In this talk I will describe my experience with Bayesian foraging. First, I will describe my background up to my encounter with Oaten’s (1977) paper, suggesting that I was pre-adapted to study Bayesian foraging. Then I will describe my early thinking about Oaten’s model. This is the story of mistakes, at least in part. Next I will talk about some related work, especially the paper by Iwasa et al. (1981). Finally, I will look at the bigger picture, part of which is to be seen in the book by Stephens and Krebs (1986).

MY BACKGROUND

I was born and raised in Duluth, Minnesota. I was interested in nature as a boy, but unlike some of my childhood friends, I did not study Biology in high school or in college. In college I majored in Math and minored in Physics and Philosophy. I was also interested in psychology, but did not take any Psychology courses. However, I did take part in an NSF Undergraduate Research Program in Statistics, in which I helped conduct and analyze a psychology experiment.

I went to graduate school at the University of California, Berkeley, where I studied Statistics. My major professor, Jerzy Neyman, was interested in stochastic population models. He was particularly interested in cancer, and thought of tumors as populations of cells. This (the level of tumors) is not the most fruitful level at which to study cancer, but the methods used to model tumors (and other populations) were good to see.

More important for the present story is that while I was a Statistics graduate student I worked for a year and a half for George Barlow in the Zoology Department, analyzing data on fish behavior. George Barlow had gone to the Statistics Department to find someone to help with statistics and Mr. Neyman recommended me because I needed a job and he knew that I was interested in psychology. I spent four hours a day in Dr. Barlow’s lab, reading and talking to people. It was great! I was encouraged to read about behavior and ecology. When I was about to go home for Christmas in 1967, I asked Dr. Barlow to recommend a book that was heavy on the mathematics and light on the biology. He recommended MacArthur and Wilson’s (1967), *The Theory of Island Biogeography*. I read the book and enjoyed it very much.

I enjoyed the reading, and I also enjoyed working in a lab and being about to talk to people daily about their work, about what I was reading, and about what was happening in the world. [A lot of things were happening in the world, and at Berkeley, in the
1960s.] Richard and Marian Dawkins were in the behavior group at Berkeley—but not in Barlow's lab—when I was there. I got to know them and liked them.

I left the lab in 1969. [In fact, I returned to Duluth for spring quarter and taught logic in the Philosophy Department.] David Noakes, who was the senior graduate student in Barlow's lab got his degree in 1969 and went to Edinburgh as a Demonstrator. He called himself the “Demonstrator from Berkeley.” In 1970 the Commonwealth Games were held in Edinburgh and David and his wife Pat invited me to visit them and attend the games. I went, but on the way I visited Richard and Marian Dawkins in Oxford. This was before optimal foraging theory, but one of the problems being studied was the search pattern of blackbirds foraging on lawns. Blackbirds move in a series of hops, and one can measure the angle between the directions moved on successive series of hops. If a piece of food is found (the birds were offered wafers, whose location was known, so it was known when and where food was found), the angle between the sequences of hops before and after finding the food is sharper than if no food is found. Showing that the angles are different is a statistical problem, which I discussed with Richard Dawkins and then Mike Cullen, who was the “ideas man.” After a conversation with him I understood him to say, “You are the kind of person we like to have around here.” He may not have said anything of the kind, but I got the idea that sometime I might return to Oxford, and I did, seven years later.

After the summer of 1970 I returned to Berkeley and found a problem that had nothing to do with biology, and eventually I got my degree. In 1972 I got a job teaching in the Statistics Department of the University of California, Riverside. The Department, which was started by F. N. David, was biologically inclined, and I got a chance to teach what we called “Statistical Ecology” (because we were a Statistics Department), but was based on Pielou's (1969) book, Introduction to Mathematical Ecology. I taught that course for six years, and I also took part in an animal behavior seminar run by Lew Petrinovich in the Psychology Department. While I was not an expert in anything, I was pre-adapted to work in optimal foraging theory by (a) having learned about stochastic population models, (b) having read and heard about ethology, and (c) having taught and read about ecology.

I spent the 1977-8 academic year on sabbatical in the Animal Behaviour Research Group at Oxford. I was not particularly interested in foraging, but I had a copy of MacArthur's (1972), Geographical Ecology, and I had read Chapter 3: “The economics of consumer choice.” I had also read Eric Charnov's thesis. I shared an office with Alex Kacelnik, who was interested in foraging [Krebs, Kacelnik and Taylor 1978 was in the works], and with Adeline Nunez, a young American woman, whom I later married. Adeline and I later published a paper on central-place foraging (about a single-prey loader in a variable environment). Adeline, Alex and I also wrote a paper about a multiple-prey loader, but that paper was never finished or submitted.

One important foraging paper that I read in Oxford was Krebs, Ryan and Charnov (1974), which made two important contributions: (1) it considered several alternative patch-leaving rules a forager might use, and (2) it described an experiment to determine
which rule was actually used. There are a lot of things wrong with that paper, as I
pointed out much later (Green 1987a), but it is one of the most useful papers in the
history of foraging theory. Richard Cowie was a student of John Krebs at this time, and
his Nature paper came out in 1977. Richard was a fellow bird-watcher and we discussed
foraging.

OATEN’S (1977) PAPER

In January, 1978, Richard Cowie showed my a copy of a preprint of Oaten’s (1977)
paper. He had gotten a copy from John Krebs with a facetious comment: “Some light
bedtime reading,” or some such. John Krebs didn’t know what to make of the paper,
Richard didn’t, and it turned out, I didn’t either. I looked at the paper and saw a couple
of trivial examples and the use of EG/ET for the long-term rate of finding prey [here I use
T to mean S + t, where S is the time spent searching a patch, and t is the travel time
between patches], while I thought that it should be E(G/f).

While the idea of using a stochastic model was appealing to me as a statistician, I thought that Oaten was wrong
and I told everyone who would listen. I was interested in competition, not optimal
foraging theory. But I was not making any progress thinking about competition. I
realized that foraging was relevant to competition and decided to look at Oaten’s model
and do it right! As soon as I started thinking seriously about Oaten’s model I realized
that he was right [the long-term average rate of finding prey does equal EG/ET, not E(G/T)]
and that I was wrong.

I wanted to find a realistic, non-trivial example of Oaten’s model. Having taken a
course in Bayesian statistics taught by David Blackwell, who used DeGroot’s 1970 book,
Optimal Statistical Decisions, the first example of a prey distribution that came to mind
was a gamma mixture of Poissons. That is, each patch has a Poisson-distributed number
of prey—whose locations in the patch are random—but the Poisson parameter varies
from patch to patch according to a gamma distribution. Search was to be systematic. I
believed that an optimal forager would leave a patch when the instantaneous rate of
finding prey, given the number of prey found by that time, equaled the highest possible
long-term average rate of finding prey. This is the “instantaneous rate rule.” This is not
the optimal strategy, but I did not realize this until after I had solved this (wrong version
of the) problem. I realized that it was harder to solve this problem than I thought, so I
picked an easier problem. I considered discrete time. Each patch would have a
binomially-distributed number of prey, with binomial parameter n fixed—all patches
would be the same size—but with parameter p varying according to a beta distribution.

This time I was successful. I found the best strategy for this example using dynamic
programming. The key idea was that if an animal wants to achieve the highest possible
long-term average rate of finding prey, at any point in a patch the forager has the option
of leaving the patch, going on to another patch, and continuing to search using the best
strategy. Therefore, the only reason to stay in a patch is that there is some rule for which
the ratio of expected gain to expected time after a particular time is at least as good as
the highest possible long-term average rate. That is, the rate at a particular time is not
what matters, but rather what might happen in the patch from that time on. I had a
method for finding the optimal foraging strategy for a reasonable case, I knew what rate it achieved, and I could compare the rate with that achieved by a "naive" forager that did not use experience obtained in a patch, but rather stayed until each patch had been searched completely. I could also vary the parameters to see the effect of more or less patch variability on the performance of an optimal forager. Two results of my calculations were that (1) if patch variability is great enough and travel time is short enough, an optimal forager could find prey much faster than a naive forager, and (2) the optimal rule had quite a simple form, one simple enough so that it might be imagined that an animal might be able to use it.

In working out my example I had made two technical mistakes, which I had discovered. These mistakes were plausible, and having made—and discovered—them was important, because other people had made, or were to make those same mistakes. Another mistake, but not a technical one, was that I did not talk publicly about my foraging work before I left Oxford. I had agreed to give two other talks, one on competition, and the other on a graph-theoretical test of nest site interference, and I did not have time to prepare a talk on my example of Oaten's model. I did give a talk about my "Bayesian birds" work at Oxford, but this was not until I returned for a single-quarter leave in 1983.

OTHER WORK ON OATEN'S MODEL

Upon returning to Riverside in 1978 I sent copies of a manuscript on my work on Oaten’s model to Allan Oaten (Allan Stewart-Oaten by this time) and to Eric Charnov. Both sent detailed comments on my paper and suggested the names of other people interested in foraging. In particular, Allan Stewart-Oaten mentioned the thesis by Jim Breck, which considered a variety of prey distributions for Oaten’s model (it also tried another optimization criterion—maximize the chance of finding at least one prey—as well as the usual rate maximization). Breck’s thesis was never published, as far as I know, but the paper by Iwasa et al. (1981) covered much of the same ground.

Before I published my “Bayesian birds” paper (Green 1980), I received a manuscript from Yoh Iwasa that treated various prey distributions for continuous time and random search. This was a mathematically sophisticated and biologically interesting paper. Much of my subsequent work, including my best published paper (Green 1987a), was basically an elaboration of the ideas found in Iwasa et al. (1981).

Eventually I found the optimal foraging strategy and compared its performance with that of other strategies, including the “giving-up-time rule,” for several prey distributions for (1) systematic search and discrete time, and (2) systematic search and (3) random search for continuous time.

Mistakes

The mistakes that I made when I first looked at Oaten’s paper were also made by others, who published them. The most fundamental of these mistakes was the confusion
of EG/ET with E(G/T). Oaten (1977) used EG/ET for the long-term average rate, as he should have, while I originally thought that he should have used E(G/T). While I realized my mistake before I tried to publish my paper, Templeton and Lawlor (1981) did publish a paper in which they made this mistake: "the fallacy of the averages." Their mistake was pointed out by Stephens and Charnov (1982), by Gilliam et al. (1982) and by Turelli et al. (1982).

The other technical mistake that I made when I looked at Oaten's paper was to use the instantaneous rate rule as the optimal strategy. This mistake assumes that the rate of finding prey in a patch is all that matters, and information gain is ignored. In some cases, the instantaneous rate rule is best, but it is not best in all cases. Pyke (1978) and Iwasa et al. (1981) used the instantaneous rate rule as optimal. That this is a mistake was made clear by McNamara (1982), who pointed out that while foragers search a patch, they may be gaining information as well as prey.

Another prominent mistake, although one that I did not make myself, was to believe that by using the giving-up-time rule a forager could satisfy the marginal value theorem. The paper by Krebs et al. (1974) exemplifies this mistake. Iwasa et al. (1981) also used the giving-up-time rule for comparison with other rules, and found it best for a negative-binomial prey distribution, but they did not claim that it was best overall. McNair (1982) pointed out that the giving-up-time rule did not satisfy the marginal value theorem and that if a giving-up-time rule were used in an environment with different patch types, it would be a mistake to use the same giving-up time in all patch types.

Revisit to Oxford in 1983

In the spring of 1983 I had a single-quarter leave and my wife and I returned to Oxford as a guest of Alex Kacelnik. He was working on central-place foraging in starlings. The three of us wrote a paper on central-place foraging (for a multiple-prey loader), but it was never finished or submitted for publication. Adeline and I wrote a paper on central-place foraging for a single-prey loader in a stochastic environment that was eventually published (Green and Nunez 1986). Alex also showed me a preprint of Lima's 1984 paper on downy woodpeckers, which was, as far as I know, the first, and still is one of the very few papers which attempts to test a version of Oaten's model.

I gave talks to three different groups at Oxford in 1983. One group was interested in foraging and included John Krebs, Alex Kacelnik, Alasdair Houston, John McNamara, Sara Shettleworth, Paul Schmid-Helpel, Patrick Miere, and Robin McCleery. After my talk John Krebs and Robin McCleery asked questions that I could not answer, but which I eventually answered years later. Krebs asked how the performance of the payoff depended on the exact form of the strategy used, and McCleery asked about the variability in the actual payoff achieved (not just the long-term average rate). I worked out a kind of answer to Krebs' question: the payoff is insensitive to the exact form of the rule used if the right general type of rule is used. One particular case of this [a modification of Lima's (1984) model] was published in 1990 (Green 1990a), and a better example was written up and illustrated (Green 1990b), but never published. The answer
to McCleery's question was that—for my favorite examples of quite variable patches—there is a lot of variability in the actual rate achieved. One consequence of this is that a forager who happened to be the most sophisticated statistician would be unlikely to detect a difference in the performance of the best assessment strategy and the (sub-optimal) instantaneous rate rule.

Another talk was for a broader audience. I tried to think of a reason the average zoologist at Oxford should be interested in optimal foraging theory, and the best that I could come up with is that people there were interested in the subject, so it was interesting to know what other people were interested in. Another point was suggested by my reading some papers written at Oxford between the times of my visits. These were to some extent experimental, and they did not seem to use theory well. I made three comments about how to do experiments: (1) Present animals with problems that they face in nature, (2) Make sure that the animal is answering the same question that the experimenter is asking, and (3) Ask whether any behavioral difference that is being investigated is large enough to matter. I expanded upon these suggestions, offering recent examples of work in which they were not met, in a paper submitted to *Ethology* in 1995. This paper was accepted subject to revision, but never revised, and therefore never published.

A third talk was given to the Animal Behaviour Research Group. This after-dinner talk went on for two hours, mainly because David McFarland kept trying to ask what my theory had to do with real animals. I could not give an answer that satisfied him. Later I though that maybe I should have just replied: "I am not talking about real animals. These are imaginary animals. But, aren't they nice." One thing that I realized was that it was so much easier to say that prey have a negative-binomial distribution (say) and have people accept that without question (because they know what it means, and know that this is a familiar mathematical assumption). Of course, if I were only to talk to people who will understand and accept mathematical assumptions, I would not have to be clear in my own mind what the model really says about the world. Perhaps McFarland questioned me so closely because he wanted to know how to describe my results himself. In fact, he did include a description of my work in his textbook (McFarland 1985), and his treatment there is quite accurate.

While we were in Oxford in 1983, several of the foraging people left for a meeting on foraging at Harvard [the proceedings were published in Commons *et al.* (1987)]. I also learned that there was to be a foraging conference to be held at Brown University in 1984. I arranged to give a talk at the Brown meeting, and I worked on that talk, and details that come out of it, for the next five years.

**STEPSHENS AND KREBS (1986)—THE END OF OPTIMAL FORAGING THEORY**

In 1987 there appeared three books on foraging. One, with a copyright date of 1986, was *Foraging Theory* by Stephens and Krebs, which presented a particular view—perhaps the predominant view—of optimal foraging theory. The other two books,
Foraging Behavior, edited by Kamil, Krebs and Pulliam, and Foraging, edited by Commons, Kacelnik and Shettleworth, were the proceedings of conferences held at Brown University in 1984 and at Harvard University in 1983, respectively. The emphasis of the Harvard conference was psychological, but some of the participants were biologists, or theorists with biological interests. The Brown conference was more general, but there was more emphasis on experiments than on theory. The book by Stephens and Krebs was almost entirely theoretical, with experiments being described as tests of the theory.

The book by Stephens and Krebs (1986) was a landmark of optimal foraging theory. It provided a clear, definitive statement of optimal foraging theory, and it is by now the most cited review of optimal foraging theory. It may also have marked the end of optimal foraging theory. The title, Foraging Theory, might be more descriptive than "Optimal Foraging Theory" would have been, since some of the theory concerned sub-optimal foraging behavior, but in their arguments for the value of "foraging theory," Stephens and Krebs used as examples optimization models that have nothing to do with foraging. In fact, I think that the absence of "Optimal" from the title reflects a failure of nerve. On the other hand, the use of "Foraging Behavior" for the title of the Brown conference proceedings reflects the general emphasis on behavior, the lack of emphasis on theory, and repeats the title of the proceedings of the previous foraging conference (Kamil and Sargent 1981).

Everyone who studies foraging should read the book by Stephens and Krebs (1986). It clearly describes the basic foraging models and some later modifications. It reviews experimental studies of the predictions of the basic foraging theory. It also refutes arguments against the optimal foraging approach. Overall, it presents the Oxford view of optimal foraging theory, in which a mathematical theory, based on evolutionary arguments, provides qualitative predictions that are tested experimentally. The survey of experimental tests in Stephens and Krebs (1986) is a repeat of what appeared in Krebs, Stephens and Sutherland (1983), who refer to the "success" of optimal foraging theory. I think that what they mean by success is popularity. Optimal foraging theory was popular because it gave ecologists new ways to organize their data, and it provided "predictions" to "test."

Reviewers of Stephens and Krebs (1986) who had done technical work on foraging tended to make technical criticisms (Green 1987; Pyke 1987; Real 1988). My criticisms centered on the use of the idea of the "marginal value theorem," which was used in a number of different ways without making the differences clear. Graham Pyke (1988), who had done work on optimal movement of foragers, pointed out that Stephens and Krebs did not consider the problem of how foragers move. Pyke also criticized the way that Stephens and Krebs characterized the results of his empirical work. Tom Getty (1988) pointed out that Stephens and Krebs had little to say about how real animals actually forage. Les Real (1988) pointed out that Stephens and Krebs use too much jargon. I think that the problem was not so much with jargon which might make the book difficult for outsiders to understand, but with the use of language for rhetorical purposes.
to influence insiders. Tom Getty, Les Real and I all criticize Stephens and Krebs for dismissing the consideration of the population consequences of foraging behavior.

Stephens and Krebs (1986) dealt with Bayesian foraging more by dismissal than by careful consideration. Their treatment was rhetorical. For example, the essence of Oaten’s (1977) model is stochasticity. Following Stephens and Charnov (1982) in their criticism of Oaten, Stephens and Krebs distinguished two kinds of stochastic models, “information” models and “risk” models. There certainly has been more experimental work on “risk” models and “risk-sensitive” behavior, with an interesting distinction between “risk-prone” and “risk-averse” foraging. Oaten’s model is an “information” model in this classification. There is also the distinction between patch “types” and “sub-types” (different “types” are identifiable immediately, without cost, when a forager enters a patch, which is encountered at random, independently of type; different “sub-types” are superficially indistinguishable, but may be distinguished statistically by using information obtained while foraging). Charnov’s (1976a) marginal value theorem paper took different “types” into account, while ignoring “sub-types.” Oaten (1977) dealt with “sub-types,” while ignoring “types.” Stephens and Krebs criticized Oaten and his followers for not dealing with the problem of patch “types.” In fact, it is much harder to deal with “sub-types” than “types,” and one can add “types” to the treatment of “sub-types” quite easily (see Green 1990 for an example). On the other hand, it is very difficult to add the treatment of “sub-types” if all that one has is a way to treat “types,” as Charnov (1976a) had. [Aside: One advantage of my trying to treat the problems of “types” and “sub-types” simultaneously was that I realized how narrow were the assumptions that Charnov used in his treatment of patch types. Stephens and Krebs reduced the four basic foraging problems listed by Pyke, pullian and Charnov (1977) to two: the “prey” problem and the “patch” problem. Their “patch” problem was really a residence-time problem, and a “patch” might be either a real patch or an individual prey, while their “prey” problem was really a choice problem, and a “prey” might be with a real prey of a patch. The “patch” problem of Stephens and Krebs corresponds to a single problem of Pyke, Pulliam and Charnov (1977)—the patch residence-time problem—but the Stephens and Krebs “prey” problem combines the prey choice and the patch choice problems of Pyke, Pulliam and Charnov. Stephens and Krebs can combine the prey and patch choice problems into one “prey” problem only by ignoring how patches are found and exploited. Further, Stephens and Krebs can ignore the Pyke, Pulliam and Charnov problem of movement if they avoid the question of how foragers find patches and ignore the question of how and when patch “types” are distinguished.]

The disciplinary approach of Stephens and Krebs (1986) is narrower than the full treatment of foraging. They are not interested in the abilities or strategies that animals must use to find prey, and they explicitly ignore the ecological consequences of foraging. There are a number of approaches to foraging, two or three of which are covered in the book by Stephens and Krebs. In a sense, Stephens and Krebs exemplify the evolutionary approach to behavioral ecology promoted by Krebs and Davies (1978, and later editions). There are three kinds of behavioral ecology, an ethological behavioral ecology, which studies the impact of ecological conditions on behavior, an ecological behavioral ecology, which tries to use knowledge of behavior to understand its ecological
consequences, and there is the best known version, evolutionary behavioral ecology, which studies the advantage to individuals to particular forms of behavior.

It is not clear how great the differences are among the topics covered by various terms used for foraging, because several different terms may be used to refer to the same thing. However, a look at the frequency of terms found in the Web of Science database suggests that the interest in foraging remains strong, while optimal foraging theory is of little interest. Doing a General Search in the Web of Science (for 1997-2003 data through 7-13-03) showed the following numbers of references under the following topics: foraging 7757, foraging behavior 1393, foraging behaviour 705, foraging theory 207, foraging ecology 271, optimal foraging 288, optimal foraging theory 110. It is possible that authors prefer two-word terms to three-word terms and this accounts for the low frequency of "optimal foraging theory." The data show that "foraging" is used over 1000 times per year, while "optimal foraging theory" is used little more than 15 times per year. "Foraging behavior" (with or without the "u") is used about 300 times per year.

DIFFERENT APPROACHES TO FORAGING

If one studies the history of foraging one sees, at different times and places, quite a variety of approaches which are quite distinct, if not mutually exclusive. Here I will list six approaches.

(1) Optimal foraging is usually traced to two papers that appeared in 1966 on prey (and patch) choice, one by MacArthur and Pianka, the other by Emlen. Other well-known early work included the review by Schoener (1971) and a chapter in the book, Geographical Ecology, by MacArthur. These men were all ecologists, and they were interested in field work as well as theory. They were interested in foraging behavior because of its ecological importance, and they used foraging to connect ecological conditions with ecological consequences. For example, if prey density is low, foragers should be expected to take a wider variety of prey and thus show more overlap (and therefore more competition) in their diets. These men were interested in foraging strategies, which consideration became the basis of optimal foraging theory. Their work was sometime referred to as evolutionary ecology.

(2) I trace the beginning of optimal foraging theory proper to two papers by Charnov in 1976. The idea was to produce mathematical models of foraging that yielded explicit, experimentally testable predictions. Pyke, Pulliam and Charnov (1977) reviewed the early work, both theoretical and experimental. Charnov was not the first or the only person to say what he did, but after 1976 everyone knew what optimal foraging theory was. The work following Oaten (1977) which I am discussing in this paper is part of this mathematical line, but there was not the same emphasis on predictions or behavioral tests. I would characterize this approach as mathematical.
(3) Once predictions were derived from foraging theory, laboratory experiments were conducted by behavioral ecologists. Krebs, and his students and colleagues, were pioneers in this work, beginning with the study of black-capped chickadees by Krebs, Ryan and Charnov (1974), and continuing with other work (Krebs et al. 1977; Krebs et al. 1978). This work was summarized by Krebs, Stephens and Sutherland (1983), and this summary was repeated in Stephens and Krebs (1986). This work is what is called behavioral ecology (in the sense of Krebs and Davies 1978).

(4) Experimental psychologists had long conducted experiments on laboratory animals, which were often motivated by food. One kind of experiment was to study the preferences of animals for various reinforcement schedules. Reinforcement schedules resemble the “gain function” used in Charnov’s (1976) “marginal value theorem” paper. The similarities of the work by biologists and psychologists became apparent at a meeting of the Animal Behavior Society in 1978, whose proceedings were published as Foraging Behavior (Kamil and Sargeant 1981). A symposium emphasizing the psychological approach to foraging was the one held at Harvard in 1983 (Commons et al. 1987). Alex Kacelnik and his students and colleagues continue work along this line. Work of along lines (2), (3) and perhaps (4) are what is considered under the head “foraging theory” by Stephens and Krebs (1986). Two other lines continue the work of line (1) which led to optimal foraging theory, but these lines are quite independent of (2), (3) and (4), and they are not mentioned by Stephens and Krebs.

(5) An old approach to foraging, which is of continuing interest, is ethological. The book, The Ethology of Predation (Curio 1976), was reviewed by Krebs (1977), but was not cited by Stephens and Krebs (1986). [Schoener (1977) wrote a review of Curio’s book along the evolutionary ecology line.] Bell’s (1991) book, Searching Behavior, continues in the tradition of Curio. Neither Curio nor Bell are much interested in foraging theory; they are interested in behavioral mechanisms rather than strategies. The study of behavioral mechanisms may not lose much by ignoring function. However, it is strange that people interested in the function of foraging behavior, as the behavioral ecologists were, should have been so uninterested in the mechanisms that foragers use to achieve their goals.

(6) Population ecology is also an old area of biology in which there is place for foraging theory. Some of the most sophisticated students of foraging: Robert MacArthur, Allan Oaten, and Yoh Iwasa, were interested in population ecology. Important papers using foraging theory in order to understand population questions include Hassell and May (1974) and Murdoch and Oaten (1975). Hassell and May (1985) and Schoener (1986) exhorted biologists to use individual behavior to understand population phenomena. A number of attempts have been made to use individual behavior to understand population consequences, but they do not always use optimal foraging theory properly.
Certainly some use it incorrectly. Hassell and May (1974) and Murdoch and Oaten (1975) provide examples of this.

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