

## **THE FUTURE OF OPTIMAL FORAGING THEORY—IN 1990**

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### **INTRODUCTION: A FIVE-MINUTE HISTORY OF OPTIMAL FORAGING THEORY**

The history of optimal foraging theory consists of two ten-year periods. The first, from 1966 to about 1976, was a period of development. The second period, from about 1976 to about 1986, was the heyday of the theory. The beginnings and endings of these periods were marked by the publication of important papers.

Optimal foraging theory began with two papers, published back-to-back in the November-December 1966 issue of *The American Naturalist*. One, by MacArthur and Pianka, considered how the optimal choice of prey and foraging location would affect the niche breadth of the forager. The other, by Emlen, developed an explicit mathematical model to predict the diet of a forager offered a choice of prey. Both of these early papers, and some that were soon to follow, were written by mathematically-inclined ecologists who wanted to use foraging behavior in order to understand ecological questions.

The mathematical treatment of foraging in the earliest papers was rather crude, but as time went on, clearer and more explicit models were developed, for example, with Pulliam (1974) offering a model of problem of prey choice, and Charnov (1976a, b) modeling prey choice and patch residence time. The basic theory was firmly established and known to all with the 1976 papers by Charnov and the review by Pyke, Pulliam and Charnov (1977), who listed four problems facing a forager: (1) which prey to take, and if prey are distributed in patches, (2) which patches to search, (3) how long to remain in a patch, and (4) how to move, within and among patches. Krebs (1978) wrote a paper on foraging for the first edition of the collection of papers, "Behavioural Ecology," edited by Krebs and Davies (1978).

During the heyday of optimal foraging theory there were many tests of the qualitative predictions made by the basic models of prey choice and patch residence time. Much of this work was summarized in the review by Krebs, Stephens and Sutherland (1983) and in the ninth chapter of the definitive treatment of foraging theory by Stephens and Krebs (1986). This work was in the spirit of behavioral ecology as expounded by Krebs and Davies (1978) and their colleagues. The idea is that animals face problems, which they solve by using strategies that can be understood in evolutionary terms. Mathematical models of behavior yield predictions that can be tested by using experimental methods similar to those used by experimental psychologists.

During the late 1970s and early 1980s there was work modifying the assumptions of the basic models to make them more realistic biologically—for example, by assuming

that prey could not be identified perfectly, or without cost—and a number of other problems were considered, including central-place foraging, risk-sensitive behavior and group foraging. The effect of these changes was not to refine the basic, early models, but to diversify the subject.

There are three very well-known reviews of optimal foraging theory. The first, by Schoener (1971) described the emerging subject, which was still basically ecological. The second, by Pyke, Pulliam and Charnov (1977), described some attractive models that appealed to the authors, and, it turned out, to many other workers. Their emphasis was more on behavior than ecology. The third review was the book by Stephens and Krebs (1986), which concentrated on theoretical models and neglected ecology and behavior, except insofar as behavioral experiments had been used to test the theory. Stephens and Krebs said that they believed that the theory needed more testing before it could be applied safely to ecology. [It is interesting that the three major reviews of the subject have about 200, 100 and 400 references, respectively, but there are only two works that they cite in common, the two *American Naturalist* papers of 1966.]

The main line of the story of optimal foraging theory is the story of a small set of ecological problems that were offered mathematical solutions, which proved attractive to practitioners of the new field of behavioral ecology. The optimal foraging approach helped to organize observations that might be made anyway, but the ideas being tested were not very interesting in themselves, and eventually interest in the theory declined.

However, at the same time there were other lines of work on foraging. Two lines were behavioral, one based on ethology (Curio 1976, Bell 1991) and the other on psychology (Kamil and Sargent 1981; Kamil, Krebs and Pulliam 1987; Commons, Kacelnik and Shettleworth 1987). Another line was in population ecology (Hassell and May 1974; Murdoch and Oaten 1975). There is still some interest in optimal foraging theory in the sense of Stephens and Krebs (1986), but as Table 1 shows, there are many more references to “foraging behavior” or “foraging behaviour” than to “optimal foraging,” “optimal foraging theory,” and “foraging theory” in the recent literature, suggesting that a more-or-less theory-free approach to foraging is now more popular than optimal foraging theory. There is also interest in the use of individual behavior to understand population ecology, for example, by assuming that foragers distribute themselves in an “ideal free distribution,” or by using “individual-based” models; but these approaches do not use optimal foraging theory as far as I can see.

## **TWO PAPERS ON THE FUTURE OF OPTIMAL FORAGING THEORY AND ONE PAPER ON AN ALTERNATIVE POINT OF VIEW**

In 1990 David Stephens and I each published a paper discussing optimal foraging theory as it appeared to us at the time and made some suggestions about what the future might hold. These two papers were similar in some ways. Both papers summarized the basic models of optimal foraging theory, and both emphasized the importance of connecting foraging models in ecology. Both papers paid special attention to stochastic models, but they considered different aspects of stochasticity, with Stephens (1990)

considering risk, and risk-sensitive foraging, while Green (1990) considered information use, as described in Oaten's (1977) model.

These two papers (Green 1990; Stephens 1990) were different in the ways that they visualized modeling, and in the ways that they viewed the connection between foraging and other areas of behavior and ecology. Stephens visualized modeling in terms of three classes of assumptions: decision assumptions, currency assumptions and constraint assumptions, while Green visualized modeling in terms of (ecological) problems that animals face, the behavior that they might or that they do use to solve those problems, and the (ecological) consequences of that behavior. Stephens viewed the connection between work on foraging theory and work on other subjects in terms of the disciplines of the people doing the work, for example, psychologists who could study foraging behavior experimentally, and ecologists who could combine ecological questions, like predator avoidance, with questions about foraging. Green, on the other hand, concentrating on ecology, looked at the problems that foragers face, for example, how prey are distributed, and the consequences of foraging, for example, whether optimal foraging might stabilize a predator-prey model, as ecological questions. While there was substantial agreement over substance—the idea that optimal foraging theory should be studied more broadly—there was a difference in point of view, between looking at who should ask the questions and what questions should be asked.

### **Green (1990): “Putting ecology back into optimal foraging theory”**

The paper by Green (1990) was an invited contribution to a new (and now defunct) journal, *Comments of Theoretical Biology*. The point of this paper was to criticize the more-or-less ecology-free approach to foraging theory offered by Stephens and Krebs (1986) in their definitive treatment of the subject. Stephens and Krebs had paid little attention to the ecological context in which foraging takes place, and they explicitly rejected attempts to apply foraging theory to population ecology, because more experiments still needed to be done to see if the theory was correct. The first draft of the Green paper was basically a statement of personal opinion about foraging theory. One reviewer said that it was the “most childish paper” that he or she had ever read. The revision that was eventually published was much more constructive, containing three substantive examples, one of which had been suggested to me years before by Stephens.

The most important example in Green (1990) showed that optimal foraging might stabilize a predator-prey system if prey are aggregated, but only for certain patterns of change in the prey distribution as overall prey density is changed by foraging. This example shows that the problem that a forager faces, and the behavior that the forager uses to solve that problem, have consequences that are important for populations. One might guess this without foraging theory, but to work out the details, and to do it correctly, requires theory.

The point of my paper (Green 1990) was to argue that people who think about optimal foraging theory should pay more attention to ecology, both in defining the problems that foragers face, but in studying the consequences of foraging behavior. The point of

studying foraging is to understand how animals forage well enough to use that understanding in dealing with other problems, including predator-prey dynamics. I tried to advocate the quantitative treatment of particular models. I did not deal with how people do foraging experiments in my 1990 paper. However, I sent a copy of that paper to George Barlow, who suggested that I write a commentary piece for *Ethology*, making a similar argument that foraging theory could be improved by paying more attention to behavioral issues like those studied by ethologists (such as species-specific behavior). Eventually, such a paper was submitted to *Ethology* and was accepted subject to revision. Unfortunately, it was never revised, and therefore never published.

In my *Ethology* manuscript I made three points which I had made about foraging experiments in a talk I gave at Oxford in 1983 (where I finally described the work that I had started there in 1978). People who do foraging experiments should ask themselves: (1) Am I setting a realistic problem? (2) Is the animal answering the same question that I am asking? (3) Does it matter what the animals do? When I finally wrote my *Ethology* manuscript around 1994 I was able to cite papers whose authors had failed to ask one of those questions (or who did not care that the answer was “no”). One of the papers that I chose as a bad example for my *Ethology* manuscript was used as a good example by Stephens (1990).

In my 1990 paper and my *Ethology* manuscript together, I make two of the three points that Stephens (1990) makes, that workers on foraging should look both up and down in a disciplinary sense.

### **Stephens (1990): “Foraging theory: up, down and sideways.”**

In 1990, David Stephens, coauthor with John Krebs of the best-known review of foraging theory (Stephens and Krebs 1986), published a paper, which he began with the statement:

In this paper I discuss current and future directions for foraging theory. I pay special attention to directions that empiricists might follow most profitably. (p. 444)

I think that this is a worthy aim.

Stephens continued by objecting to the use of the name “optimal foraging” for what he prefers to call “foraging theory.” He gave two reasons for his objection. (1) “Optimal foraging” may be read to indicate that there is a single best way to forage. [In many cases such a reading could be correct, but a proper understanding of the theory suggests a comparison between the best and other ways to forage.] (2) Other factors (perception, development of behavior) may be important in understanding foraging and the use of the name “optimal foraging” may lead to the belief that these factors can be ignored. [In a way, what Stephens is saying is that using the term “optimal foraging” may lead readers to be stupid. I don’t think that one term is much more likely than another to lead readers to be stupid.]

In a sense, the term “foraging theory” is a more accurate description of models of foraging than “optimal foraging theory” because many of the rules that have been considered are not optimal, but I think that Stephens has another reason for “foraging behavior.” In their book, “Foraging Theory,” Stephens and Krebs (1986) explain the reason for their choice of a title. A colleague [Gordon Orians] observed that when he talked about “optimal foraging” his audiences were likely to react with hostility, but they were not hostile if he used the less charged term, “foraging theory.” However, in arguing for their approach, Stephens and Krebs include examples that use optimization but do not involve foraging. That is, it is optimization that they want to sell, even though for political reasons they choose a title that is non-provocative.

I prefer the term “optimal foraging” to “foraging theory.” Most other authors have the same preference, as may be seen from the frequencies of use of the terms as tallied in the Web of Science (see my Table 1). Insofar as the terms “optimal foraging” and “foraging theory” are descriptive and suggest a real difference in meaning, I prefer “optimal foraging,” because it points to the fact that optimal strategies are found or desired, while “foraging theory,” might (properly) be used for modeling that does not lead to optimal strategies. I think that some important work on foraging and population ecology by well-known workers was flawed because it did not use optimal foraging.

After his argument about the name of his subject, with which I disagree, Stephens states the main goals of his paper, with which I agree:

This paper, reflective of my own biases and interests, is about how empiricists can most effectively influence foraging theory and foraging theorists. I would like to encourage others to do the kind of work that would tell foraging theorists what kinds of new models and new ideas are necessary to build a more accurate and general body of theory. My second motive is answering a question I am often asked: “Where is foraging theory going?” The title reflects the whimsical answer that I usually give to this question. I think that foraging theory is going in three directions—up, down, and sideways. I think students of foraging must go *sideways* by pursuing those questions they have traditionally asked: They must continue to ask evolutionarily motivated questions about the costs and benefits of, and constraints on, the foraging behavior of individuals. Students of foraging theory also find themselves stepping *down* one level of organization to ask questions about the mechanisms of foraging behavior. Moreover, many students of foraging theory have as their eventual goal stepping *up* one level of organization by using an understanding of foraging behavior to deduce things about population and community dynamics. (p. 444)

Stephens (1990) breaks the body of his paper into three parts, corresponding to the three directions that he saw for foraging theory to go.

### **Sideways**

It is not perfectly clear what Stephens (1990) means by saying that foraging theory might go sideways. Roughly speaking, he seems to mean that foraging theory might develop by considering different sets of assumptions. Stephens begins by discussing the encouraging aspects of foraging theory. On the empirical side, he lists the success of the simplest predictions of the two basic models that “the time spent exploiting a depleting patch should increase as the time required to travel between patches increases” (p. 446) and that “foragers selectively attack prey items that are most profitable.” On the conceptual side, foraging theory changed the way that students think about foraging.

Two examples are given of discouragement. Both examples are relevant to the assumption that optimal foragers should maximize the long-term average rate of finding prey (or of net energy intake). Both examples are based on empirical observations. One is risk-sensitive behavior. If foragers are offered two different reward schedules, both with the same average rate of return, but with one schedule more variable than the other, then foragers tend to prefer the less variable schedule if they are being well fed, but they prefer the more variable schedule if they are being starved.

The other example is the preference for immediacy. When offered different schedules, some animals prefer schedules that are more likely to return a reward quickly, even though the alternative schedules are no worse in the long run.

Risk-sensitive behavior and the preference for immediate rewards are certainly interesting phenomena, especially to psychologists. It is not clear to me what natural conditions, if any, are being mimicked in the experiments. In my (theoretical) work, variability may have an effect on the rate of finding prey, with foragers sometimes able to find prey faster when patches are more variable, even when the average prey density is the same (Green 1980, 1997a), while in one example of central-place foraging foragers find prey at a slower rate when the environment is more variable (Green and Nunez 1987). It is certainly possible that offering foragers different reward schedules with the same average but different amounts of variability is unnatural.

Caraco and Gillespie (1987) developed a model based on risk to interpret the decisions of orb-web spiders about whether to move the location of their webs. The idea was that spiders could choose between two strategies, to remain at one site, or to move independently of success at the current site, to another site. Moving would result in averaging over sites and would decrease the variability in reward, while maintaining the same overall rate as remaining in the same site. The prediction was that spiders should move if the environment is good and stay if the environment is bad, because the ration would be sufficient under good conditions and risk-averse behavior (moving) would then be favored, while under bad conditions, it would be better to remain, because then the ration would be bad and the spider should be risk-prone. Using the same model as Caraco and Gillespie, I showed (Green 1987b) a spider that simply remained in a site when it found a prey there and left a site where it found no prey would achieve a much higher average success rate than spiders using either of the alternatives considered by Caraco and Gillespie. My paper was rejected by *Ecology* (I did not find the optimal rule that spiders should use, I just found a simple rule that was better than those considered by

Caraco and Gillespie), but my vigorous response to the referees' comments led to the invitation to write the paper (Green 1990) that I mentioned in above.

I think that it is clear that animals do not always maximize the long-term average rate of finding prey. An animal that starves today in order to get a big meal tomorrow is still dead. On the other hand, an animal that has to avoid starvation today might do better to find prey at a high rate today. I do not think that models which assume that foragers choose between alternatives that are equally good, on average, are very realistic. Certainly they are not general.

Psychological experiments provide a rich source of facts about animal feeding behavior. These facts would be a useful part of a broad theory of feeding behavior, but at least two other things are needed for this theory. One is an understanding of how the behavior observed in the laboratory corresponds to behavior that might be found in nature. The other is that a model should be developed that shows the connection between the problem that the animal faces and the behavior that it shows. Stephens makes a good point when he says that thinking about foraging theory helped students understand foraging behavior, but gaining this understanding once or twice is not enough. Students of foraging behavior should be persistent in their use of foraging theory to understand what they are observing.

## **Down**

Under the heading of "down" Stephens (1990) has two ideas in mind. One idea is to think about mechanisms that foragers use to solve problems and the other is to think about work that psychologists do. Stephens gives two examples, both of which could be said to involve learning. In each case there is a choice between two patches, in each of which reward schedules may change. The difference is in how the schedules change.

The first example involves patch choice. One patch is sometimes good and sometimes bad. The other patch is always mediocre. If a good session in the variable patch is likely to be followed by another good session, foragers learn this and stay for another session, but when a session is bad, the forager may switch to the mediocre choice. If good and bad sessions alternate unpredictably, the forager uses stereotyped behavior, concentrating its search in the variable patch or in the fixed patch, whichever is better.

In another experiment, Blue jays were offered a choice between a patch that was good to begin with and then became bad, and a mediocre patch. The problem for the forager was to decide when the good-bad patch had become bad. Foragers moved from the good-bad patch after a run of bad luck there, but the rule that the foragers used is not of a simple form.

While the problem is different, the behavior to be analyzed in this experiment resembles that which was studied by Haccou et al. (1989) in their studies of parasitic wasps. The parasitoids foraging in a patch of hosts, leaving after going some time without having encountered a host. Haccou and her colleagues used reliability theory to

analyze the probability of leaving a patch of hosts as a function of the time since the previous host was encountered.

## Up

By up Stephens (1990) refers to problems in population or community ecology, which foraging theory might help solve. Stephens distinguishes between two ways to combine foraging theory and ecology. One of these ways he calls, “separate but equal,” and the other he calls the “integrated approach.”

By “separate but equal” Stephens means that foraging is used to solve a fixed problem from ecology, such as determining the “functional response” of predator foraging success to prey density. The problem of how to use foraging theory to determine functional response had been treated before, perhaps most famously by Hassell and May (1974) and by Mucdoch and Oaten (1975). However, this earlier work was flawed by the fact that the optimal foraging strategies had not been worked out at that time. By the time Stephens wrote, the theory was available, but he did use it but instead referred to a model of Getty using signal detection theory to distinguish between mimics. This, it seems to me, was quite a different problem than was considered earlier.

By the “integrated approach” Stephens means treating a problem as a whole with foraging theory coming in only as needed, and perhaps being designed for the occasion. Stephens gives as an example the work of Earl Werner and his colleagues, who studied the foraging of bluegill sunfish in the presence or absence of their predator, the largemouthed bass. In the absence of their predator, small sunfish feed in open water, where there is more prey, but in the presence of their predator they forage under cover, where there are fewer prey, but it is safer. Larger sunfish that are not subject to attack of the predator search wherever there is more prey. This is, indeed, exemplary work, but Stephens does not make it clear how foraging theory comes in. There is more to the story than Stephens can include in a short paper, including the fact that risk in the sense of danger from predators, is sometimes traded off against the need for food in hungry fish.

Near the end of his paper, Stephens (1990) contrasts the ecological approach to modeling, which he described as “descriptive,” with the approach of foraging theory, which he says is “explanatory.” I don’t think that this is a useful distinction. Behavioral ecology in general and foraging theory in particular use functional explanations, but it seems to me that a useful goal of foraging theory would be to characterize (describe in detail) foraging behavior in particular cases. Perhaps the difference between my point of view and that of Stephens is that I think of foraging “models,” which are mathematical representations of a problem that an animal faces and a solution to the problem, while Stephens thinks about foraging “theory” as a body of facts and ideas that include not only mathematical models and their solutions but also all the biological and psychological knowledge that is relevant to foraging.

Stephens refers to his “cautious approach” to applying foraging theory to ecological problems. In a way, this cautious approach is an advance on the position taken by

Stephens and Krebs (1986) who said that foraging theory should not be applied to ecological problems until it had been tested further. I would go much further than Stephens' cautious approach. Ecologists will do population modeling whether or not they understand foraging theory. If they don't know how to do the modeling correctly, they will probably do it incorrectly. I don't see what it will hurt to try to use foraging theory. In fact, foraging theory might have developed more and be better if behavioral ecologists had paid more attention to population ecology.

Stephens (1990, p. 454) comments that “[m]any would-be testers do not understand the theory well enough to perform meaningful tests.” I agree. But the list of testers who do not understand the theory include some of the founders and developers of the theory. In particular, one of the most important on the patch residence-time problem (Krebs, Ryan and Charnov 1974) was flawed because the authors did not understand the theory [which had not been developed in 1974, but see Oaten 1977 and Iwasa et al. 1981]. The paper is still a valuable contribution to the literature because it raised the question of what patch-leaving rule a forager might use, and it tested various alternatives experimentally. If one does not do any work until a theory is completely developed then not much work will be done.

Stephens concludes with a mention of radical critics of optimal foraging theory (Gray 1987; Pierce and Ollason 1987). He says that foraging theory might be “limping along,” but the critics do not offer any alternative. That may be a good response, but I think that, in fact, the critics do offer an alternative. The strong criticism that Ollason (1980) offered to optimal foraging theory (that mechanistic explanations may be just as good as functional explanations), which was rudely dismissed by Krebs et al. 1983, seems to have been taken to heart by Stephens and Krebs (1986) and Stephens (1990) in his preference for the name “foraging theory” over “optimal foraging theory.” I would say (as I tried to say in 1990) that an alternative to foraging theory would be a better foraging theory that would pay attention to the problems that animals face and that and that was suited to answer questions that population and community ecologists ask. This did not happen. What happened was that ecologists looked at different problems, and used different methods.

[If people ask questions about foraging, and if there are no good methods of answering the questions, maybe the people will ask other questions for which there are methods that yield answers.]

In fact, an alternative to foraging theory arose about the time that Stephens and I were writing our papers. This alternative comes from a change in viewpoint. Instead of looking at a predator and asking how it should look for and choose prey, why not look at potential prey animals and ask how they might avoid predators. The review of this subject by Lima and Dill (1990) is one of the best-known papers in the subject of behavioral ecology. It is being cited almost as frequently as the book by Stephens and Krebs (1986).

**Lima and Dill (1990): “Behavioral decisions made under the risk of predation: a review and prospectus”**

Lima and Dill (1990) reviewed a large literature on the effect of the fear of predators on the behavioral decisions of their potential prey. Theirs is an excellent paper. They summarized the results of behavioral observations according to the components of a model. First, they represented the risk of death with a simple equation:

$$P(\text{death}) = 1 - \exp(-\alpha dT)$$

where  $\alpha$  = the rate of encounter between predator and prey,

$d$  = the probability of death from an encounter, and

$T$  = the time spent subject to attack.

The probability of death from an encounter itself can be broken up into subcomponents. In one case the predator detects the prey before the prey detects the host. In another case, the prey detects the predator first. In each case there are there are a number of steps, for example, pursuit and capture, before death.

This model provides a good scheme to use to organize experimental results, and Lima and Dill summarize a lot of work, especially on fish (Dill’s specialty) and birds (Lima’s specialty). A large number of examples provide weight to the argument that avoidance of predators influences the behavioral decisions of many animals.

Most of the examples used as illustrations by Lima and Dill (1990) involve animals that must avoid predators while they themselves forage, although some examples are given in which animals must avoid predators while they are engaged in other activities, including courting and mating. There are some examples in which foraging animals give up better opportunities to forage in order to avoid predators, but there is no attention paid explicitly to any tradeoffs between foraging success and predation risk. In fact, the authors begin by making the point that being killed by a predator is the most important event in an animal’s career, and that animals should try hard to avoid predators.

Other people have tried to include the risk of predation and other mortality risks in models of foraging, especially people who want to use a fixed lower threshold for the daily ration that a forager should achieve in order to survive to another day. This method became popular after behavioral ecologists began using what they called “stochastic dynamic programming” (SDP) (for expositions of the ideas, see: Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000). In SDP models the decision that an animal should make at any time depends on the state of the animal (for example, its nutritional state) and on the state of the environment (for example, predators are [believed to be] present). A typical result of the theory is that an animal that faces a high probability of starvation should take more chances than animal that is well fed. It might be mentioned that the word “risk” is used in a completely different way in the two

phrases “risk of predation,” which refers to the chance of being attacked by a predator and “risk-sensitive behavior,” which refers to the fact that the results of the behavior (the number of prey found during a foraging bout, for example) is subject to chance and that the animal has a preference for less (or, in some cases, more) variability in the outcome.

The literature that Lima and Dill (1990) review concerns behaviors that animals, mainly foragers, use to avoid predation. Optimization theory is not used, either to evaluate tradeoffs or study the efficiency of predator avoidance. I do not know any published work on the optimal avoidance of predators, but I showed (Green 1988) that one can take the idea of optimal foraging (maximizing a predator’s rate of encountering prey) and reverse an inequality to obtain “pessimal foraging” (the worst type of foraging), which corresponds minimizing a prey animal’s rate of encountering predators. Such a model might be realistic if the prey is much more likely to see the predator than the predator is to see (this probability is part of the model given by Lima and Dill) and if the cost of encountering a predator is merely down time (when the forager remains still instead of foraging or carrying on with its usual activities). Reviewers for *The American Naturalist* did not think that mine was a realistic model of optimal predator avoidance, and my paper was rejected.

### **WHAT HAPPENED TO OPTIMAL FORAGING THEORY AFTER 1990?**

Even before 1990 interest in optimal foraging theory was waning. There was little advance in the basic theory after the early 1980s, and under the aegis of behavioral ecology, optimal foraging theory had lost contact with population and community ecology. Instead of modifying and adapting the older models to particular cases, new problems were considered (such as central-place foraging and group foraging), and crude foraging models were used by workers applying new methods like stochastic dynamic programming and individual-based models. There was no call for an improved optimal foraging theory from workers who were not asking questions that required an improved theory.

There is still a great deal of interesting in foraging (the term “foraging” is used about 1000 times per year in scientific papers), but there is much more interest in what is called “foraging behavior” (or “foraging behaviour”) than there is in “optimal foraging theory” (or “optimal foraging” or “foraging theory”). The paper by Lima and Dill (1990) has been cited about 2000 times, a comparable number to the citations of Stephens and Krebs (1986), which has been cited about 2500 times in a slightly longer time (see Table 1). It seems to me that the papers that cited Lima and Dill (1990) are themselves cited more than the papers that cited Stephens and Krebs (1986), based on my tally of the first 100 papers from about 1993 on (the earliest date available from the Web of Science at UMD). The early Lima and Dill-citing papers were cited a median of 32 times, while the Stephens and Krebs-citing papers were cited a median of 19 times (Table 2). Treating these 200 values as independent random samples, I found a significant difference between the two at the 1% level using a Kolmogorov-Smirnov two-sample test [ $D = 0.24$ ]. I am not sure what to make of this or of the methodology, but at the least, I would say that there is a lot of interest in the question of how animals behavior in order to avoid

predators, and at most, that there may be more interest in predator-avoidance than in foraging.

Another approach to foraging (other than optimal foraging theory) was developed by Patsy Haccou and her colleagues around 1990 (Haccou et al. 1991; Hemerik et al. 1993). This approach considered the giving-up time (the time between the last encounter between a predator and prey [here a parasitoid and host] and patch leaving) in terms of renewal theory. What they did was use a statistical method to study an ethological problem.

Still another approach to foraging [also applied to parasitoids] was to treat patch-leaving rules in terms of hypothetical behavioral mechanisms like that suggested by Waage (1979). In Waage's mechanism, a parasitoid has a certain tendency to remain in a patch of hosts. As time goes on, that tendency decreases until the parasitoid leaves the patch. However, if a host is encountered, the tendency to remain jumps up, but then begins to decline as time passes without finding another host. But, if another host is found, the tendency to remain takes another jump up, and so on. Driessen et al. (1995) generalized Waage's model for parasitoids by considering another possibility, that when a host is encountered, a parasitoid's tendency to remain in a patch might jump down. There is evidence for jumps up under some conditions and jumps down in others.

These two approaches and empirical evidence are reviewed in a paper by van Alphen et al. (2003), who emphasize the importance of information use by parasitoids foraging for hosts. A meeting on "Bayesian foraging" held in Lund, Sweden, in 2003 emphasized the importance of information use by foragers. The papers from this meeting were published in the February, 2006 issue of *Oikos*.

## CONCLUSION

Work on foraging theory during the 1980s moved from the basic models to other, quite different foraging problems. That movement has continued. Instead of working through optimal foraging theory, work on foraging tended to move around the theory, considering new models at roughly the same superficial level as the original models. In some cases, excellent work was done by concentrating on ecological problems and developing foraging theory as needed (the sunfish work of Werner and his colleagues mentioned by Stephens [1990] is such an example, the parasitoid work of Waage [1979] is another). There has been a tendency to bypass theory and just go from an ecological problem to a behavioral mechanism that an animal might use to solve the problem.

There may be a tendency for work on behavior and/or ecology to move from the general (it is part of ecology) to the specific (it is part of mammalogy or entomology). If I am asked what happened to optimal foraging theory, I would say (as part of the answer) is that it became part of the study of insect behavior. Or, if I am asked what is the best book on foraging after Stephens and Krebs (1986), I would probably say, Godfray (1994).

If one were to take the papers by me (Green 1990) and Stephens (1990) as predicting the future of optimal foraging theory, I would say that Stephens is much more accurate. Stephens expressed the hope that empiricists would tell foraging theorists what questions to ask. I think that ecologists have asked many questions involving foraging, but they have not addressed these questions to foraging theorists. I expressed the hope that foraging theory would be improved by being made more ecological. In fact, I think that optimal foraging theory has been pretty much ignored by ecologists.

I think that the best that can be said of optimal foraging theory is that it was a collection of nice ideas that were centered around the idea that one can ask what the best form of behavior is in particular cases. If the answers are all forgotten, but the idea that the question can be asked, perhaps that is as much as one can expect, and it is far from negligible.

**Table 1.** Numbers of times phrases and works are cited in Web of Science

Word or phrase	Times cited	Cited in title only
Foraging	17372	4307
Optimal foraging	689 (418)	102 (87)
Optimal foraging theory	271	15
Foraging theory	508 (237)	37 (22)
Foraging behavior	3221	465
Foraging behaviour	1472	371

Note: The numbers in parentheses are the numbers of times that the phrases “optimal foraging” or “foraging theory” are used minus the number of times that they are part of the longer phrase, “optimal foraging theory.”

Work	Number of times cited
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Reviews of optimal foraging theory

Schoener (1971)	1741
Pyke, Pullian and Charnov (1977)	1399
Pyke (1984)	595
Stephens and Krebs (1986)	2488

Review of work on predator avoidance

Lima and Dill (1990)	1978
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Two papers on the future of optimal foraging theory in 1990

Green (1990)	8
Stephens (1990)	25

These numbers of citations are as on May 19, 2007. Notice that there are many more references to “foraging behavior” or “foraging behaviour” (4693) than to “optimal foraging,” “optimal foraging theory,” or “foraging theory” (926 for all three), and that “optimal foraging” (418) is used nearly twice as often as “foraging theory” (237). In fact, “optimal foraging” by itself is used more than “optimal foraging theory” (271), which, in turn, is used more than “foraging theory” by itself. The most interesting thing about the references to major reviews, other than the large numbers of times these papers are cited, is that the most recent, and best known of these (Stephens and Krebs 1986), is being cited at about the same rate as the review on predator avoidance by Lima and Dill (1990). Overall, this table shows that there is great interest in foraging, that there is more interest in foraging behavior than in foraging theory, and that there is interest in looking at foraging from the point of view of the prey and not just the point of view of the predator.

**Table 2a.**

Number of times cited for 100 early papers (Web of Science) citing Stephens and Krebs (1986). These are the first papers listed in the Web of Science beginning about 1993.

Stem	Leaves	Sum	Total
0	0 1 1 1 2 2 3 3 4 4 4 4 4 5 5 6 6 7 7 7 8 8 8 8 9 9 9	27	27
1	0 0 0 0 1 1 1 1 1 2 3 3 4 4 4 4 5 5 5 7 8 8 9 9 9	25	52
2	0 1 1 2 3 4 5 7 7 7 7 7 8 9	14	66
3	0 0 0 0 1 2 6 8	8	74
4	0 1 4 5 6 6 8	7	81
5	2 3 5 8 9 9	6	87
6	4 6 6 7	4	91
7	1 1 9	3	94
8		0	94
9		0	94
10	113 118 139 168 329 391	6	100
or more			

**Table 2b.**

Number of times cited for 100 early papers (Web of Science) citing Lima and Dill (1990). These are the first papers listed in the Web of Science beginning about 1993.

Stem	Leaves	Sum	Total
0	0 4 4 5 5 6 7 7 7 8 8 8 9 9 9 9	16	16
1	0 0 0 2 2 2 3 4 6 6 6 7 8 9	14	30
2	0 2 2 2 2 2 2 4 4 5 5 5 5 6 7 7 8 8	18	48
3	0 0 0 2 3 4 5 6 6 7 7 7 8 8 8	15	63
4	0 0 6 9	4	67
5	0 0 0 1 2 5 5 6 9 9	10	77
6	0 3 4	3	80
7	1 2 6 6 6 8 8	7	87
8	7	1	88
9	1 2 8	3	91
10	100 102 120 122 123 127 191 283 329 or more	9	100

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