

A COMMENT ON OPTIMAL FORAGING THEORY

Abstract

Optimal foraging theory is one of the most popular parts of modern evolutionary biology. Much of the attraction of optimal foraging theory is due to its explicitly mathematical approach. However, the full power of mathematical modeling has not been brought to bear on optimal foraging theory. In this paper I will describe some of the ideas of optimal foraging theory and suggest why it is such a popular success, despite some serious failings. I will discuss some criticisms of optimal foraging theory and try to predict what the future holds. In particular, I will try to show how optimal foraging theory might help to bridge the gap between individual behavior and population biology.

INTRODUCTION

In order to evaluate optimal foraging theory it is important to distinguish between its great popular success, which has been the main reason for criticism as well as for enthusiasm, and its limited scientific value in helping to understand foraging behavior. It is also important to distinguish between the relatively small amount of theoretical work on foraging and the large amount of experimental work. Theoretical work generally has been done by one group of people and experimental work by another. Theoretical and experimental papers have tended to be published in different journals, which are read by different people. Most people who have done theoretical work on foraging have published one or two papers on the subject and then gone on to work on different problems. Some of this work is wrong, or has limitations not noticed by its authors, and the fact that the authors were no longer interested and did not correct their mistakes has meant that these mistakes have persisted.

WHAT IS OPTIMAL FORAGING THEORY AND WHY HAS IT BEEN SUCH A POPULAR SUCCESS?

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 theory asks the question in the form: How *should* animals look for and select food? The first papers to ask the question in this way were published in 1966.^{1,2} They and other early papers were mainly about optimal diet. An early review of the subject was written by Schoener,³ and a well-known account was given by MacArthur.⁴ A great impetus was

provided by Charnov, ^{5,6,7,8} 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. Schoener ¹⁰ has written an informative, personal history of the early years of optimal foraging theory. Schoener treats optimal foraging as an ecological theory. The recent book by Stephens and Krebs ¹¹ treats foraging theory as almost exclusively behavioral. I take Schoener’s history ¹⁰ and the book by Stephens and Krebs ¹¹ as statements of the more-or-less established view of what optimal foraging theory is. While I accept these authors’ statements about what the facts and ideas of optimal foraging theory are, I am a good deal less enthusiastic in my assessment of the subject.

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; (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 ¹¹ 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 [(3)], which they refer to as the “patch” problem. Stephens and Krebs ¹¹ ignore problem (4). I will confine myself to problems of diet choice and patch residence-time and will concentrate on the problem of how a forager should decide how long to remain in a patch, which I think is the most interesting problem theoretically.

The basic conclusions of optimal foraging are not very surprising. Generally speaking, the diet model says that, given a choice among a number of types of prey, a forager should choose the better types, while the residence-time model says that a forager should leave a patch when it becomes depleted. These conclusions could be reached without any mathematical theory, but optimal foraging theory goes further and gives rules to decide what type, or types, of prey to take and how far a patch must be depleted before it should be abandoned. The theory goes still further than this, however. It also shows how the choice of prey should change if the density of prey changes in particular ways, and how the length of time to remain in a patch before abandoning it should change if the overall distribution of patch quality changes in particular ways. There has been a great deal of experimental work on optimal foraging theory and most of this work is concerned with these second-order effects—how does behavior change when conditions change?

The popular success of optimal foraging theory.

Judging by the amount of interest in the subject, optimal foraging theory is one of the most popular areas in modern evolutionary biology. Schoener’s review ³ is one of the

most often-cited paper in all of ecology, with 860 citations by last year, ¹² and the more recent review by Pyke, Pulliam and Charnov ⁹ has been cited almost as many times. Stephens and Krebs ¹¹ list over 200 papers attempting to test one or another of the predictions of optimal foraging theory.

The large number of papers testing optimal foraging theory or referring to its ideas do not reflect just interest in the theory itself, but also the fact that many people study food habits of animals. Optimal foraging theory makes this subject more interesting. The mathematical conclusions of optimal foraging theory are used as predictions to be tested. The predictions tested do not always follow from the assumptions, however, and even when they do, experimenters do not always check to see that the assumptions are correct. I have been particularly critical ¹³ of one early paper, ¹⁴ but many more recent papers are subject to the same criticism. I do think that optimal foraging theory has made a significant contribution to natural history by drawing attention to aspects of ecology and behavior that might have been ignored, for example, by encouraging field biologists to pay attention to the food value and handling time of various types of prey. However, simply counting the number of papers that refer to optimal foraging theory would greatly exaggerate its importance.

Criticism of optimal foraging theory.

Optimal foraging theory has received a great deal of criticism, some intended to discredit the subject completely. ^{15,16} The harsher criticisms of optimal foraging theory have been answered, ^{11,17} and I think that the defenders are correct in asserting that, contrary to Pierce and Ollason, ¹⁶ optimal foraging theory is not a "complete waste of time." I do not think, however, that any great enthusiasm is justified. A hard look would reveal that the accomplishments of optimal foraging theory are real, but modest. A reader may get an idea of how limited the accomplishments are by looking at the list (pp. *x-xi*) of discoveries that Stephens and Krebs ¹¹ believe have come directly from optimal foraging theory.

Stephens and Krebs ¹¹ respond in some detail to the criticism of adaptationism leveled by Gould and Lewontin, ¹⁸ who ridicule it as Panglossian optimism. Gould and Lewontin warn that characteristics of animals, including behavior, are subject to developmental and other constraints, and that it is a mistake to view particular characteristics as optimal without taking constraints into account. Gould and Lewontin are not telling foraging theorists anything new. Foraging theorists know that behavior is limited by constraints, but they are not sure what these constraints are.

Some critics (for example, Myers ¹⁹) make it sound as though optimal foraging theory is impossible because the problems faced by animals are too complicated to be represented by simple models, and because even if this were not the case we would not know what these problems are. It seems to me that the critics expect too much of foraging theory, but the reviewers and defenders (Pyke, ²⁰ Stephens and Krebs ¹¹) seem to have similarly exaggerated expectations. The defense seems to be that foragers would be seen

to be optimal if only we knew what they were trying to do. I think that this view is mistaken. We should not expect animals to be perfect.

What I suggest is that we work harder on models, trying to make realistic, biologically meaningful assumptions. It is impractical to try to account for everything in one model, but it is important to consider a variety of models for a particular problem. We should work out the consequences of the models, including a description of the behavior expected and the ecological consequences of that behavior. When a model is tested, it is important to check whether the assumptions of the model are satisfied. If the assumptions are not satisfied the test is not valid. This point is sometimes overlooked by biologists. For example, Stephens and Krebs¹¹ criticize a model of Oaten's²¹ and mine²² because it fails to account for an observation reported by Pyke²³ in a case which our model explicitly ignores. [I think that the model can be extended quite easily to cover the case discussed by Pyke. However, Pyke's treatment contains a statistical error and it is not clear that he has established the fact which Stephens and Krebs want our model to explain.] A model does not fail because it does not apply in all cases. It is a misunderstanding of theory to expect it to do so. I sometimes tell math students that the answer to a question depends on the question. Biologists should be aware of this as well.

MY VIEW OF OPTIMAL FORAGING THEORY

The argument between the supporters of optimal foraging theory and its critics is largely over observations. I do not know how this argument will be resolved. One thing is clear: optimal foraging theory has not made full use of the power of mathematical modeling. Mathematical models are useful for two reasons. First, they require explicit assumptions, and the effort to formulate these assumptions draws attention to the details of the situation being modeled. Second, a mathematical formulation may permit the use of powerful mathematical tools that reveal conclusions not otherwise apparent. I will try to show that it is possible to use the power of modeling by describing a model that makes ecological assumptions and that permits the quantitative treatment of particular cases.

I think that optimal foraging theory is in an early stage of development, and that it is not as important to worry about imperfections in the theory as it is to ask whether the subject is interesting and useful. Animals must eat, and this is important to them and to their food, but this fact is not interesting in itself. If one could explain all feeding behavior in one simple theory this would be worthwhile, but any attempt to find such a theory is doomed by the complexity of the data. I do not think that the goal of optimal foraging theory is to understand how animals forage. It is important to understand foraging behavior only insofar as this helps us understand larger questions (in population and community ecology) or smaller ones (in learning theory). I am interested in the ecological consequences of foraging. Stephens and Krebs¹¹ list the ecological consequences of foraging as one of the problems that foraging theory could solve, but they suggest that people should wait until foraging models have been tested more thoroughly. After hundred of tests of a handful of ideas it is not clear how much longer they

would have us wait. My opinion is that the economic approach championed by Stephens and Krebs is ill-suited to the study of the ecological consequences of foraging, and the sooner these consequences are considered seriously the sooner will the deficiencies of the economic approach become clear. I will describe my own model, a version of Oaten's ²¹ general stochastic model for the patch residence-time problem, which can be used to study the consequences of foraging behavior.

A stochastic model of optimal foraging

I assume that prey are located in patches, with the number of prey per patch being a random variable with a specified distribution. A forager searches a patch in some pattern (randomly or systematically) and decides when to leave one patch and go on to another based on the success that it has had in the present patch. I find the strategy which maximizes the long-term average rate of finding prey and compare the rate achieved by an optimal forager with the rate that would be achieved by foragers using other strategies that have been suggested.

This is only one approach to one problem, but it does have several advantages. My treatment is stochastic, it describes the foraging problem in terms of the environment, and it uses particular cases which permit a quantitative treatment of the ecological consequences of foraging behavior. I will discuss these advantages one at a time.

The model is stochastic, it takes account of the variability in patch quality. This is a biologically important consideration. Charnov's ⁸ treatment of the residence-time problem, solved by his famous "marginal-value theorem," is deterministic. Charnov ⁸ claimed that his results could be extended to a stochastic case, but this claim applied to variability in capture times within patches, and not to variability in quality among patches. My model takes account of variability within and among patches, but it does not treat long-term changes in prey distribution in the environment. This is an important problem which has not been treated satisfactorily. I think that any successful treatment of this problem of higher-level variability must take into account lower-level variability as well.

In specifying the problem that an animal faces, my model includes an explicit representation of the environment, given in terms of the distribution of prey in patches. This is important because the form of the optimal foraging strategy depends on the prey distribution (Iwasa *et al.*,²⁴ Green ¹³). The early paper by Krebs, Ryan and Charnov ¹⁴ was important for suggesting an experimental test of optimal foraging theory, but the authors failed to specify the problem that the forager had to solve, and they also failed to work out the theory properly. Part of the problem lies in the use of an economic approach, most recently advocated by Stephens and Krebs, that begins with a "gain function," which is the number of prey found, or the net energy intake, represented as a function of the length of time in a patch. This economic approach begs the ecological question of how prey are distributed and the behavioral question of how the gain function depends on the animal's pattern of search. In my approach this gain function,

which would be a stochastic process, can be understood in terms of explicit ecological and behavioral assumptions. The experimental psychologists' "reinforcement schedule" plays the same role as the gain function, but the reinforcement schedule *does depend* on the animal's behavior. Neither the economic approach, using a gain function, nor the psychological approach, using a reinforcement schedule, requires a description of the environment. Use of an economic approach may add the prestige of a field with a well-developed mathematical theory, and at the same time avoid the calculations required of an approach using explicit ecological and behavioral assumptions, but this approach leads to a theory that is, at best, uninteresting ecologically, and at worst, wrong mathematically.

My model uses particular cases which can be treated quantitatively, revealing behavioral and ecological consequences of optimal foraging. I think that the best general theoretical work on the residence-problem—the papers by Oaten ²¹ and McNamara ²⁵—is too general to be of any immediate use to biologists. What I have done is add simplifying assumptions to make the model of Oaten tractable and find optimal foraging strategies using a method which is equivalent, in the cases I study, to that proposed by McNamara. ²⁵ Generality is no advantage if cases with important differences cannot be treated separately. However, Oaten's model is general in that it encompasses many models as special cases, and it is possible to treat these different cases separately. I have shown ^{13,22} that in some particular cases, chosen to be biologically plausible, the form of the optimal foraging strategy is quite simple, perhaps simple enough to expect that an animal might use it.

Once an optimal foraging strategy is found, the rate of finding prey may not be very sensitive to moderate changes in the rule used, as long as the rule is of the right general type. I think that it is important to be able to distinguish between differences in behavior on the one hand, and the differences in the consequences of the behavior (here I have in mind the rate of finding prey achieved by an animal using the behavior) on the other. This distinction is sometimes ignored. For example, the "classical"²⁶ approach to optimal foraging theory did not permit a comparison of the consequences of different strategies, and this led to some confusion. In particular, one model of prey choice leads to the conclusion that optimal foragers should either specialize or generalize completely, and should never prefer one prey but sometimes, not always, take another. Unfortunately for the theory, animals do show "partial preferences," and this has caused some consternation,²⁰ leading one critic ¹⁵ to go so far as to say that optimal foraging theory should be rejected, partly on this ground. A variety of explanations for partial preferences have been proposed (see, for example, Krebs and McCleery ²⁷) but no one seems to have asked the question: How much better is it to use a pure strategy than to show a partial preference? Since their theory was only qualitative, early theorists were not in the position to answer such a question. This qualitative theory asks what the optimal behavior looks like, but not whether it is enough better than any other behavior to matter to an animal.

There are a number of ecological implications of foraging theory: for example, at

the same average prey density but different levels of prey aggregation, an optimal forager can find prey faster (sometimes much faster) when prey are aggregated. The ecological consequence of foraging that interests me most is the functional response of predation rate to overall prey density. The form of the functional response is important in determining whether a predator-prey system is stable. Murdoch and Oaten²⁸ investigated the effect of foraging on functional response, in particular, on the patterns of change of prey distribution that would permit the functional response to be stabilizing in a particular predator-prey model. They found that, for several patterns of changing prey distribution, the rate of finding prey achieved by a predator using a fixed foraging strategy would increase fast enough with overall prey density to stabilize the system. I think that Murdoch and Oaten's results were, to some extent, an artifact of their choice of strategy. (They chose a strategy which was suboptimal in each case, but which was relatively worse at low overall prey density, thus permitting a relatively greater increase in rate as density increased than an optimal forager would show.) I do think that the approach used by Murdoch and Oaten is worth following, but their treatment can be improved.

There have been several recent exhortations^{29,30} to ecologists to try to use individual behavior to understand population ecology. There certainly is a gap between behavioral ecology on one hand and population ecology on the other. I think that this gap is due to the nature of behavioral ecology, which is basically the study of behavior in an ecological context. I think that the ecological context sometimes is forgotten. On the other hand, most models of population ecology that take predation rate into account bypass any consideration of foraging behavior and *begin* by assuming that the predation rate has some specified functional form. An exception is the model of Comins and Hassell³¹ which does incorporate foraging behavior, but does so in a biologically unrealistic way, assuming that parasites are omniscient and go to whichever site has the most hosts.

How should optimal foraging be tested?

In order to test a behavioral model it is important to work out the model theoretically, to determine what behavior is optimal, and to consider alternative behaviors and their value relative to the best. This is not always done because some tests of optimal foraging theory are of qualitative hypotheses. For example, if there are fewer good prey available, foragers should settle for poorer prey than when more good prey are available. If travel time between patches is longer, foragers should spend longer in each patch. Such hypotheses can hardly fail to be true, and they are usually confirmed. Other, more interesting, hypotheses have been tested, for example, the idea that a forager might use a "giving-up-time" rule to decide when to leave a patch. It has been claimed a couple of times^{14,32} that evidence supports this hypothesis, but in neither case did the authors look at their data properly to test the hypothesis. Not only should the optimal behavior be determined theoretically, but methods should be devised to test predictions statistically.

I doubt that anyone expects animals to be optimal in any way that can be simply and precisely stated. On the other hand, in the life of each animal there is probably

some time when it is important to be able to choose the best prey or to be able to find prey as rapidly as possible. What I expect is that if one strategy is substantially better than another, and if the better strategy is simple enough that an animal might be expected to use it, then the animal will use the better strategy. Most work on optimal foraging theory is concerned with the optimum, but not with how much better the optimum is than various alternatives. For example, in a test of a model much like one of mine, Lima³³ concluded that agreement with predicted behavior was good qualitatively, but not quantitatively. Woodpeckers showed behavior that looked like the optimal on average, but they showed some variation about the optimal. If one used the coefficient of variation as a measure of the deviation from the optimal behavior then the deviation from the mean was about 20 or 30%. But if one compared the maximum possible rate of finding prey and the rate achieved by a variable strategy such as that observed, then the difference was only about 3 or 4%. It is this second difference that we should look at, not the first.

CONCLUSION

It is enjoyable developing mathematical models in behavior and ecology. Mathematicians and statisticians will want to work on these problems if they are interesting mathematically and statistically, as I think some are. However, this work will be more useful if biologists are in a position to insist on the relevance of the work. This would be easier if they knew exactly what problems they wanted solved. It will not be much good to anyone if a great deal of modeling is done that owes its mathematical rigor to biology and its biological relevance to mathematics.

Behavioral experiments will be done as long as people are interested in the animals and behavior studied, whether the theory that the experiments are nominally designed to test is trivial or profound, whether it has many implications in other fields or few. It would be better to test non-trivial, relevant theory. The much-heralded interaction between behavioral ecologists and experimental psychologists will be a good thing if ecologically meaningful questions are studied in carefully controlled experiments. It would be a bad thing if the two groups simply exchange bad habits and combine "just so" stories about adaptation with carefully described observations from biologically irrelevant experiments.

The current direction of theoretical work on foraging is to treat an increasing variety of problems, with each problem treated superficially. One, or a few, examples, each biologically unrealistic, are considered for each problem. Foraging problems will be increasingly joined with other problems, such as predator avoidance, for joint treatment. This will be a good thing if the individual flavor of each problem is retained when the problems are treated together, but this does not seem to be happening. Mangel and Clark³⁴ have written a paper titled, "Toward a unified foraging theory," that proposes a framework for the simultaneous treatment of a number of behavioral problems, including foraging, but their treatment leaves no place for any real question about foraging.

The problem is that their treatment requires a common currency for different behaviors, and such a currency generally cannot be found. Instead of treating problems which have their own intrinsic interest, this approach requires treatment of problems chosen on the basis of their theoretical simplicity. I do not think that there is any value in an increasingly superficial treatment of an increasing variety of problems. I think that most of the early theoretical work in foraging was done by clever people who were good at having ideas, but were not interested in working the ideas out mathematically or testing them experimentally. I do not think that the early ideas of optimal foraging theory were developed in order to solve any important biological problems. I think that what optimal foraging needs most are some problems that are worth solving and some people who want to solve them.

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