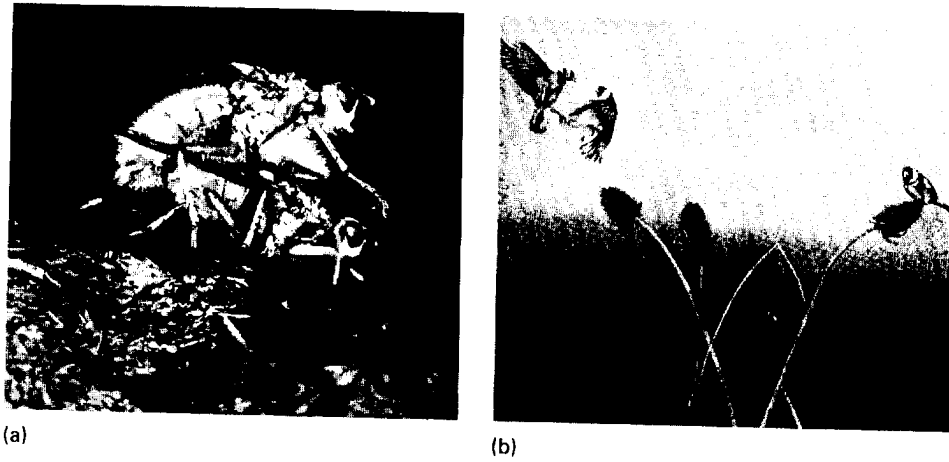


Fig. 3.3 (a) The model in Fig. 3.2 can be used to predict the duration of copula in dungflies (Box 3.1) and (b) to make predictions about many other examples of animals exploiting patchily distributed resources, such as these goldfinches (*Carduelis carduelis*) feeding on teasel heads.

ment (the time required to travel, the shape of the loading curve) and in the experiment of Kacelnik, they were clearly identifiable. Another important assumption about constraints is that the starling is assumed to 'know', or at least to behave as if it knows, the travel time and the shape of the loading curve. When we worked out the optimum load size we assumed that these were known. The experimental results supported the predictions of the model, and in so doing they supported the hypotheses about the currency and the constraints that were used to construct the model. Kacelnik did actually compare the predictions of models based on several different currencies, and he found for example, that one based on energetic efficiency (energy gained/energy spent) as opposed to rate gave a rather poor fit to the data.

The model of load size (usually called the 'marginal value theorem' (Charnov 1976)) is applicable to lots of situations in which an animal exploits a resource that occurs in discrete sites or patches, and within a patch it experiences diminishing returns (see Box 3.1 and Fig. 3.3).

BEEES

A similar problem to that of the starling is faced by a worker honey bee as it flies from flower to flower filling its honey crop with nectar to take back to the hive. Bees, like the starlings, often return to the hive with less than the maximum load they could carry and their behaviour can be explained by a model

The importance of comparing alternative models

How much nectar should a bee carry home?

In bees, diminishing returns arise from the cost of carrying nectar

similar to that used for the starling. There is, however, an important difference: the bee experiences a curve of diminishing returns neither because the nectar in its crop makes it less able to suck more flowers nor because of resource depression (Box 3.1) but because the weight of nectar in the crop adds an appreciable energetic cost to flight. The more the bee loads up its crop the more of its load it will burn up as fuel before it gets home. As a consequence, while the gross quantity of nectar harvested increases at a constant rate, the *net* yield of energy for the hive increases at a diminishing rate as the crop fills (producing, in effect, a loading curve like that of the starling).

Paul Schmid-Hempel (Schmid-Hempel *et al.* 1985) tested whether these diminishing net returns influence the bee's decision about when to go home and empty its crop. He trained bees to fly from the hive to a cluster of artificial flowers, each containing 0.6 mg of nectar. By varying the amount of flight the bee had to do between each flower in the cluster, he could alter the total cost of carrying the crop load and therefore the extent to which the bee experienced diminishing net returns. If, for example, the bee could collect a load of 10 flower's-worth of nectar while flying for a total of 5 s, it would experience little decrease in returns as it loaded up, while a bee collecting the same load by flying for a total of 50 s would suffer sharply diminishing returns. As predicted, the bees went home with smaller loads when they were forced to fly a greater distance between flowers (Fig. 3.4a). Figure 3.4a also shows two predicted lines based on maximizing two different currencies. One is based on the currency used for the starlings, net rate of energy delivery, while the other is based on a currency that did not work for the starlings, energetic efficiency. In contrast to the starlings, the second currency but not the first accounts for the bees' behaviour.

Bees maximize efficiency and not rate of energy gain

Box 3.1 *The marginal value theorem and reproductive decisions.*

The model of load carrying for starlings is applicable to many other situations in which animals experience diminishing returns within a patch. It has been used to predict how much time an animal foraging for itself (as opposed to carrying loads) will spend in each site before moving on (Cowie 1977). Diminishing returns in each patch (generally referred to as 'resource depression') might arise, for example, simply because of depletion, or because prey in the patch take evasive action and become harder to catch, or because the predator becomes less likely to search new areas in the

patch (it crosses its own path more) as time goes by, or because the predator starts with the easy prey and then goes on to hunt for those that are more difficult to catch or are less rewarding. An example of the last of these is when bumblebees or other nectar-feeders visit the biggest and most rewarding flowers on an inflorescence first, and then go on to the smaller flowers which hold less nectar (Hodges & Wolf 1981).

Reproductive decisions can be analysed as though they are foraging decisions with the same model. An example is Geoff Parker's (1978) analysis of how male dungflies search for mates. Males compete with one another for the chance to mate with females arriving at cowpats to lay their eggs. Often one male will succeed in kicking another off a female during copulation and take her over. When two males mate with the same female the second one is the individual whose sperm fertilizes most of the eggs. Parker (1978) showed this by the clever technique of irradiating males with cobalt-60, which sterilizes them but does not alter sperm activity (the sperm can still fertilize an egg but the egg does not develop). If a normal male is allowed to mate after a sterile one about 80 per cent of the eggs hatch, whereas if the sterile male mates second only 20 per cent of them hatch. The conclusion from these 'sperm competition' experiments is clear: the second male's sperm fertilizes about 80 per cent of the eggs. It is not surprising, therefore, that after a male has copulated he sits on top of the female and guards her until the eggs are laid, only relinquishing his position to a rival male after a severe struggle.

When a second male takes over (or when a male encounters a virgin) how long should he spend copulating? Parker carried out sperm competition experiments in which he interrupted the second male's copulation after different times; this showed that the longer the second male mates the more eggs he fertilizes, but the returns for extra copulation time diminish rapidly (see Fig. on p. 56). There is a cost associated with a long copulation: the male misses the chance to go and search for a new female. After the male has copulated for long enough to fertilize about 80 per cent of the eggs, the returns for further copulating are rather small and the male might do better by searching elsewhere for a new mate.

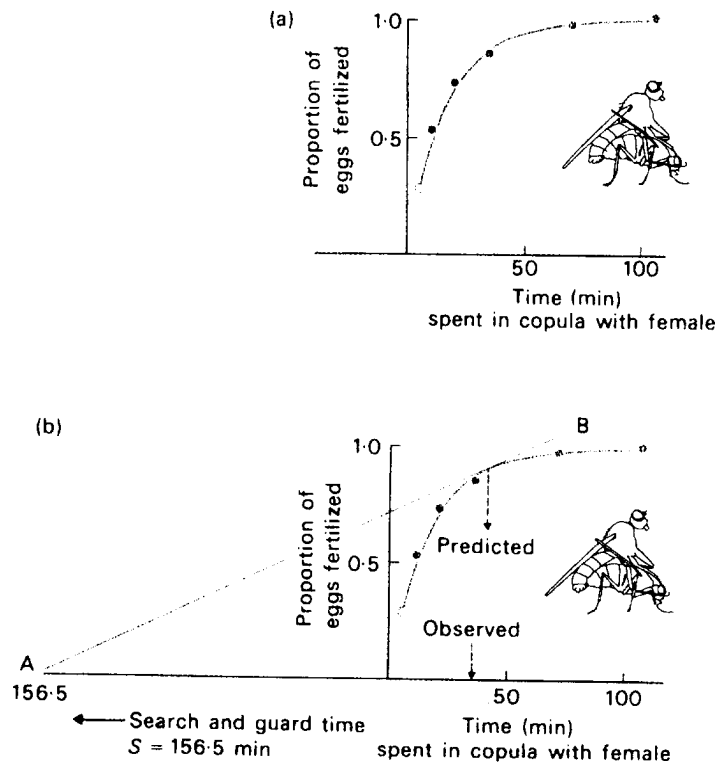
The analogue of travel time in the starling model is the time the male dungfly must spend guarding the present

Continued on p. 56

Box 3.1 Continued

female until she has laid her eggs plus the time he spends searching for a new female. This total is 156 min on average. As shown below, this estimate of travel time can be used to predict with reasonable accuracy how long the male spends copulating with a female.

Some other reproductive decisions that can be analysed in a similar way are discussed by Charnov and Skinner (1984).



(a) The proportion of eggs fertilized by a male dungfly (*Scatophaga stercoraria*) as a function of copulation time: results from sperm competition experiments. (b) The optimal copulation time (that which maximizes the proportion of eggs fertilized per minute), given the shape of the fertilization curve and the fact that it takes 156 min to search for and guard a female, is 41 min. The optimal time is found by drawing the line AB. From Parker (1978).

Why should there be this difference between bees and starlings? A simple example shows why the 'starling currency' is normally a sensible one to consider. Compare a starling that forages for

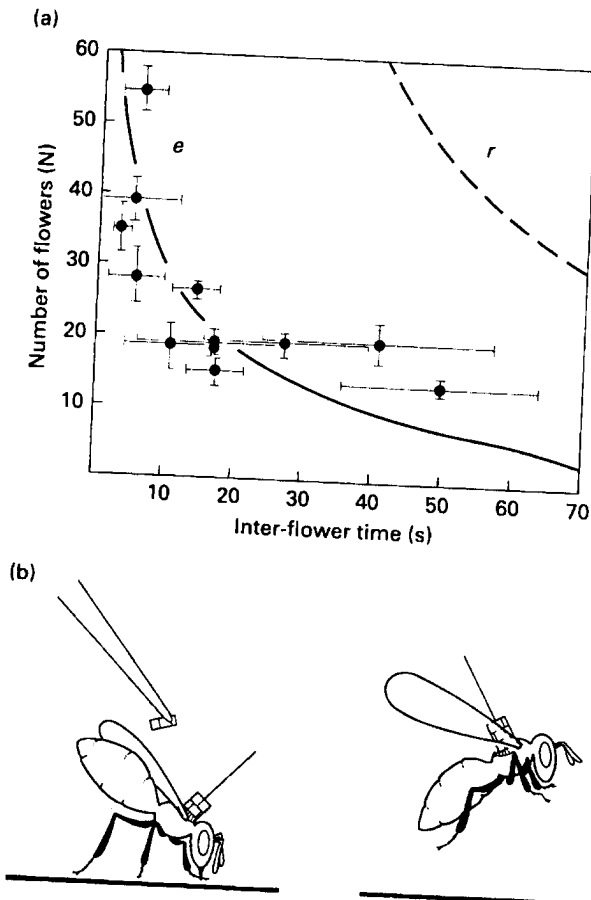


Fig. 3.4 (a) The relationship between load size (expressed as number of flowers visited) carried home by worker bees and flight time between flowers in a patch. Each dot is the mean of an individual bee and the two lines are predictions based on maximizing efficiency (e) and maximizing rate (r). From Schmid-Hempel *et al.* (1985). (b) By placing tiny weights on the bee's back while it is foraging Schmid-Hempel was able to study the bee's rule of thumb for departure from a patch to go home to the hive with a load of nectar. The weights, in the form of brass nuts, are placed on a fine rod that is permanently glued to the bee's back. They can be added or removed to simulate loading and unloading. From Schmid-Hempel (1986).

1 hour, spending 1 kJ and gaining 9 kJ with one that spends 10 and gains 90. Both have the same efficiency (9) but the former has 8 kJ to spend on its chicks and the latter has 80. In other words net rate $\{(gain - cost)/time\}$ tells us how much the animal has left at the end of the day to spend on reproduction or survival while efficiency does not. On the other hand efficiency may be a sensible currency when the crucial variable for the animal is not

Life expectancy of bees depends on work load

just the amount of gain, but also the amount spent. If, for example you have to drive from A to B on a fixed amount of fuel, efficiency might be very important indeed. It turns out that bees may be in this position. The equivalent for a foraging bee to having a fixed amount of fuel would be if it had a more or less fixed total lifetime capacity for expenditure of energy. Wolf and Schmid-Hempel tested this idea by manipulating the rate of energy expenditure of individuals, either by varying the time they were allowed to forage each day (Schmid-Hempel & Wolf 1988) or by fixing different sized permanent weights onto their backs (Wolf & Schmid-Hempel 1989). Both experiments showed that the bees that worked hardest survived for a shorter time than controls. For example, when workers carried a permanent weight of >20 mg, their survival was reduced from 10.8 to 7.5 days. These experiments lend some support to the hypothesis that workers, by maximizing efficiency, might extend their lifespan and thus contribute more nectar overall to the colony than they would by maximizing net rate.

The contrast between bees and starlings serves to underline the point that one of the aims of economic cost-benefit analyses is to compare alternative currencies and to try to understand why a particular currency is appropriate in each case. In each study one of the major advantages of the quantitative analysis was that it allowed us to see when there was a *discrepancy* between observed and predicted results. Without this potential for discrepancy it would have been impossible, for example, to tell whether bees were maximizing rate or efficiency, or nothing at all.

Adding weight to the bee's back causes it to fly home with a smaller load

The bee example also illustrates another important point. We have been thinking of animals as well-designed problem solvers making decisions that maximize an appropriate currency, but of course we do not believe that bees and other animals calculate their solutions in the same way as the behavioural ecologist. Instead the animals are programmed to follow rules of thumb which give more or less the right answer. The bees, for example, might use a rule that involved a threshold body weight ('if weight greater than x then go home'). Schmid-Hempel (1986) investigated this by adding tiny (7 mg) weights to the bee's back while it was foraging (Fig. 3.4b). He found that when he added five weights at intervals during a foraging bout the bees went home with a smaller load, as predicted if they were using a threshold weight rule. However, another experiment showed that the rule is not this simple. Instead of adding five weights gradually, Schmid-Hempel added five weights at the start of a foraging bout and then took them off gradually as the bee filled its crop. These bees

also went home with smaller loads than unmanipulated bees (or than controls where the weights were placed on the bee's back for a brief moment). The most reasonable interpretation of these results is that the bee in some way integrates the total weight it has carried since arriving at the foraging site.

The economics of prey choice

The same kind of economic approach that we have used for bees and starlings can also be used to account for the kinds of prey items that predators decide to eat.

When shore crabs are given a choice of different sized mussels they prefer the size which gives them the highest rate of energy return (Fig. 3.5). Very large mussels take so long for the crab to

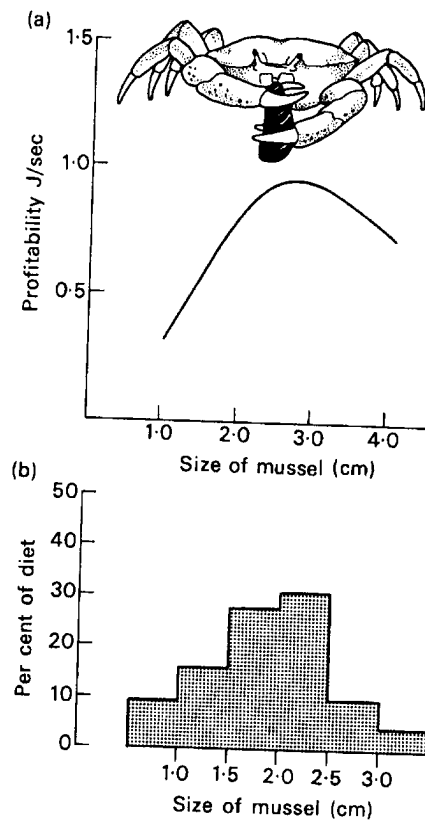


Fig. 3.5 Shore crabs (*Carcinus maenas*) prefer to eat the size of mussel which gives the highest rate of energy return. (a) The curve shows the caloric yield per second of time used by the crab in breaking open the shell and (b) the histogram shows the sizes eaten by crabs when offered a choice of equal numbers of each size in an aquarium. From Elner and Hughes (1978).

Optimal prey choice
depends on energy values,
handling time ...

... and search time

A test of the optimal
diet model

crack open in its chelae that they are less profitable in terms of energy yield per unit breaking time (E/h) than the preferred, intermediate sized, shells. Very small mussels are easy to crack open, but contain so little flesh that they are hardly worth the trouble. However the story cannot be as simple as this, because the crabs eat a range of sizes centred around the most profitable ones. Why should they sometimes eat smaller and larger mussels? One possible hypothesis to explain why several sizes are eaten is that the time taken to search for the most profitable sizes influences the choice. If it takes a long time to find a profitable mussel, the crab might be able to obtain a higher overall rate of energy intake by eating some of the less profitable sizes.

In order to calculate exactly how many different sizes should be eaten we need to develop a more precise argument based on handling time, searching time, and the energy values of the various prey (Box 3.2). The equations in Box 3.2 show the following for the simple example of a predator faced with a choice of two sizes of prey. First, when the more profitable type (higher E/h) is very abundant the predator should specialize on this alone. This is intuitively obvious: if something giving a high rate of return is readily available, an efficient predator should not bother with less profitable items. Secondly the availability of the less profitable prey should have no effect on the decision to specialize on the better prey. This also makes sense: if good prey are encountered sufficiently often to make it worthwhile to ignore the bad ones, it is never worth taking time out to handle bad prey regardless of how common they are. The third conclusion from Box 3.2 is that as the availability of the good prey increases, there should be a sudden change from no preference (the predator eats both types when encountered) to complete preference (the predator eats only the good prey and always ignores the bad ones).

An experiment which tested these predictions is illustrated in Fig. 3.6. The predators were small birds (great tits) and the prey were large and small pieces of mealworm. In order to control precisely the predator's encounter rate with the large and small worms the experiment involved the unusual step of making the prey move past the predator rather than vice versa (Fig. 3.6a). The big worms in the experiment were twice as large as the small ones ($E_1/E_2 = 2$) and h_1 and h_2 could be accurately measured as the time needed for the bird to pick up a worm and eat it. During the experiment the bird's encounter rate with large worms was varied so as to cross the predicted threshold from non-selective to selective foraging (equation 3.2) in Box 3.2. The results were qualitatively but not quantitatively as predicted, the main difference between observed and expected results being that the switch

Box 3.2 *A model of choice between big and small prey.*

Consider a predator which encounters two prey types, big prey₁ with energy value E_1 and handling time h_1 , and small prey₂ with energy value E_2 and handling time h_2 . The profitability of each prey (energy gain per unit handling time) is E/h . Imagine that the big prey are more profitable, so

$$\frac{E_1}{h_1} > \frac{E_2}{h_2}$$

How should the predator choose prey so as to maximize its overall rate of gain? Let us assume that the predator has encountered a prey — should it eat it or ignore it?

(a) If it encounters prey₁, it should obviously always eat it. Therefore choice of the more profitable prey₁ does not depend on the abundance of prey₂.

(b) If it encounters prey₂, it should eat it provided that

Gain from eating > gain from rejection and searching for a more profitable prey₁

i.e. if

$$\frac{E_2}{h_2} > \frac{E_1}{S_1 + h_1} \quad (3.1)$$

where S_1 is the search time for prey₁.

Re-arranging, the predator should eat prey₂ if

$$S_1 > \frac{E_1 h_2}{E_2} - h_1 \quad (3.2)$$

Thus the choice of the less profitable prey, prey₂, does depend on the abundance of the more profitable prey, prey₁.

This model makes three predictions. First, the predator should either just eat prey₁ (specialize) or eat both prey₁ and prey₂ (generalize). Second, the decision to specialize depends on S_1 , not S_2 . Third, the switch from specializing on prey₁ to eating both prey should be sudden and should occur when S_1 increases such that equation (3.2) is true. Only when the two sides of the equation are exactly equal will it make no difference to the predator whether it eats one or both types of prey.

was not a step but a gradual change (Fig. 3.6b). When big worms were abundant the birds, as predicted, were selective even if small worms were extremely common.

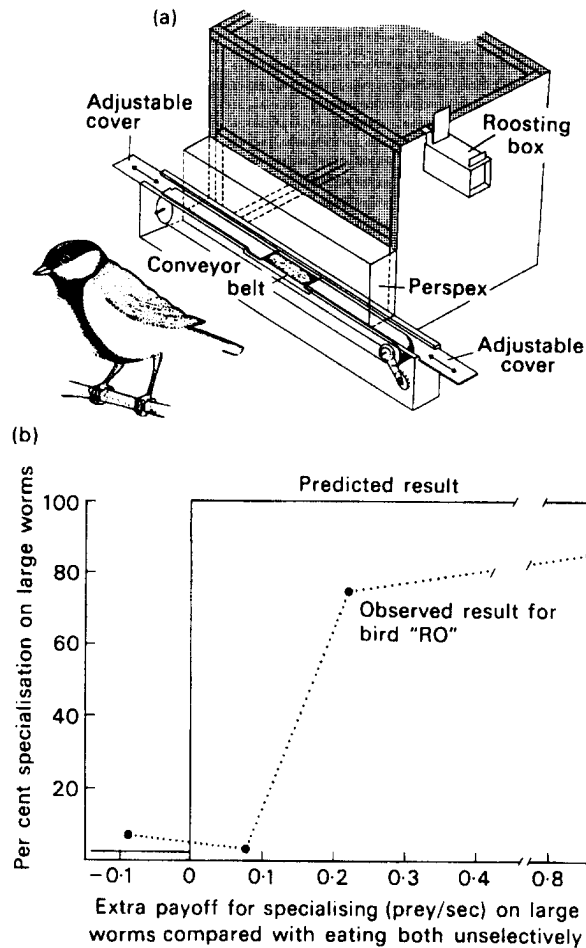


Fig. 3.6 (a) The apparatus used to test a model of choice between big and small worms in great tits (*Parus major*). The bird sits in a cage by a long conveyor belt on which the worms pass by. The worms are visible for half a second as they pass a gap in the cover over the top of the belt and the bird makes its choice in this brief period. If it picks up a worm it misses the opportunity to choose ones that go by while it is eating. (b) An example of the results obtained. As the rate of encounter with large worms increases the birds become more selective. The x-axis of the graph is the extra benefit obtained from selective predation. As shown in Box 3.2, the benefit becomes positive at a critical value of S_1 , the search for worms. The bird becomes more selective about the predicted point, but in contrast with the model's prediction this change is not a step function. From Krebs *et al.* (1977).

Sampling and information

The discussion so far has referred to animals that know their environment. In Fig. 3.2a, the model assumes that the animal knows the quality of each patch and the travel time before it

Optimal sampling by
woodpeckers

starts. Sometimes this may be a reasonable assumption, but at other times it may be more realistic to assume that the animal learns as it goes along. Steve Lima (1984) studied this kind of problem in downy woodpeckers. He trained woodpeckers in the field to hunt for seeds hidden in holes drilled in hanging logs. Each log had 24 holes and in each experiment some logs were quite empty and others had seeds hidden in some or all of the holes. The woodpeckers could not tell in advance which were the empty logs so they had to use information gathered at the start of foraging on each log to decide whether or not it was likely to be empty and therefore should be abandoned. When the logs contained 0 or 24 seeds the task was easy: looking in a single hole in theory gave sufficient information to decide and the woodpeckers in fact took an average of 1.7 looks. The task was more complicated when the two kinds of log contained 0 and 6 or 0 and 12 seeds: finding one empty hole is not longer enough to reject a log, but there must be some point at which the information gained from seeing a succession of empty holes makes it worthwhile giving up. Lima calculated how many empty holes the woodpeckers ought to check before giving up on a log in order to maximize their rate of food intake. The calculated values were 6 and 3 while the observed means were 6.3 and 3.5; thus, the woodpeckers use information gleaned while foraging in a way that comes close to maximizing their overall rate of intake.

The risk of starvation

Two kinds of currency for foraging animals — rate of food intake (starlings, great tits) and efficiency (bees) — have come up so far. Another currency that may be important for foraging animals is the risk of starvation. This is especially likely to be important when the animal lives in an environment that is unpredictable; the exact amount of food the animal will obtain is uncertain.

For example, imagine you are offered the choice of two daily food rations: one is fixed at 10 sausages per day, the other is uncertain; on half the days you get 5 sausages and on the other half, 20 sausages. Although the *average* of the second diet is higher than that of the first, it is a riskier option since there is no way of telling whether you will get 5 or 20 on any particular day. Which is the better option? The answer depends on the benefit (or 'utility' in economic jargon) of eating different numbers of sausages per day. If a diet of 10 is enough to survive on while 5 is not, then nothing is to be gained by choosing the risky option. If, on the other hand, 10 is not quite enough to survive on, the only viable option may be to take the risk and hope for 20 sausages.

Choosing a variable
foraging option may
minimize the risk of
starvation

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'Risk-sensitive'
behaviour

This option offers a 50 per cent chance of survival while the certain option offers no chance.

In short, animals should be sensitive not only to the mean rate of return from a particular foraging option but also the variability. Whether or not animals prefer high variability should depend on the relationship between the animal's needs (usually called its *state*) and the expected rewards. If energy requirements are less than the average expected reward, it pays to choose the less variable option (*risk-averse behaviour*) whilst, if requirements are above average, it usually pays to choose the more variable option (*risk-prone behaviour*).

Cold juncos are risk
prone

This idea has been tested in an experiment by Caraco *et al.* (1990). They offered yellow-eyed juncos (*Junco phaeonotus*) (small birds) in an aviary a sequence of choices between two feeding options: one variable and one with a fixed pay-off. For example, the variable option in one treatment was either 0 or 6 seeds with a probability of 0.5 each, whilst the corresponding fixed option was always 3 seeds. The experiment was carried out at two temperatures: 1°C and 19°C. At the low temperature the rewards from the fixed option were inadequate to meet daily energy needs, whilst at 19°C they were sufficient. As predicted by the theoretical argument, the birds switched from risk-averse behaviour at 19°C to risk-prone behaviour at 1°C. An equivalent result was obtained by Cartar and Dill (1990) in a study of bumblebee foraging. They augmented or depleted the energy reserves of the nest, and found that workers switched to risk-prone behaviour when the reserves were low. In this case the reserves of the colony as a whole were treated as equivalent to the reserves of an individual.

These experiments suggest that foragers are able to respond to variability in the amount of reward obtained, and that preference depends on state. However, they do not investigate the question of whether preference changes with time. Two examples of how time of day could be important are suggested by Houston and McNamara (1982, 1985). First, if the animal starts off the day risk-prone, but has good luck in its first few choices, it might be expected to become risk-averse later on. Second, as dusk approaches, for a diurnal forager the long period of enforced overnight fasting might favour a switch to risk-prone behaviour to increase the likelihood of overnight survival. These hypotheses still remain to be tested.

Variability in searching or handling time

The theoretical discussion and experimental studies described above refer only to variability in amount of food obtained (e.g. 0

or 6 seeds in Caraco *et al.*'s experiment). It has been implicitly assumed that there is no difference between options in search or handling time. In fact many experiments have shown that animals usually strongly prefer foraging options with variability in time. Most of these studies have been done by psychologists with rats or pigeons in a 'Skinner box' in which rewards are obtained by pressing a lever/pecking a key. If pecking one of the keys results in a standard reward after a fixed time, say 5 s, and pecking the other key produces rewards after a variable time but with a mean of 5 s, pigeons prefer the variable option (e.g. Mazur 1984).

Discounting the future
may explain preference
for variable delays

The theoretical interpretation of this is probably different from that for risk-prone and risk-averse behaviour with respect to amount of food. The animals behave as if they are 'future discounting', that is, placing a high value on rewards obtained soon rather than on rewards obtained after a long delay. If the weighting given to immediate rewards is sufficiently high, the animals will prefer the variable time option because the occasional very short time delays far outweigh the occasional long ones in terms of perceived benefit.

Why should animals discount the future in this way? Humans do it 'because you never know what might happen between now and then'. For foragers under natural selection a similar logic might well apply. Rewards in the future are less valuable than rewards here and now because interruptions, death by predator attack, or other changes may mean that future rewards are never collected.

Environmental variability, body reserves and food-storing

Small birds in winter often experience large daily fluctuations in body mass: the 20-g great tit, for example, typically loses 10–15 per cent of its body mass overnight in winter and regains the mass during the following day (Owen 1954). The daily gain and overnight loss is almost entirely made up of fat, which acts as fuel for overnight survival: thus each day in winter a small bird faces an uphill struggle to build up sufficient reserves for surviving the next night. Given this observation, should we expect small birds to carry as much fat as possible at all times, as an insurance against starvation? Both empirical observation and optimality models suggest that in fact birds usually carry less than the maximum reserves. In winter, birds are usually heaviest on the coldest/harshest days, suggesting that on other days they are carrying fewer reserves than the maximum. Furthermore, if one examines the trajectory of weight gain through the day one finds that birds increase their weight rapidly in the afternoon (Owen

Small birds carry optimal,
not maximal reserves

Small birds may carry more reserves in a variable environment

1954; Bednekoff 1992), implying that earlier in the day they do not carry as much fat as they could. Lima (1986) and McNamara and Houston (1990) explained these observations by hypothesizing that the reserves carried by a bird reflect an optimal trade-off between costs and benefits. The benefit of carrying extra reserves is reduced risk of overnight starvation, whilst the cost is increased danger of death from predation. The danger might arise simply because heavier birds are less agile at escaping or, more subtly, because birds with more reserves spend more time foraging rather than hiding from predators. This hypothesis predicts that the optimal level of reserves will increase (i.e. birds will be heavier) when the energy cost of overnight survival is higher, or more unpredictable, or when the danger of predation is lower (Fig. 3.7a).

Some birds store food instead of fat

Many animals store food reserves in the environment as well as on their bodies (VanderWall 1990). Among the best studied species are members of the corvid family such as Clark's nutcracker (*Nucifraga columbiana*) and the European jay (*Garrulus glandarius*) and members of the tit family such as the black-capped chickadee (*Parus atricapillus*) and marsh tit (*Parus palustris*). Nutcrackers and jays store seeds from pine and oak trees respectively in the autumn and retrieve them the following spring or summer to feed themselves and their young. The smaller tit species, on the other hand, seem to store and retrieve their food on a much shorter cycle of hours to days (Stephens & Krebs 1986; Brodin 1992). In both corvids and tits, food storing is an adaptation to survive in a variable environment. The long-term storers take advantage of the autumn abundance of seeds and utilize the food at other times of year when seeds would otherwise be scarce. The short-term storers use storing, like fat reserves, as an insurance against overnight starvation in an unpredictable environment (McNamara *et al.* 1990) (Fig. 3.7b).

Feeding and danger: a trade-off

If you watch a squirrel eating chocolate chip cookies in the park, as Steve Lima and colleagues did (Lima *et al.* 1985) you will notice that the squirrel generally comes to your picnic table, grabs a cookie and retreats to a tree to eat it. If you put out small fragments of cookie the squirrel will often make repeated sorties to the table and take each morsel back to the tree to eat it. This is obviously not a very efficient way to eat food: if maximizing net rate of energy intake or efficiency was the only important factor for a squirrel it would simply sit on the table and eat pieces of cookie until it was full. One interpretation of the

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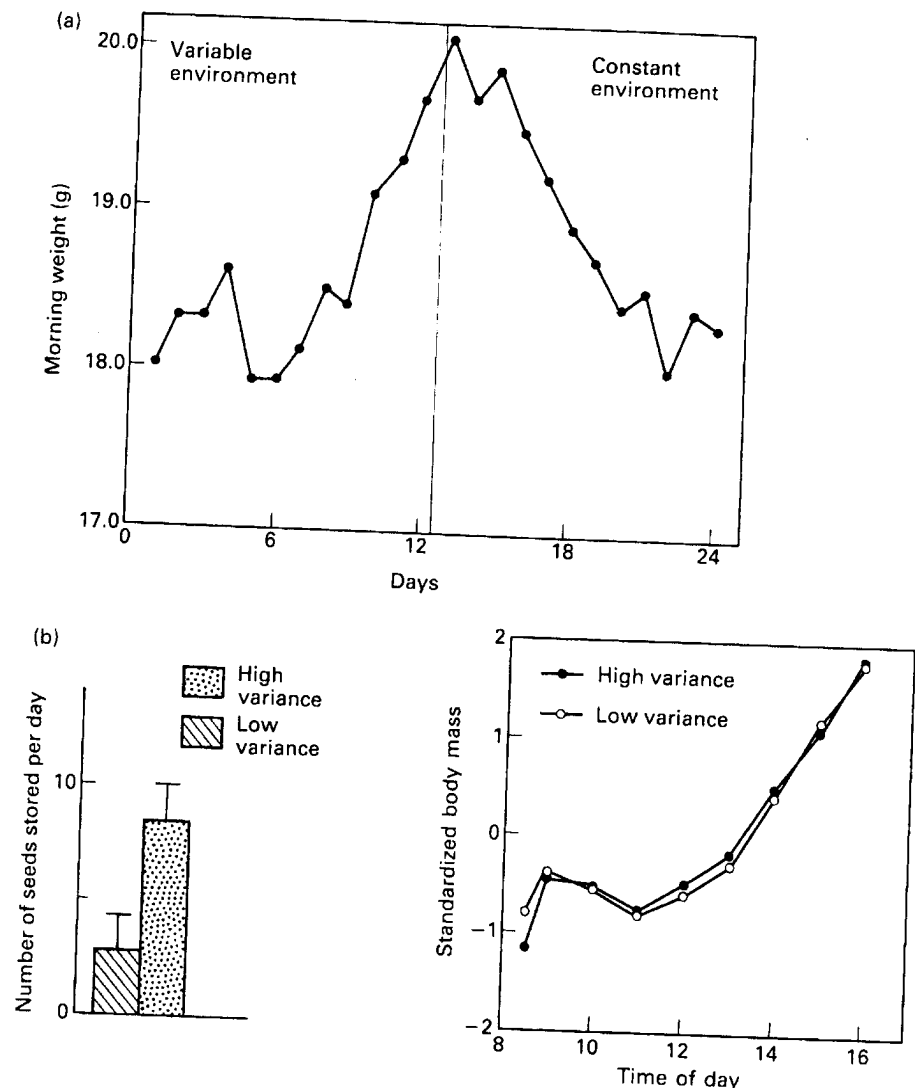


Fig. 3.7 (a) Body reserves and environmental variability. The graph shows the body mass of a captive great tit (one of eight in the experiment) which was transferred from a constant to a variable environment for 12 days before returning to the constant environment. Variability in this experiment was produced by randomly altering the length of the night-time period of no foraging. From Bednekoff (1992). (b) Food-storing and variability. In this experiment, captive marsh tits (one example is shown) stored more food (left), but did not put on more body reserves (right), in a more variable environment. These results suggest that food-storing, like fat storage, is a method of coping with environmental variability: whilst great tits, which do not store food, cope with environmental variability by putting on extra fat reserves, marsh tits store extra food in the environment. The right-hand graph also shows the daily weight trajectory of a marsh tit. In the afternoon, the bird transfers food from its hoards to its body, so reserves rise steeply towards the end of the day. From Hurly (1992).

squirrel's behaviour is that it is balancing the demands of feeding and safety from predators. It could feed at maximum rate and run a good chance of being killed by a cat by staying on the table or it could be completely safe from cats but die of starvation in the trees. Neither of these is the best solution to maximize survival, so the squirrel does a mixture of the two. Lima *et al.* argued that the squirrel should be more prone to seek safety in the trees while feeding when this involves a smaller sacrifice in terms of feeding rate. Consistent with this they found that when the feeding table was close to the trees the squirrels were more likely to take each item to cover. Big pieces of cookie were more likely to be taken to cover than small ones; they take a long time to eat and are therefore more dangerous to handle out in the open and when handling time is long the relative cost of travelling back and forth is reduced.

Hungry sticklebacks accept danger of predation to obtain high intake rates

The balance between the benefits of feeding and of avoiding danger is also influenced by an animal's hunger. On a very cold day in winter normally shy birds become quite tame at the garden bird table, presumably because their increased need for food overrides the danger of coming into the open. Manfred Milinski and Rolf Heller (1978, 1979) studied a similar problem with sticklebacks (*Gasterosteus aculeatus*). They placed hungry fish in a small tank and offered them a simultaneous choice of different densities of water fleas, a favourite food. When the fish were very hungry they went for the highest density of prey where the potential feeding rate was high, but when they were less hungry the fish preferred lower densities of prey. Milinski and Heller hypothesized that when the fish feeds in a high density area it has to concentrate hard to pick out water fleas from the swarm darting around in its field of vision, so it is less able to keep watch for predators, as shown by Milinski (1984b). A very hungry fish runs a relatively high chance of dying from starvation and so is willing to sacrifice vigilance in order to reduce its food deficit quickly. When the stickleback is not so hungry it places a higher premium on vigilance than on feeding quickly, so it prefers the low density of prey. The balance of costs and benefits shifts from feeding to vigilance as the stickleback becomes less hungry.

Consistent with this hypothesis Milinski and Heller found that predation risk influences choice of feeding rate. When they flew a model kingfisher (*Alecedo atthis*) (a predator on sticklebacks) over a tank containing hungry fish they found that the sticklebacks preferred to attack low rather than high prey densities (Fig. 3.8). This is to be expected if the hungry fish, in spite of its high chance of starvation, places a very high premium on vigilance when a predator is in the vicinity.

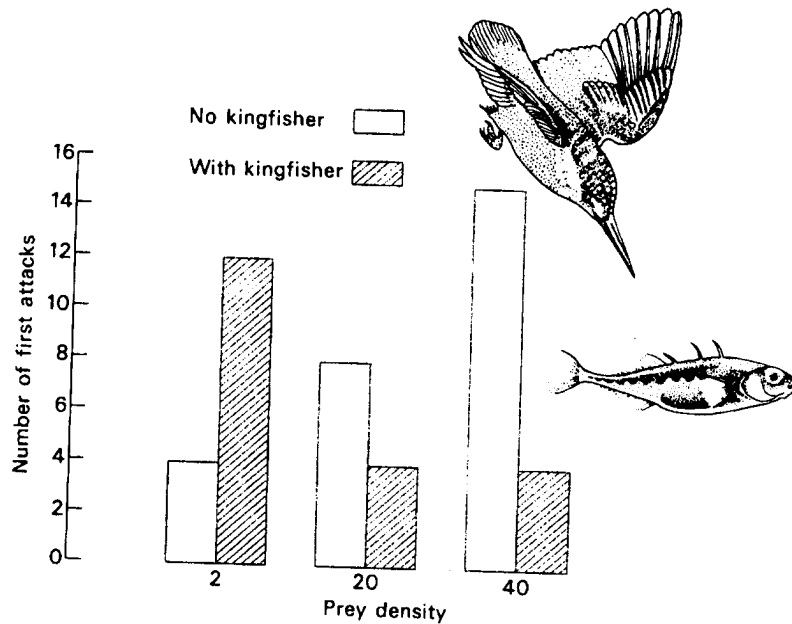


Fig. 3.8 Hungry sticklebacks normally prefer to attack high density areas of prey but after a model kingfisher was flown over the tank they preferred to attack low density areas. From Milinski and Heller (1978).

An important difference between Milinski and Heller's analysis of foraging and those described earlier is that the cost-benefit calculations include the animal's hunger state. An optimization model in which the animal's state changes as a result of its behaviour (the fish becomes less hungry as a result of feeding) is referred to as a dynamic, as opposed to static, model. In fact the traditional view that an animal's internal state controls its behaviour can be turned on its head and the animal can be seen as using its behavioural repertoire to control the internal state in an optimal way. The influence of the kingfisher on the stickleback is to alter the optimal allocation of time to feeding and vigilance, so that the fish decreases its hunger at a slower rate.

The idea of a dynamic feedback between foraging, body reserves and danger of predation has been used by Jim Gilliam (1982) to predict how an individual should shift between habitats as it grows up. His analysis applies to the bluegill sunfish (*Lepomis macrochirus*). In experimental ponds in Michigan, Earl Werner found that these fish could obtain a higher rate of food intake by foraging on benthic invertebrates such as chironomid larvae than they could by foraging either on the plankton or near the emergent vegetation at the edge of the pond. As might be expected the fish

Bluegill sunfish start off in safe habitats and move to dangerous places as they grow bigger

spend most of their time (more than 75 per cent) foraging on the benthos. However, when predators in the form of largemouth bass (*Micropterus salmoides*) were added to the pond, a significant change in habitat use by the sunfish was seen. The bass could eat only the smallest sunfish (the others were too big) and these fish now spent more than half their foraging time in the reeds feeding on plankton where they were relatively safe, even though as a result their food intake was reduced by about one-third and their seasonal growth rate by 27 per cent. The bigger sunfish continued to forage with equanimity on the benthos (Werner *et al.* 1983). The little fish thus face a trade-off: is it better to stay in the relative safety of the reeds and grow slowly, prolonging the period of vulnerability to predators, or is it better to gamble on rapid growth to a safe size in the benthos? Gilliam was able to show that the best thing (to maximize its total chance of survival) for the fish to do is to stay in the safety of the reeds until a certain size is reached and then to go for the benthic prey. This accords with observation: the young fish in the presence of predators tend to feed in safe places, and as they get bigger they shift to the better feeding areas.

Nutrient constraints: herbivores and plants

The examples we have described so far have illustrated the variety of currencies that might be important for foraging animals, but we have said little about the range of constraints that might be important. The diet of herbivores is a good example to illustrate the importance of constraints.

As a general rule nutrient quality of food is more important to herbivores than to carnivores and insectivores. This is because plants often lack essential dietary components and only by careful selection of plant species can a herbivore obtain a balanced intake. For example, the diet of moose (*Alces alces*) on the shores of Lake Superior in Michigan is strongly influenced by sodium requirements. The moose feed in two habitats: forest, where they browse on deciduous leaves, and small lakes, where they crop plants growing under water. The aquatic plants are rich in sodium but relatively poor in energy, while terrestrial plants have little sodium but a high energy content. The moose need both energy and sodium to survive and therefore have to eat a mixed diet, but to predict the exact mixture involves making an optimality model.

Since the diet of the moose contains two components we can plot it as a point on a graph, the axes of which are intake of terrestrial and aquatic plants (Fig. 3.9a). If, for example, the moose

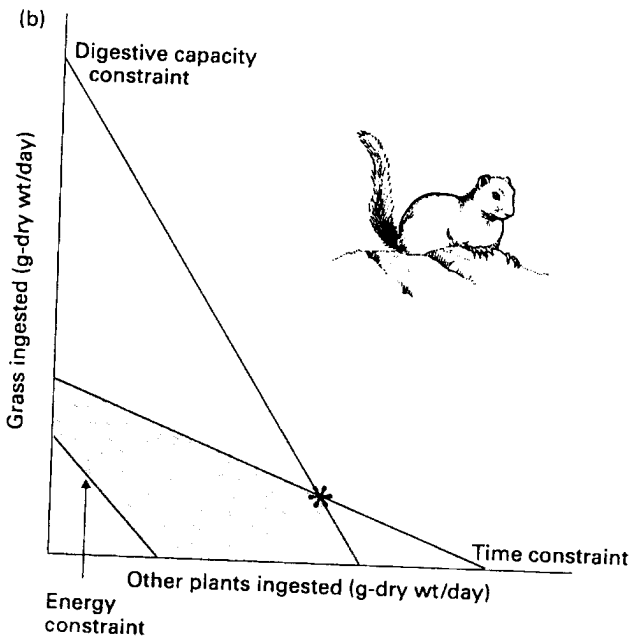
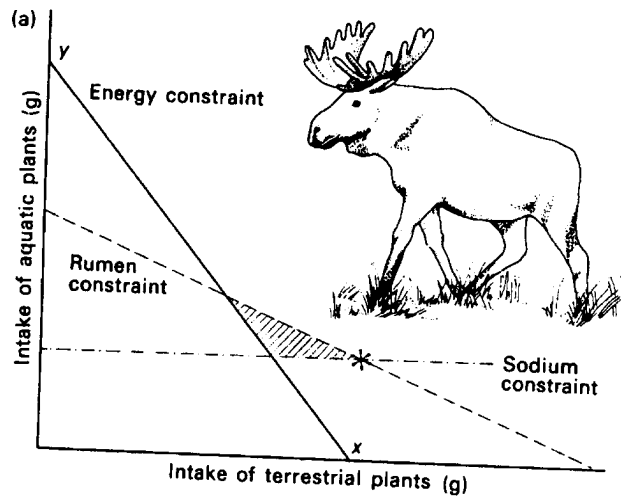


Fig. 3.9 (a) The diet of moose is constrained by the requirements for sodium and energy: the daily requirements are shown as the dot-dash and solid lines respectively and the moose has to eat a mixture of plants which lies in the space above these two lines. The third constraint is the size of the moose's rumen (broken line). Aquatic plants are bulkier than terrestrial ones so fewer grams of these can be fitted into the rumen. The moose's diet was found to lie at the point inside the triangle that maximizes daily energy intake (indicated by a star). From Belovsky (1978). (b) The Columbian ground squirrel (*Spermophilus columbianus*) also maximizes daily energy intake subject to constraints. In this case digestive capacity (equivalent to the moose's rumen constraint), time available and minimum energy requirements define the feasible set of diets. From Belovsky (1986a).

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Moose maximize daily intake

ate largely terrestrial plants with just an occasional aquatic, its diet would be represented by a point at the lower right-hand side of the graph. Now as we have already said, the daily diet has to contain a certain minimum amount of sodium. This is represented in the graph as a constraint line: the horizontal dot-dash line shows the minimum intake of aquatic plants needed to satisfy sodium requirements. But this is not the only constraint on the animal's diet. It also needs a certain amount of energy per day. This could be obtained by eating a pure diet of y grams of aquatic plants or x grams of terrestrial plants or a mixture of the two, as shown by the solid line in Fig. 3.9a. This line shows the mixture of plants that would provide just enough energy to survive the day. Finally, the diet is constrained by the size of the moose's rumen. The moose has a specially modified stomach, the rumen, in which food is slowly fermented by micro-organisms prior to digestion. The size of the rumen sets an upper limit on the amount of food that can be processed at any one time, and therefore limits the total daily intake. The broken line on Fig. 3.9a shows the maximum amount of food that could be eaten per day with different combinations of terrestrial and aquatic plants.

Constraints on maximization: rumen capacity, sodium requirements and energy needs

The total effect of these constraints can now be assessed. Only the diets inside the small shaded triangle on Fig. 3.9a satisfy all three constraints. The diet has to be above the sodium line, above the energy line, and below the rumen line. But where inside the triangle is the optimal diet? This depends on the goal or optimality criterion. If the moose is designed, for example, to maximize its daily sodium intake, the diet should include as much aquatic material as possible and lie in the top left corner of the triangle. If the moose was designed to minimize the time spent in water each day, its diet might be near the bottom right of the triangle. Gary Belovsky (1978) carried out a detailed study of the diet and found that the mixture of plants eaten was at the point within the triangle which would be predicted if the moose maximizes its daily energy intake subject to the constraints of sodium need and rumen size. This point is at the right-hand corner of the triangle (marked with a star). To see why, think of lines parallel to the energy constraint line (energy isoclines) at different distances from the origin. Any point along one of these lines is a point of equal energy intake per day, while lines further from the origin represent higher energy intake. The highest energy isocline that the moose could achieve is at the bottom right-hand corner of the triangle of feasible diets.

Belovsky (1986a,b) has extended his conclusions from the moose study to attempt to identify the currencies and constraints that determine herbivore diets in general. He concluded that

herbivores maximize energy intake and that digestive capacity is often the key constraint. In other words, herbivores tend to select plants with the highest density of energy per unit of bulk. However, Hobbs (1990) has criticized Belovsky's conclusions. Belovsky assumes that the daily capacity of the digestive tract in herbivores is measured by the bulk (total of dry matter and water) of plants that can be ingested. Hobbs points to evidence that only the dry matter of plants limits daily intake, the water being relatively rapidly absorbed. Hobbs also shows that quantitative predictions of Belovsky's models are rather sensitive to the exact value assumed for the digestive constraint, so the uncertainty about what exactly limits daily intake is all the more of a problem.

The need for more physiological information

What should one conclude from this debate? First, it illustrates the point that all optimality models are dependent on assumptions about physiological processes. Sometimes, as in the herbivore model, the optimality analysis helps to identify areas of physiology where more detailed knowledge would help in predicting behaviour. Second, the sensitivity of Belovsky's model to its assumptions illustrates a general advantage of models that make quantitative predictions: you know exactly where you stand. Third, Belovsky's conclusion that herbivores maximize daily energy gain must remain a tentative hypothesis for the moment.

Optimality models and behaviour: an overview

In this chapter we have seen how optimality models can be used to analyse decisions about foraging and mating. This approach is an extension of the idea of interpreting behaviour in terms of costs and benefits that we introduced in the last chapter. Let us now try to summarize some of the advantages and limitations of optimality modelling. Three main advantages that are illustrated by this chapter are the following.

Optimality models: testability, explicit assumptions, generality

1 Optimality models often make testable, quantitative predictions so that it is relatively easy to tell whether the hypotheses that are represented in the model are right or wrong. For example, the honeybee workers were shown not to be maximizing net rate of energy delivery to the hive, but were maximizing efficiency in their foraging. The hypotheses that were tested in the bee study, and in all optimality studies, were hypotheses about the *currency* (net rate or efficiency) and about the *constraints* on the animal's performance (energy costs, handling times and so on). The currency is a hypothesis about the costs and benefits impinging on the animal, for example for bees energetic costs and benefits seem to be much more important than, say, predation and other dangers. The constraints are hypotheses about the mechanisms of

behaviour and the physiological limitations of the animal, whether it is able to recognize differences in nectar concentration, how fast it can fly and so on.

2 A second advantage is that the assumptions underlying the currency and constraint hypotheses are made explicit. In the model used to analyse load size of starlings, for example, we had to make explicit assumptions about the loading curve, about the fact that the bird could encounter only one patch at a time, about the time taken to fly to the nest, and so on. By making these things explicit in the model one is forced to think clearly about the problem.

3 Finally, optimality models emphasize the generality of simple decisions facing animals. The starling model applied equally to dungflies, and we could have illustrated it with reference to many other animals and other decisions.

Now for a difficulty with the optimality approach: deciding what to do when the model fails to predict what the animal does. Take the dungflies as an example: the model predicts reasonably well, but not exactly, the duration of copula. What should be done about the discrepancy? Should we ignore it, assuming it is within the acceptable range of error, or should we try to analyse it further? Assume for the moment that we wanted to take the latter course. One possibility is that the currency of the model was incorrect; dungflies may trade-off feeding and mating, or danger and mating, rather than simply maximizing rate of fertilization. A second possibility is that the currency is correct but that the constraints have not been identified correctly; perhaps males run out of energy reserves while in copula. Finally, the whole idea of dungflies or other animals maximizing a currency may be incorrect. Animals may simply not be that well tuned by the process of natural selection or they may be lagging behind when some aspect of the environment changes. This kind of argument, although it is often put forward, should really be saved as a last resort, since it is not very fruitful in leading to new experiments or observations. There is, however, no straightforward recipe for distinguishing between the first two possibilities, although one useful step is, as we saw in the honeybee and moose examples, to compare different currencies (or equally, different constraints). Another important step is to analyse more thoroughly the mechanisms underlying behavioural decisions.

Summary

Behaviour can be viewed as having costs and benefits and animals should be designed by natural selection to maximize net benefit.

Table 3.1 A summary of the decisions, currencies and constraints discussed in this chapter

Animal	Decision	Currency	Some constraints	Test
Starling	Load size	Maximize net rate of gain	Travel time, loading curve, energetic costs	Load versus distance
Bee	Crop load	Maximize efficiency	Travel time, sucking time, energetic costs	Load versus flight time
Dungfly	Copulation time	Maximize fertilization rate	Travel time, guarding time, fertilization curve	Predict copulation duration
Great tit	Size of worms	Maximize net rate of gain	Handling time, search time	Choice of large or small prey
Downy woodpecker	Patch time	Maximize net rate of gain	Travel time, recognition time	Number of holes inspected
Yellow-eyed junco	Where to feed	Minimize risk of starvation	Handling time, daily energy budget	Choice of variable or certain reward
Great tit/marsh tit	Body reserves/hoard size	Maximize survival	Energetic cost of carrying reserves	Body reserves/hoard size in predictable and unpredictable environments
Squirrel	Where to eat	Maximize survival	Travel time, handling time	Vary size of food and distance
Stickleback	Where to feed	Minimize danger and starvation	Vigilance and foraging incompatible	Vary hunger and danger
Bluegill sunfish	Habitat choice	Maximize survival	Growth depends on food intake, danger related to size	Habitats used at different ages
Moose	Food choice	Maximize daily energy intake	Sodium need, digestion limit, energy limit	Per cent composition of diet

This idea can be used as a basis for formulating optimality models in which the criterion of maximum benefit, the constraints on the animal, and the currency for measuring benefit are specified. Different kinds of currency might be appropriate for measuring benefits and costs of different behaviours, for example, with feeding behaviour rate of intake might be a good currency and with male mating behaviour rate of fertilizing eggs seems reasonable (Table 3.1).

The emphasis of this approach is on quantitative testable predictions. Often the results of experiments deviate from the predictions of simple models; these deviations can be just as valuable as successful predictions in helping to understand how behaviour is designed.

Further reading

The paper by Maynard Smith (1978) discusses some of the pros and cons of optimality modelling. Three books which contain useful reviews of foraging economics are the monograph by Stephens and Krebs (1986) for a summary of mathematical models, the volume edited by Kamil *et al.* (1987) for empirical studies and two more general reviews by Russell Grey (who is very critical of the approach) and by Kacelnik and Cuthill; Krebs and Kacelnik (1991), Houston *et al.* (1988) and Hughes (1990) provide recent overviews.

Topics for discussion

- 1 Do animals have to be clever to forage optimally?
- 2 Are laboratory experiments on decision-making in simple environments useful for understanding behaviour in the field?
- 3 Is average net rate of intake a sensible currency for foraging animals?
- 4 How might one investigate the mechanisms by which animals discriminate between fixed and variable amounts of food.