

**AN EXAMPLE OF PARASITOID FORAGING: *TORYMUS CAPITTE* (HUBER;
HYMEMOPTERA: TORYMIDAE [CHALCIDOIDEA]) ATTACKING THE
GOLDENROD GALL-MIDGE *ASTEROMYIA CARBONIFERA* (O. S.; DIPTERA:
CECIDOMYIIDAE)**

Richard F. Green
Department of Mathematics and Statistics
University of Minnesota Duluth
Duluth, MN 55812 U. S. A.

INTRODUCTION

Van Alphen and Vet (1986) refer to the work of Arthur E. Weis (1983) on a torymid wasp that attacks a gall midge on goldenrod. This system seems to be quite well-studied, particularly, but not exclusively, by Weis. Van Alphen and Vet point out that the parasitoids tend to attack about the same proportion of hosts in patches (galls) with varying numbers of hosts. This has implications for the foraging strategy that the parasitoids use.

In this note I want to do three things: (1) outline the basic biology of the organisms involved, (2) describe the results of a foraging experiment conducted by Weis (1983), and (3) interpret the results in terms of Oaten's stochastic model of optimal foraging.

Arthur E. Weis is coauthor of a book (Abrahamson and Weis 1997) on the biology of a three trophic-level system involving a goldenrod stem-gall maker *Eurosta solidaginis*, its host plant and its enemies. The work described here is earlier work, done on a different species.

The biology of the system

The species of greatest interest are the torymid parasitoid *Torymus capite*, which is a larval parasitoid of the gall midge *Asteromyia carbonifera*, which itself makes blister-like galls on the leaves of goldenrod, especially Canadian goldenrod, *Solidago canadensis* L. (Compositae). There are three generations of gall midge (and its parasitoids) each year. The last generation overwinters in the gall. Field experiments conducted in northern Illinois showed a guild of five parasitoids attacking *Asteromyia carbonifera* (Weis 1982b). *T. capite* tended to attack hosts at a later stage than three of the four other parasitoids. The adult female parasitoid sometimes feeds on the haemolymph of midge larvae, but she does not oviposit on the individual larvae that she feeds upon. The parasitoid larvae sometimes consume plant matter, sometimes they consume other parasitoids, and sometimes they consume more than one host.

A study of phytophagous insects associated with goldenrod species in Gainesville, Florida (Tontes et al. 1994), identified 123 species that attacked goldenrod, although only 14 of the species were specific to goldenrod and asters. Among these were

Asteromyia carbonifera and six other dipteran species in the same family, Cecidomyiidae.

In another study of a goldenrod community, Root and Cappuccino (1992) surveyed the herbivores on *Solidago Altissima* (a member of the *Solidago canadensis* tribe) near Ithaca, New York. Over a period of six years, they observed 138 species of herbivores. It appears that goldenrod support an extremely rich fauna.

Weis (1982a) studied the presence of a fungus *Sclerotium asteris* (Schw.; Mycelia Sterlia), which is symbiotic with the gall-maker, *Asteromyia carbonifera*. The fungus produces a stroma [described by Weis (1982a, p. 1602) as “a tough, dense vegetative structure”], which causes the gall to become rigid. Presence of the gall-maker seems necessary for the fungi to form stroma. The parasitoid *T. capite* is unable to flex its ovipositor inside a gall that has become rigid, and it has much less chance of finding a host in such a gall. Weis’s (1982a) Table 1 shows that in 58 cases in which the parasitoid encountered mature (hardened galls), only two received successful ovipositions, but in 79 cases in which immature galls were offered, 23 received successful ovipositions. Weis (1982a, p. 1604) reported that as many as 80% of galls become hardened and therefore are “false targets” for their potential parasitoids. That is, the parasitoids do not distinguish between galls where their potential hosts are accessible and hardened galls where their potential hosts are inaccessible. CSIRO (1991, p. 749) mentions that some Cecidomyiidae (midge) larvae feed on fungi introduced by the ovipositing female.

Parasitism and foraging by parasitoids

In the field, parasitism on gall-makers commonly ranges between 50 and 90% (references in Weis 1982b). A two-year study by Weis (1982b) showed an overall average attack rate of 52.6% for a guild of five parasitoids. Heaviest parasitism was by *Tetrastichus tesserus*, 22.6%; *Torymus capite*, 14.1%; and *Tetrastichus fumipennis*, 11.2%. Studies on parasitoid foraging concentrated on *T. capite* because it is an ectoparasite, and its eggs could be detected easily by dissecting a gall. In a foraging experiment, Weis (1983) offered young individual parasitoids (each assumed to possess twelve eggs) a cage full of nine goldenrod stems, each with a gall on one of its leaves. Parasitoids were given 24 hours to oviposit. Weis (1983) was interested in two questions: (1) In how many galls did the parasitoids attack at least one host? and (2) What fraction of all the hosts available in an experiment were attacked? Weis was particularly interested in how the rates of attack measured these two ways depended on the number of hosts in each gall. It turned out that galls with more hosts are more likely to receive attack, but that the proportion of available hosts attacked did not depend on the number of hosts available in a gall.

In one experiment there were eighty galls available overall and the distribution of the number of galls was as follows:

Table 1. Number of hosts per gall observed in Weis' (1983) foraging experiment

Number of hosts in a gall	1	2	3	4	Total
Frequency	25	36	15	4	80

For these observations the mean and variance are: $\mu = 1.97$ and $\sigma^2 = 0.699375$. Here I am treating the values as a population, not a sample. That is, I calculate the variance by dividing by n , not by $n - 1$.

Parasitoids were observed to spend an average of 9.2 minutes per probe (S. E. = 1.58, $n = 86$), and they made an average of 5.5 probes (S. E. = 1.7, $n = 6$) per gall (Weis 1983). Thus, they spent about 50 minutes per gall. Travel time between galls was not measured, but in the next section I will infer a value for travel time based on the other observations and optimal foraging theory.

APPLICATION OF OPTIMAL FORAGING THEORY

Qualitative interpretation by Weis (1983) and by van Alphen and Vet (1986)

Weis (1983) discussed the results of his foraging experiments in terms of optimal foraging theory. He suggested that his inferred increase in the number of hosts attacked per discovered gall (curve (c) in his Fig. 6) could have been due to a weak aggregative response in the sense of Oaten (1977a). [That is, the forager tends to spend longer and infect more hosts in patches with more hosts.] However, Weis mentioned that population modelers (Hassell and May 1974, Murdoch and Oaten 1975) pointed out that an aggregative response was of adaptive significance in models in which the lowest and highest density patches differed by an order of magnitude. Weis pointed out that Iwasa et al. (1981) had suggested that foragers lacking the aggregative response would be more efficient when the variance of the frequency distributions of hosts is small relative to the mean. Weis claimed that when there is little variability in host numbers, "taking a fixed number of prey per patch (Gibb 1962) or spending a fixed amount of time per patch (Krebs 1973) will yield greater capture rates than mechanisms which use current rate of encounter in the decision when to leave the patch." [Weis makes a small technical mistake here; both the fixed number rule and the fixed time rule are based on the expected current rate of encounter.] I will show below that both the fixed time and fixed number rules are, in fact, quite good for the distribution of hosts that Weis observed.

Van Alphen and Vet (1986) also discussed Weis' observations in terms of optimal foraging theory. They repeat Weis' reference to an assertion by Iwasa et al. (1981) that host distributions with little variability call for fixed time or fixed number patch-leaving rules. But they also point out that the parasitoids certainly did not use a fixed time rule. Parasitoids did not spend the same time in each patch. Van Alphen and Vet (1986) add that there is no strong evidence that parasitoids use a fixed giving-up time rule [despite the fact that the giving-up time rule is a favorite of theorists].

Quantitative treatment of Weis' observations

Iwasa et al. (1981) gave a qualitative treatment of a number of examples of Oaten's (1977b) stochastic model of optimal foraging. Assuming random search within a patch, they compared the performance of several patch-leaving rules: (1) fixed time, (2) fixed number, and (3) fixed giving-up time. They pointed out that—of these rules—the fixed time rule is best for a Poisson prey distribution, the fixed number rule is best for a regular prey distribution (all patches have the same number of prey), and the fixed giving-up time rule is best for a negative binomial prey distribution. Iwasa et al. also plotted the expected rate of finding prey against time in a patch for a particular pattern of experience (times at which prey are found within a patch). They showed how the expected rate depends on prey distribution by considering four different distributions, regular, binomial, Poisson and negative binomial. Their illustration for a negative binomial prey distribution resembles the illustration of Waage's (1979) behavioral mechanism for patch leaving in a parasitoid.

Green (1987) provided a quantitative treatment for regular, Poisson and negative binomial prey distributions for random and for systematic search within patches. More details were provided for the case of random search in an unpublished technical report, which added the binomial prey distribution (Green 1988).

Most of the work on optimal foraging models concentrates on particular examples of prey distributions that are biologically reasonable (like negative binomial) and/or are mathematically convenient. For a Bayesian treatment, the negative binomial distribution has a particularly nice interpretation. In each patch, prey numbers have a Poisson distribution, but the Poisson parameter (average prey density in a patch) itself varies from patch to patch, and this variability is represented by a gamma-distributed Bayesian prior.

Recently I started finding optimal foraging strategies for other prey distributions that are not generally chosen for Bayesian analysis (Green 2006). This is important, because the prey or host distributions that animal foragers face are not necessarily the ones usually used by human Bayesians. Nature, or experimenters, may present foragers with problems chosen for their own convenience or their own sense of beauty. It turns out that the calculations for general problems are not really more difficult than those used for the simple, familiar examples.

In order to find the optimal foraging strategy for some particular distribution, such as the one found by Weis (1983) and given in my Table 1, it is also necessary to know that the travel time is between patches. Travel time is seldom measured, so it must be inferred. I assumed that travel time would be approximately equal to the time for which the foraging behavior observed in patches would be optimal. Weis observed that the foragers took slightly more than 20% of the hosts available. I tried to find a travel time value, τ , such that a model forager using the fixed-time (“naïve”) rule would find approximately the same percentage of hosts as observed. I also wanted a round number.

I found that $\tau = 0.02$ was too small and that $\tau = 0.04$ was too big. Therefore, I settled on the value $\tau = 0.03$.

One advantage of a quantitative treatment is that we can see how much difference it makes what patch-leaving rule a forager uses. The advantage of using the best rule for the distribution that Weis (1983) observed over a naïve rule, which ignores host distribution, is not great. A naïve forager would achieve a rate that is only about 7% below that achieved by the best rule. This may be seen in Table 2.

Table 2. Rates for the Weis host distribution for different patch-leaving rules

Rule	Rate achieved
Best	1.68107
Fixed time ($t = 0.23525$)	1.56064
Fixed number ($x = 1$)	1.55642

In each case it is assumed that travel time is $\tau = 0.03$, search within patches is random, and search rate equals one (one patch per unit time; in the terminology of Rogers 1972, “searching efficiency,” $a' = 1$). Host distribution is as in Table 1. The fixed time rule is the rule that would be best for a Poisson distribution of host numbers in patches. I have referred to this as the “naïve” rule, because it does not take into account of the foragers’ experience in a patch.

In Table 2 I have compared the performance of three different rules for the same (observed) distribution. Another treatment would be to see how well optimal foragers might do searching patches with different distributions with the same average number of host per gall as observed by Weis (1983).

Table 3. Performance of best rules for various host distributions, all with the same average as Weis observed (1.975 hosts per patch)

Distribution	Patch mean	Patch variance	Rate
Poisson	1.9750	1.9750	1.56064
Binomial (4, 0.49375)	1.9750	0.9998	1.62862
Weis (Table 1)	1.9750	0.6994	1.68107
Fixed number (2)	2.0000	0.0000	1.88679
(Above)*1.975/2	1.9750	0.0000	1.86321
Two point	1.9750	0.0244	1.84332

In each case, search is random at rate one and travel time between patches is $\tau = 0.03$. Since the average is not an integer, I cannot find a fixed distribution with the same average number of hosts per patch as Weis observed. However, since he observed an average of 1.975, a fixed distribution with exactly two hosts per patch has mean nearly equal to 1.975. The table includes the best rate for this

distribution (the best rule is to attack one host in each patch). The next row gives a rate equal to 1.975 times the original value. The final row uses a patch distribution with one host in one patch out of 40 and two hosts in thirty-nine patches out of 40. I assumed that a fixed number rule (with the fixed number equal to one) would also be best in this case.

What the best rule looks like for Weis' distribution of hosts

The optimal foraging strategy for the distribution of host numbers observed by Weis (1983) and listed in Table 1 is very simple. An optimally foraging parasitoid should remain in a patch for some time, $t(0)$, and then leave if no hosts are encountered. If a host is encountered before that time, the parasitoid should infect that host and leave. The reason that such a rule is best is this: a forager using this rule can achieve a foraging rate of about 1.68 hosts encountered per unit time searching. If no hosts are found for some time, it is quite likely that the gall contains only one host. The expected additional time to find a host if the gall contains only one host is one, which means that the rate achieved until finding that one host equals one—much less than the average rate of 1.68. On the other hand, if a host is found soon after entering the patch, the expected number of hosts remaining in the patch is less than it was before the host was found and the parasitoid should also abandon the gall.

In the following table, the expected number of hosts encountered, $E(G)$, the expected time spent searching, $E(S)$, and the expected rate achieved by the forager that tries to achieve a rate C is given for Weis' host distribution (Table 1), and travel time $\tau = 0.03$. The rule (that is, the stopping points) are given. The last row gives the travel times for which the rules given above would be best.

Table 4. Rules and rates for foragers that use strategies of the best type

C	1.6811	1.6000	1.2000	0.8000
$E(G)$	0.5781	0.6754	0.9738	1.2728
$E(S)$	0.3139	0.3726	0.5858	0.8864
$t(0)$	0.4700	0.6275	1.8825	*
$t(1)$	**	**	0.1750	0.8125
$t(2)$			**	0.1325
$t(3)$				**
Rate	1.6811	1.6753	1.5813	1.3890

New τ 0.0300 0.0490 0.2257 0.7046

* never stop ** always stop

Table 4 gives four different rules for a potentially optimally-foraging parasitoid searching for hosts that have the distribution observed by Weis (1983). The particular form of each rule depends on the rate, C , that the parasitoid “tries to achieve.” The highest possible rate, $R = 1.6811$, is achieved by a parasitoid that tries to achieve this same rate, $C = 1.6811$, when travel time is $\tau = 0.03$, which I assumed is correct for Weis’ experiment. The rule for this case (the first column of Table 4) is to leave the patch if no host has been found by time $t(0) = 0.4700$, and to leave whenever one host has been found. If the parasitoid tries to achieve a lower rate, $C = 1.2000$ (the third column of Figure 4), then the forager should leave a patch if no hosts have been found by time $t(0) = 1.8825$, if one host has been found by time $t(1) = 0.1750$, and whenever two host have been found. In Table 4 I have included the value of C that produces the highest possible rate ($C = 1.6811$), and three values that give lower values ($C = 1.6000$, 1.2000 and 0.8000 , respectively). If one tries values of C that are much larger than the optimal, the parasitoid would expect too much of the environment and would leave each patch without searching it, resulting in a foraging rate of $R = 0$.

The rule given in the third column, which “tries to achieve” rate $C = 1.2000$, is not best when travel time is actually $\tau = 0.03$, which I assumed, but it is almost as good as the best rule, achieving a rate of $R = 1.5813$ instead of $R = 1.6811$, which is the highest possible rate when $\tau = 0.03$. However, the rule shown in the third column would be best for the Weis distribution if travel time were $\tau = 0.2257$. If the travel time were actually $\tau = 0.2257$, then the rule shown in the third column would be best, and it would achieve rate $R = 1.2000$, which is the rate that the rule tries to achieve.

Table 5. The probability of finding a host using the best rule (first column in Table 4)

Number of hosts in a gall	Probability of finding a host	Proportion of hosts found
1	0.3750	0.3750
2	0.6094	0.3047
3	0.7559	0.2520
4	0.8474	0.2118

For the best rule a parasitoid should leave a patch as soon as one host has been found, or at time, $t(0) = 0.47$, whichever comes first. Thus, the probabilities given in Table 5 are also the expected numbers of hosts attacked on a gall with the number of hosts specified in the first column. If y is the number of hosts on the gall, these probabilities are given by $1 - \exp[-y t(0)]$.

Generally speaking, the best patch-leaving rules for a host distribution like that observed by Weis (1983) is to remain in the patch for a longer time when fewer hosts

have been found and to leave sooner when more hosts have been found. This rule resembles the best rule for the case in which host numbers have a binomial distribution.

For the particular case shown in the first column of Figure 4 and used to calculate the values in Figure 5, a parasitoid is more likely to find at least one host on a gall with more hosts to find, as is seen in column two of Table 5, but the proportion of available hosts found is lower when the number of hosts is higher, as in seen in column three.

CALCULATIONS

An annotated Turbo Basic program that calculates the best rate for Weis' (1983) observed distribution is included as an appendix. Algebraic details are given in Green (2006). The calculations are numerical, and are only approximate. The model is for continuous time, but the calculations are done for discrete time. A unit interval is broken into 400 intervals. Unlike systematic search, for which a forager can reach the end of a patch, random search never exhausts a patch completely. To use dynamic programming for random search, I choose some time (greater than one, the time that it would take to search the patch completely with systematic search and searching rate of one, which I use for both systematic and random search), which I treat as the end of the patch, and move backward toward the beginning of the patch. Here I treat $t = 3$ as the end of the patch (actually, I start at $1199 = 3 \cdot 400 - 1$, which is one step before the end. At time $t = 3$, proportion $1 - \exp(-3) \approx 0.95$ of a patch will have been searched, and about 95% of the prey or hosts should have been discovered.

DISCUSSION

Oaten's (1977b) model differs from earlier work on optimal foraging because it offers a place for the distribution of prey. The theoretical importance of this was made clear by Iwasa et al. (1981) who showed that the form of the optimal patch-leaving rule depends on the distribution of prey numbers in patches.

Green (1980, 1987) provided a quantitative treatment that permitted a comparison of the performance of several patch-leaving rules for each of a number of different prey distributions. Green (1987) considered systematic search as well as random search, which had usually been assumed (for example, by Murdoch and Oaten 1975; and by Iwasa et al. 1981).

The examples chosen for theoretical treatment were familiar and mathematically convenient. The beta-binomial distribution assumed by Green (1980) is convenient for Bayesian analysis, as is the negative binomial distribution treated by Murdoch and Oaten (1975), by Iwasa et al. (1981) and by others. The binomial and Poisson distributions, also treated by Iwasa et al., are familiar and tractable.

However, prey or host distributions found in nature—for example, by Weis (1983)—or distributions used in experiments—for example, by Lima (1984)—are not the ones that

theorists choose for mathematical convenience. Recently, I showed how to find optimal patch-leaving rules for any prey or host distribution as long as whatever prey or hosts are in a patch are located at random there, and (1) search is systematic (for either discrete time or continuous time), or (2) search is random for continuous time (Green 2006).

In my 2006 paper, I used as an example Lima's (1984) experiment on downy woodpeckers searching for "prey" (bits of sunflower seeds) hidden in some (or no) holes drilled in artificial "trees" (wooden dowels). Holes were opened one-at-a-time and examined for food. The birds searched systematically. This example illustrates systematic search and discrete time. Continuous time could be approximated by using the same method with small time increments.

In this paper I assume that Weis' parasitoids search randomly, and I approximate continuous time by considering small increments of time. While the purpose of this paper is to find the optimal patch-leaving rule for a parasitoid facing the host distribution described by Weis (1983) and given here in Table 1, it might better be thought of as an illustration of a method of calculation given in a Turbo Basic program included in the Appendix.

Unfortunately, my analysis does not fit Weis' observations perfectly. (1) It is not clear whether parasitoid foraging is systematic, random, or something else. However, (2) it is quite clear that search is not continuous. Search consists of inserting the ovipositor into a gall. On each insertion, a host is found or not. A small number of insertions are made and a host will be found only if one happens to be in range of the point of insertion. Some hosts may not be in range of the ovipositor for any point where it can be inserted.

If one wanted an accurate theoretical treatment of the observations made by Weis (1983), it would be necessary to modify the theory to represent the search of the parasitoids for their hosts more realistically. This would require information about how the oviposition attempts are distributed around the gall, and how the hosts are (or might be) distributed inside the galls. One question is how great a cross-section to the hosts occupy, or, perhaps equivalently, what is the probability that a particular insertion of the ovipositor will encounter a particular host. Perhaps this can be inferred from the data.

REFERENCES

- Alphen, J. J. van and Vet, L. E. M. 1986. An evolutionary approach to host finding and selection. In: J. Waage and D. Greathead (eds.), *Insect Parasitoids: 13th Symposium of the Royal Entomological Society of London*, pp. 23-61. Academic Press, London.
- CSIRO. 1991. *The Insects of Australia: A Textbook for Students and Research Workers*. Cornell University Press, Ithaca, New York.

- Gibb, J. A. 1962. L. Tinbergen's hypothesis on the role of specific search images. *Ibis* 104:106-111.
- Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theoretical Population Biology* 18:244-256.
- Green, R. F. 1987. Stochastic models of optimal foraging. In: Kamil, A. C., Krebs, J. R. and Pulliam, H. R. (eds.), *Foraging Behavior*, pp. 273-302. Plenum Press, New York.
- Green, R. F. 1988. Optimal foraging for patchily distributed prey: random search. Technical Report 88-2, Department of Mathematics and Statistics, University of Minnesota Duluth.
- Green, R. F. 2006. A simpler, more general method of finding the optimal foraging strategy in Bayesian birds. *Oikos* 112:274-284.
- Hassell, M. P., and May, R. M. 1974. Aggregation in predators and insect parasites and its effect on stability. *Journal of Animal Ecology* 43:567-594.
- Iwasa, Y., Higashi, M., and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist* 117:710-723.
- Krebs, J. R. 1973. Behavioral aspects of predation. In: P. P. D. Bateson and P. H. Klopfer (eds.), *Perspectives in Ethology*, pp. 23-63. Blackwell, Oxford.
- Lima, S. L. 1984. Downy woodpecker foraging behavior: efficient sampling in a simple stochastic environment. *Ecology* 65:166-174.
- Murdoch, W. W., and Oaten, A. 1975. Predation and population stability. *Advanced in Ecological Research* 9:1-123.
- Oaten, A. 1977a. Transit-time and density-dependent predation on patchily distributed prey. *American Naturalist* 111:1061-1075.
- Oaten, A. 1977b. Optimal foraging in patches: a case for stochasticity. *Theoretical Population Biology* 12:263-285.
- Rogers, D. 1972. Random search and insect population models. *Journal of Animal Ecology* 41:369-383.
- Root, R. B., and Cappuccino, N. 1992. Patterns in population change and the organization of the insect community associated with goldenrod. *Ecological Monographs* 62(3):393-420.

Tontes, E. M. G., Habeck, D. H., and Slansky, F., Jr. 1994. Phytophagous insects associated with goldenrods (*Solidago* spp.) in Gainesville, Florida. *Florida Entomologist* 77(2):209-221.

Waage, J. K. 1979. Foraging for patchily distributed hosts by the parasitoid, *Nemeritis canescens*. *Journal of Animal Ecology* 48:353-371.

Weis, A. E. 1982a. Use of symbiotic fungus by the gall maker *Asteromyia carbonifera* to inhibit attack by the parasitoid *Torymus capite*. *Ecology* 63(5):1602-1605.

Weis, A. E. 1982b. Resource utilization patterns in a community of gall-attacking parasitoids. *Environmental Entomology* 11(4):809-815.

Weis, A. E. 1983. Patterns of parasitism by *Torymus capite* on hosts distributed in small patches. *Journal of Animal Ecology* 52(3):867-877.

APPENDIX

Here is an annotated program that calculates the best rate of parasitizing hosts for Weis' (1983 data. The theoretical ideas and the notation are found in Green (2006), but some of the arguments of the functions are suppressed in the program.

The travel time, τ , is given as t_0 in line 30, multiplied by 400, since the patch is broken up into units of size $1/400$. Since search is random, the chance of finding a particular host in the next short interval of size $1/400$ is as given in line 60, and the probability of not finding that host is given in line 50. The distribution, $f(y)$, of the number of hosts, y , in a patch for Weis' observations is given in lines 100-130. The logarithms of factorials are calculated in lines 200-230. These are used to calculate combinations in line 730.

Rates of finding hosts, C , are guessed, and the rules that they "try to achieve" are calculated inside the C -loop from line 250 to line 1200. The loop in this program considers only values of C very close to the optimum. In fact, one calculates the rates achieved by rules that try to achieve a wider variety of rates, and eventually narrow in on the best rate. In this example, the best rule is very close to 1.68, which equals 400 times the starting value, $C = .0042$.

For each value of C , the decisions must be determined at all times, t , and for all possible number of hosts, x , found by that time. The t loop goes from lines 400 to line 1000. The times, t , begin at the "end" of the patch, corresponding to $t = 3$. I start one step before the end, at $t = 1199$, which is one unit below $400 \cdot 3$, and work backward toward the beginning.

For each t there is an x loop, from line 450 to line 990, where x ranges over all the possible numbers of host in a patch, from 1 to 4. At each point, (t,x) , it is necessary to determine whether the forager should remain in the patch or not [$d(x) = 0$, as in line 950 if the forager should leave the patch, or $d(x) = 1$, as in line 960, if the forager should remain—in the program, the dependence on time, t , is suppressed for notational convenience.]

It is also necessary at each point to calculate the expected gain $G(t,x)$ and expected time $S(t,x)$ *from that point on in the patch*, given that the forager uses the strategy that has been discovered by working backward. [In fact, these values also depend on C , but it is tedious to include all the arguments all the time.] The values for $G(t,x)$ and $S(t,x)$, called $g(x)$, and $s(x)$, respectively in the program, are found in lines 970 and 980, using the decision function, $d(x)$, and the expected gain and time, $g(t,x)$ and $s(t,x)$, respectively, called $g(x)$ and $s(x)$ in the program, which are the expected gain and expected time from point (t,x) on, *assuming that the forager decides to continue from point (t,x)* . The decision whether to continue is determined by the inequality in line 960, which corresponds to equation (6) in Green (2006).

When the expectations, $G(t+1,x)$ and $S(t+1,x)$ have been calculated, the new values of $g(t,x)$ and $s(t,x)$ are calculated in lines 930 and 940. These correspond to equations (14)

and (15) in Green (2006), but the summation is over only three terms, corresponding to finding no hosts, one host or two hosts.

The probabilities for finding zero, one or two hosts, (r_0 , r_1 , and r_2) respectively, are given in lines 900, 910 and 920, respectively. These probabilities are given in equation (17) in Green (2006). These probabilities are calculated for each t and x by iterating over all the values y , for the number of hosts in a patch. The y loop goes from lines 700-840, but additional terms have to be added for the case in which $x = y$, which is in lines 620-640. The y loop contains the calculation of conditional probabilities using Bayes' rule. Line 730 calculates a , which is $p(x|y)$, given by equation (18) in Green (2006). The joint distribution of x and y , namely $p(x,y)$ is the product, $f(y)*a$, seen in lines 790-810 and 830. These products are added (through the y loop) to get the denominator, $d1$, for the conditional probabilities, called r_0 , r_1 and r_2 , of finding 0, 1 or 2 hosts, respectively, in the next short interval after point (t,x) . The numerators of r_0 , r_1 and r_2 are calculated in lines 800, multiplying the product, $f(y)*a$, by b_0 , b_1 and b_2 , the probabilities of finding 0, 1 and 2 hosts, respectively, in the next short interval, given that $y - x$ hosts remain to be found. These probabilities, b_0 , b_1 and b_2 , which are calculated in lines 760-780, correspond to equation (16) in Green (2006).

The sums over y have to be initialized for each value of x , and this is done in lines 500-540.

```

5 Print "Weiscopy"
10 Print "Random calculations for Weis"
20 n = 4
30 t0 = 0.03 * 400
40 Dim d(n), g1(n), s1(n), g(n + 1), s(n + 1), f(n), l(n)
50 q2 = Exp(-1 / 400)
60 p2 = 1 - q2

100 f(1) = 25 / 80
110 f(2) = 36 / 80
120 f(3) = 15 / 80
130 f(4) = 4 / 80

200 l(0) = 0
210 For i = 1 To n
220 l(i) = l(i - 1) + Log(i)
230 Next i

250 For c = 0.0042 To 0.00422 Step 0.000001

260 g(n + 1) = 0
270 s(n + 1) = 0

300 For i = 0 To n
310 g(i) = 0
320 s(i) = 0
330 Next i

400 For t = 1199 To 0 Step -1
450 For x = 0 To n - 1

```

```

500 r0 = 0
510 r1 = 0
520 r2 = 0
530 n1 = 0
540 n2 = 0

600 p1 = 1 - Exp(-t / 400)
610 q1 = 1 - p1
620 a = p1 ^ x
630 d1 = f(x) * a
640 n0 = f(x) * a

700 For y = x + 1 To n
730 a = Exp(l(y) - l(x) - l(y - x)) * p1 ^ x * q1 ^ (y - x)
760 b0 = q2 ^ (y - x)
770 b1 = (y - x) * p2 * q2 ^ (y - x - 1)
780 b2 = (y - x) * (y - x - 1) * 0.5 * p2 * p2 * q2 ^ (y - x - 2)
790 d1 = d1 + f(y) * a
800 n0 = n0 + f(y) * a * b0
810 n1 = n1 + f(y) * a * b1
820 If y = x + 1 Then GoTo 840
830 n2 = n2 + f(y) * a * b2
840 Next y

850 If d1 = 0 Then GoTo 930

900 r0 = n0 / d1
910 r1 = n1 / d1
920 r2 = n2 / d1
930 g1(x) = r0 * g(x) + r1 * (1 + g(x + 1)) + r2 * (2 + g(x + 2))
940 s1(x) = 1 + r0 * s(x) + r1 * s(x + 1) + r2 * s(x + 2)
950 d(x) = 0
960 If g1(x) / s1(x) > c Then Let d(x) = 1
970 g(x) = d(x) * g1(x)
980 s(x) = d(x) * s1(x)
990 Next x
1000 Next t

1100 Print using; "###.##### "; c; g(0); s(0); g(0) / (t0 + s(0));
400 *
g(0) / (t0 + s(0))

1200 Next c

```