

OPTIMAL FORAGING AND FUNCTIONAL RESPONSE

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INTRODUCTION

Predator-prey and host-parasite systems must persist in nature for a long time. In constructing mathematical models of natural systems it is important to find biologically plausible mathematical assumptions which allow the model system to persist. Certain simple predator-prey models will be locally stable if the predator's functional response to prey density is sigmoid.

A number of people have been interested in showing that predator behavior, and, in particular, predator response to prey aggregated in patches, may produce a sigmoid functional response (Hassell & May 1974; Hassell, Lawton & Beddington 1977; Murdoch & Oaten 1975; Oaten 1977a; Waage 1979). While this work shows that predators may take a larger proportion of prey in dense patches than in sparse patches, it says nothing about the predators' functional response to overall prey density. But it is overall prey density that is important if the predator-prey system is to be stable. In this paper a simple stochastic model of optimal foraging is considered. Such

a model can produce a sigmoid functional response to overall prey density and not simply to prey density within patches.

The idea of a predator's functional response to prey density was developed by Holling (1959) who distinguished three types. In all three types predators achieve a constant high rate of responding to prey at sufficiently high prey densities. At lower prey densities a Type 1 functional response means that an individual predator's rate of taking prey increases in direct proportion to prey density. A Type 2 response increases with prey density but at an ever-decreasing rate. A Type 3 (sigmoid) functional response increases with prey density at an increasing rate over some range of prey densities.

The theoretical importance of functional response is that for certain models a Type 3 functional response stabilizes the system while a Type 2 (or Type 1) response destabilizes the system. This is true for differential equation models (Murdoch & Oaten 1975). Difference equation models tend to be less stable than the corresponding differential equation models. Hassell & Comins (1978) have claimed that a Type 3 functional response cannot by itself stabilize an otherwise unstable host-parasite model but Nunney (1980) has shown that their argument does not apply to predator-prey models. I am not concerned here with the conditions under which a Type 3 functional

response stabilizes a system, but rather with the fact that optimal foraging may produce a Type 3 functional response. It is the influence of the functional response on stability which makes the whole question interesting.

It was believed for some time that Type 3 functional responses were found in vertebrates while invertebrates showed Type 2 responses (Hassell et al. 1977). Most of the work on predator-prey systems, both theoretical and experimental, has been done on invertebrates, especially insects. The belief that invertebrates usually show Type 2 functional responses may be an experimental artifact (van Lenteren & Bakker 1976). Accumulating experimental evidence indicates that invertebrates also show Type 3 functional responses (Hassell et al. 1977) when confronted with patches of varying prey densities. This result may be due to the predators spending a smaller fraction of their time in poor patches actually searching for prey. Given the opportunity to leave poor patches the predators would probably do so. This has been modeled and studied experimentally by Waage (1979). It has been shown theoretically that if predators aggregate in patches with more prey (Hassell & May 1974), or if individuals spend more time feeding in patches with more prey (Oaten 1977a), or if they simply use an optimal foraging strategy (Green 1979), then they may show a sort of Type 3 functional response to prey density within patches. That is,

the number of prey taken per patch by an individual predator will tend to increase, as a function of prey density, more rapidly than prey density. This does not say, however, that the rate of taking prey per unit time in a patch will show a Type 3 functional response to prey density.

If the ultimate question is system stability, then it is not functional response to different prey densities between patches that is important, but functional response to different overall prey densities for the environment. It is likely that patch quality will vary no matter what the environmental conditions, but under good conditions there will be more good patches or better patches or both. Under any environmental conditions predators will probably aggregate in better patches. The question is how much better predators will do under better environmental conditions than under poorer ones.

In this paper the functional response of predators to prey density under different environmental conditions is investigated using a simple, parametric model. It is assumed that prey are distributed in patches of two types: "good" and "bad." The relative frequency of good and bad patches and their quality may change with changing environmental conditions. The optimal rule for leaving patches is found under each set of environmental conditions and the overall rate of finding prey is calculated. The

best stopping rule is quite simple and is almost identical to one suggested in a behavioral model by Waage (1979).

For certain patterns of changing the environmental parameters and for certain foraging strategies, a Type 3 functional response of predators to overall prey densities is found, while for other patterns and other strategies Type 1 or Type 2 responses may be found. This points out the importance of understanding the predator's foraging strategy and the pattern of prey distribution in various environments.

THE MODEL

The effect of foraging behavior on functional response may be studied by constructing a simple model. There are two components of the model: the distribution of prey in the environment and the foraging strategy used by predators.

The environment is assumed to consist of discrete, superficially similar patches, which are actually of two types, "good" and "bad." The number of prey in a patch of a given type has a Poisson distribution. The environment is characterized by four parameters:

- 1) p_1 = the proportion of bad patches ($p_2 = 1 - p_1$ is the proportion of good patches).
- 2) λ_1 = the expected number of prey in a bad patch.
- 3) λ_2 = the expected number of prey in a good patch.

- 4) τ = average time for a predator to travel between patches. It is assumed that it takes one unit of time to search each patch.

The predator is assumed to be unable to distinguish between patch types except by assessing its success in each patch. Searching is systematic with patches not being revisited and each patch visited being searched systematically until the end ($t = 1$), or until the predator decides to leave. The predator is assumed to use the best possible strategy based on a knowledge of the environmental parameters and its experience in each patch. This general kind of foraging model was suggested by Oaten (1977b) as a stochastic alternative to Charnov's (1976) deterministic model and has been considered for a discrete time case by Green (1980).

In the model considered here the predator has to decide, in effect, whether a patch is good or not. If whatever prey are to be found in a patch are located randomly within the patch, then after searching a patch for some time, t , the number of prey encountered up until that time, $X(t)$, is a sufficient statistic for the decision. That is, if $X(t)$, the number of prey caught by time t , is known, knowing the capture times does not add any information relevant to the decision whether the patch is good or bad. At any time in a patch the predator must decide whether to remain in the patch or to leave. A

foraging strategy will consist of a stopping rule: stop searching a patch and leave if certain numbers of prey have been found at certain times, otherwise continue. For a given set of environmental parameters the best stopping rule will maximize the average rate of finding prey, given by

$$(1) \quad R = EG/(ET + \tau),$$

where EG is the expected number of prey found per patch using a given stopping rule, and ET is the expected time spent searching a patch using a given rule.

The best stopping rule may be characterized by a number of prey, x^* , such that a predator should remain in a patch until the end if at any time it has found x^* or more prey, and stopping times $\{t_k: k = 0, 1, 2, \dots, x^*-1\}$ such that a predator should leave a patch at time t_k if only k prey have been found after that much time in a patch.

The optimal stopping rule is found by backward recurrence in a way similar to that used in an earlier paper (Green 1980). The details of the calculation are given in the Appendix. An example of the best rule for a particular case is illustrated in Figure 1.

The model used here is parametric; it makes precise assumptions about prey distribution and predator behavior. The particular assumptions made are not likely to accurately describe nature, but it is hoped they do reflect general

biological reality. The assumptions have been chosen to make possible the calculation of the best stopping rule, the best rate of finding prey, and the functional response. With these assumptions and these calculations it is possible to see the effect of certain ecological variables.

RESULTS

The best stopping rule.

The best stopping rules have been calculated for several sets of parameters. Figure 1 illustrates the best stopping rule for the parameter set: $p_1 = p_2 = .5$, $\lambda_1 = 2$, $\lambda_2 = 8$, $\tau = .125$. The resulting best stopping rule is characterized by the values: $x^* = 5$, $t_0 = .2098$, $t_1 = .4104$, $t_2 = .6049$, $t_3 = .7893$, and $t_4 = .9517$. That is, if at any time 5 or more prey have been encountered in a patch the predator should remain in the patch to the end. If no prey have been found by time $t_0 = .2098$ then the predator should leave at that time. If a prey has been found by time $t_0 = .2098$, but only one prey has been found by time $t_1 = .4104$, then the predator should leave the patch at that time. If at least one prey has been found by time t_0 and two prey have been found by time t_1 , but only two prey have been found by time $t_2 = .6049$, then the predator should leave the patch at that time.

The rate of finding prey achieved by using the best rule for the parameter set given above is $R = 5.1043$.

This is almost 15% better than the rate which would be achieved by an animal which stayed until the end of each patch. I have referred to such a rule (Green 1980) as the "naive" rule. It is in this case the best version of what has been referred to as the Time Expectation rule (Breck 1978). The rate achievable with this rule would be $R = (p_1\lambda_1 + p_2\lambda_2)/(1 + \tau) = (.5 \times 2 + .5 \times 8)/(1 + .125) \doteq 4.4444$.

The rate achievable if the predator were to stay until the end of each patch is a useful standard with which to compare the rates achievable using other rules. If all patches were similar, with a common $\lambda = p_1\lambda_1 + p_2\lambda_2$, then the best strategy would be this naive strategy of staying to the end of each patch. For any environment the naive rate is proportional to the overall prey density in the environment.

The best stopping rule, illustrated in Figure 1, not only results in a higher rate of finding prey than the naive rule, but it is also very simple. The stopping points fall almost on a line and the rule may be quite accurately summarized as follows: if one prey has not been found for every 1/5 of a unit time searched, leave the patch, otherwise remain.

The best rule is found by maximizing a certain mathematical expression using dynamic programming, with the help of a computer. There is nothing in the argument about how an animal could actually implement the rule.

However, the simplicity of the rule suggests that it might be possible to suggest a mechanism that animals might use to implement the rule. Except for two details, Waage (1979) has suggested just such a mechanism.

The best stopping rule and Waage's behavioral model.

In Waage's model a parasitic wasp arriving at a patch which it will search for hosts begins the search with a certain level of responsiveness, which is set by a chemical stimulus provided by the hosts in the patch. The parasite's level of responsiveness decreases linearly with time until it reaches a threshold, at which time the parasite would leave the patch, or until a host is encountered and oviposited on. After each oviposition the parasite's level of responsiveness increases some constant amount (or less if the time between ovipositions is too short) and the process continues until the parasite's responsiveness eventually reaches the threshold and the animal leaves the patch.

The only differences between Waage's model and my best rule, other than a slight non-linearity in my stopping rule, are 1) I do not assume that the initial level of responsiveness can vary depending on host density in the patch, and 2) I assume that the increase in responsiveness due to oviposition on a host is constant and does not depend on the interval since the last oviposition.

An example using the rule given above for the parameters $p_1 = p_2 = .5$, $\lambda_1 = 2$, $\lambda_2 = 8$, $\tau = .125$, will serve to illustrate the similarity between Waage's model and the best stopping rule for my model. Imagine a patch in which an animal would find prey at times $t = .15$, $t = .25$ and $t = .7$ if it were to continue the search for unit time. This (possible) outcome is illustrated in Figure 2a as a stochastic process, $X(t)$, which takes a unit increment each time a prey is (or would be) encountered. The stopping points for the best rule are indicated by open circles. Notice that an animal using the best rule would leave the patch at time $t_2 = .6049$, having found two prey at that time. Waage's model is illustrated for the same example (changed only slightly by treating the stopping rule as linear) in Figure 2b. Notice the similarity between the two pictures. In my representation the stochastic process, $X(t)$, remains constant until its unit increments when prey are found, and the animal remains in the patch until the process hits one of the stopping points, which (almost) lie on a straight line of positive slope. In Waage's representation the responsiveness is a process which decreases at a constant rate except for unit increments whenever a host is found, and the parasite remains in the patch until the process hits the threshold, which is a horizontal line.

Waage's model is behavioral, involving proximal

causes of behavior. His model is simple, plausible, intuitively understandable, and capable of being generalized. Mine is an optimization model and permits the explicit calculation of the rate of finding prey. While the approaches are very different the resulting rules are almost identical.

For different sets of parameters the best stopping rules will be different, but they all follow the same pattern. Figure 3 gives the best stopping rules for several sets of environmental parameters, including the set given in Figures 1 and 2. In each case the time between patches is the same ($\tau = .125$), good and bad patches are equally likely ($p_1 = p_2 = .5$), and good patches are four times as good as bad patches on average ($\lambda_2 = 4\lambda_1$). The only thing that varies is the overall quality of the environment (or, equivalently, the quality of individual patches). Notice that while in each case the stopping rule is almost a straight line, the lines are different for different sets of parameters, becoming steeper for better environments.

What this says is that, while the stopping rules should be qualitatively similar for different environments, they should be quantitatively different. Animals should be more reluctant to leave patches of given quality in a bad environment than in a good environment. Waage (1979) has suggested a similar possibility for his model. That is,

animals should show a greater responsiveness to a given patch stimulus when the overall host density is lower.

Functional response.

For each set of parameters, characterizing a model environment, we can find the best stopping rule and the rate of finding prey achieved by the rule. The functional response of predators to differences in prey density may be studied by considering particular sets of environmental parameters. I have done this by letting the parameters vary in four ways. For each environment the rate of finding prey using the best strategy for that environment is compared with the rate achieved using the "naive" rule of systematically searching each patch to the end. For all the cases considered here, the time between patches will be $\tau = .125$, so we can identify the overall prey density in the environment with the "naive" rate:

$$R = (p_1\lambda_1 + p_2\lambda_2)/(1 + \tau).$$

Example 1. One simple way of varying the environmental parameters is to change the quality of all patches uniformly. This is illustrated by the cases described above in which "good" and "bad" patches are equally frequent and good patches are exactly four times as good as bad patches. For this example Table 1 gives parameter values, best rate, "naive" rate, and average time in each patch using the best rule. Figure 4 shows the functional response by plotting the overall average rate of finding prey in

the environment using the best foraging strategy against the rate achievable using the naive rate, which is proportional to the overall prey density.

Two things should be noticed here. First, the functional response is Type 3, with the best rate of finding prey an accelerating function of the overall prey density in the environment. In this and the other examples, handling time is ignored and so the functional response appears to keep increasing. Second, the average time foraging in each patch, given in Table 1, decreases as overall prey density increases. This happens because, as overall patch quality increases, the difference between good and bad patches is easier to distinguish and predators waste less time assessing patch quality.

Example 2. In this case good and bad patches are again assumed to be equally frequent, but the quality of bad patches is assumed to be constant ($\lambda_1 = 1$), perhaps to be thought of as "background," while the quality of good patches (λ_2) varies with environmental quality. Table 2 gives various values for λ_2 , the best rate achievable, the naive rate, and the average time in patches. Figure 5 illustrates the functional response by plotting the best rate against the naive rate. Again the functional response is Type 3 and the average time per patch is a decreasing function of environmental quality.

Example 3. In this case the quality of good and

bad patches does not change ($\lambda_1 = 1, \lambda_2 = 10$) with environmental quality, but their relative frequencies do. As environmental quality increases the frequency of good patches increases. Table 3 gives values of p_2 (the proportion of good patches), the best rate, the naive rate, and the average time per patch. Figure 6 illustrates the functional response. Notice that the functional response is not an accelerating function of prey density. However, the ratio of the rate of finding prey to overall prey density is an increasing function of prey density for low prey density (small p_2) and this is what is needed for predator-prey system stability. Unfortunately, the range of p_2 values for which this is true is small. It seems unlikely that optimal foraging could stabilize a predator-prey system if the environment varied simply by changing the frequency of good and bad patches.

Example 4. In this case all patches are assumed to have the same prey density, but this density varies with the environment. In this case the naive rule is best, the functional response would be Type 1 (ignoring handling time) and the average time per patch would be the same in all environments.

DISCUSSION

The idea of the functional response of an individual

predator to prey density is an important one in the theoretical consideration of predator-prey system stability. However, it is the predator's response to overall prey density in the environment that is important. Most experimental work on predation, as well as modeling of predator behavior, has been concerned with differences in predator behavior in patches (and not environments) of different prey density.

For predators foraging in patches of varying prey density it has been suggested that predators should spend more time in good patches than bad. This will result in a larger proportion of prey being taken from good patches than from bad. This would be true of optimal foragers in my model as well. However, in two of my examples the predators would spend an average of less time per patch in good environments than in bad. This itself produces a Type 3 functional response because animals in good environments need spend less time deciding whether a patch is good or not. Of course this result depends on exactly how patch quality varies in good and bad environments. As I showed with a similar model (Green 1980), even if average patch quality is constant, increasing the variance in patch quality may, by itself, increase the rate of finding prey for an optimal forager.

The reason that some of my examples demonstrate a Type 3 functional response to average prey density within environments is that in these examples the differences

between good and bad patches is greater and easier to detect in environments that are better overall. This is plausible. However, if patch quality within environments varies in other ways, being uniform in an environment of given quality, for example, then optimal foraging cannot produce a Type 3 functional response.

My results also depend on the foraging rule used. If an animal uses the naive rule then it is impossible to achieve a Type 3 functional response no matter what the pattern of patch quality is. However, it does seem that the best rules which I have found are simple enough for animals actually to use them. Other foraging strategies might or might not result in Type 3 functional responses.

Much recent work on foraging strategies traces its origins to the experimental work of Krebs, Ryan & Charnov (1974) and the theoretical work of Charnov (1973, 1976). Oaten (1977b) pointed out that Charnov's results, which were for a deterministic model, could not be extended unambiguously to the stochastic case. Oaten developed a general stochastic model of optimal foraging, but his assumptions were too general to be mathematically tractable. The model considered here and another considered earlier (Green 1980) are special cases of Oaten's general model of optimal foraging. Other, generally suboptimal, foraging strategies have been considered by Breck (1978) and Iwasa, Higashi & Yamamura (1981), whose graphical representation of stopping rules is like mine in Figures 1, 2 and 3.

Breck and Iwasa et al. give examples for which some of the foraging strategies they describe are optimal. Breck's (1978) thesis is the most extensive work I know of on stochastic foraging models, but it is, unfortunately, still unpublished. The only published work I know of that connects an explicit stochastic foraging model and functional response is Murdoch & Oaten (1975), which only considers differences in prey density between patches. This is not directly relevant to the question of predator-prey system stability.

Predator-prey systems do persist in the natural world and a Type 3 functional response of the predator to prey density is not the only mechanism that can contribute to this persistence. (For a discussion see Hassell 1978). However, functional response may be an important stabilizing mechanism.

The model described here is a simple one, which is not intended to describe the world exactly. But it does incorporate several aspects of the environment in its parameters and it makes it possible to study the predator's response to different prey densities and distributions theoretically. Certain patterns of prey distribution in different environments may permit an optimal forager to produce a Type 3 functional response. It seems to be worthwhile to see whether prey distribution and predator behavior are actually such that a system-stabilizing, Type 3 functional response might be produced.

SUMMARY

(1) The nature of the functional response of predators to prey density is important because it may influence the stability of the predator-prey system.

(2) Previous work has indicated a system-stabilizing, sigmoid functional response of the number of prey taken per predator to the prey density in a patch, due to predators spending more time in patches with more prey. This is irrelevant to the question of predator-prey system stability, however, because what matters is the functional response to overall prey density in the environment.

(3) The functional response to overall prey density is investigated using a simple stochastic optimal foraging model. The best foraging strategy and the best possible rate of finding prey are calculated for several sets of environmental parameters.

(4) The best foraging strategy is found to be quite simple. It is almost the same as that suggested in a behavioral model by Waage (1979).

(5) Functional response can be calculated by computing the rate of finding prey in various environments. Optimal foraging may produce a sigmoid functional response for certain patterns of prey distribution in different environments, but not for others.

(6) A sigmoid functional response may arise because at overall high prey densities the difference between

good and bad patches is greater than at overall low densities and predators need spend less time assessing patch quality.

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APPENDIX

Theoretical treatment of the model.

An animal searches for prey in two superficially indistinguishable types of "patches," each type with a Poisson distribution of the number of prey in a patch. Within each patch type prey become available at random times, at rate λ_1 in "bad" (Type 1) patches and rate λ_2 in "good" (Type 2) patches. Patches of the two types are arranged at random, with bad patches occurring with relative frequency p_1 and good patches with relative frequency $p_2 = 1 - p_1$. An animal can stay in each patch for no more than some fixed time, which may be considered to be unity without loss of generality. The average time to travel between patches is τ .

The probability density of the number of prey in a given patch of Type i (where $i = 1$ or 2) will be

$$(A1) \quad f_i(x) = \exp(-\lambda_i)(\lambda_i)^x/x! .$$

The number of prey that become available if an animal remains in a patch of Type i for time $t \leq 1$ will have probability density

$$(A2) \quad f_i(x,t) = \exp(-\lambda_i t)(\lambda_i t)^x/x! .$$

The probability that a given patch in which x prey have become available by time $t \leq 1$ is, in fact, Type i , is given by

$$(A3) \quad P_i(x, t) = p_i \exp(-\lambda_i t) (\lambda_i t)^x / \sum_{i=1}^2 p_i \exp(-\lambda_i t) (\lambda_i t)^x .$$

In a patch in which x prey have been encountered by time $t \leq 1$ the (expected) instantaneous rate at which prey are becoming available is

$$(A4) \quad \mu(x, t) = P_1(x, t)\lambda_1 + P_2(x, t)\lambda_2 .$$

The animal's foraging strategy.

An animal's foraging strategy consists of a rule that tells it when to leave one patch and go on to another. Such a rule is based on an animal's knowledge of the environment and its experience in a patch. In this model we assume that the animal knows the distribution of patch quality and also the distribution of prey within a patch of given quality. However, an animal cannot know whether a given patch is good or bad without spending some time in the patch.

In our model all the information about the quality of a patch obtained up to time $t \leq 1$ is contained in $X(t)$, the number of prey made available up to that time. We will find the strategy that maximizes the average rate of finding prey, which rate is given by

$$(1) \quad R = EG / (ET + \tau) ,$$

where R is the rate, EG is the expected number of prey obtained per patch visited when the strategy is used, and ET is the expected time per visit. Of course, R , EG and ET

depend on the strategy used. The best strategy will consist of a sequence of stopping times: $\{t_k \text{ for } k = 0, 1, \dots, x^*-1\}$, with $0 \leq t_0 \leq t_1 \leq \dots \leq t_{x^*-1}$, where the animal leaves a patch at time t_k if it has only found k prey by that time. If at any time the animal has found x^* or more prey it remains in the patch until the end ($t = 1$).

The best stopping rule is found by using the dynamic programming method of backward recurrence. The method used here is very similar to that used for a similar problem by Green (1980). An important difference is that the model considered here uses continuous time and the stopping times must be found by numerical approximation.

The method used to find the best strategy consists of two parts:

1) A value C is chosen (as a guess at the best possible rate of finding prey) and that strategy is determined which would achieve rate C if C were, in fact, the best possible rate.

2) The actual rate achieved using the strategy found in 1) using value C --call this rate $R(C)$ --is compared with C . If $R(C) = C$, the best rule has been found. If not, another value of C is chosen and steps 1) and 2) are repeated. If $R(C) < C$, a smaller value is chosen for C , while if $R(C) > C$, a larger value is chosen for C .

Finding the best stopping rule, given C .

If C^* is the best long-term rate that can be achieved,

then the best strategy will consist of remaining in a patch at any point (x,t) , where x prey have been found at time t , if there exists a strategy such that the ratio of expected gain to expected time after reaching the point (x,t) exceeds C^* . There exists some smallest number of prey, x^* , such that if at any time x^* prey or more have become available within a patch, the best strategy is to finish searching the entire patch. Then x^* is the smallest integer such that

$$(A5) \quad \mu(x^*,1) \geq C^* ,$$

where $(x^*,1)$ is given by (A4).

For each number of prey $x < x^*$ there exists a stopping time t_x such that the ratio of expected gain to expected time in the patch after point (x,t_x) just equals C^* if the animal stays in the patch for a short time after reaching (x,t_x) . For any point (x,t) the animal should continue in the patch if and only if $t < t_x$.

The best rate C^* is not known, so a value, C , is chosen and a stopping rule is sought which would be best if, in fact, the chosen value were actually C^* , the best rate possible. First x^* is found from (A5) using C in place of C^* . Then, working backward, the stopping times t_{x^*-1} , t_{x^*-2} , ..., t_0 are found in succession.

In general, if t_{x+1} , t_{x+2} , ..., t_{x^*-1} and x^* are known, then for $0 < t < t_{x+1}$, consider:

Rule 1: At point (x,t) continue in the patch for a short time, Δt . If no prey are found leave the patch. If a prey is found continue, using the stopping rule that has been built up by backward recurrence, using the chosen value of C as if it is C^* .

Then define:

$EG'(x,t,C)$ = the expected number of prey gained in a patch after (x,t) using Rule 1.

$ET'(x,t,C)$ = the expected time in a patch after point (x,t) using Rule 1.

Then for $x = x^*-1, x^*-2, \dots, 0$ we solve successively,

$$(A6) \quad EG'(x,t,C)/ET'(x,t,C) = C$$

for $t = t_x$. For $x = x^*-1$ we have

$$\begin{aligned} EG'(x,t,C)/ET'(x,t,C) &= C = \\ &= \frac{\mu(x^*-1,t)\Delta t(1 + \mu(x^*,t)(1 - t - \Delta t))}{\Delta t + \mu(x^*-1,t)t)\Delta t(1 - t - \Delta t)} \end{aligned}$$

which, after canceling the Δt and eliminating terms of order smaller than Δt , yields

$$(A7) \quad \frac{\mu(x^*-1,t)(1 + \mu(x^*,t)(1 - t))}{1 + \mu(x^*-1,t)(1 - t)} = C .$$

Expression (A7) is solved for t, yielding t_{x^*-1} .

For values of $x < x^*-1$ it is simpler to break up the terms involved in (A6) by separating patches of Types 1 and 2.

In order to obtain the values of $EG'(x,t,C)$ and $ET'(x,t,C)$

needed in (A6) it is necessary to find the probability of reaching each of the possible stopping points from the point $(x+1, t)$. In general, for given $p_1, \lambda_1, \lambda_2$ and C , and known $t_k, t_{k+1}, \dots, t_{x^*-1}$ and x^* , the desired probability of going from (k, t) to (g, t_g) for $t < t_k$ and any $g \geq k$, is given by

$$(A8) \quad P(g, t_g | k, t) = \sum_{i=1}^2 P_i(k, t) \left[Q_{\lambda_i}(t_g - t)^{(g-t)} - \sum_{l=k}^{\min(x^*-1, g-1)} P_i(l, t_l | k, t) Q_{\lambda_i}(t_g - t_l)^{(g-l)} \right]$$

where $Q_{\lambda}(x) = \exp(-\lambda)\lambda^x/x!$ is the Poisson probability and $P_i(l, t_l | k, t)$ is the probability of going from (k, t) to (l, t_l) in a patch of Type i and equals the coefficient of $P_i(k, t)$ on the right hand side of (A8).

Now for any point (x, t) such that $t < t_x$ we can define:
 $EG(x, t, C)$ = the expected gain in a patch after point (x, t)

using the rule that aims at achieving rate C .

$ET(x, t, C)$ = the corresponding expected time in a patch.

Then we have

$$(A9) \quad EG(x, t, C) = \sum_{g=x}^{\infty} (g-x)P(g, t_g | x, t), \text{ and}$$

$$(A10) \quad ET(x, t, C) = \sum_{g=x}^{\infty} (t_g - t)P(g, t_g | x, t) .$$

In general, expression (A6) becomes

$$(A11) \quad EG'(x, t, C)/ET'(x, t, C) = C = \frac{\mu(x, t)(1 + EG(x+1, t, C))}{1 + \mu(x, t)ET(x+1, t, C)} ,$$

which can be solved numerically for t . For a given set of parameters $p_1, \lambda_1, \lambda_2$ and a choice of C , a stopping rule is found by solving (A5) for x^* , then solving (A7) for t_{x^*-1} , and solving (A11) for $t_{x^*-2}, t_{x^*-3}, \dots, t_1, t_0$, successively.

Finding the rate $R(C)$, given the strategy.

Once the strategy is found the rate that it actually achieves, $R(C)$, may be calculated from (1), using $EG = EG(0,0,C)$ and $ET = ET(0,0,C)$ calculated using (A9) and (A10), respectively. The resulting value is

$$(A12) \quad R(C) = EG(0,0,C)/(ET(0,0,C) + \tau) ,$$

which is compared with C . If $R(C) = C$, the best possible rate C^* and the best possible strategy have been found. If $R(C) \neq C$, choose a new value of C , a smaller value if $R(C) < C$ and a larger value (slightly larger than $R(C)$) if $R(C) > C$. Continue until $R(C) = C$.

TABLE 1. Example 1: Rate of finding prey for environments varying only in overall prey quality; $p_1 = p_2 = .5$, $\lambda_2 = 4\lambda_1$, $\tau = .125$. Values are given for various values of λ_1 and corresponding best rate, naive rate and average time in patch. Notice that average time per patch decreases as environmental quality increases.

<u>λ_1</u>	<u>Best rate</u>	<u>Naive rate</u>	<u>ET</u>
0.5	1.1556	1.1111	.7022
1.0	2.4123	2.2222	.6212
1.5	3.7352	3.3333	.5851
2.0	5.1043	4.4444	.5650
2.5	6.5077	5.5556	.5524
3.0	7.9372	6.6667	.5438
3.5	9.3866	7.7778	.5377
4.0	10.8454	8.8889	.5333

TABLE 2. Example 2: Rate of finding prey for environments varying only in the quality of good patches; $p_1 = p_2 = .5$, $\lambda_1 = 1$, $\tau = .125$. Values are given for various values of λ_2 and corresponding best rate, naive rate and average time in patch.

<u>λ_2</u>	<u>Best rate</u>	<u>Naive rate</u>	<u>ET</u>
1	0.8889	0.8889	1.0000
2	1.3348	1.3333	.9449
3	1.8372	1.7778	.7223
4	2.4123	2.2222	.6212
5	3.0387	2.6667	.5695
6	3.7009	3.1111	.5418
7	4.3887	3.5556	.5251
8	5.0955	4.0000	.5146
9	5.8164	4.4444	.5080
10	6.5478	4.8889	.5035

TABLE 3. Example 2: Rate of finding prey for environments varying only in relative proportions of good and bad patches; $\lambda_1 = 1$, $\lambda_2 = 10$, $\tau = .125$. Values are given for various values of p_2 ($p_2 = 1 - p_1$) and corresponding best rate, naive rate and average time in patch.

<u>p_2</u>	<u>Best rate</u>	<u>Naive rate</u>	<u>ET</u>
.0	0.8889	.8889	1.0000
.025	1.1815	1.0889	.3073
.05	1.6579	1.2889	.2435
.075	2.1148	1.4889	.2383
.1	2.5394	1.6889	.2444
.2	3.9509	2.4889	.2954
.3	5.0216	3.2889	.3589
.4	5.8639	4.0889	.4285
.5	6.5478	4.8889	.5035
.6	7.1189	5.6889	.5844
.7	7.6090	6.4889	.6723
.8	8.0432	7.2889	.7692
.9	8.4465	8.0889	.8783
.95	8.6500	8.4889	.9387
1.0	8.8889	8.8889	1.0000

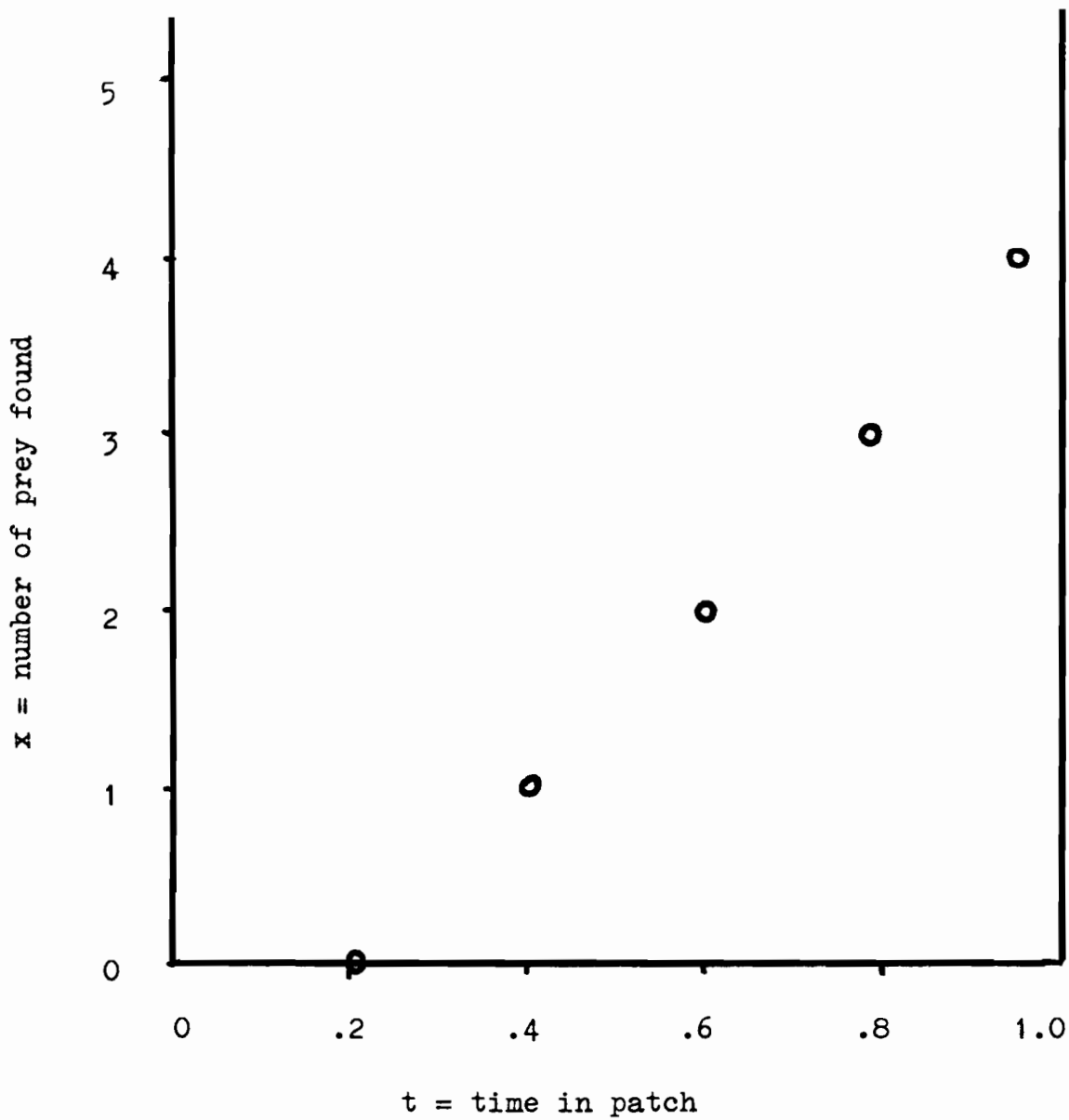


FIGURE 1. Best stopping rule for the parameter set:
 $p_1 = p_2 = .5$, $\lambda_1 = 2$, $\lambda_2 = 8$, $\tau = .125$. The open circles
are the stopping points. Notice that the stopping points
lie nearly on a straight line.

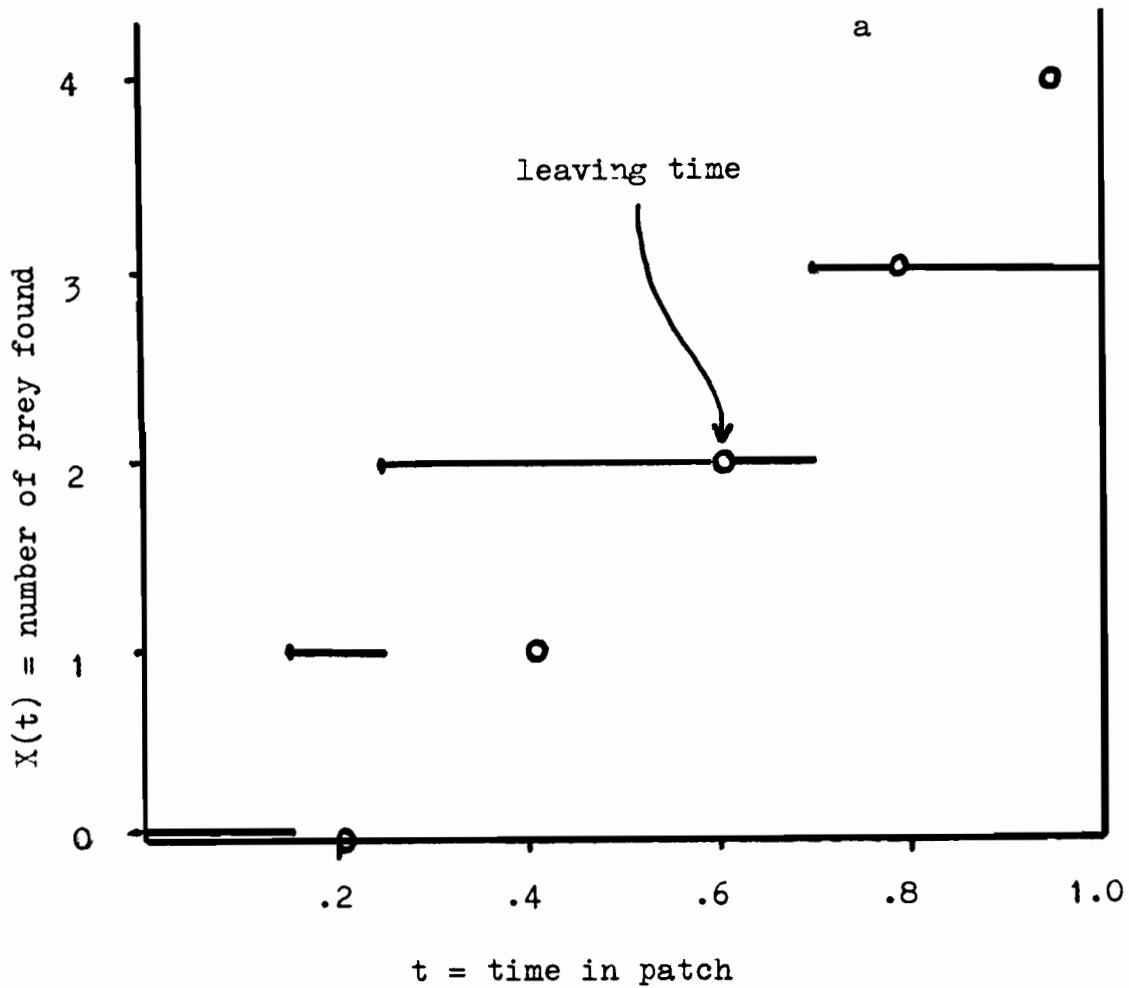


FIGURE 2a. The best stopping rule illustrated for a particular outcome. $X(t)$ is the number of prey found by time t . In the example illustrated prey become available at times .15, .25, and .7. The animal using the best rule (plotted with open circles for the parameters; $p_1 = p_2 = .5$, $\lambda_1 = 2$, $\lambda_2 = 8$, $\tau = .125$) would leave a patch when one of the stopping points is hit. For this example the animal should leave the patch at $t_2 = .6049$, having found 2 prey by that time.

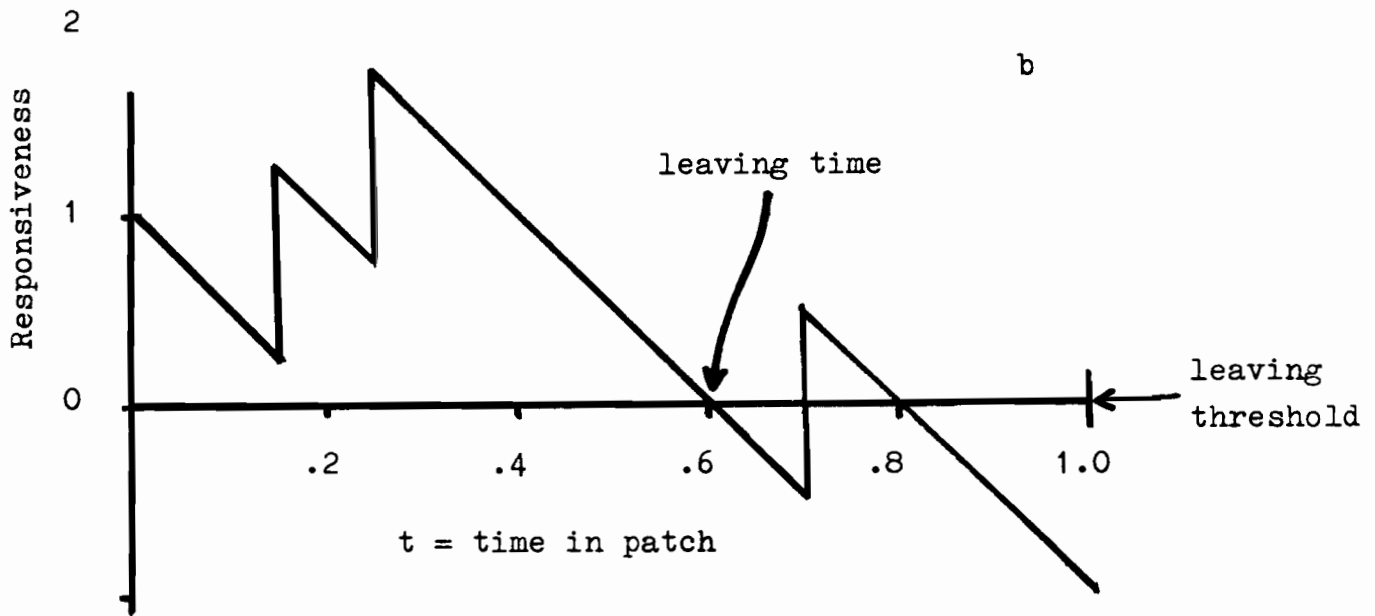


FIGURE 2b. Responsiveness of an animal to a patch. This version of Waage's behavioral model is illustrated for the same example as in Figure 2a. Responsiveness starts at some level and declines at a constant rate until a prey is found, which increases responsiveness by a unit. The animal stays in a patch until a threshold is reached and the animal leaves the patch. For this example the animal would leave the patch at time $t \doteq .6$.

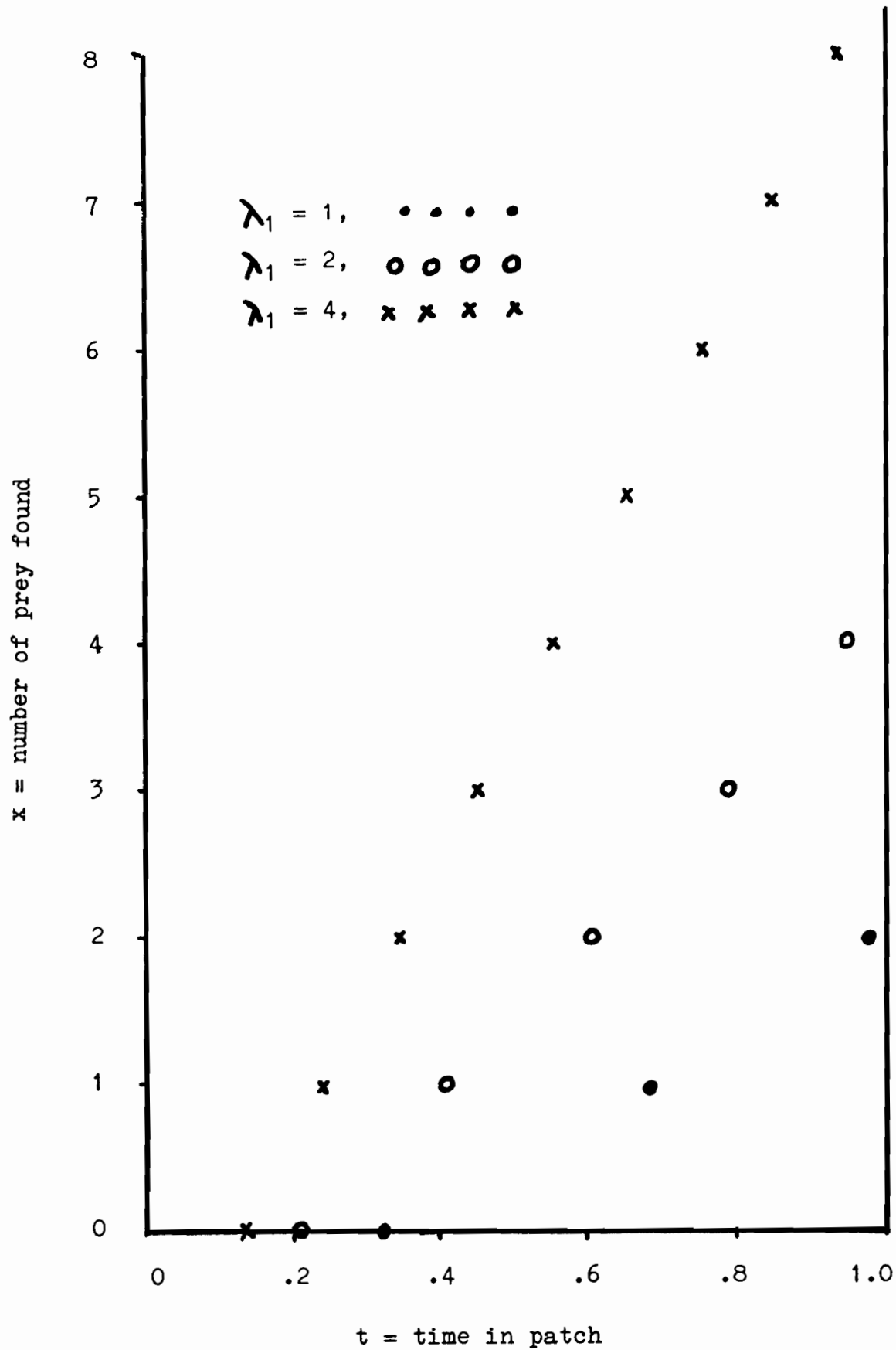


FIGURE 3. Best stopping rules for three similar environments, differing only in overall prey density; $p_1 = p_2 = .5$, $\lambda_2 = 4\lambda_1$ (good patches four times as good as bad patches), $\tau = .125$.

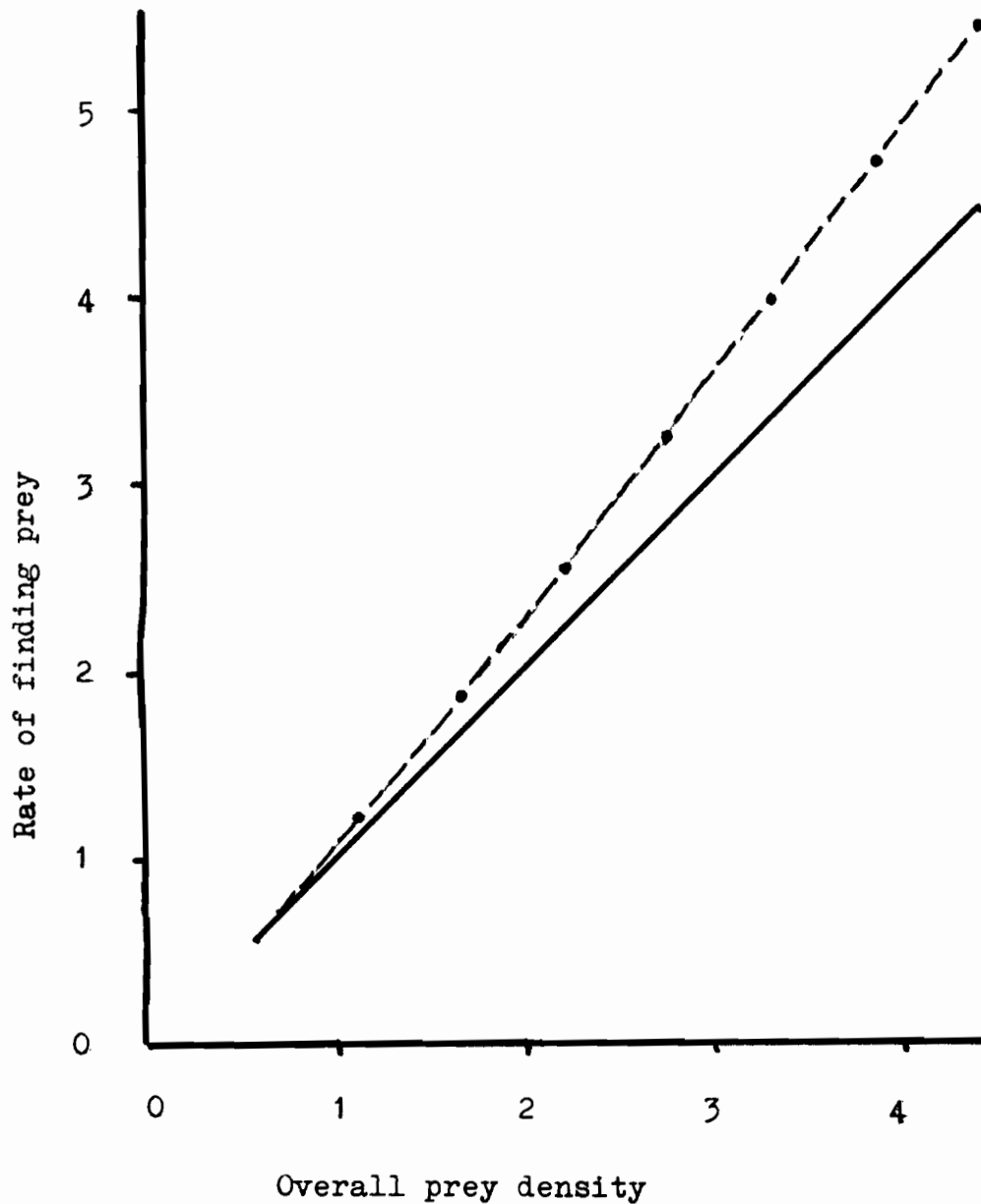


FIGURE 4. Functional response. Environments only differ in overall quality; $p_1 = p_2 = .5$, $\lambda_2 = 4\lambda_1$, $\tau = .125$, λ_1 (and λ_2) varies. Rate of taking prey plotted against overall prey density. Broken line is for best rule; solid line is for naive rule.

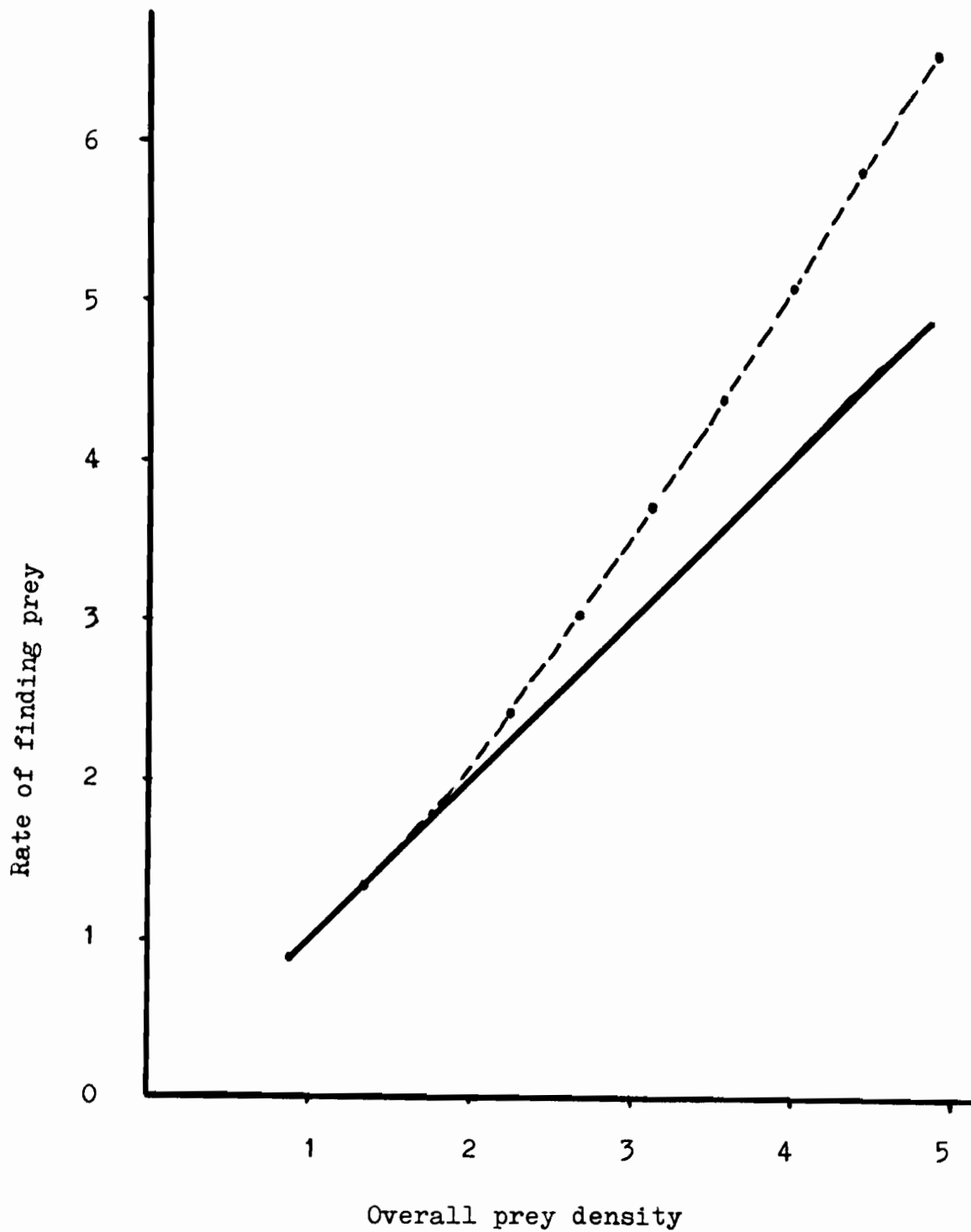


FIGURE 5. Functional response. Environments differ only in the quality of good patches; $p_1 = p_2 = .5$, $\lambda_1 = 1$, $\tau = .125$. Rate of taking prey plotted against overall prey density. Broken line is for best rule, solid line if for naive rule.

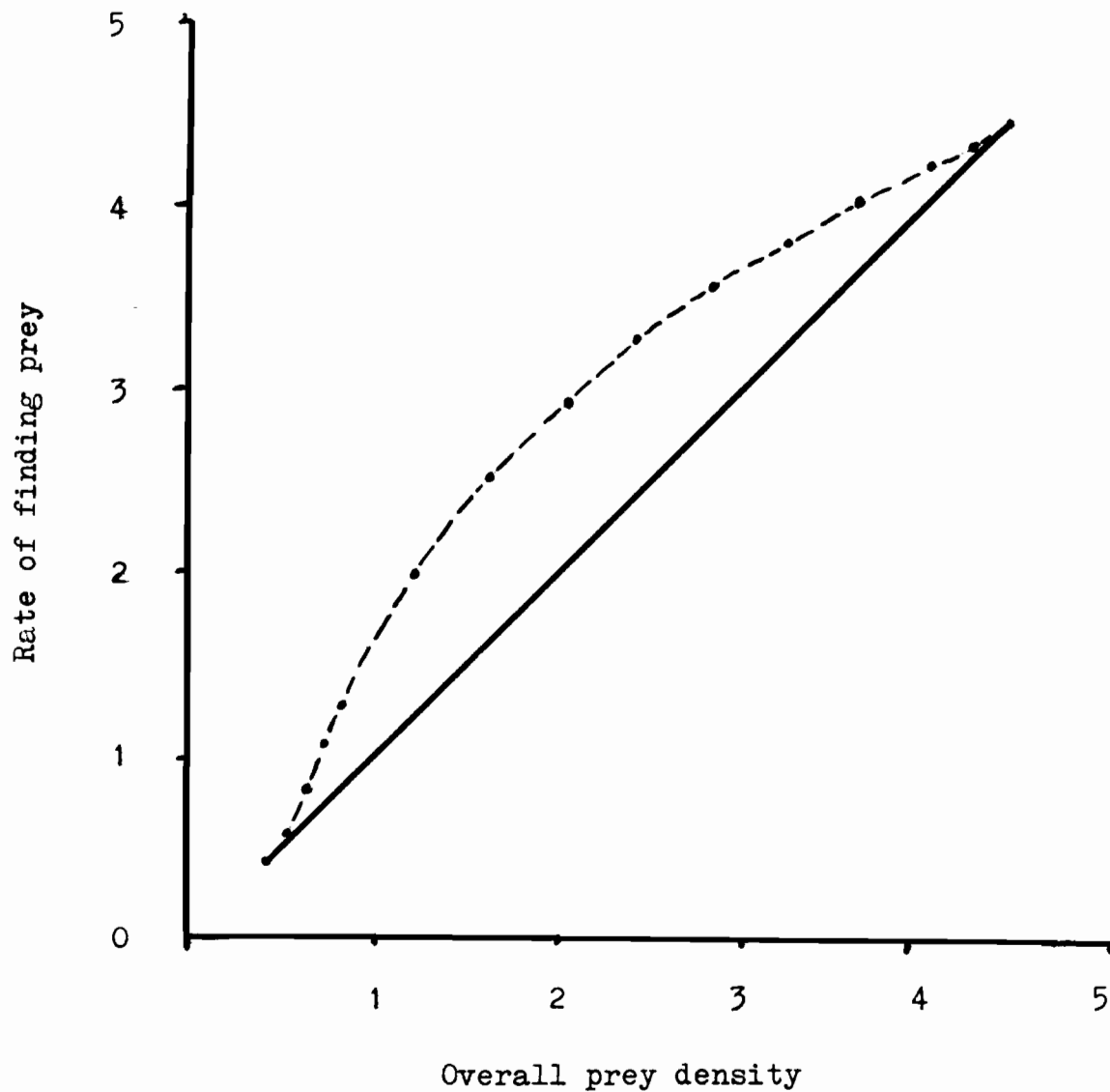


FIGURE 6. Functional response. Environments differ only in relative proportions of good and bad patches; $\lambda_1 = 1$, $\lambda_2 = 10$, $\tau = .125$. Rate of taking prey plotted against overall prey density. Broken line is for best rule, solid line is for naive rule.