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OPTIMAL FORAGING THEORY: A CRITICAL REVIEW

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INTRODUCTION

Proponents of optimal foraging theory attempt to predict the behavior of animals *while they are foraging*; this theory is based on a number of assumptions (133, 155, 210, 231). First, an individual's contribution to the next generation (i.e. its "fitness") depends on its behavior while foraging. This contribution may be measured genetically or culturally as the proportion of an individual's genes or "ideas", respectively, in the next generation. In the former case, the theory is simply an extension of Darwin's theory of evolution.

Second, it is assumed that there should be a heritable component of foraging behavior, i.e. an animal that forages in a particular manner should be likely to have offspring that tend to forage in the same manner. This heritable component can be either the actual foraging responses made by an animal or the rules by which an animal learns to make such responses. In other words, optimal foraging theory may apply regardless of whether the foraging behavior is learned or innate. Given these first two assumptions, it follows that the proportion of individuals in a population foraging in ways that enhance their fitness will tend to increase over time. Unless countervailed by sufficiently strong group selection (see 287, 242), foraging behavior will therefore evolve, and the average foraging behavior will increasingly come to be characterized by those characteristics that enhance individual fitness.

The third assumption is that the relationship between foraging behavior and fitness is known. This relationship is usually referred to as the *currency* of fitness (231). In general, any such currency will include a time scale, although in some cases it may be assumed that fitness is a function of some *rate*.

The fourth assumption is that the evolution of foraging behavior is not prevented by genetic constraints such as the physical linkage of genes that affect a number of traits or the effects of single genes on multiple traits (155). Such genetic linkage of traits could impede the rate of evolution, but it is assumed that mutations will eventually arise that circumvent these linkages.

The fifth assumption is that the evolution of foraging behavior is subject to “functional” constraints that have been realistically determined. When focusing on foraging behavior (rather than on foraging traits in general), it is assumed that the morphologies and physical properties of the animals are known and evolutionarily fixed. Assumptions may also have to be made about the level of information available to an animal and about the animal’s ability to store and process this information (e.g. 125, 189, 268). Animals might obtain information through either direct experience or observation of others (e.g. 274). Such functional constraints can also be considered as evolutionary variables within a broader framework.

The final assumption is that foraging behavior evolves more *rapidly* than the rate at which the relevant conditions change (210). Thus, the evolution and adaptation of foraging behavior should approximately reach completion with individuals foraging in ways close to (i.e. statistically indistinguishable from) those that *maximize* their expected fitness, subject to any functional constraints. In this sense, it is hypothesized that animals forage “optimally.”

This approach to animal foraging behavior began to develop about 18 years ago with papers by MacArthur & Pianka (150) and Emlen (64). The number of papers published annually that either include the *optimal foraging* in the title or clearly develop or test predictions based on optimal foraging theory appears to have increased rapidly between 1973 and 1981 and to have decreased since then (Figure 1). It will be interesting to see what happens in the future.

During the last 18 years, the literature on optimal foraging theory has been reviewed a number of times (46, 76, 132–135, 137, 199, 209, 210, 229, 231). Nevertheless, at this stage another review seems timely. Past reviews have tended to take a relatively positive view of the value of optimal foraging theory and to take apparent tests of predictions derived from this theory at face value. Optimal foraging theory has engendered considerable controversy, however (e.g. 118, 178). Furthermore, in many optimal foraging studies, the theory and the observations may not be appropriately matched because, for example, the assumptions are unrealistic or unsupported or the mathematical calculations are incorrect (see 209 and discussion below). It is therefore time, I believe, to review the various points of view concerning optimal foraging theory, to derive criteria for evaluating *studies* that attempt to test this theory, and to begin to judge its usefulness on the basis of studies that meet these criteria. In order to achieve these goals, it is also necessary to review both the theoretical and empirical developments that have occurred. I shall attempt below to carry out

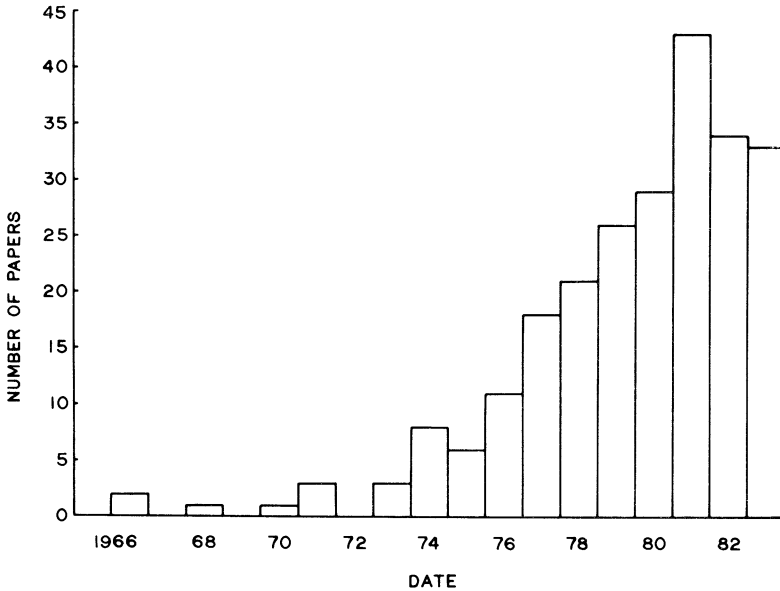


Figure 1 Yearly numbers of published papers from author's reprint collection that either contain the words *optimal foraging* in the title or include the development or tests of optimal foraging predictions.

such a review. I will deal with the behavior of animals *while they are foraging* but not with the *amount* of time that animals allocate to foraging nor with *when* animals choose to forage (see 38, 56, 92, 93, 102, 198). I shall also omit consideration of the recent attempts to relate optimal foraging theory to experiments on "matching" (see 101, 106) and to apply it in a variety of contexts (e.g. 1, 39, 62, 94, 95, 191, 192, 207, 235, 286).

ATTITUDES TOWARD OPTIMAL FORAGING THEORY

The most critical view of optimal foraging theory is that it is "tautological" (178) or "not scientific" (118). This view arises from the following properties of this theory: First, when predictions and observations do not agree, it is not clear which assumptions are at fault (155, see also 50). Authors have tended to rationalize such discrepancies between observed and predicted results by attributing them to faulty assumptions regarding constraints or the currency of fitness rather than those assumptions about the heritability of behavior, the lack of genetic constraints, or the rate of evolution. They thereby seem to invite the criticism (e.g. 85, 149) that they are unwilling to abandon certain assumptions. Second, it is difficult to obtain independent tests of most, if not all, of the

assumptions that underlie optimal foraging theory. Probably few would doubt the assumption about the heritability of foraging behavior, but confirmatory experiments (e.g. 54) are mostly lacking. Foraging behavior almost certainly affects animal fitness, but unless the effects of this behavior on survival and reproduction can be demonstrated for animals that differ only in terms of selected aspects of their foraging, the currency of fitness cannot be verified. Under carefully controlled circumstances, an animal will do as it pleases, and consequently, it is difficult to obtain more than a *minimum* estimate of an animal's capabilities for information acquisition, storage and processing. Elaborate breeding experiments would be necessary to verify the existence of any linkage between foraging behavior and other traits. There also does not appear to be any information available on rates of evolution and of changes in conditions.

To view optimal foraging theory as tautological or unscientific seems unreasonable. Like other scientific theories, it is based on assumptions. The existence of a number of assumptions in the case of this theory makes it difficult, but not impossible, to evaluate it fully. Some of the assumptions are easier to relate to observations than others. A sound knowledge of an animal's natural history may well determine how realistic the assumptions concerning the currency of fitness and functional constraints are (see 210), but it is of little help with regard to the other assumptions. It is also relatively easy to alter the theoretical treatments of foraging and the data collection schemes to accommodate alterations in the assumptions concerning fitness currency and functional constraints. For example, the assumption that an animal is simply maximizing the net rate of energy gain can easily be modified to allow for a minimum requirement of some nutrient (e.g. see 188). At present, however, there is no obvious way to incorporate deviations in other assumptions into the theory. Such deviations should lead to "suboptimal" foraging behavior, but unless some way can be found to predict the magnitude and direction of any departures from optimal behavior, there seems little point in pursuing this (but see 90, 213, 238, 239). The most logical approach to differences between predictions and observations is therefore to explore the consequences of variation in the currency and constraints assumptions and to devise experiments and observations from which the most realistic assumptions about these variables can be deduced. If the most realistic currency and constraints assumptions and the most careful development of theory do not lead to reasonably close agreement between observed and predicted results a reasonable fraction of the time, then optimal foraging theory should properly be judged as not very useful (see below). Therefore, its usefulness cannot be determined on the basis of only one or a few studies (see also 280).

A second view of optimal foraging theory, which is also unflattering, is that it is doomed to failure because of the complexity of the natural world. In other

words, according to this view, the effort to develop this theory is hopeless because one or more of the basic assumptions is almost certain to be false. This view would seem to be overly pessimistic, however, and if it were applied in analogous fashion to the motion of falling objects, it would surely produce a table of falling coefficients, rather than the law of gravity. The success of many optimal foraging studies also argues against this view.

A third view of this theory, highly flattering but clearly inaccurate, is that there are already so many studies supporting its predictions that it can be regarded as well-established and verified; hence there is no need for further development and tests of its predictions. However, the large and growing number of studies in which some discrepancy has been found between the predictions of optimal foraging theory and observations—especially in terms of precise quantitative predictions—mitigates strongly against this view.

A final view of this theory, to which I subscribe, is that it is still too early to pronounce judgment and that further development and testing are warranted. Though the number of “optimal foraging studies” is already quite large (Figure 1), none of them fulfills all of the criteria for evaluating this theory outlined below. When those studies that come closest to satisfying all the criteria are examined, some patterns emerge in terms of the degree of success of the theory, and these patterns suggest avenues for future investigation.

THE DEVELOPMENT OF THEORY

In 1977 it was reasonable to consider development (and tests) of optimal foraging theory in the following four roughly independent categories: (*a*) diet, (*b*) patch choice, (*c*) when to leave a patch; and (*d*) movement (e.g. 210). Some 7 years later, these categories are still useful and convenient, but several new developments have occurred. The first of these is the addition of a fifth category, namely central place foraging (e.g. 179), which deals with situations in which an animal has a central foraging base, such as a nest, from which it goes on foraging bouts and to which it returns with at least some of what it has gathered while foraging. In such situations, the choices of where to forage (patch choice), when to leave a patch, and what to eat (diet) are interrelated, and hence a separate category is required.

A second general development has been an increased realization of the potential importance of the stochastic or variable nature of the world (e.g. 23, 159, 174, 195, 253). From the outset of optimal foraging theory, it was realized that most, if not all, parameters—such as the amount of energy obtained from an individual of a particular prey type—are random variables (i.e. they take different values with certain probabilities). In the initial models, this kind of randomness was adequately dealt with by the use of mean values for the various parameters (e.g. 32). In some situations, however, the fitness of a foraging

animal is a function not only of the mean values of the various parameters but also of their variances. In these situations, an animal should make its foraging decisions on the basis of these variances as well as the means. Animals that prefer lower variance, all else being equal, are termed “risk averse,” while animals that prefer higher variance are “risk prone” (23).

The variable nature of the world also means that animals cannot be omniscient and that they will have only an imperfect knowledge of what they may encounter at a future time and place (199). In such situations, an animal should be a statistician—collecting and storing information as it forages and using this information to make foraging decisions. For example, there may be a positive correlation among the nectar volumes in flowers on the same plant, in which case an animal feeding on this nectar might base its decisions about when to move to another plant on the amount of nectar obtained so far from the present plant. Therefore, it should be less likely to change plants the more nectar it has obtained from the flowers of the present plant.

It has also been recognized that the world is always changing and that animals should accordingly devote time to “sampling” their environment in order to obtain necessary information for subsequent foraging decisions (245). For example, if the relative quality of two food patches switches from time to time, then an animal that can feed in either patch should always spend some time in what at the time might be the worse patch so that it could make the appropriate adjustments when conditions change. At present, however, there appears to have been no mathematical development of such sampling regimes.

A final general development has been the alteration of a number of the assumptions in the original foraging models. For example, in the original model of optimal diet (see 210), it was assumed that animals recognize distinct food types almost instantaneously. More recently, recognition time has been included, which has altered the original predictions of the theory (63, 111).

1. Risk Aversion and Risk Proneness

In general, the fitness of a foraging animal will be some function of a number of foraging parameters such as the amounts of energy obtained from the various food types, the handling times involved, the rates of encounter, and so on. If these foraging parameters are random variables, the average or expected fitness will usually depend not only on the mean values of the parameters but also on their variances. Optimal foraging theory began with two kinds of exception to this rule.

The first kind of exception resulted from the initial assumption that the fitness of a foraging animal is a linear function of the net rate of food gain while foraging. In algebraic terms, it was implicitly assumed (e.g. 210) that fitness $F = a + bR$, where R is the net rate of food gain and a and b are constants. In this case, since $E(F) = a + bE(R)$, any variance associated with R does not affect

the expected fitness, and the maximization of the expected fitness is equivalent to the maximization of the expected net rate of food gain. As the following example illustrates, however, the situation becomes quite different when fitness is assumed to be a nonlinear function of R (or its equivalent) (see also 23, 214, 252). Suppose that fitness $F = 0$ if $R < T$ (i.e. some threshold) and $F = 1$ (i.e. an arbitrary constant) if $R > T$. Suppose also that R is a random variable with probability distribution $P(R = r) = P(r)$. Then the expected value of F is simply the *probability* that the animal meets its minimum food requirements (i.e. $\int_T^\infty P(r)dr$), which depends on the general shape of the probability distribution for R . Suppose further that the variance of the probability distribution for R (but not the mean) depends on which of two (or more) foraging possibilities the animal chooses and that the probability distributions of R are always symmetric. Then the choice that maximizes the expected fitness will depend on whether the mean R (i.e. $E(R)$) is greater or less than the threshold T . If $E(R) > T$, the animal should opt for the smaller variance (i.e. be risk averse); but if $E(R) < T$, the animal should be risk prone and preferentially select the higher variance. In other words, if an animal is likely to starve, its best chance for survival will come from the most variable situation (assuming no differences in means). On the other hand, if it can expect to exceed its food requirements, it should prefer the lowest variance.

In general terms, the optimal response to variance in R (assuming a constant mean) depends on the shape of the relationship between fitness and R at the point where R equals its average or expected value. If the relationship is convex (i.e. bowed downwards), an animal should be risk prone; if it is concave (i.e. bowed upwards), an animal should be risk averse. If fitness is a sigmoidal (i.e. S-shaped) function of R and the frequency distributions of R are symmetric with the same mean, then an animal should be risk averse or prone to the right or left of the inflection point, respectively (from 23). If both the mean and variance of R depend on an animal's foraging decisions, the situation is more complicated (253).

The second kind of exception to the general rule that the expected fitness will depend on the means and variances of the various foraging parameters arises from the assumption that foraging events are independent of one another and of previous foraging decisions. Suppose, for example, that encounter rates with different kinds of food types are not affected by any aspect of past history, such as the food types previously encountered or consumed. Then the foraging process can be modeled as a renewal process, and the expected rate of food gain depends only on the averages of the food gain from each food type, the handling time for each food type, and the time between encounters with food items (e.g. 32, 33; see below). In this case, if fitness increases linearly with food gain, the optimal diet will depend on these averages and not on any associated variances. On the other hand, if foraging events are influenced by past history, the

variances and covariances of any foraging parameters should affect the expected rate of food gain and hence the optimal foraging strategy (e.g. 87, 174, 202).

2. *Optimal Diet*

The original and simplest model of optimal diets was based on the following assumptions: (a) The fitness of a forager increases linearly with the expected rate of food intake, where food value is measured in calories or weight. The costs of handling and searching for food are assumed to be equal. (b) Each food type has an associated average food value and average handling time, both of which are known to the forager. (c) The forager requires negligible time to recognize food types and does not make any mistakes in doing so. (d) Handling and searching for food are mutually exclusive. In other words, the forager decides whether or not to eat a particular food item at the instant it encounters that item. This assumption was implicit during the early developments of optimal diet theory. (e) The rates of encounter with the different food types are constant and independent of each other and of past history. (f) Handling times and food yields are independent of past history. (g) Food items are encountered sequentially rather than simultaneously. (h) Food items, if eaten, are totally consumed. (i) Dietary choices are constant. (j) The foraging time is long compared with the time spent handling and searching for food. (k) There are no constraints on total food volume or the rate of food intake.

Under these assumptions, foraging can be thought of as a renewal process where the renewal event is the recommencement of searching for a food item and where the expected food gains and times taken between renewal events are independent of past experience. Therefore, the optimal diet depends only on the average values of the food gains and handling times for each food type and on the encounter rates with the different food types (32, 253). It also follows (see 117 and references in 210) that in the optimal diet, a food type is either always eaten or always ignored; the optimal diet is found by starting with the food type having the highest average food gain to average handling time ratio (i.e. the highest rank) and adding food types with successively lower ratios until R reaches a maximum. Consequently, the optimal diet in the *present* case has the following testable properties (210):

1. Whether or not a food type should be eaten is independent of its abundance and depends only on the *absolute* abundances of food types of higher rank. An animal should never specialize on a relatively low-ranked food type regardless of its abundance (see also 68, 236).
2. As the abundance of a relatively high-ranked food type increases, lower-ranked types should eventually be dropped from the diet, starting with the lowest-ranked type included. So, increasing overall food abundance should

lead to greater specialization. Increasing abundance of relatively low-ranked food types may, however, have no effect on the optimal diet.

3. As mentioned above, a food type is either completely included in the optimal diet or completely excluded from it—animals should never exhibit “partial preferences.”

Many studies have attempted to test one or more of these three predictions (e.g. 51, 52, 59, 67, 78, 81, 84, 141, 241, 246, 248, 257, 266). A much smaller number have tried to determine the exact optimal diet using the above model and to compare this diet with the observed one (65, 66, 75, 82, 83, 136, 163, 190, 263, 278). (These studies will be evaluated below.) There are also many recent studies that examine the dietary preferences of animals and the factors correlated with these preferences (e.g. 10, 18, 57, 60, 61, 74, 112, 114, 121, 122, 148, 151, 164, 220, 222, 223, 225, 255, 260, 265, 276). Further developments in optimal diet theory have occurred through alterations to the assumptions in the above model.

DIFFERENTIAL COSTS OF HANDLING AND SEARCHING FOR FOOD The simplest possible variation of the above model is to assume that fitness is an increasing linear function of the *net* rate of food gain rather than the gross rate. The distinction is real so long as the costs of handling and searching for food are different. This alteration produces potential differences in the exact optimal diet, but it does not change the three more qualitative predictions outlined above (31).

NUTRIENT CONSTRAINTS Significant departures from the above optimal diet predictions result from the simplest of models that include nutrient requirements. Suppose, for example, that fitness is maximized when the rate of food gain is maximized, subject to the constraint that the rate of gain of some nutrient must at least equal some threshold value. In this case (see 188), “partial preferences” should result (i.e. some food types, when encountered, should be eaten with probabilities between 0 and 1), and the preference for a particular food type should depend not only on the abundances of more preferred food types but also on its own abundance (and probably the abundances of less preferred food types). Similar predictions arise from other models that include nutrient requirements (153, 211, 212). After allowing for nutrient requirements, increases in abundance of preferred food types should still lead to greater dietary specialization (from 188).

RECOGNITION TIME, MISIDENTIFICATION, AND CRYPTICITY The optimal diet model can easily be modified to allow for the time required for recognition of food types by adding recognition times to the handling times (107, 111).

When an animal encounters a food item, it *must* spend some time (which may vary with the food type) to recognize the food type, and it may also incur handling time if it chooses to eat the food item. This version of the optimal diet model does not predict partial preferences, but it does predict that whether or not a particular food type is included in the diet should depend on its own abundance (absolute and/or relative), as well as the abundances of more preferred food types (63, 107, 111). In fact, a suboptimal food type may be included in the optimal diet if it becomes abundant enough (111). Furthermore, food types may be ranked in terms of energy/handling time ratios, increasing the abundance of preferred food types should lead to greater dietary specialization, and food types should be added or deleted from the optimal diet in rank order. Allowing for misidentification of food types leads to the same set of predictions. The same predictions also arise if recognition time is only required when an animal specializes (see 66).

Crypticity of food types can lead to yet another variation in the predictions of the optimal diet model (66, 111). Hughes (111) allowed for the possibility that an animal might mistake inedible objects for an otherwise valuable food type, spending some time before discovering the error and rejecting the object. If the density of the more valuable food type were sufficiently low, the optimal diet might consist of specialization on less valuable food types with total exclusion of the more valuable but cryptic one. Hence, with decreases in the abundance of the more valuable food type, the forager might first switch from specializing on the more valuable food type to generalizing and then to specializing on the less valuable food type. Otherwise, this version of the optimal diet model produces the same predictions as the model including recognition times and misidentification.

THE DEPENDENCE OF DIET ON THE DEGREE OF SATIATION An animal's diet may not be constant but may depend on its degree of satiation. Suppose, for example, that an animal requires only a small amount of food to reach "satiation" (i.e. the food level above which further increases do not enhance fitness) and that it has just encountered a low-value food item that would normally be excluded from the diet. If fitness is maximized when the time required to reach satiation is minimized, then the optimal strategy might be to consume the food item rather than to continue searching for a more preferred food type (221). In other words, an animal might specialize until it has almost reached satiation and then expand its diet. Richards (221) showed that for two prey types A and B, such diet expansion should only occur if the animal requires less than the amount of food in the higher ranked item to reach satiation. This variation in the optimal diet model is therefore most applicable to animals that forage for food items that are large relative to total intake.

THE EFFECTS OF FORAGER EXPERIENCE ON HANDLING TIMES AND FOOD YIELDS As the rate of encounter with a food type increases, the handling time for that food type will probably decrease (43, 111, 157, 281); handling time may also decrease with increasing "hunger" (e.g. 129, 277).

Hughes (111) modified the original diet model by setting each handling time equal to a function of the encounter rate. He then showed that partial preferences should not develop; that whether or not a particular food type is included in the optimal diet depends on its own abundance, as well as on the abundances of more preferred food types: and that as changes in the abundance of food types occur, the optimal diet could switch from specialization on one food type to specialization on another, with or without generalization in between (111). McNair (157) obtained similar results.

Food yields per food item may also be influenced by an animal's past diet (22, 183). Though this possibility apparently has not been modeled, it is clear that allowing for it considerably complicates the determination of optimal diets and probably requires knowledge of an animal's past diet. Rates of encounter with detected food items may also depend on past experience. Animals might, for example, develop "search images" whereby they are more (or less) likely to detect food types they have encountered before (e.g. 157, 166, 184). The formation of such search images may explain frequency-dependent dietary selection (e.g. 73, 105, 167).

NONRANDOM ENCOUNTERS WITH FOOD ITEMS In the original optimal diet model, it was assumed that encounter rates with food types are constant and independent of past history and of each other. This type of food encounter pattern is termed random, and it produces a probability distribution (negative exponential) of the time between an animal's beginning to look for food and the next food encounter independent of past history (e.g. 187, 219). This probability distribution still could depend on past history, however. Suppose, for example, that there is a single food type, items of which "arrive" when an animal is both handling and searching for food. Food items that arrive during search time have been "encountered." Suppose further that the handling time for a food item and the time interval between successive food arrivals are independent random variables. The expected interval between the time when the animal finishes handling a food item and simultaneously recommences searching and when it encounters the next food item will then depend on the length of the handling time. This expected time interval would be very short if, for example, handling times and interarrival times were constant, with the former slightly shorter than the latter.

In general, the relationship between past history and the time interval between the point when an animal recommences searching and its next food

encounter will be complex. Continuing the above example, suppose that successive handling times and successive interarrival times are all independent of one another. Even then, it is possible that any number N of food items will arrive during the handling time for the last item. The probability density function for the required time interval T will be a function of N and the handling time H . Hence, the expected time interval between the end of handling one food item and the end of handling the next (i.e. $T + H$) will depend on the probability density function of H and the conditional probability function of N given $H = h$ and $N = n$. The situation becomes even more complicated if there are two or more food types, each with its own associated probability distributions of handling times and interarrival times.

Krebs et al (136) considered the following special case. They supposed that there are two food types with constant values $2E$ and E , that the interarrival time t between successive food items is constant, that the handling times associated with each food type are random variables ($H1$, $H2$) such that $2E/E(H1) > E/E(H2)$, and that food types occurred in one of the following three sequences, where $L = \text{large}$ and $S = \text{small}$: $L, S, \dot{L}, S, -L, L, L, S, L, L, L, S, -L, S, S, L, S, S, -$. They defined p as the probability that $H2 < t$ and argued that the optimal strategy of the animal is to specialize on the larger food type if $p < 1/2$, independent of the sequence of food types. As Rechten et al (219) pointed out, however, this formulation is incorrect; the correct optimal strategy apparently has not been determined. They argue that if there is a single food type and if an animal recommences searching *at random* during any interarrival interval, then the expected time until the next food encounter is $0.5 [\mu + (\sigma^2 \div \mu)]$, where μ is the rate of food arrival and σ^2 is the variance of the interarrival time. But recommencement times are only likely to be distributed randomly over interarrival times if the average handling times are much larger than the interarrival times. Consequently, Rechten et al's deductions for the case of two food types are unlikely to be correct in most cases.

McNair (156) considered a more general situation by assuming that the search time (after handling time has ended) required to encounter a food item has a probability distribution that depends on both the prey types last encountered and the one that will be found next. In this case, prey types are not necessarily added to the optimal diet in decreasing order of the energy to handling time ratio; whether or not a food type is included in the optimal diet will depend on its own abundance instead (156).

Pulliam (187) also examined nonrandom encounters with food items by assuming that an animal encounters clumps of food; that every item in these clumps can be consumed without further search time; and that during searching time, encounters with clumps occur at random. The qualitative predictions of the simple optimal diet model remain unchanged, but if overall food densities

are constant, increased clumping of food items tends to shift the optimal diet towards greater specialization (187).

DECLINING RATES OF FOOD ENCOUNTER If an animal forages amongst patches and if the rate of encounter with a food type declines with the removal of that food type from a patch, then the optimal diet within a patch and the optimal time of departure from it are interrelated. Under these circumstances, the optimal diet may depend on the time spent in a patch so far and on the abundances of nonpreferred food types, and it may consist of partial preferences (99). The optimal diet may also depend on the average time spent in a patch (99), just as foraging strategies may, in general, depend on the time scale involved (see 48, 115, 210, 224).

OTHER POSSIBLE VARIATIONS IN THE OPTIMAL DIET MODEL The optimal diet model has not been modified to allow for simultaneous encounters with food items. In such situations, however, partial preferences may be optimal because a food item will probably be eaten if it is encountered along with less preferred items or ignored if a more preferred item is present.

The optimal diet model might also be modified to allow for nonlinear relationships between fitness and the expected rate of food intake (i.e. to include risk) or to allow fitness to be affected by factors other than food (e.g. 177). Some theoretical treatments of diets have not been included in the above discussion (e.g. 17, 48, 89, 181, 249–251, 258).

SUMMARY OF PREDICTIONS The qualitative predictions that arise from the simple optimal diet model break down under relatively straightforward and realistic variations to the model. Partial rather than absolute preferences are expected if fitness depends on more than one food value (e.g. energy and nutrients or the energy intake mean and variance). Preferences for food types that depend on the abundance of each food type rather than on the abundances of better food types should develop if fitness depends on more than one food value, if recognition of food types requires time or is imprecise, if food types are cryptic, or if handling times or food yields depend on experience. In the last two situations, the optimal diet may also involve specialization on an inherently inferior food type or switching between specialized diets. This breakdown of the simple qualitative predictions means that much care should be exercised in testing them.

3. Optimal Patch Choice

Patch choice is analogous to dietary choice and can be modeled in exactly the same manner if two conditions are met: first, food patches must always be

encountered before being accepted or rejected and second, the within-patch food yield and time spent must be independent of which patch types are accepted and of the overall rate of food gain. There are no obvious examples that satisfy all of these assumptions, however, so it is not surprising that apparently no one has focused on this kind of patch choice.

In general, one of the above assumptions will not be met. The various possible departures from these assumptions determine an array of different patch-choice situations that I shall consider below.

The simplest kind of patch-choice situation involves the following assumptions: (a) the locations and "qualities" of all patches are known to the foraging animal; (b) these locations and qualities are constant; (c) there is no resource depletion during the time the animal spends in a patch; and (d) fitness is an increasing linear function of the animal's net rate of food gain. Under these assumptions, the animal's optimal strategy is to spend *all* its time in the most conveniently located patch with the greatest net rate of food gain. A variety of patch-choice situations can be obtained by altering one or another of the above assumptions as follows:

THE CURRENCY OF FITNESS Fitness may be a nonlinear function of the net rate of food gain or may depend on the rates of both nutrient and food gains. If it is not a linear function of the net rate of food gain, then the expected fitness for a particular strategy will depend on the mean, variance, and possibly the general shape of the frequency distribution of that net rate. Suppose, for example, that the expected fitness is given by $E(F) = aE(R) - bV(R)$, where $V(R)$ is the variance of R and a and b are positive constants (i.e. an animal is risk averse) (e.g. 214, 215). Suppose also that there are two patch types, that the amount of food obtained during time t_i in patch type i has mean $R_i t_i$ and variance $V_i t_i$ (i.e. each time period is independent of other time periods), that an animal spends a proportion p of total time T in patch I , and that the costs of travel between patches are negligible. Then the animal's overall rate of food gain will have mean $E(R) = pR_1 + (1 - p)R_2$ and variance $V(R) = (pV_1 + (1-p)V_2)/T$, and the expected fitness $E(F)$ will be maximized with respect to p when $p = 1$ or 0 , depending on whether $aT(R_1 - R_2)$ is greater than or less than $b(V_1 - V_2)$. In other words, the animal should allocate all of its time to one or another patch type depending on the difference in means relative to the difference in variances between the two patch types [i.e. $(R_1 - R_2)/(V_1 - V_2)$] and the relative importance in determining fitness of the mean and variance of the *total* amount of food obtained during the foraging time T (i.e. aT/b). If one of the patch types has both the highest R and the lowest V , then the animal should spend all its time in a patch of that type. If the expected fitness is not a linear function of the mean and variance of the rate of food gain, however, the optimal strategy may consist of allocating time to both patches.

An identical situation prevails if fitness depends on the rate of intake of two or more food values, such as food weight and the amount of some nutrient. If fitness is a linear function of the rate of intake of food and a nutrient, then the optimal strategy will be to allocate all available time to one patch type, the identity of which will depend on the quantitative details of the fitness function and the available patch types. If the fitness function is nonlinear, then allocating time to more than one patch may be optimal. Patch choice may also affect other aspects of fitness such as predation risk to a forager (e.g. 91, 100, 161, 163, 238).

IMPERFECT KNOWLEDGE ABOUT THE QUALITY OF PATCHES If an animal does not know the quality of the available patch types, then its optimal allocation of time should depend on how much foraging time remains, on its experience so far in each patch type, and on any a priori knowledge about the kinds of patches available (138). If a lot of foraging time remains, an animal should devote some time to sampling the available patch types before deciding how to allocate the remaining time. If its experience indicates that one patch type is much worse than the others, the animal should stop foraging in that patch type. If the animal knows the array of available patch qualities but not which ones are which, it should spend less time sampling than if it knows only that patch quality varies.

There is no comprehensive theoretical treatment of this foraging problem. Krebs et al (138), however, have considered the following special case for two patches: (a) In each patch, an animal's foraging consists of trials for which the probability of obtaining a food reward is a constant but unknown P_i . In their examples, P_1 and P_2 are (0.50, 0.00), (0.40, 0.10), (0.35, 0.15), and (0.30, 0.20). (b) The P_i each have an a priori beta probability distribution with parameters $(\alpha_i, \beta_i) = (0, 0), (0, 2),$ or $(2, 0)$. This distribution has the desirable property that the a posteriori probability distribution of P_i after n_i trials with r_i successes in patch i also has a beta distribution with new parameters $(\alpha_i + r_i, \beta_i + n_i - r_i)$ (138). (c) The time and effort required by an animal to move between the two patches is negligible. (d) An animal samples each of the two patches equally and then exploits just one of them. (e) The total number of foraging trials is $2N$ of which M are spent sampling the two patches. (f) An animal adopts the value of M that maximizes the expected number of food rewards during the $2N$ foraging trials. Krebs et al (138) then derived the optimum M . For each combination a_1, a_2, n , where n is the number of foraging trials carried out so far in each patch and a_i is the number of food rewards obtained so far in each patch, they determined whether the expected future gain was greater if the animal allocated the next two trials to sampling each patch and then specialized on the apparent better patch (*Es*) or if it specialized immediately (*Ed*). They worked backwards in n from $n=N$ and found that, if only two trials remained, spe-

cialization was better than continued sampling for all combinations of a_1 and a_2 . They also found that the higher the value of n , the more “consistently higher” (138) Ed was than Es (in, presumably, the proportion of a_1, a_2 combinations).

It is not clear from their paper, however, how they subsequently derived the optimal M . One possible way to determine it would be to estimate the probability associated with each combination of a_1, a_2 , and n , use these probabilities to calculate the expected difference between Ed and Es for each n , and set M equal to the n at which this expected difference first becomes negative as n decreases from N . Krebs et al reported that the optimum M decreases as the difference between P_1 and P_2 increases. They also found that for a given a_1, a_2 combination, the likelihood that Ed would exceed Es decreases as the total number of trials ($2N$) increases. That is, sampling should last longer for larger N 's.

TEMPORAL VARIATION IN PATCH QUALITY If the qualities of the available patches vary over time, the optimal strategy may not be to allocate all of the available time to one patch, but it will sometimes include time spent sampling the various patches (245). However, no theoretical model of this situation has apparently been developed.

4. Optimal Patch Departure Rules

As an animal spends time in a food patch, it may obtain information about the quality of the patch *while* depleting the food available in it. An animal may therefore leave a patch because of information gained or resource depletion or both. The failure to appreciate fully these dual reasons for patch departure has resulted in some confusion concerning the development and testing of predictions concerning rules of patch departure.

Charnov (33) developed the first model of patch departure, and he incorporated seven assumptions: (a) fitness increases linearly with the expected net rate of energy intake; (b) the expected net energy gain from a patch $g_i(t)$ depends on the patch type i and is a continuous function of amount of time t allocated to the patch, (c) the slope of $g_i(t)$ decreases with increasing t because of resource depletion; (d) the foraging animal “knows” the quality of each patch (i.e. the function $g_i(t)$ for each i); (e) the average travel time between patches (t_b) is known to the animal; (f) the proportion of visited patches of type i (P_i), and the energy costs per unit time in traveling between patches (e_b) and while searching within a patch (e_w) are constant and known to the forager; (g) an animal bases its decision to depart from a patch only on the patch type and the amount of time spent in the patch. From these assumptions, it follows that the foraging process can once again be modeled as a renewal process (33, 34) and that the forager should allocate time T_i to each patch of type i such that the instantaneous or “marginal” rate of net energy gain (i.e. $\partial g_i(t)/\partial t$, when $t = T_i$) has dropped by

time T_i to the overall rate for the habitat (33). Hence, the instantaneous rates of net energy gain at the times of departure should be equal for each patch type and should be higher in habitats whose overall net rate of energy intake is higher (33). The times allocated to patches should therefore be greater for consistently better patches but should decrease as habitat quality increases (33). Essentially the same theory and predictions have been derived by Cook & Hubbard (42) and Parker & Stuart (182). This theory has been modified in the following ways:

DIFFERENT POSSIBLE DEPARTURE RULES An animal's departure may depend on the amount of food obtained in a patch rather than on the length of time spent there. Assuming that food occurs in discrete food items, the amount of food obtained in a patch is a discrete rather than a continuous variable. From Charnov's theoretical work (33), it follows that in such a situation an animal should leave a patch as soon as it obtains an amount of food such that the marginal rate of energy gain from the amount of food consumed equals the overall rate in the habitat. So, the interval between the time the last food item was obtained in a patch and departure from that patch [i.e. the "giving-up times" (139)] should be zero.

It might also be assumed in the case of discrete food items that an animal's departure from a patch depends only on a giving-up time for each patch type (139). The expected marginal rate of energy gain in a patch should then depend on *both* the patch type and the time since the last food item. Krebs et al (139) predicted that giving-up times should be the same in different patch types within a habitat. This prediction should only be correct in the above model, however, if the departure decisions and the expected marginal rates of energy gain in the patches depend solely on the giving-up times. In general, giving-up times should be longer in patches that are consistently better than others (158).

Iwasa et al (113) have compared the above three departure rules, involving time per patch, food per patch, and giving-up time, respectively, for the case when identical food items are encountered at random within patches that all have the same initial number of food items. They also assume that the food handling times are negligible. When the maximum rates of food gain are determined for each departure rule, the optimized fixed-number (i.e. the fixed amount of food) strategy is best, followed by the fixed-time strategy and then by the fixed giving-up-time strategy (113). This conclusion seems reasonable, since the instantaneous rate of food gain should be most *directly* affected by the number of food items removed (or remaining), less directly by the elapsed time, and least directly by the time since the last food item was consumed. If patch quality varies but the animal knows the quality of each patch before entering it and is able to adopt a different number, time, or giving-up-time threshold for each patch type, then the three optimal strategies should yield the

same result. McNair (158) found, however, that it is possible to construct situations in which the fixed giving-up-time strategy is better than the fixed-time strategy.

THE DEPENDENCE OF FITNESS ON THE MEAN AND VARIANCE OF ENERGY INTAKE If fitness is a nonlinear function of an animal's net rate of energy intake and if some of the parameters that determine this rate are random variables, then the net rate of energy intake will also be a random variable; and the expected fitness will be a function of its mean, variance, and possibly the general shape of its frequency distribution (see above). Stephens & Charnov (253) considered this possibility for the above model of patch departure. They assumed that the expected fitness is maximized when the probability that an animal obtains less than some threshold amount of food is minimized; that all of the parameters in the model are constants, except travel time between patches; that there is one patch type; and that encounters with patches occur at random so that between-patch travel time has a mean of $1/q$ and a variance of $1/q^2$. Then they used renewal theory (see 47) to derive the mean (μ_τ) and variance (σ_τ^2) for the energy gain (e_τ) during a foraging period of length τ . They had previously shown that if τ is large relative to the time between foraging decisions, then e_τ will be approximately normally distributed; also minimizing the probability of starvation will be equivalent to maximizing the ratio $(R - \mu_\tau)/\sigma_\tau$, where R is the net energy requirement. Finally, they contrasted the optimal time spent in each patch if the probability of starvation is minimized (t_1) with that if the mean rate of energy gain is maximized (t_2). They found that there is a critical level of R (R^*) such that t_1 is greater or less than t_2 if R is less or greater than R^* , respectively (253).

UNKNOWN PATCH QUALITY The situation is rather different if the foraging animal does not know the qualities of patches before it enters and samples them. The animal may leave a patch long before there has been any resource depletion if the initial sampling of the patch suggests that it is inferior to others. To develop models of optimal patch departure, it is therefore necessary to consider the sampling procedures that animals might adopt. Sampling by a foraging animal may be defined as acquisition and storage of information that is correlated with future foraging success. It should be widespread, since food densities should be correlated both temporally and spatially.

The array of possible kinds of information that an animal may usefully acquire while foraging is large. For example, an animal feeding on discrete food items may store the magnitudes of all time intervals between successive food items, the time intervals between arrival in a patch and the first encounter with a food item, and the time since the last food item was encountered, and it may also store the food values of all food items encountered. This information

may be correlated with the value of and time to the next food item. Assumptions about the level of information foraging animals possess are critical in the development of models of optimal patch departure. Since an animal's ability to store information may decay over time, assumptions concerning an animal's memory are also important.

The range of ways in which animals might use their information is also large. It is usually assumed that foraging animals are constantly making decisions based on the values of a number of parameters (e.g. 159, 199). These relationships between the parameters and the decisions are termed decision rules (e.g. 199). The general aim of optimal foraging models is to determine the optimal decision rules.

Several distinct optimal patch departure models have been developed and these are considered separately below.

ANIMALS FORAGING FOR NECTAR IN FLOWER CLUSTERS For an animal that is foraging for nectar, any cluster of flowers such as an inflorescence or a plant may be thought of as a patch. Since these animals do not remain indefinitely in a single patch, they must be making decisions about whether to stay in or leave the patch. Such decisions could be made on a continuous basis, but it seems more likely that they are made just after the animal has consumed the nectar in a flower. As an animal visits more flowers relative to the number available in the patch, the probability of revisiting flowers should increase. There should also be a positive correlation between the nectar volume in any two flowers within the same cluster because these flowers are likely to have been visited previously at about the same time, and they may have relatively similar rates of nectar production. Consequently, the amount of nectar that the animal can expect at the next flower on the present cluster should rise with increases in either the amount of nectar obtained at the present flower or the number of flowers available in the cluster, and it should decrease with increases in the number of flowers within the cluster visited so far.

With this view of foraging by a nectarivore in mind, I considered the following model for departure from a flower cluster (194):

1. Fitness is assumed to increase linearly with the overall net rate of energy gain.
2. The probability p that the next flower visited by the animal within the present flower cluster is a revisit increases as the number of flowers already visited within the cluster (n_v) increases and as the number of available flowers (n_a) decreases.
3. The nectar volume obtained by the animal at the present flower is positively correlated with the nectar in the next flower that the animal would visit if it continued to forage within the present flower cluster.

4. After consuming the nectar in a flower, the animal decides whether to visit another flower in the same flower cluster or to leave and visit a flower on another cluster.
5. The animal leaves a cluster if the amount of nectar obtained from the present flower (or the average nectar obtained from the last m flowers) is less than a threshold (T), which depends on n_v and n_a . If the animal is foraging optimally, it should be more likely to visit another flower within the present cluster the greater its expected nectar at the next flower within that cluster is. Consequently, the optimal threshold T should increase with either an increase in n_v or a decrease in n_a .
6. The time and energetic costs incurred by an animal in moving between flowers within a cluster, moving between clusters, or removing nectar from a flower are all constant.
7. The animal obtains little or no nectar at a revisited flower.
8. The animal is assumed to know the above relationships and parameters and the overall rate of energy gain in the habitat.

It follows from points 2, 3, and 7 above that the probability density function for the amount of nectar (μ_n) in the next flower that the animal would visit if it continued to forage within the present cluster is given by $f(\mu_n|\mu_p, n_v, n_a) = f(\mu_n, \mu_p, n_v, n_a) = f$, where μ_p is the amount of nectar obtained at the present flower (or the mean amount obtained at the last m flowers). If $E_n = E(\mu_n|\mu_p, n_v, n_a) = \int \mu_n f d\mu_n$ is the expected value of μ_n , then it would also be the case that $\partial E_n/\partial \mu_p > 0$, $\partial E_n/\partial n_v < 0$, and $\partial E_n/\partial n_a > 0$. In order to find the set of optimal thresholds for different numbers of visited flowers and available flowers, it is apparently necessary to carry out computer simulations of the above foraging model (e.g. 202). Three solutions have been deduced without proof, however, from the “marginal value theorem” that Charnov (33) developed, which was outlined above for situations in which patch qualities are known (103, 195; J. M. Pleasants, personal communication).

In all cases, the optimal threshold T for a given n_v and n_a is assumed to depend on the animal’s overall rate of energy gain in the habitat (R) and the times and costs required to move between flowers within a cluster (t_f and c_{ftf}) and to handle a flower and remove its nectar contents (t_h and c_{ht_h}). The three proposed solutions for the optimal T are given by the following equations:

$$E(\mu_n|\mu_p \geq T) - (c_f t_f + c_h t_h) = R(t_f + t_h), \quad 1.$$

i.e. the expected rate of energy gain obtained by moving to the next flower on the present cluster, *given that the animal chooses to do so*, is equal to the overall rate of energy gain in the habitat (195). This statement is *not* equivalent, as

Hodges (103) implied, to the prediction that an animal should leave a plant whenever the expected rate of energy gain obtained by probing the next flower within the present cluster is less than the overall rate in the habitat.

$$E(\mu_n | \mu_p = T) - (c_f t_f + c_h t_h) = R(t_f + t_h), \quad 2.$$

i.e. the threshold T is such that if the animal obtains *exactly* that amount of nectar at the present flower and chooses to visit another flower on the present flower cluster, its expected rate of energy gain for so doing is equal to the overall rate of energy gain in the habitat (103; J. M. Pleasants, personal communication).

$$\frac{E(\mu_n | \mu_p = T) - (c_f t_f + c_h t_h)}{t_f + t_h} = \frac{\mu - (c_c t_c + c_h t_h)}{t_c + t_h} \quad 3.$$

where t_c and $t_{c.c}$ are the time and cost required to move between flowers on different flower clusters and μ is the expected nectar at the *first* flower on another cluster (103). Hodges (103) allowed t_h to depend on the amount of nectar energy obtained. He justified only considering the first flower on another flower cluster on the basis of his observations that the animals he studied (bumbees) visited one flower per flower cluster most of the time.

Though each of these proposed foraging strategies will produce one desired result—i.e. the likelihood of departure from a flower cluster will decrease with increases in the amount of nectar obtained at the present flower—none is the correct optimal strategy (202). Nor do we know the extent to which these proposed strategies tend to be good approximations of the correct one.

Computer simulations indicate that the optimal thresholds will usually rise with increases in the numbers of visited flowers and fall with increases in the number of available flowers, even if there is no immediate risk of revisiting a flower (202). In other words, if a flower cluster still has many unvisited flowers, the animal should tend to continue sampling the cluster before rejecting it. This finding is analogous to the sampling situation Krebs et al (138) consider.

FORAGING IN PATCHES FOR RANDOMLY ENCOUNTERED PREY ITEMS Oaten (174) considered the optimal patch departure rule in the following situation: (a) Fitness increases linearly with the expected rate of food intake. (b) Food consists of prey items that are all identical and that occur in patches that differ in terms of the initial number of prey present. Food items are not replaced as they are eaten. (c) The proportion p_k of patches encountered by the animal that initially contain k prey is known to the animal. (d) The animal also knows the probability density function $f(t_1, \dots, t_j, k)$ for the time between

arrival in a patch and the first food encounter (t_1) and the time t_i between the $(i-1)$ th and i th food encounter, given that the patch initially contains k food items and that the animal obtained j food items from the patch. (e) The time required for the animal to travel between patches has an expected value that is known to the animal. (f) The animal's decision concerning whether or not to stay in its present patch depends on the time intervals t_1, \dots, t_j up to the last food item obtained and the time v_{j+1} since the last food item was encountered. More precisely, it is assumed that after j food items the animal employs a threshold V_j (i.e. the giving-up time) that is a function of t_1, \dots, t_j such that if and when $v_{j+1} = V_j$, the animal leaves its present patch. (g) The handling times of food items are negligible.

Based on these assumptions, Oaten (174) derived implicit equations for V_j and showed that an optimally foraging animal will tend to stay longer in a patch than an animal that leaves when its instantaneous probability of capture per unit time has fallen to the overall rate in the habitat. Continued foraging in the patch provides not only food but valuable information as well (159, 174).

Green (87) modified Oaten's model by adopting the following assumptions: (a) Each patch consists of n bits (i.e. places where food items may be found). (b) The animal takes unit time to search each bit. (c) Within each patch, the number of bits containing one food item follows a binomial distribution with parameters n and p . Remaining bits contain no food. The value of p then determines the patch type. (d) In terms of patch quality, the animal knows only that p is distributed over patches with a beta distribution whose parameters are α and β . (e) As the animal searches a patch, the probability that it will find food in the next bit does not change. (f) The animal will leave its present patch if it has searched t_k bits and found only k food items.

Green (87) then compared the rate of food gain for the optimal t_k 's for three alternative cases: (a) The naive strategy—The animal is assumed to learn nothing about the quality of its present patch from its experience in it; the optimal strategy is to search all n bits in each patch visited. (b) The omniscient strategy—The animal is assumed to know the qualities of each patch before visiting them. Therefore, the animal should thoroughly search the best patches and ignore the others (as in the optimal diet model above). (c) The instantaneous rate strategy—The animal is assumed to leave a patch when the probability of finding a prey in the next bit falls below some critical value. In this case, the optimal critical value is typically lower than the overall rate of food gain in the habitat. An optimal forager in Green's model should therefore tend to stay longer in each patch than an animal that adopts the best instantaneous rate strategy. Green (87) found that the omniscient strategy is the best if it can be used, the naive strategy is the worst, and for the parameter values he considered, the instantaneous rate strategy is almost as good as the strategy of employing the optimal t_k 's.

Iwasa et al (113) also developed a modified version of Oaten's (174) model. They made the following additional assumptions: (a) Within each patch encounters with food items occur at random and (b) The instantaneous rate of food encounter in a patch is proportional to the number of food items remaining in the patch. They then showed that the expected number of food items remaining in a patch, given that n have been eaten in time t (including any time since last food item), is a function of the p_i 's (i.e. the distribution of patch quality) and t and n , but it does not *also* depend on the t_1, \dots, t_j and $v_{(j+1)}$ of Oaten's model. The optimal strategy is therefore to leave a patch whenever t and n are such that this expected number of remaining food items is less than some threshold (n_t) (113). Iwasa et al also showed that this optimal departure rule becomes a fixed-number (per patch) strategy when all patches have the same known number of food items and a fixed-time strategy when the number of food items per patch has a Poisson distribution. It is not clear whether a fixed-number, a fixed-time, or a fixed giving-up-time strategy generally would, when optimized, yield the highest rate of food gain in the present model. They suggested, however, that the fixed giving-up-time strategy is the best of the three only when the distribution of food is highly contagious.

Stewart-Oaten (254) modified his earlier model (174) in the same manner as Iwasa et al (113) and showed that if the number of food items per patch has a Poisson distribution, then the optimal strategy is to "leave after constant time T " (i.e. a fixed-time strategy). He also demonstrated that in this situation, the following three strategies are all equivalent to the optimal strategy: (a) employ a departure rule such that the average instantaneous capture rate at the time of departure from a patch is equal to the overall capture rate; (b) leave a patch when the instantaneous probability of capture per unit time is equal to the overall capture rate; and (c) leave when this instantaneous capture probability is equal to an optimum threshold. McNamara (159) also developed two special cases of Oaten's foraging situation model (174).

FORAGING IN PATCHES THAT VARY OVER TIME If patch quality varies over time, then an animal may sometimes do better if it moves to a new patch than if it remains where it is. The optimal strategy will be determined by the frequency and magnitude of *potential* changes in patch quality and the extent to which patch quality tends to remain constant over time. For example, if patch quality may change at time t , and if patch qualities at time t_{n+1} are likely to be the same as at time t_n , then an animal should remain in its present patch at time t_n if it is in a high quality patch and move to a new patch if it is in a low quality patch. This strategy would be called "win-stay" (see 288). In contrast, if patch qualities tend to reverse themselves every time they change, an animal should adopt a "win-leave" strategy (see 288) and leave its patch if it was of high quality during the last time interval.

Janetos (119) developed a model of this foraging situation based on the following assumptions: (a) Fitness increases linearly with the expected rate of food gain. (b) There are two kinds of patches, good and bad, which may change in quality after each day. Good and bad patches change quality with probabilities a and b respectively. (c) The daily food gains in good and bad patches are G and B respectively. (d) The cost of changing patches is C (measured in food units). Janetos considered the two possible strategies: (a) sit-and-wait, where the animal never moves from its present patch, and (b) active forager (win-stay), where the animal remains in its present patch for another day if it has just had a good day and changes patches otherwise. Two other possible strategies that Janetos does not consider are: (c) active forager (win-shift), where the animal changes patches if it just had a good day and otherwise remains in its present patch for another day and (d) active forager (always shift), where the animal changes patches at the end of every day. The average daily food gain from strategy (d) (i.e. $(bG+aB-C)/(a+b)$) is always less than that from strategy (a) (i.e. $(bG+aB)/(a+b)$) (see 119). Consequently, we need not consider strategy (d) further. Strategy (b) is better than strategy (a) if $(G-B)/C > (a+b)^2/b(a+b-1)$. Similarly, strategy (c) is better than strategy (a) if $(G-B)/C > (a+b)^2/a(a+b-1)$. Since $1-a-b$ must be either positive or negative and since $(G-B)/C$ is positive, it follows that the optimal strategy is either (b) or (c). Using Janetos's methods, (119) it can easily be shown that if $(a+b) < 1$, strategy (b) is better than strategy (c) as long as $[(G-B)/C > (a-b)(a+b)^2/ab[1-(a+b)^2]]$; and if $(a+b) > 1$, (b) is better if the reverse inequality holds. Consequently, if $a+b < 1$ and $a < b$, then strategy (b) is always optimal; whereas if $a+b > 1$ and $a > b$, then strategy (c) is always optimal. In the other cases, the optimal strategy depends on the difference between good and bad patches relative to the cost of moving between patches and on the magnitudes of a and b . Janetos & Cole (120) consider two other possible strategies.

5. Optimal Movements

Many animals undergo movement relative to the medium in which they are foraging. This movement may result from activities of the foraging animal, as in the case of a mobile animal that walks, flies, swims, etc., while in search of food or of a stationary feeder that exerts some control over the rate at which its foraging medium passes by (e.g. a suspension feeder that controls the rate of movement of water through its filtering apparatus). Movement may also occur independently of an animal's behavior as, for example, in the case of stream-living animals that rely on the movement of the water to bring them food. This section will deal with the active movement of foraging animals.

THE PATTERN OF MOVEMENT As animals move from one place to another while foraging they exhibit various movement patterns (see references in 209,

210). If, for example, the movements of an animal are divided (naturally or artificially) into linear segments, then there may be some tendency for the segment lengths and angular changes in direction to assume particular values. There may also be some relationship between the present rate of food intake and the size of the linear segments and direction changes. Many animals, for example, exhibit "area-restricted searching" whereby they alter their movements in response to food so that they tend to remain in the local area.

Two models dealing with such movement patterns have been developed (see 36, 193, 194). One assumes that the animal does not know where food may occur (36, 193), while the other assumes that the animal knows the exact locations of a number of "resource points" that may contain food (194). Both models assume that fitness increases linearly with the rate of food gain.

In the first model, the foraging animal is visualized as moving among points on a uniform bounded grid in the following manner (193): (a) Movements can only occur between a point in the grid and one of its four nearest neighbours (Hence movements are of constant length). (b) The direction of a movement depends only on the direction of the previous movement. (c) The animal turns right, continues straight ahead, turns left, or goes backwards with probabilities P_r , P_s , P_l , and P_b respectively. These probabilities are obtained by discrete approximation to a normal distribution that has a mean angle 0° and is truncated at $+180^\circ$ and -180° . The probabilities are then uniquely determined by $P_r - P_b$, which in this case is the directionality of movement (see 146). (d) The animal obtains no food at revisited grid points. The optimal directionality minimizes path recrossing. (36, 193). Using computer simulation, I showed that this optimal directionality increases with increases in the size of the grid and with decreases in the length of the foraging bout and that it depends on the behavior of the animal at the grid boundary (193). For realistic boundary behavior and a wide range of grid sizes and bout lengths, the model predicts directionalities between 0.8 and 1.0 (i.e. movements with relatively little turning) (1930).

In the second model, the movements are visualized as follows (194): (i) Food occurs at "resource points," which are randomly distributed but the locations of which are known to (e.g. can be seen by) the foraging animal. (b) The animal cannot tell how much food is available at a resource point before it gets there. (c) The animal chooses the next resource point just before leaving the present one. (d) The animal moves linearly between resource points. (e) The animal chooses the next resource point by aiming its departure in some direction relative to the direction of the last movement, scanning a sector of angular width $2w$ about this aimed direction and then choosing the closest resource point. Heinrich (98) pointed out, however, that animals may not always choose the closest detected resource point. (f) The difference between the arrival and aimed departure directions and the width of the scanning sector may depend on

the direction of previous movement or on the amount of food obtained at the present resource point. In other words, the animal is able to "remember" certain information. These relationships are adjusted in order to maximize fitness. (g) Food is renewed at a constant, relatively low rate. (h) There is a positive correlation between the amounts of food in neighboring resource points. The closer the points are, the higher this correlation will be. I have argued that this correlation pattern arises from the tendency of the animal (or other animals) to move between closely neighboring resource points, thereby creating similarities among neighboring points in terms of the time since the last visit (194). (i) The area containing the resource points is large, so that encounters with its boundaries can be ignored.

I went on to deduce that the optimal rule of movement will have the following properties (194): (a) The mean angular change in direction should be 0° . (b) The animal should alternate right and left hand turns. (c) The width of the scanning sector should increase as the amount of food obtained at a resource point increases. Consequently, the variance of the angular change in direction should increase simultaneously (i.e. the directionality should decrease). (d) The frequency distribution of the distances moved between resource points should resemble a negative geometric distribution. If the animal cannot obtain or store some of the information it is assumed to know in the model, then these predictions will have to be modified accordingly (194). In addition, as Zimmermann (296) pointed out, the optimal directionality should decrease if the rate of food renewal is rapid or if the animal removes only a fraction of the available food during a visit to a resource point. In some circumstances, random movement (i.e. no directionality) could be expected. The exact optimal rule of movement has not been determined for the present model (209). Such an exercise would almost certainly require a large-scale computer simulation (209).

THE SPEED OF MOVEMENT OF MOBILE ANIMALS As foraging animals travel faster, the rates of energy expenditure and of encounters with the locations of food items should increase (e.g. 77, 171, 204, 273, 275). If food items are cryptic, however, the probability that encountered food items will actually be detected should decrease at the same time. Gendron & Staddon (77) developed a model incorporating all of these potential consequences of increasing speed, which is based on the following assumptions: (a) Fitness increases linearly with the net rate of energy gain. (b) Searching for and handling food items are mutually exclusive activities. (c) There is only one food type. (d) The rate of encounter with food items is $S \times D$, where D is the density of food items and S is the search rate (measured by the area searched per unit time). (e) The probability P_d that the animal detects an encountered food item is: $P_d = [1 - (S/M)^k]^{(1/k)}$, where M is the search rate at which no food items are detected and k is a conspicuousness index. (f) The rate of energetic expenditure while searching

increases linearly with the search rate. (g) The rate of energetic expenditure while handling food items is negligible. (h) The animal adopts the search rate that maximizes the net rate of energy gain.

Gendron & Staddon discovered that the optimal search rate could only be found using computer simulations based on particular parameter values but noted that it is lower than the rate that maximizes the gross rate of energy gain. They also modified the above model to allow for two food types that are eaten whenever encountered and detected and found that the optimal search rate in this case depends on the density and crypticity of each food type, as well as on their energetic values and handling times.

I developed a simpler model by omitting any consideration of crypticity and implicitly assuming that all encountered food items are detected (204). The optimal search rate is then the maximum speed that the animal can sustain over the search period. If the energetic cost of searching at this search rate increases more rapidly than a linear function would, however, the optimal search rate in my model may be some intermediate speed.

FILTERING RATE BY STATIONARY SUSPENSION FEEDERS For animals that obtain their food by filtering water (or air), increases in the filtering rate should be accompanied by increases in the rate of ingestion of food particles and in the energetic costs of filtering and by a decrease in the energy absorption efficiency for each particle ingested. Three similar models of this foraging situation have been developed (142, 144, 256). All of them incorporate the following assumptions: (a) Fitness increases linearly with the net rate of energy gain. (b) The rate of food (energy) ingestion is proportional to the filtering rate F (measured as volume per unit time). (c) The energetic cost of filtering, E_F , is: $E_F = bF^x$, where b and x are constants ($x=3$ in 142; $x=2$ in 144). (d) The animal adopts the filtering rate that maximizes the net rate of energy gain. The three models basically differ only in their assumptions concerning absorption efficiency. Lam & Frost (142) assumed simply that energy gain is equal to the amount of energy ingested (i.e. the absorption efficiency is 100%) and that energetic costs increase with increasing body length. They derived the optimal filtering rate and showed that it increases with increasing particle density or decreasing body length. Lehman (144), in contrast, assumed that there is a constant number N of food particles in the animal's gut. Consequently, the time t that each particle spends in the gut is given by $N = FDt$, where D is the particle density. He also assumed that the gut has a maximum volume and that the amount of energy obtained per ingested particle increases with increasing passage time (t) in the gut. Therefore, the animal should maintain a full gut, and the optimal filtering rate is found by plotting the net rate of energy gain against the filtering rate after assigning particular values to the various parameters. Finally, Taghon (256) assumed that the fraction of energy obtained from ingested particles decreases with increases in the filtering or ingestion rates. He calculated the optimal

filtering rate for constant absorption efficiency and for absorption efficiencies that decline linearly or exponentially with rising filtering rates. He concluded that in all cases, the optimal filtering rate increases with increasing energy value per food particle.

FORAGING MODE Alternate foraging modes have received little attention to date (6, 170, 172). Norberg (170) considered two alternate modes, one of which resulted in a higher rate of energy gain at a given food density and in a higher rate of energy expenditure than the other. He showed that the higher the food density, the more likely it is that the more efficient, but more expensive, strategy will lead to a higher net rate of energy gain (170). He also considered the special case of birds that climb or hop vertically in trees while searching for food and then fly between trees (172). He assumed that the birds could hop up each tree and fly to the next tree using gliding as much as possible (Strategy A), hop down each tree and fly up to the top of the next (Strategy B), or alternate hopping up and down each tree and fly horizontally between trees (Strategy C). He showed that Strategy B is never optimal; Strategy C produces a better net rate of energy gain than Strategy A if and only if the distance between successively visited trees is less than about half the distance coverable in gliding flight, with height loss equal to the foraging height zone within each tree (172).

6. *Optimal Central Place Foraging*

For a central place forager, one cannot consider diet, patch choice, departure from patches, and movement rules independently of one another. The transportation distance for food gathered will depend on the animal's location at the time of return, and this location may depend on previous movements or on where the animal has chosen to forage. At the same time, the frequency of trips back to the central place will depend on the animal's diet and on the amount of food obtained at each location.

Present models of central place foraging focus on just one aspect of foraging: (a) movements while searching for food, (b) the relationships between diet and distance from the central place, and (c) the association between distance and both patch choice and the rule of departure from a patch. Consequently, I shall deal separately with each of these foraging categories. In all three cases, it is assumed that the cost of transporting food items to the central place depends only on the time required, and not on the size of the load (cf 54).

SEARCHING MOVEMENTS According to Morrison's (165) model, a foraging animal leaves its central place, searches for a patch of food using the movement rule described below, returns to the central place with a food item, and then makes $(n-1)$ more trips to and from the patch, obtaining the same amount of

food each time; then it resumes the search for another patch. His model is based on the following assumptions (165): (a) Fitness increases linearly with the expected rate of food gain. (b) The locations of patches are initially unknown. (c) The animal searches for patches by traveling a constant distance (D) in between turns, which results in new movement directions that are *independent* of previous events. During the search, the animal detects all patches that occur within a detection radius (r). Every time the animal changes direction, it re-searches areas searched during the previous movement interval. The overlap between areas searched during nonsuccessive movement intervals is assumed to be negligible. (d) The animal adopts the distance (D) that produces maximum fitness. Morrison then showed that as D increases, the rate of searching new areas increases, the expected search time to find a patch consequently decreases, the expected final distance from the central place increases, and the costs of each visit to the patch therefore increase. He derived an expression for the average time per feeding visit to a patch and showed that this is minimized (i.e. the expected rate of food gain is maximized) for values of D that decrease as n increases. In other words, if an animal revisits a patch many times, it should adopt a movement rule that keeps it near its central place. Because the locations of patches are initially unknown, in the present model the animal will tend to visit patches more distant than the nearest patch (165).

DIET VS DISTANCE FROM CENTRAL PLACE Schoener (232) considered the situation where an animal encounters food items that differ in terms of their net energy yield and handling time and where any chosen food item is transported to a central place. He assumed that fitness increases linearly with the average net rate of energy gain. The optimal strategy is obtained in the same manner as the optimal diet in the above diet models; encountered food items should be ranked according to the ratio: (net energy gain - transportation cost) \div (handling time + transportation time). He also assumed that both net energy gain and handling time are functions of prey length. For several choices for these functions, if transportation time is independent of prey length, then as transportation time (i.e. distance) increases the length of the best prey should increase and the range of prey lengths taken should shift upwards. These effects can be reversed, however, if transportation time increases with prey length (232).

Lessells & Stephens (145) considered an animal that forages in patches and adopted the following assumptions: (a) Fitness increases linearly with the expected rate of food gain. (b) Patches occur at different distances (i.e. travel times t_T) from a central place. (c) Each chosen food item is transported to the central place. (d) Within a patch, the animal accepts the first food item of "value" (i.e. energy) C or greater, where C may vary with transportation time or distance. (e) Handling times other than transportation time are negligible. (f)

The animal "chooses" the relationship between C and t_T that maximizes fitness. For each C , there will be an expected energy gain e and a search time t_s per patch; the optimal C is obtained graphically from a plot of e against t_s in essentially the same way as Charnov's marginal value theorem is solved (see 33, 145). Lessells & Stephens also showed that the optimal threshold C increases with increases in the distance of a patch from the central place. In other words, the animal should tend to take food items of higher energy value from more distant patches.

PATCH CHOICE AND PATCH DEPARTURE VS DISTANCE FROM CENTRAL PLACE If there is no resource depletion during foraging in available patches, then an animal should forage in the closest patch exclusively. If resource depletion does occur, however, then the animal should forage in a number of patches, and the overall allocation of *time* to the various patches will depend not only on patch choices but also on the rules for departure from each patch. Consequently, in the context of central place foraging, patch choice and the patch departure rule must be considered together. In all of the models discussed below, the animal's diet is assumed to be independent of patch location.

Andersson (4) formulated a continuous model for this foraging situation based on eight assumptions: (a) Fitness increases linearly with the amount of food obtained during a fixed time S or decreases with the time required to obtain a fixed amount of food. (The same results should apply if the rate of food gain is the currency of fitness.) (b) Stationary, identical food items are distributed randomly and with density λ throughout the total foraging area, which is circular with radius R . (c) When searching, the animal is surrounded by a detection area of radius r_d , which is much smaller than R . (d) $t(r)$ is the total time that each point of distance r from the central place remains within the animal's detection area. (e) Given that a food item occurs at a certain point at distance r from the central place, the item will be discovered and removed with probability $P[t(r)]$ where P increases with increasing t , but with decreasing slope (i.e. diminishing returns set in as the animal spends more and more time searching at each point). (f) Removed food items are not replaced. (g) Each food item obtained at distance r from the central place entails a transportation time $C_r(r)$. (h) The animal adopts the functional relationship $t(r)$ that maximizes fitness. Andersson then derived an expression for the average time required per food item for food obtained from the circular belt ($r, r+dr$) given $t(r)$; defined *marginal cost* as the cost per food item from this belt during an additional time $dt(r)$ as $dt(r)$ tends to 0; and showed that for general forms of $P[t(r)]$, the total search time has been optimally allocated if and only if this marginal food cost is equal throughout the foraging area. In addition, if $P(t) = 1 - \exp[-at(r)]$, where a is the instantaneous rate of detection, and $C_r(r) = r/vz$, where v is the transport velocity and z is the number of food items per load, then the optimal $t(r)$ is given by:

$$t(r) = [\ln(M - r/vz) a \lambda \pi r_d^2] / a, \quad 4.$$

where M is the marginal food cost under optimal time allocation. Finally, Andersson found that over a variety of parameter values, the optimal $t(r)$ (i.e. the time per unit area) decreases approximately linearly with r (4).

Several authors (80, 128, 179) have developed a discrete model that deals with the same foraging situation. They assume that after an animal has foraged for time t in a patch, its expected food gain is $f(t)$, where $f'(t) > 0$ and $f''(t) < 0$; that after foraging in each patch, the animal transports the food obtained to a central place at a time cost T (i.e. the time for a return trip), and that fitness increases linearly with the expected rate of food gain. These assumptions form the basis for a mathematical model identical to Charnov's (33) model of the allocation of time to patches, and the solution is found in the same manner as for Charnov's model (80, 128). If there is only *one* patch, since T increases with the increasing distance d of a patch from the central place, the optimal time spent in the visited patch and amount of food obtained there will both increase with increasing d (80, 128). If, however, there are two or more patches at different distances, then the animal should spend decreasing amounts of time per patch as the distance from the central place increases (see 33). Whether the time per patch (i.e. time per unit area) should decrease linearly with distance (as predicted in 4) will depend on the relationships between time and energy yield per patch and between patch abundance and distance.

The above model has not been modified to allow for some (but not instant) food renewal. However, food renewal underlies a simple model Evans (70) developed. He made the following assumptions: (a) An animal forages in food patches that last one day. (b) Patches of food arise anew at the beginning of each day. (c) A unit area (e.g. 1 m²) contains a food patch on any given day with probability p . (d) The animal, after leaving its central place, searches each consecutive circular belt (perhaps by moving in a spiral) until it finds a patch, and then it forages in that patch for the rest of the day. The probability P_k that the animal will forage in the circular band between $(k-1)$ and k distance units (corresponding to area units) is given then by $P_k = [1 - q^{(2k-1)}]q^{(2k-2)}$, where $q = 1 - p$. In this case, the search time per unit area, which is proportional to $P_k / (2k-1)$, might follow the same general pattern, but it would reach a peak earlier than P_k . In contrast to Andersson's (4) predictions, any decrease would not be linear.

EVALUATING OPTIMAL FORAGING THEORY

1. Criteria for Accepting Optimal Foraging Studies

Because of both the many assumptions that form the basis for any optimal foraging predictions and the difficulty of devising independent, direct tests of some of these assumptions, the usefulness of the optimal foraging approach will only become clear after a large number of optimal foraging studies have

been conducted. Not all studies, however, provide equally valid contributions to the overall evaluation of optimal foraging theory, and I propose that only those studies that satisfy the following criteria be considered acceptable.

1. When the assumptions about the foraging animal can be assessed independently, they should be as realistic as possible, and they should be justified. Such assumptions normally include those made about the currency of fitness, the information possessed by the animal, and any behavioral constraints. For many herbivores, for example, it would not be realistic to assume that fitness is measured solely in terms of the net rate of energy gain (see 72). Very few studies explicitly justify the assumptions made, however (e.g. 194, 197).

2. The foraging model should correspond as closely as possible to the actual foraging situation. It is inappropriate, for example, to apply a model based on an assumption of random food encounters to a situation in which food encounters occur after constant intervals (219) or to use Charnov's (33) marginal value theorem in situations where an animal is likely to be sampling rather than depleting each patch.

3. The predictions should follow logically from the underlying model. In some cases, the mathematics may be controversial (e.g. 34, 259, 264).

4. Parameters that determine the optimal diet should be estimated in an unbiased manner. For example, encounter rates with food types should be determined "from the animal's point of view."

5. Because many foraging parameters are random variables, there will usually be some error associated with any optimal foraging predictions. Consequently, such predictions should usually be determined and expressed in terms of means and standard errors or of confidence intervals. I know of no published studies in which this has been done.

6. Confidence intervals should also be determined for observed foraging behavior, followed by appropriate statistical comparisons of the observed and predicted confidence intervals.

7. In laboratory studies, the experimental foraging situation should mimic natural foraging situations as closely as possible (206), even though unnatural foraging situations may, of course, tell us much about the capabilities of animals.

8. In laboratory studies, animals should be given sufficient experience with the experimental foraging situation to allow their behavior to reach an equilibrium. Like Bayesian statisticians, animals are likely to have a priori assessments of food distributions, among other factors, and their foraging decisions will therefore be influenced by past experience (e.g. 116). Only after an animal's behavioral response to a foraging situation has reached an equilibrium is it reasonable to assume that this response has not been affected by the animal's experience before the experiment began. Even then, this assumption may not be valid. Studies of animals with limited experience may, however, tell us much about how they learn to forage.

Unfortunately, there appear to be no studies (including my own) that satisfy all of these criteria. However, studies that fail to include confidence intervals for predictions but satisfy the other criteria can provide some idea of the usefulness of optimal foraging theory. If there is no significant difference between the confidence interval for the observed behavior and a *point* prediction (e.g. the mean) for the optimal behavior, then the same result would hold if a confidence interval had been used for the optimal behavior. If the first difference is significant, however, using a predicted confidence interval for the optimal behavior may fail to reveal a significant difference between the observed and predicted values. Failure to develop confidence intervals for predictions should therefore lead to a bias towards rejecting optimal foraging hypotheses.

In the following sections, I shall review tests of optimal foraging theory, concentrating on those studies that come closest to satisfying the above criteria.

2. Diet

THE CURRENCY OF FITNESS Most optimal diet models assume that fitness is positively correlated with the gross or net rate of food or energy gain. There is a growing literature that indicates, however, that nutrients affect growth and/or the maintenance and food preferences of herbivores (11, 13, 27, 28, 72, 127, 162, 168, 169, 175, 180, 186, 224, 226, 227, 233, 234, 265, 282, 283), granivores (40, 86, 148, 190), and predators (88, 185). Some nectarivorous animals may maximize their net rates of energy gain while foraging (e.g. 194), but the small amounts of amino acids and other nutrients in nectars may have nutritional significance (8, 9). For animals foraging on food items that appear to differ only in terms of their size, it is probably realistic to express fitness as food or energy gain (e.g. 63, 66, 82, 107, 136, 138, 139, 199, 216, 217, 269, 271, 278, 284, 296).

Most optimal diet models are also based on the assumption (usually implicit) that the relation between fitness and food or energy gain is linear and consequently that fitness is maximized when the expected net rate of food or energy gain is maximized. It is also always assumed that dietary choice does not influence an animal's ability to perform other tasks, such as avoiding predators. For the foraging situations considered so far, this seems a reasonable assumption.

THE DETECTION OF FOOD ITEMS In most optimal diet models, it is assumed that animals cannot determine the values of food items at a distance and that encounters occur sequentially rather than simultaneously. This assumption is likely to be unrealistic for many animals, however. In particular, among those animals for which optimal diet predictions have been tested, detection and evaluation of food items at a distance occurs in nectarivores (e.g. 152, 195,

200, 203, 271), fish (e.g. 75, 78, 266, 278), back swimmers (81), and swallows (263). The time an animal needs to move to a detected food item should be included in the handling time for that item, so the value of a food item may depend on the distance at which it is detected. If a number of food items are encountered simultaneously, an animal may neglect a food item that it often eats if a better item is present. The only diet choice situations considered so far for which food evaluation at a distance should not occur and for which the net rate of food or energy gain should be a reasonable currency of fitness are predation by crabs on mussels (63), predation by great tits on pieces of mealworm presented through a small window over a conveyor belt (66, 107, 136), pigeons "searching" for food in a Skinner box by pecking at a key (143), and redshank searching for worms of different sizes (82). In all these cases, encounters with food items should be sequential rather than simultaneous. I shall discuss the results of these studies below and then briefly consider the results of other studies.

STUDIES IN WHICH FOOD ENCOUNTERS ARE SEQUENTIAL, FOOD EVALUATION AT A DISTANCE DOES NOT OCCUR, AND FOR WHICH THE NET RATE OF FOOD OR ENERGY GAIN IS A REASONABLE CURRENCY OF FITNESS It is usually assumed in optimal diet theories that the expected time to the next food encounter is independent of the time spent handling the last food item. This assumption will be correct if food encounters occur at random but incorrect if they are nonrandom and if the encounter process continues while the animal is handling food. In the conveyor belt studies by Krebs et al (136), Houston et al (107), Erichsen et al (66), and Rechten et al (218), the interval between food encounters was constant and the encounter process (i.e. the movement of the conveyor belt) continued while the bird handled the food. These studies therefore require modifications in the optimal diet theory, as Krebs et al (136) and Rechten et al (219) have attempted to do. Neither modification appears to be correct (see 219 and above), but I shall assume below that the correct theory would produce negligible changes in the predictions generated during the above conveyor belt studies.

In these studies and in Lea's (143) Skinner box study, animals (birds in all cases) were sequentially presented with two types of food items, which could be accepted or rejected. Depending on the values of the various parameters, the optimal diet was therefore either always to accept the better food type and never accept the other (i.e. specialize) or to accept both food types (i.e. generalize) (see the above discussion of optimal diet theory).

Krebs et al (136) varied the encounter rates with the 2 food types and tested their predictions on 5 individual birds in each of 5 experimental tests. They found that in all 25 instances, the optimal diet predictions were upheld in the sense that the birds preferentially selected the better food type when specializa-

tion was predicted (assuming that food types were instantly and correctly recognizable) and did not select preferentially when generalization was predicted. They also discovered, however, that when specialization was predicted, the birds continued to include some of the worse food type in their diets. In other words, the birds exhibited partial preferences.

Houston et al (107) varied the encounter rates and in some cases added a recognition time to each food type. They tested 4 individual birds in 3 experimental treatments; the observed and predicted dietary selections were consistent with each other in 11 of the 12 instances. In one instance, a bird was predicted to specialize but did not. They also found partial preferences.

Erichsen et al (66) included food items that resembled the better food type but yielded no return and varied the encounter rates with the 3 food types. As the birds always rejected the fake food items, this was essentially a two-food-type situation. They tested 5 birds in 2 treatments; the observed and predicted dietary selections were consistent 9 out of 10 instances. In one case, a bird was selective when it should not have been. They too reported partial preferences.

Rechten et al (218) used essentially the same experimental design as Krebs et al (136), alternating two food types that were regularly spaced on the conveyor belt. They found that when specialization is predicted, the birds make two kinds of "errors," namely, rejecting a profitable item (RP error) and taking an unprofitable item (TU error). They also discovered that at higher food presentation rates (i.e. shorter distances between food items), there were more RP errors and fewer TU errors, as one would expect if the birds sometimes misidentify the food types. They showed, however, that the birds could have adopted error probabilities that would have yielded higher rates of food gain, so misidentification does not completely account for the observed partial preferences. Rechten et al also observed that on the average, the birds rejected more items per item taken than would be expected if the birds were including sampling in their strategy and that hungry birds came closer to the optimal foraging predictions than partially satiated birds.

Lea's (143) results contrast with the relatively favorable ones obtained in the conveyor-belt studies. He varied the search time between the handling of one food item and the encounter with the next, the handling times associated with each food type, and the magnitude of the food reward associated with each food type. As expected, the 6 pigeons he studied became less and less selective as the search time lengthened; but they did not change from specializing to generalizing in a predicted stepwise manner, and they did not demonstrate a rapid decrease in selectivity at the predicted threshold search time. Lea also found, contrary to expectation, that the rate of encounter with the worse prey type affected its level of inclusion in the diet.

The different levels of success of optimal foraging theory in the above conveyor-belt and Skinner-box studies could be due to a greater similarity

between the conveyor-belt foraging situation and the natural foraging situations of the birds in the studies. In the conveyor-belt situation, a bird sees potential food items through a small open window above the conveyor belt and either allows an item to pass or else picks up the item for eating and/or inspection (e.g. 136). Food value is varied by changing the size of a food item; handling time is varied by enclosing the food items in containers from which they must be extracted; recognition time is varied by making the containers clear or opaque. In Lea's (143) Skinner-box study, the pigeon made dietary decisions (i.e. "searches") by pecking a certain number of times on a key, chose to accept a particular food type by pecking on a key and then waited for a period of time before gaining access to a food bin for another period of time. The conveyor-belt studies seem to mimic natural foraging situations more closely than the Skinner-box study.

Elnor & Hughes (63) studied different-sized crabs feeding on mussels of different sizes. When mussel availability was unlimited, the crabs chose mussel sizes close to the optimal size and that the crabs included bigger and smaller mussels as the supply of optimally sized mussels was depleted. Since crabs must spend some time recognizing mussel size, the abundance of a particular mussel size should determine whether it is included in the optimal diet (see the above discussion of optimal diet theory). Elnor & Hughes discovered that the foraging of the crabs was consistent with this expectation. Contrary to expectation, however, they also found some partial preferences.

OTHER STUDIES IN WHICH FOOD EVALUATION AT VARIOUS DISTANCES MAY NOT OCCUR Granivorous birds that essentially search areas of ground beneath them may not evaluate food at different distances. If the density of seeds is sufficiently low, seed encounter should also be sequential rather than simultaneous. However, seeds of different species are apparently not equivalent in terms of their nutrients (e.g. 40, 86), so the theory of optimal diets for granivores should take nutrient constraints into account (188, 190).

Pulliam (190) studied chipping-sparrows that were feeding on seeds in oak woodland. Some seed species were never eaten by caged or wild birds, and Pulliam assumed that these seeds were nutritionally unsuitable. When attention was restricted to the remaining seed types, he discovered that as predicted, seed types with ratios of energy yield to handling time above a threshold value tended to be included in the birds diet and vice versa. He also found partial preferences, which he interpreted in terms of the nutritional qualities of the seeds.

EXPERIMENTAL STUDIES WITH NECTARIVORES A nectarivore will often be able to see many flowers or plants from its present location. Thus, the optimal diet theory must be modified to allow for detection at a distance and for

simultaneous encounters. Waddington & Holden (271) assumed that in such situations, a nectarivore that can only plan one step at a time should always choose the next flower (or plant, etc.) so as to achieve the maximum expected ratio of net energy gain divided by the time required to move to and exploit the next flower. As pointed out above, this will not be precisely the optimal strategy, but I shall assume that it is a good approximation.

Waddington & Holden (271) observed honeybees foraging for nectar among two types of randomly distributed artificial flowers that differed in color and shape. They varied the average nectar yield per flower of each type by varying the proportions of flowers containing 2 μ l of unscented 25% sucrose solution, varied the densities of the 2 flower types, and for each of 7 cases, determined the proportions of visits to each flower type if the bees foraged optimally. The observed and predicted proportions were all similar, although a few significant differences were found (271).

Real and his colleagues (216, 217) also observed nectarivores (bumblebees and wasps) foraging for nectar among two kinds of differently colored, randomly distributed artificial flowers. In both studies, the densities of each flower type were equal, and the value of each type was varied by changing the probability distribution of the nectar volume per flower. The insects exhibited flower preferences that increased with increases in the average nectar yield per flower and decreased with increases in the variance (216, 217).

Waddington et al (269) also considered the importance of reward variance in determining flower preferences. They observed bumblebees foraging among four flowers of two color types arranged in a square with diagonally opposite flowers of different colors. Each time a bee left a flower, the nectar in that flower was replenished according to a probability distribution of nectar rewards. The bumblebees preferred flower types with constant rewards to ones with the same mean but variable rewards (269). In addition, the bumblebees exhibited partial rather than absolute flower preferences (269).

In all of the above studies of nectarivore foraging, the animals were risk averse and did not always maximize their expected net rate of energy gain. This result seems surprising in view of the large numbers of flowers (or plants) that many nectarivores (especially bees) are likely to visit during a day.

Marden & Waddington (152) observed honeybees choosing between two artificial flowers that differed in color and sometimes distance. When the flowers were equidistant from a bee, 14 of the 15 bees always chose one color or the other, while the last one showed no color preference. When the flowers were at different distances from a bee (but not in different directions), 8 of 10 bees tended to choose the closest flower independently of its color; one bee was initially constant to a particular color and later tended to choose the closest flower; another bee remained color constant. Thus, almost all the bees eventually tended to forage optimally. The preferences were partial rather than absolute, however.

OTHER STUDIES In other diet studies, fewer of the criteria outlined above are satisfied. Nevertheless, these studies yield results that tend to be similar to those just discussed. Many studies have found that animals exhibit partial rather than absolute food preferences (e.g. 3, 51, 59, 76, 86, 104, 115, 141, 263, 266, 278, 294). Some studies have indicated that an animal's preference for a particular food type depends only on the abundances of better food types (e.g. 52, 53), while others have found that the abundance of the particular food type is also important (e.g. 78, 115, 263, 266).

3. Patch Choice

THE CURRENCY OF FITNESS The same comments made about optimal diets as to whether or not it is realistic to assume that fitness increases linearly with the net rate of food or energy gain also apply to optimal patch choice. In addition, fitness associated with patch choice should often depend on predation, etc.

PATCH CHOICE IN THE ABSENCE OF RESOURCE DEPLETION WITH KNOWN LOCATION AND QUALITY OF PATCHES Most studies of patch choice focus on patches where there is no resource depletion, the locations are known, and factors other than food mass or energy are unimportant. In the earliest of these studies, the patches differed in the average rate of food or energy gain, and the variance was ignored. The animals preferred the patch with the highest rate of food or energy gain, but preferences were partial rather than absolute (147, 243, 245, 279, 291). Recently, several studies have considered how the variance in the rate of food intake affects patch preferences. Two kinds of birds—juncos and white-crowned sparrows—were found to prefer a patch with a relatively low variance in the rate of food intake (i.e. they were risk averse) when they could expect to meet their food (i.e. energy) requirements and to be risk prone when unable to do so. Preferences in these studies were also partial rather than absolute (24–26).

In another set of recent studies, the patches differed not only in the food supplied but also in predation risk (91, 100, 161, 163, 238). Sticklebacks in the simulated presence of an avian predator tended to feed in low rather than in high density swarms where the fish are less able to pay attention to predator approaches. In the absence of the predator, the fish preferred the high density swarms. (161). Sparrows sometimes prefer a distant patch providing shelter from predators to a closer, exposed patch (91). Small bluegills did not switch habitats when expected, and this may have been due to differential predation risk (163). Patch choice by back swimmers was related to a balance between feeding rate and predation risk (238).

If there is no resource depletion within patches and if fitness increases linearly with the rate of food or energy gain, then the optimal strategy is to

forage all the time in the best patch. If fitness also depends on some other aspect of food intake such as the variance in the rate of intake or the intake rate of some nutrient, however, then allocating time to more than one patch may be optimal (see the discussion of theories of optimal patch choice). The presence of other factors affecting fitness may explain the partial preferences observed in the above studies.

Two studies indicate the importance of factors other than energy. Belovsky (12) studied the foraging behavior of moose, for which diet and patch choice are equivalent because the various food types occur in patches. He assumed that moose are subject to constraints in the maximum feeding time available each day, daily rumen processing capacity, sodium requirements, and energy metabolism. He found that a model based on the assumption that fitness increases linearly with daily energy gain accurately predicts the amounts of aquatic vegetation, deciduous leaves, and forbs consumed by a moose each day. In turn, nectar-gathering workers of social bee species appeared to choose sunflower cultivars on the basis of energy production per plant, whereas solitary bees, which collect pollen as well as nectar from these plants, did not (260).

PATCH CHOICE WHEN RESOURCES ARE DEPLETED AND RENEWED In most natural situations, an animal will deplete the available food resources as it forages in a patch. At the same time or in between foraging bouts, these resources may be renewed. The optimal patch choice (assuming the locations of patches are known) will therefore depend on the patterns of resource depletion and renewal. For example, if resource renewal is rapid relative to depletion, then an animal should always forage in the best patch. If renewal is slow, the optimal strategy would be to avoid recently depleted patches.

Cole et al (37) explored the extent to which hummingbirds can learn the appropriate patch choice strategy if both resource depletion and renewal occur. Their patches were two artificial flowers, one of which supplied nectar while the other did not. In between foraging bouts, the positions of the two flower types either remained constant or were switched. The birds had an initial bias towards shifting between flower locations on successive bouts, and they learned this strategy more rapidly than they learned to return to the same flower location. The authors attributed this difference to the relatively slow renewal of flower nectar, so that the "win-shift" strategy is more appropriate under natural conditions. Two other studies concluded that animals distribute themselves between two patches so that the rates of food or energy intake in the patches are equal (160, 200).

4. Rules of Departure from a Patch

The amount of time an animal spends in a patch may affect its rate of food intake, its predation risk, and the time it spends elsewhere performing other

important tasks, such as monitoring potential intruders. Consequently, these factors may all enter into determining the currency of fitness for an animal's rule of departure from a patch. So far, the currency for all models of patch departure has been the net rates of food or energy gain; the tests of these models have involved situations for which this is a reasonable choice. Other factors—e.g. predation (97), intrusions (123), and thermoregulation (49)—will clearly have to be included in some situations, however. If one only considers food, an animal may leave a patch because its rate of food or energy intake has decreased through depletion of the available food or through movement into poorer regions of the patch, or because sampling experience indicates that it is a relatively poor patch. The theory of patch departure has concentrated, however, on resource depletion rather than on sampling (see the above discussion of the optimal rules of departure). It is assumed that the locations and qualities of patches are known. The theory should therefore be tested only in situations where this assumption is justified. In the discussion below, I shall first consider studies that satisfy this requirement, then a study that deals mostly with sampling, and finally research that involves both depletion and sampling (see also 209).

RESOURCE DEPLETION IN PATCHES OF KNOWN QUALITY AND LOCATION When food items are discrete, the optimal rule of patch departure will depend on the information used by the animal. An animal may base its departure decisions on the amount of food obtained so far, the amount of time spent in the patch, the time since the last food encounter, or other intercapture intervals, among other factors. In the absence of independent tests, assumptions about information use must be taken at face value.

Krebs et al (139) were the first to attempt to evaluate optimal patch departure. In one of their experiments, the locations and qualities of the patches should have been known to the foraging animals (chickadees). All of the patches were artificial pine cones containing a single food item (mealworm pieces) randomly assigned to one of six covered holes. The authors found that the birds obtained 0.26 food items per patch on average. This number is much smaller than the optimum of 1.0 that would prevail if the birds base their departure on the number of food items obtained so far. It could be close to the optimum, however, if the birds base their departure from a patch on the total time spent in the patch or on the time since consuming the last (and first in this case) food item. Krebs et al carried out some other experiments indicating that the chickadees based their departures on the time since the last food item was consumed (i.e. on the giving-up time) rather than on the time spent in a patch or the amount of food obtained so far. Zach & Falls (292) reported similar results for ovenbirds. Bond's (20) analysis of the probability distributions of giving-up times suggested that departure decisions may be affected by other factors as

well. Giving-up times for caddis larvae were unaffected by the previous level of feeding (262). Giving-up times of parasitoid wasps were approximately constant in patches of different qualities, and the wasps reduced the prey to about the same level in each patch (110).

Several studies have implicitly assumed that foraging animals base their departure from patches on the time spent in a patch so far (42, 45, 123, 135). Cowie (45) varied the predicted times per patch by changing interpatch travel times and found that the observed average times and the predicted times were similar. Cook & Hubbard (42) considered six patches that differed in food density and predicted the percentages of the foraging animal's time that should be spent in each patch type. They found that the animals spent some time in patches they should not have visited at all, but that otherwise the difference between the observed and predicted values was minimal. Krebs & Cowie (135) applied this same approach to Smith & Sweatman's (245) and Zach & Falls's (291) data (see 209). Resource depletion was minimal in the latter two studies, however, so I included them in the previous discussion of patch choice. Kacelnik et al (123) studied great tits that could obtain food in a patch by hopping on a perch. They simulated resource depletion by requiring increasing numbers of hops to obtain the next food item. The most common numbers of hops were equal to the predicted number for 3 out of 4 birds, one bird having considerably longer hopping bouts than predicted. In all of these studies, the average or most common time spent per patch agrees reasonably well with the predicted time per patch, but the time spent per patch is not a constant as was predicted. A number of studies have obtained results that support more qualitative predictions of optimal patch departure (e.g. 16, 41, 58, 79, 124, 140, 237).

PATCHES OF UNKNOWN QUALITY To nectivores that feed at flowers in inflorescences or on plants, these clusters of flowers represent patches. As such an animal moves among the flowers within a patch, it may be increasingly likely to revisit a flower (e.g. 195, 202, 208), it may visit flowers that tend to contain less nectar than others (e.g. 103, 196, 205), or it may obtain information about the otherwise unknown quality of its present patch (e.g. 103, 195, 202). Such foraging situations are therefore ideal for developing and testing models of optimal patch departure. In general, however, these models must include sampling as well as depletion.

The only study in which sampling and depletion are included in both the model and the data collection is one of mine (202). I observed honey eaters feeding at inflorescences that almost always had seven flowers in a regular arrangement. As these birds visited flowers within an inflorescence, the probability of a revisit increased slightly until seven flowers had been visited, and then it became close to one. There was a positive correlation among the nectar volumes of flowers from the same inflorescence, so the birds could have

estimated patch quality on the basis of their sampling experience in a patch. I assumed that fitness increases linearly with the expected net rate of energy gain; that the birds base their departure decisions on nectar thresholds with respect either to the nectar volume obtained from the last flower visited or to the average nectar volume obtained from the flowers visited within a patch so far; and that these thresholds will vary with the number of flowers that have been visited. I used a computer simulation based on the observed probabilities of flower revisitation, the patterns of nectar distribution, and the times associated with various activities of the birds to derive the optimal nectar thresholds and from them, the optimal frequency distributions of the numbers of flowers probed per inflorescence. The observed and predicted frequency distributions were qualitatively similar but significantly different. The direction of this discrepancy is what would be expected if the birds tend to be transient (202), a characteristic verified by subsequent bird banding (G. H. Pyke & H. F. Recher, unpublished data).

Other attempts have been made to test predictions of optimal patch departure using foraging by nectarivores (15, 103, 108, 109, 195, 284). In all these cases, however, the development of the predictions is inappropriate to the foraging situation (see the above discussion of optimal patch departure theory; also 209, 230). The same is true for Davies' study (52) of spotted flycatchers foraging among nondepletable patches of flying insects (see 209).

5. *Rules of Movement*

MOVEMENT PATTERNS AND SPEED OF MOVEMENT Relatively little attention has been given to developing and testing models of optimal patterns of movement (see 209, 210, 270). Many studies have shown that animals become less directional in movements or tend to engage in area-restricted searching after their encounter with large amounts of food or food odor (19, 21, 55, 69, 194, 210, 247, 267, 285, 289, 293, 295). Such behavior is expected whenever food is patchily distributed (e.g. 210). However, there are as yet no predictions as to exactly what the directionality, or more generally, the rule-governing patterns, of movement should be in different situations (see the above discussion of optimal movement patterns). Consequently, quantitative tests of the predictions are not feasible. The degree of directionality exhibited by animals varies widely (2, 130, 196, 203, 210, 228, 240, 296–298).

In addition, where animals can see food items at a distance, they tend to move to the closest and the best items (best in terms of the rate of food gain) (e.g. 152, 176, 203, 297, 298). Animals may also tend to alternate left and right turns (e.g. 194) or to turn in one direction rather than the other (e.g. 35).

The speed of movement of foraging animals has received even less attention than movement patterns (see 204). In one of the few studies, Ware (272) found

that the average swimming speed of bleak, a planktivorous fish, is close to the speed that maximizes the net rate of energy gain.

FORAGING MODE Animals sometimes exhibit a variety of foraging modes while feeding in the same area and on the same food types. Kestrels, for example, may hunt while hovering or while sitting on a perch (225). Hummingbirds and honey eaters may perch and hop or hover while feeding among flowers within an inflorescence or plant (201). I deduced that in two observed foraging situations, hovering hummingbirds and perching honey eaters would have obtained lower net rates of energy gain if they had adopted the alternative mode of foraging (201). Hovering seems to enable a bird to move more rapidly between flowers within an inflorescence than perching and hopping, but at a higher energetic cost (201). Zach (290) found that crows, which break whelks by dropping them on rocks, minimized the total amount of ascending flight required when choosing the height of the drop. No other tests of optimal foraging modes have apparently been carried out.

6. *Central Place Foraging*

All quantitative tests of optimal central place foraging have assumed that fitness increases linearly with the rate of food or energy intake. Other factors may also be important (e.g. 154), however.

For central place foragers, patches may differ in their quality and distance from the central place, and animals should vary their time and load size per patch accordingly (see the above discussion of optimal central place foraging). Several researchers found that the rate of food gain in a patch decreases as more time is spent in the patch, and they have used this relationship and the theory of optimal central place foraging (see 80, 128, 179) to derive predicted times and load sizes for different patches. In these cases—as required by the theory—there is effectively only one patch, and the animal is not simultaneously choosing among patches. Close agreement between the observed and predicted load sizes was reported (30, 126, 128, 261). However, chipmunks consistently spent less time and collected smaller loads than predicted (80). In all cases, the load sizes and patch times increased with increasing distance or time from the central place (80, 126, 128, 261). This qualitative result is consistent with Carlson & Moreno's (29) and Nunez's (173) findings.

A central place forager must also choose which patches to visit, and it would be expected to allocate different amounts of time to patches at different distances from the central place. But the predicted pattern of time allocation is sensitive to assumptions about the knowledge of patch locations and the rate of food renewal (see above), so quantitative tests of such predictions seem premature. Central place foraging has also been the subject of a number of other studies (e.g. 5, 7, 14, 44, 71, 96, 131, 224, 244).

CONCLUSIONS

Optimal foraging theory can only be expected to be useful when its assumptions, mathematical development, and testing are appropriate for the studies to which it is applied. Future optimal foraging studies should therefore deal explicitly with these problems and satisfy the kind of criteria I have presented above. As in many other areas of research, the achievement of these goals should be enhanced by better communication between theoreticians and empiricists.

Up to this point, the predictions of optimal foraging theory have been supported to some extent but not completely. In many cases, the (correct) prediction is some kind of all-or-nothing behavioral response, yet animals invariably exhibit more gradual and incomplete responses (e.g. partial diet preferences, variable patch times). Many explanations for these discrepancies have been proposed (e.g. sampling, mistakes), but further development and testing of these rationalizations remain to be carried out.

If attention is restricted to those studies that provide genuine tests of optimal foraging theory, the level of agreement between predicted and observed foraging behavior has been reasonably good, except for the findings of gradual rather than all-or-nothing behavioral responses. Consequently, the optimal foraging approach seems worth pursuing. Nevertheless, there are still extremely few studies that come close to meeting my proposed criteria, and it is therefore premature to form a firm opinion regarding the usefulness of the approach.

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