

**POPULATION CONSEQUENCES OF FORAGING BEHAVIOR
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RESULTS FROM PRIOR NSF SUPPORT

I have received no NSF support in the last five years.

PROJECT SUMMARY

I propose to do a theoretical study of two population consequences of the foraging behavior of animals that search for prey which are distributed in patches. First, I will investigate how the rate of finding prey changes with prey density [the functional response] for predators using an almost-optimal foraging strategy when the prey distribution changes with prey density in a variety of ways. Second, I will study the change in prey distribution when patches are exploited by an optimal forager, and I will calculate the rate of finding prey that a forager may achieve by revisiting patches. I will find optimal and almost-optimal strategies and will calculate the rates of finding prey that they would achieve for a particular version of Oaten's (1977) general stochastic model of optimal foraging. The form of the functional response determines whether a certain version of the Lotka-Volterra predator-prey model is stable, while the effect of patch exploitation is important in determining the value of maintaining feeding territories and of partitioning resources.

PROJECT DESCRIPTION

INTRODUCTION

I am interested in how animals which forage for prey that are distributed in patches should decide when to leave one patch and move on to another. I have found optimal foraging strategies for a number of particular models and have studied the performance of these and other strategies. I propose to study the population consequences of nearly optimal foraging for a particular, biologically realistic model, in which the number of prey per patch has a negative binomial distribution. In particular, I ask: a) How does the rate of finding prey change with changing prey density—that is, what is the functional response—for various patterns of change of prey distribution with prey density? and b) What is the distribution of the number of prey left in a patch that has been searched and what is the rate of finding prey achieved by a forager revisiting these patches? The functional response is important in determining the stability properties of certain predator-prey models, while the cost of revisiting already-searched patches is important in determining the value of resource partitioning and the maintenance of feeding territories.

Foraging theory.

Early work on foraging theory, beginning with MacArthur and Pianka (1966) and Emlen (1966), was ecological. Schoener's (1971) review is one of the most frequently cited papers in all of ecology. MacArthur's (1972) book has a chapter on foraging theory, and Emlen's (1973) textbook discusses the subject of foraging. Hassell and May (1974) introduced a foraging model in the second of their pair of papers on host-parasite models, and Murdoch and Oaten (1975) discussed the effect of foraging behavior on the stability of predator-prey systems. There has been little serious use of foraging theory in population ecology since 1975.

Most of the recent work on foraging has been ethological, studying foraging behavior itself rather than its consequences. This approach to the subject, which was reviewed by Krebs (1973) and stimulated by experimental studies of the theoretical ideas of Charnov (1976 a,b), was enriched by the addition of techniques from experimental psychology. A recent view of this approach is found in the symposium volume edited by Commons, Kacelnik and Shettleworth (1987). I think that the ethological approach to foraging has been valuable because it made the subject of food habits more interesting and stimulated many natural history observations. This approach has not been of much use in population ecology, however.

Pyke, Pulliam and Charnov (1977) gave an excellent review of the ideas of foraging theory to that time. They listed several problems that a forager has to face. I am interested in the problem: What rule should a forager use to decide when to leave one patch and move on to another? Charnov (1976a) gave a solution to this problem for a forager in a deterministic environment and claimed that his ideas could be extended to

a stochastic model. Disagreeing, Oaten (1977) developed an explicitly stochastic model to expose Charnov's claim. Oaten assumed that an animal forages in a patchy environment in which patches may vary in the number of prey that they contain. Foragers are assumed to "know" the distribution of the number of prey per patch, the joint distribution of capture times within a patch, given the number of prey to be found there, and the travel time between patches. Given this knowledge and its experience in a patch, an optimal forager uses the strategy that maximizes its long-term average rate of finding prey. The environment is assumed to be unchanging and patches are superficially similar.

Oaten's approach to the patch residence-time problem is one of three that have been used. The first, which is exemplified by Charnov's (1976a) model, is basically economic. A forager's experience in a patch has no place in this approach. Instead a forager has a "gain function," which represents the energy gained (somehow) during its time in a patch. Optimal foraging is given in terms of the gain function, rather than any behavior of the forager or any experience that it has. Oaten's approach is to describe the environment a forager faces and to determine the optimal strategy in terms of the forager's experience in patches. A third approach, which is that used by experimental psychologists, and now by some behavioral ecologists, is to specify a reinforcement schedule that determines the experience of an animal in an operant experiment. This psychological approach does take the experience of experimental animals into account, but it does not generally include a description of the natural environment that the experimental situation is intended to mimic. I use Oaten's approach.

Functional response.

Functional response is the principle population consequence of foraging that I want to consider. I will follow Murdoch and Oaten (1975) who attempted to incorporate foraging behavior into a modification of the simple Lotka-Volterra model:

$$\begin{aligned} \frac{dH}{dt} &= aH - bHP \\ \frac{dP}{dt} &= -cP + dHP \end{aligned} \tag{1}$$

where H is the number of prey (or hosts) and P is the number of predators (or parasites) at a particular time, t , and a, b, c and d are constants. The rightmost terms in (1) may be understood to mean that an individual predator will find prey at a rate proportional to the number of prey. Murdoch and Oaten (1975) modified (1) to permit a more general relationship between the number of prey and the predation rate. If, using slightly different notation than Murdoch and Oaten, we write the rate of taking prey, per predator, as a function of overall prey density, μ —which is proportional to H —as

$R(\mu)$, then equations (1) become:

$$\begin{aligned}\frac{dH}{dt} &= aH - bPR(\mu) \\ \frac{dP}{dT} &= -cP + dPR(\mu)\end{aligned}\tag{2}$$

A condition for stability of the system given by (2) is that at equilibrium the ratio $R(\mu)/\mu$ will be increasing in μ . Murdoch and Oaten (1975) explored this condition and I plan to do the same.

Work on Oaten's model.

While there has been little experimental work on Oaten's model—except for that of Lima (1984, 1985)—most of the theoretical work of the patch residence-time problem uses Oaten's approach. Breck (1978), Iwasa, Higashi and Yamamura (1981), McNair (1982), Stewart-Oaten (1982), McNamara and Houston (1987), and I (Green 1980, 1984, 1987a) have treated a number of particular cases, and McNamara (1982) gave a general theorem specifying a condition that an optimal foraging strategy must satisfy.

Recently I have written a series of technical reports (Green 1987 b, c, d, 1988), and hope to finish another one this summer, elaborating the ideas that I outlined at the International Foraging Conference held at Brown University in 1984 (Green 1987a). These technical reports, and the work that I propose here, should form the basis of a monograph on stochastic models of optimal foraging.

I have used the same approach as Breck (1978) and Iwasa *et al.* (1981). That is, I make particular assumptions about the distribution of the number of prey per patch, the locations of these prey within patches, and the pattern of search the forager uses. I compare the performance of a number of strategies, including the optimal strategy for each case. Most people who consider the pattern of search, including Hassell and May (1974), Murdoch and Oaten (1975), Breck (1978) and Iwasa *et al.* (1981), assume that search within a patch is random. I have found the optimal foraging strategies and the rates of finding prey they achieve for a few cases assuming random search (Green 1987a, and in prep.), but I have concentrated on systematic search, which I think is more realistic biologically [a few references are given in Green (1987a)].

In the foraging model whose population consequences I propose to study I will assume that an animal searches for prey distributed in superficially similar patches of the same size, with a forager being able to search each patch completely in unit time. I assume that the number of prey per patch has a negative binomial distribution, that the prey within a patch are distributed at random within the patch, and that search is systematic within each patch—that is, a forager does not retrace its steps within a patch. I think of the negative binomial distribution of prey as meaning that patches vary in quality. That is, the number of prey per patch has a Poisson distribution with parameter λ ,

and the parameter λ is itself a random variable, having a gamma distribution with parameters α and β . Using that notation, the probability that a randomly chosen patch will contain exactly x prey is given by

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

I have found the optimal foraging strategy for this model, using dynamic programming (Green 1987a, more details given in Green 1987b).

If the number of prey per patch has a negative binomial distribution and search is systematic, then the optimal foraging strategy for a particular choice of travel time and of the parameters of the prey distribution will be characterized by a number, n , such that the forager should remain in a patch until it has been searched completely whenever $n + 1$ or more prey have been found there, and a sequence of times, $t(0), t(1), \dots, t(n)$, with $0 < t(0) < t(1) < \dots < t(n)$, such that the forager should leave a patch at time $t(k)$ if exactly k prey have been found by that time. The points $\{t(k)\}$, for $k = 0, 1, \dots, n$ lie very close to a line and this suggests consideration of a linear stopping rule:

stop searching and leave a patch at time $t(k) = a + bk$ if exactly k prey have been found by that time, otherwise remain in the patch until it has been searched completely.

Such a linear stopping rule has not only simplicity to recommend it, but its performance is almost as good as that of the best rule. I have compared the best linear stopping rule with the best stopping rule for three sets of parameters for which I have found the best rule and in each case the long-term average rate of finding prey for the linear rule was within 0.1% of the rate for the best rule. What this means is that, for practical purposes, we need consider only linear stopping rules if we are interested in optimal and near-optimal foraging for negative binomial prey distribution and systematic search.

Table 1. Comparison of the best linear rule with the best rule for three sets of parameters.

Parameters:			Rates of finding prey* achieved by forager using:		
α	β	τ	Best linear rule	Best rule	Relative difference
0.25	0.05	0.1	10.71822	10.72812	0.092%
0.5	0.1	0.1	8.070463	8.07443	0.049%
0.5	0.2	0.1	3.601957	3.602655	0.019%

* Assuming that handling time $h = 0$. The form of the best rule does not depend on the value of h , but the rate achieved does.

Linear stopping rules are simple enough that animals might be expected to use them [see, for example, Waage's (1979) simple mechanism that might result in a giving-up-time rule, and its extension to rules such as mine by Stephens and Krebs (1986, pp. 174-5)], and they are efficient. I propose to use linear stopping rules to study the population consequences of (almost-) optimal foraging behavior.

WHAT I PROPOSE TO DO

I intend to study how the rate of finding prey per forager depends on the prey density *and on the pattern of change of prey distribution as prey density changes* when the number of prey per patch has a negative binomial distribution and the forager searches systematically within patches and uses a linear stopping rule. I will also look at the distribution of the number of prey left in a patch by a forager using a linear stopping rule and will calculate the rate of finding prey achieved by a forager which uses a given linear stopping rule and unknowingly revisits patches that have already been searched by a forager using the same rule.

Functional response.

The first, and most important, part of the proposed research examines the *functional response* of a predator to its prey. My model is specified by four parameters, α , β , τ and h . The prey distribution is specified by α and β , where α is equivalent to the more familiar negative binomial parameter, k , and the average number of prey per patch is $\mu = \alpha/\beta$. The time to travel between patches is τ , and the time to handle each prey is h . The strategies that I consider are linear stopping rules specified by the coefficients of a line, a and b . A given strategy for a given set of model parameters will produce some expected number of prey found per patch, EG , and some expected time spent

searching each patch, ET , and these produce the long-term average rate of finding prey $R = EG/[ET + hEG + \tau]$. There are too many variables to consider them all simultaneously, so what I plan to do is to choose sets of parameter values, find the best linear stopping rule for each set of parameters α, β , and τ (the best rule does not depend on handling time, h), and then calculate the rate, R , as I change the parameters in each of two ways: (1) let β change, while keeping the other parameters constant, and (2) let α change, while keeping the other parameters constant.

Consider an example: $\alpha = 0.5, \beta = 0.1$ and $\tau = 0.1$. In this case the average number of prey per patch is $\mu = \alpha/\beta = 5$. The best linear rule has the form: stop if k prey have been found by time $t(k) = 0.0754 + 0.1300k$. If handling time is zero, then the long-term average rate of finding prey achieved by this rule would be 8.070463, compared with the rate of 8.074433 for the best rule. The relative loss due to using a linear rule rather than the best rule is slightly less than 0.05%. As I vary the parameters I will calculate the rate achieved for the new sets of parameters by the rule given above, which is the best linear rule for the original case. What this will show is how the rate of finding prey will change with changing parameters, given that the forager continues to use a strategy that is (almost) best for the original set. If the set of parameter values $\alpha = 0.5, \beta = 0.1$ and $\tau = 0.1$ is considered as a starting point, the question is how fast the rate of finding prey achieved by a particular strategy will change as the parameters change in different ways. Fixing the other parameters and either increasing α or decreasing β will increase the average number of prey per patch, μ , and either kind of change will increase the rate, which I write $R(\mu)$. That is, $R(\mu)$ will increase with μ . More important is how $R(\mu)/\mu$ changes with μ , since a condition for the stability of some predator-prey models is that the ratio $R(\mu)/\mu$ be increasing at equilibrium. What I expect to find is that $R(\mu)/\mu$ will increase for a while as μ increases due to a decrease in β , but that it will not increase at all as μ increases due to an increase in α .

A particular example is illustrated in Fig. 1. The ratio $R(\mu)/\mu$ is plotted against μ for a forager using the linear stopping rule that is best when $\alpha = 0.5, \beta = 0.1$ and $\tau = 0.1$. In the example illustrated in Fig. 1 the value $\alpha = 0.5$ is fixed and it is assumed that prey density changes because of changes in β alone. It is seen from the figure that if handling time, h , is small then the ratio $R(\mu)/\mu$ increases at prey populations whose densities are around $\mu = 5$, the density for which the strategy studied is the best of all linear stopping rules.

Much evidence (see, for example, Taylor 1984) shows that if a negative binomial distribution is fitted to insect numbers then α increases and β decreases as density increases. Thus it is of interest to determine, for particular starting points in parameter space and a particular strategy, what patterns of change in α and β result in the ratio $R(\mu)/\mu$ increasing with prey density and what patterns result in a decrease. I think that this can be done by drawing a topographic map of $R(\mu)/\mu$ in the space of parameters α and β .

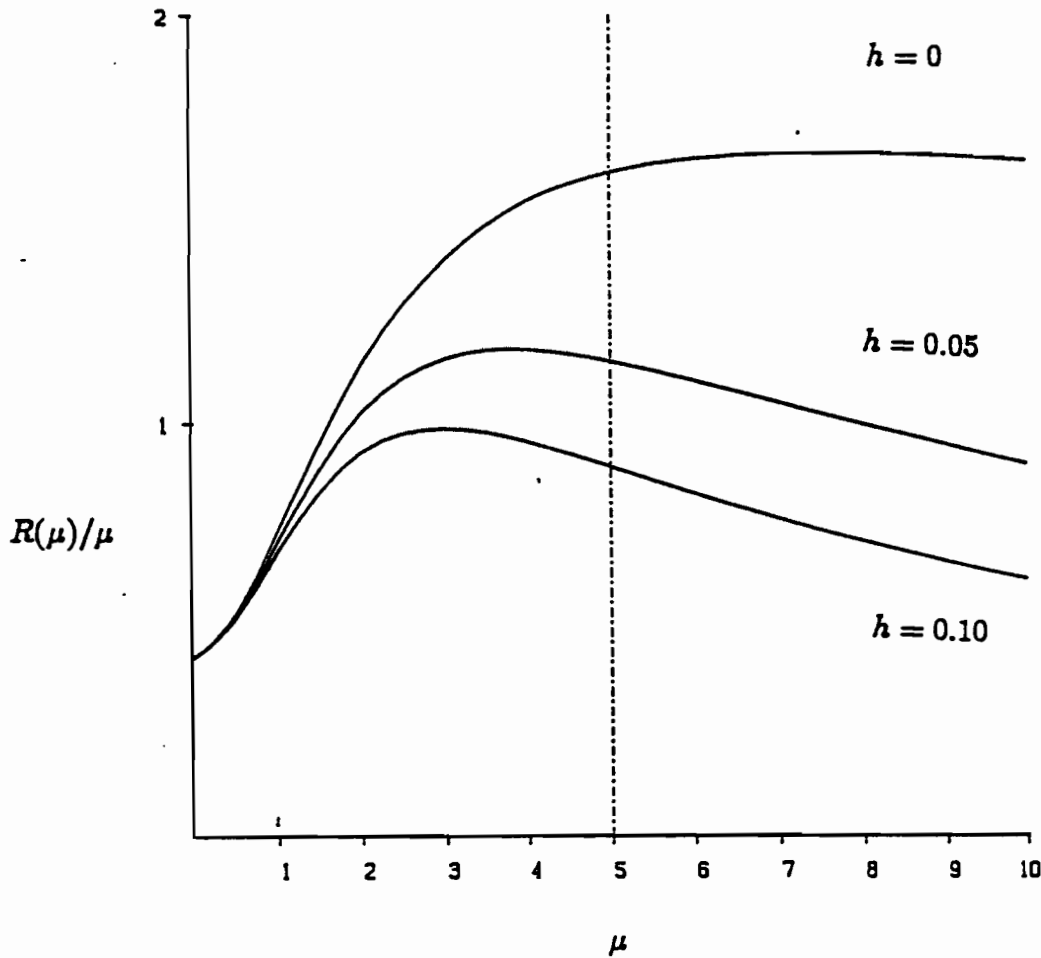


Figure 1. Ratio of rate of finding prey to average prey density, $R(\mu)/\mu$, plotted against average prey density, μ . The number of prey per patch has a negative binomial distribution and search is systematic. The forager is assumed to use the linear patch-leaving rule that is best for the case $\alpha = 0.5$, $\beta = 0.1$ and $\tau = 0.1$. In this figure the parameter α is fixed and μ is varied by varying β . The important point is that the modification of the Lotka-Volterra model given by (2) is stable if the equilibrium prey density is such that $R(\mu)/\mu$ is increasing. For negligible handling time ($h = 0$) the figure shows that $R(\mu)/\mu$ increases until about $\mu = 7.5$, which is well beyond the density $\mu = \alpha/\beta = 5$ [indicated by the dotted vertical line] for which the rule studied is best, while for $h = 0.05$ and 0.10 this ratio stops increasing by densities $\mu = 3.75$ and $\mu = 3.0$, respectively.

I want to study how the rate of finding prey achieved by a particular linear stopping rule changes with changes in parameter values from the original set of values for which the rule is the best. I want to do this starting at a number of different sets of parameter values. I would also like to see how the rate of finding prey depends on the parameters of the prey distribution if foragers are assumed to be able to change rules as the parameters of the prey distribution change and to use the best rule for each set of parameters. This assumption that the strategy changes with (even small) changes in the prey distribution may be implausible biologically, but, at least for one case, I would like to compare this assumption with the assumption that a fixed strategy is used while the prey distribution changes.

The reduction in prey numbers by a forager.

The second part of this proposed research is to find the distribution of the number of prey left in a patch that has been searched by a forager using a particular strategy. I expect that an optimal forager will not only reduce the number of prey in a patch but that it will tend to homogenize slightly the prey distribution as well. If this is true, then not only will foragers reduce the number of prey available to themselves and others, but the maximum possible rate of finding prey will be reduced out of proportion to the reduction in the average number of prey per patch. I plan to calculate the rates of finding prey achievable by foragers revisiting patches already searched by others which have used the best linear patch-leaving rule. I will calculate the rates achieved by foragers who revisit patches and use either the best linear patch-leaving rule for the original prey distribution or the best linear patch-leaving rule for the new prey distribution for exploited patches.

The question of how many prey a forager leaves in a patch is of interest to people who want to determine what strategy foragers actually use [Gibb (1962), Lima (1984)], but I think that it is also important in determining the value of maintaining a feeding territory and the value of resource partitioning. Work on feeding territories has concentrated on their size and the amount of food needed by the territory holder. The rate of finding prey is also important and this rate depends not only on the amount of food available, but also on its distribution, and on information that the forager has about prey distribution. One advantage of holding a feeding territory is that it permits a territory holder to sequester information about patch quality and possibly to maintain a feeding rate that is out of proportion to the average prey distribution within the territory. I am interested in measuring the theoretical advantage of sequestering information about prey distribution.

I have made attempts to solve the problems that I have described [Green (1979, 1981)], and have presented some results of these attempts at meetings (at the International Conference on Population Biology at Edmonton in 1982 and at the American Society of Zoologists meeting at Denver in 1985). I hope that the proposed work will be better than the earlier work because (1) the assumption that prey have a negative binomial distribution is more realistic than the assumptions that I made earlier, and (2)

the use of a single, linear stopping rule is more plausible than assuming that a different, optimal stopping rule is used for each prey distribution as prey distribution changes.

Plan for the execution of the proposed work

The proposed work involves three sets of calculations. First, as a preliminary, I plan to investigate the efficiency of linear stopping rules for my model. A comparison of the best linear rules with the best rules is given in Table 1 for three cases. I plan to give a more coherent and comprehensive treatment of efficiency. Second, I plan to study how the rate of finding prey depends on prey density for various patterns of change of prey distribution with prey density. An example is illustrated in Fig. 1. Third, I plan to study how the distribution of prey in patches—and, consequently, the rate of finding prey—depends on the number of times that patches have been visited. The results of these calculations will provide components which may be used in population models.

I hope to be able to present a preliminary account of this work at the Ecological Society of America meeting at Toronto during the summer of 1989 and to submit the completed work to the *Journal of Animal Ecology* before the tenure of this grant is over. I will describe the details of the computations in one or two technical reports. All of this work is part of a larger whole which I hope to publish as a monograph on stochastic models of optimal foraging. If I receive support I should be able to finish this monograph during the 1989-90 academic year.

Budget justification

I am requesting support to pay half my salary during the academic year so that I can be relieved from half my teaching load, which is usually two courses per quarter. I am also requesting support at half the rate of my regular salary for two months during the summer of 1989. I have already done much of the basic theoretical work for this project at home on a PC clone, which is very convenient, but is also slow. Most of the remaining work involves intensive computing, so I am requesting a faster computer system to help. I will continue to need the support of the Computer Center for advice, software and high-quality printing. I am also requesting support in order to attend the ESA meeting in Toronto and to produce and publish the papers that result from the proposed work.

IMPORTANCE OF THIS WORK AND RELATION TO OTHER WORK IN POPULATION ECOLOGY

If one is interested in understanding the dynamics of populations then it is important to understand how individual behavior influences populations of individuals. Recently Hassell and May (1985) and Schoener (1986) have exhorted ecologists to think more about the consequences of individual behavior for population ecology. The foraging behavior of individual animals may be important in determining the population stability of predators and prey, or of hosts and parasites. The reduction of prey numbers by

predators may determine the value of maintaining feeding territories or of partitioning resources. I have studied aspects of foraging theory relevant to these issues and want to look at some of the implications of the theory.

I think that understanding the theory will be useful in trying to understand population ecology, but I also think that the attempt to understand population ecology will stimulate the study of foraging theory and will improve it by requiring attention to details that have been ignored by people using foraging theory to explain foraging behavior. In fact, some details can be ignored safely when studying foraging behavior because, at least for the models that I have studied, the performance of different foraging rules in a particular environment may be quite insensitive to the rule used, and a given rule that is best in one environment may be nearly best in quite a different environment. On the other hand, a change in the environment may lead to a substantial change in the performance of a given rule, and this may have important ecological consequences. I think that understanding foraging theory may be more important for ecologists than for behaviorists.

Several conclusions have emerged from the study of the problem of how a forager should decide when to leave one food patch and go on to another. (1) The form of the optimal strategy depends on the form of the prey distribution, and not just on travel time, the size of patches and the average prey density. (2) Optimal strategies are often very simple, and if the correct general form of strategy is used, then it does not matter much if the strategy used is not exactly the best. (3) The rate of finding prey achieved by an optimal forager depends on the variance as well as the average of prey density. These conclusions are not surprising, but they were missed by early workers on foraging theory, and were not noticed until the development of Oaten's (1977) model and the treatment of particular cases, especially by Iwasa *et al.* (1981).

The model that I plan to use is almost exactly the same as that used by Murdoch and Oaten (1975): they used the negative binomial prey distribution, computed the functional response of a randomly searching forager using a particular strategy as the parameters of the prey distribution were varied in particular ways, and used the functional response to study the stability of a modification of the Lotka-Volterra predator-prey model. For a number of sets of values for travel time and handling time they varied the parameters of prey distribution in a number of particular ways and found the largest prey density for which stable coexistence of predators and prey is possible. They found that stability is possible for at least some values of prey density for most of the sets of parameters they considered, but I do not expect to find this. I think that their conclusion was due, in part, to their choice of the giving-up-time rule, with a small value of the giving-up time, for each parameter set.

What Murdoch and Oaten (1975) did was to use a rule which (in a sense) tries to use information about feeding success within patches, even though such information is useless in the case in which the number of prey per patch has a Poisson distribution.

My interpretation of their result is that they use a rule that is never optimal, and performs worst at low prey densities but is not quite so bad for higher densities. The apparently population-stabilizing functional response that they observed was due to the fact that for some values of prey density the foraging strategy used was becoming less bad as prey density increased. The results do follow from the model, but quite different results would be obtained if the forager were assumed to use an optimal or near-optimal strategy. Murdoch and Oaten (1975, p. 51) are careful not to overstate their results and conclude that, "The question of the effect on stability of variability in patch densities, as a function of average patch density, remains open." I suspect that I will find a much smaller number of ways than did Murdoch and Oaten (1975) to vary the parameters of prey distribution and get a stabilizing functional response.

Looking at Murdoch and Oaten's (1975) paper one sees the difficulties of trying to put foraging behavior into a population model. [In a more recent paper Murdoch and Stewart-Oaten (1988) have treated some of the same questions of population ecology, but have not used any ideas of foraging theory.] I hope to have better success than they did, in part because I have the benefit of Oaten's (1977) later work. There have been a few other attempts to combine foraging behavior and functional response; for example, Comins and Hassell (1979) and Abrams (1982), but neither of these papers treats foraging behavior. Comins and Hassell (1979) simply assumed that at any time each forager goes to whichever patch has the highest prey density at that time. Abrams (1982) was not interested in foraging per se, but rather the question of whether an animal should forage or not. Abrams assumed that if the animal forages it does so optimally, but he was not interested in what that means.

The other problem that I am interested in is the way that an optimal forager reduces the number of prey by searching a patch. An optimal forager that is able to search systematically within patches should soon leave poor patches and take a small fraction of whatever prey are there. A good patch should be searched for a longer time and a larger proportion of the prey found. I do not think that this kind of density-dependent exploitation (in which a larger proportion of the prey are taken in those patches with more prey) should be confused with the sigmoid functional response (in which, for certain prey densities, the overall rate of finding prey per predator increases with prey density faster than prey density does) that may tend to stabilize a predator-prey system. I did confuse the two when I tried to treat exploitation [Green (1979)] and I think that Hassell, Lawton and Beddington (1977) confused the two when they interpreted experimental data on the number of prey attacked during a fixed time for different prey densities. There has been a recent surge of interest in the detection of density-dependence (for example, Stiling 1987), but it is important to realize that the consequences of density-dependence depend on the level at which it occurs.

It seems to me that there is a gap between behavioral ecology and population ecology and that this gap might be bridged by foraging theory. If the recent symposium volumes are any indication then foraging theory is moving downward into a consideration of behavioral mechanisms and questions of interest to psychologists (Commons, Kacelnik

and Shettleworth 1987), or sideways into a variety of questions of interest to behavioral ecologists and psychologists (Kamil, Krebs and Pulliam 1987), but not upward into population ecology. If population ecologists mention foraging behavior at all they take it as given, as Comins and Hassell (1979) and Abrams (1982) do, and go on from there.

In his "brief history of optimal foraging ecology," Schoener (1987) comments that among the ecology textbooks published in the 1970's after the emergence of optimal foraging theory, one [Krebs 1972, and 1978 (second edition), and 1985 (third edition)] did not mention feeding strategies at all, while others did not agree about where to put feeding strategy ecology. While I think that Schoener's comments are intended as criticism of the treatment of foraging theory by Charles Krebs and other ecologists, I take the fact that an ecologist as cautious and accurate as Krebs does not discuss foraging theory in his text as implying a justifiable criticism of foraging theory itself. While there has been work on diet selection that has, quite properly, been incorporated into ecology texts, I think that there has been little, if any, work of general ecological interest on the problem of patch residence-time. I hope to make up part of this deficit.

BIBLIOGRAPHY

- Abrams, P. A. 1982. Functional responses of optimal foragers. *American Naturalist* 120:382-390.
- Breck, J. E. 1978. Suboptimal foraging strategies for a patchy environment. Ph. D. dissertation, Michigan State University.
- Charnov, E. L. 1976a. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9:129-136.
- Charnov, E. L. 1976b. Optimal foraging: attack strategy of a mantid. *American Naturalist* 110:141-151.
- Comins, H. N., and Hassell, M. P. 1979. The dynamics of optimally foraging predators and parasitoids. *Journal of Animal Ecology* 48:335-351.
- Commons, M. L., Kacelnik, A., and Shettleworth, S. J. (eds.) 1987. *Quantitative Analysis of Behavior, Volume VI: Foraging*. Laurence Erlbaum Associates, Hillsdale, New Jersey.
- Emlen, J. M. 1966. The role of time and energy in food preference. *American Naturalist* 100:611-617.
- Gibb, J. 1962. L. Tinbergen's hypothesis of the role of specific search images. *Ibis* 104:106-111.
- Green, R. F. 1979. Functional response and the effect of a Bayesian predator on prey distribution. Department of Statistics, University of California, Riverside, Technical Report No. 56.
- Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theoretical Population Biology* 18:244-256.
- Green, R. F. 1981. Optimal foraging and functional response. (Unpublished manuscript)

- Green, R. F. 1984. Stopping rules for optimal foragers. *American Naturalist* 123:30-43.
- Green, R. F. 1987a. Stochastic models of optimal foraging. In: *Foraging Behavior*, (ed. by A. C. Kamil, J.R. Krebs, and H. R. Pulliam), pp. 273-302. Plenum Press, New York.
- Green, R. F. 1987b. A stochastic model of optimal foraging: systematic search for negative-binomially distributed prey. Computer Science, Mathematics and Statistics, University of Minnesota, Duluth, Technical Report No. 87-2.
- Green, R. F. 1987c. The giving-up-time rule as a strategy for animals foraging systematically in a patchy environment. Computer Science, Mathematics and Statistics, University of Minnesota, Duluth, Technical Report No. 87-3.
- Green, R. F. 1987d. Optimal foraging in patches, each of which contains the same number of prey. Computer Science, Mathematics and Statistics, University of Minnesota, Duluth, Technical Report No. 87-4.
- Green, R. F. 1988. Optimal foraging and pessimal foraging, or the optimal avoidance of predators. Computer Science, Mathematics and Statistics, University of Minnesota, Duluth, Technical Report No. 88-1.
- Green, R. F. (In preparation.) Optimal foraging for animals that search randomly in a patchy environment.
- Hassell, M. P., Lawton, J. H., and Beddington, J. R. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. *Journal of Animal Ecology* 46:249-262.
- Hassell, M. P., and May, R. M. 1974. Aggregation in predators and insect parasites and its effects on stability. *Journal of Animal Ecology* 43:567-594.
- Hassell, M. P., and May, R. M. 1985. From individual behaviour to population dynamics. In: *The British Ecological Society Symposium, Volume 25: Behavioural Ecology*, (ed. by R. M. Sibly and R. H. Smith), pp. 3-32. Blackwell Scientific Publications, Oxford.
- Iwasa, Y., Higashi, M., and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist* 117:710-723.
- Kamil, A. C., Krebs, J. R., and Pulliam, H. R. (eds.) 1987. *Foraging Behavior*. Plenum Press, New York.
- Krebs, C. J. 1972. *Ecology: The Experimental Analysis of Distribution and Abundance*. Harper and Row, New York. (Second Edition, 1978; Third Edition, 1985.)

- Krebs, J. R. 1973. Behavioral aspects of predation. In: *Perspectives in Ethology* (ed. by P. P. G. Bateson and P. H. Klopfer), Chapter 3. Plenum Press, New York.
- Lima, S. L. 1984. Downy woodpecker foraging behavior: efficient sampling in simple stochastic environments. *Ecology* 65:166-174.
- Lima, S. L. 1985. Sampling behavior of starlings foraging in simple patchy environments. *Behavioral Ecology and Sociobiology* 16:166-174.
- MacArthur, R. H. 1972. *Geographical Ecology*. Harper and Row, New York.
- MacArthur, R. H., and Pianka, E. R. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603-609.
- McNair, J. N. 1982. Optimal giving-up times and the marginal value theorem. *American Naturalist* 119:511-529.
- McNamara, J. 1982. Optimal patch use in a stochastic environment. *Theoretical Population Biology* 21:269-288.
- McNamara, J. M., and Houston, A. I. 1987. Foraging in patches: there's more to life than the marginal value theorem. In: *Quantitative Analysis of Behavior, Volume VI: Foraging* (ed. by M. L. Commons, A. Kacelnik, and S. J. Shettleworth), pp. 23-39. Laurence Erlbaum Associates, Hillsdale, New Jersey.
- Murdoch, W. W., and Oaten, A. 1975. Predation and population stability. *Advances in Ecological Research* 9:2-131.
- Murdoch, W. W., and Stewart-Oaten, A. 1988. Aggregation by parasitoids and predators: good for control, bad for stability. Submitted for publication.
- Oaten, A. 1977. Optimal foraging in patches: a case for stochasticity. *Theoretical Population Biology* 12:263-285.
- Pyke, G. H., Pulliam, H. R., and Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 52:137-154.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:369-404.
- Schoener, T. W. 1986. Mechanistic approaches to community ecology: a new reductionism? *American Zoologist* 26:81-106.

- Schoener, T. W. 1987. A brief history of optimal foraging ecology. In: *Foraging Behavior* (ed. by A. C. Kamil, J. R. Krebs, and H. R. Pulliam), pp. 5-67. Plenum Press, New York.
- Stephens, D. W., and Krebs, J. R. 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Stewart-Oaten, A. 1982. Minimax strategies for a predator-prey game. *Theoretical Population Biology* 22:410-424.
- Stiling, P. D. 1987. The frequency of density dependence in insect host-parasitoid systems. *Ecology* 68:844-856.
- Taylor, L. R. 1984. Assessing and interpreting the spatial distribution of insect populations. *Annual Review of Entomology* 29:321-357.
- Waage, J. K. 1979. Foraging for patchily distributed hosts by the parasitoid, *Nemeritis canescens*. *Journal of Animal Ecology* 48:353-371.