

**THE GIVING-UP-TIME RULE  
AS A STRATEGY FOR ANIMALS  
FORAGING SYSTEMATICALLY  
IN A PATCHY ENVIRONMENT**

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## THE GIVING-UP-TIME RULE AS A STRATEGY FOR ANIMALS FORAGING SYSTEMATICALLY IN A PATCHY ENVIRONMENT.

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*ABSTRACT* In this paper I give a method for finding the long-term average rate of finding prey achieved by a systematic forager using a giving-up-time rule to decide when to leave patches in which prey are distributed continuously and randomly. The method is illustrated in the case that patches are all of the same size and the number of prey per patch has a negative binomial distribution. The best giving-up-time and the rate that it achieves are found for particular cases, and the rate achieved for each is compared with the rates achieved by other strategies .

### INTRODUCTION

Animals that search for prey which are distributed in patches, for example, woodpeckers that search for insects on trees, must have some way of deciding when to leave one patch and go on to another. If an animal is to achieve a high long-term average rate of finding prey it should leave patches having few prey after only a short visit, and should remain for a longer time in patches having more prey. The question is, how can an animal decide when to leave a patch? Or, how should an animal use information about a patch to decide when to leave a patch? If the only information that an animal obtains about a patch is the time and/or place at which prey are found, the question is, how should the times (and/or places) at which prey are found be used to decide when to leave a patch? One simple rule that has been suggested is to leave a patch as soon as the time that has passed without finding a prey reaches some critical value,  $g$ . This time,  $g$ , is referred to as the "giving-up-time," and the associated leaving rule is referred to as the "giving-up-time rule."

At one time (Krebs, Ryan, and Charnov 1974) the giving-up-time rule was thought to permit optimal foraging, but it is now realized that this is not the case (McNair 1982,

Green 1984). However, the giving-up-time rule is simple, and one can argue that it should be considered, not as an optimal foraging strategy, but as a "rule of thumb" that animals might use (Janetos and Cole 1981; Krebs, Stephens, and Sutherland 1983). While the giving-up-time rule is undeniably simple, it is unlikely that animals would actually use it unless it were also reasonably efficient, or if no other simple foraging strategy were possible.

In this paper I study the relative efficiency of the giving-up-time rule in a particular, biologically realistic, case by comparing the long-term average rate of finding prey achieved by the giving-up-time rule and by other rules, including one that achieves the highest possible rate among all rules based on the animal's experience in each patch. It is seen that the giving-up-time rule is quite good (It is certainly better than nothing, that is, using a rule that ignores experience in each patch.), but it is not optimal in any of the cases that I consider. Further, in these cases it is seen that there exists a rule that is simpler and more efficient than the giving-up-time rule.

The main point of this paper is the calculation of the long-term average rate of finding prey achieved by the giving-up-time rule under the assumptions that a) the forager searches patches systematically, and b) the time at which prey are found is continuous. A method for finding the long-term average rate of finding prey by foragers using the giving-up-time rule has been found by several people, including Iwasa, Higashi, and Yamamura (1981) for random search, and a method has been given for systematic search in the case in which prey are found in discrete "bits" of time (Green 1984). The case considered here is more difficult.

## METHOD

### 1. *Finding the long-term average rate of finding prey for a forager using the giving-up-time rule.*

#### *The problem.*

The animal forages in a *patch*, which I will treat as the interval  $(0, 1)$ . I assume that all patches are the same size, and differ only in the number and location of prey that they contain. I think of a patch as an interval of time during which the animal can search for prey.

The *number of prey in a patch*,  $N$ , will be a random variable, whose distribution is specified by some probability function,  $f(n)$ . I am most interested in the cases in which  $N$  has a negative binomial distribution.

The *locations* of the  $n$  prey in a patch will be distributed at random. That is, the locations of the  $n$  prey will be independent variables, each having a uniform distribution

on  $(0, 1)$ . Search is assumed to be systematic. That is, the forager starts in a patch at the beginning (time = 0) and continues searching at a constant rate until deciding to leave a patch. A forager using the giving-up-time rule has some number,  $g$ , the “giving-up-time,” such that a patch is left if no prey are found during the first time interval of length =  $g$  in the patch, or if exactly  $g$  units of time have passed since the last prey was found. The forager will leave a patch when the end is reached, even if there has been no interval longer than  $g$  without prey.

The *number of prey,  $X$ , found in a patch*, and the *amount of time,  $T$ , spent searching a patch* are random variables whose values depend on the number and location of prey in the patch. I want to find the long-term average rate of finding prey,

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

where  $EX$  and  $ET$  are the expected number of prey found and the expected amount of time spent searching, respectively, per patch searched, and  $\tau$  is the average travel time between patches, which I assume is known.

*Ideas used to solve the problem.*

The required values of  $EX$  and  $ET$  are found by conditioning on  $N$ , the number of prey in a patch. For a given number of prey,  $N = n$ , we can think of the locations of the  $n$  prey as breaking up the interval  $(0, 1)$  into  $n + 1$  subintervals. We may think of the (sub-)intervals as being long (length  $\geq g$ ) or short (length  $< g$ ). The number of prey found will equal the number of short intervals encountered before the first long one, unless all the intervals are short, in which case all  $n$  prey will be found. The search time will equal the sum of the lengths of the short intervals encountered before the first long interval, plus the giving-up-time,  $g$ . If all the intervals are short then the search time equals one.

We can write

$$EX = \sum_{n=1}^{\infty} E(X|n)f(n), \quad \text{and} \quad (2)$$

$$ET = \sum_{n=0}^{\infty} E(T|n)f(n), \quad (3)$$

where  $E(X|n)$  is the expected number of prey found and  $E(T|n)$  is the expected search time per patch having exactly  $n$  prey. These expectations are found by first finding the distribution of the number of short intervals in patches containing exactly  $n$  prey (What I actually do is find the distribution of the number,  $m$ , of long intervals, but, of course, the number of short intervals equals  $n + 1 - m$ ), and then using this distribution to find the average length of a short interval in patches with exactly  $m$  long intervals and  $n + 1 - m$  short intervals.

*Notation and formulas.*

The long-term average rate of finding prey depends on the distribution of the number of prey per patch,  $f(n)$ , the travel time between patches,  $\tau$ , and the strategy used, here specified by the giving-up-time,  $g$ . I assume that  $f(n)$  is negative binomial, which I interpret as a mixture of Poisson distributions, where the Poisson parameter  $\lambda$  is a random variable having a gamma distribution with parameters  $\alpha$  and  $\beta$ . I use the notation:

$(\alpha, \beta)$  = the parameters that specify  $f(n)$ , that is,

$$f(n) = \binom{\alpha + n - 1}{n} \left( \frac{\beta}{\beta + 1} \right)^\alpha \left( \frac{1}{\beta + 1} \right)^n. \quad (4)$$

This expression is used in (2) and (3).

$\tau$  = travel time (or average travel time) between patches. This term is used in (1).

$g$  = the giving-up-time. The forager will leave a patch when it has spent a time interval which equals  $g$  in a patch without finding a prey.

The main problem here is to calculate  $E(X|n)$  and  $E(T|n)$  for specified values of the giving-up-time,  $g$  (I could write  $E(X|n, g)$  and  $E(T|n, g)$ , but I suppress the  $g$  for notational simplicity.), for all values of  $n \geq 1$ . I use the following notation:

$N$  = the number of prey in a patch.

$X$  = the number of prey found by the forager in a patch.

$T$  = the time spent searching in a patch.

$M$  = the number of long intervals (inter-prey intervals, plus the intervals before the first prey and after the last prey) in a patch.

$P_{\{m\}}$  = the probability that a patch contains exactly  $m$  long intervals. (These probabilities depend on the values of  $N(=n)$  and  $g$ , but I suppress this dependence of  $n$  and  $g$  for notational simplicity.)

$A_k$  = the probability that a specified set of  $k$  intervals, for example, the first  $k$  intervals, are all long.

$S_k$  = the sum (over all sets of  $k$  intervals) of the probabilities that specified sets of  $k$  intervals are all long.

$L$  = the length of a specified interval, in particular, the last interval.

$L_s$  = the length of a specified interval, given that it is short.

$L_l$  = the length of a specified interval, given that it is long.

The conditional expectations  $E(X|n)$  and  $E(T|n)$  are found using

$$E(X|n) = \sum_{m=0}^n E(X|n, m)P_{[m]}, \quad (5)$$

$$E(T|n) = \sum_{m=0}^{n+1} E(T|n, m)P_{[m]}, \quad \text{for } n \geq 1, \text{ and} \quad (6)$$

$$E(T|0) = g,$$

where  $E(X|n, m)$  and  $E(T|n, m)$  are the expected number of prey found and the expected time spent searching, respectively, per patch containing exactly  $n$  prey and having exactly  $m$  long intervals.

The values of  $P_{[m]}$  will be non-zero for  $m = 1, 2, \dots, n + 1$  if  $(n + 1)g < 1$ , and for  $m = 0, 1, 2, \dots, [1/g]$  if  $(n + 1)g \geq 1$ .  $[1/g]$  is the greatest integer less than or equal to  $1/g$ . The problem now is to find  $P_{[m]}$ ,  $E(X|n, m)$  and  $E(T|n, m)$ . These all depend on  $g$ , and  $P_{[m]}$  depends on  $n$  as well, but I suppress these to simplify the notation.  $P_{[m]}$  is found using a theorem in Feller (1968, IV.3.1):

$$P_{[m]} = S_m - \binom{m+1}{m} S_{m+1} + \binom{m+2}{m} S_{m+2} - \dots \pm \binom{n+1}{m} S_{n+1} \quad (7)$$

We have

$$S_k = \binom{n+1}{k} P(A_k) \quad (8)$$

by symmetry. We find  $P(A_k)$  using

**LEMMA 1.**

$$\begin{aligned} P(A_k) &= (1 - kg)^n \quad \text{for } k < 1/g, \\ &= 0 \quad \text{for } k \geq 1/g. \end{aligned} \quad (9)$$

**PROOF:** The case  $k \geq 1/g$  is trivial. Assume that  $k < 1/g$ .

The probability  $P(A_k)$  is equivalent to the probability that the first  $k$  intervals are each long, by symmetry. Now, consider the event,  $A'_k$ , that the first  $k$  intervals are long. Then we have

$$\begin{aligned} P(A'_k) &= P\{X_{(1)} \geq g, X_{(2)} \geq X_{(1)} + g, X_{(3)} \geq X_{(2)} \\ &\quad + g, \dots, X_{(k)} \geq X_{(k-1)} + g\}. \end{aligned} \quad (10)$$

Including  $X_{(k+1)}, \dots, X_{(n)}$ , we have

$$P(A'_k) = P\{X_{(n)} \geq X_{(n-1)} \geq \dots \geq X_{(k+1)} \geq X_{(k)} \geq X_{(k-1)} + g \geq X_{(k-2)} + 2g \geq \dots \geq X_{(1)} + (k-1)g \geq kg\}. \quad (11)$$

Now let  $Y_{(n)} = X_{(n)}, Y_{(n-1)} = X_{(n-1)}, \dots, Y_{(k)} = X_{(k)}; Y_{(k-1)} = X_{(k-1)} + g, Y_{(k-2)} = X_{(k-2)} + 2g, \dots, Y_{(2)} = X_{(2)} + (k-2)g, Y_{(1)} = X_{(1)} + (k-1)g$ . Then we have

$$P(A'_k) = P\{Y_{(n)} \geq Y_{(n-1)} \geq \dots \geq Y_{(1)} \geq kg\}, \quad (12)$$

where the  $Y_{(i)}$ 's are shifted uniform order statistics and the restriction on them is equivalent to the restriction on the  $X_{(i)}$ 's. From (12) we have

$$P(A'_k) = (1 - kg)^n, \quad \text{and, therefore} \\ P(A_k) = (1 - kg)^n. \quad (13)$$

*Q. E. D.*

A patch with  $n$  prey is broken into  $n+1$  intervals. If exactly  $m$  of these are long and  $n+1-m$  are short, and if the intervals are arranged at random, then the probability that a randomly chosen short interval will lie to the left of all the long intervals is  $1/(m+1)$ . Therefore,

$$E(X|n, m) = (n+1-m)/(m+1). \quad (14)$$

It is more difficult to find  $E(T|n, m)$ . If one can find  $E(L_s|n, m)$ , the expected length of a short interval, given exactly  $m$  long and  $n+1-m$  short intervals in a patch, then

$$E(T|n, 0) = 1, \\ E(T|n, n+1) = g, \quad \text{and} \\ E(T|n, m) = E(L_s|n, m)E(X|n, m) + g \quad \text{for } m \neq 0, m \neq n+1. \quad (15)$$

The problem is to find  $E(L_s|n, m)$ . In order to do this I will use a theorem on conditional expectation and will concentrate, for definiteness, on the length of the last (right-most) interval. I make use of

**LEMMA 2.** If  $L$  is the length of the last interval, and if the first  $k$  intervals are long (this requires that  $k < 1/g$ ), then the expected length of the last interval is given by

$$E(L|n, k) = 1/(n+1), \quad \text{if } k = n+1, \text{ and} \\ E(L|n, k) = (1 - kg)/(n+1), \quad \text{if } k \leq n. \quad (16)$$

*PROOF:* Using the idea used to prove Lemma 1, we can think of the event that the first  $k$  intervals are long as being equivalent in a sense to all the points lying in the interval  $(kg, 1)$ , in fact, being independent and uniform on  $(kg, 1)$ . In this case, the expected

length of the last interval is  $(1 - kg)/(n + 1)$ , if  $k$  is not equal to  $n + 1$ . The case  $k = n + 1$  is trivial.

Q. E. D.

Notice that conditioning on  $n$  and  $m$ , for example, in  $E(T|n, m)$ , means that the patch contains  $n$  prey and *exactly*  $m$  intervals are long. When I condition on  $n$  and  $k$ , for example, in  $E(L|n, k)$ , this means that the patch contains  $n$  prey and the *first*  $k$  intervals are long.

I find the values of  $E(L_s|n, m)$  by solving the equation for conditional expectation:

$$E(L|n, k) = \sum_{m=k}^n E(L_s|n, k, m, 0)P(n, k, m, 0|n, k) + \sum_{m=k+1}^{n+1} E(L_l|n, k, m, 1)P(n, k, m, 1|n, k) \quad (17)$$

where  $E(L_s|n, k, m, 0)$  is the expected length of the last interval, given that it is short, that the patch contains  $n$  prey, of which exactly  $m$  are long, including the first  $k$ .  $E(L_l|n, k, m, 1)$  is the corresponding expected length of the last interval, given that it is long.  $P(n, k, m, i|n, k)$  is the probability that exactly  $m$  intervals are long (including the last one if  $i = 1$ , excluding the last one if  $i = 0$ ), given that the patch contains  $n$  prey and the first  $k$  intervals are long. We can simplify the notation in (17) and write

$$E(L|n, k) = \sum_{m=k}^n E(L_s|n, m)P(m, 0|n, k) + \sum_{m=k+1}^{n+1} E(L_l|n, m)P(m, 1|n, k), \quad (18)$$

which we want to solve for  $E(L_s|n, m)$ , for  $m = 1$  to  $n$  if  $(n + 1)g < 1$  (*Case 1*), and for  $m = 0$  to  $[1/g]$  if  $(n + 1)g \geq 1$  (*Case 2*). We solve (18) iteratively for  $E(L_s|n, m)$  and  $E(L_l|n, m)$ , starting with the largest possible value of  $k$  ( $k = n + 1$  in Case 1 and  $k = [1/g]$  in Case 2). We use three facts:

a)  $E(L|n, k)$  is given by (16).

b)

$$P(m, 0|n, k) = P_{[m]} \binom{n-k}{m-k} / \left[ \binom{n+1}{m} P(A_k) \right] \\ P(m, 1|n, k) = P_{[m]} \binom{n-k}{m-k-1} / \left[ \binom{n+1}{m} P(A_k) \right]. \quad (19)$$



c)  $E(L_s|n, m)$  and  $E(L_l|n, m)$  are related by

$$mE(L_l|n, m) + (n + 1 - m)E(L_s|n, m) = 1 \quad (20)$$

and each can be expressed in terms of the other.

A BASIC program which does these calculations is given in an Appendix.

## 2. Finding the long-term average rate of finding prey for a forager using Lima's rule.

Steve Lima (1984) performed an experiment in which downy woodpeckers foraged for "prey" hidden in holes drilled in artificial "trees," each of which had either no prey or a fixed number of prey. Excluding the possibility that the foragers could count the number of prey obtained in a tree and leave when exactly the fixed number of prey were found, the best strategy is to begin by searching a particular number of holes in each tree, leaving if no prey are found, and remaining until the tree has been searched completely if any prey are found at the beginning of the search. This strategy is simpler than the giving-up-time rule, which it resembles.

Lima's rule is the optimal strategy for the birds in his experiment, and it also works quite well for my model. Not only is Lima's rule conceptually simple, but it is easy to analyze. For my model I will characterize the rule as follows: If no prey is found within time  $t = t_0$  of entering a patch, leave; otherwise stay until the patch has been searched completely ( $t = 1$ ). If the number of prey per patch has a negative binomial distribution with parameters  $\alpha$  and  $\beta$ , then the probability of finding no prey by time  $t_0$  is given by

$$p(0, t_0) = [\beta/(\beta + t_0)]^\alpha. \quad (21)$$

The expected number of prey remaining in a patch left by a forager at time  $t_0$ , without having found any prey, is given by

$$E(N|0, t_0) = (1 - t_0)\alpha/(\beta + t_0). \quad (22)$$

Therefore, the expected number of prey found by a forager using Lima's rule is given by

$$E(X|t_0) = \alpha/\beta - (1 - t_0)p(0, t_0)\alpha/(\beta + t_0). \quad (23)$$

The expected time spent foraging per patch is given by

$$E(T|t_0) = 1 - (1 - t_0)p(0, t_0). \quad (24)$$

## 3. The optimal foraging strategy and a strategy that ignores experience in a patch.

If the number of prey per patch has a negative binomial distribution, then the optimal foraging strategy based on experience obtained while foraging may be found by dynamic programming (Green 1987a,b). The optimal strategy has roughly the form: Leave

a patch if the rate of finding prey in the patch falls below some critical value, otherwise continue until the patch has been searched completely.

Perhaps the simplest strategy is to remain in each patch until it has been searched completely. This strategy may be used as a (lower) standard against which to measure the performance of other strategies. The long-term average rate of finding prey achieved by this "naive" strategy is

$$R = \alpha / [\beta(1 + \tau)]. \quad (25)$$

## RESULTS

The long-term average rates of finding prey are given in Table 1 for four different strategies: 1) the best assessment rule, 2) Lima's rule, 3) the giving-up-time (GUT) rule, and 4) a naive rule that ignores an animal's experience in patches. Rates are given for four cases with different levels of variability in the number of prey per patch, but with the same average number of prey per patch ( $\mu = \alpha/\beta = 5$ ) and the same travel time ( $\tau = .1$ ). The advantage of using information is greater for more variable patches, as is the advantage of using the best assessment rule over the GUT rule or Lima's rule. Lima's rule is better than the GUT rule.

In Fig. 1 the long-term average rates of finding prey achieved by the GUT rule and Lima's rule are plotted against the GUT and the stopping time  $t_0$ , for four different levels of patch variability. The rates achieved are rather insensitive to the GUT and the value of  $t_0$  in regions around the optimal values. The optimal giving-up-times are greater when patches are less variable. It can also be seen that the optimal value of the GUT is greater than the optimal value of  $t_0$ . This is because an animal using Lima's rule only stops if no prey are found by time  $t_0$  (or if the patch has been searched completely), while an animal using the GUT rule would stop at such times, but would also stop if some prey have been found, but an interval equal to the GUT has passed since the last prey was found.

## DISCUSSION

While the GUT rule has been described (Krebs, Ryan and Charnov 1974) as if it were optimal, in general it is not (see McNair 1982). McNamara (1982, Example 2, p. 276) did provide an artificial example in which the GUT rule is optimal, but he did not mention this fact. Recently, there has been an attempt to resurrect the GUT rule, not as an optimal foraging strategy, but as a simple rule (a "rule of thumb") that a forager might be able to use. For systematic search and a negative binomial distribution of prey in patches, the best assessment rule is nearly as simple as the GUT rule, and achieves a

substantially higher rate of finding prey if patches are highly variable. In this case the rule suggested by Lima is also better than the GUT (although not as good as the best rule) and is simpler as well. For less variable patches there is little to choose among the rules except simplicity.

I have treated the GUT rule as a strategy that might be used by a systematic forager. However, the rule was not intended for this purpose. It is more sensible to use such a rule if the rate of finding prey in a patch decreases with the time that the forager has spent in the patch, perhaps because the forager searches randomly. I think that the assumption of random search, although widespread in models of foraging (Hassell and May 1974, Murdoch and Oaten 1975, Breck 1978, Iwasa, Higashi and Yamamura 1981), is not very realistic. There is a good deal of evidence that search within patches is systematic (Lima 1984, Baum 1987), or at least non-random (Gill and Wolf 1975, Kamil, 1978). Even if search is random, the GUT is not optimal (see Green (1987b) for the case of negative binomial prey distribution), but its performance relative to other strategies is worth considering. I will consider this in more detail in the future.

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## APPENDIX

Here is a BASIC program that calculates the long-term average rate of finding prey achieved by a systematic forager using a giving-up-time rule to search for negative-binomially distributed prey. The program divides by zero repeatedly for small values of giving-up-time, but it seems to work anyway. The negative binomial parameters used in equation (4) are given in statements 10 and 20, and the travel time used in equation (1) is given in statement 30 as  $T_0$ . The negative binomial probabilities, denoted as  $P(*)$ , are calculated in statements 100 to 130, and the partial sums of the probabilities and the partial sums of the products of the variable values and their probabilities, denoted by  $S1(*)$  and  $S2(*)$ , respectively, are also calculated. These partial sums are used to calculate the approximations in statements 1510 to 1700. The giving-up-time used is given in statement 200.

The expressions  $EX$  and  $ET$  needed in equation (1) are indicated by  $X$  and  $T$  in the program. The conditional expectations  $E(X|n)$  and  $E(T|n)$  are denoted by  $X(*)$  and  $T(*)$  in the program. The probability  $P_{[m]}$ , given in equation (7), that there are exactly  $m$  long intervals (given that there are exactly  $n$  prey in the patch) is denoted by  $Q(*)$  in the program and is calculated in statements 320 to 410 for the case  $(n+1)g \geq 1$  [Case 2], and in statements 500 to 590 for the case  $(n+1)g < 1$  [Case 1]. The terms  $S_k$  are denoted by  $S(*)$  in the program and are calculated using logs of factorials, denoted by  $L(*)$  in the program, and calculated in statements 50 to 80.

The values of  $E(L_s|n, m)$ ,  $E(L_l|n, m)$  [which are denoted by  $E1(*)$  and  $E2(*)$ , respectively, where  $*$  stands for  $m$  and  $n$  is implicit] and  $E(X|n)$  and  $E(T|n)$  are calculated in statements 610 to 795 for Case 1 and in statements 1000 to 1180 for Case 2, and the values for  $E(X|n)$  and  $E(T|n)$  are put into equations (5) and (6) in statements 800 and 810 or statements 1190 and 1200. The  $E(L|n, k)$  in equation (16) is denoted by  $E(*)$  in the program, where  $*$  stands for  $k$ , while  $P(m, 0|n, k)$  and  $P(m, 1|n, k)$  in equations (19) are denoted by  $P1(*, *)$  and  $P2(*, *)$  in the program, where  $*, *$  stands for  $m, k$ . The values of the expressions in (19) are calculated in statements 700, 708, 730 and 740 or in statements 1070, 1120 and 1130.

Finally, the sums given in (2) and (3) are taken over infinitely many terms. The program sums for  $n = 0, 1, 2, \dots, 99$ . The approximate values of  $EX$  and  $ET$  are given for those sums, along with two pairs of approximations to the infinite sums, one providing a lower bound, the other providing an upper bound for the true value of  $R$  given in (1). In one approximation  $(n/99)E(X|99)$  is substituted for  $E(X|n)$  and  $E(T|99)$  is substituted for  $E(T|n)$  in (2) and (3) for  $n > 99$ . Since, for  $n > 99$ , the ratio  $[(n/99)E(X|99)]/E(T|99)$  is less than the ratio  $E(X|n)/E(T|n)$ , but both ratios are larger than the remaining terms in the ratio given by (1) [and (2) and (3)], and  $E(T|99)$  is less than  $E(T|n)$ , we have that this approximation, printed as  $X2/(T2 + T0)$  in statement 1600, is a lower bound for the true value of  $R$ . In the other approximation,  $n$  is substituted for  $E(X|n)$  and 1 is substituted for  $E(T|n)$  in (2) and (3), for  $n > 99$ . Since 1 is greater than  $E(T|n)$  and  $n (= n/1)$  is greater than the ratio  $E(X|n)/E(T|n)$ , and since that ratio and  $n$  are both larger than the remaining terms given by (1), we have that this approximation, printed as  $X3/(T3 + T0)$  in statement 1700, is an upper bound for the true value of  $R$ . These approximations are very good.

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1 PRINT "Calculating rate for GUT rule and systematic search"
2 DIM S1(100)
3 DIM S2(100)
4 DIM S(100)
5 DIM P(100)
6 DIM Q(100)
7 DIM L(100)
8 DIM X(100)
9 DIM T(100)
10 A = .5
12 DIM E(100)
13 DIM E1(100)
14 DIM E2(100)
15 DIM P1(20,20)
16 DIM P2(20,20)
20 B = .1
30 T0 = .1
40 LPRINT "alpha =",A;"beta =",B;"tau =",T0
50 L(0) = 0
60 FOR I = 1 TO 100
70 L(I) = L(I-1) + LOG(I)
80 NEXT I
100 P(0) = (B/(B+1))^A
105 S1(0) = P(0)
107 S2(0) = 0
110 FOR N = 1 TO 100
120 P(N) = P(N-1)*(A+N-1)/(N*(B+1))
125 S1(N) = S1(N-1) + P(N)
127 S2(N) = S2(N-1) + N*P(N)
130 NEXT N
200 G = .25
210 X = 0
220 T = P(0)*G
300 FOR N = 1 TO 99
305 X(N) = 0
310 IF N+1 < INT(1/G) THEN GOTO 500
320 S(0) = 1
330 FOR K = 1 TO INT(1/G)
340 S(K) = EXP(L(N+1) - L(K) - L(N+1-K))*(1 - K*G)^N
350 NEXT K
360 FOR M = 0 TO INT(1/G)
370 Q(M) = 0
380 FOR J = M TO INT(1/G)
390 Q(M) = Q(M) + S(J)*EXP(L(J) - L(M) - L(J-M))*((-1)^(J-M))
400 NEXT J
410 NEXT M
420 GOTO 600
500 FOR K = 1 TO N+1
510 S(K) = EXP(L(N+1) - L(K) - L(N+1-K))*(1 - K*G)^N
520 NEXT K
540 FOR M = 1 TO N+1
550 Q(M) = 0
560 FOR J = M TO N+1
570 Q(M) = Q(M) + S(J)*EXP(L(J) - L(M) - L(J-M))*((-1)^(J-M))
580 NEXT J
590 NEXT M
600 IF (N+1)*G >= 1 THEN GOTO 1000
610 E(N+1) = 1/(N+1)
620 E1(N+1) = 0
630 E2(N+1) = 1/(N+1)
640 E(N) = (1 - N*G)/(N+1)
645 P2(N+1,N+1) = 1
650 P1(N,N) = Q(N)/((N+1)*((1 - N*G)^N))
660 P1(N+1,N) = 0

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670 P2(N+1,N) = Q(N+1)/((1 - N*G)^N)
675 E1(N) = (E(N) - E2(N+1)*P2(N+1,N))/P1(N,N)
680 E2(N) = (1 - (N+1-N)*E1(N))/N
685 X(N) = Q(N)/(N+1)
688 T(N) = Q(N)*E1(N)/(N+1)
690 FOR K = N-1 TO 1 STEP -1
695 X(N) = X(N) + Q(K)*(N+1-K)/(K+1)
700 P1(K,K) = Q(K)*EXP(L(K) + L(N+1-K) - L(N+1))/((1 - K*G)^N)
705 E(K) = (1 - K*G)/(N+1)
708 P2(N+1,K) = Q(N+1)/((1 - K*G)^N)
710 E1(K) = (E(K) - (E2(N+1)*P2(N+1,K)))/P1(K,K)
720 FOR M = K+1 TO N
730 P1(M,K) = Q(M)*EXP(L(N-K)-L(N-M)-L(M-K)-L(N+1)+L(M)+L(N+1-M))/((1 - K*G)^N)
740 P2(M,K) = Q(M)*EXP(L(N-K)-L(N-M+1)-L(M-K-1)-L(N+1)+L(M)+L(N+1-M))/((1-K*G)^N)
750 E1(K) = E1(K) - (E1(M)*P1(M,K) + E2(M)*P2(M,K))/P1(K,K)
760 NEXT M
770 E2(K) = (1 - (N+1-K)*E1(K))/K
780 T(N) = T(N) + E1(K)*((N+1-K)/(K+1))*Q(K)
790 NEXT K
795 T(N) = T(N) + G
800 X = X + X(N)*P(N)
810 T = T + T(N)*P(N)
850 GOTO 1400
1000 N1 = INT(1/G)
1010 E(N1) = (1 - N1*G)/(N+1)
1020 E1(N1) = E(N1)
1030 E2(N1) = G + (1 - N1*G)/(N+1)
1040 X(N) = Q(N1)*(N+1-N1)/(N1+1)
1050 T(N) = Q(N1)*(G + E1(N1)*(N+1-N1)/(N1+1))
1055 X(N) = X(N) + N*Q(0)
1057 T(N) = T(N) + Q(0)
1060 FOR K = N1 - 1 TO 1 STEP -1
1070 P1(K,K) = Q(K)*EXP(L(K)+L(N+1-K)-L(N+1))/((1 - K*G)^N)
1080 E(K) = (1 - K*G)/(N+1)
1090 E1(K) = E(K)/P1(K,K)
1100 X(N) = X(N) + Q(K)*(N+1-K)/(K+1)
1104 IF N1 <= N THEN LET N2 = N1
1106 IF N1 > N THEN LET N2 = N
1110 FOR M = K+1 TO N2
1120 P1(M,K) = Q(M)*EXP(L(N-K)-L(N-M)-L(M-K)-L(N+1)+L(M)+L(N+1-M))/((1 - K*G)^N)
1130 P2(M,K) = Q(M)*EXP(L(N-K)-L(N-M+1)-L(M-K-1)-L(N+1)+L(M)+L(N+1-M))/((1 - K*G)^N)
1140 E1(K) = E1(K) - (E1(M)*P1(M,K) + E2(M)*P2(M,K))/(P1(K,K))
1150 NEXT M
1160 E2(K) = (1 - (N+1-K)*E1(K))/K
1170 T(N) = T(N) + Q(K)*(E1(K)*(N+1-K)/(K+1) + G)
1180 NEXT K
1190 X = X + X(N)*P(N)
1200 T = T + T(N)*P(N)
1400 NEXT N
1450 LPRINT "GUT =",G
1500 LPRINT "First",X,T,X/(T+T0)
1510 X2 = X + (A/B - S2(99))*X(99)/99
1520 T2 = T + T(99)*(1 - S1(99))
1590 LPRINT A/B - S2(99),1 - S1(99)
1600 LPRINT "Second",X2,T2,X2/(T2 + T0)
1610 X3 = X + (A/B - S2(99))
1620 T3 = T + 1 - S1(99)
1700 LPRINT "Third",X3,T3,X3/(T3 + T0)

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**Table 1.** Long-term average rates of finding prey achieved by foragers using four different rules, for four different levels of patch variability (low values of  $\alpha$  mean high patch variability). In each case the number of prey per patch has a negative binomial distribution with parameters  $\alpha$  and  $\beta$  (with mean =  $\alpha/\beta = 5$ ) and travel time between patches,  $\tau = 0.1$ .

	Assessment rule ( $t_0$ )		Lima's rule ( $t_0$ )		GUT rule (GUT)		Naive rule
$\alpha = 0.25$	10.728	(.0531)	9.979	(.0464)	8.804	(.150)	4.545
$\alpha = 0.5$	8.074	(.0748)	7.509	(.0650)	6.977	(.190)	4.545
$\alpha = 1.0$	6.377	(.1063)	6.003	(.0925)	5.819	(.235)	4.545
$\alpha = 2.0$	5.393	(.1524)	5.179	(.1338)	5.141	(.282)	4.545

*Note:* For the GUT rule the rate achieved by the best choice of GUT is given, as is the value of the best choice of GUT. For the assessment rule and Lima's rule the rates achieved are given for the best such rules, as is the value of  $t_0$ , the time at which a patch should be left if no prey have been found by then. A forager using the "naive" rule would remain in each patch until it has been searched completely.



- i) the giving-up-time (GUT) rule, and
- ii) Lima's rule.

The rates achieved are plotted against the giving-up-time or against  $t_0$ . The rates are not given for small values of the giving-up-time because the calculations took too long on my home computer, but the rate is approximately linear (starting at 0 for GUT = 0) for small values of the GUT.

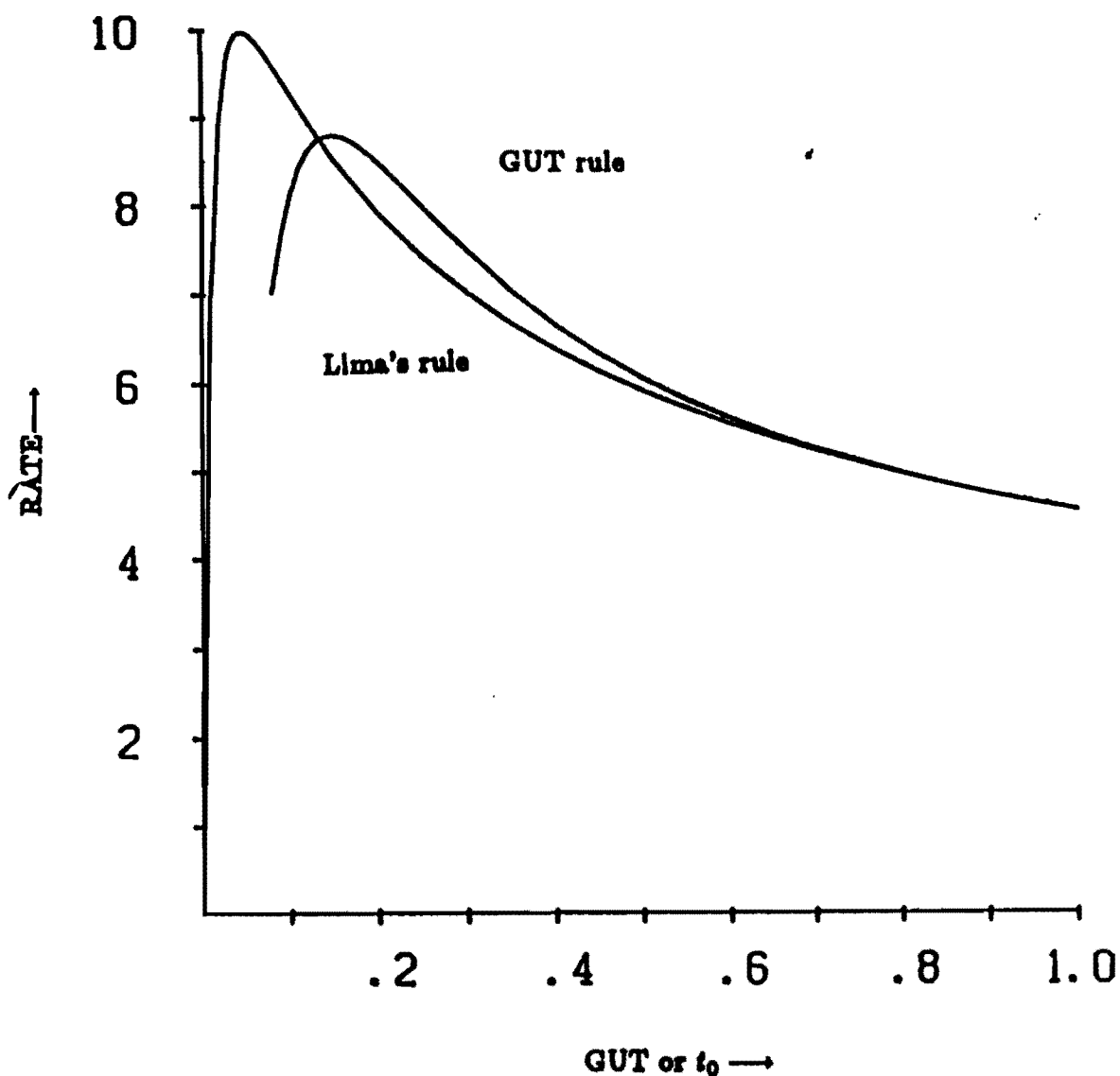


FIG 1a. The number of prey per patch has a negative binomial distribution with  $\alpha = 0.25, \beta = 0.05$ . Travel time  $\tau = 0.1$ .

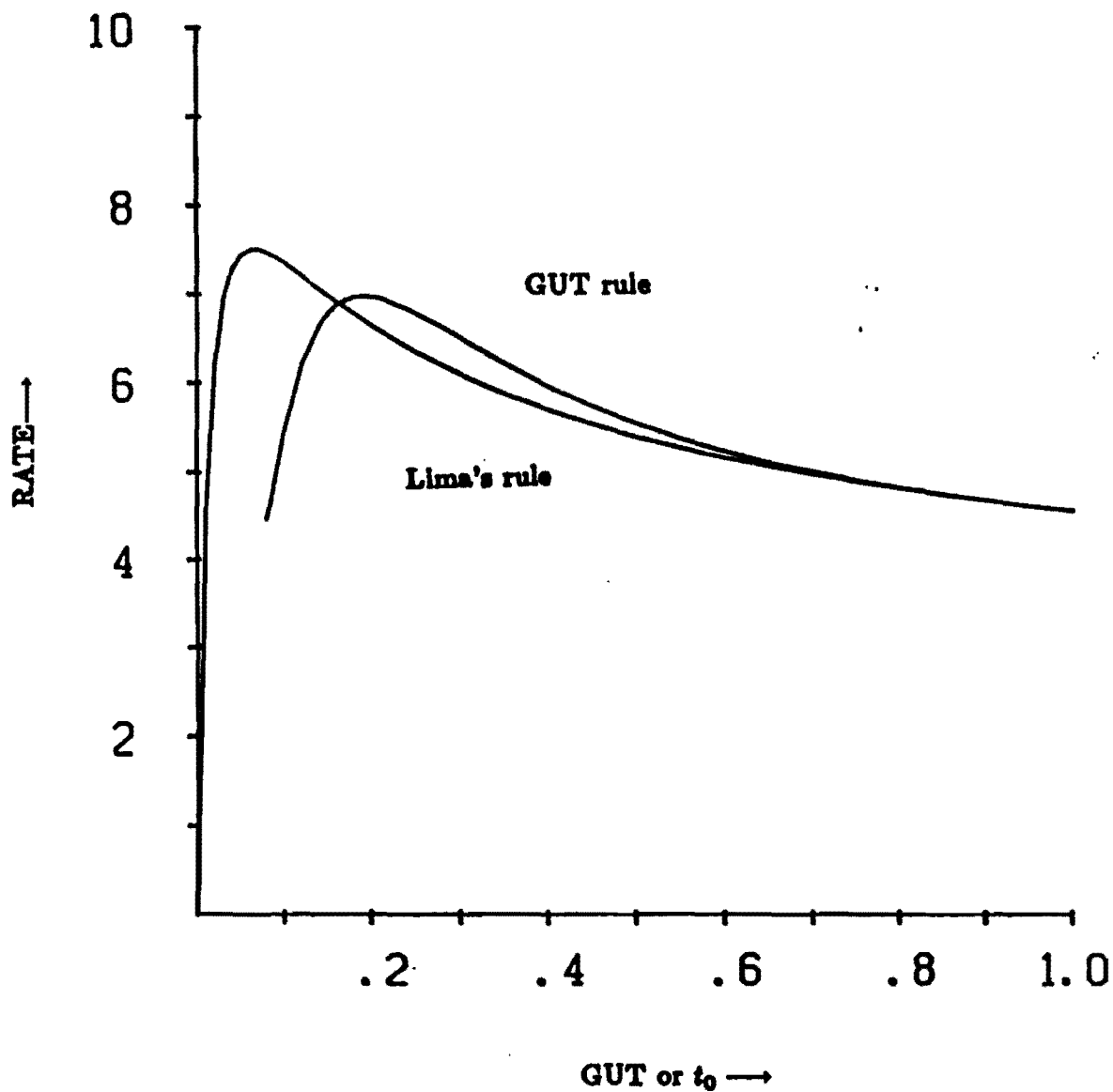


FIG 1b. The number of prey per patch has a negative binomial distribution with  $\alpha = 0.5, \beta = 0.1$ . Travel time  $\tau = 0.1$ .

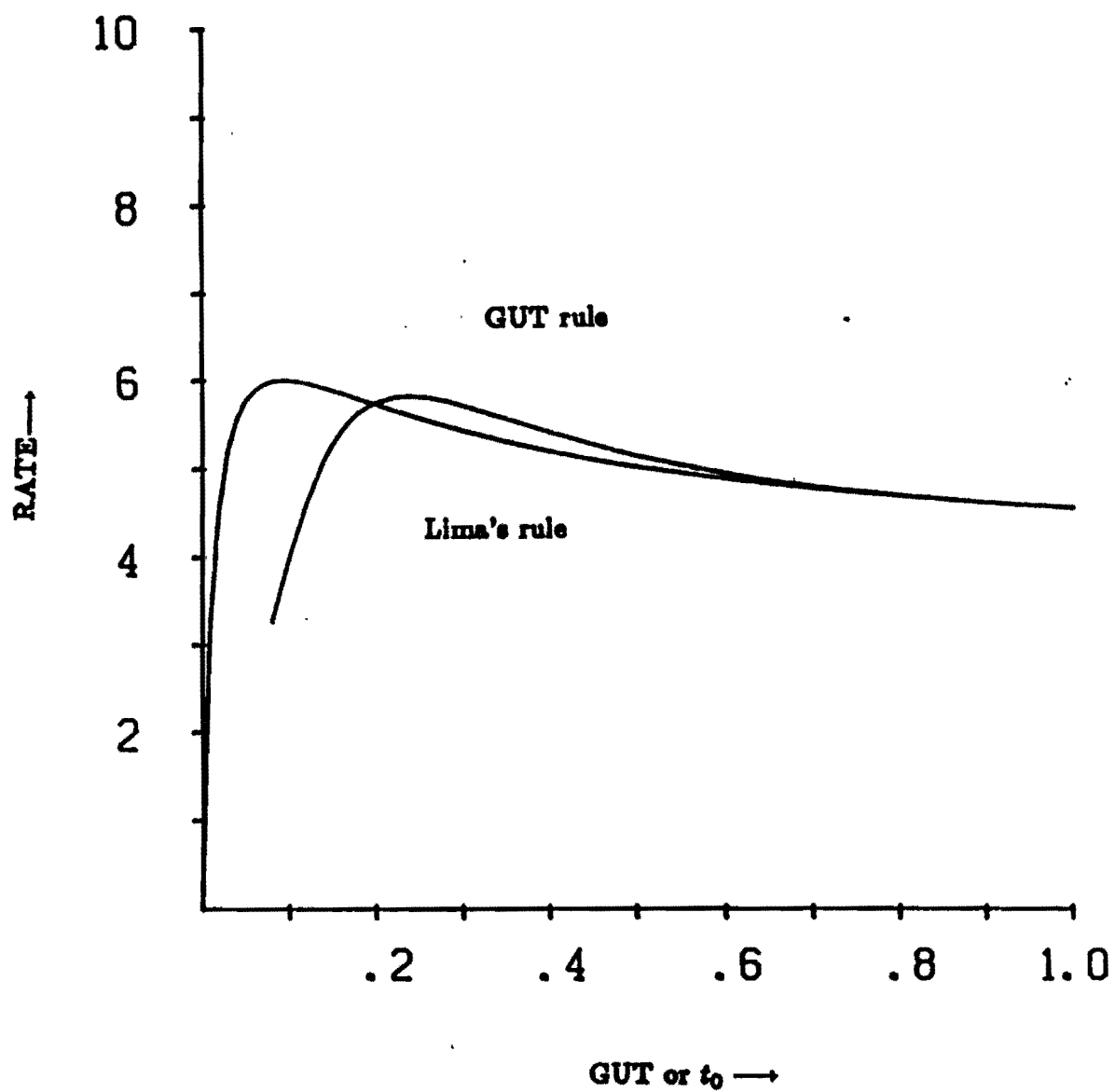


FIG 1c. The number of prey per patch has a negative binomial distribution with  $\alpha = 1.0, \beta = 0.2$ . Travel time  $\tau = 0.1$ .

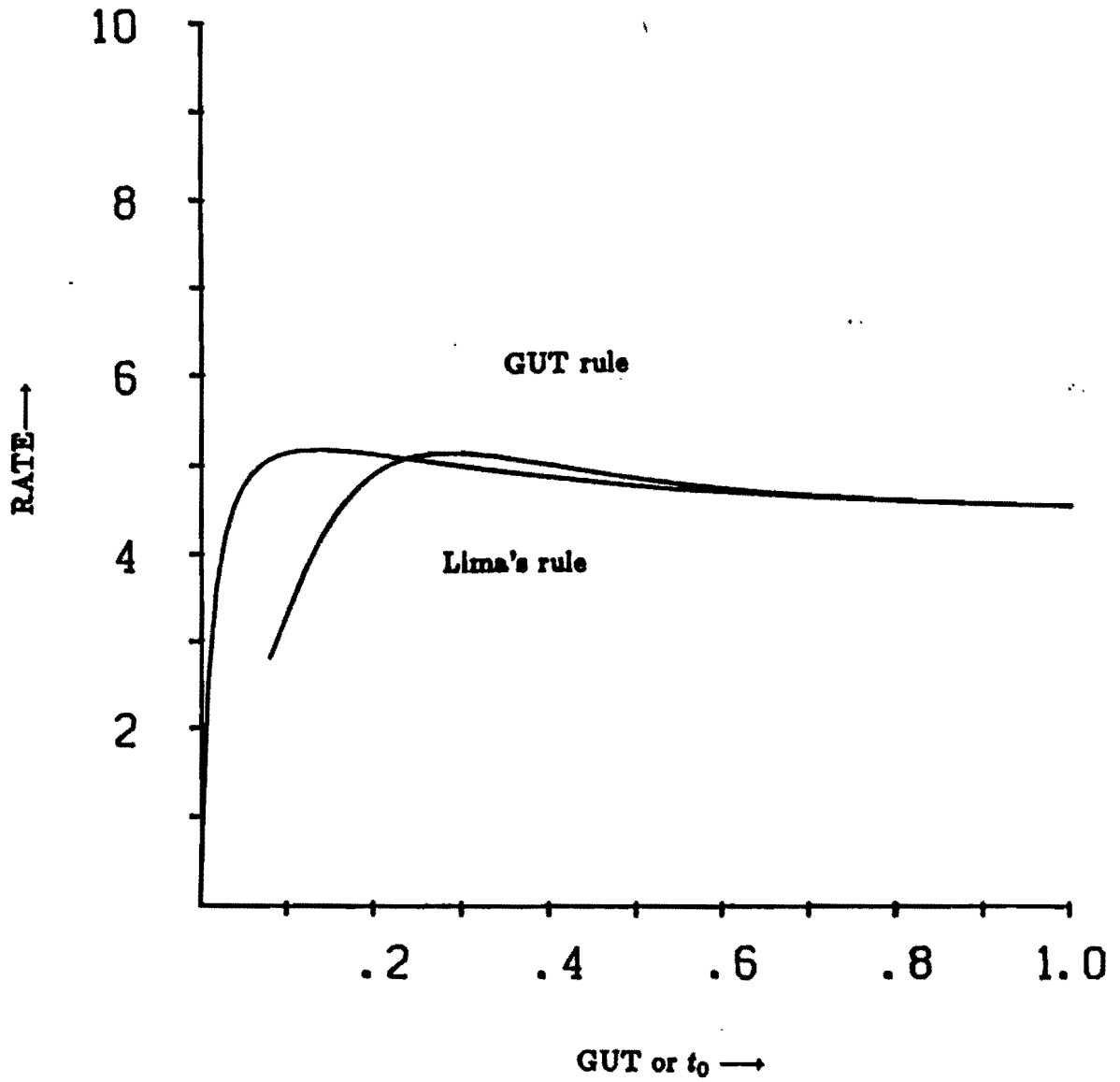


FIG 1d. The number of prey per patch has a negative binomial distribution with  $\alpha = 2.0, \beta = 0.4$ . Travel time  $\tau = 0.1$ .