

Dynamic information and host acceptance by a tephritid fruit fly

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ABSTRACT. 1. Female apple maggot (*Rhagoletis pomonella* Walsh) flies held in field cages usually oviposited in an unparasitized (non-pheromone marked) fruit when it was encountered.

2. Oviposition in a previously parasitized (pheromone marked) fruit depended upon the time since the last oviposition (TSLO) and the percentage of infested fruit encountered during search for oviposition sites.

3. Previous theories of host acceptance suggest that the acceptance or rejection of a host should depend dichotomously on time since last oviposition and the fraction of marked hosts in the last five encounters. The experiments, however, show considerable variability and are thus not consistent with the theory.

4. A new theory for the experiments is introduced. This model involves physiological (egg complement) and informational state variables and leads to intuitive understanding of the experimental results. In particular, the model shows how the plasticity in oviposition site selection may arise from fitness maximizing behaviour. Alternative models are also discussed. All of the models stress the importance of physiological and informational states.

Key words. Tephritid flies, oviposition strategy, foraging, learning.

Introduction

An organism searching for oviposition sites, and ovipositing when one is encountered, can often be viewed functioning as a 'decision maker'. That is, the organism encounters a potential oviposition site, assesses the quality of the site, and then decides whether or not to oviposit. In principal, this decision depends upon the physiological state of the organism, and the general state of the environment. (The actual interplay of these two will differ for different

organisms; see Singer (1982) and McDonald (1986) for discussion about butterflies and mediterranean fruit flies, respectively.) In this paper we study the interplay of host quality, physiological state and informational state for adult female apple maggots *Rhagoletis pomonella* Walsh. This tephritid fly attacks healthy (non-rotting) fruit. The fly also occasionally (to be specified below) superparasitizes fruit by ovipositing in a host that has already been parasitized and marked with pheromone by a conspecific. Superparasitism has been observed in the field (Roitberg *et al.*, 1982) and in the laboratory (Roitberg & Prokopy, 1983). In general, *R. pomonella* dis-

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criminate against previously parasitized hosts by detecting the marking pheromone deposited by a female during a previous oviposition and not ovipositing. However, if the delay between ovipositions is sufficiently high, *R. pomonella* females will accept hosts that have been previously parasitized (Roitberg & Prokopy, 1983). A delay of about 10 min leads to a four-fold jump in the proclivity to oviposit in marked fruit and a delay of 80 min leads to nearly all flies accepting previously parasitized (pheromone marked) fruit (see Fig. 1 of Roitberg & Prokopy, 1983).

Flies in natural settings or semi-natural field cages face a situation in which they will encounter mixtures of unparasitized and previously parasitized hosts. In principal, host acceptance decisions then depend upon the density of hosts and the mixture of clean (unparasitized) and marked (previously parasitized) hosts. Since flies can never completely assess host density, some proxy must be used. One choice would be the time since the last oviposition (which we denote by TSLO). A measure of the mixture of clean and marked hosts is the fraction of marked hosts in the previous N encounters. (In view of the experiments described in the next section, we chose $N=5$.) Recently developed theories of host acceptance (Iwasa *et al.*, 1984; Mangel, 1987a,b) can then be applied and lead to results summarized in Fig. 1. These theories are based

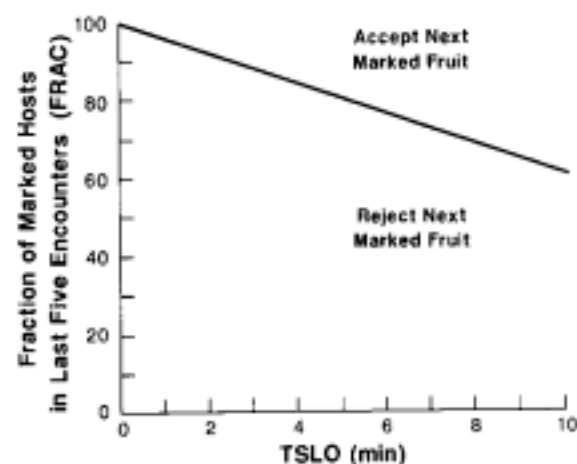


FIG. 1. Theoretical predictions of host acceptance in the plane determined by the time since last oviposition (TSLO) and fraction of marked hosts in the last five encounters (FRAC). According to the theory (Iwasa *et al.*, 1984), if a marked host is encountered for the combination of events above the line, the fly should oviposit in the marked host. If a marked host is encountered for points below the line, the fly should reject the marked host.

on the assumption that host acceptance is determined by behaviours that maximize accumulated lifetime fitness (expected number of progeny) through oviposition decisions, with clean fruit and marked fruit having different increments in fitness. The theories also consider the egg complement of the fly and survivorship over the fly's lifetime. In Fig. 1 we label the plane TSLO-fraction of marked hosts in the last five encounters (FRAC) and divide it into two regions. For the combination of events falling above the line a marked host should be accepted for oviposition when encountered, but for the combination of events falling below the line a marked host should be rejected when encountered. The intuition associated with Fig. 1 is relatively straight-forward: marked hosts should be accepted only when the mixture of hosts is such that marked hosts predominate or when host encounters are rare. In the third section we will compare experimental results with the theoretical predictions based on Fig. 1.

In this paper we further study the role of physiological and informational variables in the behaviour of *R. pomonella* females, using recently developed methods (Mangel, 1987a,b) to model the field behaviour of females. Our results not only show the interplay of the physiological and informational states, but also the natural and consistent way in which plasticity of behaviour may be produced by optimality mechanisms.

Materials and Methods

The source of larvae was *R. pomonella* maggot-infested fruit collected from hawthorn (*Crataegus mollis*) trees in Amherst, Massachusetts. The protocol for raising the flies is described in Roitberg & Prokopy (1983). The experiments were conducted using a field cage containing a tree with a canopy of about 1 m³ volume. The number of fruit in the tree varied between eight and sixty-four, in clumps of four (that is two to sixteen clumps). Each fruit in the tree was numbered. Further details of the experimental protocol are described in Roitberg *et al.* (1982). The data reported here are not given in Roitberg *et al.* (1982).

Flies were taken from the laboratory into the field and allowed to experience two ovipositions in the field cage; this provided an acclimation

period for the flies. After the first two ovipositions the clock was set equal to zero and at subsequent host encounters the type of fruit (clean, indicating no previous oviposition; or marked, indicating a previous oviposition and marked by a pheromone) and the time since the previous oviposition was recorded. Females were followed until they left the tree. For the time course of our experiments and density of the fruit, oviposition in clean fruit appeared to not be limited by egg complement. The data collected thus consist of (1) times of oviposition in fruit, (2) the type of fruit in which the oviposition occurred, and (3) the type of fruit in which a rejection occurred. From these, we can compute the time since the last oviposition and the fraction of marked fruit in the last five encounters.

Results

The data will be reported according to the following scheme. For each oviposition in a fruit, we recorded the time since the last oviposition (TSLO), whether the current fruit is unparasitized (clean, C) or previously parasitized (pheromone marked, M) and the fraction of marked fruit in the last five fruit encountered. We found essentially no relationship between acceptance of a clean host, time since last

oviposition and fraction of marked fruit in the last five encounters. That is, females essentially always accepted a clean fruit when it was encountered. (A regression of fraction of marked fruit in the last five encounters against time since the last oviposition gives a slope of 0 and a value of $r=0.01$; i.e. a straight line explains essentially nothing about the oviposition decision in clean fruit.) We observed 120 instances in which a fly encountered a marked fruit and rejected it.

We also observed a small number (2% of the total number of ovipositions) of superparasitisms in which a fly oviposited in a marked fruit. Fig. 2 shows results for ovipositions in marked fruit. In this figure, we have redrawn the line from Fig. 1 and also plotted points that show the value of time since the last oviposition and fraction of marked fruit in the last five encounters. Half of the experimental points are in accordance with the theory; those are the points falling above the line. On the other hand, half of the experimental points are in disagreement with the theory; those are the points falling below the line. We can think of a number of possible explanations for the discrepancy. First, it might be that the theoretical line is wrong and that the slope is too high. We could redraw the theoretical line so that all points fell above it. This is not very satisfying, however, since the line was drawn using our best parameter estimates. (We used laboratory based survivorship data to compute the line. If survivorship in the field is lower than in the laboratory, then the slope of the line would be lowered. However, to move the line so that all points fall above it requires an unreasonably low survivorship (Mather & Roitberg, 1987, and references therein).) Second, it might be that the flies are considerably sub-optimal, in which case the points below the line correspond to mistakes in host acceptance. Third, it might be that the system is so noisy that the points falling below the line correspond to 'noise' of an unidentified source. The second and third explanations are as unsatisfying as the first.

The alternative explanation, which is the one we propose here, is that the variability can tell us something about the behaviour of the flies and the interaction of the flies and their environment. Thus the scatter in Fig. 2 could be called a kind of 'behavioural plasticity'. The question that we address in the next section is how such plasticity might arise and what can be learned from it.

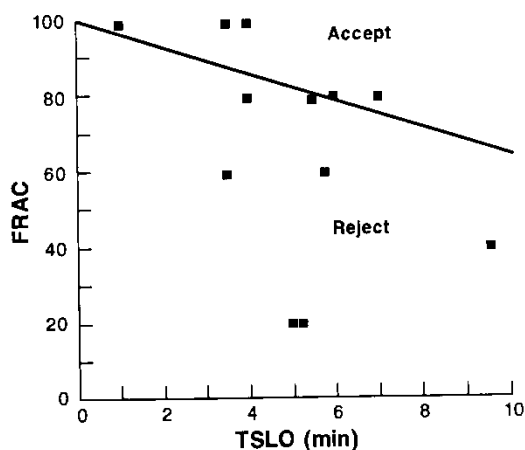


FIG. 2. Ovipositions by female *R. pomonella* in marked fruit in a tree in a field cage, as a function of time since the last oviposition (TSLO) and fraction of marked hosts in the last five encounters (FRAC). We also show the theoretical line drawn in Fig. 1. Approximately half of the points are in accordance with the theory and half do not agree with the theory.

A model for the experiments

We now introduce an explicit model for the experiments described in the previous sections. In particular, we will suggest a framework for modelling the experiments and show that this framework provides an explanation for the experimental results. We stress that there are other frameworks (modifications of the model given here) that could also be used; these are discussed in the Conclusions, where we also make certain experimental predictions.

The model uses a state variable approach for the analysis of the behaviour of the fly (Mangel & Clark, 1986; Mangel, 1987a,b). We define the state variable $X(t)$ by

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

in which time is measured discretely, so that we will consider increments of time equal to 1 unit. We assume that the periods are sufficiently short that the fly can encounter at most one fruit in a single period. The $X(t+1)$ equals either $X(t)$ (if no fruit is encountered during period t or one fruit is encountered, but rejected) or $X(t) - 1$ (if a fruit is encountered and accepted for oviposition). If a fly oviposits in a clean fruit, its total lifetime fitness is incremented by an amount f_c ; oviposition in a marked fruit leads to increment f_m . We assume that within host intraspecific competition causes $f_m < f_c$. It will be seen that the equations for total lifetime fitness that characterize the behaviour of the fly depend only on the relative values of f_c and f_m and not on the absolute values. Averill & Prokopy (1987) recently published data that can be used to compute these increments in fitness, assuming that fitness is measured by the expected number of progeny.

The probability that a fly survives from period t to period $t+1$ is denoted by $p(t)$. If T denotes the total lifetime of the fly, we use a model of the following type

$$p(t) = [(T+1)^\gamma - (t+1)^\gamma] / [(T+1)^\gamma - t^\gamma] \quad (2)$$

where γ is a parameter. If it is moderate, say about $\gamma=3$, then the survivorship curve is relatively flat for many values of t starting from $t=0$ and then drops rapidly to 0 as t approaches T . This is similar to much of the life-table data generated for fruit flies (see, e.g., Carey, 1984; Roitberg, unpublished).

In addition to the physiological state variable

represented by egg complement we introduce a state variable that summarizes information about the environment. Let S_i denote the state of i th previously encountered fruit. Thus, $S_i = C$ if the fruit was unparasitized and $S_i = M$ if the fruit was previously parasitized and pheromone marked. The vector $S(t) = (S_1, S_2, S_3, S_4, S_5)$ then represents the states of the last five fruit encountered. To find the dynamics of $S(t)$ we adopt a 'sliding window' model for the memory of the fly. (In the appendix, we describe a more general model for information about the fruit, and show how the general model and the one presented here are connected.) That is, each time a new fruit is encountered, the memory window shifts by 1 and memory of the fifth fruit is lost. Thus, if no fruit is encountered during period t , $S(t+1) = S(t)$. If a clean fruit is encountered during period t , and $S(t)$ is given above, then $S(t+1) = (C, S_1, S_2, S_3, S_4)$ whereas if a marked fruit is encountered during period t , then $S(t+1) = (M, S_1, S_2, S_3, S_4)$. In this way, we are able to treat information in a dynamical fashion during the foraging process. Gould (1984) provides data that suggest honey bees might use such a sliding window model. McNamara & Houston (1987b) described alternative models for the adaptive use of memory.

Now consider a female that starts period t with a complement of eggs given by $X(t) = x$ and informational variable $S(t) = s$. We assume that this fly stops foraging for oviposition sites at the end of period $T-1$ and ask for the behaviour that maximizes accrued fitness through oviposition decisions. Thus, introduce a fitness function defined by

$$F(x, s, t, T) = \text{maximum value of expected fitness through oviposition between period } t \text{ and } T, \text{ given that } X(t) = x \text{ and } S(t) = s \quad (3)$$

First we note that there is an 'end-condition' for this function, because we assume that there is no oviposition in period T . Therefore, no additional fitness can be accrued beyond T and so we set $F(x, s, T, T) = 0$. An equation for the fitness function can be derived by comparing the state of the organism between period t and period $t+1$. Three events may occur. First, no fruit is discovered during period t , in which case neither the state variable nor the informational variable changes. Second, a clean fruit may be discovered. We assume that the insect will always

oviposit in a clean fruit, so that the state variable representing egg complement is decreased by 1 unit. The informational state variable is shifted according to the rules described above. Thus, if the sequence was $\{S_1, S_2, S_3, S_4, S_5\}$ it now becomes $\{C, S_1, S_2, S_3, S_4\}$. Third a marked fruit may be encountered. In this case, the insect 'decides' to oviposit or not using the current time, current value of the state variable, and current value of the informational variable. In addition, the informational state variable is updated according to the rule given above.

To derive the equation for the fitness function, we must model the encounter rates with the two kinds of fruit. Consider a cluster fruit, which we will call a patch. We presume that there are N fruit in the patch, that the insect can visually determine the value of N (Roitberg, 1985) and let p_e denote the probability of encountering a fruit of either type in a single period. We use a random search model (Mangel, 1985a) so that

$$p_e = 1 - \exp(-N\varepsilon) \quad (4)$$

In this equation, ε is a parameter representing the search effectiveness of the fly. Its reciprocal is the mean time to find a single fruit, if only one fruit is present; thus ε can be determined by experimental measurement. (For more details, see Mangel, 1985a.)

When a fruit is encountered, it may be clean or marked. We must now model the way in which the fly estimates the fraction of clean fruit in the environment. To do this, introduce a 'counting function' given by $c(s_i) = 1/5$ if s_i corresponds to a clean fruit and $c(s_i) = 0$ if s_i corresponds to a marked fruit. The rationale behind the counting function is this: The sum of the $c(s_i)$ over the five entries in the information vector is 1, if all five entries in the memory window are Cs, and is 0, if all five entries in the memory window are Ms. Thus, for example, the probability that an encountered fruit is clean is estimated by $\sum_i c(s_i)$ and the probability that an encountered fruit is marked is estimated by $1 - \sum_i c(s_i)$.

Given the information vector $S(t) = s$, the probability of encountering a clean fruit in period t is then estimated by $p_e \sum_i c(s_i)$ and the probability of encountering a marked fruit in period t is $p_e(1 - \sum_i c(s_i))$. At this point, it becomes necessary to differentiate between the informational state $S(t) = s$ and the *estimate* of fraction of clean fruit in the environment. The informational state is fixed and is certain – that is, the

model we are developing here involves perfect discrimination between unparasitized and parasitized hosts, so that the fly is certain that clean fruit are clean and marked fruit are marked. On the other hand, the fraction of clean fruit in the environment is estimated by $\sum_i c(s_i)$ and since it is an estimate, there is uncertainty associated with this estimate. Dealing with the uncertainty is one of the great difficulties of stochastic dynamic programming (Mangel, 1985b). Here we assume that the fly behaves as if the estimate were perfect (no variance or uncertainty in the estimate); in Appendix 2 we discuss alternatives to this assumption.

The equation for $F(x, s, t, T)$ (Mangel & Clark, 1986, 1988; McNamara & Houston, 1986), is then

$$\begin{aligned} F(x, s, t, T) = & (1 - p_e) \rho(t) F(x, s, t+1, T) \\ & + p_e \sum_i c(s_i) [f_c + \rho(t) F(x-1, s_c, t+1, T)] \\ & + p_e (1 - \sum_i c(s_i)) \max \{ f_m + \rho(t) F(x-1, s_m, t+1, T); \\ & \rho(t) F(x, s_m, t+1, T) \} \end{aligned} \quad (5)$$

In this equation, s_c and s_m are defined in the following way. If $s = (s_1, s_2, s_3, s_4, s_5)$, then $s_c = (C, s_1, s_2, s_3, s_4)$ and $s_m = (M, s_1, s_2, s_3, s_4)$. The three terms on the right-hand side of Eq. (5) respectively correspond to not encountering any kind of fruit, encountering a clean fruit and ovipositing in it, and encountering a marked fruit and deciding whether or not to oviposit in it. When an encountered fruit is accepted, the fly obtains an immediate increment in fitness (hence the presence of f_c and f_m on the right-hand side of Eq. (5)) and uses one egg (hence the $x-1$ on the right-hand side of Eq. (5)). This equation is solved 'backwards in time', meaning that we start by setting $t = T-1$ on the left-hand side of Eq. (5), evaluating $F(x, s, T-1, T)$ using the right-hand side of Eq. (5), then decrease t to $t = T-2$, and proceed in this fashion until $t = 1$ (the first period of the problem). Further details can be found in Mangel (1987a, b). Although the actual fitness function may be of interest, for the experiments described in the previous section, it is the decision associated with the encounter of the marked fruit that we want to consider. This decision is determined directly during the evaluation of the dynamic programming equation. An important aspect of the decision actually comes from the information updating. That is, consider two sequences in which 40% of the last five fruit encountered were marked, for example: M, M, C, C, C and M, C, C, C, M . In these sequ-

ences, the first entry corresponds to the most recently encountered fruit. Each of these sequences has 60% clean fruit. Suppose that another marked fruit is encountered. The first sequence is updated according to the rule $M, M, C, C, C \rightarrow M, M, M, C, C$ but the second sequence is updated according to the rule $M, C, C, C, M \rightarrow M, M, C, C, C$. That is, although both fruit correspond to 40% marked fruit before the information state is updated, after the updating one sequence corresponds to 60% marked fruit, but the other still corresponds to 40% marked fruit. Thus, it is entirely possible that in the plane of 'TSLO/Fraction of Last Five Infested', the two sequences lead to different behavioural decisions. This means that although the fly is essentially making simple decisions based on quantities that it treats as deterministic, when the data are plotted as in Figs 1 or 2, the appearance will be one of stochasticity.

This is, in fact exactly the case. Fig. 3 shows that now the 'TSLO/Fraction of Last Five Infested' plane is divided into three regions. In one region, oviposition in a marked fruit is never optimal. In a second region, oviposition in a marked fruit is always optimal (i.e. maximizes accumulated lifetime fitness). In a third region, oviposition in a marked fruit is sometimes optimal. This middle region corresponds to the region of scatter below the line in Fig. 2.

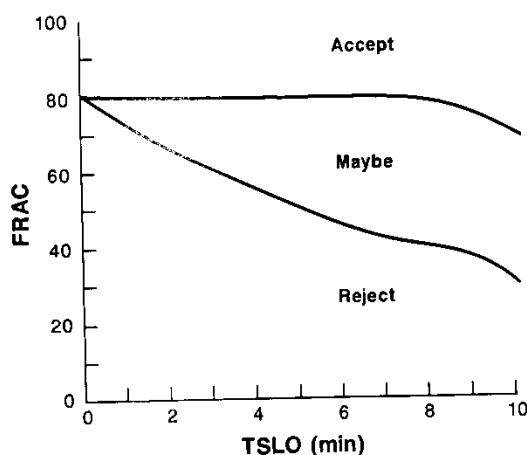


FIG. 3. Division of the 'TSLO/Fraction' plane into regions in which it is optimal to always oviposit, never oviposit, and sometimes (depending on details of the informational state) oviposit. Parameters for the calculations are $T=20$, $p_e=0.28$, $\gamma=3$, $f_c=1$, $f_m=0.2$, and the maximum number of eggs available per day is ten eggs. This figure is drawn for the case in which three eggs remain.

In Fig. 4 we have replotted the data from Fig. 2 (the stars) and the boundary curves of Fig. 3. All but two of the data points fall in the 'accept' or 'maybe' regions. In addition, we have plotted fifteen quasi-randomly selected instances (circles) in which a marked fruit was rejected by the fly. These all fall in the 'maybe' or 'reject' regions. The model has provided information and intuition for a successful interpretation of the data; this is the main point of the modelling exercise. The apparent 'noise' represents behavioural plasticity of optimally behaving organisms. Finally, we point out that we observed thirty instances in which a marked fruit was rejected but $\text{FRAC}=100\%$. According to the simple theory based on Eq. (5) – in which there is no uncertainty in the estimate of the fraction of clean fruit in the environment – flies should always accept marked fruit when $\text{FRAC}=100\%$. The observation that they don't indicates that a more complicated theory such as the one developed in Appendix 2 and taking uncertainty of estimates into account is necessary for a full understanding of this behaviour.

One could use the model to generate quantitative hypotheses that can be tested either in the laboratory or the field; we are currently working on such experiments. Two approaches would be the following: We could use the theory to try to construct a new measure – as an alternative to

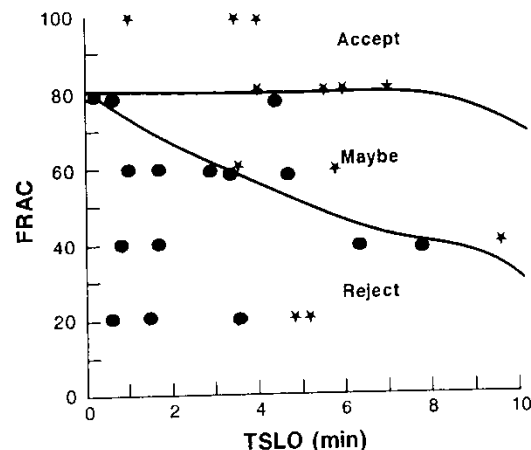


FIG. 4. Comparison of observations from Fig. 2 and the theoretical curves from Fig. 3. Instances in which a marked fruit was accepted for oviposition are indicated by a star. Also shown are fifteen quasi-randomly selected (see text for details) instances in which a marked fruit was rejected (circles). Note that nearly all acceptances fall in the 'accept' or 'maybe' regions and that the rejections fall in the 'maybe' and 'reject' regions.

'Fraction of the last five encounters that were marked' – in which decisions were indeed dichotomous. Alternatively, our theory suggests that decisions are dichotomous, but in a space larger than time since last oviposition and a simple measure of history. Our theory suggests decisions are dichotomous in egg complement/time since last oviposition/ $\sum_i c(s_i)$ space. In the appendix we describe a model in which recent encounters are weighted more heavily than past encounters.

Discussion

Our experimental results suggest that female *R. pomonella* respond to physiological (time and egg complement) and informational constraints or variables when selecting oviposition sites. We have provided a model that incorporates both kinds of variables and provides a successful explanation of the observed field data, particularly the behavioural plasticity of the flies when making oviposition decisions. Our results also show the importance of thinking clearly about the meaning of 'optimality' when viewing biological systems. If the external observer has an inaccurate model of optimal behaviour, then it may appear that the organism is highly sub-optimal, when this is in fact not the case (see, e.g., McNamara & Houston, 1987a, for a further discussion of this point). Our results suggest that we should be able to construct a quantity involving physiological state (egg load) and informational state for which decisions are essentially dichotomous (i.e. the 'maybe' region in Fig. 3 shrinks to 0).

The theory that we have presented does not provide a unique explanation of the behaviour of the flies. Other theories based on informational variables would work as well. For example, we could assume that flies are simultaneously estimating the probability of encountering any fruit at all and the fraction of clean fruit in the environment. The estimation procedures would be similar to the ones given in this paper. The key to the plasticity of behaviour, however, is the incorporation of an informational state into the host acceptance analyses.

The experimental and theoretical results presented in this paper address the question of 'why' female *R. pomonella* would oviposit in marked fruit. We have shown that a consistent explana-

tion of the behaviour can be obtained by considering maximization of lifetime fitness, subject to physiological and informational constraints. The role of theory is to guide our thinking about what the flies are doing, why they are doing it, and how we can and should characterize their behaviours. The simple theory present here could be extended to address a variety of other issues, such as patch exit decisions and the behaviour of flies when a number of different kinds of fruit are available. The concomitant question is now 'how' do the female *R. pomonella* make the decisions? It is almost surely true that they do not operate using dynamic programming algorithms such as those given here, though they may employ simple 'rules of thumb' (Roitberg & Prokopy, 1982). But this leaves the question of how the rules of thumb are developed and retained and how the flies might solve the dynamic optimization problem presented to them by nature.

Acknowledgments

This was partially supported by NSERC Canada Operating Grant to B. D. Roitberg and NSF grant BSR 86-1073 to M. Mangel. M. Mangel also thanks the Guggenheim and Fulbright Foundations for support. Much of the data was collected in collaboration with J. J. M. van Alphen, F. Galis, J. C. van Lenteren and R. Prokopy. M. Mangel thanks G. Edelman and R. Prokopy for conversations about the problem and theory.

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Accepted 22 October 1988

Appendix 1: A general learning model

In this appendix, we generalize the sliding window model developed in the paper. The generalized model is likely to be appropriate in situations other than the one described in the paper. To begin, we expand the information vector $S(t)$ to include all fruit that the fly has encountered during the current foraging bout.

Once again let s_i denote the i th element of the vector $S(t)$, so that $s_i = C$ if the i th most recently encountered fruit was clean and $s_i = M$ if the i th most recently encountered fruit was marked. In this general model, one estimates the probability that an encountered fruit is clean in the following way. Let $p_c(S(t), n)$ denote the probability that the next encountered fruit will be clean, given the vector $S(t)$ and that there are n fruit included in this vector. The estimate for $p_c(S(t), n)$ is then

$$p_c(S(t), n) = (s_1 + ws_2 + w^2s_3 + w^3s_4 + \dots w^{n-1}s_n) / (1 + w + w^2 + \dots w^{n-1}).$$

In this equation, $w \leq 1$ is a given weighting factor; it represents the rate at which past encounters are forgotten. If $w = 1$, then all previous encounters are remembered 'forever' and if $w < 1$, previous encounters are 'forgotten' at a geometric rate. The denominator in this expression is simply a weighting factor. It can be simplified by noting that

$$1 + w + w^2 + \dots w^{n-1} = (1 - w^n) / (1 - w).$$

We can then write that

$$p_c(S(t), n) = (s_1 + ws_2 + \dots w^{n-1}s_n)(1 - w) / (1 - w^n)$$

Because of the geometric series, it is extremely simple to derive an updating equation for $P_c(S(t+1), n+1)$ in terms of $p_c(S(t), n)$. This equation is

$$p_c(S(t+1), n+1) = s_{n+1}(1 - w) / (1 - w^{n+1}) + wp_c(S(t), n)(1 - w^n) / (1 - w^{n+1})$$

where s_{n+1} denotes the state of the $n+1$ st fruit encountered in period $t+1$.

If this informational picture were employed in the dynamic modelling, the information variable would be represented by the number of fruit $N(t)$ encountered up to the start of period t and the current estimate of $p_c(S(t), n)$; denote this latter quantity by $P_c(t)$. The objective function would then depend upon the egg complement $X(t) = x$, the number of fruit encountered $N(t) = n$, and the current estimate that an encountered fruit is clean $P_c(t) = p_c$. It is clear that this model would also lead to a region of apparent behavioural plasticity if the data were summarized using only TSLO and the fraction of marked fruit in the last five fruit encountered.

The sliding memory model developed in the paper can be thought of as a special case of this more general model in which w is actually a func-

tion of n , with value 1 if $n \leq 5$ and value 0 if $n > 5$. Unlike the model described in this appendix, however, the dynamics of the sliding memory model are more complicate and all of the five fruit must be tracked.

Appendix 2: Dynamic programming equation with uncertainty in the estimate

In this appendix we show how the dynamic programming Eq. (5) can be modified to include uncertainty about the fraction of clean fruit in the environment. Although there is an underlying true fraction of clean fruit in the environment (p) the fly's estimate of this value (\hat{p}) need not be perfect. This estimate that the fly develops for p depends on the encounter history of the fly. The uncertainty in the estimate means that the fly has probability distribution for p given the estimate \hat{p} . Some of the ways that this distribution could be constructed are Bayesian analysis (Mangel, 1985b; Walters, 1986; Mangel & Clark, 1988), maximum likelihood analysis, or linear operator models (McNamara & Houston, 1987b). We will not describe methods for the

construction of this distribution here, since they detract from the main attention of the paper and appendix.

What happens to the dynamic programming equation in the presence of uncertainty about the fraction of clean hosts in the environment? Given \hat{p} and a procedure for estimating the distribution, the probability of any particular value of p can be computed. This value is then inserted into Eq. (5) instead of $\Sigma_i c(s_i)$. We then obtain

$$\begin{aligned} F(x, s, t, T) = & (1 - p_e) \rho(t) F(x, s, t + 1, T) \\ & + E_{p|\hat{p}} [p_e p [f_c + \rho(t) F(x - 1, s_c, t + 1, T)]] \\ & + p_e (1 - p) \max \{ f_m + \rho(t) F(x - 1, s_m, t + 1, T); \\ & \rho(t) F(x, s_m, t + 1, T) \} \end{aligned}$$

In this equation, $E_{p|\hat{p}}$ denotes the expectation over the true values of p , given the information \hat{p} . This equation takes uncertainty into the estimates of \hat{p} into account. It leads to boundary curves similar qualitatively to the one shown in Fig. 3. Equation (5) is obtained by assuming that the distribution of p , given \hat{p} , is a spike, at $p = \hat{p}$. By doing this we avoid many of the complexities of stochastic dynamic programming (Mangel, 1985b).