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An evolutionary interpretation of the "motivation to oviposit"

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Abstract

The ovipositional behavior of parasitoids and other insects is often described by phrases such as "motivation to oviposit" or "ovipositional drive". This paper shows how an evolutionary (i.e. functional) interpretation can be given to such phrases. A detailed model for the parasitisation of Sycamore aphids by *M. pseudoplatani* is developed, using experiments by Collins and Dixon (1986). Two models are developed: i) one in which egg complement is the only state variable and ii) one in which egg complement and information concerning host densities are state variables. Comparisons of the behaviour of simulated parasitoids, using the decisions associated with the models, and the experiments suggest that both egg complement and information are important for the parasitoid's decision making. Accepting previously parasitized hosts may be optimal, and not simply an error in parasitoid perception. A number of other detailed predictions are made, such as the relative fitness of first and second eggs in superparasitized hosts and the nature of the memory of the parasitoid.

Introduction

Understanding the basis by which parasitic insects make oviposition decisions is likely to play an ever increasing role in the effective use of parasitic hymenoptera in biological control and the effective control of crop destructive insects such as tephritid fruit flies or the boll weevil. For this reason, basic studies of biological decision making are important in the practical arena, since they provide keys to understanding the why and how of biological control.

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An example of this kind of study is that by Collins and Dixon (1986) in which the oviposition behavior of the parasitoid *Monoctonus pseudoplatani* Marsh is studied. This parasitoid attacks the sycamore aphid. Collins and Dixon investigated the foraging activity of the parasitoid, particularly oviposition decision making and host discrimination. They interpret the results in terms of the parasitoid's "motivation to oviposit" as a function of egg complement. Such descriptions of insect behavior occur frequently in the literature (e. g. Fitt 1984; or Prokopy, 1981). A phrase such as "movitation to oviposit" is useful as a description of behavior, but what one would really like is a functional interpretation of the motivation (Tinbergen 1951; McFarland, 1977). A number of authors have recently begun the analysis of parasitoid behavior in terms of lifetime fitness (Charnov and Skinner 1984, 1985; Charnov and Stephens, 1988; Iwasa et al., 1984; Parker and Courtney, 1984; Mangel, 1987a, 1987b; Waage and Godfray, 1985).

This paper has a number of purposes. The first is to attribute an evolutionary explanation to the phrases "ovipositional drive" and "motivation to oviposit". This evolutionary explanation leads to an understanding of the experiments of Collins and Dixon, particularly changes in the rate of oviposition over time and the acceptance or rejection of previously parasitized hosts. The second purpose is to illustrate how the state variable approach to behavioral ecology (e. g. McNamara and Houston, 1986, Houston et. al., 1988, Mangel and Clark 1986, 1988, Mangel 1987a, b) can be applied in the analysis of a detailed experimental situation. In particular, I will show how to formulate a state variable model corresponding to the experiments of Collins and Dixon and will show how the study of the model leads to hypotheses that can be experimentally tested.

In the next section, the experiments of Collins and Dixon are described and the main experimental results are summarized. The third section contains two state variable models of increasing complexity for the experiments. The fourth section contains an analytical and numerical study of the models. A number of detailed comparisons, predictions and possible experiments are discussed. The fifth section contains discussion and conclusions.

The experiments

In the experiments, 20 aphids were placed in a small glass tube and allowed to settle for an hour. After that, a single parasitoid was introduced and allowed to forage freely. The number of encounters and the number of ovipositions (attacks) were recorded over 15 minute intervals for up to six hours. Aphids were changed periodically at intervals ranging from 1/2 hour to 3 hours. Egg complement of the parasitoid was estimated by the length of the hind tibia; Collins and Dixon show that there is excellent correlation between the cube of the hind tibia and the egg complement. In order to study host discrimination, red and green color morphs were used. One color would be previously parasitized aphids and the other unparasitized aphids. The main experimental results are the following:

Egg complement and oviposition rate

The attack on unparasitized aphids, measured by the number of ovipositions in the first 15 minutes after unparasitized aphids are introduced, increases with egg complement.

Dynamics of oviposition rate

The oviposition rate (ovipositions per 15 minute interval) changes over time. In particular, for the situation in which unparasitized aphids are introduced every hour, the following pattern emerges (Fig. 1):

– There is a 20 percent drop in the oviposition rate in the first 15 minutes of hours 2 and 3, relative to hour 1.

– There is about 40 to 60 percent drop in the oviposition rate in the first 15 minutes of hours 4 to 6, relative to hour 1.

These patterns suggest that there are two phenomena in need of explanation: the *within* hour dynamics of oviposition and the *between* hour dynamics of oviposition.

Host discrimination and acceptance

By using differently colored morphs of the aphid, Collins and Dixon determined that previously parasitized aphids were less likely to be attacked than unparasitized aphids. They conclude "Thus, *M. pseudoplatani* detected and avoided attacking parasitized aphids, although discrimination was imperfect". I will argue that it may be evolutionarily optimal to attack a parasitized aphid; the optimality of this
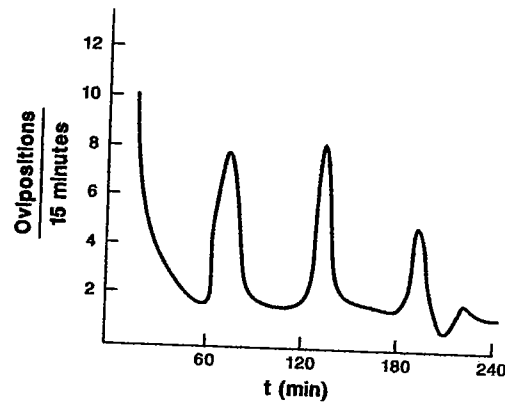

Fig. 1. Dynamics of oviposition observed by Collins and Dixon. (Drawn from their Fig. 2). The oviposition rate in each quarter of an hour is shown as a function of time, when aphid hosts are changed every hour.

decision will depend upon the parasitoid's egg complement and her assessment of the environment.

Models for the experiments

In this section, I develop two models for the experiments. The models involve increasing complexity of assumptions about biological mechanisms. The purpose of this modeling is not to exactly reproduce the experiments in the computer but to provide insight into the experiments and suggest new experiments.

The models are all based on the premise of maximization of lifetime fitness accumulated through ovipositions. When the parasitoid oviposits in the unparasitized host, her lifetime fitness is incremented by an amount f. Ovipositing in a previously parasitized host increases lifetime fitness by the amount f'. Here $f' < f$; Charnov and Skinner (1984, 1985) show how such fitness increments may be determined experimentally by measuring the survival and fecundity of offspring from unparasitized and previously parasitized hosts. The assumption underlying all of the models is that the parasitoid makes decisions in order to maximize total accumulated fitness. Total accumulated fitness depends upon survival, host densities and egg complement.

A model with egg complement as the state variable

The simplest model is one in which the parasitoid's decisions are based solely on her egg complement. Thus, define $X(t)$ by

$$X(t) = \text{egg complement at the start of period } t \tag{1}$$

If the parasitoid encounters a host and oviposits in it during period t, then $X(t + 1) = X(t) - 1$. If the host is rejected, or no host is encountered during period t, then $X(t + 1) = X(t)$. Here a period is considered short enough that at most one host encounter occurs in a single period. In the computations reported below, the length of a single period is 0.5 minutes.

The lifetime fitness function is denoted by $F(x, t)$ and defined by

$$F(x, t) = \text{maximum expected lifetime fitness accrued through}$$
$$\text{oviposition between period } t \text{ and end of the}$$
$$\text{parasitoid's life, given that } X(t) = x. \tag{2}$$

The equation that $F(x, t)$ satisfies can be derived by considering all of the events that may occur in period t and assuming that the parasitoid acts optimally (i.e. behaves to maximize total accumulated fitness) for each separate event.

In the present situation, the following three events may occur during period t;

1. the parasitoid does not encounter any kind of host,
2. the parasitoid encounters an unparasitized host or
3. the parasitoid encounters a previously parasitized host.

In order to model these events introduce:

$$\lambda = \text{Prob\{parasitoid encounters any type of host in a unit interval of}$$
time} and

$$p = \text{Prob\{an encountered host is unparasitized\}} \tag{3}$$

The parameter λ can be estimated from the data of Collins and Dixon, who report an average encounter rate of 34.5 encounters/hour. Assuming random search, λ is the parameter of a Poisson process and can be estimated from the experimental data.

Collins and Dixon report that handling time (the time required for an oviposition) is just a few seconds and since the mean time between host encounters is about 1.7 minutes, handling time can be ignored.

Next consider the parameter p. For the first model developed in this section, the parasitoid is presumed to treat p as a fixed constant. In the second model the parasitoid estimates the value of p, which thus changes as hosts are parasitized. Finally, survival from one period to the next is modeled by a parameter μ defined by

$$\mu = \text{Prob\{parasitoid survives from period } t \text{ to period } t + 1\} \tag{4}$$

Given the probabilities λ, p and μ, the law of total probability (Mangel and Clark, 1988) can be used to derive the equation for $F(x, t)$:

$$F(x, t) = (1 - \lambda)\,\mu F(x, t + 1)$$
$$+ \lambda p \, \max\{\mu\,F(x, t + 1); f + \mu\,F(x - 1, t + 1)\}$$
$$+ \lambda(1 - p) \, \max\{\mu\,F(x, t + 1); f' + \mu F(x - 1, t + 1)\} \tag{5}$$

The three terms on the right hand side of Eqn. (5) summarize the future expected fitness, based on what happens during period t. The first term corresponds to the situation in which no host is encountered (this occurs with probability $1 - \lambda$). If the parasitoid survives to period $t + 1$ (which occurs with probability μ), her egg complement is still x eggs. The second term corresponds to the encounter with an unparasitized host (which occurs with probability λp). A decision is then needed regarding oviposition; this is the source of the "max". The two terms in brackets are respectively the expected lifetime fitness $\mu F(x, t + 1)$ if the host is rejected and the expected lifetime fitness if the host is accepted. In the latter case, oviposition results in an immediate increment in fitness f which is added to expected future fitness $\mu F(x - 1, t + 1)$. Oviposition results in the decrease of the egg complement. The third term on the right hand side of Eqn. (5) corresponds to the situation in which a previously parasitized host is encountered. A similar argument is used to understand the options.

Note that μ can be factored throughout the right hand side of Eqn. (5) giving:

$$F(x, t) = \mu[\,(1 - \lambda)\,F(x, t + 1)$$
$$+ \lambda p \, \max\{F(x, t + 1); (f/\mu) + F(x - 1, t + 1)\}$$
$$+ \lambda(1 - p) \, \max\{F(x, t + 1); (f'/\mu) + F(x - 1, t + 1)\}] \tag{6}$$

Thus, it is f/μ and f'/μ that provide measures of fitness to be compared with expected lifetime fitness.

A Model with egg complement and environmental information as state variables

Now consider the case in which the parasitoid estimates the fraction of unparasitized hosts in the environment, that is estimates the parameter p. For experiments such as those by Collins and Dixon, the actual value of p will change over time since the total number of hosts is fixed. The model for estimating the parameter p is a model with decaying information. To begin, let S_i denote the state (unparasitized or previously parasitized) of the ith previously encountered host. In particular, set

$$S_i \begin{cases} 1 \text{ if the } i^{\text{th}} \text{ previously encountered host was unparasitized} \\ 0 \text{ if the } i^{\text{th}} \text{ previously encountered host was parasitized} \end{cases} \quad (7)$$

Next, introduce a memory parameter m, with $0 < m \leq 1$, which measures the rate at which the memory of previous hosts decays and let $\hat{p}$ denote the estimate for p given by

$$\hat{p} = (S_O + mS_1 + m^2 S_2 + m^3 S_3 + m^4 S_4 + \cdots)/(1 + m + m^2 + m^3 + \cdots) \quad (8)$$

For constant p, this is the weighted maximum likelihood estimate of p. In what follows, it is helpful to know that

$$1 + m + m^2 + m^3 + \cdots = 1/(1 - m).$$

Now let $\hat{P}(t)$ denote a state variable that tracks the fraction of unparasitized hosts in the environment and let $\hat{p}$ denote a particular value of $\hat{P}(t)$. What are the dynamics of $\hat{P}(t)$?

If no host is encountered during period t, then $\hat{P}(t + 1) = \hat{P}(t)$. If an unparastized host is encountered during period t, then

$$\begin{aligned} \hat{P}(t + 1) &= (1 + mS_0 + m^2 S_1 + m^3 S_2 + m^4 S_3 + \cdots)(1 - m) \\ &= (1 - m) + (1 - m) \, m \, (S_0 + mS_1 + m^2 S_2 + \ldots) \\ &= (1 - m) + m\hat{P}(t) \\ &= 1 - m(1 - \hat{P}(t)) \end{aligned} \quad (9)$$

From this equation, it follows that $\hat{P}(t + 1) - \hat{P}(t) \geq 1$, with equality holding only if $\hat{P}(t) = 1$. Thus, encounter with an uparasitized host changes the parasitoid's perception of the world, measured by an increase in the value of $\hat{P}(t)$.

Similarly, if a parasitized host is encountered during period t, then the dynamics of $\hat{P}(t)$ are found to be

$$\hat{P}(t + 1) = m\hat{P}(t) \quad (10)$$

so that encounter with a parasitized host causes a decrease in the value of $\hat{P}(t)$, unless it is already equal to 0.

In order to include information about host densities, the definition of lifetime fitness must be modified:

$$F(x,\hat{p},t) = \text{maximum expected lifetime fitness accrued through}$$

ovipositions from period t onwards, given that

$$X(t) = x \text{ and } \hat{P}(t) = \hat{p}. \tag{11}$$

The dynamic programming equation changes for two reasons. First, as the parasitoid encounters hosts, the value of $\hat{P}(t)$ changes. Second, $\hat{P}(t)$ is a random variable. This means that there is a probability distribution associated with pairs of values p and $\hat{p}$. Let $g(p/\hat{p})$ denote the probability density for the true value of p, given $\hat{P}(t) = \hat{p}$. Since the lifetime fitness is an expected lifetime fitness, the dynamic programming equation becomes

$$F(x, \hat{p}, t) = (1 - \lambda)\mu \; F(x, \hat{p}, t + 1) + \lambda \int p \; \max\{\mu F(x, 1 - m(1 - \hat{p}), t + 1);$$

$$f + \mu F(x - 1, 1 - m(1 - \hat{p}), t + 1)\}g(p/\hat{p})dp + \lambda \int (1 - p) \; \max\{\mu F(x, m\hat{p}, t + 1);$$

$$f' + \mu F(x - 1, m\hat{p}, t + 1)\}g(p/\hat{p})dp \tag{12}$$

The first term on the right hand side of this equation corresponds to the event that no host is encountered in period t. The second term corresponds to the event that an unparasitized host is encountered in period t. Then the informational dynamics given by Eqn. (9) apply and the rest of the argument is as before. The integration over p takes into account the uncertainty in $\hat{P}(t)$; it corresponds to an expectation over the true value of p, given the current information. The third term corresponds to the event that a parasitized host is encountered, in which case the informational dynamics given by Eqn (10) apply.

Additional assumptions are needed in order to actually solve Eqn (12). The most stringent set of assumptions involves developing an entire probability model for the host encounter process and from that computing the distribution $g(p/\hat{p})$. On the other hand, since p appears only linearly in Eqn (12), that equation can be rewritten as

$$F(x, \hat{p}, t) = (1 - \lambda) \; \mu F(x, \hat{p}, t + 1) + \lambda \; E\{p/\hat{p}\} \; \max\{\mu F(x, 1 - m(1 - \hat{p}), t + 1);$$

$$f + \mu F(x - 1, 1 - m(1 - \hat{p}), t + 1)\} + \lambda(1 - E\{p/\hat{p}\}) \; \max\{\mu F(x, m\hat{p}, t + 1);$$

$$f' + \mu F(x - 1, m\hat{p}, t + 1)\} \tag{13}$$

where $E\{p/\hat{p}\}$ denotes the expected value of p given the current information $\hat{p}$. Eqn (13) is completely general, and the additional assumption is now made that

$E\{p/\hat{p}\} = \hat{p}$ (i.e., that $\hat{p}$ is an unbiased estimator for p). In this case, Eqn (13) becomes

$$F(x, \hat{p}, t) = (1 - \lambda)\mu F(x, \hat{p}, t + 1)$$

$$+ \lambda \hat{p} \, \max\{\mu F(x, 1 - m(1 - \hat{p}), t + 1);$$

$$f + \mu F(x - 1, 1 - m(1 - \hat{p}), t + 1)\}$$

$$+ \lambda(1 - \hat{p}) \, \max\{\mu F(x, m\hat{p}, t + 1);$$

$$f' + \mu F(x - 1, m\hat{p}, t + 1)\} \tag{13}$$

The model developed in this section can be extended to include imperfect discrimination of hosts by introducing a probability of accurate discrimination of previously parasitized hosts. In that case, the increment in fitness f when an apparently unparasitized host is encountered must be replaced by an expected increment in fitness, taking into account the chance that an apparently unparasitized host is actually parasitized. The dynamics of $\hat{P}(t)$ also change.

Results and predictions

For the results reported here, stationary solutions (Mangel and Clark, 1986, 1988; McNamara and Houston, 1986) of the dynamic programming equations (5) and (12) are used. Such stationary solutions are independent of time, so that decisions only depend on the values of the state variables. For example, the stationary version of Eqn (13) is

$$F(x, \hat{p}) = (1 - \lambda) \, \mu F(x, \hat{p})$$

$$+ \lambda \hat{p} \, \max\{\mu F(x, 1m(1 - \hat{p})); f + \mu F(x - 1, 1 - m(1 - \hat{p}))\}$$

$$+ \lambda(1 - \hat{p}) \, \max\{\mu F(x, m\hat{p}); f' + \mu F(x - 1, m\hat{p})\} \tag{14}$$

This equation can be solved by an iterative method (Mangel and Clark, 1988) and as it is solved one obtains the decision rule of the wasp (to oviposit or not) as a function of the current value of the state variables (egg complement in the first case or egg complement and estimating fraction of unparasitized hosts in the environment in the second case).

After solution of the dynamic programming equations, the experiments of Collins and Dixon were simulated in the following manner. One hundred identical "computer" wasps each with an initial complement of 70 eggs were presented with 20 "hosts" in separate "experiments". The hosts were encountered randomly according to the Poisson process described previously and the density of unparasitized and parasitized hosts changed as the wasps parasitized hosts. Thus, the true fraction of unparasitized hosts changes over time. As in the experiments, hosts were changed every hour so that at the start of each hour the number of unparasitized hosts was 20. The simulations tracked the mean and variance of the number of encounters and ovipositions.

Decision rules

The decision rules can be summarized by a curve in the plane of physiological and environmental variables. Figure 2 shows how the "fraction of unparasitized hosts (p)/egg complement (x)" plane is divided by the solution of Eqn (6). The curve shown in this figure separates the plane into two regions, one in which previously parasitized hosts are rejected and one in which previously parasitized hosts are accepted for oviposition. For a combination of events (p, x) falling above this boundary, the wasp will oviposit in a parasitized host. Note that since this is based on Eqn (6), the value of p is actually fixed (there is no updating of p as encounters occur). The boundary curve is determined by the interplay of egg complement, encounter rate and probability of survival. When egg load is high, accepting previously parasitized hosts becomes optimal because the expected number of future encounters is not sufficient to insure that all eggs can be placed in unparasitized hosts. For example, for the parameters used here, the probability of encountering a host in a singe period is about 0.3 and the expected lifetime of the parasitoid is about 200 periods. If only unparasitized hosts were encountered, the wasp would need of the order of 233 periods, slightly larger than the expected lifetime, to oviposit all of her eggs (70 eggs divided by 0.3). This leads to the optimality of accepting previously parasitized hosts when egg complement is high.
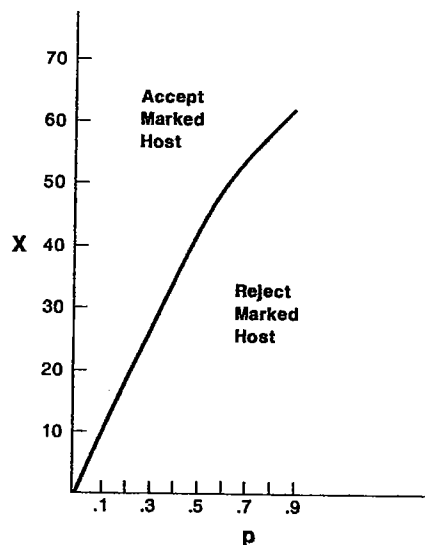
Fig. 2. Division of the probability of encountering an unparasitized host (p)/egg complement (x) plane according to accepting or rejected a previously parasitized hosts for the model with no information updating. Parameters used in the computation are $\mu = .995, f = 1, f' = .1$, and $\lambda = .289$. Since there is no updating of information in this model, the dynamics of the egg complement $X(t)$ will sit on a vertical line, determined by the initial value of p.

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If the mortality rate increases, the boundary curve will shift downwards. This can be summarized by the following prediction:

Prediction 1

If two parasitoids have the same egg complement, the older one will be more likely to accept previously parasitized hosts.

Note that although p is used in the construction of Fig 2, by the assumptions in Eqn (6) the parasitoid behaves as if p were constant (it will be changing as ovipositions occur and new hosts are introduced). Thus a "trajectory" in this plane will be a vertical line, beginning at a large value of x and fixed value of p and moving downwards in x but with p fixed. This means that the boundary curve will be crossed only once.

Figure 3 shows the comparable division of the "environmental information $(\hat{p})$/egg complement (x)" plane for the model in which both egg complement and environmental information are state variables. The boundary curve is similar to Fig. 2. The difference is that since both $\hat{P}(t)$ and $X(t)$ change as the result of encounters and ovipositions, trajectories may cross the boundary curve more than once. For
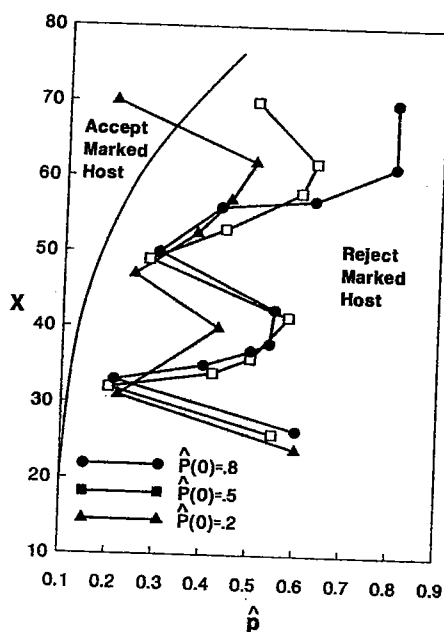

Fig. 3. Division of the probability of encountering an unparasitized host $(\hat{p})$/egg complement (x) plane according to accepting or rejected a previously parasitized hosts for the model with information updating. All parameters as in the previous figure and $m = 0.9$. Also shown are the average trajectories of the 100 simulated parasitoids that start with egg complement $X(0) = 70$ eggs and information variable $\hat{P}(0) = 0.2$, 0.5 or 0.8. Note that the effect of initial information decays as time increases (X decreases) so that the trajectories coalesce.

Prediction 2

The second egg in a host provides little or no fitness to the mother, relative to the first egg. For example, survival of second eggs should be noticeably smaller than survival of first eggs.

During the review of this paper, Prof. A. F. G. Dixon (personal communication) reported that this prediction is correct: only one egg survives to maturity and the first egg to hatch is usually the one to survive. Prof. Dixon also reports that about 10 percent of the parasitie larvae die during development, so the fitness of the subsequent eggs is not zero. These facts suggest that values of f'/f in the range of .05 — .2 are quite appropriate for the parasitoid studied here.

Effect of adult survival

The relationship between adult survival μ and egg complement X determines the boundary curve and general nature of oviposition decisions (Mangel, 1987a, b). The expected lifetime of the wasp is roughly $1/(1 - \mu)$. Thus, for example, for the value $\mu = .995$ (used in most computations here), the expected lifetime is about 200 periods. Computations with both models showed that the experimental within hour ovipositional dynamics were not obtained unless the expected lifetime of the parasitoid (measured in periods of length .5 minutes) exceeds the initial egg complement.

The role of initial environmental information

The results shown in Fig. 3 indicate that if information updating does occur, then the initial environmental information (i.e. the value of $\hat{P}(0)$) is not particularly important. If information updating does not occur, so that the wasp behaves as if p were fixed and constant, the environmental information is unchanging and the choice of value is important. For example, results similar to the ones shown in panel b of Fig. 4 occur for values of $p = .2$ or $p = .5$ and oscillatory dynamics similar to panel a occur for values of $p = .8$. A difficult question is if the value of p would become fixed, in the evolution of the parasitoid's behavior. Even then, the expected fitness of the model with information updating is larger than the expected fitness for the model in which p is fixed and oscillatory dynamics are observed. That is, for a full egg complement $F(70, .8, 1) = 33.63$ but $F(70, 1) = 31.82$ when $p = 0.8$ in the model without information updating. The ratio of these two fitnesses is 1.056, which provides a measure of the evolutionary advantage of information updating.

The role of the memory parameter

The memory parameter m summarizes the rate at which past information is forgotten. For example, if $m = .9$, then after 5 periods an encounter is weighted

about 60 percent of its initial value and after 10 periods it is weighted at about 35 percent of its initial value. On the other hand, if $m = .6$, then after 5 periods the weighting is 8 percent and after 10 periods the weighting is less than 1 percent. Study of the model with information updating showed that when $m = .9$ the simulated parasitoids showed oscillatory ovipositional dynamics similar to the observed experimental results but that when $m = .6$ the oviposition rate was nearly constant for the first 90 minutes of the simulation. This suggests:

Prediction 3

The parasitoid has a "long-lived" or slowly decaying memory.

The effect of imperfect discrimination

An extension of the second model was developed, in which imperfect host discrimination occurs. The simulated ovipositional dynamics were oscillatory, and similar to the dynamics when host discrimination was perfect. This leads to the conclusion that acceptance of previously parasitized hosts was not caused by imperfect discrimination but was due to the optimality of accepting parasitized hosts for certain values of the state variables.

This conclusion could be tested with the following experiment: Separate two groups of parasitoids that are essentially identical from birth. Deprive one group of parasitoids of hosts for a number of hours, while allowing the second group to oviposit. Then present both groups with identical mixtures of unparasitized and parasitized hosts. The hypothesis is that the deprived group will have a much higher acceptance rate of previously parasitized hosts than the non-deprived group.

Conclusions and discussion

The objective of this paper has been to show that by applying the premise of maximization of accumulated lifetime fitness, we can derive an evolutionary explanation of the motivation to oviposit. This motivation is determined by the interplay of physiological state variables and ecological state variables. Given values of the state variables at a certain point in the parasitoid's life, the premise of maximization of accumulated fitness provides decision rules about acceptance of hosts and oviposition strategies. This premise successfully predicts the dynamical response of the parasitoids and also provides an explanation for the acceptance of previously parasitized hosts. The two main conclusions are i. Oviposition in a previously parasitized host can be an adaptive and optimal strategy, depending upon encounter history and ecology. ii. Treating the ecology in a dynamic way, in which environmental information is updating according to encounters, is important. This paper provides a specific memory model for such informational dynamics.

The model developed in this paper could be extended in a number of ways. For example, the parameters λ (host encounter rate) and μ (adult survival) were treated as constant and known. In fact, the parasitoid might have to estimate them as well. Updating and estimating λ will be important if the parasitoid lives in a world in which host density may vary greatly. Methods similar to the ones presented here could be used to update λ. Real parasitoids must also feed and rest, as opposed to "computer" parasitoids. These activities could easily be incorporated into the models developed in this paper. For example, although the parasitoid is proovigenic, it may be difficult to lay many eggs in rapid succession. Handling times might increase because eggs have further to travel to reach the ovipositor or survival might decrease. Such effects can be incorporated, once the physiology is known.

Acknowledgments

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