

FORAGING AND BEHAVIORAL ECOLOGY

The last three chapters discussed how regulatory and economic principles apply to experiments on feeding, the allocation of time among various activities, and choice between different ways of getting food. But a critical test of any approach is how well it can deal with the way animals behave in *nature*. It is hard to devise a fair test, of course, because in nature nothing is controlled, and observations will nearly always be incomplete. Nevertheless, applications of these principles to problems of diet selection and foraging in natural or close-to-natural conditions have been increasingly successful. This chapter deals with the application of optimality arguments to problems posed by natural foraging behavior.

DIET SELECTION AND FUNCTIONAL RESPONSE

In recent years, interest in foraging in natural environments has been organized around a few simple quantitative arguments, some discovered independently by several workers.¹ The basic issues are essentially the same as those discussed under the heading of “optimal behavior” in Chapters 7 and 8: how animals choose either between equivalent foods (i.e., perfect substitutes) or between imperfect substitutes. There are also close parallels between many natural situations and some of the reinforcement schedules described earlier. The starting point for theoretical analysis is the *net rate of energy intake*, and the beginning assumption is that animals act so as to maximize it. This assumption has fairly straightforward consequences for choice of diet, allocation of time to patches, search for camouflaged (cryptic) prey, and spatial pattern of search in environments with different food distributions. I will deal with each of these cases in turn.

Functional response

How does the amount a predator takes of a particular prey type depend on the density of that prey type in the environment? The answer to this question is of great interest to ecologists because of its bearing on the stability of predator-prey systems. For example, if individual prey are at greater risk when prey density is high than when it is low (negative feedback), predation will have a stabilizing effect on prey populations; but if risk is less at high densities than low (positive feedback), the stage is set for explosive increases and decreases in prey population size. The question has psychological interest, because the relation between prey density and predator intake is the natural equivalent of a feedback function, with density playing the role of schedule value, and “attack rate” (defined below) as response rate.

There are three simple ways that predation rate relates to prey density. Two of them can be derived from first principles as follows: Consider a single food type, which is uniformly and randomly distributed with spatial density D . An animal foraging at random will encounter prey items at a rate aD , where the constant a (the attack rate) is proportional to the rate at which the animal moves through its environment and is also related to the area it can scan visually — together these define the animal’s *search path*. If looking for one prey type does not interfere with looking for others (assuming prey to be randomly distributed in space), then this relation will hold for all available prey types. Thus, for prey type i , the encounter rate will be aD_i .

If a single prey type is encountered at a rate aD , then in a period of time of unit length, the total number of prey items encountered (and eaten) will be

$$R = aDt^*,$$

where t^* is the time when the animal is actually foraging which, in turn, is total time, less time taken up in handling prey. If we arbitrarily set total time equal to unity, this argument yields:

$$t^* = 1 - Rh$$

where h is the time to handle one prey item. Eliminating t^* from these two equations yields the result

$$R = aD/(1 + aDh), \quad (9.1)$$

which is known as Holling's *disk equation* (Holling, 1959, 1965). The label "disk equation" derives from Holling's first experimental test of it, in which his blindfolded secretary "foraged" for sandpaper disks scattered on a tabletop. The disk equation says that when a predator finds prey at random, his rate of eating will be a negatively accelerated function of prey density: When prey are thin on the ground, rate of predation is proportional to prey density; but as prey density increases, more and more time is taken up handling each prey item, so that additional increases in prey density have less and less effect. The disk equation corresponds to mild positive feedback: An individual prey item is protected at very high prey densities because the predator spends less and less time searching and more and more time handling prey — the predator is "swamped" by the prey. This swamping is one functional explanation for the propensity of insects and other small prey organisms to occur in "blooms" of vast numbers of individuals that all emerge at once.

The relation between rate of prey capture, R , and prey density, D , is known as the *functional response* of a predator-prey system.²

It is easy to show that the disk equation can be generalized for n prey types as

$$R_i = aD_i / (1 + \sum^n aD_i h_i). \quad (9.2)$$

Holling pointed out the three simple forms of functional response illustrated in Figure 9.1: Type

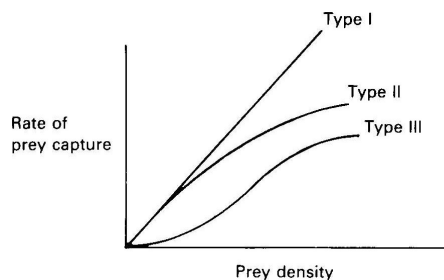


Figure 9.1. Three types of functional response.

I: Linear, with zero intercept — rate of prey capture is simply proportional to prey density. Type II: Negatively accelerated — rate of prey capture increases with prey density but at a negatively accelerated rate, because more and more time is taken up in handling the prey. Type III: Sigmoidal (S-shaped) — rate of prey capture at first increases with prey density at a positively accelerated rate, but then at high densities reverts to the negatively accelerated form.

The type I (linear) functional response is shown only by filter feeders (whales filtering krill, sponges filtering microorganisms, etc.) and other animals where the prey require negligible handling time; it is just a special case of the type II response where $h = 0$. Consequently, the disk equation provides a description of both type I and type II responses. The type II response is the commonest, shown by many predators dealing with a single prey species.³ The type III response seems to reflect psychological mechanisms in ways I discuss in a moment.

Diet choice

Dietary items such as insects, seeds, nuts, and so forth differ in their energy content and in the time it takes to eat them. For example, a hazel nut will generally take longer to unpack and eat than an ear of grain, although it may also yield more energy. If we ignore for the moment the different *types* of food, it is obviously convenient to summarize the value of each food item by the *ratio* of energy content, E , to *handling time*, h ; the ratio E/h is known as the *profitability* of a food item.

Given prey species of equivalent nutritive value, but differing profitabilities, the first question to ask about diet choice is: How many different prey types should the predator take in order to maximize net energy intake? The obvious answer — *all* — is false, as the following

argument shows. Consider just two prey types, with densities D_1 and D_2 , energy contents E_1 and E_2 , and handling times h_1 and h_2 . We need consider just two possibilities: that the predator takes both prey types, or just the most profitable. If the capture rate in the single-prey case is R_1 , the net rate of energy intake is just $R_1 E_1$. Thus, at any instant of time, the animal can expect an average rate of energy intake equal to $R_1 E_1$. Suppose it encounters a prey item of a less profitable type. If it attacks the item, its expected rate of energy return is just the profitability of the item, that is, E_2/h_2 . Clearly, if E_2/h_2 is less than $R_1 E_1$, the predator does better to pass up the less profitable prey and continue looking for the more profitable one. As this argument shows, the predator's decision is *independent* of the density of the less profitable prey. For a given pair of prey types there will be a threshold density of the more profitable prey above which it will pay the predator to specialize on the more profitable type.

The same argument obviously holds for more than two prey types. If prey types are ranked according to profitability, as the density of the more profitable types increases, the predator should drop more and more of the low-ranked types from its diet.

The strong prediction of this analysis is that animals should be absolutely rigid in their selection of prey types. This does not always happen. In most tests, animals take a few items outside the "optimal set." For example, in one experiment (Werner & Hall, 1974) a group of ten Bluegill sunfish (*Lepomis macrochirus*) was allowed to hunt for water fleas (*Daphnia*) of three different size classes. The fish were exposed to three different "mixes" of *Daphnia*, and the proportions caught were estimated by examining the stomach contents of the fish. The proportions of small, medium, and large fleas were the same in all three mixes (equal numbers of each size), but the total numbers of fleas (i.e., absolute prey density) varied. The handling time for all classes of fleas was similar (and small), so that their profitability depended mainly on their size. When absolute density was low, the fish ate fleas in proportion to the frequency with which they were encountered. But as density increased, the fish increasingly favored the more profitable types, although at no density was their preference exclusively for the most profitable type. This study, like a number of others, found that as the density of the more profitable prey type increases, animals become more selective.

There are several reasons why animals might not conform to the strict stereotypy prescribed by simple optimal-diet models: The most obvious is that the assumptions of the simple model — uniform prey distribution, known profitability — are not met. If prey are not uniformly distributed, then prey choices should shift and what is measured will be an average of two or more different choice patterns. Animals must sample to learn about prey profitabilities, and this will produce nonexclusive choice. If many different prey types are encountered, the animal may forget about the profitabilities of some of them (a memory constraint) and may continue sampling to update his information.

An interesting limitation derives from the kind of positively accelerated cost function discussed in Chapter 7. An investor of limited means should spread his investment over several different securities, so that he doesn't lose his shirt if a single stock crashes — the probability that several independent stocks will all crash being much lower than the probability a single stock will fail. For the same reason, an organism is well advised to sample more than one prey type, so that a change in the abundance of any given prey type will have less effect on his total intake. It can be shown that this *risk-aversion* corresponds to non-substitutability of prey types, and a negatively accelerated utility function (positively accelerated cost function) of the type discussed earlier.⁴ This argument implies nonexclusive choice even if different prey types are nutritionally identical, and even if the rate of energy intake is thereby less than maximal.

There is experimental evidence for this tendency to diversify choice, even among identical alternatives. In an ingenious series of experiments, Catania (1980a,b) has shown that pigeons

will choose an alternative that gives them several additional choices over an alternative that gives them only one — even if all choices are identical in terms of food delivery. In one experiment, for example, a pigeon was confronted with two rows of response keys: two below and four above. At the beginning of a cycle, only the two lower keys were lit. A peck on the left key occasionally (on a VI schedule) turned it off and turned on the four top keys, three lit green and one red: Each green key delivered food for pecks on the same fixed-interval schedule; pecks on the red key were ineffective (extinction). A peck on the right, lower key occasionally turned it off (according to the same VI schedule) and turned on the four upper keys, as before, but now three were red and one was green. After food delivery, the four keys went off and the two lower ones were re-illuminated, to begin the next cycle.

Thus, by pecking left and then pecking any of the three green keys in the second link of this *concurrent-chain* VI-FI schedule (see note 6, Chapter 8), the pigeon obtained exactly the same frequency and spacing of food as by pecking right and then pecking the single green key in the second link. The two lower keys were exactly equivalent in terms of food delivery. Nevertheless, pigeons showed a bias in favor of the left key, which yielded a choice among three green keys, over the right key, which permitted no choice. In other experiments, Catania showed that it was the *number* of keys in the second link rather than their size that was important to the pigeons. Clearly this result is consistent with the idea that animals have a built-in tendency to diversify their behavior, when diversification costs them little in terms of overall payoff rate.

Switching and functional response

Nothing I have said so far conflicts with the idea that given two prey types of equal, high profitability, both should be taken whenever encountered. If we restrict ourselves to the ideal case in which the two types occur at random in the same area (so that the predator cannot look for one type in one kind of habitat and the other in another), this means that each prey type should be taken in proportion to its frequency of occurrence (D , in Equation 9.1). For a pair of such equivalent prey types, the expected relation between relative density (that is, $D_1/[D_1 + D_2]$) on the x -axis and relative capture rate ($R_1/[R_1 + R_2]$) on the y -axis is shown by the diagonal in Figure 9.2: Relative capture rate should match relative density. (Matching can be derived in one step from Equation 9.2. Note: “Matching” here is not the same as the matching on concurrent schedules discussed in Chapter 8. Matching here is between obtained relative payoff rates and relative payoff (prey) densities; matching on concurrent schedules is between relative *response* rates and obtained relative payoff rates.)

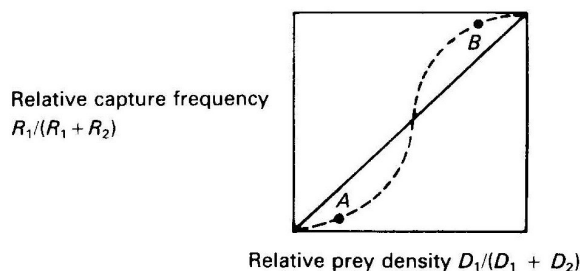


Figure 9.2. Predator “switching.” The straight line shows the relation between proportion of prey taken and relative prey density when the predator is unselective. The sigmoidal function corresponds to switching, that is, disproportionately more prey taken at high relative densities, disproportionately few at low relative densities.

This ideal situation occurs rarely in nature: The number of prey types is usually variable, and they are not usually equal in profitability. Hence it is not surprising that measured relations between prey density and proportion of prey in diet deviate from the matching form. The commonest form of deviation is shown by the dotted line in Figure 9.2: A given prey type is taken disproportionately *less* often when its relative density is low, and disproportionately *more* often

when its relative density is high. This has been termed *switching* (Murdoch, 1969) because it corresponds to a switch in preference in response to a change in relative prey density. For exam-

ple, suppose that at time t_0 prey types 1 and 2 have densities 10 and 50 per unit area and the animal's diet is made up of 1 and 2 in the proportions 1:10. This corresponds to point A in Figure 9.2. Suppose that after a period of time, the density of prey type 1 increases to 50 and the density of 2 falls to 10. The predator now prefers 1, in the proportion of 10:1, and relative choice corresponds to point B in Figure 9.2.

It is often difficult to be sure of the reasons for the deviation from matching; there are at least four possibilities:

1. *Absolute density changes.* Figure 9.2 shows relative measures plotted against one another, hence gives no information about changes in absolute density. As the example shows, relative changes may reflect changes in the absolute levels of either or both prey types. If one prey type is, in fact, slightly more profitable than the other these absolute changes can lead to relative changes in choice of the kind shown by the dotted curve in Figure 9.2. For example, if prey type 1 is, in fact, somewhat more profitable than type 2, then at low densities of lit will pay the predator to take both prey types, but if the absolute (and relative) density of 1 rises, it may be better to specialize on 1. This shift in the absolute density of 1 will thus lead to a "switching" pattern of relative choice.

2. *Nonrandom spatial distribution.* If the spatial distribution of one prey type changes so that it occurs in "patches," rather than being randomly intermixed with the other type, then it may pay the predator to specialize. Thus, if prey type 1 (one of two equivalent prey types) is randomly distributed at low (absolute) density, but distributed in patches at high density, the predator should sample both types when the absolute density of 1 is low, but concentrate on 1 when its absolute density is higher.

Patchy distribution can be further subdivided, into cases where the patches of one prey type are recognizable (i.e., associated with a particular habitat, as when moths of a certain type are associated with a certain type of tree) and cases where the patches are not associated with a reliable signal. When patches are signaled, then obviously the predator would do well to spend most of its time in the signaled area. Even if in the patch it takes prey in proportion to the frequency with which they are encountered, since it encounters disproportionately more of one type, it will take more of that type. If patches are not signaled, they can still be detected by means of *area-restricted search*; this is the vertebrate equivalent of the klinotaxis discussed in Chapter 2: Even without special training, many animals increase their rate of turning when a prey item is encountered; and most species can learn to behave in this way if exposed to patchily distributed prey. If prey are patchily distributed, this pattern of movement obviously increases the animal's chance of encountering additional prey. The result is the same as in the signaled case: Patchily distributed prey are encountered, and taken, disproportionately more often than evenly distributed prey.⁵

3. *Changes in profitability with experience.* With repeated encounters, predators can often become more efficient in handling prey. If the ease with which they do this depends upon the *absolute frequency* with which prey are encountered, then a change in absolute frequency alone may cause a change in effective profitability, leading to a change in preference of the type discussed under (I), above. There is much evidence that with experience animals become better at handling prey. Oystercatchers (*Haematopus ostralegus*), for example, do not mate until a year or two after attaining sexual maturity, because it takes them that long to learn to open shellfish effectively enough to support a family. If a low-profitability prey can increase in profitability when it is encountered at high density, then presumably the predator should continue to sample it even when it occurs at low density. If profitability depends upon absolute density, then prey choice need not be independent of the absolute density of any prey type.

4. *Changes in effective density with experience.* I have assumed that the rate at which a predator encounters a prey type is proportional to prey density. This will not be true if animals must

learn to discriminate camouflaged prey from their background, or to identify particular objects as potential food. The second kind of learning certainly occurs, and the first kind is very probable. Hence, the assumption that encounter rate is proportional to prey density is not always valid.

The possibility that encounter rate can change with experience is interesting because it is a striking instance of an intimate relation between the processes of learning and memory and a behavior pattern — relative predation — critically important to the distribution and abundance of species. I have not yet discussed learning and memory in any detail, but uncontroversial assumptions about memory point to features that are likely to be important. For example, a predator will be more easily able to remember features of a prey item if items of the same type are encountered in “runs,” without intervening items of a different type; in this way interference from the other type is minimized. In nature, runs of the same prey type are much more likely if prey are patchily distributed, so that learning to detect a prey type, as a cause of “switching,” is often likely to be confounded with nonrandom distribution.

There are at least two kinds of learning that might lead to changes in encounter rate: learning that a particular object is in fact a potential prey, and “learning to see” a cryptic prey type, that is, formation of what has been termed a *specific searching image*.⁶ The first type, classification learning, is relatively straightforward; the second, perceptual learning, is less so.

Chicks provide an example of classification learning as they learn to select nutritive over nonnutritive objects. All omnivores sample new foods and learn either to avoid them or incorporate them into their diet. These cases involve learning the significance of readily identifiable objects, not learning to discriminate the object from its background. An experiment with captive jays (*Garrulus garrulus*) and chaffinches (*Fringilla coelebs*) is a less clear case: de Ruiter (1952) found that the birds initially failed to treat stick caterpillars as food, but after they found one accidentally (perhaps by treading on it and causing it to move) they quickly found others. At first they treated the caterpillars like twigs, but afterward they treated them as prey. The birds in this experiment learned that a familiar object is, in fact, prey, and to this extent these results require no perceptual interpretation. But they may also have been learning to discriminate stick caterpillars from sticks, which does imply perceptual learning.

Search image

The idea of a search image derives initially from human subjective experience. von Uexküll, the great German ethologist, describes his own experience as follows:

During an extended stay at the home of a friend, an earthen water jug was always set before my place at lunchtime. One day, however, the servant broke the jug and in its place put a glass carafe. At the next meal, when I looked for the jug, I did not see the carafe. Only after my host assured me that the water stood in its accustomed place did the various glittering reflections off knives and plates suddenly fly together through the air to form the glass carafe...The Searching Image obliterates the Receptor Image. (von Uexküll, 1934, p. 13 — trans., Croze, 1970)

Many people have had similar experiences, and they make plausible the idea that animals and people have to “learn to see” new objects, especially camouflaged objects. Nevertheless, when subjective experience is ruled out, as it must be when we are dealing with nonverbal organisms, these two types of learning — to identify a new prey type, and search-image formation — are difficult to distinguish in practice.

Consider, for example, Marian Dawkins’ ingenious experiments (1971a,b), in which domestic chicks were allowed to search for colored rice grains on various backgrounds. Three results are of special interest: (a) Confronted with green and orange grain on a green background, the chicks consumed the orange grains first. The green (cryptic) grain was only consumed after a delay; moreover, the cryptic grains were consumed at an increasing rate, once they had been detected. (b) The lag in consuming cryptic grains was not due either to color preference (green and orange grain and backgrounds were counterbalanced) or simply to classifying them as non-

prey. For example, chicks that had just been eating conspicuous orange grains (i.e., on a green background) were still deficient in taking (cryptic) orange grains on an orange background. (c) The ability to take cryptic grain was abolished both by the passage of time and interpolated experience with another type of grain: The chicks forgot within 24 hr, and the peck latency to a cryptic grain type was inversely related to time since the chick pecked the preceding grain of that type. Apparently, the chicks were learning something specific about green or orange grain *in its cryptic context*.

Compelling as these results are, they still do not force us to the conclusion that the chicks were undergoing a perceptual change of the same kind as von Uexküll with the water carafe. Key facts are the transience and susceptibility to interference of the learning in Dawkins' experiments. One is inclined to attribute the changes in performance to perceptual modification, because chicks probably do not as readily forget to attack non-cryptic prey (although this has not been rigorously established, as far as I know — indeed, it might be quite hard to prove, given that chicks have a predisposition to peck at certain kinds of objects, quite apart from particular

		Attack?			
		No	Yes		
Prey	Present	30	70	100	$p(Y P) = .7$
	Absent	50	50	100	$p(Y \sim P) = .5$

Table 9.1.

task, the more likely that time and interpolated tasks will interfere with its retention (see Chapter 12). Hence, learning to recognize cryptic prey may just be more difficult than other kinds of learning, not necessarily different in kind.

ROC analysis

One *objective* concomitant of the search-image hypothesis is that animals should improve their ability to *detect* cryptic prey, in the detection-theory sense touched on in Chapter 5. The meaning of “detect” is illustrated by example in the accompanying contingency table (Table 9.1), which shows 200 hypothetical “encounters” between a predator and a cryptic prey. The prey (e.g., caterpillar) was only present on half the occasions; on the remainder, the animal was looking at something else (twig). When there was no prey, the animal nevertheless attacked 50% of the time: $p(Y | \sim P) = .5$; but when prey was present, the animal attacked on 70% of occasions: $p(Y | P) = .7$. The fact that $p(Y | P) > p(Y | \sim P)$ shows that the animal was able to detect the prey, albeit imperfectly.⁷

These two values of $p(Y | \sim P)$ and $p(Y | P)$ are plotted at the filled dot labeled “A” in the contingency space of Figure 9.3. The curve through A illustrates the limitations on the animal’s ability to de-

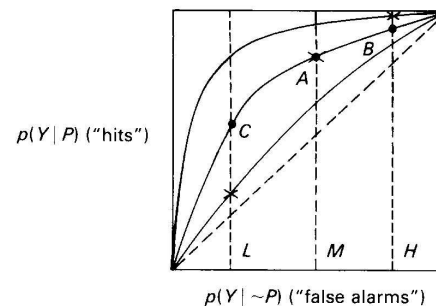


Figure 9.3. Search image as detectability change. Three ROC curves, corresponding to high, medium, and low detectability. Filled circles indicate the hypothesized relation between hits and false alarms on the assumption that different densities of cryptic prey affect only response bias (all three points are on the same ROC curve). The x 's correspond to the search-image view: Detectability is low at low prey densities, but high at high densities.

test this hypothetical cryptic prey type. The curve is traced out by considering what we would expect if the animal were more or less cautious in his attacks. For example, suppose he becomes less cautious, attacking when he merely suspects that the twig is a caterpillar: Obviously the number of “hits” ($p(Y | P)$) will go up; but since he cannot detect prey any better, so also will the number of “false alarms.” This rasher policy corresponds to point B in Figure 9.3. Conversely, if he really hates to peck at twigs rather than caterpillars, he can be more conservative, and not peck unless he is really sure he sees a caterpillar and not a twig. This strategy, point “C” in the figure, reduces $p(Y | \sim P)$, but also drops $p(Y | P)$, so that he misses more prey items.

The curve through points A, B, and C is called an *isosensitivity curve*; another name is *ROC curve* (the initials stand for “receiver operating characteristic” — this kind of analysis was first used for evaluating the properties of telecommunications equipment). The difference between the ROC curve and the diagonal in Figure 9.3 is a measure of *detectability* (sometimes abbreviated as d' , which is one measure of detectability). The diagonal corresponds to complete inability to detect the prey, and obviously the more the ROC curve pushes up into the upper left-hand corner, the better the animal is able to detect the prey.

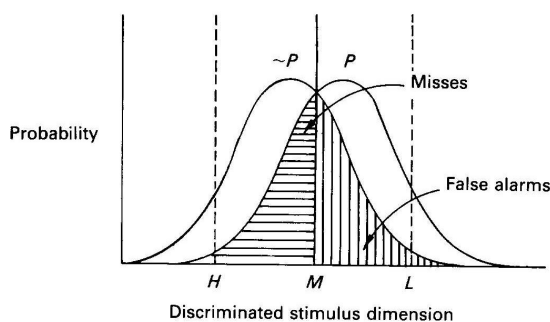


Figure 9.4. One-dimensional signal-detection analysis: The distributions represent the relative frequency with which either prey (right distribution) or non-prey (distractors: left distribution) occur at different values of the discriminated stimulus dimension. The vertical, solid line is the response criterion: Items to the right are attacked, to the left, not attacked. The crosshatched areas represent the probability of the two kinds of error: misses ($p(N | P)$) and false alarms ($p(Y | \sim P)$).

Curve ABC corresponds to a more cryptic prey (or a less able animal) than the curve above and to the left, to a less cryptic animal than the curve below and to the right. The shape of the ROC curve is determined by the distribution of prey items (caterpillars: the *signal*) and distractors (twigs: the *noise*) along all the stimulus dimensions that are important for detectability.

The idealized one-dimensional case is illustrated in Figure 9.4, which shows overlapping “signal” and “noise” distributions. Because the two distributions overlap, it is impossible for the animal to get everything right: Wherever he sets his *criterion* (the solid vertical line in the figure: potential prey items falling to the right he attacks, items to the left he doesn’t), he will make some false alarms (the vertically crosshatched area of the left distribution) and miss some positive cases (the horizontally crosshatched area of the right distribution). As the animal

shifts his criterion (sometimes also called *bias*) from left to right, the areas under the distributions corresponding to false alarms and hits (the two areas to the right of the criterion) shift in the way shown by the ROC curve. Points on the ROC curve corresponding to Low, Medium, and High criterion settings are indicated in Figure 9.3 and by the dashed lines in Figure 9.4. The separation of the two distributions in Figure 9.4 defines the detectability of the prey: the less the overlap, the better the detectability. The three ROC curves in Figure 9.3 correspond to different separations between the signal and noise distributions.

The position the animal sets his criterion should depend on the relative costs of the two kinds of errors: misses and false alarms. Two things affect this ratio: costs of each type of error and their relative frequency. The cost of a false alarm will depend on the time lost in responding mistakenly, the danger of attacking something dangerous, and the physical effort involved. The cost of a miss will depend on the animal’s state of hunger and the profitability of the prey. The relative frequency of the two types of error depends on prey density. If prey density is high, then in the nature of things, the animal will be more likely to encounter prey than if prey density is low — the total in the upper row of Table 9.1 will be higher. Consequently, the animal can afford to be more lenient in his criterion (move it more to the left) when prey density is high than

when it is low. It turns out that the optimal criterion level is directly related to the ratio of prey and distractor densities: The higher the density of the prey in relation to the density of things confused with the prey, the more lenient the animal should be, and the farther to the right in Figure 9.3 should be the point representing his behavior.⁸

Two things follow from this argument: (a) The risk to an individual cryptic prey item should increase as prey density increases; thus optimal adjustment of predator bias alone, with no increase in detectability, should have a stabilizing effect on the prey population (more on this in a moment). (b) Because the effects of a change in bias are different from the effects of a change in prey detectability, we should be able to see experimentally whether change in prey density has one effect, both effects, or neither. Figure 9.3 shows three ROC curves, corresponding to Low, Medium, and High levels of detectability. The filled circles show the expected effect of changing the absolute density of prey, from *Low*, through *Medium*, to *High*, on the hypothesis that this affects bias only: As the absolute frequency of prey increases, $p(Y|P)$, the probability of attacking a distractor (a “false alarm”), and $p(Y|P)$, the probability of attacking P (a hit), increase along the same ROC curve. The x 's show the effect of increasing prey density, on the hypothesis that detectability increases: As the absolute frequency of A increases, $p(Y|P)$ and $p(Y|P)$ increase along successively higher ROC curves.

It is simple in principle to test these two hypotheses. In practice, uncertainty about the proper form for the ROC curves makes testing less sure. One possibility is to compare the ROC curves generated by varying prey frequency with those obtained by varying choice payoffs.⁹ Since there is no reason to expect that variations in payoff will affect detectability, we might accept the form of the ROC curve obtained under these conditions as the norm. If a different curve is obtained when frequency is varied we might want to conclude that frequency variation affects detectability, as the search-image hypothesis requires. As far as I know, this test has not been carried out.

Ecological implications.

Experimental results agree in showing that animals take some time to learn to attack cryptic prey, and that this hard-won ability is easily lost either after lapse of time, or after the interpolation of some other learning. This susceptibility to interference is sometimes referred to as the “incompatibility of search images,” since it implies that animals will find it more difficult to look for two different cryptic prey types than for one. These two factors — difficulty in learning to detect cryptic prey, and enhanced difficulty of detecting more than one cryptic type — have implications for the composition and size of populations. For example, if predator efficiency increases as absolute prey density increases, this will constitute a negative feedback tending to limit the size of prey populations.

I just showed that a stabilizing effect of crypticity on prey population can be derived without assuming perceptual learning. Bias in favor of attack, which we can measure by $p(Y|P)$, should increase with prey density. But $p(Y|P)$ is just the risk incurred by an individual prey item. Hence, the risk to each individual cryptic prey item should increase with absolute prey density. Thus, crypticity in and of itself should tend to exert a stabilizing effect on population growth since it provides less protection at high population densities than low.

Moreover, this process will tend to shift a type-II functional response (Figure 9.1) in the direction of the type-III response, because it will cause a given cryptic prey to be taken disproportionately less at low densities. In terms of the disk equation (Equation 9.1), this change in bias means that the attack rate parameter, a , instead of being constant, increases with prey density, D . The simplest possible quantitative assumption is that a is proportional to D , that is, $a = kD$, which yields the modified equation:

$$R = kD^2/(1 + h k D^2). \quad (9.3)$$

It is easy to see that Equation 9.3 has the required properties: When density is low (D close to zero), the equation reduces to $R = kD^2$, a curve of positive, rather than negative, acceleration; but when D is large, acceleration is negative as the function approaches its asymptote of $1/h$.

The obtained form of functional response for vertebrate predators foraging for cryptic prey quite often corresponds to the sigmoidal form of Equation 9.3 (Holling, 1965; Murdock & Oaten, 1975). Available data are not sufficient to decide whether the type III response is uniquely characteristic of cryptic prey, as this analysis implies. There are some indications that attack rate increases with prey density — the “feeding frenzy” of sharks and many other predators in a patch of abundant prey is a well-known example. But again, we have no evidence that the effect is stronger in the case of cryptic prey and competition among predators provides another functional explanation for feeding frenzy.

There is evidence that prey distributions in nature are in accordance with what one might expect from this analysis. For example, cryptic prey are usually dispersed, keeping density as low as possible, whereas aposematic (bad-tasting, poisonous) potential prey are usually clumped (Benson, 1971; Ford, 1945; Tinbergen, Impeken, & Franck, 1967).

Equation 9.3 can readily be generalized to N prey types; for two prey types it takes the form:¹⁰

$$R_1 = aD_1^2 / (1 + ah_1D_1^2 + ah_2^2D_2^2), \quad (9.4)$$

where D_1 and D_2 are the densities of the two prey types, h_1 and h_2 their handling times, and a is the attack-rate parameter.

It is easy to derive switching from Equation 9.4. For two prey types, the relation between the ratio taken and the ratio of densities is

$$R_1/R_2 = (D_1/D_2)^2, \quad (9.5)$$

or, in terms of proportions

$$R_1/(R_1 + R_2) = [D_1^2 / (D_1^2 + D_2^2)], \quad (9.6)$$

which is a sigmoidal function.

Thus, both switching and the type-III functional response can be derived from the assumption that animals foraging for cryptic prey adjust their response criterion in an efficient way.¹¹ These effects need not depend on the predator being able to improve its ability to detect more frequent prey, nor even on interference between two prey types: It is not necessary that a predator be able to forage more efficiently for one cryptic prey than for two - although that is usually taken as an essential implication of the search-image idea. It is important to make this point, because all these effects have at one time or another been tied to the concept of search image - which assumes more than is necessary to account for them.

Theory aside, learning to detect cryptic prey is susceptible to interference; consequently it is, in fact, more efficient for animals to forage for one prey type than two. For example, in an experimental test of the search-image notion, Pietrewicz and Kamil (1979) found that captive bluejays (*Cyanocitta cristata*) are better able to identify color slides of cryptic *Catocala relictata* moths if they are presented alone, than if they are intermixed with slides of *C. relectata*, another cryptic species. It is easy to show that an advantage of this sort should always lead to specialization on one or other prey type, that is, to extreme switching (Staddon, 1980b).

This experiment is perhaps the best evidence that learning about cryptic prey does involve an improvement in detectability, not just a shift in response bias: In the Pietrewicz and Kamil study, net percentage of correct responses (that is, correct positives plus correct negatives, a measure of detectability) improved within runs of the same prey type, but not across a series where the two types were intermixed. Hence this study provides real evidence for the search-

image idea. Few other studies do so. Some can be dismissed because of inadequate experimental design, but many cannot. For example, there are numerous experiments on attention in human subjects, and a few with animals,¹² that could provide the necessary evidence, but for the most part do not. In these experiments, cryptic prey are represented by a small set of symbol types (e.g., x 's and z 's) that must be spotted by a subject in briefly presented video displays. These target symbols are always embedded in a larger number of distractor symbols, so they are hard to pick out. The number of types of target symbols is termed the *memory-set size*, and the idea that search images are incompatible would lead one to expect that the accuracy with which members of the memory set are detected should be inversely related to memory-set size: the more different types the subject is looking for, the worse his performance on any given type. The surprise is how little difference memory-set size makes: Most experiments show that subjects can search for two, three, or even four types almost as easily as for one. Of course, these subjects are very well trained, so once again one is led to the idea that the changes in detectability go along with learning, and may not represent an intrinsic limitation of animals' perceptual systems.

The possibility that search images interfere with one another — that animals can forage more efficiently for one cryptic prey type than for two — implies that cryptic prey populations should tend to be *polymorphic*: If low density affords relative protection then rare morphs should be favored. This steady selection pressure for variation in crypsis might be expected to lead to polymorphism in the population as a whole. Poulton (1888) pointed out many years ago that polymorphism probably reduces the risk to individual prey organisms, and several natural populations (*Cepea* snails, some butterflies) have been looked at from this point of view. There are limitations on the possibilities, however, because the different cryptic morphs must satisfy two conflicting conditions: to be cryptic with respect to the common background, but not to be confusable with each other. The more heterogeneous the background, the more possibilities for polymorphism, but there will be some limit in every case.

There is no doubt that animals learn something about cryptic prey, that such learning can be difficult and is unusually subject to decay and interference, and that these limitations mean that it is often advantageous for predators to specialize on an abundant cryptic prey type. There is also some evidence that such learning involves an improvement in detectability, as opposed merely to a change in response tendency (bias). Nevertheless, it is also true that phenomena such as switching and type-III functional response that are sometimes attributed to these properties of search image may simply reflect an adaptive adjustment of the attack threshold for cryptic prey. The set of data for which search image is a necessary explanation is, in fact, rather small and to some degree inconsistent with laboratory results.

Nutrient constraints and sampling

The analysis so far is simplified in two important respects: It ignores qualitative differences among foods, and it assumes an unchanging environment. Both these factors are important to real (as opposed to model) animals foraging in natural environments, although neither is easy to tackle theoretically or experimentally.

The need for specific nutrients such as vitamins and minerals means that foods cannot always be compared just in terms of their energy content. There are two possibilities to consider: (a) when the animal must choose among a set of "pure" foods, that is, foods each containing just one nutritional ingredient; and (b) when the animal must choose among a set of foods each of which contains a mix of essential ingredients in approximately constant proportions. The second case obviously corresponds more closely to reality. In both cases, the situation confronting the animal can be described most compactly using the economic techniques introduced in Chapter 7.

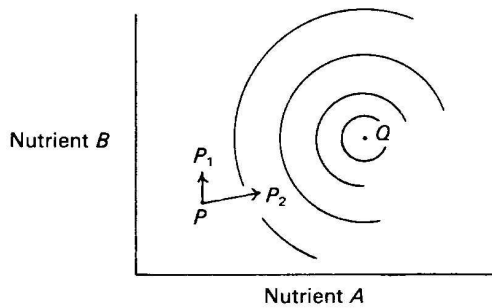


Figure 9.5. State-space representation of diet choice, given nutrients of different types. Point Q is the optimal mix of the two nutrients, point P is the animal's actual nutritional state. Vectors P_1 and P_2 represent the improvements in nutritional state to be expected from two food items: an item containing nutrient B only, and an item containing both A and B .

time can be represented by a point in this space (P in Figure 9.5). P will generally be some distance from point Q , the “ideal” nutritional state. Surrounding Q , we assume, will be a set of closed, concentric indifference contours representing the animal's ordered preferences for nutritional states different from Q (see Figure 7.12). Consider now a particular food item of nutrient B . If ingested, the item will (the animal's individual and evolutionary history tells it) move the animal's nutritional state from P in Figure 9.5 to point P_1 . I will term the line joining P and P_1 the *improvement vector* for the food item in question. An alternative food item contains both A and B ; if ingested it will move the animal's state from P to P_2 . Clearly, the animal's preference in this case will be for the second item, since it shifts the total state closer to Q , the “ideal” state. In this way, the animal can choose from any set of potential food items. This analysis of the problem can obviously be extended to any number of essential nutrients.

This is strictly a regulatory analysis. It does not incorporate environmental features, such as taste and circadian factors, dealt with by the linear model of Chapter 6. However, it does, of necessity, incorporate information about the environment, in the form of the animal's estimate of the improvement vector.

This scheme converges on the one discussed at length in Chapter 7 if we make three transformations. First, a space of potential actions (behaviors) is set up, corresponding to the space in Figure 7.2 and several subsequent figures. Second, the axes of the space in Figure 9.5 are rescaled so that the lengths of the improvement vectors are proportional to the “real” improvement in physiological state associated with a given action.¹⁴ Third, a set of indifference contours corresponding to the real improvement associated with any action is drawn in the behavior space.

The general conclusion is that the problem of a balanced diet is just one aspect of the broader problem of allocating time and energy to particular activities. Although it is sometimes convenient for us to distinguish dietary problems from others that the animal faces, the animal itself cannot really do so: Since all action draws from the same common stock of time and energy, the animal must balance all against all.

In practice, it is highly unlikely that animals make choices on the basis of a scheme like this. Rather, they have evolved sets of relatively simple rules that can handle the vagaries of their natural environments and ensure a plentiful and balanced diet. For example, rats and many other animals when confronted with a number of novel foods will sample them one at a time, waiting a sufficient time between new choices to see if each new food has (delayed) bad effects.

The way an animal should treat each of these situations obviously depends upon its metabolic needs. Since nutritional ingredients such as amino acids are always utilized to form combinations, a sensible animal's preference for one ingredient should depend upon the amount it already has of the other ingredients that enter into the compounds. Hence preferences will rarely be independent of one another.

The problem can be illustrated by considering a simplified creature that requires only two essential nutrients. Its needs can be represented as shown in Figure 9.5.¹³ The horizontal axis shows the animal's nutritional state with respect to nutrient A , the vertical axis its nutritional state with respect to nutrient B . Thus, the animal's total nutritional state at any

Similarly, a rat suffering from experimentally induced vitamin deficiency will widen its choice of foods, and, by a slow process of learning add foods to its diet that can reduce the deficiency (Rodgers & Rozin, 1966; see Rozin & Kalat, 1971, for a review). Contrary to the implications of the economic model, animals are rarely able by taste or sight to evaluate foods in terms of their specific nutritional constituents (specific hungers for taste for sugar, salt, and specific aversions to some poisonous substances are exceptions, but there is no special sensitivity to the great majority of essential vitamins and minerals). As the analysis in Chapter 6 suggested, environmental factors are exceedingly important in motivating the animal to eat versus doing something else; they are much less important in guiding it in a selective way to particular foods. Omnivores become “bored” with a monotonous diet or, to say the same thing a bit differently, a given food type becomes more attractive the longer the time since it was last sampled. Specific satiation-deprivation mechanisms like this function to promote dietary diversity and thus ensure dietary balance in general while not guiding the animal toward particular nutrients. These mechanisms also ensure that the animal will not become too fixed in its behavior (although there are some striking exceptions to this, to be discussed later) and will continue to sample alternatives that may be useful in the future as the environment changes.

NATURAL FEEDBACK FUNCTIONS

Prey in nature are distributed in various often nonrandom ways, are subject to depletion by predators, and may also recover after lapse of time. These three characteristics — nonrandom, particularly patchy, spatial distribution, depletion and repletion — interact with the behavior of the predator to define a *feedback function*, precisely equivalent to the feedback function defined for operant reinforcement schedules that was discussed extensively in earlier chapters.

For example, if prey are patchily distributed, the activity of a predator foraging in a patch is subject to diminishing returns, as shown schematically in Figure 9.6 (a slightly modified version of Figure 8.4).

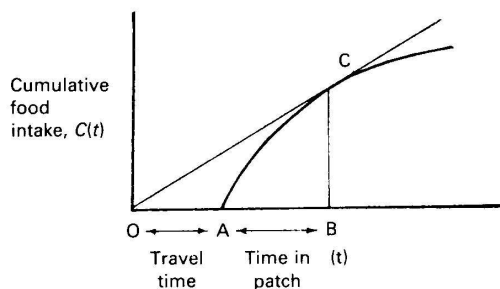


Figure 9.6. The marginal-value theorem. Optimal time in a patch (AB) is defined as the point where the instantaneous rate of prey capture (slope of cumulative curve at point C) is equal to the overall mean capture rate, that is, cumulative food intake divided by travel time plus time in patch ($[OA + AB]/OB$).

At first, the predator can take prey at a high rate (indicated by the steep initial slope of the cumulative curve); but as the patch is depleted, the density of prey drops and the rate of return decreases. This situation is equivalent to an operant-conditioning experiment in which the rate of return for responding to one alternative decreases with time, while the rate of return to be expected from another alternative (i.e., other patches, in the natural case) remains constant. An example might be a two-choice procedure: On one response key a ratio schedule where the size of the ratio increases with each food delivery and on the other a constant ratio schedule, the decreasing ratio would be reset to its initial value after each switch to the constant ratio (Hodos & Trumbule, 1967; Lea, 1976). Obviously, the optimal course is for the

predator to leave a patch when the “instantaneous” rate of return drops below the rate of return from the habitat as a whole. If all patches are of equal richness, this optimal strategy is illustrated by the diagonal line in Figure 9.6. The average rate of return is just BC/OB , that is, the mean cumulative food intake per patch divided by the mean travel time between patches (OA) plus the mean time in a patch (AB); point C is where the instantaneous rate of return within a patch just equals this average, hence AB represents the optimal time in a patch (Charnov, 1976; Parker & Stuart, 1976).

One way to test this analysis is to let animals forage in an artificial environment where

the richness of patches and the travel time between them can be controlled. Cowie (1977) did this with great tits (*Parus major*) in a large artificial aviary. The birds were looking for mealworms hidden in sawdust-filled plastic cups (the patches) on the branches of artificial trees. Travel time was manipulated by putting loose or tight lids on the plastic cups — a tight lid was assumed to have the same effect as a longer travel time. The cumulative food-intake curve was measured directly as the bird consumed the mealworms in each identical cup. Cowie looked to see if the average time spent on a branch varied with the travel time as predicted from the optimal-foraging analysis. The birds did indeed spend longer in each patch when the travel time was longer, but on the average they seemed to spend even longer than predicted by the analysis. When the energetic, as well as time, costs of traveling were taken into account, the fit between theory and data was quite good. Other studies, with bumblebees, water-skaters, and other animals have also provided support for the marginal-value approach, although it is not clear that it works in every situation (Whitham, 1977; Cook & Cockrell, 1978; Davies, 1977; see Krebs, 1978, for a review; see Shettleworth, 1998, for a more recent survey).

There is no standard reinforcement schedule precisely equivalent to foraging in depleting patches. But there are common natural situations analogous to both interval and ratio schedules. Within a non-depleting patch — a large cloud of insects or *Daphnia* prey, for example — return is directly proportional to attack rate (if handling time is excluded). This is the natural equivalent of a ratio schedule. Correspondingly predators in such situations usually respond at a high rate.¹⁵

When a food source replenishes itself after lapse of time, the predator faces a situation analogous to an interval schedule. For example, a predator that has exclusive access to a self-renewing foraging area should follow a foraging path that allows each region the optimal time for replenishment. Studies of wagtails (*Motacillidae*) patrolling their territory along a river bank at which insect prey arrive more or less randomly show that the feedback function here corresponds to a random-interval schedule. The birds seem to adjust their search path appropriately.¹⁶ Hawaiian honeycreepers (*Loxops virens*) defend territories of nectar-producing flowers; here the pattern of repletion is more predictable and corresponds to a fixed-interval schedule. This study and others have shown that predators under these conditions adjust their foraging patterns so that depleted flowers are not revisited until their nectar stores have substantially recovered (Kamil, 1978; Gill & Wolf, 1978).

SUMMARY

The study of natural foraging is difficult because of uncertainties about the feedback function relating the animal's behavior to its consequences. Nevertheless, much has been learned about diet choice and foraging patterns by looking at foraging in terms of energetic return and by making simple assumptions about foraging patterns. For example, logic suggests that animals should specialize more when food is abundant than when it is scarce, and they do, although not as strictly as theory implies. Exceptions seem to reflect either the animal's lack of knowledge about its environment, or an evolutionary bias that favors nonexclusive choice (risk aversion).

The natural equivalent to a feedback function is the predator's *functional response*: the relation between prey density and predation rate. Two types of functional response can be derived from simple arguments about random search and prey-handling time. The third type, often associated with foraging for cryptic prey, seems to involve psychological mechanisms that take the form either of changes in the animal's criterion for attack, or in the actual detectability of prey (*search image*), as a function of experience. Simple type I and type II functional responses correspond quite closely to ratio feedback functions. Situations where the prey replenish with time (foraging by nectar feeders, for example) resemble interval schedules. Animals seem to behave as these characterizations imply, responding rapidly under ratio-like conditions, but allowing time to elapse between visits when the probability of finding prey increases with time away.

NOTES

1. Reviews of this work appear in Schoener (1971), Pyke, Pulliam, and Charnov (1977), Kamil and Sargent (1981), and Krebs (1973, 1978). The principle (discussed later in the chapter) that an optimal diet from a set of nutritionally equivalent prey differing in profitability is just the N most profitable types (where N depends on the relative profitabilities and abundances of the most profitable types) was independently proposed by at least nine different people. Some other principles were borrowed from economic theory.

2. See Murdoch and Oaten (1975) and Hassell (1976) for reviews of predation and population stability.

The disk equation is a feedback function, in the sense that it says how the animal's obtained rate of reward depends upon its "attack rate," a . The hyperbolic form is reminiscent of the result I derived earlier for a VI schedule, but this similarity is probably misleading. The natural foraging situation corresponds to a ratio schedule, in the sense that encounter rate is strictly proportional to attack rate during the time the animal is searching. The negative acceleration derives from the increasing time taken up with handling prey, not from the animal's inability to predict when reinforcement is set up.

3. See, for example, the review in Hassell (1978); an introductory summary of much of the same material is Hassell (1976).

4. This argument has been made by Real (e.g., 1980).

5. The general point is that any departure from randomness introduces *redundancy*, in the information-theory sense, into the spatial distribution of prey. Providing the predator has some way of taking advantage of the extra information provided by non-randomness, experienced prey densities will always be higher than average levels. Consequently, predictions about optimal diet based on average levels will usually be wrong.

6. This concept is originally due to von Uexküll (1934). It was first applied by L. Tinbergen (1960) as an explanation for variations in the diet of bird predators in pine forests. Tinbergen found that the proportion of different cryptic insect prey species in the birds' diets bore no simple relation to the relative abundance of the insects in the birds' environment: An increase in the proportion of a prey type was generally followed by an increase in its proportion in the birds' diet only after some delay. Tinbergen interpreted this lag as the time taken for the birds to "learn to see" the new type.

7. Dawkins' (1971a) data show that, in fact, birds make very few "misses," rarely pecking at non-prey — perhaps because this entails some risk. One way to increase prey detectability is to adjust foraging speed, searching more slowly for cryptic prey. Gendron (1982; Gendron & Staddon, 1983) has shown that quail adjust their search speed as this suggestion implies, searching more slowly for more cryptic prey. This choice to trade off speed for accuracy makes no difference to the optimality analysis in the text. It poses a problem for the animals when foraging simultaneously for prey of differing crypticities, however, since the search speed appropriate for the more cryptic type is unnecessarily slow for the less cryptic, the speed for the less cryptic too fast for the more cryptic. This is another way in which foraging for two prey types is less efficient than foraging for one.

8. *The effect of prey density on prey risk.* The optimal adjustment to changes in the density of cryptic prey can be derived quite simply from the ROC analysis. First, we need to estimate the costs and benefits for the four outcomes in Table 9.1. These are shown in the *payoff matrix* in Table N9. 1.

Thus, the cost of a false alarm is u , of a miss, v , and the benefit of a hit is B ; I assume that a correct failure to attack carries neither cost nor benefit. The net benefit, H , to an animal of a particular strategy (criterion) is proportional to these costs and benefits, multiplied by their probabilities of occurrence and weighted by the densities of prey and distractors (non-prey):

		Attack?	
		No	Yes
Prey	Present	v	B
	Absent	0	u

Table N9.1.

$$H = D_p[p(Y|P)B - (1 - p(Y|P)v] - D_N p(Y|\neg P)u,$$

where D_p and D_N are the densities of prey and nonprey, respectively, and costs u and v , are expressed as nonnegative numbers. For readability we can replace $p(Y|P)$ with p and $p(Y|\neg P)$ with q ; simplifying then yields

$$H = D_p[p(B + v) - v] - D_N q u. \quad (\text{N9.1})$$

In this equation p and q are not independent; they are related by prey detectability, which defines a particular ROC curve (see Figure 9.3). A simple approximation to standard ROC curves is the power function

$$p = q^s, 0 < s \leq 1, \quad (\text{N9.2})$$

where the exponent, s , is a measure of crypticity: The larger the value of s , the more closely the ROC curve approaches the diagonal $p = q$, hence the more cryptic the prey. Substituting Equation N9.2 in Equation N9. 1 and simplifying yields

$$H = p D_p (B + v) - v D_p - p^{1/s} \cdot D_N u. \quad (\text{N9.3})$$

In these equations p represents the animal's criterion, since he can set p anywhere he wants by being more or less stringent. Consequently, finding the best criterion is equivalent to finding the value of p in Equation N9.3 that maximizes H . Differentiating Equation N9.3 with respect to H , setting the result to zero to find the maximum, and simplifying yields

$$\hat{p} = [s(D_p/D_N)((B + v)/u)]^r, \quad r > 0, \quad (\text{N9.4})$$

where $r = s/(1 - s)$.

It is easy to see that Equation N9.4 has the properties one might expect: Prey risk, \hat{p} , is directly related to prey density, D_p , and inversely related to density of non-prey, D_N ; \hat{p} is directly related to the sum of the benefits of a hit, B , and the cost of a miss, v , and inversely related to the cost of a false alarm, u . In addition, the steepness of the function depends on the crypticity, s : The more cryptic the prey (the higher the value of s), the more sensitive \hat{p} should be to prey density. (See Staddon & Gendron, 1983, for a fuller account.)

9. This would have to be done using a modified version of the operant conditioning procedure used by Pietrewicz and Kamil (1979), discussed later in the chapter. One way to proceed is as follows. Pigeon or bluejay subjects could be confronted with three response keys. A color slide of either a potential cryptic prey item, against a background ("signal + noise": S) or a background without prey ("noise": N) would be projected on the center key at the beginning of each

trial. A few pecks on this “sample” stimulus would then turn on the two outer keys. A peck on the left key would be correct if the sample were “S”; a peck on the right key would be correct if the sample were “N.” Both types of error could be “punished” by timeouts (i.e., periods in the dark when no reward is possible). Correct responses would be reinforced with food. After reward or timeout, a new sample would be presented and the cycle would continue as before.

Prey frequency would be varied by varying the proportion of *S* and *N* trials; payoff could be varied either by rewarding correct responses on an intermittent basis, by varying amount of reward, or by varying the magnitude of punishment. ROC curves could easily be traced out by any of these methods. If the curve derived by varying prey frequency shows at high prey frequencies significantly higher values for d' than the other curves, one would have strong evidence for the search-image idea.

10. Switching and functional response. The general form of Equation 9.4 is

$$R_i = aD_i^2 / (1 + a\sum h_i D_i^2), \quad (\text{N9.5})$$

for *N* prey types. It is also not necessary to assume that attack rate, *a* in equation 9.1, is strictly proportional to prey density, *D*. Almost any positive monotonic relation can be well fitted by the power function

$$a = kD^m, \quad m \geq 0. \quad (\text{N9.6})$$

Substituted in Equation N9.5 this yields a general formula for functional response:

$$R_i = aD_i^{m+1} / (1 + ah_i D_i^{m+1}). \quad (\text{N9.7})$$

Equation N9.7 is similar to the general form suggested by Real (1977). When $m = 0$ the equation corresponds to the type I ($h_i = 0, \forall i$) or type II ($h_i > 0$) response; when $m > 0$, it corresponds to the type III response. When $m = 1$, and $N = 2$, Equation N9.6 is reduced to Equation 9.4. The relative choice function derived from Equation N9.7 is obviously

$$R_1/R_2 = (D_1/D_2)^{m+1}, \quad (\text{N9.8})$$

which corresponds to switching when $m > 0$.

11. This analysis implies that “switching,” in Murdoch’s (1969) sense, does not require a type III functional response for each prey type considered separately (i.e., with the densities of all others held constant). However, if each prey type shows the type III response in isolation, then the predator should show switching when confronted with both, assuming that it treats each type independently: The type III response implies switching, but not conversely.

12. Blough (1979) presents elegant experimental data on visual search in pigeons. Experimental results with humans are described in Schneider and Shiffrin (1977), Shiffrin and Schneider (1977), Green and Swets (1966), and Rabbitt (1978).

13. McFarland and his associates have pioneered the application of models of this sort to the analysis of motivational systems. See, for example, McFarland and Houston (1981) and McCleery (1978). An analysis of the nutrient-constraint problem is provided by Pulliam (1975).

14. Fitness and utility — again. The definition of “real improvement” is not a trivial matter. Early approaches to animal motivation (e.g., Hull, 1943) identified physiological state as the key factor. Hull, for example, supposed something termed “tissue need” to be the driving force behind action. I argued at length in Chapter 6 that this cannot be correct: It is very poor design indeed to arrange that the animal becomes hungry only when it is beginning to suffer real resource

depletion. Hull (1952) eventually recognized this deficiency and added *incentive* as a determinant of behavior: Thus food-related behavior was presumed to be proportional to the *product* of “drive” (“tissue need”) and incentive (roughly, the expected rate of energy acquisition) (see also McCleery, 1977).

The final extension was made by thoroughgoing selectionists (e.g., Sibly & McFarland, 1976) who identified Darwinian *fitness* as the key variable. Thus “improvement” in Figure 9.5 must be “improvement in fitness.” This has become the working assumption for evolutionary biologists (see Oster & Wilson, 1978; Maynard Smith, 1978) and is the contemporary version of the adaptationist manifesto that essentially every phenotypic feature serves some adaptive function. Although theoretically more justifiable than the much simpler assumption that some measurable aspect of food intake (say) is maximized, it suffers from two practical problems: All motivational systems (for food, water, sex, exploration, etc.) are now lumped together, since all must deal in the common currency of Darwinian fitness. And fitness is essentially impossible to measure directly. It is after all not even *current* fitness that is required, but fitness in the ancestral populations in their “selection environments.” In addition, the mechanisms of embryonic and post-embryonic development, plus the availability of appropriate variation (in the form of gene combinations and mutations), constrain the set of possible phenotypes in ways that are impossible to pin down in detail. As a practical matter, fitness is impossible to measure directly, and the existence of unknown developmental constraints means that some phenotypic features are likely not to be optimal.

The practical resolution of all this is to deal with measurable aspects of behavior, such as energetic efficiency, but to recognize that these are plausible surrogates for fitness. Despite the obvious philosophical flaws of this position, no real alternative exists. The approach is an essential part of any attempt to understand adaptive behavior and, warts and all, has been exceedingly successful.

15. The alert reader will notice that according to my argument, herbivores are also on a ratio schedule, yet are not noted for the tempo of their foraging. One difference lies in the relation between the cost of foraging activity and its energetic return: For herbivores the relative return on foraging is modest, because of the low energy content of their food. Thus, their ratio schedule is a high-valued one. But as we saw in Chapter 7, on very high ratios, animals will respond slowly; it is only at intermediate values, yielding payoff rates close to the peak of the bitonic response function, that ratio schedules generate high response rates. Thus the leisurely foraging of herbivores does not constitute a paradox.

As a practical matter, herbivores may also be limited by the time it takes them to process their food: Since processing takes so long, and holding capacity is limited, there is also a limit to the useful rate of foraging.

16. *Foraging in a repleting food source.* Davies and Houston (1981) assumed that insects and other prey items arrive in a random way at the wagtail’s riverbank territory. Hence, the number of food items arriving within a unit length of territory since the wagtail’s last visit is given by

$$x(t) = K(1 - \exp(-wt)), \quad (\text{N9.9})$$

where t is the time since the last visit (the *return time*) and K and w are constants (for a given observation period). Equation N9.9 is of the same form as Equation 8.6, which describes reinforcement probability as a function of interresponse time on (random) variable-interval schedules where K is the magnitude of reinforcement and w is the average rate of reinforcement.

Davies and Houston develop the analogy more fully, as follows. If the wagtail’s territory is of length L , then the total number of items obtained is

$$N(t) = Lx(t) = LK(1 - \exp(-wt)), \quad (\text{N9.10})$$

assuming that the same return time holds for all points on the territory, and that there are no invasions by other wagtails (a strong assumption, sometimes!). The return time is given by

$$t = L/v,$$

where v is the speed at which the wagtail walks. If the animal's rate of energy consumption is proportional to v , then the net rate of energy gain is given by

$$N(t)/t - kv = [LK(1 - \exp(-wt)) - kL]/t, \quad (\text{N9.11})$$

where k is a constant.

Now consider an animal working on a VI schedule with scheduled reinforcement rate, w . If the animal adopts a constant interresponse time, t , then the expected reinforcement rate, R , is given by Equation N9.10, where K is the reinforcement magnitude. If each response has a constant energetic cost, k , then, obviously, the net energy gain is given by Equation N9.11.

It seems likely animals adapt so well to standard reinforcement schedules because the schedules resemble common natural situations.