

**CAN OPTIMAL FORAGING STABILIZE  
A PREDATOR-PREY SYSTEM?**

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Running Head: Optimal foraging and predator-prey stability

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## SUMMARY

- (1) An optimal foraging model is presented for predators that search for prey which are aggregated in patches, with the number of prey per patch having a negative binomial distribution. The rate of finding prey is calculated for an optimal forager and for an almost-optimal forager which uses a very simple foraging strategy. The performance of foraging strategies of the best general form is shown to be insensitive to changes in the exact form.
- (2) The rate of finding prey depends on the strategy used by the predator and on the distribution of prey in patches. For a particular foraging strategy, the rate of finding prey is calculated as a function,  $R(N)$ , of average prey density,  $N$ , as the prey distribution changes in particular ways. This rate,  $R(N)$ —the “functional response”—is put into a modification of the Lotka-Volterra predator-prey equations suggested by Murdoch & Oaten (1975).
- (3) The condition for an equilibrium to be locally stable in Murdoch and Oaten’s model is that the rate of finding prey per predator per prey,  $R(N)/N$ , must be increasing at equilibrium. I plot the rate  $R(N)/N$  against  $N$  for two patterns of change of prey distribution: (a) the negative binomial parameter,  $k$ , is constant, and (b)  $k$  increases in proportion with  $N$ . Each of these plots is done in two ways: (i) keeping the foraging strategy the same, no matter what the prey distribution, and (ii) letting the predator use whatever foraging strategy is best for the prevailing prey

distribution.

- (4) The stability of the model depends on how the prey distribution changes with prey density. If foragers use the strategy which is optimal when the prey density is at equilibrium, then, for small handling time, the model is stable if the parameter  $k$  is constant, but not if  $k$  increases in proportion to average prey density. The conditions on predator behavior and prey distribution that lead to stability are quite limited. It appears to be more difficult for optimal foraging behavior to stabilize a predator-prey model than Murdoch & Oaten (1975) suggested.
- (5) A conclusion similar to mine also holds for a host-parasitoid model considered by May (1978), in which aggregation occurs in predation risk rather than in prey distribution. I show that the stability seen in May's model is due not only to the degree of aggregation of predation risk, but it also depends on the way in which the degree of aggregation changes with predator density.

## INTRODUCTION

In recent years, ecologists have been exhorted to try to use individual behavior to understand population ecology (Hassell & May 1985, Schoener 1986). In particular, it might be possible to use optimal foraging theory to help understand the dynamics of predator-prey and host-parasitoid systems. Two early attempts (Hassell & May 1974, Murdoch & Oaten 1975) showed that this was possible, but this early work was not as successful as it might have been because the appropriate optimal foraging theory had not been worked out, and the biological factors responsible for the stability of the population models were not clear. Since then, there has been substantial development of optimal foraging theory, in particular, the work by Oaten (1977) and his followers on stochastic models, and a better understanding of the biological interpretation of host-parasitoid models has been developed, in particular, by Hassell (1978) and coworkers,

including May (1978), and by the reinterpretation by Chesson & Murdoch (1986) of the earlier models.

In this paper, I concentrate on the functional response of predators to prey numbers, that is, the relationship between  $R(N)$ , the rate of finding prey per predator, and the overall prey density,  $N$ . Solomon (1949) distinguished between the way that predator numbers change with prey density—the “numerical response”—and the way that the predation rate changes with prey density—the “functional response.” Holling (1959) classified different forms of the functional response according to whether  $R(N)$  is linear (Type I), negatively accelerating (Type II), or positively accelerating (Type III) at low prey density. For my purposes, Holling’s classification corresponds to whether the rate of finding prey per predator per prey,  $R(N)/N$ , is constant (Type I), is decreasing (Type II), or is increasing (Type III) when the prey population is at equilibrium.

In this paper, I will first introduce the predator-prey model treated by Murdoch & Oaten (1975) and show how foraging comes into the model. Then I will describe my optimal foraging model, and I will illustrate some basic results. In particular, I will show that the optimal strategy is not only efficient, but it is also simple and robust. My treatment of the predator-prey model will follow that of Murdoch and Oaten quite closely, except that I will find the optimal foraging strategy and will consider what happens when the predators use the strategy which is optimal when the prey population is at equilibrium. I will show that the stability of the model depends on how the prey distribution changes as the average prey density changes.

### THE PREDATOR-PREY MODEL

In order to study the effect of foraging behavior on a predator-prey model, Murdoch & Oaten (1975) offered a modification of the Lotka-Volterra model. In the Lotka-Volterra model, the numbers of prey,  $N$ , and the numbers of predators,  $P$ , are governed

by the differential equations:

$$dN/dt = aN - bNP, \quad (1)$$

$$dP/dt = -cP + dNP. \quad (2)$$

The first terms of the right-hand sides of equations (1) and (2) say that in the absence of predators, prey numbers increase exponentially, while in the absence of prey, predator numbers will decrease exponentially. The second terms are more interesting. These terms say that there is an effect of predation on prey numbers, and a corresponding effect of predation on predator numbers, and that these effects are proportional to the product of the numbers of predators and prey. One interpretation of this is that population change is proportional to the overall rate of predation, and that in any small interval of time, each predator has a small chance of finding and eating each prey. That is, the rate of total predation is proportional to  $NP$ ; the rate of finding prey, per predator, is proportional to  $N$ ; and, most simply, the rate of finding prey, per predator per prey, is constant.

An interesting mathematical property of the Lotka-Volterra model is that it is neutrally stable. That is, if a system is started at some point  $(N, P)$  other than equilibrium, then the system will move in a closed orbit about the equilibrium point. In particular, if the system is started at some point close to the equilibrium, then the system will move about the equilibrium in an orbit very close to an ellipse, never getting much closer or farther away from the equilibrium point than at the start. This local analysis is described by Pielou (1977).

Murdoch & Oaten (1975) modified the simple Lotka-Volterra model by assuming that the rate of finding prey, per predator, might be some general function of  $N$ . If we

write this rate as  $R(N)$ , then the Lotka-Volterra equations become

$$dN/dt = aN - bR(N)P, \quad (3)$$

$$dP/dt = -cP + dR(N)P. \quad (4)$$

If there exists an equilibrium such that  $R(N)/N$  is increasing in  $N$  at equilibrium, then that equilibrium is locally stable. That is, if the system is started at a point near the equilibrium, then the system will approach that equilibrium.

It is possible that the predation rate, per predator per prey, depends on the number of predators,  $P$ , but not on the number of prey,  $N$ . That is, for some general function,  $S(P)$ , we have

$$dN/dt = aN - bNS(P), \quad (5)$$

$$dP/dt = -cP + dNS(P). \quad (6)$$

In this case, an equilibrium will be stable if  $S(P)$  is an increasing function, but  $S(P)/P$  is a decreasing function of  $P$  at equilibrium. One way of interpreting these models is that a predator-prey system may be locally stable if predators become more efficient as prey density increases [equations (3) and (4)], or if predators become less efficient as their own density increases [equations (5) and (6)]. In this paper I will concentrate on the effect of changing prey density.

### THE OPTIMAL FORAGING MODEL

The optimal foraging model that I use is a particular case of Oaten's (1977) general stochastic model. Following Oaten, I assume that:

- (i) Prey are located in superficially similar patches of the same size, with a known distribution of the number of prey per patch.
- (ii) The joint distribution of capture times, given the number of prey in a patch, is known.
- (iii) A forager spends travel time,  $\tau$ , going from each patch to the next, and spends time  $h$  handling each prey that is captured (I assume that prey which are found are captured).
- (iv) The forager decides when to leave a patch based on the “knowledge” specified in (i)-(iii), and on its experience in a patch.
- (v) For a given foraging strategy it is possible to calculate the long-term average rate of finding prey, given by

$$R = EG/[ET + \tau + hEG], \quad (7)$$

where  $ET$  and  $EG$  are the expected time spent searching per patch and the expected number of prey found per patch, respectively.

- (vi) The optimal foraging strategy is the one which maximizes the value of  $R$ .

I make the particular assumptions that

- (i) The number of prey per patch has a negative binomial distribution with parameters  $k$  and  $m$ , where  $k$  is a measure of aggregation, and  $m$  is the mean.
- (ii) The prey that are found in a patch are distributed at random there, and predator search within a patch is systematic, with the time required to search a patch completely equal to one. This means that the times of finding prey within a patch are independently and uniformly distributed on the interval  $(0,1)$ .

The assumption that the number of prey per patch has a negative binomial distribution is biologically realistic, and is an assumption commonly made in modeling the distribution of individual organisms in particular areas (Southwood 1966; Pielou 1977). The assumption that search is systematic is sometimes correct (Lima 1984), although animals sometimes seem to forage randomly (Marschall, Chesson & Stein 1989; DeVries, Stein & Chesson 1989). Modelers often assume that search is random for mathematical convenience (for example, Hassell & May 1974; Murdoch & Oaten 1975; Iwasa, Higashi & Yamamura 1981), but search is certainly non-random in many cases (Gill & Wolf 1975; Kamil 1978; Baum 1987).

In calculating a predator's rate of finding prey for a predator-prey model, handling time is of great importance and must be included, but it is irrelevant in the determination of the optimal foraging strategy. That is, the strategy that maximizes expression (7) for one particular value of handling time will maximize it for all other values. Therefore, I will assume that  $h = 0$  and ignore the term,  $hEG$ , in expression (7) when I do my calculations and present my results for the optimal foraging model.

The optimal foraging strategy for my model is found by using dynamic programming. The details are given in Green (1987) and will not be repeated here, except for the calculation of the rate of finding prey that is achieved once a particular foraging strategy has been chosen. This calculation is given in an Appendix. The general idea in finding the optimal strategy is that a value is guessed for the highest possible rate of finding prey,  $R$ , and a strategy is found that "tries to achieve" that rate. Then the rate that the strategy actually achieves is found, and this value is compared with the value guessed. When the rate achieved equals the value guessed, then the optimal strategy has been found. It turns out that for a negative binomial prey distribution and systematic search the optimal foraging strategy has quite a simple form. In general, a forager in such a situation should stay longer in patches in which more prey have been found, and

should leave patches in which fewer prey have been found. In particular, there is a set of times,  $t(x)$ , such that the forager should leave a patch at time  $t(x)$  if exactly  $x$  prey have been found by that time. If enough prey are found, the forager should remain in the patch until it has been searched completely ( $t = 1$ ).

## RESULTS

### *The optimal foraging strategy*

The optimal foraging strategy (that is, the stopping points) for the particular case:  $k = 0.5$ ,  $m = 5$  and  $\tau = 0.1$  is illustrated in Fig. 1a. When the values of  $x$ , the numbers of prey found in a patch, are plotted against  $t(x)$ , the times at which the forager should leave a patch if exactly  $x$  prey have been found by that time, it can be seen that the resulting points lie almost on a line. In Fig. 1b is plotted a similar rule (this one slightly sub-optimal) for which the stopping points do lie on a line. The stopping times for such a rule can be written as:

$$t(x) = a + bx. \quad (8)$$

The rule illustrated in Fig. 1b is the best linear stopping rule for the same case:  $k = 0.5$ ,  $m = 5$  and  $\tau = 0.1$ . For this rule,  $a = 0.0754$  and  $b = 0.1301$

Not only are the rules illustrated in Figs. 1a and 1b very similar, but the rates of finding prey that they achieve are virtually indistinguishable. The best rule (Fig. 1a) achieves rate  $R = 8.0744$ , while the best linear rule (Fig. 1b) achieves rate  $R = 8.0705$ , which differs from the best rate by less than 0.05%. Table 1 compares the performance of the best rule and the best linear rule for several sets of prey distribution and travel time.

In none of the cases that I have looked at is the difference between the performances of the best rule and of the best linear rule very large. For practical purposes there seems

to be no difference between the best rule and best linear rule. However, linear stopping rules are easier to describe, being characterized by the constants  $a$  and  $b$ . A forager using a linear stopping rule would behave like a simple wind-up toy that leaves a patch whenever it becomes wound down. Such a toy might be wound up some amount ( $= a$ ) upon entering a new patch, and it would be wound up an additional amount ( $= b$ ) every time a prey is found. Such a mechanism was suggested by Waage (1979) for a parasitic wasp searching for patchily-distributed hosts.

*Robustness of the optimal foraging strategy*

The optimal foraging strategy that I have found—or, rather, a linear stopping rule (8), which is essentially the same, and which I will treat here instead of the optimal strategy as a matter of conceptual convenience—is not only simple, but it is also robust in the sense that a rule which is best for one particular prey distribution is likely to be quite good for another, quite different, prey distribution that is of the same type. For a particular prey distribution, the rate of finding prey achieved by a forager that uses a strategy of the right general form is not very sensitive to which particular rule is used. The insensitivity of the rate of finding prey to the exact form of the rule used is illustrated in Fig. 2 for several sets of prey distribution. This figure gives topographic maps, in which elevation is the rate of finding prey, measured in terms of efficiency relative to the best rule, and the  $a$  and  $b$  coordinates represent the coefficients for linear stopping rules (8). Points along the horizontal axis ( $a > 0, b = 0$ ) represent rules in which a forager remains in each patch for a fixed amount of time equal to  $a$ , then leaves, no matter how many prey have been found. The point ( $a = 1, b = 0$ ) represents the “naive” rule (Green 1980) in which a forager searches each patch completely, ignoring the number of prey found there. Points along the line  $a + b = 1$  represent rules in which a forager leaves a patch if no prey are found by time  $a$ , and remains until the patch has been searched completely if one or more prey is found before time  $= a$ . A similar rule was found to be

optimal for a foraging experiment performed by Lima (1984). Points along the vertical axis ( $a = 0$ ) represent a forager which leaves each patch immediately upon entering it. A forager using such a rule would find no prey.

It can be seen that quite a wide range of coefficients give rules that achieve rates which are 90% or 95% of the maximum possible. One way to interpret the relative efficiency of a particular foraging strategy is to compare it with the relative efficiency of the “naive” strategy. For example, in the case  $k = 0.5$ ,  $m = 5$  and  $\tau = 0.1$ , illustrated in Fig. 2a, the highest possible rate of finding prey is 8.0744, while the “naive” rate is  $m/(1 + \tau) = 4.54545$ . Thus, the relative efficiency of the “naive” rule is  $4.54545/8.0744 = 56\%$ . For many sets of coefficients,  $a$  and  $b$ , a linear rule does much better than the naive rule.

A comparison of the maps given in Fig. 2a-d shows that, while the coefficients of the best linear rules differ with differing prey distributions, a rule that does well for one distribution is likely to do well for a different distribution of the same general type. For example, the prey distributions illustrated in Figs. 2a and 2c differ in average by a factor of two, but the rule that is best in either case will, when used in the other case, achieve a rate about 90% of that achieved by the best rule in that case.

In short, linear stopping rules are simple, efficient, and robust.

### *Functional response*

In order to investigate the stability of Murdoch & Oaten’s (1975) model, the rate of finding prey is calculated for particular prey distributions as prey density changes. Then the rate of finding prey, per predator per prey,  $R(N)/N$ , is plotted against overall prey density,  $N$ , as prey distribution (and possibly the foraging strategy) changes in particular ways with overall prey density. An equilibrium with prey density  $N^*$  will be

stable if  $R(N)/N$  is increasing at  $N = N^*$ . Since  $N$  represents density, its units are arbitrary, and  $N$  may be identified with  $m$ , the average number of prey per patch for the negative-binomial prey distribution. In Fig. 3,  $R(N)/N$  is plotted against  $N$ , with travel time ( $\tau = 0.1$ ) and the negative binomial parameter ( $k = 0.5$ ) remaining constant as  $N$  changes. In Fig. 3a the predator is assumed to use the strategy which is optimal when overall prey density = 5 ( $k = 0.5, m = 5$ ), and this same strategy is used no matter what the prey density is. In Fig. 3b the predator is assumed to use whichever strategy is best for the prey distribution that prevails at the time. In both Figs. 3a and b the rate  $R(N)/N$  is plotted for three different handling times. If the equilibrium prey density is  $N^* = 5$  (indicated by a broken vertical line), then it is seen that—for the shortest handling time ( $h = 0$ )— $R(N)/N$  is increasing at  $N = N^* = 5$  for either a fixed foraging strategy (Fig. 3a) which is best at that prey density, or for a changing strategy that is always best (Fig. 3b). However, for the larger handling times of  $h = 0.05$  and  $h = 0.10$ ,  $R(N)/N$  is decreasing at  $N = N^* = 5$ , and the system given in equations (3) and (4) is unstable.

In Fig. 4, the rate  $R(N)/N$  is plotted against  $N$  assuming that travel time ( $\tau = 0.1$ ) is constant but the negative binomial parameter  $k$  for the prey distribution changes with density, remaining proportional to prey density. In order to make the cases illustrated in Fig. 4 comparable to those in Fig. 3, it is assumed that  $k = 0.1N$ . In Fig. 4a the forager is assumed always to use the strategy that is best for  $k = 0.5$  and  $m = 5$ , while in Fig. 4b the forager is assumed to use whichever strategy is best for the prey distribution which prevails at the time. In this example, it is seen that  $R(N)/N$  decreases with  $N$  at all prey densities, and for all handling times, whether the foraging strategy used remains constant or changes with prey density. In particular, an equilibrium with  $N^* = 5$  (indicated by the broken vertical line) would be unstable if the predator used the strategy that was optimal at that prey density (Fig. 4a).

A comparison of Fig. 3a with 3b, and of Fig. 4a with 4b, indicates that it makes little difference, at least around the equilibrium, whether a predator always uses a fixed strategy that is best at equilibrium, or uses a changing strategy that is always best for the prey distribution at the time. However, a comparison of Fig. 3 with Fig. 4 shows that it does make a difference how the parameters of the prey distribution change as overall prey density changes. It seems that the conditions under which optimal foraging can contribute to predator-prey system stability are rather limited, especially in terms of handling time, but such conditions do exist, and they depend on how the prey distribution changes with overall prey density.

While it is possible, indeed it is likely, that a predator will not use an optimal foraging strategy, it may be reasonable to assume that a predator's foraging strategy will not change with very small changes in prey distribution. That is, the cases illustrated in Figs. 3a and 4a are most likely to hold. Now, looking at Fig. 3a—the most interesting, because it offers hope of stability—we see that there may be stability if handling time is zero ( $h = 0$ ), and if the prey equilibrium is five prey per patch ( $N^* = 5$ ), where five prey per patch is the overall prey density for which the foraging strategy is best. However, we might want to make the realistic assumption that the equilibrium prey density is not the one for which the foraging strategy used is the best. For example, perhaps the equilibrium prey density is  $N^* = 2$ , while the foraging strategy used by predators is that which is best when prey overall prey density is 5. We can see from Fig. 3a that  $R(N)/N$  is increasing at  $N = N^* = 2$ , not only for  $h = 0$ , but also for  $h = 0.05$  and  $0.10$ . On the other hand, if the prey equilibrium is  $N^* = 10$ , and the foraging strategy used is that which is best when overall prey density is 5, then we see from Fig. 3a that  $R(N)/N$  is decreasing, albeit slightly, even for  $h = 0$ . This shows that the stability of the model depends not just on the prey distribution and how prey distribution changes with prey density, but it also depends on the particular foraging strategy that the predator uses.

## DISCUSSION

Despite the exhortations to put individual behavior into population models (Hassell & May 1985; Schoener 1986), and despite the developments in foraging theory summarized by Stephens & Krebs (1986), there has been little attempt since Hassell & May (1974), and Murdoch & Oaten (1975) to use foraging theory to understand predator-prey and host-parasitoid population models. Among the few exceptions are Abrams (1982) and Bernstein, Kacelnik & Krebs (1988). However, Abrams (1982) does not consider foraging behavior per se, but rather the decision whether to forage or not, and Bernstein, Kacelnik, & Krebs (1988) do not consider population dynamics, although their paper is intended as a first step in that direction.

Both the Lotka-Volterra predator-prey model as modified by Murdoch & Oaten (1975), and the Nicholson-Bailey model as modified by a number of authors, whose work is summarized by Hassell (1978), contain terms in which predation (or parasitism) rate is given as an explicit function of predator and prey (or parasitoid and host) numbers. It seems to be natural to ask the question what these functions would look like for optimal foragers, especially now that a theory of optimal foraging is available to help answer the question.

An advantage of studying foraging behavior in order to understand population ecology is that foraging occurs over a small enough scale (in space and time) that it might be possible to comprehend. On the other hand, the dynamics of an entire population may involve too much time and space to be studied in detail. An extreme example of this is Schaffer's (1984) complaint that the time series provided by the Hudson Bay Company's hare-lynx data is too short for him to test his ideas about the dynamics of that system. If no series of population data is long enough to permit an understanding of population dynamics, perhaps it is necessary to pay more attention to the behavioral

mechanisms underlying population change.

Using the predator-prey population model of Murdoch & Oaten (1975), in which the system is locally stable if the rate of finding prey per predator per prey,  $R(N)/N$ , is increasing at equilibrium, I show that the conditions for stability are met if the predator forages optimally and a number of other conditions are satisfied. The stability of Murdoch & Oaten's (1975) model depends on the predators' foraging strategy, the time spent handling each prey, the prey distribution, and the way that prey distribution changes with prey density. If prey are aggregated in patches, with the number of prey per patch having a negative binomial distribution, and if the predators use the foraging strategy which is best when prey density is at equilibrium, then stability is possible if handling time is short enough, and the degree of aggregation of prey does not decrease very rapidly with prey density (that is,  $k$  is constant, or slowly changing with the average number of prey per patch,  $m$ ).

An equilibrium is more likely to be stable if foragers use a strategy which is best for a prey density higher than that at equilibrium. This fact is the basis of the difference between my conclusions and those of Murdoch & Oaten (1975) who find that foraging can stabilize their model in three patterns of changing prey distribution. Murdoch & Oaten (1975) showed that the foraging strategy that they considered could stabilize their model in both of the cases that I consider: (i) negative binomial prey distribution and constant  $k$ , (ii) negative binomial distribution and  $k$  proportional to the mean, and another case as well: (iii) Poisson prey distribution. Murdoch & Oaten (1975) did not find the optimal foraging strategy for their predators but, assuming that search within patches was random, they calculated the predation rate for predators that use a fixed-giving-up-time rule to decide when to leave a patch. That is, a predator was assumed to leave a patch as soon as it had spent a fixed length of time,  $T$ , in the patch without (or since) finding a prey. Murdoch & Oaten (1975) found that foraging stabilized

their model, not because the foraging strategy that they considered was sub-optimal, but rather because the particular giving-up time,  $T$ , that they chose was small, being relatively better for higher prey densities. Thus, the predation rate might increase rapidly with prey density and stabilize the system because the foraging strategy considered was better adapted for high prey densities, and foraging tended to become less inefficient as density increased.

A look at the topographic maps in Fig. 2 shows that if foragers are to use rules which are not optimal, it is better to err on the side of remaining in patches longer than they should, that is, to use rules better adapted to lower overall prey densities. A cautious predator might be expected to err in the direction that would reduce its predation rate the least, but such an error would tend to destabilize the system.

Data on insect populations (Taylor 1984) suggest that if aggregated prey distributions are negative binomial, then the parameter,  $k$ , tends to increase with density, but slower than proportionally. That is, the change in prey distribution with prey density would lie somewhere between the two cases that I have considered, one of which permits stability, the other of which does not.

The safest conclusion to draw from my analysis is that while optimal foraging can contribute to the stability of a predator-prey model under some circumstances, the range of conditions under which it does produce stability are quite limited. Certainly they are more limited than Murdoch & Oaten (1975) suggested. It seems to me to be worthwhile to check particular systems to see whether the conditions for stability are met.

#### *Other models*

The Lotka-Volterra predator-prey model [(1) and (2)] can be stabilized by letting the predation rate depend on prey numbers [equations (3) and (4)] or by letting the predation rate depend on predator numbers [equations (5) and (6)]. More attention has

been paid to the effect of prey numbers, the “functional response,” and this is what I have looked at in this paper. However, the negative quality of my results suggests that more attention might be paid to the effect of predator numbers. I have not done this, but people studying host-parasitoid models have.

*The Nicholson-Bailey host-parasitoid model*

In fact, Hassell & Comins (1978) have shown that if the Nicholson-Bailey host-parasitoid model is written as:

$$N(t + 1) = bN(t)\exp[-aP(t)] \quad (9)$$

$$P(t + 1) = cN(t)\{1 - \exp[-aP(t)]\}, \quad (10)$$

where  $a$  is the attack rate per host per parasitoid,  $N(t)$  and  $P(t)$  are the host and parasitoid numbers, respectively, in the present generation, and  $N(t + 1)$  and  $P(t + 1)$  are the host and parasitoid numbers, respectively, in the next generation, then the system cannot be stabilized by letting the attack rate,  $a$ , depend on host numbers. If we think of  $a$  as being the functional response, this result says that functional response cannot stabilize this (usual) host-parasitoid model. Nunney (1980) pointed out that this result does not apply to all difference-equation models, but that it applies here because of the assumption that chance of escaping attack is an exponentially decreasing function of the number of attacks.

*May's "phenomenological model"*

Host-parasitoid models can be stable if there is interference among parasitoids (Rogers & Hassell 1974; Beddington 1975), and May (1978) has shown that his “phenomenological model” is stable if the degree of aggregation of attacks is sufficiently great. May’s model can be written:

$$N(t + 1) = bN(t)[1 - aP(t)/k]^k \quad (11)$$

$$P(t + 1) = cN(t)\{1 - [1 - aP(t)/k]^k\}, \quad (12)$$

where the term

$$f(N, P) = [1 - aP/k]^k, \quad (13)$$

the chance that an individual host will escape attack, is the zero term of a negative binomial distribution with parameter  $k$ . The parameter,  $k$ , is a measure of the degree of aggregation of attack (smaller  $k$  means more aggregation), or equivalently, the distribution of the number of parasitoids per host patch.

There are two points to emphasize about May's (1978) model. First, the modification of the original, unstable Nicholson-Bailey model [(9) and (10)] that permits stability in May's model [(11) and (12)] involves an effect of parasitoid numbers and parasitoid aggregation, not of host numbers and host aggregation. This point has been emphasized by Chesson & Murdoch (1986). Second, the stability of May's model does not depend simply on the degree of aggregation of attack, but it also depends on the pattern of change in aggregation with parasitoid numbers. This is the same point that I made above for the effect of prey aggregation in a predator-prey model. This point can be made for May's model by writing:

$$f(N, P) = [1 - aP^*/k]^{kP/P^*}, \quad (14)$$

where  $P$  is the parasitoid density and  $P^*$  is the equilibrium parasitoid density. It can be seen that (14) is just an exponential function of  $P$ , and a model incorporating (14) reduces to the unstable Nicholson-Bailey system [(9) and (10)]. However, at equilibrium ( $P = P^*$ ), the value of (14) would be the same as the value of (13), and would have the same biological interpretation—that attack is aggregated with negative binomial parameter  $k$ . There is no difference between (13) and (14) at equilibrium, but there is a difference around equilibrium, and this difference is critical. In May's (1978) model (13),  $k$  is

constant, while in (14),  $kP/P^*$  plays the same role, but it is proportional to parasitoid density,  $P$ .

### *Conclusion*

Early work (Hassell & May 1974) may have been misleading in suggesting that host-parasitoid models can be stabilized if hosts are aggregated, and parasitoids aggregate their attacks in areas where hosts are more numerous. Aggregation of prey in patches where predators can concentrate their search may contribute to the stability of predator-prey models such as that proposed by Murdoch & Oaten (1975) and treated in this paper, but it is important to realize that in models such as May's (1978) the stability that is seen is due to the fact that some hosts are more likely to be attacked than others, and because parasitoids become less efficient as their density increases. Chesson & Murdoch (1986) point out that a host-parasitoid system is more likely to be stable if the aggregation of attack occurs independently of host density than if attack is concentrated in areas with more hosts.

The predator-prey model that I have considered, and the host-parasitoid models, such as those treated by Hassell (1978), are usually examined for local stability. That is, if a system is perturbed slightly from equilibrium, does it tend to return to equilibrium? The stability of such models depends on what happens around equilibrium. It may be that populations are not locally stable, and that they persist because some mechanism, or mechanisms, prevents extinction when one or another population is low. Some behavioral mechanisms have been suggested that could promote persistence, for example, switching of prey when prey density is low (Murdoch & Oaten 1975, and, more recently, Abrams 1987), or cessation of foraging when prey density is low (Abrams 1982). Such mechanisms would have obvious effects on the predation rate. These effects, and the more subtle effects due to changes in prey distribution with prey density, all are important in determining the dynamics of interacting populations.

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**APPENDIX.** The rate of finding prey for a forager that uses a patch-leaving rule based on the number of prey found.

*Foraging strategy.*

I assume that foragers search systematically within a patch and that they leave a patch when it has been searched completely. The time to search a patch completely is set equal to 1, and expected travel time,  $\tau$ , between patches is then defined in terms of this time. There is a non-negative integer  $n$  and a set of times,  $\{t(x)$ , for  $x = 0, 1, 2, \dots, n\}$ , with  $t(0) < t(1) < t(2) < \dots < t(n)$ , such that a forager should leave a patch if  $x$  prey have been found by time  $t(x)$ . If more than  $n$  prey are found in a patch, then a forager should remain in the patch until it has been searched completely.

If we identify the location of prey in patches with the time that it would take a forager to find them if it remained in the patch long enough to find them, then we can write

$v(x)$  = the probability that there are exactly  $x$  prey in the interval  $[0, t(x)]$ , for  $x = 0, 1, 2, \dots, n$ ;

$w(i, j)$  = the probability that there are exactly  $j - i$  prey in the interval  $[t(i), t(j)]$ , given that there exactly  $i$  prey in the interval  $[0, t(i)]$ , and

$p(x)$  = the probability of finding exactly  $x$  prey by time  $t(x)$ , but having found more than  $i$  prey at time  $t(i)$ , for all  $i < x$ .

In order to determine how well a particular rule does, we need to specify the prey distribution and find the values of  $p(x)$  for the particular rule and for the specified prey distribution. In general, we will have

$$p(0) = v(0) \tag{A1}$$

$$p(x) = v(x) - \sum_{i=0}^{x-1} p(i)w(i, x), \tag{A2}$$

for  $x = 1, 2, \dots, n$ .

*The prey distribution.*

I assume that the number of prey per patch is a random variable having a negative binomial distribution. I interpret this distribution in a Bayesian framework, using the notation of DeGroot (1970), thinking of a negative binomial distribution as a gamma-distributed mixture of Poisson distributions. That is, in a patch of “quality” =  $\lambda$ , the distribution of the number of prey,  $Y$ , will have a Poisson distribution with probability function:

$$f(y|\lambda) = \frac{e^{-\lambda} \lambda^y}{y!} \tag{A3}$$

Patch quality is assumed to vary, with  $\lambda$  itself being a gamma-distributed random variable with probability density function:

$$\xi(\lambda|\alpha, \beta) = \frac{\beta^\alpha \lambda^{\alpha-1} e^{-\beta\lambda}}{\Gamma(\alpha)} \tag{A4}$$

Using this notation, we may think of “patch quality” =  $\lambda$  as being a parameter that the forager has to estimate, and the values of  $\alpha$  and  $\beta$  are the parameters of the prior distribution of  $\lambda$ . If a forager spends time  $t$  in a patch and finds  $x$  prey during that time,

then the prior parameters  $\alpha$  and  $\beta$  are updated by this experience in the patch and become the posterior parameters  $\alpha + x$  and  $\beta + t$ .

Using the parameters  $\alpha$  and  $\beta$ , the negative binomial distribution for the number of prey in a patch may be written:

$$f(y|\alpha, \beta) = \binom{\alpha + y - 1}{y} \left( \frac{\beta}{1 + \beta} \right)^\alpha \left( \frac{1}{1 + \beta} \right)^y \quad (A5)$$

In this notation, the gamma parameter  $\alpha$  is the same as the negative binomial parameter  $k$ , and the ratio  $\alpha/\beta$  is the same as the negative binomial mean,  $m$ . The distribution of the number of prey to be found during the first  $t$  units of time in a patch may be written:

$$f(x, t|\alpha, \beta) = \binom{\alpha + x - 1}{x} \left( \frac{\beta}{t + \beta} \right)^\alpha \left( \frac{t}{t + \beta} \right)^x \quad (A6)$$

The probability of there being exactly  $j$  prey in the interval  $[0, t(j)]$ , given exactly  $i$  prey in the interval  $[0, t(i)]$ , for  $i < j$ , may be written:

$$f(j - i, t(j)|\alpha, \beta, i, t(i)) = \binom{\alpha + i - 1}{j - i} \left( \frac{\beta + t(i)}{\beta + t(j)} \right)^{\alpha+i} \left( \frac{t(j) - t(i)}{\beta + t(j)} \right)^{j-i} \quad (A7)$$

*The rate of finding prey*

The expressions given in (A6) and (A7) may be used to calculate the probabilities needed to find the values  $p(x)$ . We have

$$p(0) = v(0) = f(0, t(0), |\alpha, \beta) \quad (A8)$$

$$v(x) = f(x, t(x)|\alpha, \beta) \quad (A9)$$

$$w(i, j) = f(j - i, t(j)|\alpha, \beta, i, t(i)) \quad (A10)$$

If the average travel time between patches is  $\tau$ , then the rate of finding prey will equal

$$R = EG/[ET + \tau], \quad (A11)$$

where  $EG$  is the expected number of prey found per patch, and  $ET$  is the expected time spent searching each patch.  $ET$  will equal the time to search a patch completely ( $t = 1$ ) minus the average time saved by leaving patches early, while  $EG$  will equal the average number of prey per patch ( $\alpha/\beta$ ) minus the average number of prey missed by leaving patches early.

A forager that has found  $x$  prey after spending time  $t$  in a patch expects to be finding prey within that patch at rate

$$r(x, t) = (\alpha + x)/(\beta + t), \quad (A12)$$

and such a forager could expect to find  $r(x, t)(1 - t)$  additional prey if it were to remain in the patch until it had been searched completely.

Using the values obtained by using expressions (A2), (A8-10), and (A12), the expectations  $ET$  and  $EG$  may be found:

$$ET = 1 - \sum_{x=0}^n p(x)[1 - t(x)] \quad (A13)$$

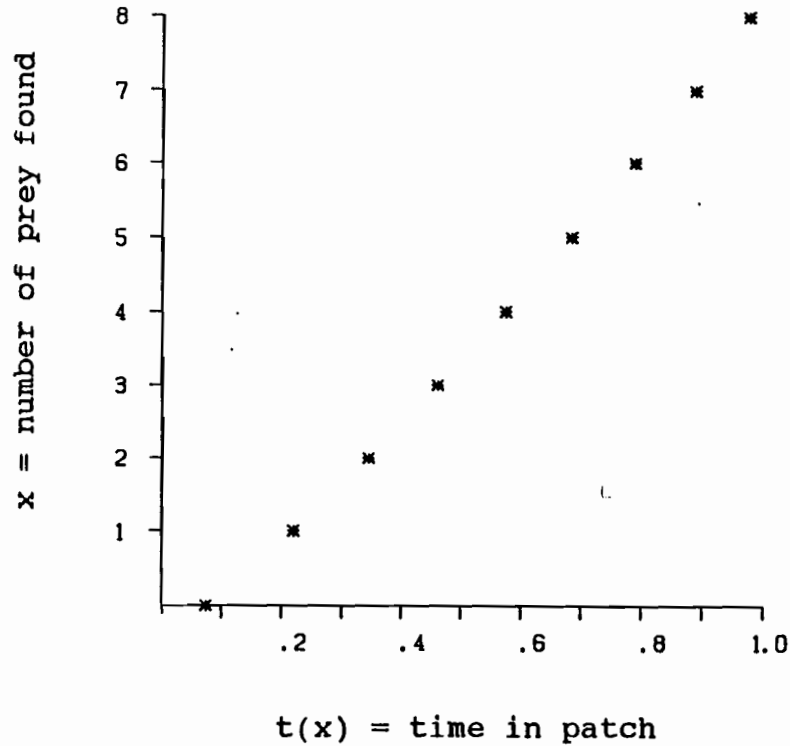
$$EG = \alpha/\beta - \sum_{x=0}^n p(x)r(x, t(x))[1 - t(x)]. \quad (A14)$$

TABLE 1. Efficiency of the optimal foraging strategy and the best linear stopping rule

Prey distribution		Travel time	Linear rule		Rates achieved*	
k	m	tau	Intercept a	Slope b	R(linear)	R(best)
0.5	5.0	0.1	0.0754	0.1301	8.0705	8.0744
1.0	5.0	0.1	0.1070	0.1526	6.3757	6.3770
0.5	2.5	0.1	0.1171	0.2682	3.6020	3.6027
1.0	2.5	0.1	0.1676	0.3054	2.9183	2.9184
0.5	5.0	0.2	0.1089	0.1624	6.3157	6.3174
1.0	5.0	0.2	0.1552	0.1806	5.2438	5.2444
0.5	2.5	0.2	0.1694	0.3248	2.8844	2.8847
1.0	2.5	0.2	0.2440	0.3430	2.4491	2.4492

\* Rates of finding prey may be compared with the rate achieved by a "naive" forager that ignores experience in a patch and searches each patch completely. A "naive" forager achieves rate  $R = m/(1 + \text{tau})$ .

(a) Best stopping rule



(b) Best linear stopping rule

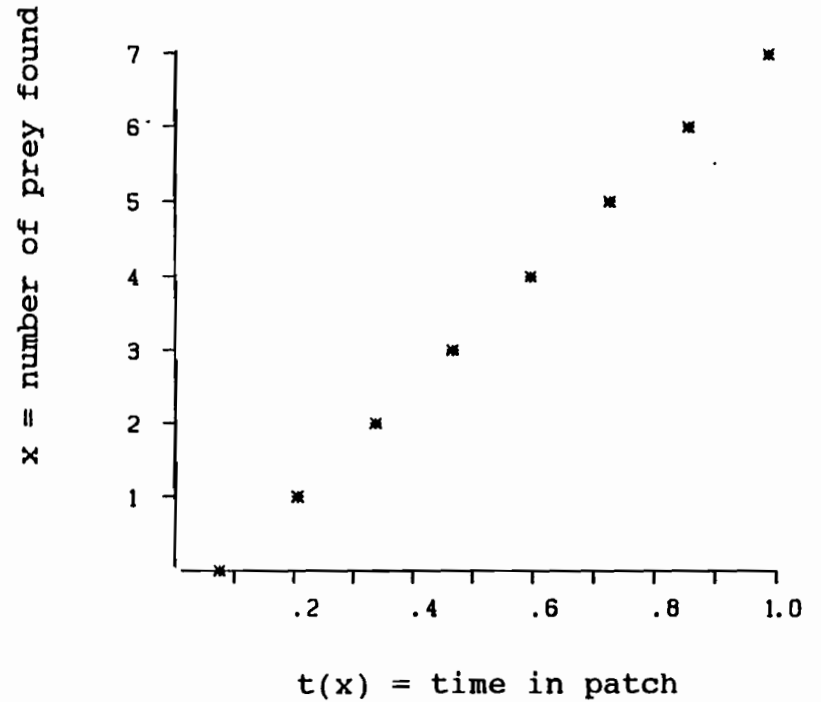


FIG. 1. Stopping rules for a systematic forager searching for negative binomially distributed prey. (a) An optimal forager leaves a patch when the patch has been searched completely ( $t = 1$ ), or if exactly  $x$  prey have been found by time  $t(x)$ . (b) The best linear stopping rule is very similar to the optimal rule, but the stopping times,  $t(x) = a + bx$ , increase linearly with the number of prey,  $x$  (here  $a = 0.0754$  and  $b = 0.1301$ ). In the case considered here, the parameters of the prey distribution are  $k = 0.5$  and  $m = 5$ , and travel time is  $\tau = 0.1$ .

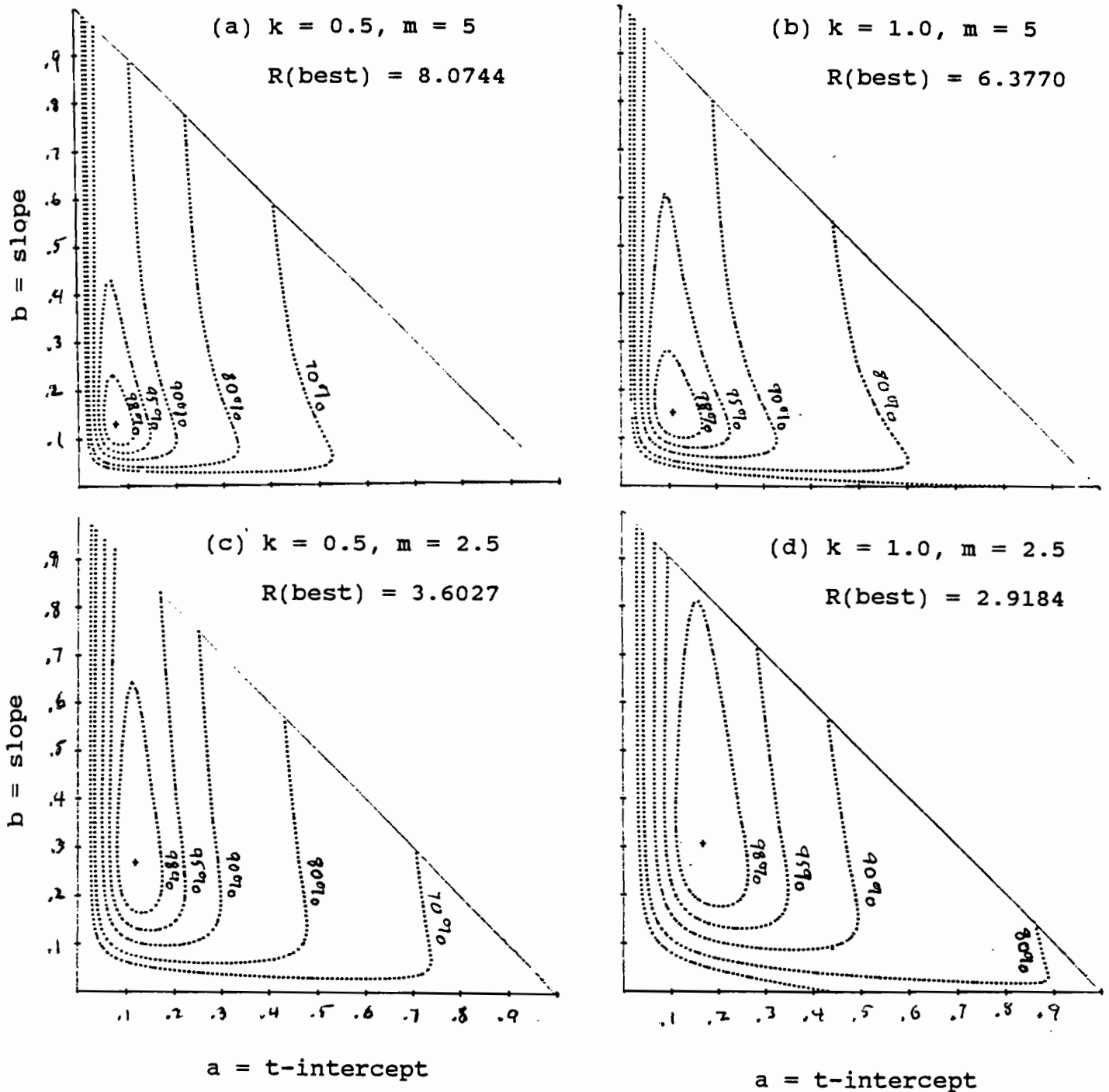


FIG. 2. Topographic maps of the rate of finding prey for linear stopping rules. Isoclines represent sets of values of the coefficients  $a$  and  $b$ , where stopping times are given by  $t(x) = a + bx$  (such a rule is illustrated in FIG. 1b), that achieve fixed rates that are the specified percentages of the rate achieved by the best rule. The coefficients for the best linear rule for each prey distribution are indicated by a small cross. The rate achieved by the best rule,  $R(\text{best})$ , is given for each of four prey distributions, specified by the negative binomial parameters,  $k$  and  $m$ . In each case, travel time,  $\tau = 0.1$ .

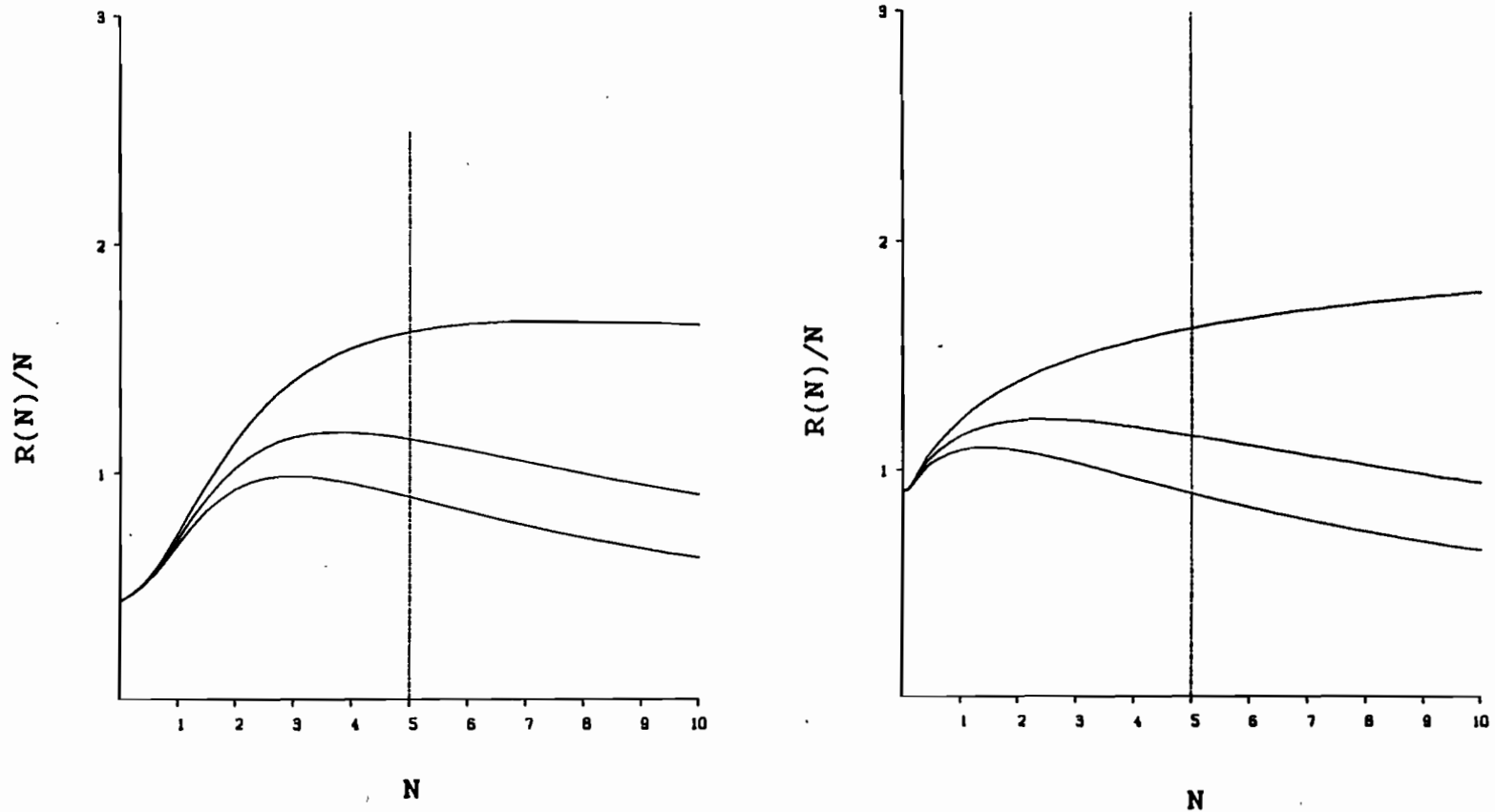


FIG. 3. Rate of finding prey per predator per prey,  $R(N)/N$ , plotted against overall prey density,  $N$ , when the negative binomial parameter  $k$  for the prey distribution remains constant ( $k = 0.5$ ) as overall prey distribution changes, but travel time remains constant ( $\tau = 0.1$ ). Rates are plotted for three different values for the time spent to handle each prey,  $h = 0$ ,  $h = 0.05$  and  $h = 0.10$ .

(a) The forager is assumed to use the same foraging strategy, no matter what the prey distribution. The stopping rule used is the one illustrated in FIG. 1a, which is best for prey parameters  $k = 0.5$  and  $m = 5$ , and travel time = 0.1. The overall prey density for which the foraging strategy is best,  $N = m = 5$ , is indicated by a dotted vertical line. (b) The forager is assumed to use whatever strategy is best for each particular prey distribution.

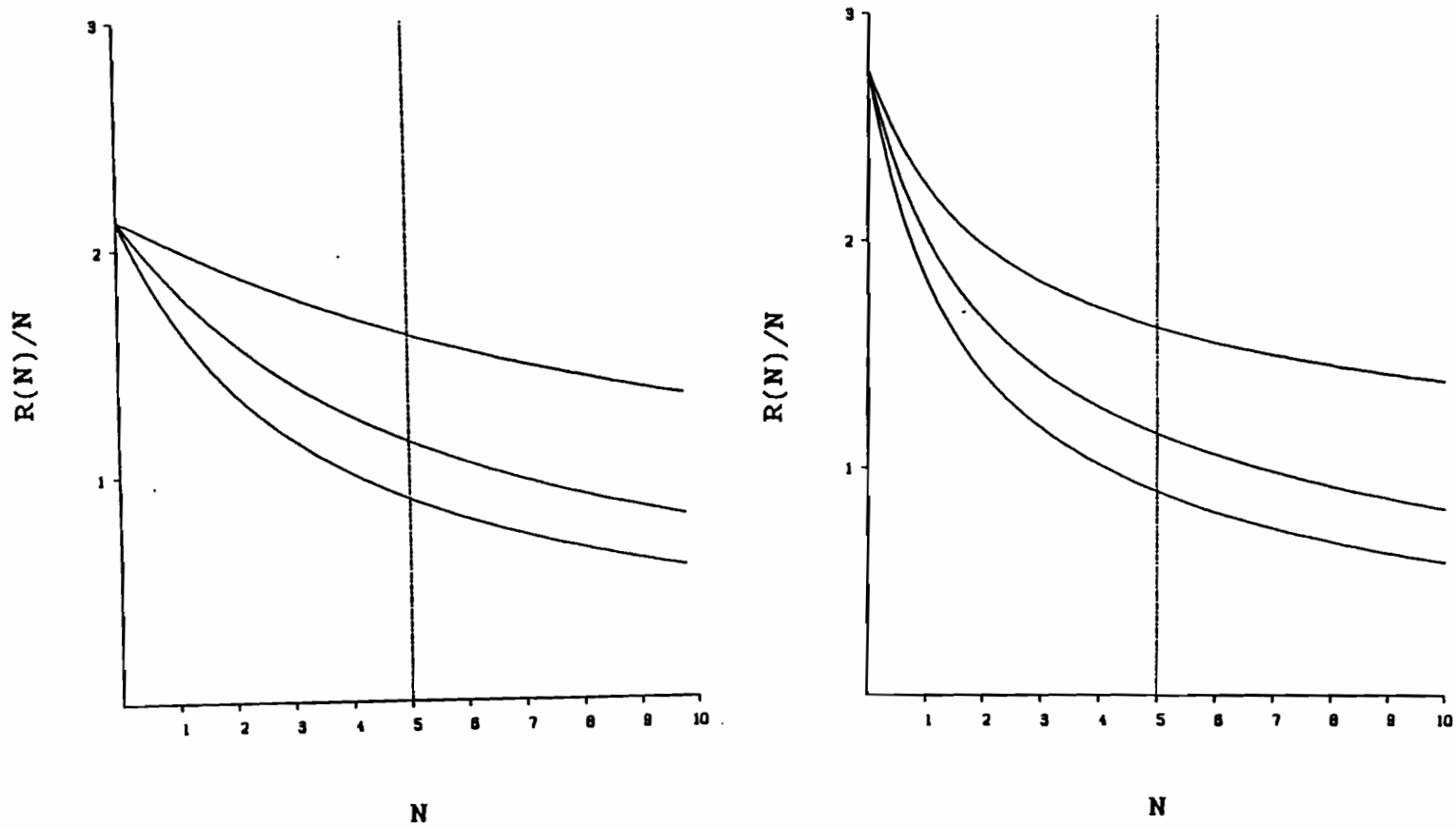


FIG. 4. Rate of finding prey per predator per prey,  $R(N)/N$ , plotted against overall prey density,  $N$ , when the negative binomial parameter  $k$  for the prey distribution is proportional to overall prey density ( $k = .1N$ ). Travel time,  $\tau = 0.1$ , is constant. Rates are plotted for three different values of time spent to handle prey,  $h = 0$ ,  $h = 0.05$  and  $h = 0.10$ . (a) The forager is assumed to use the same foraging strategy, no matter what the prey distribution. The stopping rule used is the one illustrated in FIG. 1a, which is best for prey parameters  $k = 0.5$  and  $m = 5$ , and travel time = 0.1. The overall prey density for which the foraging strategy is best,  $N = m = 5$ , is indicated by a dotted vertical line. (b) The forager is assumed to use whatever strategy is best for each particular prey distribution.