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Foraging behavior has attracted much attention in the last two decades, and many efforts have been made to use theoretical models to understand it. Most of these models are intended to apply to predators, which are usually assumed to maximize the rate of finding prey or the net rate of energy intake while foraging [see Stephens and Krebs (1986) for a recent review]. Under this assumption a forager that searches for prey which are distributed in patches should remain in a patch until the the patch is depleted, or until the forager decides that the patch is not a good one. An optimally foraging predator has no reason to ignore suitable prey or to leave a patch in which there is a good chance of finding enough suitable prey.

Insect parasitoids constitute a special life-form in which the adult (imago) stage is a free-living organism, but the larva is a parasite of another insect. This life style, which is common among Hymenoptera and Diptera, is generally treated by ecologists as a special case of predation: the free-living imago consumes its "prey" indirectly through its parasitic larva (Hassell 1978). Despite some excellent work on the foraging behavior of parasitoids (*e.g.,* Waage 1978, 1979, 1983), there is no special foraging theory for parasitoids. Yet, there is a special theory of optimal oviposition for parasitoids (*e.g.,* Godfray 1987), which deals with the optimal number and sex of eggs laid in various hosts.

The Nicholson-Bailey model (Nicholson and Bailey 1935) is widely used to describe host-parasitoid population dynamics (Hassell 1978). This model and its various descendants assume that reproductive success of parasitoids is directly proportional to the number of hosts encountered. In fact, it has been argued (Hassell and Waage 1984) that host-parasitoid systems are particularly convenient to model because it is easy to calculate the reproductive success of parasitoids by counting the number of hosts encountered. Thus, the number of hosts attacked is assumed to be equal to the number encountered and to be proportional to host density.

We suggest that foraging parasitoids are subject to different constraints than real predators are. The most important of these constraints is that the pre-imago stages of parasitoids are subject to attack by hyperparasitoids. A result of this constraint is that the reproductive success of a parasitoid need not be proportional to the number of suitable hosts it is able to locate. We will argue that in the presence of hyperparasitism, it may pay the parasitoid to ignore some suitable hosts in one patch and move to another patch in order to reduce the risk to its offspring of being attacked by hyperparasitoids.

We will illustrate our argument by describing an aphid-parasitoid-hyperparasitoid system in which the aphids are clumped in colonies, and hyperparasitism often reaches high levels. We will show that the optimum number of hosts for a parasitoid to attack may be far fewer than the total number of aphids in the attacked colony. The optimum number of hosts to infect should depend not only on the number of aphids per colony, but also on (a) the number of hyperparasitoids that are expected to visit the aphid colony, (b) the cost to the parasitoid of traveling to the next aphid colony, and (c) the expected number of aphids which are already infected by conspecific females. We will show that the optimal foraging strategy of a parasitoid is influenced by two different selective factors, namely, the host distribution and density on one hand and the hyperparasitoid density and foraging tactics on the other.

THE APHID-PARASITOID-HYPERPARASITOID SYSTEM

The cabbage aphid, *Brevicoryne brassicae,* is a common aphid that attacks crucifer plants in temperate climates. The species is gregarious, forming colonies of up to several thousand individuals. As a serious pest of crucifer crops, its life history has been studied in detail (George 1957, Hafez 1961). On wild crucifers, colonies are found mainly on flower heads (Markkula 1951, Ayal pers. obs.). The distribution of aphids is clumped at two levels: (a) the number of aphids within colonies, and (b) the number of colonies within a plant (or a plant patch). Colonies consist of adult females and their offspring (nymphs at different nymph-stages).

Diaeretiella rapae, an Aphidiid wasp, is the major parasitoid of *B. brassicae.* The adult female wasp is attracted to the crucifer plant by the plant's smell (Reed *et al.* 1970). When on a plant, she moves over its surface searching for aphid colonies by using her antennae to detect chemical and tactile stimuli, including aphid honeydew (Ayal 1987). Aphids are recognized and accepted as hosts only as a result of direct contact and examination with the antennae. The time required to handle a single aphid is short and lasts less than 15 seconds, but each attack effort is followed by intensive grooming which may last 1-3 minutes. The female parasitoids attack only those aphids which are near the perimeter of the colony. The egg complement of a parasitoid is 200-400 (Hafez 1961), and females have been observed parasitizing over 50 aphids within a single colony in a single bout (Ayal, unpublished data).

Alloxysta victrix, a Cynipid wasp, is the main hyperparasitoid of *Diaeretiella,* and its life history and basic foraging behavior have been described by Gutierrez (1970a-d), Gutierrez and van den Bosch (1970a-b) and Berkeley (1989). The female hyperparasitoid detects whether or not an aphid has been parasitized by inserting the ovipositor with its special sensilae at the tip into the body of the aphid. Unlike *Diaeretiella, Alloxysta* moves freely over all the aphids within the colony and examines an aphid for a parasite by riding on its back. It takes *Alloxysta* approximately 30 seconds to check an aphid for a parasitoid larva; if the results are negative, the hyperparasitoid moves to another aphid. Detecting an infected aphid leads to intensive search for the parasitoid larva, often by taking the ovipositor out and inserting it in a new point until it hits the parasitoid larva. This process lasts 5-15 minutes. Hyperparasitoids which do not detect infected aphids in a colony leave it after only a few aphids have been checked. Locating a parasitized aphid increases sharply the number of aphids inspected before leaving (Ayal pers. obs.). Rates of hyperparasitism in the field vary during the season from 10%

early in the season to as much as 60-80% or more later in the season (Hafez 1961). Hyperparasitism is often blamed for the ineffectiveness of parasitoids in controlling aphids and other pests in agroecosystems (Hafez 1961, DeBach 1964).

THE MODEL AND ITS ASSUMPTIONS

We want to find the number of aphids that a parasitoid, which is subject to attack by hyperparasitoids, should infect in a colony of aphids in order to maximize its lifetime reproductive success. Maximum reproductive success is achieved by maximizing the number of adults eclosing from all the eggs that the female parasitoid lays during her lifetime. We analyze a simple model which contains the following assumptions:

(1) The number of aphids per colony is a fixed number, N.

(2) The number of eggs laid by a parasitoid that visits a colony of aphids is c (we ignore superparasitism).

(3) After the aphid colony has been visited by a parasitoid, it is visited by hyperparasitoids which search for infected aphids. The number of hyperparasitoid visits to a given aphid colony is a random variable having a Poisson distribution with mean $= H$.

(4) The hyperparasitoids that visit an aphid colony search independently of each other.

(5) Hyperparasitoids search systematically within aphid colonies (that is, during a visit they do not re-examine aphids that they have already examined during that visit), and they use a fixed "giving-up-time rule" in which they leave a colony when G consecutive aphids searched do not contain a parasitoid larva.

(6) The cost for a parasitoid to move from the colony it is searching to the next one is τ, expressed in terms of units of the average time (or effort) that it takes the para-

sitoid to find and handle an aphid within a colony.

Using assumptions (1) - (5) and particular choices of the parameters N, H, and G, we will calculate $s(c)$, the expected number of parasitoid offspring in an aphid colony that will escape attack by hyperparasitoids and survive to eclosion, as a function of the number of aphids attacked, c. We will look at these calculations in two ways.

(a) We will find the number of aphids to be attacked per colony, c, that maximizes the expected number of parasitoids surviving to eclosion in that colony, $s(c)$.

(b) We will find the value of c that maximizes the parasitoid's long-term average rate of producing surviving offspring, given by

$$R = s(c)/[c + \tau] \tag{1}$$

First, we will argue that R is a reasonable proxy for parasitoid fitness. If a parasitoid is unlikely to find more than one aphid colony in her lifetime, then in any colony that she does find, the optimal number of aphids to infect is the number c that maximizes $s(c)$. On the other hand, if a parasitoid is able to find many aphid colonies in her lifetime, but lack of time limits her reproductive success, then she should maximize the rate of reproduction. If time is measured in terms of the time spent to find, attack and recover from attacking each aphid, and τ is the average time spent finding another aphid colony, measured in the same time units, then the number of aphids to infect per colony that maximizes the long-term average rate of reproduction is the number c that maximizes R in equation (1) above.

This idea is the basis of Charnov's (1976) "marginal value theorem" for optimally foraging predators. While Charnov's theorem was given for a deterministic model, he asserted, quite correctly, that his result could be extended to a stochastic model, but he did not make it clear exactly how this was to be done. There has been some dispute (Templeton and Lawlor 1981) over what it is that an optimal forager should maximize in a stochastic model, but it now seems quite clear that if a forager visits many patches then, by the law of large numbers, the maximum long-term average rate of finding prey (or producing offspring) is found by maximizing R (Gilliam *et al.* 1982; Turelli *et al.* 1982). If a small number of colonies are visited, then it is difficult or impossible to express simply what an optimal forager/ovipositor should maximize.

RESULTS

In order to simplify the execution of the model simulation and the interpretation of its results, we deal with one variable at a time, holding all others fixed. In each case we are interested in the form of $s(c)$, the expected number of parasitoids successfully eclosing, as a function of c, the number of aphids infected by the parasitoid per aphid colony. The form of the function, $s(c)$, is of critical importance, whether we are interested in the clutch size, c, that maximizes $s(c)$ itself, or the clutch size that maximizes R.

Two parameters of the model involve the aphid hosts: the number of aphids per colony, N, and the travel time between colonies, τ, which will be small when there are many aphid colonies (*i.e.,* τ is negatively correlated with aphid density in the habitat). Two parameters involve the hyperparasitoids: the average number of hyperparasitoid visits per infected aphid colony, H, which is a measure of overall hyperparasitoid density, and G, the fixed giving-up time which each hyperparasitoid is assumed to use to decide when to leave an aphid colony. There is a wide range of values that the parameters N, H and τ may assume, but we doubt that G is likely to vary widely. We concentrate on the effects of varying N and H and τ as seen when $s(c)$ is plotted against c.

The effect of hyperparasitoid numbers

Fig. 1 shows the effect of different average numbers of hyperparasitoid visits, H, to each aphid colony, assuming a "giving-up time," $G = 5$, with the number of aphids per colony set equal to $N = 100$. The average number of parasitoids eclosing per aphid colony, $s(c)$, is plotted against parasitoid clutch size, c, for six different hyperparasitoid densities (see Appendix for details of how $s(c)$ is calculated). The straight line represents the case in which there are no hyperparasitoids ($H = 0$) and all eggs eclose as adults. However, an average of one hyperparasitoid visit per aphid colony ($H = 1$) dramatically reduces the number of eclosing adults. After a certain number of parasitoid eggs have been laid (about 45), any additional eggs laid will reduce the expected number of eclosing adults, and only if many more eggs are laid does the number of eclosing adults increase slightly.

[Put Fig. 1 about here]

This effect of hyperparasitism becomes more pronounced as the average number of hyperparasitoid visits to a colony increases. Thus, when the expected number of hyperparasitoid visits is greater than two, the maximum number of adults eclosing is reached when the number of eggs laid is less than 40 (*i.e.*, 60% of the aphids in the colony should be bypassed). Any additional eggs laid would result in a reduction in the expected number of parasitoid adults eclosing.

The effect of aphid colony size

Fig. 2 shows the effect of varying aphid colony size $N = 25$, 50 and 100, assuming that foraging hyperparasitoids use the giving-up-time rule with $G = 5$. These figures exhibit the same qualitative results as Fig. 1, but the optimal proportion of aphids to infect per colony is not constant: in larger colonies the proportion of infected aphids which maximizes the parasitoid adult output is slightly larger than the proportion in smaller colonies. This result is due, in part, to the assumption of a fixed giving-up time for the hyperparasitoids, which means that for smaller aphid colonies a larger proportion of aphids is screened by each hyperparasitoid. That is, the same hyperparasitoid density will tend to have a greater impact on parasitoids in smaller patches, as long as the same foraging strategy is used by hyperparasitoids in small as in large aphid colonies. It is possible that the hyperparasitoid foraging strategy changes with changes in aphid colony size, but we have not considered this here.

[Put Fig. 2 about here]

The effect of travel time

When $s(c)$ is plotted against c for a given set of parameters, N, H and G, the maximum rate $R = s(c)/(c + \tau)$ may be found for a given travel time between colonies, τ, by plotting the tangent line from the point $(-\tau, 0)$ to the set of $s(c)$ points. Fig. 3a presents such a plot for three different values of travel time ($\tau = 10, 20$ and 40) for hyperparasitoid density, $H = 1$. From this figure one can see that the optimal number of eggs, $c*$, that a parasitoid should lay in an aphid colony is lower than the number which gives the highest expected number of eclosing adults per colony. One can also see that the value of $c*$ decreases as the cost of travel time decreases.

[Put Fig. 3 about here]

Fig. 3b shows that for a fixed travel time, but different hyperparasitoid densities, the optimal clutch size, $c*$, is lower for higher hyperparasitoid densities. These results are summarized in Table 1, which presents the optimal number of aphids a parasitoid should attack in a single colony, $c*$, and the expected number of adult parasitoids emerging from them, $s(c*)$, for five different levels of hyperparasitoid density, five different values of travel time, and three colony sizes. It may be seen from this table that the relative differences in reproductive success for different hyperparasitoid densities are slightly greater when travel time is longer. In the limiting case in which travel time is infinite, all parasitoid reproduction would take place in a single aphid colony, and the optimal clutch size would be the value $c*$ that maximizes $s(c*)$.

[Put Table 1 about here]

The effect of visits by several parasitoids to the same aphid colony

In our model we have assumed that an aphid colony is visited by only one parasitoid, and that all parasitoid eggs laid there are hers. If an aphid colony contains exactly c infected aphids, all attacked by the same parasitoid, then her gain by attacking another aphid is the difference $s(c+1) - s(c)$. If the parasitoid seeks to maximize the expected number of her offspring eclosing from a patch she should lay another egg if $s(c+1) - s(c)$ is greater than zero, but if she seeks to maximize the rate of reproduction she should lay another egg if the difference $s(c+1) - s(c)$ exceeds the maximum reproductive rate, R.

In general, an optimally ovipositing parasitoid must weigh the gain due to laying an additional egg against the loss due to increasing the risk to eggs she has already laid in the colony. If a parasitoid visits an aphid colony in which some aphids have been infected by other parasitoids, she should make her oviposition decisions based on the gain due to laying an egg in addition to all the eggs already laid in the colony by herself and other parasitoids, and the loss due to increasing the risk to the eggs that she has laid there. If all infected aphids in a colony are equally likely to produce eclosing adult parasitoids, then in an aphid colony with c infected aphids, e of which have been attacked by a particular parasitoid, the expected number of her offspring that will survive to eclosion in the colony is given by

$$s(e,c) = es(c)/c. \tag{2}$$

The gain due to laying another egg is given by

$$d(e,c) = s(e+1, c+1) - s(e,c). \tag{3}$$

The decision whether or not to attack an additional host in a colony depends on the value of $d(e, c)$. A parasitoid which seeks to maximize the number of offspring should attack another host as long as $d(e, c)$ is positive, while a parasitoid seeking to maximize the rate of reproduction should attack another host if $d(e, c)$ is greater than the maximum achievable rate, R.

The values of the differences $d(e, c)$ can be viewed as the slope of line segments connecting points whose coordinates are $(e, s(e, c))$ and $(e + 1, s(e + 1, c + 1))$. These line segments can be connected in a continuous (but not smooth) curve for fixed values of $o = c - e$, which is the number of aphids in a colony that are infected by parasitoids other than the one making the decision. A series of such curves is illustrated in Fig. 4 for the case: $N = 50$, $H = 3$, $G = 5$. In this case, for small or moderate values of o, it can be seen that as the value of o increases, the number of eggs e a particular parasitoid should lay decreases. Yet, the total number of aphids infected in a colony, c, increases as o increases. Thus, in the case that $o = 10$ aphids infected by other parasitoids it can be seen that a parasitoid seeking to maximize her per-colony success should lay $e = 9$ additional eggs, resulting in a total of $c = 19$ eggs laid in the colony. On the other hand, a parasitoid should attack 14 aphids if she is the only one to visit a colony.

[Put Fig. 4 about here]

DISCUSSION

The main point that we want to make is that the foraging goals of predators and parasitoids are different. Optimal foraging theory often includes the assumption that predators maximize the long-term average rate of finding prey, or the long-term net rate of energy gain (Stephens and Krebs 1986). There is some question about this, since it might be best to optimize over a shorter amount of time. It is far from clear that the fitness of a predator is linearly related to the rate of finding prey or gaining energy, as is implied by the Lotka-Volterra predator-prey model, but it is reasonable to assume that predator fitness is at least a monotonic function of the rate of energy intake.

Our model suggests that when a risk of hyperparasitism exists, then depending on the magnitude of this risk, parasitoids should neglect readily available hosts. There is nothing that the parasitoids' larvae can do to avoid attack by hyperparasitoids, but it is possible that ovipositing parasitoids can distribute their eggs in such a way as to decrease the loss due to hyperparasitoids. A key point in our model is the assumption that foraging hyperparasitoids use a strategy that tends to concentrate their attacks in aphid colonies that have suffered a higher rate of infection by parasitoids.

It has been asserted (Hassell 1978) that host-parasitoid models have an advantage over predator-prey models because the rate of attack of hosts by parasitoids is directly proportional to the growth rate of the parasitoid population. We point out that this need not be true if parasitoids are subject to attack by hyperparasitoids. On the contrary, we suggest that parasitoids should maximize the total number of offspring successfully eclosing, and that in some cases this will be achieved by judiciously restricting the number of hosts infected in each colony (or host patch). This restriction in the number of hosts attacked per colony will increase the proportion of time spent traveling between colonies and will reduce the total number of hosts attacked by each parasitoid.

The main result of our paper, illustrated in Fig. 1, is that if parasitoid larvae are subject to attack by efficiently foraging hyperparasitoids, then the optimal number of hosts to attack per colony may be substantially smaller than the number of hosts present in the colony. If the hyperparasitoid risk is high enough, then a parasitoid which has laid a certain number of eggs in a host colony may actually decrease the expected number of her offspring eclosing from that colony by laying another egg. If the time available to lay eggs, or the number of eggs available for laying, is small, than the optimal number of hosts attacked per colony (that is, the number that maximizes the parasitoids' lifetime reproductive success) may be less than the number that maximizes the average number of offspring eclosing per colony. The optimal number of hosts to attack per colony thus may depend on travel time, as illustrated in Fig. 3a, but this dependence seems quite weak for our model. Similarly, the optimal number of hosts to attack depends on the level of risk due to hyperparasitoid attack, as illustrated in Fig. 3b, but the effect of quite large differences in hyperparasitoid risk on the optimal clutch size seems quite small.

Our model relies on a number of particular assumptions for which there is little evidence. We do know that aphid parasitoids are sometimes subject to intense attack by hyperparasitoids (Hafez 1961, and see Sullivan 1987 for a review), that parasitoids concentrate their search where there is evidence that there are more, or larger, aphid colonies (Ayal 1987 and pers. obs.), and that hyperparasitoids seem to use a foraging behavior that would tend to concentrate their attack in aphid colonies which have suffered more infection by parasitoids (Ayal, pers. obs.). However, it is not known what foraging tactics hyperparasitoids actually use. We have assumed systematic search and a fixed giving-up-time rule because they are biologically plausible and mathematically convenient, but we are not sure that these assumptions are biologically correct. There has been a lot of theoretical work on the fixed giving-up-time rule, beginning with Krebs *et al.* (1974), who believed that it provided a mechanism for foragers to satisfy the "marginal value theorem" (Charnov 1976) and thus produce optimal foraging. Others have treated the giving-up-time rule theoretically, but generally with the assumption that foraging is random within patches (Murdoch and Oaten 1975, Iwasa *et al.* 1981). Green (1984) treated the giving-up-time rule and systematic search, and the method introduced there is used to do the calculations described in the Appendix of this paper.

It is not known what parasitoids and hyperparasitoids "know," and how they can adjust their behavior to changing conditions. The size and number of aphid colonies certainly change over a season (Hafez 1961), as do the numbers of parasitoids and hyperparasitoids. Our Fig. 2 shows that the optimal number of hosts to attack per colony depends on colony size, but it is not clear how sensitive parasitoids are to colony size, even though it is known that they spend longer in colonies from which they detect more honeydew (Bouchard and Cloutier 1984). As the aphid population increases, both the size and number of aphid colonies increase. While increasing colony size increases the optimal parasitoid clutch size, increasing the number of colonies decreases the time, τ, necessary to find another colony, and this tends to decrease optimal parasitoid clutch size. We think that increasing parasitoid numbers should increase the total number of aphids attacked per colony, but should decrease the optimal number of aphids for each parasitoid to attack per colony. Increasing numbers of hyperparasitoids tend to decrease the optimal number of aphids for a parasitoid to attack per colony. All these changes are important to foraging parasitoids, but it is not clear to which of these changes, if any, they are sensitive.

The main conclusion of our model is that parasitoids faced with the risk to their offspring of attack by hyperparasitoids should sometimes limit the number of hosts they attack in each patch and quickly move in search of another patch. This conclusion may be compared with the idea of "spreading the risk" (den Boer 1968). As in our model for parasitoids seeking to avoid hyperparasitism, animals that "spread the risk" should limit their reproduction within each patch, try to visit many patches, and sometimes reduce the total number of eggs laid in order to lay them in more patches. There is evidence that parasitoids do readily abandon host patches and disperse in search of other patches (Strong 1989).

While our model predicts some of the same behavior as does "spreading the risk," the evolutionary mechanisms underlying the two are quite different. Our model is based on the conventional assumption that selection favors behavior that maximizes the reproductive rate. Our model does differ from conventional host-parasitoid models in that we measure reproductive success by the number of adult offspring eclosing from hosts rather than the number of hosts attacked. In our model, a parasitoid should sometimes bypass suitable hosts because attacking them would increase the risk to other offspring of attack by hyperparasitoids. A parasitoid should bypass suitable hosts because to attack them would reduce her reproductive rate. "Spreading the risk," on the other hand, is based on the idea that selection does not favor maximizing the reproductive rate, rather it favors maximizing the chance of leaving some surviving offspring. An animal that "spreads the risk" would sometimes leave a patch and move on to another even though such a move would lower the expected reproductive success of that animal. If our model of parasitoid-hyperparasitoid interaction is correct, then parasitoids should sometimes restrict reproduction within patches whether they want to "spread the risk" or simply to maximize the rate of reproduction.

SUMMARY

Foraging theory treats insect parasitoids as real predators. We argue that if the juvenile stages of a parasitoid are subject to attack by hyperparasitoids, then adult parasitoids should not maximize the number of hosts attacked, as currently assumed, but rather, they should maximize their lifetime production of eclosing adult offspring. We illustrate our argument by using a host-parasitoid-hyperparasitoid system in which the hosts are aphids which aggregate in colonies and the hyperparasitoids forage for parasitoids using a "giving-up-time" rule. We use a simulation model to investigate how many hosts the parasitoid should infect in a colony of N aphids in order to maximize the number of adults eclosing. We consider three different variables and deal with them one at a time: (1) N = the number of aphids in a colony, (2) H = the average number of hyperparasitoids visiting each colony, and (3) τ = the parasitoid travel time between colonies. We show that the optimal number of aphids to infect in a colony is sometimes

much less than the total number of aphids available. Hence, parasitoids should sometimes ignore and bypass suitable hosts. The optimal number of aphids to infect within a colony decreases with a decrease in the aphid colony size, an increase in the average number of hyperparasitoid visits, and a decrease of travel time between aphid colonies. If an aphid colony is infected by several parasitoids, the optimal number of aphids for each parasitoid to attack is not the same as the optimal number would be if she were the only parasitoid to visit the colony. We find the optimal number of aphids for a new parasitoid visitor to a colony to attack given that a particular number of aphids have already been infected by other parasitoids. For lightly infected colonies a new parasitoid visitor should attack fewer aphids than if she were the only visitor to the colony, but the total number of aphids infected would be higher than if she were the only visitor.

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LITERATURE CITED

Ayal, Y. 1987. The foraging strategy of *Diaeretiella rapae* McIntosh I. The concept of the elementary unit of foraging. J. Anim. Ecol. 56:1057-1068.

Berkeley, E. 1989. Foraging behaviour and host location by the hyperparasitoid *Alloxysta victrix* Westwood. Ph. D. Dissertation, University of London.

Bouchard, Y., and C. Cloutier. 1984. Honeydew as a source of host-searching kairomones for the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae). Can. J. Zool. 62:1513-1520.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Biol. 18:244-256.

DeBach, P. 1964. Biological control by natural enemies. Cambridge University Press, Cambridge UK.

den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18:165-194.

George, K. S. 1957. Preliminary investigations on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.). Bull. Entomol. Res. 48:619-629.

Gilliam, J. F., R. F. Green, and N. E. Pearson. 1982. The fallacy of the traffic policeman: a response to Templeton and Lawlor. Am. Nat. 119:875-878.

Godfray, H. C. J. 1987. The evolution of clutch size in parasitic wasps. Am. Nat. 129:221-233.

Green, R. F. 1984. Stopping rules for optimal foragers. Am. Nat. 123:30-43.

Gutierrez, A. P. 1970a. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae) 3. Host suitability studies. Ann. Entomol. Soc. Am. 63:1485-1491.

Gutierrez, A. P. 1970b. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae) 4. The effect of age of host on host selection. Ann. Entomol. Soc. Am. 63:1491-1494.

Gutierrez, A. P. 1970c. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae) 5. Host selection. Ann. Entomol. Soc. Am. 63:1495-1498.

Gutierrez, A. P. 1970d. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae) 6. Description of sensory structures and a synopsis of host selection and host specifity. Ann. Entomol. Soc. Am. 63:1705-1709.

Gutierrez, A. P., and R. Van den Bosch. 1970a. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae) 1. Review of hyperparasitism and the field ecology of *Charips victrix.* Ann. Entomol. Soc. Am. 63:1355-1360.

Gutierrez, A. P., and R. Van den Bosch. 1970b. Studies on host selection and host specifity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae) 2. The bionomics of *Charips victrix.* Ann. Entomol. Soc. Am. 63: 1360-1365.

Hafez, M. 1961. Seasonal fluctuations in population density of the cabbage aphid *Brevicoryne brassicae* (L.) in the Netherlands, and the role of its parasitoid *Aphidius (Diaeretiella) rapae* (Curtis). Tij. Plant. Nedr. 67:445-548.

Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, NJ.

Hassell, M. P., and J. K. Waage. 1984. Host-parasitoid population interactions. Ann. Rev. Entomol. 29:89-114.

Iwasa, Y., M. Higashi, and N. Yamamura. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. Am. Nat. 117:710-723.

Krebs, J. R., J. C. Ryan, and E. L. Charnov. 1974. Hunting by expectation or optimal foraging? Anim. Behav. 22:953-964.

Markkula, M. 1953. Biologische okologische Unterzuchungen uber die Kohlblattlaus, *Brevicoryne brassicae* L. (Hem.: Aphididae). Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo 15:6-113.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res. 9:2-125.

Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. Part I. Proc. Zool. Soc. London 2:9-65.

Reed, D. P., P. P. Feeny, and R. B. Root. 1970. Habitat selection by the aphid parasite *Diaeretiella rapae* (Hymenoptera: Braconidae) and hyperparasite *Charips brassicae* (Hymenoptera: Cynipidae). Can. Entomol. 102:1567-1578.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton NJ.

Strong, D. R. 1989. Density independence in space and inconsistent temporal relationships for host mortality caused by a fairyfly parasitoid. J. Anim. Ecol. 58:1065-1076.

Sullivan, D. J. 1987. Insect hyperparasitism. Ann. Rev. Entomol. 32:49-70.

Templeton, A. R., and L. R. Lawlor. 1981. The fallacy of the averages in ecological optimization theory. Am. Nat. 117:390-393.

Turelli, M., J. H. Gillespie, and T. W. Schoener. 1982. The fallacy of the fallacy of the averages in ecological optimization theory. Am. Nat. 119:879-884.

Waage, J. K. 1978. Arrestment responses of the parasitoid *Nemeritis canescens* to a contact chemical produced by its host *Plodia interpunctella*. Physiol. Entomol.

3:135-146.

Waage, J. K. 1979. Foraging for patchily-distributed hosts by the parasitoid *Nemeritis canescens*. J. Anim. Ecol. 48:353-371.

Waage, J. K. 1983. Aggregation in field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera: Ichneumonidae). Ecol. Entomol. 8:447-453

APPENDIX

Finding the expected number of eclosing adult parasitoids, $s(c)$,

when their larvae are subject to attack by hyperparasitoids using the giving-up-time rule.

a) First we find the probability distribution of the number of parasitoid larvae attacked in an aphid colony visited by one hyperparasitoid, where

$N =$ the number of aphids per colony,

$c =$ the number of aphids in the colony that contain parasitoid larvae,

$g =$ the giving-up-time that the hyperparasitoid uses. The hyperparasitoid searches the aphid colony systematically (without revisiting aphids already examined), and the colony is abandoned if the hyperparasitoid examines g consecutive aphids which do not contain parasitoid larvae.

Given the values N, c and g, we find the probability, $P(x,t)$ that a hyperparasitoid will leave an aphid colony after having examined exactly t aphids and having found exactly x parasitized aphids. The key idea is to find the number of ways arranging t aphids, x of which contain parasitoid larvae, in such a way that the last g aphids contain no parasitoid larvae, the $t-g$th aphid does contain a parasitoid larva, and for the first $t-g-1$ aphids, there is no run of g consecutive aphids which contain no parasitoid larvae. This idea was used by Green (1984) for a similar problem, but with slightly different notation. If we denote this number of arrangements by $n(x,t)$, we have

$$n(0,g) = 1, \text{and} \tag{A1}$$

$$n(0,t) = 0 \quad \text{for} \quad t \neq g.$$

$$n(1,g+i) = 1 \quad \text{for i = 1,2,\ldots, g} \tag{A2}$$

$$n(1,t) = 0 \quad \text{otherwise.}$$

Now we can iterate, for $x = 2, 3, 4, \ldots, N + g$:

$$n(x,t) = \sum_{i=1}^{g} n(x-1, t-i). \tag{A3}$$

For $t < N$ we will have the values of $n(x,t)$ we want. However, hyperparasitoids which forage systematically should leave an aphid colony in which all aphids have been searched. If we write

$$n'(x,N) = \sum_{t=N}^{N+g} n(x,t) \tag{A4}$$

then we have, for the final time, $t = N$:

$$n(x,N) = n'(x,N).$$

The probability, $P(x,t)$, is then given by

$$P(x,t) = n(x,t) \frac{\binom{c}{x}\binom{N-c}{t-x}}{\binom{N}{t}} \tag{A5}$$

for $t = x + g, x + g + 1, \ldots, x + N - c$. The numerator of (A5) is the number of ways of arranging the N aphids such that a hyperparasitoid would leave after having searched t of them and have found x parasitized larvae, while the denominator is the total number of ways of choosing t out of N aphids.

For a given set of values N, c and g we can obtain the probability that exactly x parasitoid larvae are found by summing the terms found in (5) over time

$$P(x) = \sum_{t=x}^{N} P(x,t) \tag{A6}$$

b) Now for a given set of values N, c and g, the expected number of parasitoid larvae that will be found during a single visit to an aphid colony by one hyperparasitoid is given by

$$E(c) = \sum_{x=1}^{c} xP(x), \tag{A7}$$

and the expected number that will escape equals

$$p(c) = c - E(c).$$

If we assume that parasitized and non-parasitized aphids are searched in random order, then the probability that a given parasitized aphid will be escape detection by a hyperparasitoid is given by

$$q(c) = [c - E(c)]/c. \qquad (A8)$$

If hyperparasitoids do not mark aphids in which they attack parasitoid larvae, and if when several hyperparasitoids visit the same aphid colony they search independently of each other, then the chance that a parasitoid larva will escape attack from v hyperparasitoids will be $q(c)^v$.

If the number of hyperparasitoids that visit a given aphid colony (v) is a random variable having a probability function, $f(v)$, (We use Poisson distribution:

$$f(v) = [exp(-H)H^v]/v! \qquad (A9)$$

where H is the average number of hyperparasitoids that visit each aphid colony.) then the probability that a given parasitoid larva escapes detection is

$$Q(c) = \sum f(v)q(c)^v, \qquad (A10)$$

and the expected number of parasitoids that escape attack is

$$s(c) = cQ(c). \qquad (A11)$$

Table 1. Optimum number of eggs laid ($c*$) and the expected number of eclosing adults [$s(c*)$] per colony, for different aphid colony sizes (N), different hyperparasitoid densities (H), and different costs of travel between colonies (τ). In each case it is assumed that hyperparasitoid giving-up-time $G = 5$.

	τ	5		10		20		40		∞	
	H	$c*$	$s(c*)$	$c*$	$s(c*)$	$c*$	$s(c*)$	$c*$	$s(c*)$	$c*$	$s(c*)$
$N = 25$	1	7	4.49	8	4.78	25	9.20	25	9.20	25	9.20
	2	5	2.56	6	2.79	6	2.79	7	2.89	7	2.89[1]
	3	4	1.67	5	1.83	5	1.83	6	1.90	6	1.90
	4	4	1.25	4	1.25	5	1.31	5	1.31	5	1.31
	5	3	0.84	4	0.93	4	0.93	4	0.93	5	0.94
$N = 50$	1	13	10.3	15	11.3	17	12.0	18	12.3	21	12.7[1]
	2	10	6.9	12	7.8	13	8.1	15	8.5	16	8.6
	3	9	5.4	10	5.7	12	6.2	13	6.4	14	6.4
	4	8	4.2	9	4.5	11	4.9	11	4.9	13	5.0
	5	7	3.6	9	3.8	10	4.0	10	4.0	11	4.0
$N = 100$	1	26	22.9	31	26.4	35	28.7	38	30.0	45	31.4[1]
	2	21	17.1	25	19.6	29	21.7	32	22.8	38	23.7
	3	19	14.4	22	16.0	26	17.8	28	18.5	34	19.3
	4	17	12.0	20	13.6	23	14.8	26	15.7	31	16.3
	5	16	10.6	19	11.9	22	13.0	24	13.5	29	14.0

1. The maximum is a local one. The overall maxima are:

$s(25) = 3.38$ for $N = 25$ and $H = 2$,

$s(50) = 18.4$ for $N = 50$ and $H = 1$,

$s(100) = 36.8$ for $N = 100$ and $H = 1$.

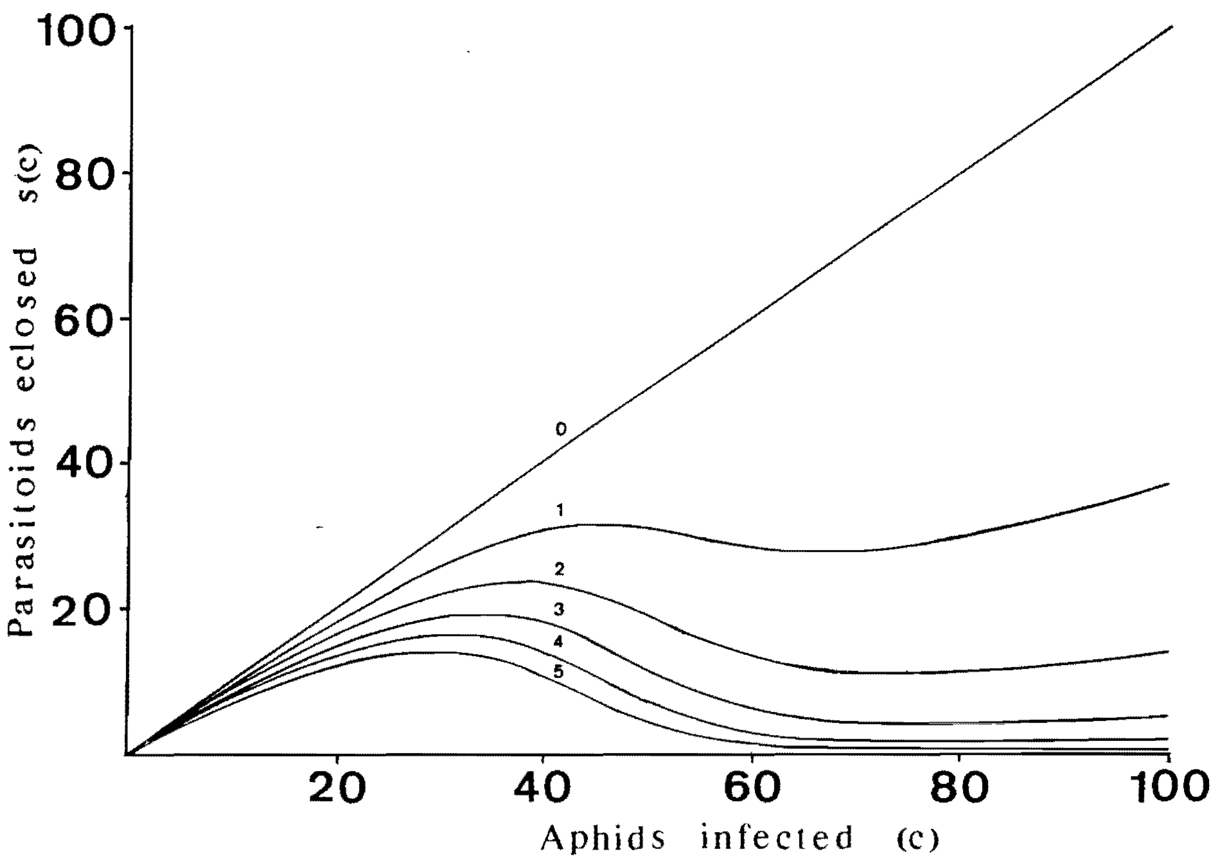
Legends for Figures

Fig. 1. Number of adult parasitoids eclosing, $s(c)$, as a function of the number of eggs laid by a female in a colony for different average numbers of hyperparasitoid visits to a colony. Giving-up-time rule $G = 5$. Colony size $N = 100$. The numbers next to each curve represent the average numbers of hyperparasitoid visits to each aphid colony, H. For explanation see text.

Fig. 2. The number of adult parasitoids eclosing, $s(c)$, for three different aphid colony sizes N (figures next to each curve). The average number of hyperparasitoid visits per colony is $H = 3$. For explanation see text.

Fig. 3. The optimal number of eggs a female parasitoid should lay in a colony ($c*$) assuming (a) different travel times (τ). $N = 100$, $H = 1$, and (b) for three different hyperparasitoid densities ($H = 1$, 3 and 5) and a fixed traveling time ($\tau = 10$). $N = 100$. Asterisks denote the points where the lines are tangent to the curves. For explanation see text.

Fig. 4. The number of eclosing adults of a certain female parasitoid, $s(e, c)$ infecting e aphids in a colony in which o aphids are already infected by other females, as a function of the number of aphids she infects. Figures next to each curve give the corresponding number of aphids in the colony infected by other females (o). For explanation see text.



Parasitoids eclosed s(c)
100
80
60
40
20
0
1
2
3
4
5
20
40
60
80
100
Aphids infected (c)

Fig. 2.

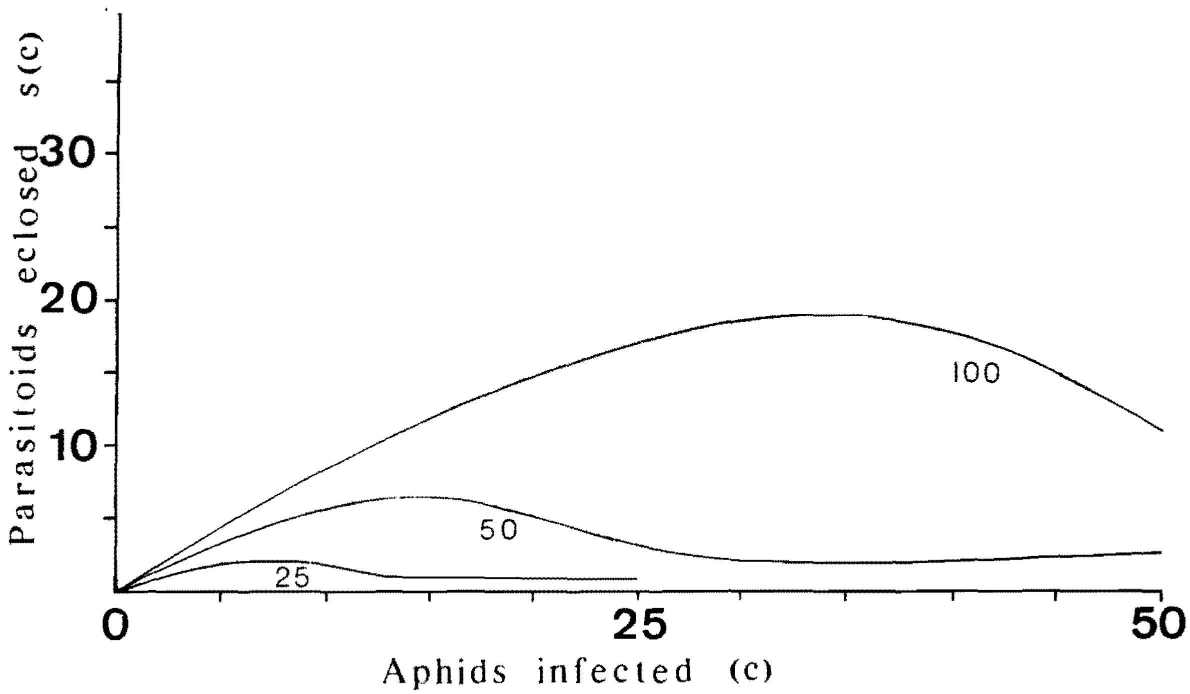
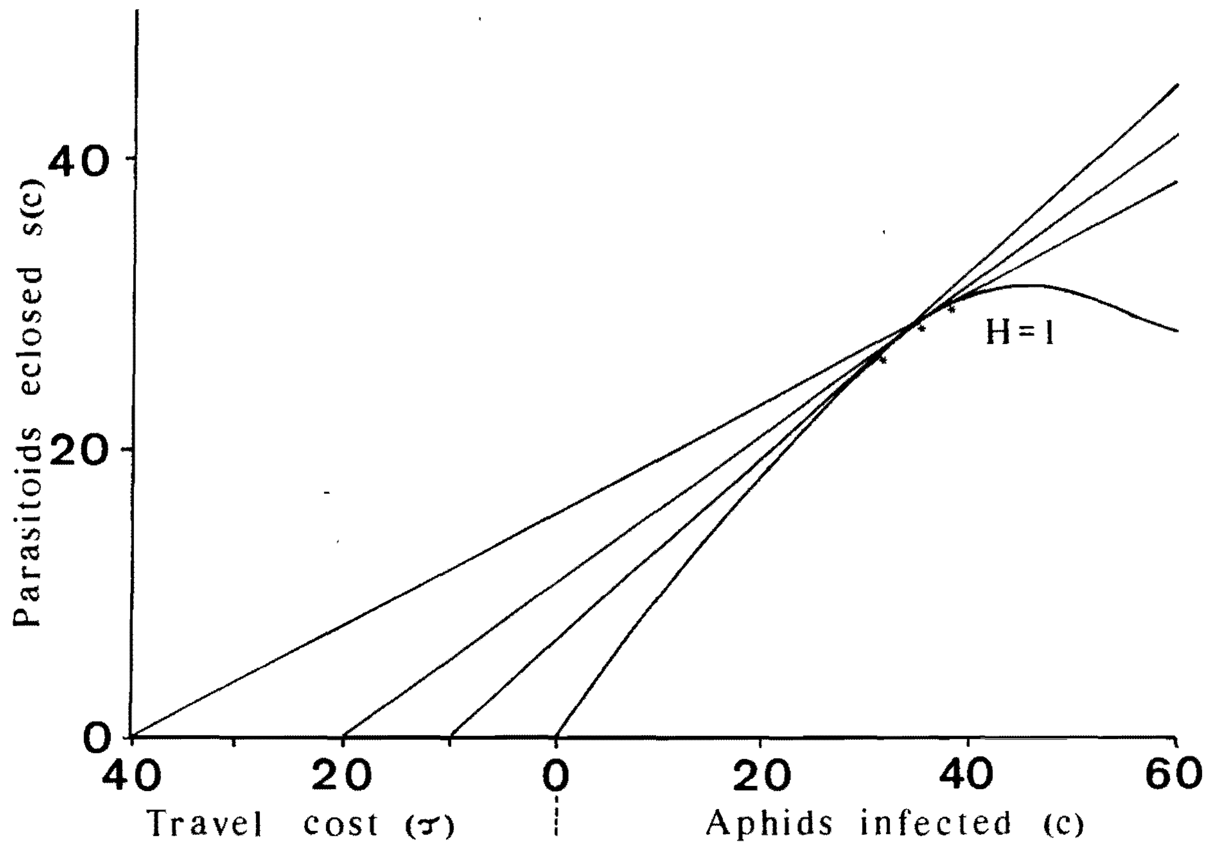

Parasitoids eclosed s(c)
30
20
10
100
50
25
0
25
50
Aphids infected (c)

Fig 3a



Parasitoids eclosed s(c)
40
20
0
H = 1
40
20
0
20
40
60
Travel cost (τ)
Aphids infected (c)