PUTTING ECOLOGY BACK INTO OPTIMAL
FORAGING THEORY

by

Richard F. Green

Technical Report 89-11

Department of Mathematics and Statistics
University of Minnesota
Duluth, Minnesota 55812

October 1989

PUTTING ECOLOGY BACK INTO OPTIMAL FORAGING THEORY

Abstract: Optimal foraging theory is one of the most popular areas in modern evolutionary biology. In this paper, I outline some of the main ideas of optimal foraging theory and describe two basic foraging models in detail. I argue that one of these models is less interesting than it should be because it does not include realistic assumptions about the environment or about the behavior of the forager. Then I describe a model that does make explicit behavioral and ecological assumptions. I argue for the use of particular, quantitative models and describe an experimental test of one such model. I discuss some criticisms of optimal foraging theory and will try to predict what the future holds. In particular, I show how optimal foraging theory might help to bridge the gap between individual behavior and population biology.

INTRODUCTION

For many years ecologists have been interested in the food habits of animals. Their question is, How *do* animals look for and select food? Optimal foraging asks the question: How *should* animals look for and select food? The first papers to ask the question in this way were published in 1966.[1,2] These and other early papers were mainly about optimal diet. An early review of the subject was provided by Schoener,[3] and a well-known account was given by MacArthur,[4] who pointed out that as the overall density of prey decreases, predators should be less selective in their choice of prey. A consequence of this is that predators which compete with each other for prey should show greater overlap in their use of prey and should compete more strongly as prey density decreases.

A great impetus to the study of foraging theory was provided by Charnov,[5−8] who provided an explicitly mathematical theory and used the striking phrase "optimal foraging" to refer to what Schoener[3] referred to, perhaps more accurately, as "feeding strategies." A broad view of foraging theory was laid out in an influential review by Pyke, Pulliam and Charnov,[9] and most experimental work on foraging behavior has been based on the ideas contained in this review. Recently, three volumes have been published on foraging. Two of these are the proceedings of symposia, one[10] held at Harvard University in 1983 and the other[11] held at Brown University in 1984. The third volume is a monograph by Stephens and Krebs.[12] I think that a reader interested in learning about optimal foraging theory would do best to begin with the book by Stephens and Krebs, which gives an excellent description of foraging models and the strategy of modeling and

its criticisms, and with Schoener's[13] informative, personal history of the early years of optimal foraging theory.

Early work on foraging theory was basically ecological, and Schoener's historical sketch reflects this point of view. More recently, foraging theory has been treated as almost exclusively behavioral, and ecological aspects have been neglected. This modern view is seen in the monograph by Stephens and Krebs, [12] who seek to understand foraging as a behavioral adaptation, with little attention being paid to its ecological context and none to its ecological consequences. In the next section, I will begin by following Stephens and Krebs in their treatment of the two basic foraging models, but I will present an alternative to one of these models and try to show that foraging theory can be made more interesting by paying attention to the ecological context of the behavior. The model that I present permits a quantitative treatment of foraging behavior, which is more useful than the older, qualitative treatment because it permits the investigation of some ecological consequences of foraging behavior.

OPTIMAL FORAGING MODELS

In their review of optimal foraging theory, Pyke, Pulliam and Charnov[9] described four problems that a forager must face: (1) What prey to take, and if prey are distributed in patches, (2) What patch types to search; (3) When to leave a patch, and (4) How to move between patches. Foraging theory may be divided into parts according to which of these questions it addresses. Most work on foraging theory has been done on problems (1) and (3). The least amount of work has been done on (4), perhaps because it is difficult to give a realistic, yet tractable, formulation of the problem. Stephens and Krebs[12] have lumped the problems involving choice [(1) and (2)] into one, which they refer to as the "prey" problem. They contrast this with the problem involving residence time, which they refer to as the "patch" problem. I will describe the basic prey and patch models as Stephens and Krebs describe them, and then I will present an alternative to the basic patch model. For all the models, an optimal forager is one that maximizes its long-term average rate of energy uptake or its long-term average rate of finding prey while foraging.

The prey problem: What types of prey should a forager accept?

The prey problem is to decide which of several types of prey (indexed by the subscript i) the forager should take. The basic prey model assumes:

(1) Foragers cannot search for prey and handle prey at the same time.

(2) Individuals of each prey type are encountered one at a time, at random, independently of other types, according to a Poisson process.

(3) The net energy gain, e_i, the handling time, h_i, and the encounter rate, λ_i, are fixed for each type i, and do not depend on the choices that the forager makes.

(4) The forager is able to discriminate among prey types perfectly and instantaneously, without cost.

(5) The forager has complete information about the parameters of the model, but does not use information acquired while foraging.

The basic prey model predicts that:

(1) A forager will choose the most profitable prey types, where profitability is measured by the ratio e_i/h_i.

(2) Foragers will be more selective when encounter rates are higher (that is, prey are more abundant).

(3) Whether a particular type of prey will be taken depends only on the abundance of more profitable prey; it does not depend on the abundance of the prey in question, or the abundance of less profitable prey.

(4) Prey of a given type should be accepted always or never. There should be no "partial preferences," with the forager taking some, but not all, items encountered of a particular prey type.

Stephens and Krebs[12] (following Krebs, Stephens and Sutherland[14]) cite many studies that test some or all of these predictions of the prey model. Most of these studies are classified as giving at least qualitative support to the theory. The most frequently tested prediction is that foragers prefer the most profitable prey. It is not surprising that this prediction is usually confirmed.

The patch model: How long should a forager spend in a patch?

In the patch problem prey are distributed in patches and a forager must decide when to leave one patch and go on to another. The basic patch model assumes:

(1) Searching for patches and searching for prey within patches are mutually exclusive activities.

(2) Patches are encountered at random according to a Poisson process with fixed rate λ_i for each patch type i.

(3) The time chosen to leave a patch is independent of the forager's experience within that patch.

(4) For each patch type, i, the net expected energy gain is a fixed, continuous function, $g_i(t)$, of the time that a forager remains in the patch. For each patch type, this function takes value 0 at time 0, increases initially, and is eventually negatively accelerating.

(5) A forager is assumed to have complete information about the encounter rates λ_i and the gain functions $g_i(t)$, but no additional information about patch quality is obtained while the patch is being searched.

The optimal foraging strategy for the basic patch model is given by Charnov's[8] "marginal value theorem," which says that the optimal time to remain in patch type i is the time t_i when the derivative (the "marginal value") of the gain function $g'_i(t_i) = C$, where C is the highest possible long-term average rate of energy gain. Charnov's theorem is illustrated, for one patch type, in Fig. 1a.

(Put Fig. 1 about here.)

The basic patch model predicts:

(1) Foragers should stay longer in a patch of a given type when the environment is poorer overall, or if travel time between patches is longer.

(2) A forager should search all patches encountered until the net rate of energy gain in the patches is reduced to the same level.

(3) A forager should take more resources from better patches.

Again, a large number of studies[12,14] tend to show qualitative agreement with these predictions. By far the most frequently tested prediction is the first—that foragers should remain longer in patches when conditions are worse.

There is a difficulty with Charnov's original marginal value theorem: it assumes that the gain function for a particular patch type is a continuous, deterministic function of time in a patch. For a real predator capturing individual prey, the gain function would be discontinuous and stochastic. In one patch, the gain function might look like that shown in Fig. 1b, where the slope is almost always zero, and the marginal value theorem does not apply. Stephens and Krebs[12] avoid this difficulty by referring to the net *expected* energy gain, thus making the theorem refer to stochastic models. However, a more serious problem remains: the marginal value theorem as stated by Stephens and Krebs does not specify a rule that a forager can to decide when to leave a patch.

The trouble with the marginal value theorem is that it is based on the idea of a gain function, an idea drawn from economics, illustrated by a schematic figure, and assumed to satisfy some general, mathematically convenient assumptions. The gain function is given in place of detailed assumptions about how prey are distributed within and among

patches and how foragers search for prey within patches. It is true that particular assumptions about prey distribution and predator search pattern will yield a particular gain function, but different sets of assumptions about prey distribution and search pattern, each calling for a different optimal foraging strategy, can yield the same gain function.

For example, in the original study testing a version of the marginal value theorem, Krebs, Ryan and Charnov[15] asked which of three rules a forager would use to decide when to leave a patch. One rule said that a forager should stay in each patch until a particular number of prey are found (the fixed-number rule), another said that a forager should stay for a fixed time in each patch (the fixed-time rule), while the third said that a forager should leave a patch when a fixed time has been passed without a prey having been encountered (the giving-up-time rule). Krebs *et al.*[15] treated the giving-up-time rule as optimal, and interpreted the data as being consistent with this rule, but such a strategy would not be considered possible by the version of the marginal value theorem described by Stephens and Krebs,[12] which only permits the fixed-time rule. Iwasa, Higashi and Yamamura[16] showed that if search within patches is random, then, depending on the distribution of prey within patches, each of the strategies considered by Krebs *et al.* [15] could be best of the three. If all patches contain the same number of prey, then the fixed-number rule is best (the fixed number is not necessarily the number of prey originally in each patch); if the number of prey per patch has a Poisson distribution, then the fixed-time rule is best, while if the number of prey has a negative binomial distribution (with small enough parameter k), then the giving-up-time rule is best of the three (but not best overall).

Thus, the form of the optimal rule for a forager to use to decide when to leave a patch depends on the distribution of prey within a patch, a fact obscured by treating the problem using a general gain function. Further, the rate of energy gain that an optimal forager can achieve depends on how prey are distributed in patches. The importance of prey distribution is emphasized in Oaten's[17] stochastic model, of which the examples given by Iwasa *et al.*[16] are special cases.

Oaten's stochastic model of optimal foraging

Oaten devised a new patch model in an attempt to demonstrate the importance of including more biological details than were found in Charnov's original patch model. Oaten's model assumes:

(1) Prey are found in patches, and the predator knows the distribution of the number of prey per patch.

(2) The predator knows the joint distribution of the capture times, given the number of prey in a patch. Patches are superficially similar and of the same size. (That is, they are all of one "type," in the terminology of Stephens and Charnov.[18])

(3) Prey are not replaced as they are captured.

(4) The predator knows the time τ that it takes to go from patch to patch.

(5) The predator decides when to leave a patch based on its knowledge of (1), (2) and (4), and its experience in the patch.

(6) Given a strategy we can calculate

$$R = E(G)/[E(T) + \tau] \tag{1}$$

where

$E(G) =$ the expected number of prey caught in each patch,

$E(T) =$ the expected length of time spent in each patch, and

$R =$ the long-term average rate of finding prey using the given strategy.

(7) The predator uses the strategy that maximizes R.

Oaten's model is very general, and particular predictions follow only from particular assumptions. The first prediction of the basic patch model (that foragers should remain longer in patches when travel time between patches is longer) follows from Oaten's model. The basic patch model's third prediction (that foragers should take more prey from patches that have more prey) also follows from Oaten's model, if prey are distributed at random within a patch. The second prediction of the basic patch model (that foragers should search all patches until the rate of finding prey in each has fallen to the same level) does not, in general, follow from Oaten's model.

The advantage of Oaten's model over the basic patch model is that it permits the consideration of patch variability and the use of information obtained while foraging. In its first two assumptions, Oaten's model has a place for explicit descriptions of the environment and the forager's pattern of search. Oaten's model has the disadvantage of being complicated and very difficult to work out in detail.

McNamara[19] has given a general theorem that characterizes the patch-leaving rule for Oaten's model. McNamara's theorem is given in terms of a "potential" function:

$$H(t, \mathbf{x}) = \max_S [G(t, \mathbf{x}, S) - \gamma T(t, \mathbf{x}, S)], \tag{2}$$

where γ is the highest possible long-term average rate of energy gain, and $G(t, \mathbf{x}, S)$ and $T(t, \mathbf{x}, S)$ are the expected net energy obtained and the expected time spent in a patch *from time t on*, respectively, given that the forager has had experience $\mathbf{x}$ by time t in a patch and S is some strategy. For Oaten's model, $\mathbf{x}$ represents the times at which prey

have been found, while for an example that I will describe, x is simply the number of prey that have been found by time t. McNamara's theorem, which says that an optimal forager should remain in a patch as long as $H(t, \mathbf{x})$ is positive, gives a true statement about patch-leaving rules which may be used in simple cases, and his theorem has heuristic value—it emphasizes the point that it is not just the average rate of finding prey at any particular time that is important (as is the case in the stochastic version of the marginal value theorem given by Pyke[20] or the one by Stephens and Krebs[12]). However, McNamara's theorem is difficult to apply in particular cases. Its main use in applications is to show that rules found by other methods are actually the best possible.

A number of particular cases of Oaten's model have been considered. These cases involve particular assumptions about how prey are distributed in patches. I will describe one example[21] which I think is realistic biologically.

A particular case of Oaten's model

Assume:

(1) The number of prey per patch has a negative binomial distribution. The probability function of the number of prey per patch may be written as

$$f(x|\alpha, \beta) = \binom{\alpha + x - 1}{x} \left(\frac{\beta}{1+\beta}\right)^{\alpha} \left(\frac{1}{1+\beta}\right)^{x} \tag{3}$$

(2) The prey within a patch are distributed randomly (uniformly and independently) and search within a patch is systematic. This implies that capture times within a patch will be random.

I use this notation because it is convenient to think about patches as varying in quality, with the number of prey in a patch having a Poisson distribution with parameter λ, but with λ itself varying from patch to patch, and having a gamma distribution. That is,

$$f(\lambda|\alpha, \beta) = \frac{\beta^{\alpha} \lambda^{\alpha-1} e^{-\beta\lambda}}{\Gamma(\alpha)} \tag{4}$$

This is a familiar setup for a Bayesian model.

The upshot of my assumptions (1) and (2) is that if the parameter λ is thought of as being a random variable with a gamma prior distribution with parameters α and β, and if a forager has spent time t in a patch and has encountered x prey there, then λ will have a gamma posterior distribution with updated parameters $\alpha + x$ and $\beta + t$. We can think of a forager that has found x prey in a patch by time t as finding prey at an instantaneous rate of $(\alpha + x)/(\beta + t)$ at time t. For this example, the number of prey found up to a particular time is a sufficient statistic for λ at that time, and the optimal

patch-leaving rule will consist of a set of times, $t(k)$, such that a forager should leave a patch when the patch has been searched completely, or if exactly k prey have been found by time $t(k)$.

For a given choice of α and β for the prey distribution, and travel time τ, candidate optimal patch-leaving times may be found by dynamic programming. Values, C, are guessed for the highest long-term average rate that can be achieved, and strategies are found that "try to achieve" these rates. For each of the strategies that is found, the expected number of prey found and the expected time in a patch, EG and ET, respectively, can be found, and these values can be used to calculate the rate $R(C) = EG/(ET + \tau)$ that is achieved by the rule. The optimal strategy is the one for which $R(C) = C$, and the optimal rate is the value of C for which $R(C) = C$.

For particular choices of α and β, the points (ET, EG) may be plotted for all guessed values of C, and the result will be an analogue of the marginal value theorem. I illustrate this in Fig. 2a, for two types of patches, one twice as large as the other, and having twice as many prey on average. Both patch types have the same value of α ($\alpha = 0.5$), but $\beta = 0.1$ for the large patches and $\beta = 0.2$ for the smaller patches. The optimal patch-leaving rules, corresponding to the $ET - EG$ points indicated by asterisks in Fig. 2a, are illustrated in Fig. 2b. The optimal rules are qualitatively similar for the two patch types, but it can be seen that a forager is slightly more reluctant to leave larger patches. [In this particular case, I first found the optimal strategy for the case that all patches are large and travel time $\tau = 0.1$. For this case, the optimal rate is $R = 8.074$, which may be compared with the rate $R = 4.545$, which would be achieved by a "naive" forager that ignored experience within patches and searched each patch completely. Having found the value $R = 8.074$, I used this value to find the strategy that "tries to achieve" this rate for the smaller patches.]

(Put Fig. 2 about here.)

While there is some difference between the leaving rules for large and small patches in the example that I have given, very little would be lost if the forager used the same rule in both types. On the other hand, a great deal would be lost if the forager could not use information obtained while foraging. If both sizes of patch are equally frequent, then an optimal forager can find an average of 8.074 prey per unit time (with $\tau = 0.0660$), while a forager that does not distinguish between patches of different sizes, but uses the same rule for small patches that would be best for large ones, would achieve rate 7.983, about 1% below the maximum rate. On the other hand, a forager that ignores information about patch quality obtained while foraging would achieve rate 4.596, about 43% below the maximum. In other words, in this case it is much more important to recognize differences among patches of the same size than to recognize the difference between patch sizes. While one example does not suffice to show the relative importance of differences within and between patch types in general, the important point here is that Oaten's model permits the quantitative treatment of this question for particular cases.

A quantitative treatment of foraging is important if one wants to investigate the population consequences of foraging behavior.

POPULATION CONSEQUENCES OF FORAGING BEHAVIOR

Recently biologists have been exhorted to consider the population consequences of individual behavior.[22,23] There has been little attempt to use foraging theory to understand population- and community-level phenomena, largely because behavioral ecology, of which foraging theory is a part, has been concerned with lower-level phenomena. Since the questions asked by behavioral ecologists have been generally qualitative, it has not seemed necessary to develop a quantitative theory, and it is not easy to see how the qualitative theory that has been developed is relevant to population ecology. In fact, the development of a quantitative foraging theory appropriate to the understanding of population ecology has proceeded quite independently of the development of foraging theory within behavioral ecology.[16,17,19,24-27]

One case in which foraging theory has been applied to population ecology is the predator-prey model based on the Lotka-Volterra equations considered by Murdoch and Oaten.[25] In the usual model, the rates of change of the number of prey, N, and the number of predators, P, are given by the differential equations:

$$dN/dt = aN - bNP, \quad \text{and}$$
$$dP/dt = -cP + dNP, \tag{5}$$

where a, b, c and d are positive constants. In this model, the amount of predation is proportional to the product of the number of predators and the number of prey. That is, the rate of finding prey, per predator, is proportional to the number of prey. The predator-prey system governed by the Lotka-Volterra equations is neutrally stable, and the question arises how these equations can be modified realistically to yield stability. Murdoch and Oaten modified these equations to permit the predation rate per predator to be a function, $R(N)$, of the number of prey, and they used foraging theory to determine the form of $R(N)$. The equations become:

$$dN/dt = aN - bR(N)P, \quad \text{and}$$
$$dP/dt = -cP + dR(N)P. \tag{6}$$

For an equilibrium for these equations to be locally stable, the ratio $R(N)/N$ must be increasing at the equilibrium. The value of R used in these equations is slightly different than that given in expression (2) because the time spent handling prey must be taken into account. Thus, we have:

$$R(N) = EG/[ET + \tau + hEG], \tag{7}$$

where h is the handling time per prey.

Using essentially the same assumptions as in Oaten's[17] subsequent model, except for the assumption that foragers are optimal, Murdoch and Oaten[25] assumed that prey are distributed in patches, and that search within patches is random. They assumed that predators use the giving-up-time rule with a particular, rather short, giving-up time. Then they specified the prey distributions within patches, letting these distributions change in specified ways as the overall prey population, N, changed. They assumed that prey distribution is either Poisson or negative binomial, and they varied the prey distributions in patches in three ways: (1) for the Poisson distribution, parameter λ is proportional to N, while for the negative binomial distribution, (2) the parameter k (α in my notation) is held constant, or (3) k is proportional to N. In each case, there is a range of values of N for which a stable equilibrium is possible if handling time is small enough. Murdoch and Oaten's treatment of foraging theory has the disadvantage that the giving-up-time rule is not the optimal strategy for either of the types of prey distribution considered, and the giving-up time chosen is not the best among all giving-up times for the particular cases examined. Thus, their results might be explained by saying that their model only seemed to be stabilized by foraging behavior because the foraging strategies considered are inefficient, and that the ratio $R(N)/N$ seemed to increase because the foraging strategy considered is less inefficient at higher prey densities.

I have done some calculations using the same model as Murdoch and Oaten[25], but I assume that the forager uses the strategy that is optimal at equlibrium, and that this same strategy is used for prey densities around the optimum. In Fig. 3, I have considered cases (2) and (3) of Murdoch and Oaten, and the ratio $R(N)/N$ is plotted against N for single examples for each of these two cases, for travel times $h = 0$ and $h = 0.05$. It is seen that the equilibrium can be stable if the negative binomial parmeter k is held constant (and if travel time is small), but not if k is proportional to N. If prey distribution is Poisson, the best that can be hoped for is neutral stability because the optimal strategy is to stay in each patch for a fixed time, and the number of prey found during that time will be proportional to overall prey density.

(Put Fig. 3 about here.)

By using optimal foraging theory, I find that stability is possible with Murdoch and Oaten's model, but that the conditions for stability are more limited than those suggested by Murdoch and Oaten. My calculations, and those of Murdoch and Oaten, show that foraging behavior might contribute to the stability of a predator-prey system under certain conditions, and that these conditions involve how the predator forages, how the prey are distributed in patches, and how the prey distribution changes with overall prey density. While some of this is obvious, I do not think that it has been reported that the stability of a predator-prey system depends on the pattern of change of prey distribution with changes of prey density. This is a qualitative observation, but it results from a quantitative treatment of foraging theory.

A conclusion similar to mine holds for a "phenomenological" host-parasitoid model considered by May,[28] who assumed that the probability that a given host avoids attack

can be represented by the zero term of a negative binomial distribution. May showed that the system will be stable if the degree of aggregation of attack is great enough (that is, the negative binomial parameter, k, is small enough). While May does not mention the fact, the stability of his model depends not only on the degree of aggregation of attack, but also on the way this degree of aggregation varies with parasitoid density. Hassell and May[22] interpreted the aggregation of attack in terms of aggregation of hosts, but Chesson and Murdoch[29] showed that the important thing for the stability of host-parasitoid systems such as that considered by Hassell and May[24] is aggregation of attack and not aggregation of hosts. I think that an important contribution of the models of Murdoch and Oaten, and of Hassell and May, is that they are not just models of population dynamics, but they include expressions that depend on the behavior of individual animals. One of the goals of optimal foraging theory should be to develop quantitative models that will permit the evaluation of the expressions contained in these models of population dynamics.

CRITICISMS AND TESTS OF OPTIMAL FORAGING THEORY

Optimal foraging theory has received strong criticism,[30,31] some of which is intended to discredit the whole subject. The strongest—or fiercest—criticisms have been answered,[12,32] and I do not think that the assertion that optimal foraging theory is "a complete waste of time"[31] can be sustained. Such extreme criticism can best be answered by asking whether optimal foraging theory has been of any practical use to those interested in understanding animals' food habits. The answer to this is clearly, "yes." The question of *how useful* is foraging theory remains, but the most extreme critics of the theory have not asked this question. The developers of optimal foraging theory have not been interested in applications, so the theory is not as useful as it could be. Most criticisms of the theory have been concerned with the philosophy of modeling and methodological issues. A number of critical views of optimal foraging theory are listed by Schoener.[3]

These views are of three types: (1) Optimal foraging theory says that animals forage optimally, in some sense, and any evidence to the contrary is accommodated by adding *ad hoc* hypotheses to change the model, or the sense in which foraging is to be optimal. This view sees foraging theorists insisting, "foraging is optimal," and keeping to this form even if they have to change the meaning. I do not think that this view of optimal foraging theory is a correct one because, as Stephens and Krebs [12] say, the assumption of optimality is not under test. While optimal foraging theorists are not guilty of the sin of *ad hocery*, I think that they do suffer from an excessive fear of being accused of it. If anything, they are too unwilling to modify their ideas and think them through again when they are found to be wrong.

(2) The problems faced by foragers are too complicated to be represented by simple models, and even if this were not true, we would still not know what these problems are. I think that there is some validity to this view. It is less likely to apply to the qualitative models descibed by Stephens and Krebs than to the quantitative models that I prefer. I think that it is important to consider a variety of models, and to fit the models

to the known facts. It certainly is unlikely that a single, simple, inflexible model will fit all cases. I think that working out the details of optimal foraging theory will be difficult in any case, but the question is whether it is impossible. I do not know what the answer is—the thing is to try.

(3) Optimal foraging theory has been tested and shown to be incorrect. (Or, it has been shown to be correct, and is of no further interest.) The strongest criticism and the most vigorous defense of optimal foraging theory are both based on the interpretation of experimental tests of the theory. The difference of opinion is based on the fact that supporters of optimal foraging theory take the confirmation of general, qualitative predictions as evidence that the theory is correct, while opponents take the refutation of specific, quantitative predictions as evidence that the theory is false. For example, Stephens and Krebs [12] point to scores of tests that show that foragers tend to prefer the most profitable prey as evidence that the theory is correct, while Gray [30] points to evidence that foragers show "partial preferences" as evidence that the theory is incorrect.

Two issues are raised by tests of optimal foraging theory: whether or not the assumptions of the model are general, and whether the predictions are qualitative or quantitative. There is some confusion over what is meant by generality. Models which do not refer explicitly to particular cases, such as the basic prey model which I have described above, are sometimes thought of as "general," even though their assumptions may be so restrictive that they hold for few, if any, cases. Truly general models apply to more cases, but they generate fewer, and less specific, predictions. Neither the basic prey model nor the basic patch model refer to particular cases—they are general in that way—but this does not mean that they are truly general. The basic prey model assumes that foragers are omniscient, and can discriminate among prey types instantaneously, and without mistakes. These assumptions are clearly too strong to apply to any case. That is, in a mathematical sense, this model is vacuous. The fact that one prediction tends to be confirmed—that foragers should prefer the most profitable prey—happens because this prediction would also follow from weaker, more realistic assumptions. That another prediction fails—that foragers should never show partial preferences—happens because the prediction follows from one particular, unrealistic assumption: that discrimination is perfect, but it would not follow if this assumption were relaxed.

The other issue is whether one wants qualitative or quantitative predictions. Stephens and Krebs [12] take experiments showing that foraging behavior is better than random as evidence in favor of optimal foraging theory, while Gray [30] takes evidence showing that foraging is not perfect as evidence that foraging is not optimal. I think that we can safely say that the behavior of foragers is better than random and less than perfect. It is unreasonable to expect foraging behavior to be perfect, but we might expect something better than statistically significant non-randomness. It would be good to be able to measure the efficiency of foraging quantitatively, to see whether behavior was closer to randomness or to perfection. Such measurement is possible in an experiment performed by Lima.

Lima's test of an example of Oaten's model

While there have been many experiments testing the predictions of the basic patch model, I know of only two good published tests of Oaten's model. Both of these were done by Lima.[33,34] I will describe one of these experiments, which not only provides a test of a stochastic foraging model but which also illustrates the difference between comparing the observed behavior with optimal behavior and comparing the observed payoff with the optimal payoff.

Lima observed the foraging behavior of free-living Downy Woodpeckers foraging on 60 artificial "trees," which were wooden dowels, each having 24 holes drilled in six rings of four holes each. "Prey" (pieces of sunflower seeds) were placed in some of the holes, and all of the holes were covered with pieces of tape. In each experiment, some of the trees were left with all the holes empty, while the other ("full") trees had prey in a fixed number of holes, which were chosen at random. Foraging was observed to be systematic among and within trees. Typically, a bird would search each tree beginning at the lowest holes and proceeding to the top, with all, or nearly all, of the holes being searched if prey were found in the first few holes. If no prey were found in the first few holes searched, then the bird abandoned the tree. If one assumes that the birds search all the holes in a tree in which some prey are found, then the optimal strategy is to search a fixed number of holes, k, in each tree, to leave if no prey have been found, and to stay until the end if any prey have been found. If the value of k is too large, then a bird will tend to stay too long in empty patches, while if k is too small a bird will be too likely to leave patches that are really full. If full patches contain exactly n prey, and if proportion α of all patches are full, then the rate of finding prey (per hole searched) is given by $R(k) = EG/[ET + \tau]$, where

$$ET = k + (24 - k)\alpha[1 - \binom{24 - k}{n}/\binom{24}{n}], \text{and}$$

$$EG = \alpha n[1 - \binom{24 - k}{n}/\binom{24}{n}].$$

(8)

I have calculated EG and ET for the case that "full" patches have $n = 12$ prey, and $\alpha = 0.4$, using the value $\tau = 4$, roughly obtained from the data for travel time, and I plot $R(k)$ against k as the upper histogram in Fig. 4. The observed frequencies of leaving empty trees after having searched exactly k empty holes in Lima's experiment are plotted as the bottom histogram in of Fig. 4. One way of interpreting this distribution of k values is to imagine that the birds are using rules of the type: *search exactly k holes in each tree; if no prey have been found leave; otherwise remain until all the holes have been searched—but the value of k used varies randomly from tree to tree.* That is, assume that the forager uses a mixture of pure strategies. Then the expected payoff for such a mixed strategy can be estimated by averaging the payoffs, $R(k)$, over the observed distribution of k. This average rate is plotted as the dotted line in Fig. 4, where it can be compared with solid lines above and below it. The upper line represents the highest possible value of $R(k)$, corresponding to $k = 3$ here, and the lower line corresponds

to a "naive" strategy in which a bird ignores experience in a tree and searches all holes $[R = n\alpha/(24 + \tau) = 0.1714]$.

(Put Fig. 4 about here.)

The birds in Lima's experiment showed variability in the strategy they used—that is, the k value—under the same experimental conditions. One way to interpret this variability of behavior is as a deviation from optimality. The magnitude of this deviation might be measured by the coefficient of variation of the observed k values $[\sigma/\mu = 0.4284]$. Since the mean value of k is not the optimum value, it might be better to use the mean squared-error divided by the optimum value of k. This ratio would be 0.5228. This measure represents a fairly large relative deviation of behavior from the optimum, but a comparison of the average payoff with the optimum [0.2859 *vs.* 0.2953] shows a very small relative difference [3.2%]. This reveals an important point: it is not how much *behavior* differs from the optimum that is important, but how much the *results* of the behavior differ from the optimum. This point is not seen by using qualitative models.

THE FUTURE OF OPTIMAL FORAGING THEORY

Foraging theory has shed light on the food habits of animals, for example, by drawing attention to handling time as a factor affecting the profitability of prey. Most zoologists have been less interested in whether the theory is true than in the insight that is gained by considering the assumptions of the models. Optimal foraging theory offers the prestige of an explicitly mathematical formulation and the attraction of language taken from economics, but these apparent advantages are balanced by the loss of biological insight when economic assumptions replace ecological ones.

I think that an increasing amount of experimental work on foraging animals will focus attention on particular cases. I hope that this will force theorists to pay more attention to particular cases, and this will include paying more attention to the ecological context of foraging. Details revealed by experiments will suggest new theoretical questions, which will enrich the theory—if theorists pay attention. One detail that is important in patch models is the question of how a forager knows it has reached the end of a patch. This question does not arise if foraging is assumed to be random, as is often done, or if search is assumed to be systematic and the forager knows when it has reached the end of a patch, as I assume.[26] However, Baum[35] has shown in an experiment with pigeons that foraging may be systematic but not complete, resulting in a sudden, but unsignalled, decrease in the rate of finding prey. An animal using such a pattern of search has the problem of deciding when the rate of finding prey changes. Another possibility is that patches are large, but that foragers are chased out at some random time (Cowie's "door slamming" hypothesis).[36] As far as I know, these last two cases have not been treated theoretically. Another important detail is the question of whether patches are revisited during a bout of foraging. In Oaten's model, it is assumed that there are many patches and they are not revisited, but in some experiments, patches can be revis-

ited. In these cases, a different theory is required, perhaps one extending the beginning made by Krebs, Kacelnik and Taylor[37] with their two-armed bandit model.

While there are a great number of theoretical ideas about foraging that need developing and testing, I do not think that it is necessary to conduct any more tests of the basic prey and patch models which I have described. I think that we can safely say that foragers offered different types of prey will tend to prefer the most profitable, and foragers searching for prey in patches will tend to be more reluctant to leave patches when the travel time between patches is longer. I think we can say that animals forage nonrandomly, but not perfectly. The question is, can we say more? For example, can we say how good foraging is? We can do so in some cases, as Lima's experiment shows, but to do so we need particular, quantitative models. Foraging behavior is not only of interest to people who study the behavior of individual animals, but it also important in understanding larger-scale ecological questions like competition within and between species and predator-prey relations. A quantitative theory is necessary if we want to apply optimal foraging theory to the study of these higher-level questions. In the predator-prey model of Murdoch and Oaten [25] which I described earlier, there is an explicit expression for the predation rate as a function of prey numbers. As I showed, optimal foraging theory can be used to test whether the conditions for stability are met in this model. One of the points which emerged from this examination is that whether or not the system can be stabilized by optimal foraging depends on how prey distribution varies with varying prey numbers. This point can be seen only be looking at different particular cases.

In their discussion of the uses of optimal foraging theory Stephens and Krebs[12] mention the ecological consequences of foraging, but they conclude that the time has not yet come for the study of such problems because more testing of the models is necessary. I think that this conclusion is wrong on two counts. First, there is no need to do further tests of the generally stated, qualitative models whose truth Stephens and Krebs are concerned with. Second, by paying attention to the consequences of foraging, we can see that a quite different sort of foraging theory is needed, one that pays attention to particular cases and is able to treat them quantitatively. Foraging theorists should ask the question: What good does it do to know that (some) animals forage (approximately) optimally? That is, if the theory is as close to correct as can reasonably be hoped, how can this fact be used? If one has a theory that makes particular assumptions about the environment, and that makes quantitative predictions about the foraging rate, then this theory may be used to study the population consequences of foraging. I think that what we need to do is put ecology back into optimal foraging theory by paying more attention to the context of foraging and its consequences.

Acknowledgments

RICHARD F. GREEN

Department of Mathematics and Statistics

University of Minnesota

Duluth, MN 55812

References

1. R. H. MacArthur and E. R. Pianka, Am. Natur. 100, 603 (1966).

2. J. M. Emlen, Am. Natur. 100, 611 (1966).

3. T. W. Schoener, Ann. Rev. Ecol. Syst. 2, 369 (1971).

4. R. H. MacArthur, *Geographical Ecology* (Harper and Row, New York, 1972).

5. E. L. Charnov, Optimal foraging: some theoretical explorations, Ph. D. thesis, University of Washington, Seattle (1973).

6. E. L. Charnov and G. H. Orians, Optimal foraging: some theoretical explorations, Unpublished manuscript (1973).

7. E. L. Charnov, Am. Natur. 110, 141 (1976).

8. E. L. Charnov, Theor. Pop. Biol. 9, 129 (1976).

9. G. H. Pyke, H. R. Pulliam and E. L. Charnov, Q. Rev. Biol. 52, 137 (1977).

10. M. L. Connons, A. Kacelnik and S. J. Shettleworth (eds.), *Quantitative Analysis of Behavior, Volume VI: Foraging* (Laurence Erlbaum Associates, Hillsdale, New Jersey, 1987).

11. A. C. Kamil, J. R. Krebs and H. R. Pulliam (eds.), *Foraging Behavior* (Plenum Press, New York, 1987).

12. D. W. Stephens and J. R. Krebs, *Foraging Theory* (Princeton University Press, Princeton, New Jersey, 1986).

13. T. W. Schoener, A brief history of optimal foraging ecology, in *Foraging Behavior*, ed. A. C. Kamil, J. R. Krebs and H. R. Pulliam (Plenum Press, New York, 1987) pp. 5-67.

14. J. R. Krebs, D. W. Stephens and W. J. Sutherland, Perspectives in optimal foraging, in *Perspectives in Ornithology,* eds. A. H. Brush and G. A. Clark, Jr. (Cambridge University Press, New York, 1983) pp. 165-216.

15. J. R. Krebs, J. C. Ryan and E. L. Charnov, Anim. Behav. 22, 953 (1974).

16. Y. Iwasa, M. Higashi and N. Yamamura, Am. Natur. 117, 710 (1981).

17. A. Oaten, Theor. Pop. Biol. 12, 263 (1977).

18. D. W. Stephens and E. L. Charnov, Behav. Ecol. Sociobiol. 10, 251 (1982).

19. J. McNamara, Theor. Pop. Biol. 21, 269 (1982).

20. G. H. Pyke, Am. Zool. 18, 739 (1978).

21. R. F. Green, Stochastic models of optimal foraging, in *Foraging Behavior,* ed. A. C. Kamil, J. R. Krebs and H. R. Pulliam (Plenum Press, New York, 1987) pp. 273-302.

22. M. P. Hassell and R. M. May, From individual behaviour to population dynamics, in *The British Ecological Society Symposium, Volume 25: Behavioural Ecology,* ed. R. M. Sibly and R. H. Smith (Blackwell Scientific Publications, Oxford, 1985) pp. 3-32.

23. T. W. Schoener, Am. Zool. 26, 81 (1986).

24. M. P. Hassell and R. M. May, J. Anim. Ecol. 43, 567 (1974).

25. W. W. Murdoch and A. Oaten, Adv. Ecol. Res. 9, 2 (1975).

26. R. F. Green, Theor. Pop. Biol. 18, 244 (1980).

27. R. F. Green, Am. Natur. 123, 30 (1984).

28. R. M. May, J. Anim. Ecol. 47, 833 (1978).

29. P. L. Chesson and W. W. Murdoch, Am. Natur. 127, 696 (1986).

30. R. D. Gray, Faith and foraging: a critique of the "paradigm argument from design," in *Foraging Behavior,* ed. A. C. Kamil, J. R. Krebs, and H. R. Pulliam (Plenum Press, New York, 1987) pp.69-140.

31. G. J. Pierce and J. G. Ollason, Oikos 49, 111 (1987).

32. S. C. Stearns and P. Schmid-Hempel, Oikos 49, 118 (1987).

33. S. L. Lima, Ecology 65, 166 (1984).

34. S. L. Lima, Behav. Ecol. Sociobiol. 16, 135 (1985).

35. W. M. Baum, Random and systematic foraging, experimental studies of depletion and schedules of reinforcement, in *Foraging Behavior,* ed. A. C. Kamil, J. R. Krebs and H. R. Pulliam (Plenum Press, New York, 1987) pp. 587-607.

36. R. J. Cowie, Nature 268, 137 (1977).

37. J. R. Krebs, A. Kacelnik and P. Taylor, Nature 275, 27 (1978).

a)

$g(t) =$ net
energy gain

1

-1.0   .0   1.0   2.0   3.0

$t =$ time in patch

b)

5

4

3

2

1

$g(t) =$ number
of prey found
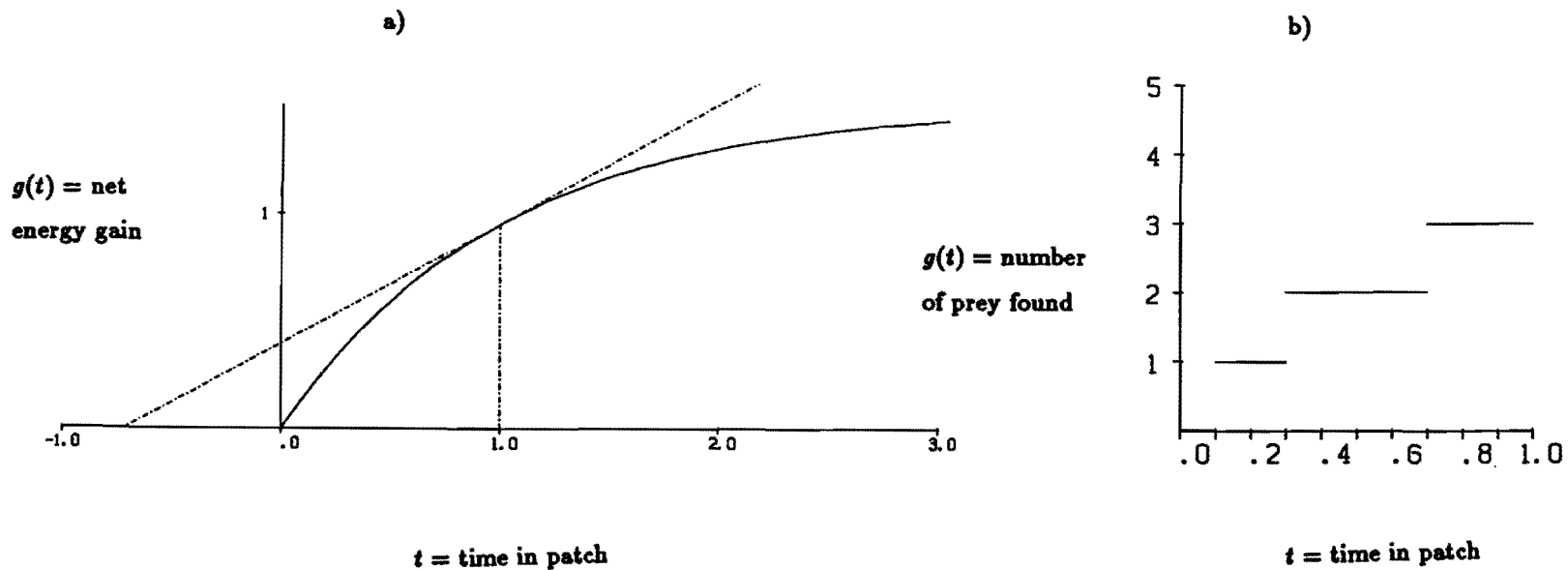
.0 .2 .4 .6 .8 1.0

$t =$ time in patch

FIGURE 1 a) Charnov's marginal value theorem for one patch type. The solid line represents the net energy gain, $g(t)$, as a function of time in a patch. The dotted tangent line from the point $(-\tau, 0)$ touches the gain function when the patch residence time equals t_0, its optimal value. At this point the derivative of the gain function, $g'(t_0)$ [its "marginal value"], equals the maximum possible long-term average rate of energy gain. b) The gain function for a forager that finds discrete prey [which here are found at times $t = 0.1, 0.3$ and 0.7]. In this case, the derivative of the gain function is almost always zero, and Charnov's marginal value theorem does not apply.

a)

E(G) = expected
number of prey
found per patch

.2   .4   .6   .8   1.0

E(T) = expected time in patch

b)

k = number
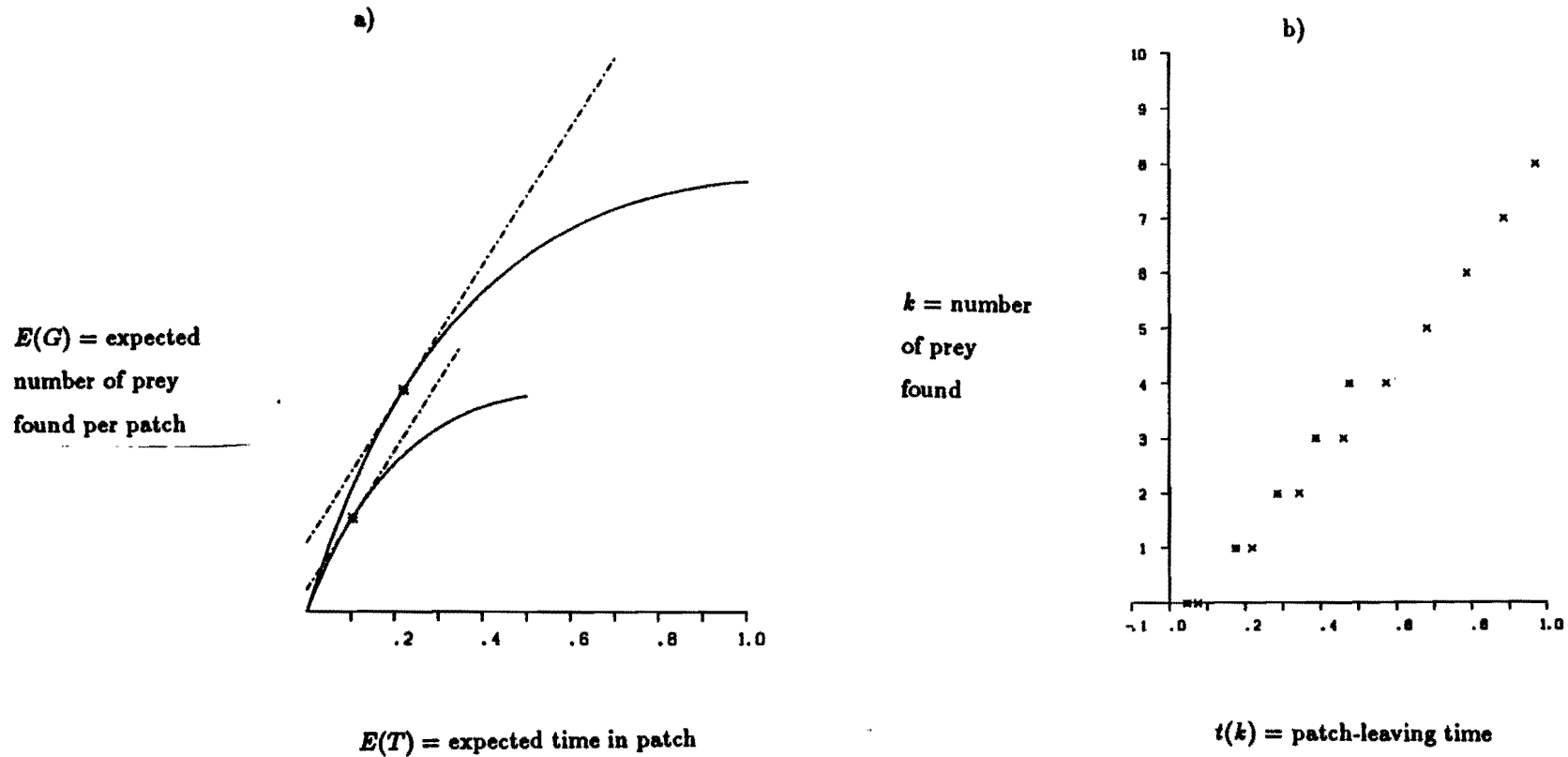of prey
found

t(k) = patch-leaving time

FIGURE 2 a) An analogue of the marginal value theorem for two patch types, one twice
as large as the other, and tending to have twice as many prey. In this case, the expected
number of prey found per patch, $E(G)$, is plotted against the expected time per patch,
$E(T)$, for a number of candidate optimal strategies. The dotted lines are the tangent
lines to the $ET - EG$ curves with slope $R = 8.074$. b) The optimal patch-leaving rules
are of the form: leave a patch at time $t(k)$ if exactly k prey have been found by that
time. Asterisks indicate stopping points for smaller patches, x's for larger patches. For
both patch types, a forager should leave a patch when it has been searched completely
[$t = 0.5$ for small patches, $t = 1.0$ for large patches]. Notice that an optimal forager
should be slightly more reluctant to leave larger patches. For each patch type, the num-
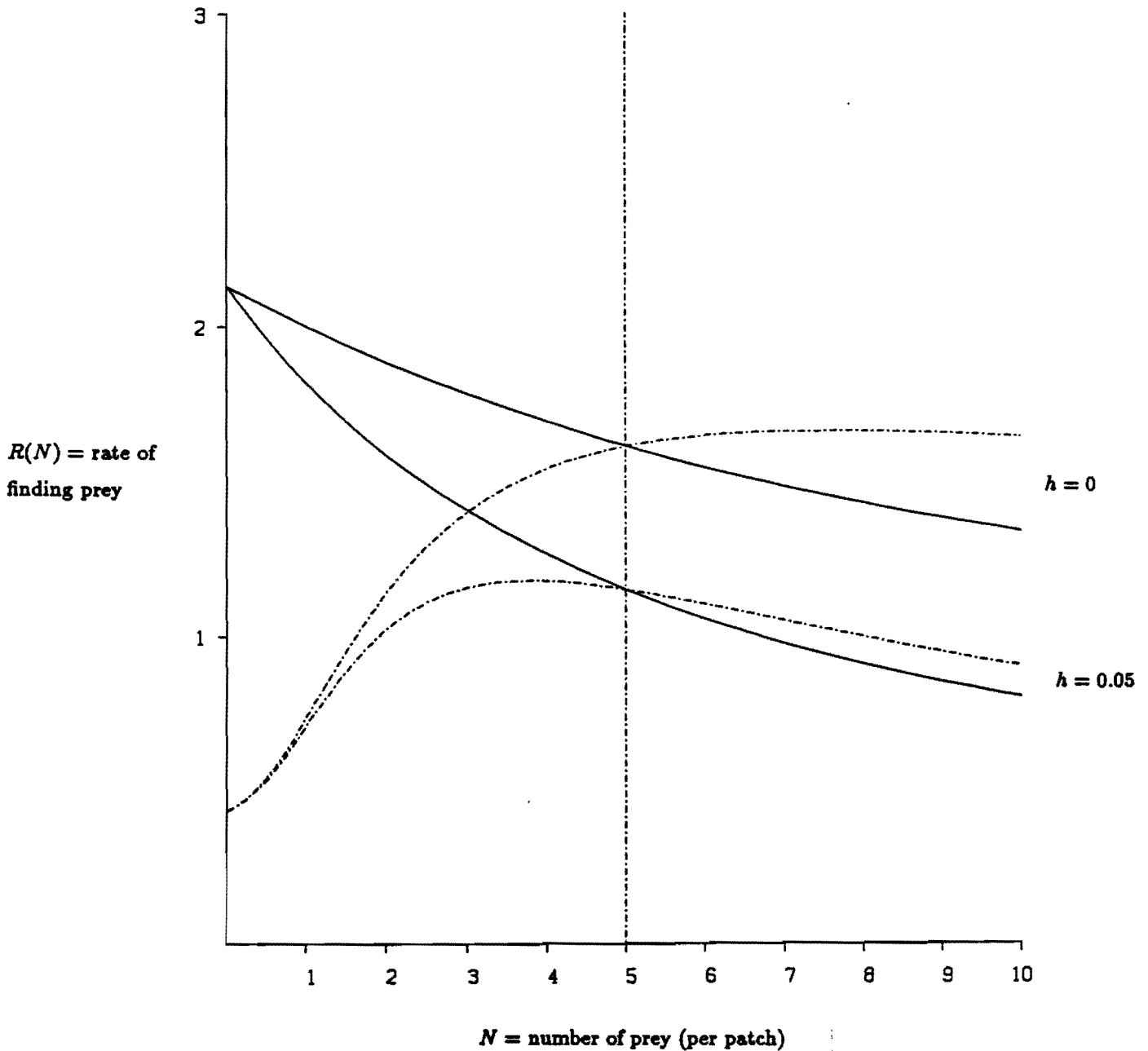ber of prey per patch has a negative binomial distribution.

FIGURE 3 $R(N)/N$, the relative per predator rate of finding prey, plotted against the overall number of prey N. The forager is assumed to use the foraging strategy illustrated in Fig. 2b [x's], which is optimal for a systematic forager when prey distribution is negative binomial with $\alpha = 0.5$ and $\beta = 0.1$, and travel time is $\tau = 0.1$. As prey numbers change, the prey distribution is assumed to change in one of two ways: the negative binomial parameter k [my α] remains constant [solid line], or k is proportional to N [broken line]. The system equilibrium will be stable if $R(N)/N$ is increasing at equilibrium. It is seen that the equilibrium having prey density averaging 5 per patch [for which case the optimal strategy is used] will be stable if k is constant and handling time $h = 0$.
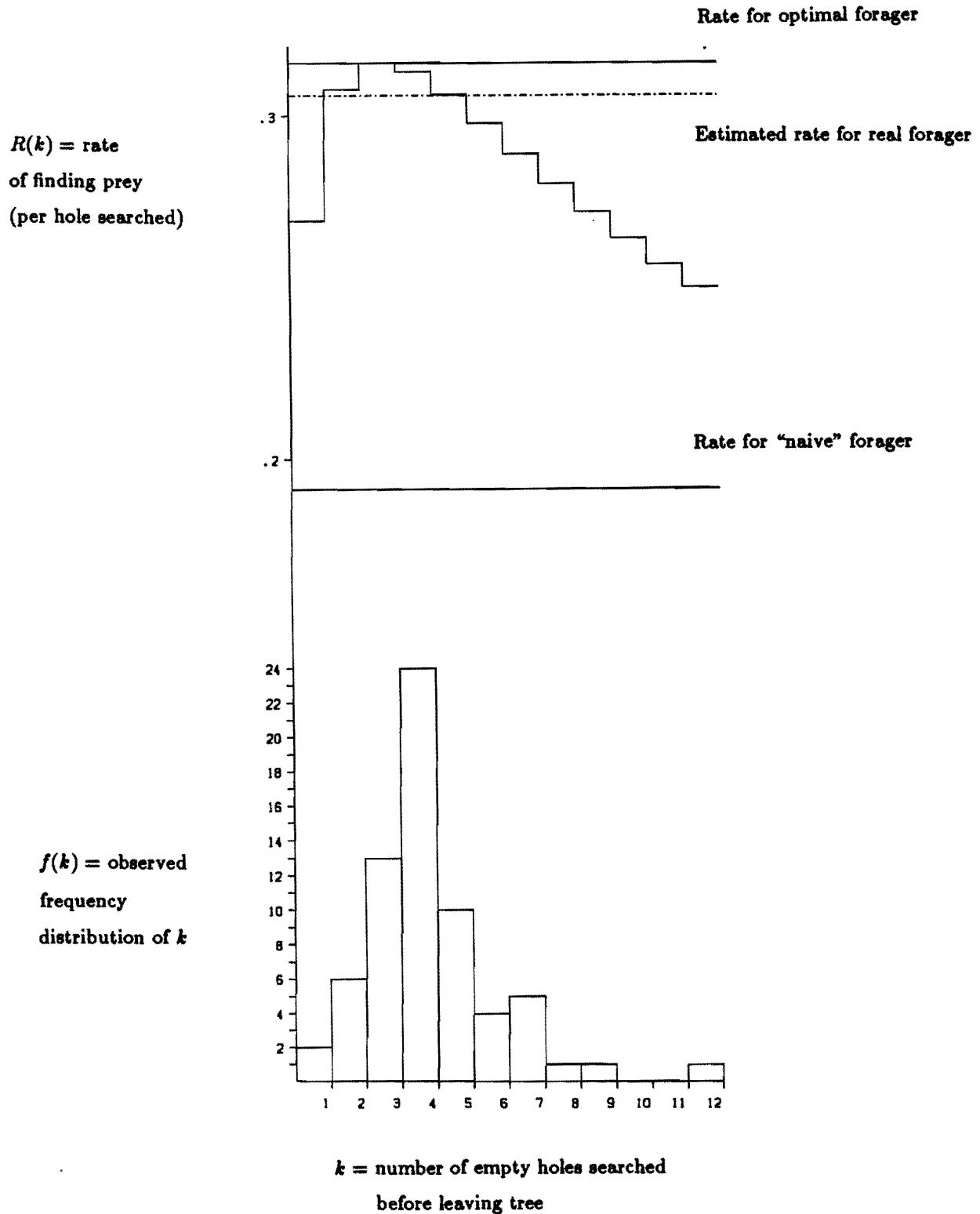
FIGURE 4 Rate of finding prey, $R(k)$, plotted against k, the number of empty holes searched before leaving a tree in Lima's experiment with Downy Woodpeckers. The upper, open histogram represents $R(k)$, while the lower, solid histogram represents the observed distribution of k. Solid horizontal lines represent the rates of finding prey that would be achieved by a "naive" forager [which searches every patch completely, $R = 0.1714$], and an optimal forager [$k = 3$, $R(3) = 0.2953$]. The dotted horizontal line represents the achieved rate [$R = 0.2859$], calculated by averaging the $R(k)$ values shown in the upper histogram, over the distribution shown in the lower histogram.