

**THE EFFECT OF FORAGING BEHAVIOR
ON THE STABILITY OF A
PREDATOR-PREY MODEL**

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INTRODUCTION

Foraging theory and predator-prey models are two pieces of ecological theory which both involve predation, but—with one notable exception (Murdoch and Oaten 1975)—the two have led separate existences. In this paper I treat the same predator-prey model as did Murdoch and Oaten (1975) and determine the functional response, which is critical for the stability of the model, by using optimal foraging theory. I study the stability of the model by assuming that a forager uses a strategy that is nearly optimal when the prey population is at equilibrium. It is seen that the predator-prey model may be locally stable *if* the variance of the prey distribution increases rapidly enough as prey density increases. The conditions on the prey distribution under which I find the equilibrium to be stable are more restricted than those found by Murdoch and Oaten (1975), who did not assume optimal foraging, but rather assumed that predators use a sub-optimal strategy that is relatively better at high than at low prey densities.

A FORAGING MODEL

Within the environment

The environment contains many superficially similar food patches which differ in the number of prey they contain. The distribution of the number of prey per patch is the same throughout the environment at any time, but this distribution may change from time to time.

Within the patches

The number of prey per patch has a negative binomial distribution, which I specify by the probability function:

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

where x is the number of prey in a patch, and α and β are the parameters, chosen for the convenience of mathematical analysis. The average number of prey per patch is $\mu = \alpha/\beta$, while α is equivalent to the more familiar negative binomial parameter, k .

The prey

The prey within a patch are to be found at random locations, they are all the same, and each prey found is handled in time h , which is small.

The forager

The forager searches each patch systematically until it has been searched completely, or until the forager decides to leave the patch and go on to another. In deciding when to leave a patch the only information that a

forager has about the patch is the number of prey it has found there and the times at which they were found. An optimal forager maximizes the long-term average rate of finding prey, given by

$$R = \frac{EG}{ET + \tau + hEG},$$

where ET and EG are the expected time spent and the expected number of prey captured per patch, respectively, and τ is the average travel time between patches.

A PREDATOR-PREY MODEL

This paper treats a modification of the Lotka-Volterra predator-prey model, which is given in terms of two differential equations:

$$dN/dt = aN - bNP, \text{ and}$$

$$dP/dt = -cP + dNP,$$

where N and P are the numbers of prey and predators, respectively, at time t , and a, b, c , and d are constants. In the calculations illustrated in this paper, I use $a = 0.05$, $b = 1$, $c = 0.25$ and $d = 0.05$, which yield equilibrium population values, $N^* = 5$ and $P^* = 0.05$. I imagine that the environment consists of patches where predators may find prey, and the values of N and P are interpreted as the average number of prey and predators per patch. For the Lotka-Volterra model, the points (N, P) determined by the population sizes at various times trace out the closed orbits illustrated in Fig. 4.

For the Lotka-Volterra model, the interaction between predator and prey involves the product of the numbers of predators and prey, NP , suggesting that the predation rate *per predator* is proportional to the number of prey, and does not depend on the number of predators. Murdoch and Oaten (1975) suggested a modification of this model in which the predation rate per predator, which may be written as $R(N)$, still does not depend on the number of predators, but it need not be proportional to the number of prey. The Lotka-Volterra equations are then modified to read:

$$dN/dt = aN - b'R(N)P, \text{ and}$$

$$dP/dt = -cP + d'R(N)P,$$

where b' and d' are new constants given by

$$b' = bN^*/R(N^*) \quad \text{and} \quad d' = dN^*/R(N^*).$$

Murdoch and Oaten point out that the critical condition for stability of this new model is that the ratio $R(N)/N$ must be an increasing function of N when N is at equilibrium.

I investigate the stability of Murdoch and Oaten's (1975) model by calculating $R(N)$ using the foraging model described earlier. In each case I am interested primarily in the stability of the model at the equilibrium point $N^* = 5$, $P^* = 0.05$. The results, illustrated in **Fig. 3**, were obtained in four ways, by varying the parameters of the prey distribution in two ways, and for each of those ways, either assuming that for all prey densities the forager uses the strategy that is optimal for a particular case (prey density = 5), or assuming that at all times the forager uses whatever strategy is optimal for the prey density that actually prevails at that time.

In **Fig. 3 (a)** and **(c)**, I assume that for the prey distribution the negative binomial parameter α is fixed (= 0.5) and that β varies, while in **(b)** and **(d)** I assume that α varies and that β is fixed (= 0.1). In **Fig. 3 (a)** and **(b)** I assume that the forager uses the strategy which is optimal for the particular prey distribution for which $\alpha = 0.5$ and $\beta = 0.1$. [Actually, I use the best linear rule, that is, the best rule of the form: *stop at time $t(k) = ak + b$ if exactly k prey have been found by that time.* This rule, with $a = 0.1302$ and $b = 0.0754$, closely resembles the optimal rule illustrated in **Fig. 1**, and the rate that it achieves is about 99.95% of the

rate achieved by the optimal rule.] In **Fig. 3 (c)** and **(d)** I use the optimal rule for each prey density.

While **Fig. 3** illustrates the dependence of $R(N)/N$ on N , and thus shows when stability is possible, I have also illustrated the convergence to (or the divergence from) equilibrium in **Fig. 5**. Instead of actually using the values of $R(N)$ that are used to plot **Fig. 3 (a)** and **(b)**, I have used a linear approximation to $R(N)$ which is tangent to the true function, $R(N)$, at the equilibrium prey density. **Fig. 5 (a)**, which illustrates convergence to the equilibrium ($N^* = 5, P^* = 0.05$) corresponds to **Fig. 3 (a)**, while **Fig. 5 (b)**, which illustrates divergence from the same equilibrium, corresponds to **Fig. 3 (b)**. In **Fig. 5 (c)** and **(d)** I approximated $R(N)$ using a linear function that is tangent to the true function used to illustrate **Fig. 3 (a)** at the new prey equilibrium values $N^* = 4$ and $N^* = 6$, respectively (with $P^* = 0.05$ in each case).

RESULTS

The illustrations in **Fig. 3** show how the functional response of predation rate depends on the foraging strategy used, the time spend handling individual prey, and the pattern of change of prey distribution with prey density. The critical condition for stability is that $R(N)/N$ increases with increasing N around equilibrium. This is unlikely to happen unless handling time, h , is small. If a predator forages optimally when prey density is at equilibrium then it makes little difference to the stability at that equilibrium whether the predator uses the same strategy when prey density changes or if the strategy is changed to match the change in prey density. However, if a predator uses a foraging strategy that is not optimal at equilibrium then the stability of that equilibrium depends on whether the strategy used is better adapted for higher or lower prey densities.

An equilibrium tends to be more stable if a forager uses a strategy adapted to a higher prey density. This point is illustrated in **Fig. 5 (a), (c) and (d)**. In each case the forager uses the strategy that is best when equilibrium prey density is $N^* = 5$. In **(a)** the equilibrium prey density is $N^* = 5$, while in **(c)** it is $N^* = 4$, and in **(d)** it is $N^* = 6$. It can be seen that the rate of convergence is greatest for $N^* = 4$ and least for $N^* = 6$. A comparison of **Fig. 3 (a) and (c)** shows that while a stable equilibrium is possible over a wider range of prey density when the predator is able to change strategy and use the strategy that is optimal at each prey density, the most stable equilibrium is achieved when a predator uses

a strategy which is adapted to a too-high prey density.

The most important things to observe are the differences between **Fig. 3** (a) and (b) and between (c) and (d). These differences show that for a negative binomial prey distribution it is very important how prey distribution changes as prey density changes. At equilibrium the aggregation of prey should increase with prey density in order for the equilibrium to be stable.

Fig. 5 confirms for a few particular cases the convergence or divergence indicated by **Fig. 3**. One thing that this figure suggests, for the convergent cases (a) , (c), and (d), is that convergence to equilibrium is very slow. When this observation is coupled with the fact that quite a number of assumptions are necessary to achieve even such weak convergence, the conclusion is suggested that real populations should not be expected to be maintained at or near local equilibria because predators forage optimally on aggregated prey populations.

DISCUSSION

There have been several recent exhortations (Hassell and May 1985, Schoener 1986) to biologists to incorporate individual behavior into population ecology. It is important to try to consider the foraging behavior of individuals in predator-prey and host-parasitoid models, in which a critical detail is the relationship between the predation rate and the numbers of predators and prey.

In this paper I follow Murdoch and Oaten (1975) and consider a modification of the Lotka-Volterra predator-prey model, in which prey are found in patches. The rate of finding prey per predator, which is denoted by $R(N)$, where N is the average number of prey per patch, is assumed to depend on the density of prey but not the density of predators. This model will have a stable equilibrium if the ratio $R(N)/N$ is increasing at the equilibrium, N^* .

Murdoch and Oaten (1975) investigated the pattern of $R(N)/N$ by calculating $R(N)$ for a foraging model in which the pattern of search by predators and their foraging strategies were specified, as well as the distribution of the numbers of prey in patches. Murdoch and Oaten assumed that search is random, and that the predator uses what has become known as the "giving-up-time rule" to decide when to leave a patch. Prey were assumed to have either a Poisson distribution or a negative binomial distribution in patches. Murdoch and Oaten found that the condition for a stable equilibrium was satisfied for three different patterns of changing prey distribution: (1) Poisson, with parameter λ proportional

to the size of the prey population, and negative binomial, (2) with parameter β constant and α varying, or (3) with parameter α constant and β varying. For each of these three patterns Murdoch and Oaten found that stability was possible for prey densities below particular values. The condition that permits stability is that the rate at which individual predators find prey must increase rapidly enough as prey density increases. I think the fact that Murdoch and Oaten found that stability is possible for all three patterns of prey distribution was due to their having assumed that predators use a particular, sub-optimal foraging strategy—one that is relatively better at higher prey densities.

In this paper I only give results for patterns (2) and (3) considered by Murdoch and Oaten (1975). I consider only one example of each pattern and assume either that predators use the foraging strategy that is optimal at the prey density that prevails at the time, or that they always use the particular strategy which is optimal when prey density is at the equilibrium, $N^* = 5$. Under these assumptions, stability is possible if α remains fixed (and handling time is small), but not if β remains fixed. That is, the stability of equilibrium depends not just on prey distribution, foraging strategy and handling time, but also on the pattern of change of prey distribution with density. This is an important point which applies to other population models as well.

Several workers have pointed out other population consequences of aggregated distributions of animals. Atkinson and Shorrocks (1981) described a model in which populations of competitors might coexist on ephemeral patches if the competitors are sufficiently aggregated. May

(1978) described a "phenomenological model" in which hosts and parasitoids might have a stable equilibrium if parasitoids are sufficiently aggregated. In earlier work, Hassell and May (1974) were at pains to suggest behavioral mechanisms to explain parasitoids' aggregation in terms of aggregated prey. Chesson and Murdoch (1986) pointed out that for host-parasitoid models it is parasitoid aggregation that is critical for stability, and that this aggregation need have nothing to do with prey aggregation. However, contrary to the assertions of these authors, it is not the aggregation, or the degree of aggregation, that is critical in these cases. What is important is the pattern of change of aggregation with changes in population density. In a sense, for stability, aggregation must tend to increase with competitor density for Atkinson and Shorrocks' (1981) model (Green 1986), and with parasitoid density for May's (1978) model.

Thus, for Murdoch and Oaten's (1975) predator-prey model, for May's (1978) host-parasitoid model, and for Atkinson and Shorrocks' (1981, or Hassell's and Comins 1976) two-competitor model, it is not aggregation, but a certain pattern of change of aggregation with density that is necessary for stability.

CONCLUSIONS

A predator-prey model may be locally stable if the functional response of predation rate to prey density has the proper form. In particular, the rate of capture of prey per predator must increase faster than overall prey density at equilibrium for the equilibrium to be stable. Whether the predation rate changes with prey density in the proper way depends on the foraging strategy of predators, the time they spend handling prey, the distribution of prey, and the way that this distribution changes with overall prey density.

The model that I consider suggests that if prey are distributed in patches which vary substantially in the number of prey that they contain, if a forager uses an efficient strategy that takes advantage of patch variability by requiring him to leave patches in which few or no prey have been found, and to remain in patches where more prey have been found, if handling time is small, and if patch variability (prey aggregation) increases rapidly with prey density, then a predator-prey model may be stabilized by the functional response. (The facts that the conditions required for stability are many, and that the stabilizing force is weak, suggest that real predator-prey systems are unlikely to be locally stable.)

I am particularly interested in the role of optimal foraging and in the pattern of change of prey distribution with prey density. Clearly, the role of foraging strategy is important since a forager which ignores the variability in patch quality and only encounters prey at a rate proportional to their overall density cannot stabilize the prey population. Similarly, if

the prey are distributed randomly (Poissonwise) in patches, an optimal forager should ignore experience in patches and will not stabilize the prey population.

In this paper I have looked at the effect of foraging behavior on functional response and the effect of functional response on a particular predator-prey model. Hassell and Comins (1978) have argued that a sigmoid functional response cannot, by itself, stabilize a host-parasitoid model. That is, for a host-parasitoid model to be stable it is necessary to include the effect of parasitoid density on the attack rate per individual parasitoid. I have not considered the effect of predator density on their foraging efficiency, and it is not clear how to do this if it is to be done. One possibility is to assume that as their density increases predators tend to visit and search again patches that have already been searched.

The most important theoretical conclusion of this paper is that the stability of a predator-prey model depends on how the distribution of prey depends on overall prey density. This conclusion applies to host-parasitoid (May 1978) and competition (Atkinson and Shorrocks 1981) models as well, but it is often overlooked because aggregation is put into models as a negative binomial parameter k (my α) which is then treated as a constant. It is important to realize that this parameter is probably not a constant in nature (Taylor, Woiwood and Perry 1979), and that its pattern of variation is critical to the stability of the models in which it is included.

ACKNOWLEDGMENTS

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OPTIMAL FORAGING STRATEGY

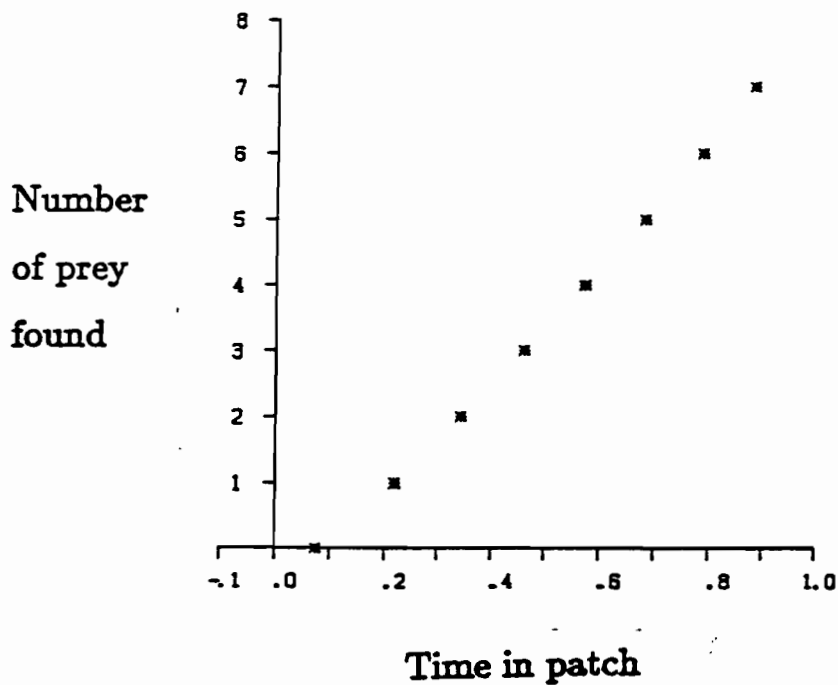


Fig. 1. A forager should leave a patch if one of the points indicated by an asterisk is reached. That is, a forager should leave a patch at time 0.0748 if no prey have been found, at time 0.2186 if one prey has been found, and so on. Search is systematic, and it takes unit time to search the entire patch. Prey distribution is negative binomial, with $\alpha = 0.5$ and $\beta = 0.1$, and travel time between patches is $\tau = 0.1$.

THE MARGINAL VALUE THEOREM

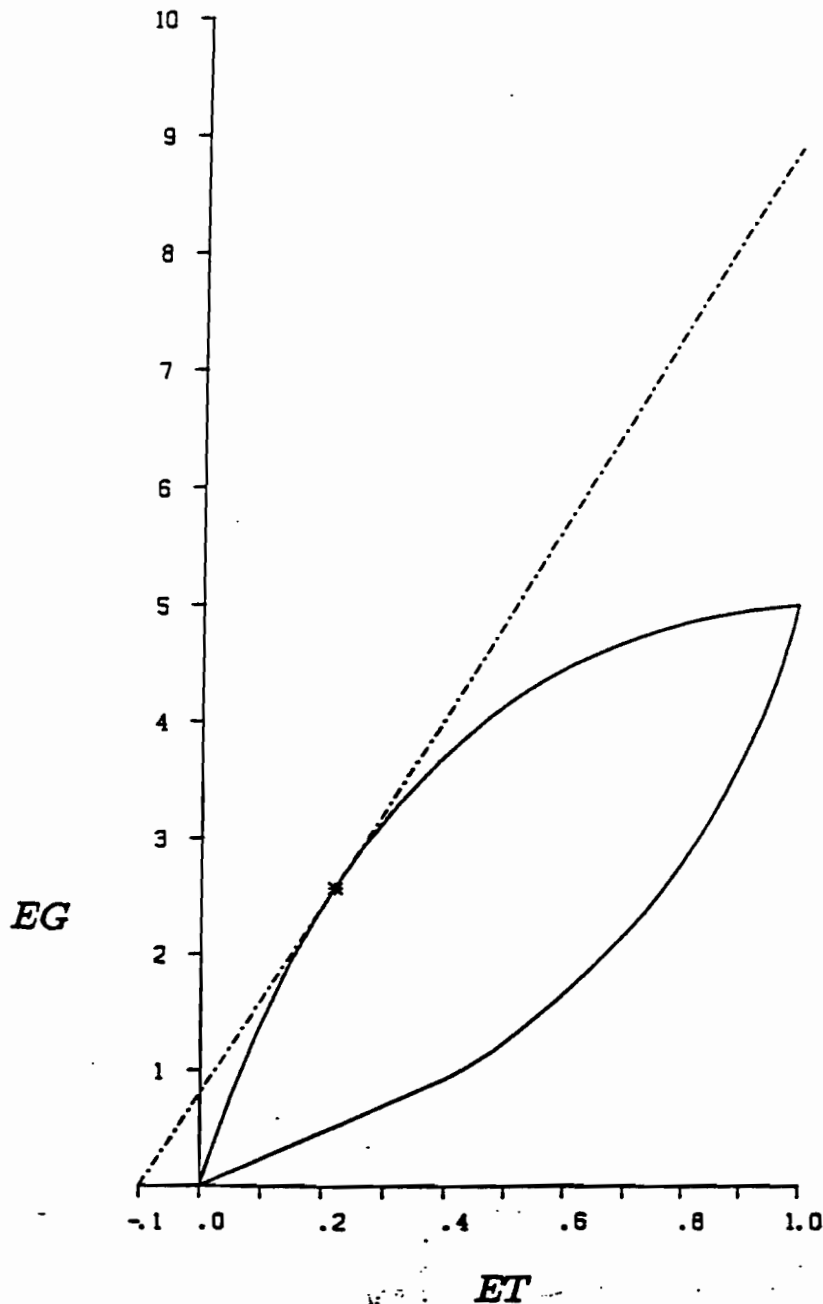


Fig. 2 (a) The football-shaped envelope contains the set of values of (ET, EG) for all possible foraging strategies for the case in which prey distribution is negative binomial with parameters $\alpha = 0.5$ and $\beta = 0.1$. The optimal strategy for $\tau = 0.1$ produces the point indicated by an asterisk, and the resulting predation rate, $R = 8.074$, is the slope of the dotted line tangent to the envelope at this point.

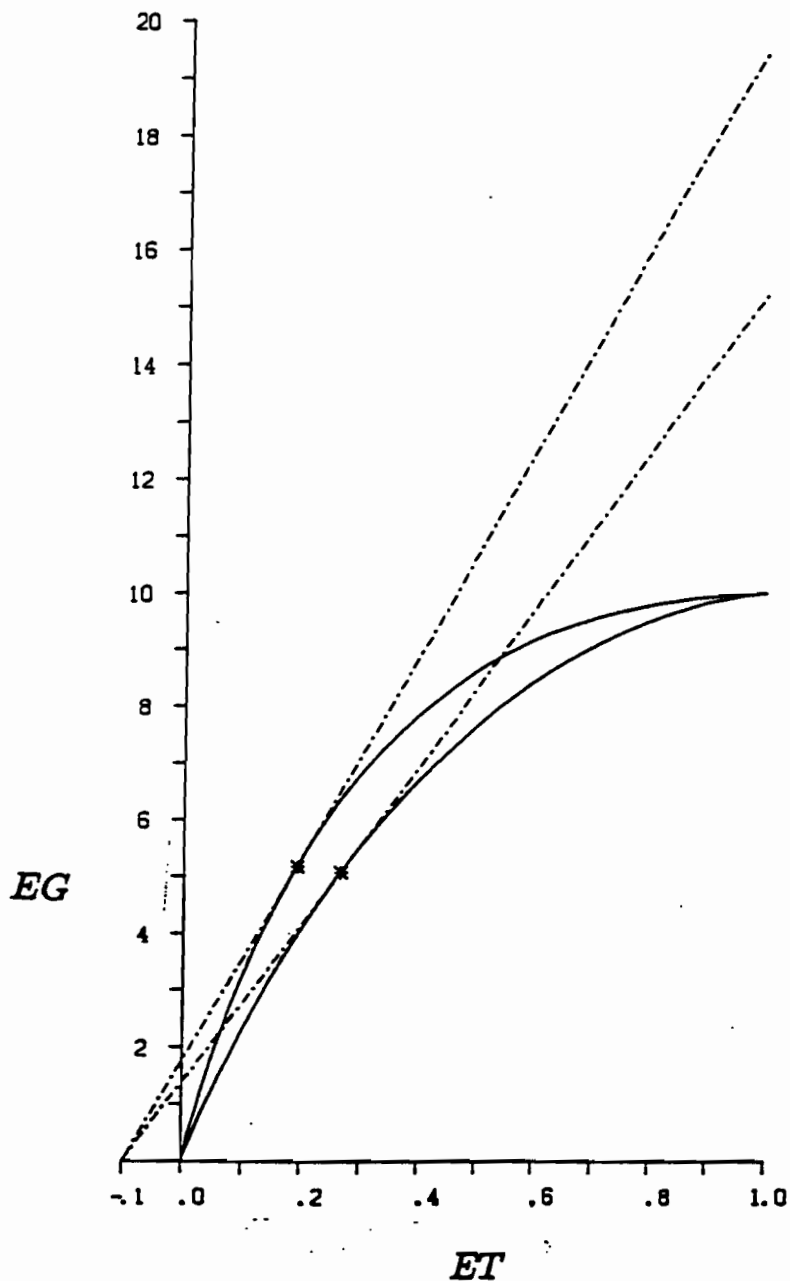


Fig.2 (b) The solid curves are upper boundaries for the (ET, EG) envelopes for two cases in which the average number of prey per patch, $\mu = \alpha/\beta$, is twice that in (a). For the upper curve, $\alpha = 0.5$ and $\beta = 0.05$, while for the lower, $\alpha = 1.0$ and $\beta = 0.1$. The vertical scale in (b) is half that in (a) so that a comparison of the slopes of the dotted tangent lines in (b) with the tangent line in (a) shows whether the predation rate increases faster or slower than the change in average prey density.

FUNCTIONAL RESPONSE (in each case $N = \mu = \alpha/\beta$)

- (a) Prey distribution parameters: $\alpha = 0.5$ (constant), β varies
 Predator uses the best strategy for the particular case:
 $\alpha = 0.5$, $\beta = 0.1$, and $\tau = 0.1$

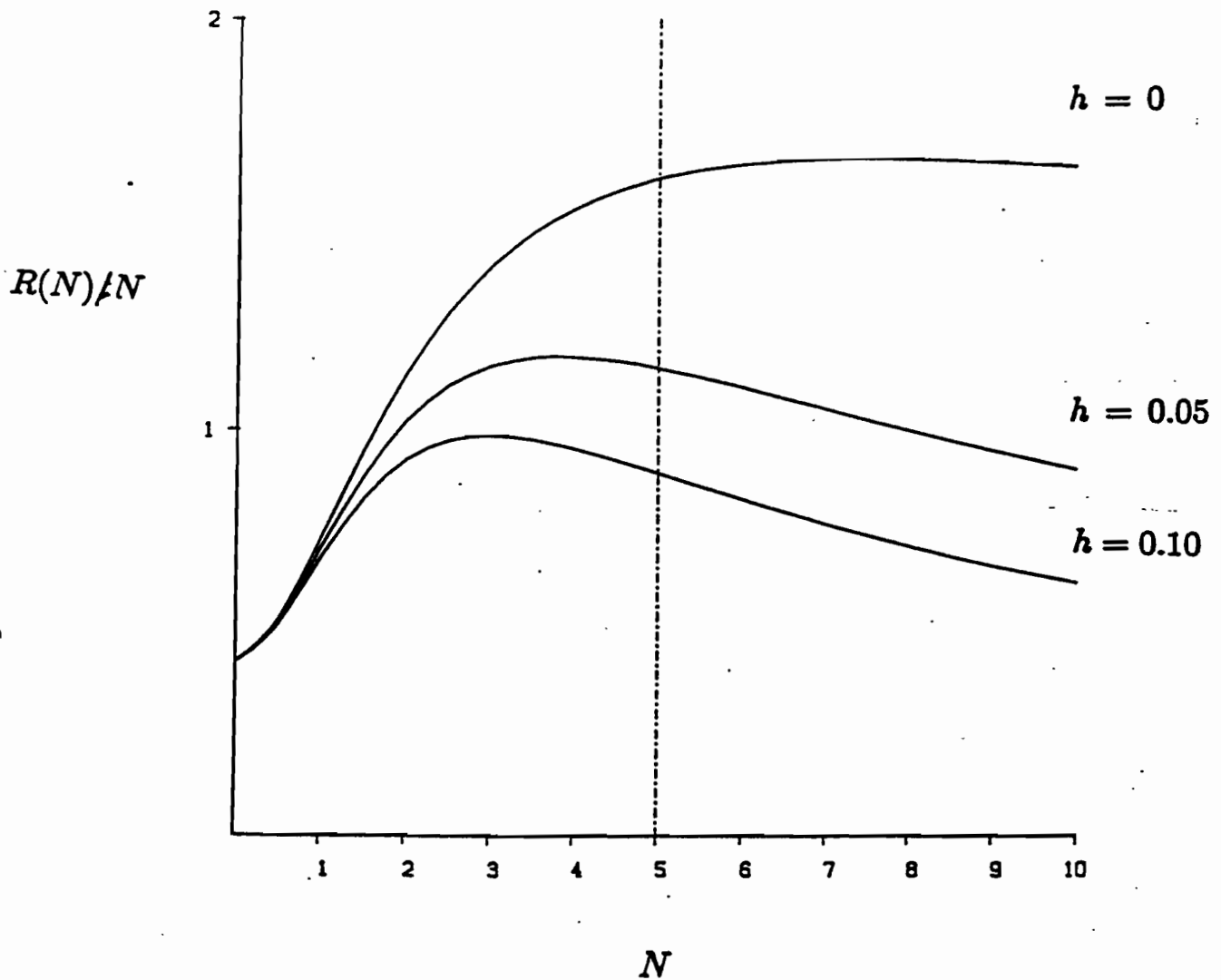
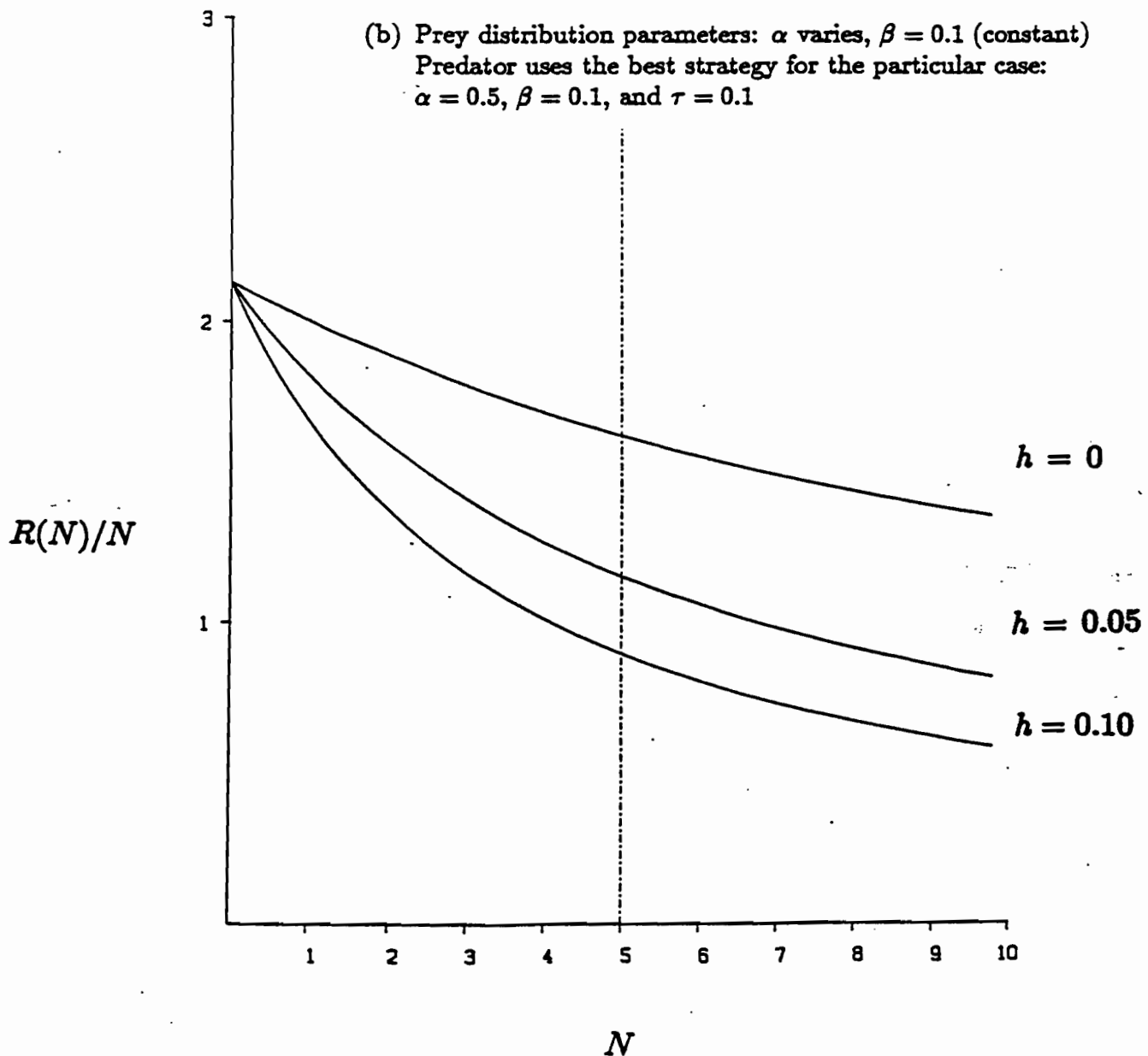
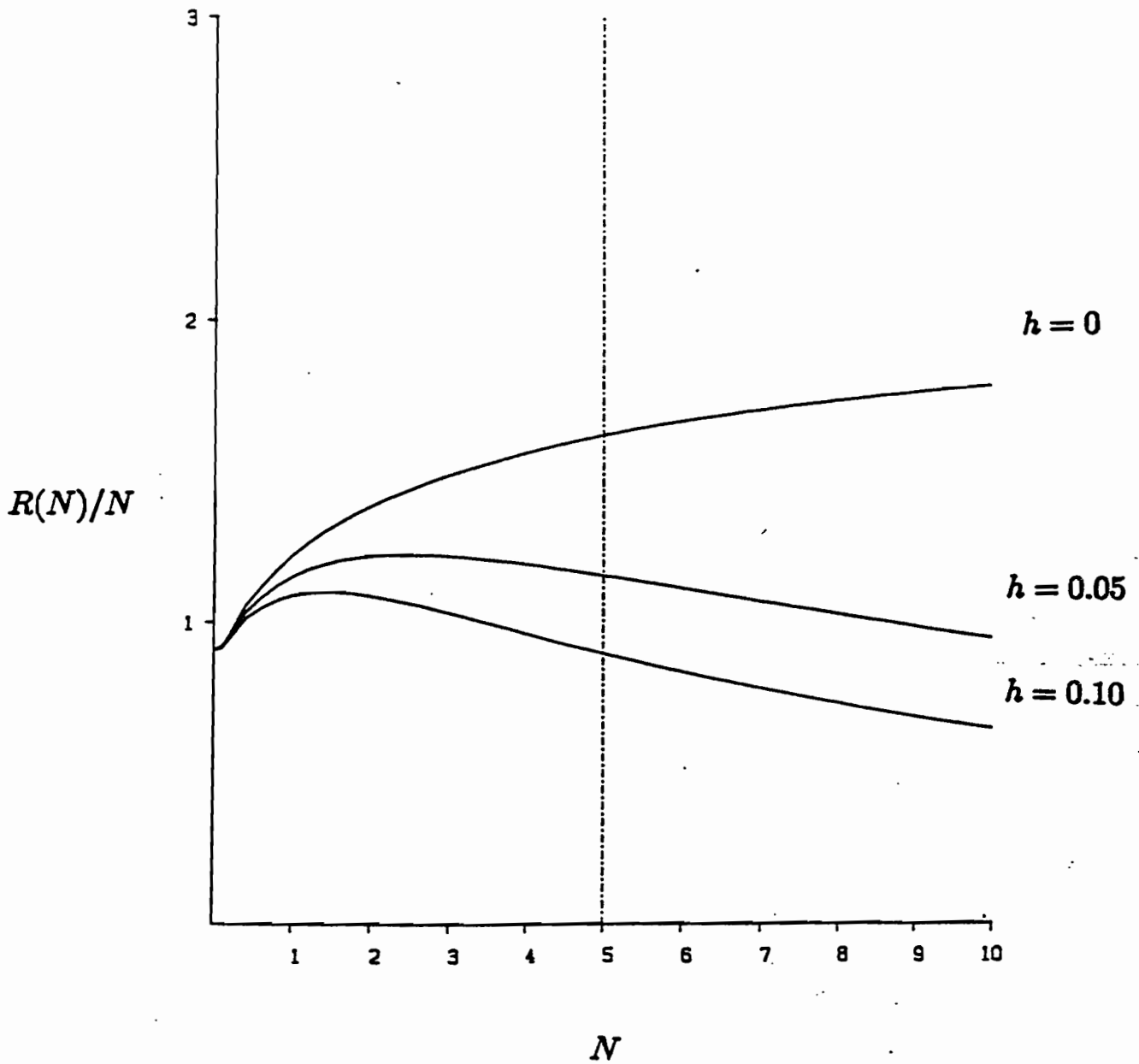


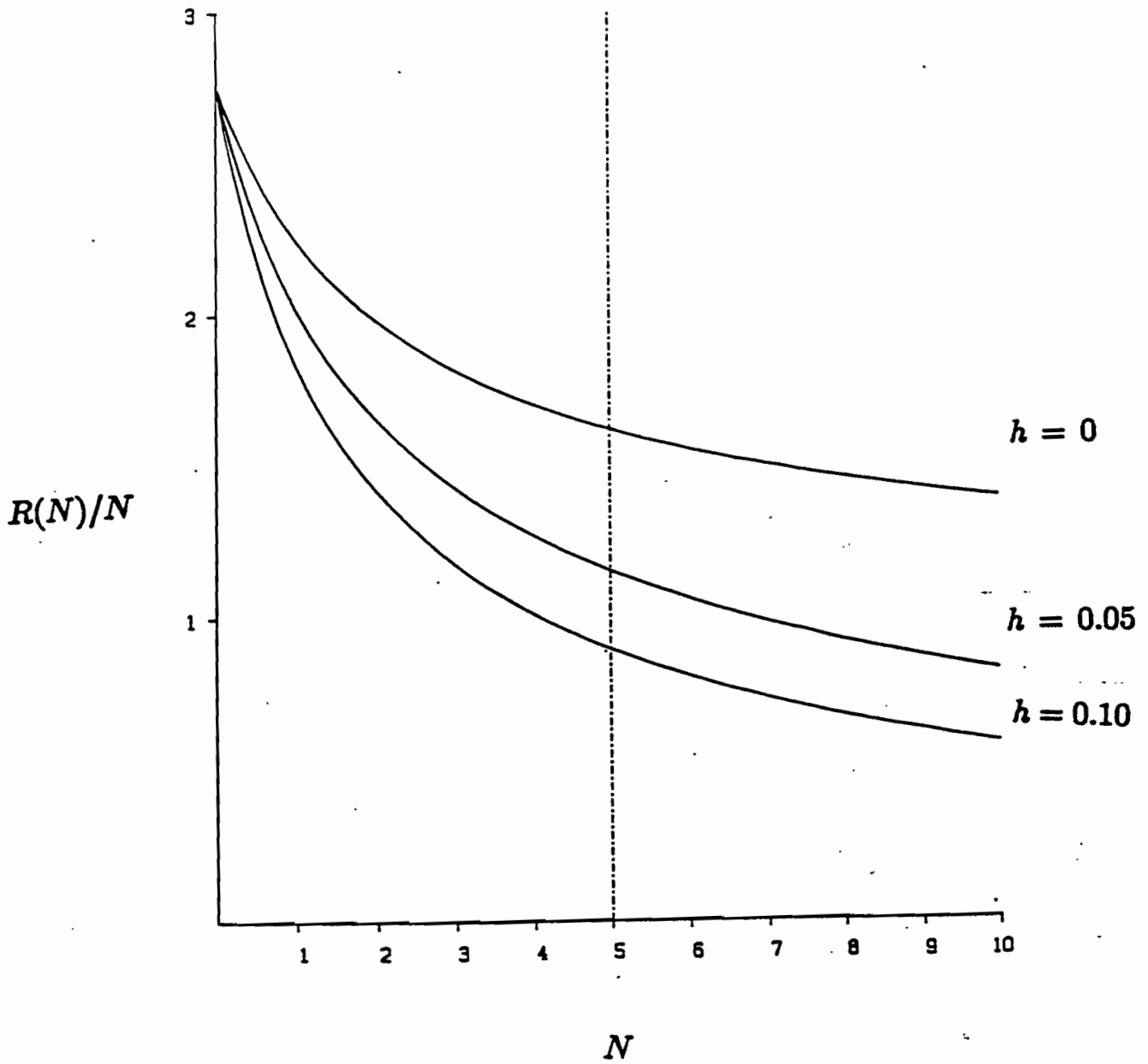
Fig. 3. Predation rate per predator per prey, $R(N)/N$, plotted against N , the average number of prey per patch. For the population equilibrium for the modified Lotka-Volterra equations to be stable it is necessary that $R(N)/N$ be increasing at the equilibrium value of the prey population. Notice that this happens (for small values of handling time, h , and low values of prey density, N) when the negative binomial parameter α remains constant as prey density changes.



(c) Prey distribution parameters: $\alpha = 0.5$ (constant), β varies
Predator uses the best strategy for each prey distribution



(d) Prey distribution parameters: α varies, $\beta = 0.1$ (constant)
Predator uses the best strategy for each prey distribution



NEUTRAL STABILITY OF THE LOTKA-VOLTERRA MODEL

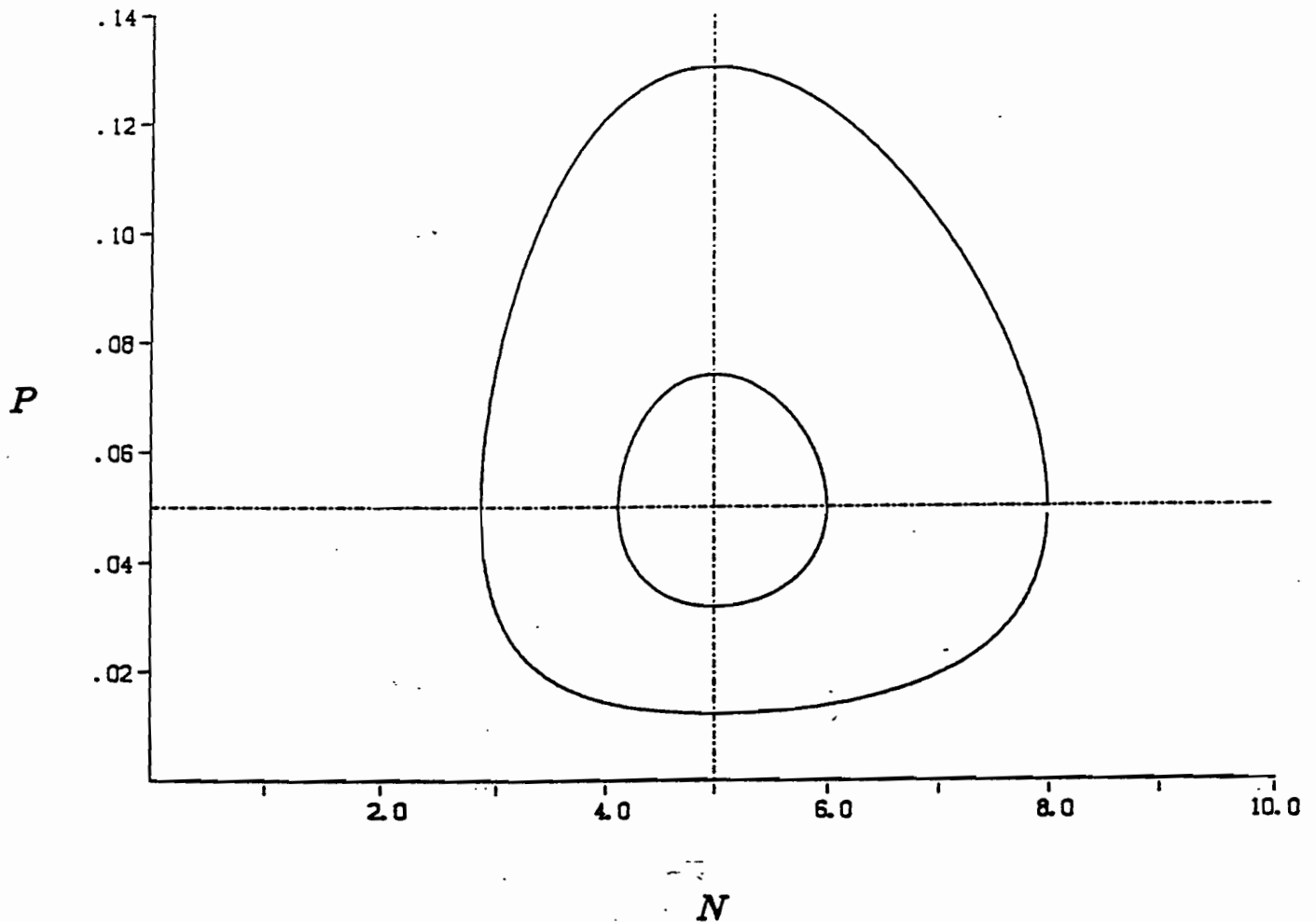


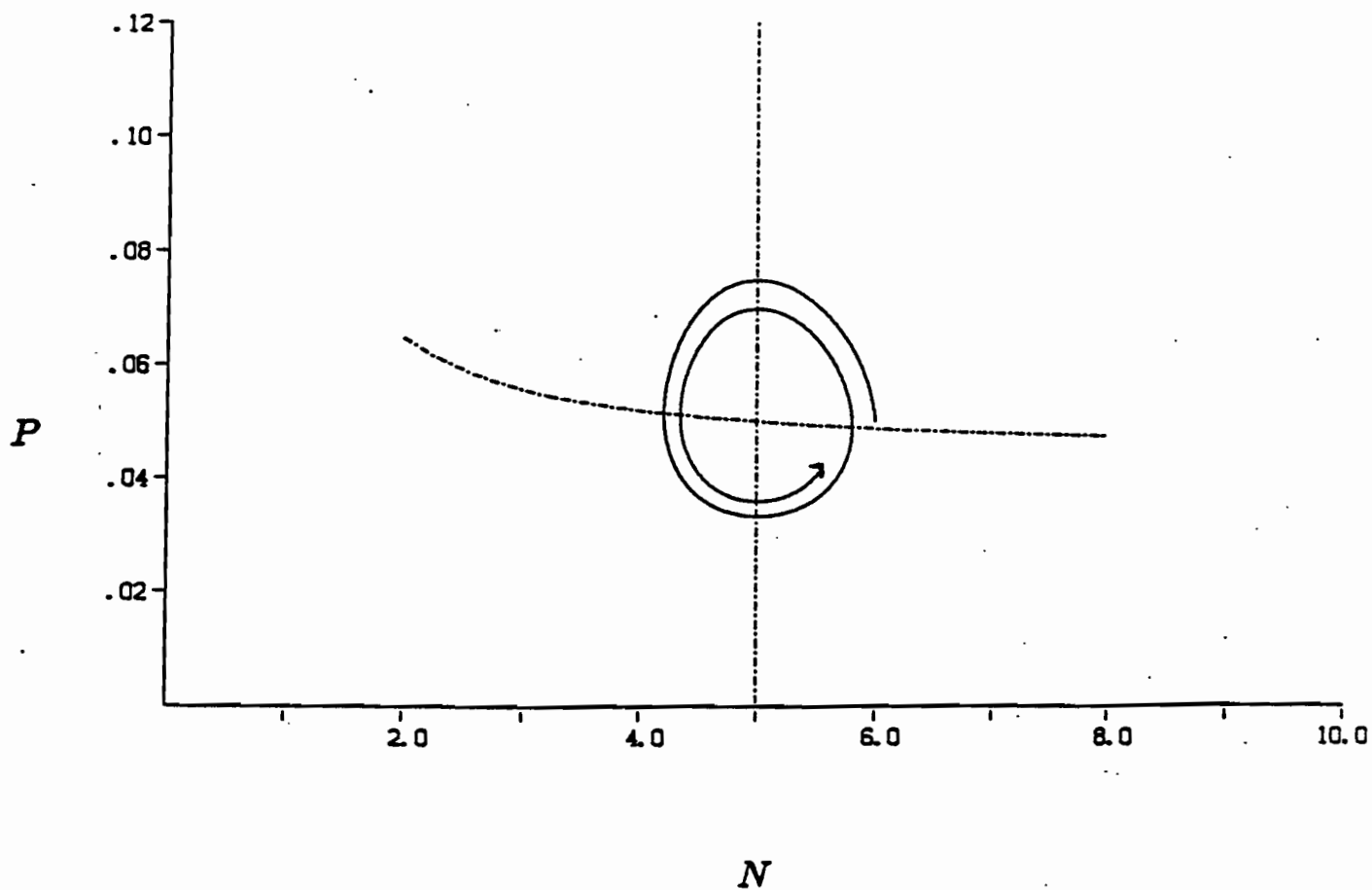
Fig. 4. The Lotka-Volterra model with $a = 0.05$, $b = 1$, $c = 0.25$, $d = 0.05$ and equilibrium $N^* = 5$ and $P^* = 0.05$. the inner orbit was begun at $N = 6$ and $P = 0.05$, while the outer orbit was begun at $N = 8$ and $P = 0.05$.

STABILITY OF THE MURDOCH AND OATEN MODEL

Fig. 5. The modified Lotka-Volterra model with $a = 0.05$, $b = 1$, $c = 0.25$ and $d = 0.05$. In each case $R(N)$ is approximated by a linear function of N given in the figure, and b and d are replaced by $b' = bN^*/R(N^*)$ and $d' = dN^*/R(N^*)$, respectively. In all cases, $P^* = 0.05$.

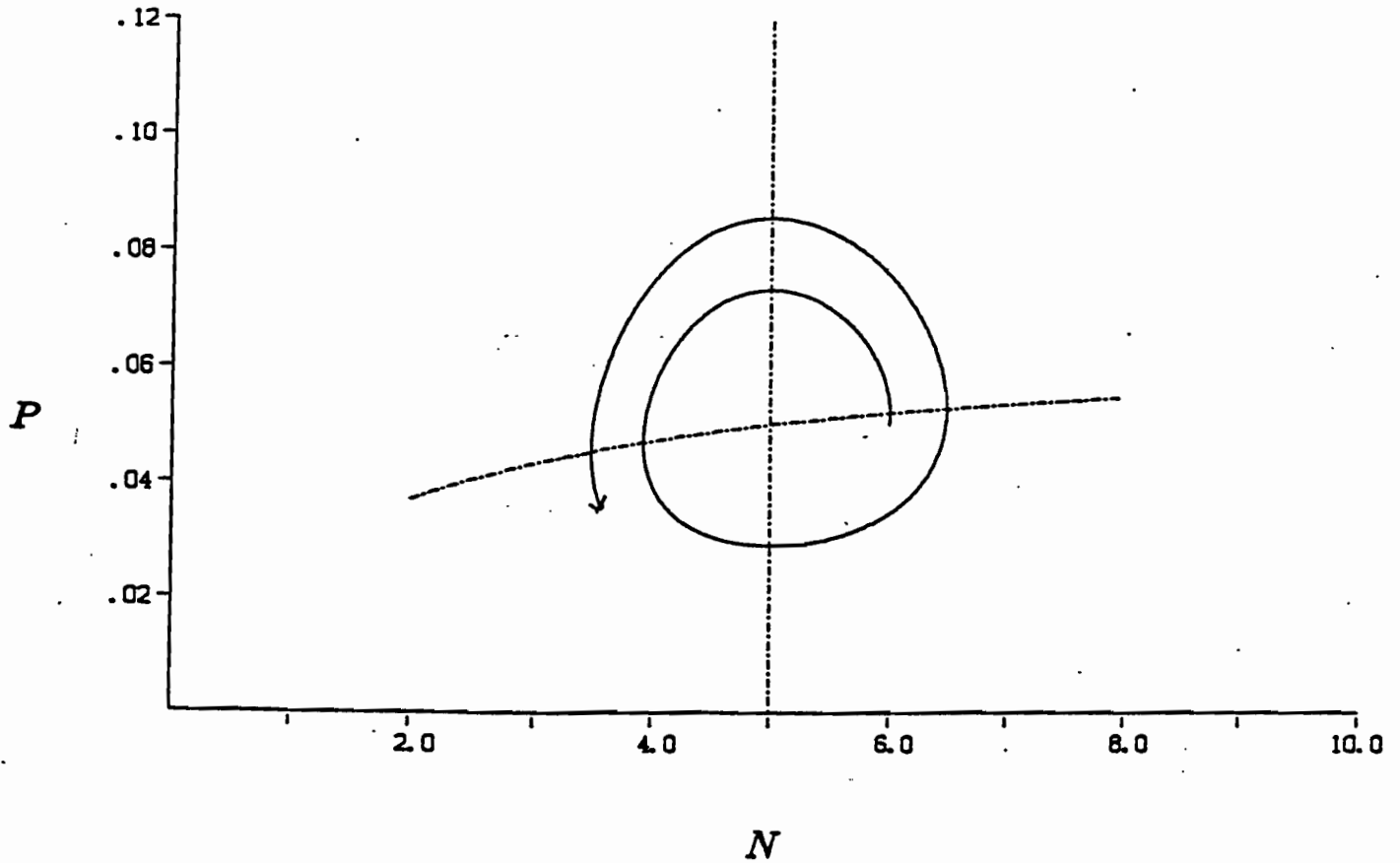
$$(a) R(N) = 1.86N - 1.226$$

$$N^* = 5, R(N^*) = 8.074$$



$$(b) R(N) = 1.2426N + 1.861$$

$$N^* = 5, R(N^*) = 8.074$$



(c) $R(N) = 1.94N - 1.59$

$N^* = 4, R(N^*) = 6.17$

