OPTIMAL FORAGING AND PESSIMAL FORAGING
OR
THE OPTIMAL AVOIDANCE OF PREDATORS

by

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Abstract. Charnov's "marginal value theorem" says that a forager that searches for prey distributed in patches should leave a patch when the rate of finding prey there falls to a value equal to the long-term average rate of finding prey. The original marginal value theorem is based on unrealistic assumptions and does not hold for foragers that must capture individual prey. This paper mentions three possible extensions of the marginal value theorem to foragers that feed on individual prey. In one of these extensions the expected number of prey found per patch (EG) may be plotted against the expected amount of time spent searching each patch (ET) for all possible strategies. The best strategy will be one yielding a point satisfying a version of the marginal value theorem applied to the set of points determined by the expectations.

In this paper I treat a particular case in which a forager searches systematically for prey distributed in patches, where the number of prey per patch has a negative binomial distribution. Any particular foraging strategy will yield a pair of values (ET, EG). For a particular negative binomial distribution the set of all such pairs forms an envelope whose upper boundary can be found by finding a set of "optimal strategies," using a method described by Green (1987a,c). The lower boundary of the envelope of possible (ET, EG) pairs is found by finding a set of "pessimal strategies." This paper describes how to find these "pessimal strategies," which, in a sense, are the worst ways to forage. However, if we think of a prey animal encountering (and hiding from or fleeing) predators rather than a forager encountering prey, then the worst way to forage corresponds to the best way to avoid predators.
INTRODUCTION

One of the old problems in the study of natural history is that of the “food habits” of animals. What food do animals eat? Where do they search for it, and how do they capture it? Over the last twenty years a new approach to this problem has developed. This approach, known as “optimal foraging theory,” asks the question, how should animals look for food? In a very useful review, Pyke, Pulliam and Charnov (1977) listed four problems that a forager faces. (1) What food to choose, (2) Where to look for food, and if food is distributed in patches, (3) How long to stay in each patch, and (4) How to move among patches. In this paper I will consider the third problem: how long to stay in a patch, or, more precisely, what rule should a forager use to decide when to leave one patch and go on to another?

This paper addresses the general problem of how to find an optimal foraging strategy. In order to do this it is necessary to choose (1) a particular problem, that is, a description of the environment that the forager has to deal with, (2) a set of strategies that the forager might use, and (3) a way to decide which strategy is best.

In this paper I assume that a forager searches for prey which are found in superficially similar patches. The number of prey per patch is assumed to have a negative binomial distribution, and the prey in a given patch are located at random. A forager is assumed to search a patch systematically and will leave a patch when it has been searched completely, or at some earlier time, but the decision to leave a patch at any time can depend only on the experience that the forager has had up to that time. It is assumed that the environment remains stable for a long time and that the optimal strategy is the one that maximizes the long-term average rate of finding prey.

There is some dispute over this last assumption. A number of alternatives have been suggested. For example, a forager might (1) maximize the probability of finding some prey, or (2) maximize the probability of finding at least \( N \) prey within some specified time, for some number \( N \), or, more generally, (3) maximize expected “fitness,” where “fitness” is some (specified) non-linear function of the number of prey found in a given time. As a criterion, the long-term average rate of finding prey has the advantage of convenience, and it is a realistic choice in some cases. None of the alternatives is more convenient mathematically, and none is better (more general and more realistic) biologically.

A forager that has to decide when to leave one patch and go on to another should leave a patch if that patch has become bad, perhaps through depletion of prey, or if the forager has obtained information, perhaps through poor success, that the patch was bad from the start. Much of the work on optimal foraging theory is based on the idea of patch depletion. I am more interested in how a forager can decide whether or not a patch is good. Generally speaking, if prey have an aggregated distribution in patches, then a forager should leave a patch in which few prey have been found and remain in a patch in which many prey have been found.
The marginal value theorem provides a method of finding the optimal foraging strategy for certain cases in which patches are depleted of prey by foragers. Several extensions of the marginal value theorem have been suggested, and two of these apply to the case of negative binomial prey distribution which I want to consider. One of these, which seems to be the one favored by enthusiasts of the marginal value value theorem (Stephens and Krebs 1986), is looked at in some detail. This version of the marginal value theorem minus the “marginal value” part—is correct, but it is trivially equivalent to the assumption that an optimal forager should maximize the long-term average rate of finding prey.

THE MARGINAL VALUE THEOREM

Charnov's marginal value theorem.

Charnov's (1976) “marginal value theorem” is perhaps the best-known idea in optimal foraging theory. The theorem says that if the net energy gained by a forager in a patch is a known, continuous, deterministic function of time in a patch, and if the function has a positive first derivative and a negative second derivative, then the strategy that maximizes the long-term average rate of energy gain is to leave a patch when the slope of the energy-gain function falls to the highest possible long-term average rate of energy gain. The term “marginal value,” which is taken from economics, refers to the instantaneous rate of energy gain. I think that one of the main attractions of the marginal value theorem to biologists is that the terminology suggests a connection with economics, a field with a well-developed mathematical theory.

Charnov's marginal value theorem is often illustrated by a picture such as Figure 1a. The optimal time to remain in a patch, \( t_0 \), is the time that maximizes the long-term average rate of energy gain, \( r = g(t_0)/(t_0 + \tau) \), where \( \tau \) is the travel time between patches. In Fig. 1a, \( t_0 \) is the time at which the tangent of the line from \((-\tau, 0)\) to the \(g(t)\) curve touches that curve. At this point the slope of the \(g(t)\) curve, given by \(g'(t_0)\), equals the slope of the tangent line. Figure 1a is very informative since it shows several things at the same time: (1) The pattern of energy gain with time is seen in the function \(g(t)\). (2) The rate of energy gain at any time is the slope of the function \(g(t)\). (3) The long-term average rate of energy gain for a forager that leaves each patch at time \(t\) is the slope of the secant line from \((-\tau, 0)\) to \((t, g(t))\).

It is possible that Charnov's mathematical assumptions do not hold and that the marginal value theorem will have to be modified if it is to remain true. Figure 1b illustrates a case in which the energy gain function consists of connected line segments. This pattern has been found by Baum (1987) in laboratory experiments with pigeons, which seem to search an area systematically, but not completely. After one search, during which the pattern of gain follows the first line segment, the pigeons make another search, during which the pattern of gain follows the next line segment. In such a case the optimal time to remain in each patch, \(t_0\), could again be found by drawing a tangent line from \((-\tau, 0)\) to the \(g(t)\) curve, but now the derivative of \(g(t)\) at the point \((t_0, g(t_0))\) would not exist. That is, the “marginal value” part of the marginal value theorem would
not hold. The point is that the idea of using a tangent line to find the optimal residence time in a patch, which is illustrated in Fig. 1a,b, is more general than the marginal value theorem, which the figure was designed to illustrate.

Charnov's marginal value theorem was applied to the case in which a forager's environment contained different patch types, each with a different energy gain function. If the gain function for each patch is known to the forager immediately upon reaching a patch, but is not recognized from a distance, then the marginal value theorem specifies the optimal residence time in each patch. Again, each patch should be left when the rate of energy gain there falls to the highest possible long-term average rate that can be achieved. There are two biologically interesting conclusions that follow from this theory. First, each patch should be left when its quality (in the sense of rate of gaining energy there) is the same as each other patch. Second, if environmental quality is lower (or travel time is longer), the highest possible long-term average rate of energy gain will be lower and optimal foragers should tend to stay longer in a patch of given quality than if environmental quality is higher. These general conclusions have been the main ideas that have been tested by people doing experimental work on the question of how animals decide when to leave one patch and go on to another. In their review of such work, Krebs, Stephens and Sutherland (1983) give the impression that no other ideas are worth testing.

There is an important difficulty with the marginal value theorem. It does not apply to cases in which foragers capture individual prey, since the gain function is not continuous in such cases. However, it might be possible to apply the marginal value theorem, not to the rate of energy gain, but the expected rate. Charnov (1976) claimed that the marginal value theorem could be applied to stochastic models, but he did not specify how this was to be done. Oaten (1977) disputed Charnov's claim and developed his own general stochastic model of optimal foraging. My work on optimal foraging theory is based on Oaten's model.

Charnov's marginal value theorem does specify an optimal foraging rule in a limited number of cases (for example, when should a bee stop sucking nectar from one flower and move on to another?), but it does not apply to most foragers. A number of extensions have been suggested to the marginal value theorem. These extensions do not, in general, specify rules that foragers could use, but they do give information about which rule is best among a given set of rules.

*Pyke's stochastic version of the marginal value theorem.*

If a forager searches for discrete prey which are found at random then we might consider the expected rate at which prey are found. For example, if a forager in a patch at time $t$ has found $n$ prey at times $t_1, t_2, \ldots, t_n$, with $0 < t_1 < t_2 < \ldots < t_n < t$, we might ask what is the probability of finding another prey in the interval $(t, t + \Delta t)$. If we divide this probability by the length of the interval, $\Delta t$, and let this value go to
zero, then the limit is the "instantaneous rate" of finding prey. Pyke (1978) offered his
stochastic version of the marginal value theorem: leave a patch when the instantaneous
rate falls to the highest possible long-term average rate. Pyke's rule is not optimal in
general, as has been pointed out by Oaten (1977), Green (1980) and McNamara (1982),
but it is optimal in some cases.

If a forager gains information about patch quality while foraging—for example, if
patches vary a great deal in the number of prey they contain—then a forager might re-
main in a patch even if the expected instantaneous rate is low because there is
information—as well as prey—to gain. That is, if there is a chance that the expected in-
stantaneous rate will increase with time in a patch, then a forager may be better off re-
mainin a patch even though the expected instantaneous rate is lower than the high-
est possible long-term average rate. Iwasa et al. (1981) considered the problem faced
by a forager searching randomly in patches which have particular distributions of the
numbers of prey per patch. They used an idea equivalent to Pyke’s to find the "opti-
mal" foraging strategy. If all patches have the same number of prey an optimal forager
should take some fixed number of prey from each patch, while if the number of prey per
patch has a Poisson distribution an optimal forager should remain in each patch for
a fixed time. A forager faced with a binomial distribution of the number of prey per
patch should leave when many prey have been found or much time has been spent in a
patch, with the critical number of prey to be found before leaving decreasing with time.
A forager faced with a negative binomial distribution should leave a patch if few prey
have been found by a given time. Pyke’s rule does give the optimal strategy in the first
three cases, but not in the case of a negative binomial distribution of the number of prey
per patch. The fact that the fixed-time rule is optimal for the Poisson distribution was
proved by Stewart-Oaten (1982). The fact that Pyke’s rule gives the optimal strategy
in this case, and in the cases of fixed number and binomial distribution of the number
of prey per patch, follows from a theorem of McNamara (1982). The negative binomial
case is different. The expected instantaneous rate of finding prey increases each time a
prey is found, and this fact must be taken into account.

Green (1980) considered an "instantaneous rate rule" for a discrete-time case anal-
ogous to the continuous-time case with a negative binomial prey distribution. The best
"instantaneous rate" rule was almost as good as the overall best rule, but it is interest-
ing to note that the best "instantaneous rate" rule did not satisfy Pyke’s version of the
marginal value theorem. That is, if we consider all rules of the form: leave a patch when
the expected instantaneous rate of finding prey there falls to a particular constant, then
the particular constant for the best such rule is not equal to the long-term average rate.

Finally, on the subject of instantaneous rate, I should point out an important dis-
tinction. When I talk about the "instantaneous rate" I refer to the probability of find-
ing a prey in a short time. A prey will either be found or not, but I do not know which.
This is true no matter how I think of the rate. The important distinction is between
whether or not this rate is a known, fixed value. For example, the rate of finding prey
might be two per unit time, where the value two is known. Or, the rate of finding prey
might be either one or three, with no way of knowing which, but with a probability of exactly one half that the true value is one and one half that the true value is three. In this second case there might be an advantage in having information about whether the rate is actually one or three. I am interested in such cases, and it is for them that I use the phrase "expected instantaneous rate," which would be two in this case.

Another marginal value theorem, using expected gain and expected time in a patch.

I think that the original purpose of Charnov's (1976) marginal value theorem was to help find optimal foraging strategies. There was the suggestion (Krebs, Ryan and Charnov 1974) that the giving-up-time rule—leave a patch as soon as a fixed time (the giving-up-time) passes without finding a prey—would satisfy the marginal value theorem and would provide optimal foraging. This suggestion was wrong, as was pointed out by McNair (1982) and Green (1984).

Now it is recognized (Stephens and Krebs 1986) that the marginal value theorem does not provide an optimal rule that a forager might use. Instead, it is claimed that the marginal value theorem provides a method of choosing the best among a set of rules. That is, once a set of rules has been specified and all have been analyzed, then the marginal value theorem may be used to choose the best. It is not clear how to choose the set of rules, or to be sure that the best rule has been included in the set. Sometimes the best rule is not included. The usual approach is to list several familiar sets of rules and (sometimes) find the best of these. Recently this approach has been dressed up by referring to "rules of thumb" (Cowie and Krebs 1979; Krebs, Stephens and Sutherland 1983), with the suggestion that since animals are not very smart they are only capable of using simple rules, and thus theorists are justified in confining their attention to rules which have occurred to them. In principle, the long-term average rate is calculated for all of the rules considered and the highest rate is found. The rule which results in the highest rate is the best of the rules considered and satisfies a sort of marginal value "theorem." This "theorem," however, is trivially equivalent to the assertion that an optimal forager should maximize its long-term average rate of energy gain.

This version of the marginal value theorem based on expectations is illustrated in Fig. 2. In this case a forager searches systematically for prey distributed in patches, with the number of prey per patch having a negative binomial distribution. A forager uses some rule based on its experience in a patch to decide when to leave that patch and go on to the next. Each strategy corresponds to a point \((ET, EG)\), where \(ET\) is the expected time spent searching each patch, and \(EG\) is the expected number of prey found per patch. The set of all possible pairs of values \((ET, EG)\) is the convex envelope illustrated in the figure. The upper boundary of the envelope corresponds to the candidate optimal foraging strategies calculated by the method described by Green (1987a,c). The lower boundary of the envelope corresponds to candidate "pessimal" foraging strategies, which are found by a method described in the next section. The optimal foraging strategy is the one which achieves the highest long-term average rate of finding prey, given by
\[ R = \frac{EG}{(ET + \tau)} \], where \( \tau \) is the average travel time between patches. Once all the candidate optimal strategies have been found (they need not all be found, but enough must be found to be able to draw a pleasingly smooth boundary for the figure), and their values \( ET \) and \( EG \) have been calculated and plotted, then the optimal strategy is the one such that the upper tangent from the point \((-\tau, 0)\) to the \((ET, EG)\) envelope passes through its \((ET, EG)\) point. (The "pessimal" strategies are ones such that the lower tangent from the points \((-\tau, -x)\) to the \((ET, EG)\) envelope passes through their \((ET, EG)\) points.) Fig. 2 does illustrate a version of the marginal value theorem that is true quite generally (unless the envelope is not closed, or unless it does not have a smooth boundary, in which case the "marginal value" part of the marginal value theorem would not hold), but it is not very useful unless one wants to defend the marginal value theorem very badly.

**McNamara's potential function.**

McNamara (1982) proved a general theorem which gives a condition for a patch-leaving rule to be optimal. At any time a forager that has searched a patch for some time should remain in the patch if there exists a strategy such that the forager, having had the experience in the patch that the forager has had and using that strategy, will have an expected additional gain, \( EG' \), and expected additional time to remain in the patch, \( ET' \), such that

\[ \frac{EG'}{ET'} > \gamma, \] (1)

where \( \gamma \) is the maximum long-term average rate of energy gain. Condition (1) resembles Charnov's marginal value theorem, which follows from it, but this condition is far more general since it does not only depend on the instantaneous rate of energy gain but on future prospects within a patch as well.

Condition (1) is nice for two reasons. It has intuitive appeal and it is very general. Not only does it include Charnov's marginal value theorem as a special case, but it also shows that Pyke's stochastic version of the marginal value theorem provides the optimal strategy if the average instantaneous rate of energy gain is almost surely monotone non-decreasing. I think that the main value of McNamara's result is that it can be used to prove other, less general, but more easily used, results. As it is, the generality of McNamara's theorem is also a weakness because the theorem does not provide a method that can be used to find the optimal patch-leaving rule in general. The cases in which McNamara's theorem has been applied directly are very simple, and in those cases the optimal rule could be found as easily without the theorem.

The condition for staying in a patch which McNamara uses is actually given in a slightly different form than condition (1). McNamara defines a "potential function," which is the maximum over all possible strategies of \( EG' - \gamma ET' \). A forager should remain in a patch if the potential function is greater than zero. This "potential function" provides an interesting analogue to what Waage (1979) referred to as "responsiveness,"
the tendency of a forager to respond to the edge of a patch by turning back into a patch and continue foraging there. However, the potential function is also a mathematical entity which must be dealt with if McNamara's theorem is to be used to find the optimal foraging strategy in any particular case. In general, the potential function is very difficult to deal with.

PESSIMAL FORAGING

Pessimal foraging, or the optimal avoidance of predators.

In order to illustrate all the possible points, \((ET, EG)\), in Figure 2 it is necessary to find a set of foraging strategies which are, in a sense, the worst possible. These strategies, which lead to the points on the lower boundary of the \((ET, EG)\) envelope in Figure 2, are found by a method which is equivalent to changing the maximization in McNamara's potential function to minimization and reversing the inequality.

It may be silly to think about how a predator might find prey most slowly ("pessimal foraging"), but it might be sensible to think about how a prey animal should behave in order to encounter predators as infrequently as possible. For example, assume that an animal must spend some time looking for food, and that it is itself subject to predation during that time. Assume that the animal searches for food distributed in patches, and that it may encounter predators (each of which has a small, fixed probability of capturing the animal) in these patches, or while travelling between patches. Assume that the average travel time between patches is \(\tau\) and the average number of predators encountered during this time is \(x\). If patches vary in the risk of predation that an animal suffers in each, then the strategy which minimizes the rate of encountering predators is one which minimizes

\[ R = (EG + x)/(ET + \tau). \] (2)

This suggests an analogue of the marginal value theorem which is illustrated in Figure 3.

In this section I describe how to find pessimal foraging strategies for the case in which the number of prey (predators) per patch has a negative binomial distribution. This is essentially the assumption made by May (1978) in a model used to investigate the stability of predator-prey communities. Since I imagine that the reason that the animal suffers a predation risk is that it is itself looking for prey, I assume that the animal must leave each patch at, or before, the time that the patch has been searched completely.

Finding the pessimal strategy.

The pessimal foraging strategy will be to leave good patches and stay in bad patches. More exactly, a pessimal forager should remain in a patch at any time if the minimum (taken over all possible strategies) of the ratio of expected number of prey found to the
expected time in the patch from that time on is less than the lowest possible long-term average rate of finding prey. If the number of prey per patch has a negative binomial distribution, then the pessimal foraging strategy will have the same general form as the optimal foraging strategy for the case in which each patch contains the same number of prey.

The pessimal foraging strategy, examples of which are illustrated in Figure 4, may be characterized by a set of times, \( t_m, t_{m+1}, \ldots, t_n \), with \( t_m < t_{m+1} < \ldots < t_n = 1 \), for some integers \( m \geq 1 \) and \( n \geq m \), such that the forager would leave a patch if \( k \) prey are found before time \( t_k \). The pessimal strategy, or the times \( \{ t_k \} \), is found by dynamic programming, using a method very similar to that used to find an optimal strategy by Green (1987b).

First, a value \( C \) is guessed for the lowest possible rate of finding prey and then a rule is found that "tries to achieve" rate \( C \). The distribution of the number of prey per patch can be written as

\[
f(x) = \left( \frac{\alpha + x - 1}{x} \right) \left( \frac{\beta}{1 + \beta} \right)^\alpha \left( \frac{1}{1 + \beta} \right)^x,
\]

where \( \alpha \) and \( \beta \) are parameters of the negative binomial distribution. This is not the usual way to write \( f(x) \). The notation I use is convenient if the negative binomial distribution is thought of as a gamma mixture of Poissons (Green 1987a,c). Then \( \alpha \) and \( \beta \) are the usual parameters of a gamma distribution. If \( k \) prey have been found by time \( t \), then the rate of finding prey at time \( t \) is given by

\[
r(t, k) = (\alpha + k)/(\beta + t).
\]

In particular, if the time to search a patch completely is taken to be 1, then a forager that has almost completed searching a patch and has found \( k \) prey will expect to find prey at about rate

\[
r(1, k) = (\alpha + k)/(\beta + 1).
\]

If we let \( n \) indicate the smallest value of \( k \) such that \( r(1, k) \geq C \), then a pessimal forager should leave a patch whenever \( n \) prey have been found there.

**Finding \( t_{n-1} \).**

Once \( n \) has been found, we find the time \( t_{n-1} \) such that a pessimal forager should leave a patch if \( n - 1 \) prey are found before that time. This is done by guessing "candidate" values, \( t \), for \( t_{n-1} \), and calculating the expected number of prey found, \( EG' \), and the expected amount of time spent, \( ET' \), in the patch from time \( t \) on, given that the forager will leave a patch whenever another prey is found, or when the patch has been searched completely. The ratio \( EG'/ET' \) is compared with \( C \). The correct value of \( t \) is
found by iteration. A larger value of $t$ is chosen if $EG'/ET' > C$, while a smaller value of $t$ is chosen if $EG'/ET' < C$. The process is continued, using the bifurcation method, until a value of $t$ is found such that $EG'/ET' = C$.

Since at most one more prey will be found after candidate time $t$, we have

$$EG' = 1 - P(1, n - 1 | t, n - 1),$$

(6)

where $P(1, n - 1 | t, n - 1)$ is the probability that no more prey will be found by time $t$, given that exactly $n - 1$ prey have been found by time $t$. In general, the probability of finding $y$ more prey by time $t_j$, given that $k$ prey have been found by time $t_i$ (with $t_i \leq t_j$), is given by

$$P(t_j, k + y | t_i, k) = \binom{\alpha + k + y - 1}{y} \left( \frac{\beta + t_i}{\beta + t_j} \right)^{\alpha + k} \left( \frac{t_j - t_i}{\beta + t_j} \right)^{y}$$

(7)

If exactly $y$ prey are to be found in the interval $(t_i, t_j)$ then the expected time to wait (after $t_i$) in order to find the $m$th prey [for $i \leq m \leq y$] in that interval is $m(t_j - t_i)/(y + 1)$, and the expected location [in the interval $(0,1)$] of the $m$th point in the interval $(t_i, t_j)$ is

$$t_i + m(t_j - t_i)/(y + 1).$$

(8)

Thus, for our candidate time $t$ we have

$$ET' = (1 - t) \sum_{y=0}^{\infty} \frac{1}{(y + 1)} P(1, n - 1 + y | t, n - 1).$$

(9)

Once we have found a value of $t$ such that $EG'/ET' = C$ we set $t_{n-1} = t$ and use that value to help find $t_{n-2}$.

Finding $t_{n-2}$.

Once $t_{n-1}$ has been found we find the value of $t_{n-2}$ by guessing a candidate value, $t$ (a good guess is $t = t_{n-2}/2$), and calculating $EG'$ and $ET'$ from time $t$ on, assuming that $n - 2$ prey have been found by time $t$, and that the forager would stop if the $n - 1$st prey is found before $t_{n-1}$, or if the $n$th prey is found before time $t = 1$. Otherwise the forager completes the search of the patch. If $EG'/ET' > C$ then a larger value of $t$ is chosen; if $EG'/ET' < C$ then a smaller value of $t$ is chosen. At each iteration the value of $t$ is changed by adding or subtracting an amount half the size of the last amount (using $t_{n-1}/4$ the first time). Once $t_{n-2}$ is found then the values $t_{n-1}$ and $t_{n-2}$ are used to find $t_{n-3}$, and the process is continued until the value $t_m$ is found, where $m$ is the smallest number of prey such that a forager should ever leave a patch if that many prey have been found.
We have

\[
EG' = 1 - P(t_{n-1}, n - 2 | t, n - 2) \\
+ P(t_{n-1}, n - 2 | t, n - 2) \{2 - 2P(1, n - 1 | t_{n-1}, n - 2) \\
+ P(1, n - 1 | t_{n-1}, n - 2)\}
\]

\[
ET' = (1 - t)P(t_{n-1}, n - 2 | t, n - 2) \{P(1, n - 2 | t_{n-1}, n - 2) \\
+ P(1, n - 1 | t_{n-1}, n - 2)\} + \\
\sum_{y=1}^{\infty} \left(\frac{(t_{n-1} - t)}{(y + 1)}\right) P(t_{n-1}, n - 2 + y | t, n - 2) \\
+ P(t_{n-1}, n - 2 | t, n - 2) \sum_{y=2}^{\infty} \left(\frac{(t_{n-1} - t) + 2\frac{1 - t_{n-1}}{y + 1}}{y + 1}\right) \\
P(1, n - 2 + y | t_{n-1}, n - 2) \tag{11}
\]

Finding \(t_{n-3}, t_{n-4}, \ldots, t_m\).

Once \(t_{n-1}, t_{n-2}, \ldots, t_{i+1}\) are found, we want to find \(t_i\). This time is found by guessing a value \(t\) (a good guess is \(t_{i+1}/2\)) and finding the values \(EG'\) and \(ET'\), the expected additional number of prey found and the expected additional time to remain in a patch for a forager that has found \(i\) prey by time \(t\) and will leave a patch when it has been searched completely, or whenever the \(n\)th prey is found, or if the \(j\)th prey is found before \(t_j\), for \(j = i + 1, i + 2, \ldots, n - 1\). Once the values of \(EG'\) and \(ET'\) are found, the ratio \(EG'/ET'\) is compared with \(C\) and another value of \(t\) is guessed, larger if \(EG'/ET' > C\), smaller if \(EG'/ET' < C\). The process is continued until a \(t\) is found such that \(EG'/ET' = C\). This value of \(t\) will be the desired value \(t_i\). Once this value has been found, the value for \(t_{i-1}\) is found in the same way, and the process is continued until the value \(t_m\) is found, where \(m\) is the smallest number of prey such that a pessimal forager should leave a patch (after a very short time) if that many prey have been found. If the process is attempted for \(m - 1\) it will be found that \(EG'/ET' < C\) for all \(t > 0\).

For each candidate value, \(t\), guessed for \(t_i\), the main problem is to find \(EG'\) and \(ET'\). This is done by breaking up the possible stopping points into cases, in terms of when the forager could leave the patch. If \(i\) prey have been found by time \(t\), then the forager deciding to go on until reaching a stopping point might leave before \(t_{i+1}\), having found one additional prey (for a total of \(i + 1\)), or in the interval \((t_{i+1}, t_{i+2})\), having found no additional prey by \(t_{i+1}\), but two additional prey by \(t_{i+1}\). In general, a forager that has found \(i\) prey by time \(t\) and that continues in a patch until it has been searched completely, or until \(n_1\) prey have been found before \(t_{n_1}\), for \(i < n_1 \leq n\), will stop either when the end of the patch is reached, \(t = 1\), having found \(n_2\) prey, where \(n_2 < n\), or will stop during the interval \((t_{n_{i-1}}, t_{n_i})\), having found a total of \(n_1\) prey, for
\( n_1 = i + 1, i + 2, \ldots, n \) [using \( t_i = t \) and \( t_n = 1 \), conventionally], but the number of prey found at time \( t_j \) will be less than \( j \) for \( j = i + 1, i + 2, \ldots, n_1 - 1 \).

The cases in which the forager leaves during the interval \((t, t_{i+1})\), and the case in which the forager stays until \( t_n = 1 \) are treated separately. For the other cases, in which the forager leaves during some interval \((t_{n_1-1}, t_{n_1})\), for \( i < n_1 \leq n \), the forager must have found some number of prey, \( j \), at time \( t_{n_1-1} \), and must never have found as many as \( k \) before \( t_k \), for \( k = i + 1, \ldots, n_1 - 1 \). Call the probability of this [given \( i \) prey found by time \( t \)], \( Q(t_{n_1-1}, j|t, i) \), for \( i \leq j < n_1 - 1 \). These probabilities are calculated for various values of \( n_1 \) and \( j \) by iteration.

\[
Q(t_{i+1}, i|t, i) = P(t_{i+1}, i|t, i) \tag{12}
\]

and, for \( n_1 = i + 3, \ldots, n \), and for \( j = i, \ldots, n_1 - 1 \), we have

\[
Q(t_{n_1-1}, j|t, i) = \sum_{k=i}^{\min[j, n_1-3]} Q(t_{n_1-2}, k|t, i) P(t_{n_1-1}, j|t_{n_1-2}, k). \tag{13}
\]

A forager that has found \( j \) prey at time \( t_{n_1-1} \) (for \( j < n_1 - 1 \)) will find the \( n_1 \)th prey in the interval \((t_{n_1-1}, t_{n_1})\) if there are \( n_2 - j \) prey in that interval (for \( n_2 \geq n_1 \)). The probability of this is \( P(t_{n_1-1}, n_2|t_{n_1-1}, j) \). Thus, the probability that a forager that has found \( i \) prey by time \( t \) and decides to remain in a patch to the end, or until \( k \) prey have been found before the time \( t_k \) (which has already been determined), will have found \( j \) prey by time \( t_{n_1-1} \), and would find \( n_2 - j \) more prey if it remained until time \( t_{n_1} \), is given by

\[
Q(t_{n_1-1}, j|t, i) P(t_{n_1}, n_2|t_{n_1-1}, j). \tag{14}
\]

In this case the forager would have found \( n_1 - i \) prey after time \( t \), and the expected time to remain in the patch after time \( t \) would be

\[
t_{n_1-1} - t + \frac{n_1 - j}{n_2 - j + 1}(t_{n_1} - t_{n_1-1}). \tag{15}
\]

This number of prey and this expected time, each multiplied by the probability (14), would contribute to the value of \( Ec' \) and \( Et' \), respectively.

If there are \( n_2 - i \geq 1 \) prey to be found in the interval \((t, t_{i+1})\), then a forager that has found \( i \) prey by time \( t \) should stop when the first of these additional prey is found. The probability of this event is \( P(t_{i+1}, n_2|t, i) \). In this case, one prey will have been found after time \( t \), and the expected time to remain in the patch after time \( t \) is

\[
\frac{t_{i+1} - t}{n_2 - i + 1}. \tag{16}
\]
The number of prey (one) and this expected time, each multiplied by the probability, would contribute to the values of $EG'$ and $ET'$, respectively.

Finally, it is possible that a forager that has found $i$ prey by time $t$ will never find $k$ prey before $t_k$, for $k = i + 1, \ldots, n$, and will stay until the patch has been searched completely. The probability of this happening, and exactly $j$ prey having been found in the patch (for $i \leq j < n$), can be written as $Q(t_n, j|t, i)$, which can be calculated using (13), with $n_1 - 1 = n$.

In this case $j - i$ prey will have been found after time $t$, and time $1 - t$ will have been spent in the patch after time $t$. Again, this number of prey and this time, each multiplied by the probability, would contribute to the value of $EG'$ and $ET'$, respectively.

Putting these cases together we have

$$EG' = 1 - P(t_{i+1}, i|t, i) + \sum_{j=i+1}^{n-1} (j - 1)Q(t_n, j|t, i)$$

$$+ \sum_{n_1=i+2}^{n} (n_1 - i) \sum_{n_2=n_1}^{n_1 - 2} Q(t_{n_1-1}, j|t, i)P(t_{n_1}, n_2|t_{n_1-1}, j) \quad (17)$$

$$ET' = \sum_{n_2=i+1}^{\infty} \frac{t_{i+1} - t}{n_2 - i + 1}P(t_{i+1}, n_2|t, i)$$

$$+ \sum_{n_1=i+2}^{n} \sum_{n_2=n_1}^{\infty} \sum_{j=i}^{n_1 - 2} [(t_{n_1-1} - t + \frac{n_1 - j}{n_2 - j + 1}(t_{n_1} - t_{n_1-1}))Q(t_{n_1-1}, j|t, i)P(t_{n_1}, n_2|t_{n_1-1}, j)$$

$$+ \sum_{j=i}^{n-1} (1 - t)Q(t_n, j|t, i). \quad (18)$$

**Finding $EG$ and $ET$, given $t_m, t_{m+1}, \ldots, t_n$**

Once the times $t_m, t_{m+1}, \ldots, t_n$ have been found for a particular choice of $C$, the values $EG$ and $ET$ are found and the rate

$$R(C) = \frac{EG + x}{ET + \tau} \quad (2)$$

is calculated. $EG$ and $ET$ are found using a method similar to that used to find $EG'$ and $ET'$, given that $i$ prey have been found by time $t$. In order to find $EG$ and $ET$ we start with zero prey having been found by time $t = 0$. We can write the probability of
having found $j$ prey by time $t_{n_1-1}$, but never having found as many as $k$ prey before
time $t_k$, for $k < n_1 - 1$, as $Q(t_{n_1-1}, j|0,0) = Q(t_{n_1-1}, j)$, which may be calculated using
\[ Q(t_{n_1-1}, j) = \sum_{k=0}^{\min[j,n_1-3]} Q(t_{n_1-2}, k)P(t_{n_1-1}, j|t_{n_1-2}, k) \] (19)

for $n_1-1 = m+1, m+2, \ldots, n$, and for $j \leq n_1-2$. For $n_1-1 = m$ and $j = 0, 1, \ldots, m-1$
we have
\[ Q(t_m, j) = P(t_m, j|0,0). \] (20)

Using the same ideas as were used to find $EG'$ and $ET'$ we have
\[ EG = m[1 - \sum_{i=1}^{m-1} P(t_m, j|0,0)] \]
\[ + \sum_{n_1=m+1}^{n} \sum_{n_2=n_1}^{\infty} n_1 Q(t_{n_1-1}, j)P(t_{n_1}, n_2|t_{n_1-1}, j) \]
\[ + \sum_{n_2=1}^{n_1-1} n_2 Q(t_{n_1}, n_2) \] (21)
\[ ET = \sum_{n_2=m}^{\infty} \frac{m n_1}{n_2 + 1} P(t_m, n_2|0,0) \]
\[ + \sum_{n_1=m+1}^{n} \sum_{n_2=n_1}^{\infty} \sum_{j=0}^{n_1-2} \left[ t_{n_1-1} + \frac{n_1 - j}{n_2 - j + 1} (t_{n_1} - t_{n_1-1}) \right] \]
\[ Q(t_{n_1-1}, j)P(t_{n_1}, n_2|t_{n_1-1}, j) \]
\[ + \sum_{n_2=1}^{n_1-1} Q(t_{n_1}, n_2). \] (22)

What I have done is to calculate the values $EG$ and $ET$ for various values of $C$. The
$(ET, EG)$ points determined in this way form the lower boundaries of the envelopes illus-
trated in Fig. 2.

For a given choice of $\alpha, \beta, x$ and $r$ we can use (21) and (22) to calculate the long-
term average rate of finding prey achieved by a forager using a rule that "tries to achieve" rate $C$,
\[ R(C) = \frac{EG + x}{ET + r} \] (2)

In order to find the "pessimal strategy", we can start with some value of $C$ that can be
achieved, namely
\[ C_0 = \frac{\alpha/\beta + x}{1 + r} \] (23)
and iterate, using $C_1 = R(C_0), C_2 = R(C_1)$, and so on, until we have $R(C) = C$. The solution of this last equation, $C^*$, will be the rate of finding prey achieved by the “pessimal forager.” This will be the lowest possible rate of finding prey, and the rule used will be the “pessimal foraging strategy.” The $(EG, ET)$ point corresponding to the “pessimal foraging strategy” for $\alpha = 0.5, \beta = 0.1, z = 0.5$ and $\tau = 0.1$ is indicated with an asterisk in Fig. 3.

RESULTS AND DISCUSSION

If we want to think of the consequences of a foraging strategy, rather than the form of the strategy itself, then we might like to consider the expected number of prey captured per patch $(EG)$ and the expected amount of time spent searching each patch $(ET)$. All possible pairs of values $(ET, EG)$ are contained in the envelopes illustrated in Fig. 2. A forager leaving each patch immediately after reaching it would spend no time there and would capture no prey. That is, $EG = 0$ and $ET = 0$. A forager searching each patch completely would find all the prey in the patches and would stay unit time in each patch. That is, for the cases considered (for which $\alpha/\beta = 5$), we have $EG = 5$ and $ET = 1$.

Fig. 2 shows that certain pairs of $(ET, EG)$ are impossible. For example, it is impossible to find a very large number of prey $(EG)$ without spending a reasonably long time $(ET)$ searching. Similarly, it is impossible to spend a very long time searching without capturing a reasonable number of prey. When patches are more variable ($\alpha$ is smaller) the envelope is fatter and it is possible to achieve higher (and lower) rates of capturing prey.

While there has been a great deal of work on optimal foraging, in particular, on the problem of how an animal should forage in order to maximize the long-term rate of encountering prey, there has been little interest in the complementary problem of how an animal should move in order to encounter predators at the lowest possible rate. The problem treated here can be interpreted in two ways as the optimal avoidance of predators.

First, as described earlier, a forager might encounter prey either while travelling between patches or while foraging within patches. If travel time between patches is $\tau$ and the expected number of predators encountered during this time is $z$, then for a particular strategy the long-term rate of encountering predators is given by $R = (EG + z)/(ET + \tau)$. If no prey are encountered while travelling ($z = 0$) then predators are best avoided by never stopping in a patch where prey (or predators) may be encountered. An animal using this strategy would spend all of its time travelling. I ignore this case.

Second, ignoring the chance of encountering predators while travelling, a forager might stop foraging and spend some time hiding within a patch whenever a predator is encountered. If such a forager would hide for an average time $c$ upon encountering a predator, and if the travel time between patches is $\tau$, then in the long run the ratio
of time wasted (spent travelling or hiding) to time spent searching for prey would be 
\[ R = \frac{(cEG + \tau)}{ET} \], which is minimized when \[ \frac{EG + \tau/c}{ET} \] is minimized. This last ratio is the slope of the tangent line from the point \((0, -\tau/c)\) to the lower boundary of the \((ET, EG)\) envelope, illustrated in Fig. 5.

If travel time is ignored, and an animal wants to spend some time in patches where prey (and possibly, predators) can be found, but wants to minimize the rate of encountering predators, then the desired strategy is one corresponding to the point \((ET^*, EG^*)\) indicated in Fig. 5. Notice that the lower boundary of the envelope of possible \((ET, EG)\) points in Fig. 3 and Fig. 5 is linear from \((0,0)\) to \((ET^*, EG^*)\). Points along this line are mixtures of pure strategies corresponding to the points \((0,0)\) and \((ET^*, EG^*)\). The strategy leading to the point \((ET^*, EG^*)\) is illustrated in Fig. 4a. One can find strategies that "try to achieve" rates lower than \(EG^*/ET^*\), but such strategies lead to points \((ET, EG)\) which lie inside the envelope.

It is interesting to note that the strategy that produces the point \((ET^*, EG^*)\) in Fig. 3 is not the obvious one: leave a patch as soon as a predator is encountered. Such a strategy is not quite best in the cases that I have considered, but it is probably good enough for practical purposes. Table 1 gives the rates achieved (the ratios \(EG^*/ET^*\)) by the pessimal strategies for each of three distributions of prey \(\alpha = .5, \alpha = 1\) and \(\alpha = 2\) with \(\alpha/\beta = 5\), for \(\tau = 0\) and \(\tau = 0\). These rates are compared with the rates achieved by the simple rule: leave a patch as soon as a predator is encountered.

The rates of finding prey (or predators) given in Table 1 can be compared with the rate, \(\alpha/\beta = 5\), which would be achieved by an animal using the naive strategy of ignoring experience in patches and searching each one completely. The ratios of the lowest rates \(EG^*/ET^*\) to the naive rate \((=5)\) show that foragers can find prey (predators) at 30%, 46% and 63% of the naive rate, for the cases \(\alpha = .5, \beta = .1; \alpha = 1, \beta = .2; \) and \(\alpha = 2, \beta = .4\), respectively. These ratios for "pessimal foragers" correspond to the ratios of the rates achieved by the optimal foragers to those achieved by a naive forager with \(\tau = 0\), for the same three cases. Optimal foragers can achieve rates 17.4, 11.2 and 8.1 for the three cases. In each case the relative advantage of using the optimal strategy and of using the pessimal strategy is about the same. For example, for \(\alpha = .5, \beta = .1\) and for \(\tau = 0\), the rate achieved by an optimal forager is more than three times the naive rate, while for a pessimal forager the rate achieved is less than one-third that of the naive rate. The advantage of using optimal (or pessimal) foraging is greatest when patch variability is greatest.

Candidate pessimal foraging strategies are illustrated in Fig. 4 for the case of the most variable prey distribution \((\alpha = .5, \beta = .1)\), for three different values of \(C\) (rates of encountering prey that the forager "tries" to achieve). The points \((ET, EG)\) that these strategies achieve lie on the lower boundary of the envelope and are indicated by the heavy dots in Fig. 5. Notice that a forager "trying to achieve" a higher rate of encountering prey (or, "willing to settle" for a higher rate of encountering predators) should be
more willing to stay in patches in which prey (predators) have been encountered than should a forager "trying to achieve" a lower rate.

There has been some interest in incorporating the need to avoid predators in foraging models. Animals do change their foraging behavior in response to the presence of predators. Some evidence of this is reviewed by Gilliam and Fraser (1987), who demonstrate experimentally that foragers may also be willing to undergo greater risk of predation to achieve greater foraging success. The work of Gilliam and Fraser incorporates risk of predation into the patch choice problem. The problem is, where should animals forage if different locations vary in the numbers of prey available and the predation risk in them? I have considered the patch residence time problem (Green 1987a,c) and suggest here that risk of predation might be incorporated into that problem as well.

If predators can be avoided (or the risk of predation while foraging reduced to the level suffered by a non-foraging animal) by waiting patiently until each predator encountered disappears, then predation risk could be incorporated in a foraging model as a time cost. An optimal forager in an environment with a given joint distribution of predators and prey (predators on and prey for the forager), would decide at any time whether or not to leave a patch based on when prey had been captured and when predators had been encountered in the patch up to that time. A model like that used in this paper might be used, assuming, for example, that the numbers of predators and prey per patch were distributed independently, each with a (different) negative binomial distribution. For such a model the optimal foraging strategy would depend only on the number of prey captured and the number of predators encountered up to a given time, and I think that this strategy might be found by dynamic programming, using a method similar to that which I have used here. I have not tried to do this.

LITERATURE CITED


APPENDIX

Here is a BASIC program that calculates a "pessimal foraging strategy" for a negative binomial prey distribution with parameters $\alpha = 0.5$ and $\beta = 0.1$, given in lines 10 and 20. Travel time is $\tau = 0.1$, given in line 30, and the expected number of prey (predators) encountered while travelling from one patch to another is $x = 0.5$, given in line 40. The forager "tries to achieve" rate $C = 3.182$, given in line 100.

A pessimal forager should always leave a patch whenever $n$ prey have been found. If $n = i$ this means that a forager should leave a patch whenever one prey has been found there. The case $n = 1$ is treated in lines 200 to 290. The probability that a patch contains no prey is given in line 220. The probabilities of there being $i$ prey in the patch, for $i = 1, 2, \ldots, 100$, given in line 240, and these probabilities are used in line 250 to calculate the expected length of time spent in each patch, given $n = 1$.

The case $n = 2$ is treated in lines 302 to 700. The stopping time $t_{n-1} = t_1$ is calculated in lines 304 to 440, with $EG'$, given by expression (6), seen in line 320, and $ET'$, given by expression (9), seen in lines 330 and 370. Once the stopping time $t_1$ has been found the probability of there being no prey in the interval $(0, t_1)$ is given in line 500, and the probability of there being no prey in the interval $(t_1, 1)$, given that no prey are in the interval $(0, t_1)$, is given in line 505. The probabilities of there being $i$ prey in the interval $(0, t_1)$, for $i = 1, 2, \ldots, 100$, are given in line 560, and these probabilities are used in line 570 to help find $ET$. The probabilities of there being $i$ prey in the interval $(t_1, 1)$, given no prey in $(0, t_1)$, are given, for $i = 1, 2, \ldots, 100$, in line 650, and these probabilities are used in line 660 to help find $ET$. Other terms are added to $ET$ in lines 530, 570 and 620. $EG$ is found in line 520. (Notice that $T$ in the text is $S$ in the program.)

The other cases ($n \geq 3$) are treated in the rest of the program (lines 800 to 2800). First, the value of $n$ is found in lines 810 to 860. Then the stopping time $t_{n-1}$ is found in lines 900 to 1060, and the result is printed in line 1070. Next, stopping time $t_{n-2}$ is found in lines 1100 to 1330, and the result is printed in line 1340. Then the other stopping times, $t_{n-3}, t_{n-4}, \ldots, t_m$ are found, if necessary, in lines 1490 to 2000, and are printed in line 1985. The smallest number of prey such that a patch should be left if that number have been found is $m$. Once a particular pessimal foraging strategy, characterized by the values of $m$ and $n$, and the stopping times $t_m, t_{m+1}, \ldots, t_{n-1}$, have been found, then the expected number of prey found per patch, $EG$, and the expected length of time spent searching each patch, $ET$, are found in lines 2080 to 2730, and these values are printed, along with the rate given in expression (2), in line 2800.
For a given guess, \( t \), for the time \( t_{n-1} \), the value of \( EG' \), given by (6), is calculated in line 940, while the value of \( ET' \), given by (9), is calculated in lines 950 and 980. For a given guess of \( t_{n-2} \), the value of \( EG' \), given by (10), is calculated in line 1170, while the value of \( ET' \), given by (11), is calculated in lines 1180, 1185, 1210 and 1250.

For a given guess, \( t \), for time \( t_{n-k} \), with \( k \geq 3 \), given the values \( t_{n-k+1}, t_{n-k+2}, \ldots, t_{n-1} \), the values of \( Q(\ast, \ast|\ast, \ast) \) are found in lines 1540 to 1710. Since the arguments \( t \) and \( i = n - k \) in \( Q(t_{n-1}, j|t, i) \) are fixed throughout the calculation, only two arguments, \( t_{n-1} \) and \( j \), are required in the expressions rendered by \( Q(\ast, \ast) \) in the program. In the program (lines 1610 and 1680), \( J \) stands for the subscript \( n_1 - 1 \) and \( Jl \) stands for \( j \) in expression (13). Expression (12) is seen in line 1570, while (13) is used to calculate \( Q(t_{n-1}, i|t, i) \) in line 1590. The loop in lines 1600 to 1700 calculates the values \( Q(t_{n-1}, j|t, i) \) for \( j > i = n - k \). Expression (13) is seen in line 1680.

\( EG' \) is calculated in lines 1560, 1770 and 1870, with the first line in expression (17) seen in line 1560, the last line in (17) seen in line 1770, and the middle line in (17) seen in line 1870 of the program. \( ET' \) is calculated in lines 1740, 1780 and 1880 with the first line in (18) seen in line 1740, the last line in (18) seen in line 1780, and the middle line(s) seen in line 1880 of the program. Once a value of \( t \) has been found such that \( EG'/ET' = C \), that value is used for \( t_{n-k} \), and that value and the later stopping times are used to help find \( t_{n-k-1} \). This process is continued until \( t_1 \) has been found, or until an integer \( i > 1 \) is found such that \( t_i = 0 \). In this case \( m \) is set equal to \( i + 1 \), where \( m \) is the smallest number of prey whose discovery would require the forager to leave the patch. If \( t_1 > 0 \) then \( m = 1 \).

In lines 2080 to 2730 the values of \( EG \) and \( ET \) are calculated for the values of \( m, n \) and \( t_m, t_{m+1}, \ldots, t_{n-1} \) for the rule that "tries to achieve" rate \( C \). First, the values of \( Q(t_{n-1}, j|0, 0) = Q(t_{n-1}, j) \) are calculated in lines 2100 to 2420. \( Q(t_m, 0) \) is given in line 2100, \( Q(t_m, j) \) for \( j = 1, 2, \ldots, m - 1 \) is given in line 2150 (if \( m \geq 2 \), \( Q(t_{n-1}, 0) \) is given in 2310 for \( 1 \leq n_1 - 1 \leq n \), while the remaining values of \( Q(t_{n-1}, j) \), which are calculated using expression (19), are found using line 2390.

The value of \( EG \), given in expression (21), is calculated in lines 2220, 2580 and 2710. The first line in (21) is calculated in line 2220 of the program, although the calculation in the program—being slightly more convenient for the calculation of \( ET \) as well—is slightly different from that in the text. The second line in (21) is calculated in line 2580 of the program, and the last line in (21) is calculated in line 2710 of the program. The value of \( ET \), given in expression (22), is calculated in lines 2230, 2590 and 2720 of the program. The first line in (22) is calculated in line 2230 of the program, the second line of (22) is calculated in line 2590, and the third line in (22) is calculated in line 2720. Finally, the calculated values for \( EG, ET \) and \( R(C) \) are printed in line 2800 of the program.

The lower boundaries of the envelopes plotted in Fig. 2 were obtained by calcu-
lating $EG$ and $ET$ for a sequence of choices of $C$. The curves have been completed by linear interpolation between the calculated points [and the point $(1,5)$], except that a smooth curve has been interpolated from the calculated point $(0.9438, 3.6727)$ to the point $(1,5)$ in Fig. 2a (and in Figs. 3 and 5), and from the calculated point $(0.9642, 4.3498)$ to the point $(1,5)$ in Fig. 2b.

1 LPRINT "Pessimal foraging: PESFOR3"
5 DIM T(20)
6 DIM Q(20,20)
7 DIM M1(20,20)
8 DIM M2(20,20)
10 A = .5
20 B = .1
30 TO = .1
40 X0 = .5
50 LPRINT A;B;TO;X0
60 FOR I = 0 TO 20
64 FOR J = 0 TO I
67 M1(I,J) = J
70 M2(I,J) = I
74 NEXT J
77 FOR J = I TO 20
80 M1(I,J) = I
84 M2(I,J) = J
87 NEXT J
90 NEXT I
100 C = 2.108416
105 LPRINT "C = "; C
110 IF C > (1 + A)/ (1 + B) THEN GOTO 300
200 G = 1 - (B/(1+B))^A
210 S = (B/(1+B)) ^ A
220 P = (B/(1+B))^A
230 FOR I = 1 TO 100
240 P = P*(A+I-1)/(I*(I+1))
250 S = S + P/(I+1)
260 NEXT I
265 LPRINT "N = 1"
270 LPRINT G;S; (G + X0)/ (S + TO); G/S
290 STOP
300 IF C > (2 + A)/ (1 + B) THEN GOTO 800
302 N = 2
303 LPRINT "N = 2"
304 T = .5
307 C1 = .5
310 FOR J = 1 TO 20
320 G1 = 1 - ((B+T)/(B+1)) ^ (A+1)
330 S1 = (1 - T) * ((B+T)/(B+1)) ^ (A+1)
340 P = ((B+T)/(B+1))^A
350 FOR I = 1 TO 100
360 P = (A+I) * P* (1-T) / ((B+1)*I)
370 S1 = S1 + P* (1-T) / (I+1)
380 NEXT I
390 IF G1/S1 > C THEN GOTO 420
400 T = T - .5*C1
410 GOTO 430
420 T = T + .5*C1
430 C1 = .5*C1
440 NEXT J
450 T(N-1) = T
460 LPRINT T(1); 1
500 Q = (B/(B+T(N-1)))^A
505 Q1 = ((B+T(N-1))/(B+1))^A
510 R1 = (1 - T(N-1))/(B+1)
520 G = 1 - Q + Q*(2 - Q1*A*R1 - 2*Q1)
530 S = (B/(B+1))^A
540 P = (B/(B+T(N-1)))^A
550 FOR I = 1 TO 100
560 P = (A + I - 1)*P*A*T(N-1)/(I*(B+T(N-1)))
570 S = S + Q*P*A*R1
580 NEXT I
590 Q = (B/(B+T(N-1)))^A
600 P = ((B + T(N-1))/(B+1))^A
610 R1 = (1 - T(N-1))/(B+1)
620 S = S + Q*P*(T(N-1) + 2*(1-T(N-1))/(I+1))
630 P = A*P*R1
640 FOR I = 2 TO 100
650 P = (A+I-1)*P*/R1/I
660 S = S + Q*P*(T(N-1) + 2*(1-T(N-1))/(I+1))
670 NEXT I
680 LPRINT G;S; (G + X0)/(S + T0); G/S
700 STOP
700 N = 1
710 FOR I = 1 TO 100
720 IF A+I >= C*(B+1) THEN GOTO 840
730 NEXT I
740 N = I
750 LPRINT "N = "; N
760 T(N) = 1
770 T = .5
780 C1 = T
790 FOR I = 1 TO 20
800 P = ((B + T)/(B + 1))^A + A - N - 1
810 G1 = 1 - P
820 S1 = (1 - T)*P
830 FOR J = 1 TO 100
840 P = (A - N - 2 + J)*P*(1 - T)/(J*(B + 1))
850 S1 = S1 + (1 - T)*P/(J + 1)
860 NEXT J
870 C1 = .5*C1
880 IF G1/S1 > C THEN GOTO 1040
890 T = T - C1
900 GOTO 1050
910 T = T + C1
920 NEXT I
930 T(N-1) = T
940 LPRINT T(N-1); N-1
950 T = T(N-1)/2
960 C1 = T
970 FOR I = 1 TO 20
980 P = ((B + T)/(B + T(N-1)))^A + A + N - 2
990 P0 = P
1000 P1 = ((B + T(N-1))/(B+1))^A + A + N - 2
1010 R1 = (1 - T(N-1))/(B + 1)
1020 G1 = 1 - P + P*(2 - 2*P1 - (A + N - 2)*P1*R1)
1030 S1 = (1 - T)*P*P1
1040 S1 = S1 + (1 - T)*P*P1*R1*(A + N - 2)
1050 FOR J = 1 TO 100
1060 P = (A + N - 3 + J)*P*(T(N-1) - T)/(J*(B + T(N-1)))
1070 S1 = S1 + (T(N-1) - T)*P/(J + 1)
1080 NEXT J
1225 P1 = (A + N - 2) * P1 * R1
1230 FOR J = 2 TO 100
1240 P1 = (A + N - J + J) * P1 * R1 / J
1250 S1 = S1 + (T(N-1) - T + Z*(1 - T(N-1)) / (J + 1)) * P0 * P1
1260 NEXT J
1270 C1 = .5 * C1
1280 IF G1 / S1 > C THEN GOTO 1310
1290 T = T - C1
1300 GOTO 1320
1310 T = T + C1
1320 NEXT I
1330 T(N-2) = T
1340 LPRINT T(N-2); N-2
1350 L = 20
1500 FOR K = 3 TO N-1
1510 T = T(N-K+1) / 2
1520 C1 = T
1530 FOR I = 1 TO 20
1535 S1 = 0
1540 P = ((B + T) / (B + T(N-K+1))) * (A + N - K)
1550 P0 = P
1560 G1 = 1 - P
1570 Q(N-K+1,N-K) = P
1580 FOR J = N - K + 2 TO N
1590 Q(J,N-K) = Q(J-1,N-K) * ((B + T(J-1)) / (B + T(J))) * (A + N - K)
1600 FOR J1 = N-K+1 TO J-1
1610 Q(J,J1) = 0
1620 FOR J2 = N-K TO M1(J1, J1-2)
1630 P = ((B + T(J-1)) / (B + T(J))) * (A + J2)
1640 IF J2 = J1 THEN GOTO 1680
1650 FOR J3 = 1 TO J1 - J2
1660 P = (A + J2 + J3 - 1) * P * (T(J) - T(J-1)) / (J3 * (B + T(J)))
1670 NEXT J3
1680 Q(J,J1) = Q(J,J1) + Q(J-1,J2) * P
1690 NEXT J2
1700 NEXT J1
1710 NEXT J
1720 FOR J = 1 TO L
1730 P0 = (A + N - K - 1 + J) * P0 * (T(N-K+1) - T) / (J * (B + T(N-K+1)))
1740 S1 = S1 + (T(N-K+1) - T) * P0 / (J+1)
1750 NEXT J
1760 FOR J = N-K TO N-1
1770 G1 = G1 + (J - N + K) * Q(N,J)
1780 S1 = S1 + (1 - T) * Q(N,J)
1790 NEXT J
1800 FOR N1 = N - K + 2 TO N
1810 FOR J = N - K TO N1 - 2
1820 P1 = ((B + T(N1-1)) / (B + T(N1))) * (A + J)
1830 FOR I = J + 1 TO N1 - 1
1835 P1 = (A + I - 1) * P1 * (T(N1) - T(N1-1)) / ((I1 - J) * (B + T(N1)))
1840 NEXT I1
1850 NEXT J
1860 FOR N2 = N1 TO L
1870 P1 = (A + N2 - 1) * P1 * (T(N1) - T(N1-1)) / ((N2 - J) * (B + T(N1)))
1870 G1 = G1 + (N1 - N + K) * Q(N1-1,J) * P1
1880 S1 = S1 + Q(N1-1,J) * P1 * (T(N1-1) - T) + (N1 - J) * (T(N1) - T(N1-1)) / (N2 - J + 1)
1890 NEXT N2
1900 NEXT J
1910 NEXT N1
1920 C1 = .5*C1
1930 IF G1/S1 > C THEN GOTO 1960
1940 T = T - C1
1950 GOTO 1970
1960 T = T + C1
1970 NEXT I
1980 T(N-K) = T
1985 LPRINT T(N-K);N-K
1990 IF T(N-K) < .000001 THEN GOTO 2040
2000 NEXT K
2010 M = 1
2020 LPRINT "M = 1"
2030 GOTO 2080
2040 M = N - K + 1
2050 LPRINT "M = ";M
2080 G = 0
2090 S = 0
2100 Q(M,0) = (B/(B + T(M)))^A
2110 P = Q(M,0)
2120 IF M = 1 GOTO 2200
2130 FOR I1 = 1 TO M - 1
2140 P = (A + I1 - 1)*P*T(M)/(I1*(B + T(M)))
2150 Q(M,I1) = P
2160 NEXT I1
2200 FOR N2 = M TO 100
2210 P = (A + N2 - 1)*P*T(M)/(N2*(B + T(M)))
2220 G = G + M^P
2230 S = S + M*T(M)*P/(N2 + 1)
2240 NEXT N2
2300 FOR N1 = M + 2 TO N + 1
2310 Q(N1-1,0) = (B/(B + T(N1-1)))^A
2320 FOR J1 = 1 TO N1 - 2
2325 Q(N1-1,J1) = 0
2340 FOR J2 = 0 TO M1(J1,N1-3)
2350 P = ((B + T(N1-2))/(B + T(N1-1)))^(A + J2)
2355 IF J2 = J1 THEN GOTO 2390
2360 FOR J3 = J2 + 1 TO J1
2370 P = (A + J3 - 1)*P*(T(N1-1) - T(N1-2))/((J3 - J2)*(B + T(N1-1)))
2380 NEXT J3
2390 Q(N1-1,J1) = Q(N1-1,J1) + Q(N1-2,J2)*P
2400 NEXT J2
2410 NEXT J1
2420 NEXT N1
2500 FOR N1 = M + 1 TO N
2510 FOR J = 0 TO N1 - 2
2520 P = ((B + T(N1-1))/(B+T(N1)))^(A + J)
2530 FOR J3 = J + 1 TO N1 - 1
2540 P = (A + J3 - 1)*P*(T(N1) - T(N1-1))/((J3 - J)*(B + T(N1)))
2550 NEXT J3
2560 FOR N2 = N1 TO 100
2570 P = (A + N2 - 1)*P*(T(N1) - T(N1-1))/((N2 - J)*(B + T(N1)))
2580 G = G + M^Q(N1-1,J)*P
2590 S = S + Q(N1-1,J)*P*(T(N1-1) + (N1 - J)*(T(N1) - T(N1-1)))/(N2 - J + 1)
2600 NEXT N2
2610 NEXT J
2620 NEXT N1
2700 FOR J = 0 TO N - 1
2710 G = G + J*Q(N,J)
2720 S = S +Q(N,J)
2730 NEXT J
2800 LPRINT G/S; (G + X0)/(S + T0); G/S
Table 1. Pessimal foraging for $\tau = x = 0$.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Lowest rate</th>
<th>Stopping times</th>
<th>&quot;Cautious&quot; rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>$\beta$</td>
<td>$t(1)$</td>
<td>$t(2)$</td>
</tr>
<tr>
<td>0.5</td>
<td>0.1</td>
<td>1.507</td>
<td>0.806</td>
</tr>
<tr>
<td>1.0</td>
<td>0.2</td>
<td>2.306</td>
<td>0.479</td>
</tr>
<tr>
<td>2.0</td>
<td>0.4</td>
<td>3.150</td>
<td>0.353 0.773</td>
</tr>
</tbody>
</table>

Note. The lowest rate ("pessimal foraging") is achieved by a forager using the rule specified by the stopping times. For $\alpha = 0.5$ and $\beta = 0.1$ a pessimal forager should leave a patch if one prey ( predator) is found before $t(1) = 0.806$, or if a second prey is found after that time. The forager should leave a patch when $t = 1$ in any case. The "cautious" rate, which is almost as low as the lowest rate, is achieved by a forager that leaves a patch whenever a prey ( predator) is found.
Fig. 1. Charnov's marginal value theorem, for one patch type. The total energy gained in a patch by time $t$, namely, $g(t)$, is plotted against time in the patch, $t$. The travel time between patches is $\tau$, and the long-term rate of energy gain for an animal that remains for time $t$ in each patch is $r(t) = g(t)/(t + \tau)$. The time, $t_0$, that maximizes $r(t)$ is the value such that the line from $(-\tau, 0)$ to $(t_0, g(t_0))$ is tangent to the gain function. a) The gain function is negatively accelerated, as Charnov (1976) assumed, and the derivative (the "marginal value") of the gain function at $t_0$ equals the highest possible long-term rate of energy gain. That is, $g'(t_0) = r(t_0) = g(t_0)/(t_0 + \tau)$. b) The gain function is piecewise linear. In this example, the gain function does not have a derivative at $t_0$, and the "marginal value" part of the marginal value theorem does not hold.
Fig. 2. Set of \((ET, EG)\) points for all possible strategies for a forager searching systematically in patches having a negative binomial distribution of the number of prey. The average number of prey per patch is \(\alpha/\beta = 5\). a) \(\alpha = 0.5, \beta = 0.1\); b) \(\alpha = 1.0, \beta = 0.2\); c) \(\alpha = 2.0, \beta = 0.4\).
c) $\alpha = 2.0, \beta = 0.4.$
Fig. 3. An analogue of the marginal value theorem for a pessimal forager. This may be interpreted as optimal avoidance of predators by a forager, if $\tau$ and $z$ are the expected time spent and the expected number of predators encountered while traveling between patches, and $ET$ and $EG$ are the expected time spent and the expected number of predators encountered within each patch, for a particular strategy. The strategy which minimizes the rate of encounter with predators is one corresponding to values $(ET, EG)$ where the tangent line from $(-\tau, -z)$ touches the $ET-EG$ curve. The $ET-EG$ curve illustrated here is the lower surface of the envelope of $(ET, EG)$ points illustrated in Fig. 2a, for the parameters $\alpha = 0.5$ and $\beta = 0.1$. The point marked with an asterisk corresponds to the optimal strategy for $\tau = 0.1$ and $z = 0.5$. 
Fig. 4. Candidate pessimal strategies for animals "trying" to achieve rates a) $C = 1.507$; b) $C = 4$, and c) $C = 8$, for a negative binomial prey distribution with $\alpha = 0.5$ and $\beta = 0.1$. The strategies illustrated yield values of $ET$ and $EG$ corresponding to points marked with asterisks on the curve illustrated in Fig. 5. There exist tangent lines to the $ET$-$EG$ curve at these points with slopes 1.507, 4 and 8, respectively. The tangent line with slope 4 is shown in Fig. 5. A pessimal forager should leave a patch if it hits (if the number of prey found [predators encountered] by time $t$ hits) one of the horizontal line segments in the figure. Each of these strategies is pessimal for an appropriate choice of $\tau$ and $x$. The rate 1.507 is the lowest rate that can be achieved for any choice of $\tau$ and $x$. 
Fig. 5. Another analogue of the marginal value theorem. This figure looks like Fig. 3, but both axes represent time. $ET$ is the expected time spent searching in a patch, $\tau$ is the time spent traveling between patches, and $EG$ is the expected number of predators encountered. If a forager wastes time $c$ hiding after encountering each predator, then the expected time wasted hiding in each patch is $cEG$. The total time wasted traveling and hiding is proportional to $cEG + \tau$ or, equivalently, $EG + \tau/c$. The optimal avoidance of predators minimizes the ratio $[EG + \tau/c]/ET$, and corresponds to pessimal foraging. The points marked with the asterisks correspond to the strategies illustrated in Fig. 4.