

MODELLING BEHAVIORAL DECISIONS OF INSECTS

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Abstract. Many problems in animal behavior can be viewed as dynamic control problems. In this paper, the dynamic viewpoint is used to analyze certain behavioral decisions of insects, in particular oviposition site selection and clutch size. The theory is motivated by work on parasitic wasps and fruit parasitic insects--particularly apple maggot (*Rhagoletis pomonella*) and medfly (*Ceratitis capitata*). The theory presented in this paper is based on Markovian decision processes in either discrete or continuous time. In these decision processes, the objective functional is a measure of fitness obtained through egg production. The paper closes with some speculations about how insects may be able to solve dynamic programming problems.

§1. Introduction: Experimental and Theoretical Motivation

The behavioral ecology of insects provides a wealth of motivation for ecological modelling. The theoretical work which is described in this paper, in particular, is motivated by a number of different sets of experiments and analyses on different types of insects. These will now be briefly described.

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Parasitic Wasps. Charnov and Skinner (1984, 1985) and Skinner (1985) studied clutch size as a function of host volume in the wasp *Nasonia*. In their analysis, they found that most observed field clutch sizes were smaller than the clutch size which maximized fitness per host; this will be called the "Lack Clutch Size" (or LCS) in analogy to David Lack's work on clutch size in birds. Charnov and Skinner provide an explanation for the apparent "non-optimality" of the observed clutches in terms of rates, in analogy to the marginal value theorem of Charnov (1976). It will be seen here that what one means by "optimal," in fact, drives what is considered non-optimal behavior.

Apple Maggot. R. Prokopy and his collaborators and students, particularly B. Roitberg have conducted an elegant series of experiments on the field behavior of *Rhagoletis pomonella* (Prokopy and Roitberg 1984, Roitberg 1985, Roitberg and Prokopy 1981,1982,1983,1984, Roitberg et al. 1982,1984).

Roitberg and Prokopy (1983) studied the effect of host deprivation on the response of *R. pomonella* to its oviposition marking pheromone (OMP). They observed the following kinds of results:

Time Since Last Oviposition (min.)	Percent of Flies Ovipositing in OMP-Marked Fruit
5	10%
10	45%
20	65%
40	66%
80	85%

These numbers were read off by eye from Figure 1 of Roitberg and Prokopy (1983), so they might be a tad off; the trend is clear however. They conclude: "Thus, acceptance of parasitized hosts by short term (< 96 h), host-deprived flies must be due to changes in physiological state associated with host deprivation" (Roitberg and Prokopy 1983, page 71). The exact nature of these physiological changes remain to be determined, but I will provide some speculations of my own in §5.

In another paper on the foraging behavior of the apple maggot (Roitberg et al. 1982), a study is made of the relationship between the number of fruit clusters on a tree, the residence time of the fly in the tree and the giving up time (GUT), which is defined here as the time since the last oviposition before emigration from the tree. The observed data are (read off from Figures 12 and 13 of Roitberg et al. 1982):

Number of Fruit Clusters	Residence Time (min.)	GUT (min.)
2	20	12
4	55	13
8	70	7
16	75	4

(Note: these are only approximate values since they are read off the figures by eye and correspond to mean values.) Note that the GUT decreases with residence time in the patch; this is an observation which is difficult to explain in terms of classical foraging theory.

Medfly. My colleague, J. Carey and his students recently developed an artificial host for field and laboratory studies of the behavior of another tephritid fly, the Mediterranean fruit fly *Ceratitis capitata*. His student, R. Freeman, studied the distribution of eggs as a function of host volume (it is difficult to determine "clutch size" in this case, but total number of eggs is easy). They find the kind of results shown in Figure 1. The key observation here is that the number of eggs per host levels off with host volume. Although it is possible, it appears that this effect is more than the medflies simply running out of eggs.

The theoretical motivation for this paper is recent work done in conjunction with Colin Clark on the theory of foraging (Mangel and Clark 1986). This theory is based on the use of Markovian decision processes for modelling of foraging actions and decisions. In the next section, this approach is described in more detail. It is applied, in the third section, to a model for the behavior of parasitic wasps (also see Mangel 1987) and, in the fourth section to a model for the rose hips fly *Rhagoletis basiola*. The second model is currently under further development and will be used to analyze field experiments by B. Roitberg. The fifth section contains a discussion and, in the spirit of a workshop, some speculations. In particular: how do organisms solve stochastic dynamic programming problems?

§2. Markovian Decision Models

In this section, an approach to modelling behavioral decisions based on Markovian decision processes is described. Mangel and Clark (1986) call this approach "unified foraging theory" since it allows one to treat the three main aspects of behavior--finding food, avoiding predation, and reproducing--in a unified manner.

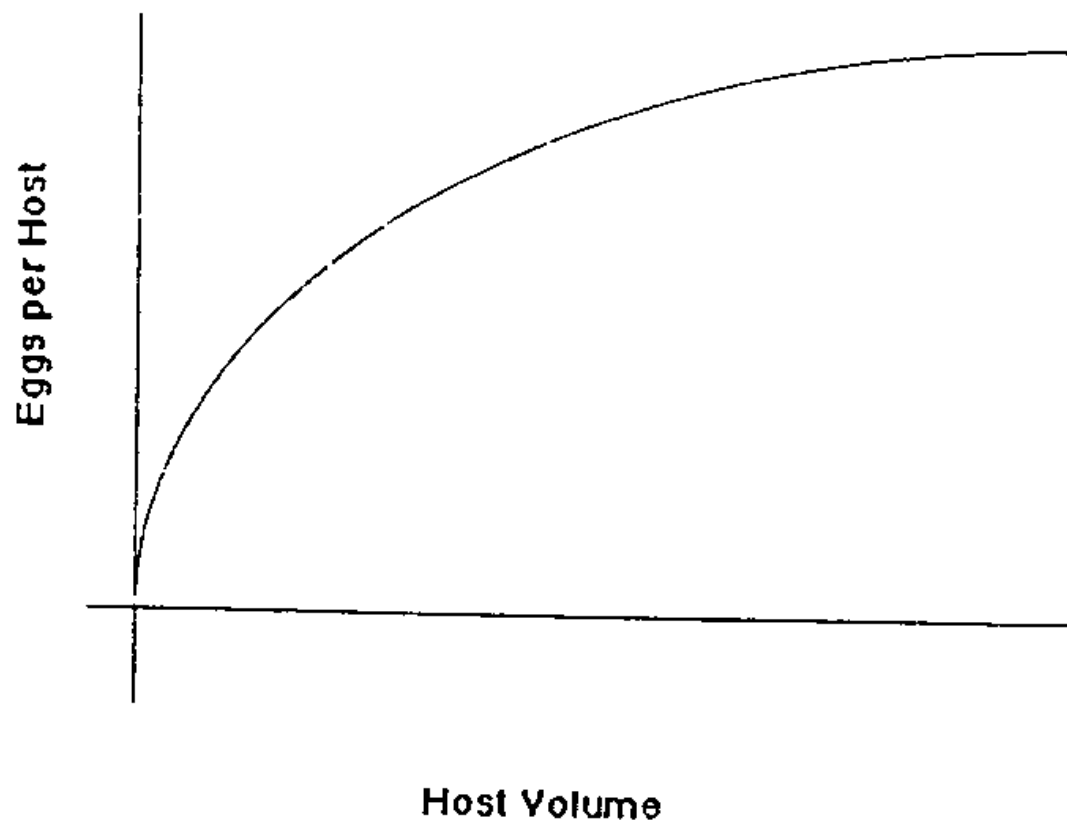


Figure 1. Results of Carey and Freeman on Medfly response to host volume.

The basic objective of these decision models is to be able to treat trade-offs in a consistent manner. One is thus able to deal with a wide variety of ethological problems (see, e.g., Huntingford 1984). There are three main components to this theory:

- 1) A state variable (variables), $X(t)$, which provides a means of assessing the current state of the organism. For example, for insects which produce a fixed number of eggs, $X(t)$ could represent the number of eggs remaining at time t . The state variable changes over time, subject to physiological constraints (it will be seen that these are very important for insect decisions), decisions by the organism, and (usually random) environmental effects. The state variable provides a means for connecting the physiological state of the organism with its behavior.
- 2) An objective functional, which depends upon the current value of the state variable and provides a measure of "value" for the current state variable when assessed at a later point in time. This objective provides a way for connecting long term and short term behaviors. For example, for insects the objective functional might be lifetime fitness obtained through egg production, given that the initial number of eggs is $X(0) = x$.
- 3) A methodology for optimizing the objective functional, subject to the stochastic dynamics of $X(t)$ and any appropriate constraints. The method from stochastic control used in this paper is stochastic dynamic programming (Aoki 1967, Bertsekas 1976, Mangel 1985). This method is actually little more than a bookkeeping technique (with probability 1 something will happen!) and clever use of computers.

The theory presented here, and in Clark (1987), Mangel (1987) and Mangel and Clark (1986), is easy to use. It involves parameters which should be easily measured in the field or laboratory; the mathematical formulation is straightforward and the required computations can be implemented on a desk top microcomputer.

§3. Clutch Size in Parasitic Insects

The results presented in this section were motivated by the work of Charnov and Skinner (1984,1985) and Skinner (1985). There is a considerable overlap between this section (summarized from Mangel 1987) and their papers, as well as with those of Iwasa et al. (1984) and Parker and Courtney (1983). The objective of this section is to

show, by means of the simplest possible model, how the state variable approach can be applied and used to understand clutch size decisions.

Imagine an insect which starts its life with a reserve $X(0) = X_0$ of mature eggs and attacks one of H different kinds of hosts. If it encounters a host of type i and lays a clutch of size ϕ in this host, then assume that its lifetime fitness increases by $W_i(\phi)$. The computation of the increment in fitness, $W_i(\phi)$, is a very nontrivial matter and Charnov and Skinner (1984) and Skinner (1985) did a great job of developing W s for a number of different insect-host systems.

The state variable, $X(t)$, is defined by

$$[3.1] \quad X(t) = \text{number of eggs remaining at time } t.$$

The dynamics of the state variable are then quite straightforward. Consider a small interval of time Δt and define

$$[3.2] \quad \lambda_i \Delta t = \text{Probability of encountering a host of type } i \text{ in } (t, t+\Delta t).$$

If a clutch of size ϕ_i (yet to be determined) is laid on a host of type i , then [3.1] and [3.2] give

$$[3.3] \quad X(t + \Delta t) = X(t) - \phi_i \quad \text{with probability } \lambda_i \Delta t.$$

The objective functional comes next. In order to define it, let T denote the maximum possible lifetime of the insect and set

$$[3.4] \quad F(x, t, T) = \text{maximum expected fitness from egg production between } t \text{ and } T \text{ when the number of eggs remaining at } t \text{ is } X(t) = x.$$

Then one certainly has

$$[3.5] \quad F(x, T, T) = 0$$

5

since there is no value to having any eggs at death. In order to develop the dynamic programming equation (DPE) that $F(x, t, T)$ satisfies, first define $\rho(t)$ by

$$[3.6] \quad 1 - \rho(t)\Delta t = \text{Probability of surviving to time } t+\Delta t, \text{ given} \\ \text{that the insect is alive at time } t;$$

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this quantity can be computed from the usual survivorship curves of demography (see, e.g. Mangel 1987).

Now reason as follows: If the insect encounters a host of type i it can lay a clutch of any size between 0 and the current number of remaining eggs. If the clutch size is ϕ , then the increment in fitness is $W_i(\phi)$ and the number of remaining eggs is decreased by ϕ . In symbols, one has

$$[3.7] \quad F(x, t, T) = \sum_{i=1}^H \lambda_i \Delta t \max_{\phi \leq x} \left\{ W_i(\phi) + (1 - \rho\Delta t) F(x-\phi, t+\Delta t, T) \right\} \\ + (1 - \sum_{i=1}^H \lambda_i \Delta t) (1 - \rho\Delta t) F(x, t+\Delta t, T).$$

Equation [3.7] is the basic DPE associated with this problem. Note how the constraint on the number of eggs arises in a most natural way. There are two ways to analyze equation [3.7]. The first is to set $\Delta t = 1$. In that case, time is measured in discrete units (although the specific unit of time is not given, so that it could be quite small). Equation [3.7] becomes

$$\begin{aligned}
 [3.8] \quad F(x, t, T) = & \sum_{i=1}^H \lambda_i \max_{\phi \leq x} \left\{ W_i(\phi) + (1 - \rho) F(x - \phi, t+1, T) \right\} \\
 & + (1 - \sum_{i=1}^H \lambda_i) (1 - \rho) F(x, t+1, T) .
 \end{aligned}$$

This equation is easily iterated backwards, starting at $t = T-1$, on a desk-top microcomputer. Its solution leads to a number of predictions which will be discussed shortly.

The alternative to $\Delta t = 1$ is the continuous time limit in which Δt approaches 0. To deal with this case, Taylor expand [3.7] in powers of Δt to obtain

$$\begin{aligned}
 [3.9] \quad F(x, t, T) = & \sum_{i=1}^H \lambda_i \Delta t \max_{\phi \leq x} \left\{ W_i(\phi) + F(x - \phi, t, T) + O(\Delta t) \right\} \\
 & + F(x, t, T) + \frac{\partial F}{\partial t} \Delta t - \left(\rho + \sum_{i=1}^H \lambda_i \right) \Delta t F(x, t, T) + o(\Delta t)
 \end{aligned}$$

where $O(\Delta t)$ and $o(\Delta t)$ represent quantities such that

$$\begin{aligned}
 [3.10] \quad \lim_{\Delta t \rightarrow 0} \frac{O(\Delta t)}{\Delta t} &= \text{constant} \\
 \lim_{\Delta t \rightarrow 0} \frac{o(\Delta t)}{\Delta t} &= 0 .
 \end{aligned}$$

Dividing by Δt and letting Δt approach 0 gives the equation

$$[3.11] \quad - \frac{\partial F}{\partial t} = \sum_{i=1}^H \lambda_i \max_{\phi \leq x} \left\{ W_i(\phi) + F(x - \phi, t, T) \right\} - \left(\rho + \sum_{i=1}^H \lambda_i \right) F(x, t, T) .$$

This is a nonlinear, partial differential-difference equation. It is much harder to solve than the discrete time version [3.8]. Some techniques for solving such equations are discussed by Ahmed and Teo (1981) and Teo and Wu (1984).

Returning to the discrete time version [3.8], one finds the following predictions arising from the solution (see Mangel 1987 for more details).

- P_1 : Older insects should be less choosy about where they lay their eggs. For example, there should be more superparasitism near death.
- P_2 : A cohort of identical insects which start life together will, at later times, have a distribution on the values of the number of eggs remaining (caused by weather, food, host encounters, etc.). This will lead to a distribution in clutch sizes.
- P_3 : As the chance of finding hosts for which the optimal clutch size ϕ^* is larger increases, the observed distribution of clutches should change so that smaller clutches are more frequent.
- P_4 : As the conditional probability of survival decreases, the frequency of large clutches should increase.
- P_5 : As the time horizon $T - t$ decreases, for example by host deprivation, the frequency of larger clutches should increase.

Some of these predictions (e.g. P_1 , P_2 , P_4) can be seen by qualitative examination of the dynamic programming equation [3.8]. Others (e.g. P_3 , P_5) are less obvious--it helps to solve [3.8] to see them--but are easily understood when one starts thinking in the paradigm that UFT provides. It is the paradigm of constrained, Markovian dynamics which guides the prediction.

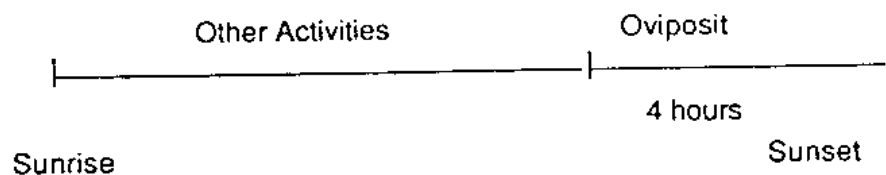
§4. A model for *Rhagoletis basiola*

A model for *Rhagoletis basiola* is described in this section. It differs in many ways from the model of the previous section. The differences are based on a number of biological details. The most important are these: upon encountering a host fruit, the fly either lays one egg or no eggs. The fitness accrued to the mother from this egg depends upon whether or not the host was previously parasitized and if so, when. For

example, one could develop the following kind of data (B. Roitberg, personal communication):

i	Host Type	Relative Fitness, W_i
1	Unparasitized	2.00
	Previously parasitized	
2	1 day before	1.50
3	2 days before	1.00
4	3 days before	0.75
5	4 days before	0.50
6	Larva present (host parasitized 5 or more days previously)	0.20

The lifetime of the fly is about 15 days; each day is divided into 20 hours in which the fly does activities other than search for oviposition sites and 4 hours in which it searches for oviposition sites. A "timeline" for each day can be developed as follows:



Finally, in this model there are two state variables defined as follows:

$X(t, D)$ = number of mature eggs being held at the start of period t on day D

[4.1]

$Y(t, D)$ = number of oocytes (potential eggs), remaining at the start of period t on day D .

The variable $X(t, D)$ has a capacity constraint such that

$$[4.2] \quad X(t, D) \leq C$$

where C is the maximum number of mature eggs that the fly can hold at any time. The variable $Y(t, D)$ satisfies the constraint that

$$[4.3] \quad Y(t, D) \leq Y_M$$

where Y_M is the maximum number of potential eggs.

Now define a fitness function $F_D(x, y, t, T)$ as follows:

$$[4.4] \quad F_D(x, y, t, T) = \text{maximum expected fitness through egg production when } D \text{ days remain, when } X(t, D) = x, Y(t, D) = y, \text{ and } T - t \text{ is the number of periods remaining in day } D.$$

That is, T is the time horizon for foraging for oviposition sites within a day. When analyzing [4.4], it will be understood that $D = 1$ corresponds to the last day of the fly's life. Thus one has the end condition

$$[4.5] \quad F_1(x, y, T, T) = 0.$$

The end condition connecting day D and $D - 1$ is more complicated. Suppose that a fly ends day D with x mature eggs and y potential eggs remaining. During the night, it can, in principle, mature enough eggs to reach the capacity C . Thus, it starts the next day with C mature eggs, as long as $y \geq C - x$. Otherwise it starts the next day with $x + y$ mature eggs. Thus, in addition to [4.5], one has

$$[4.6] \quad F_D(x, y, T, T) = \begin{cases} F_{D-1}(C, y-C+x, 0, T) & \text{if } y \geq C-x \\ F_{D-1}(x+y, 0, 0, T) & \text{if } y < C-x \end{cases}$$

Now consider the dynamic programming equation for behavior within a given day. The discrete time formulation will be used. Let

$$[4.7] \quad 1 - p_D(t) = \text{Probability that the fly is alive at the start of period } t+1 \text{ given that it is alive at the start of period } t \text{ with } D \text{ days remaining.}$$

Also assume that the length of a period is sufficiently great that an egg can be matured in a period, if any potential eggs remain. Finally, introduce the following notation

$$[4.8] \quad \lambda_i = \text{Probability of encountering a host of type } i \text{ in a period (note: } \lambda_i \text{ could easily be a function of } D \text{ and } t \text{ with no change in the algorithm)}$$

and the "indicator functions"

$$I_{x < C} = \begin{cases} 1 & \text{if } x < C \\ 0 & \text{if } x = C \end{cases}$$

$$I_{y > \hat{y}} = \begin{cases} 1 & \text{if } y > \hat{y} \\ 0 & \text{if } y \leq \hat{y} \end{cases}$$

Finally, set

$$\lambda_0 = 1 - \sum_{i=1}^H \lambda_i$$

and $W_0 = 0$. With this notation, the same kind of logic that leads to [3.8] leads to the following dynamic programming equation

$$\begin{aligned}
 [4.9] \quad F_D(x, y, t, T) = & \sum_{i=1}^H \lambda_i \max \left[(1 - p_D(t)) \left\{ F_D(x+1, y-1, t+1, T) I_{x < C} I_{y > 0} \right. \right. \\
 & + F_D(x, 0, t+1, T) I_{x < C} (1 - I_{y > 0}) + F_D(C, y, t+1, T) (1 - I_{x < C}) \left. \right\} ; \\
 & W_i + (1 - p_D(t)) \left\{ F_D(x, y-1, t+1, T) I_{y > 0} + F_D(x-1, 0, t+1, T) (1 - I_{y > 0}) \right\} \left. \right].
 \end{aligned}$$

Although it looks formidable, equation [4.9] is no harder to solve than [3.8]--it's just that the indicator functions make it look more complicated.

Equation [4.9] is somewhat complex, but it is easily solved on a desk-top microcomputer. More interestingly, one can develop Monte Carlo simulations in which insects behave "optimally" according to the solution of [4.9] but encounter host types randomly. By using the simulation, one can perform "computer experiments" analogous to the field and lab experiments on real flies. (Mangel 1987 provides a further discussion of such computer experiments.) For example, a simulation was programmed for the following situation: 100 flies start the last day of their lives, which lasts for 40 periods, with 2 mature eggs and 14 potential eggs. They encounter the six host types randomly, each with equal probability, and make oviposition decisions according to equation [4.9]. Using this simulation, one can perform "host deprivation" experiments by reducing the time horizon. Figure 2 shows the results of such an experiment in which one sees an increase in the oviposition rate in either marked fruit (upper panel) or very inferior hosts (lower panel) with increased host deprivation (which for this problem corresponds to decreased time horizon). This pattern compares very well with the results of Roitberg and Prokopy (1983) discussed previously.

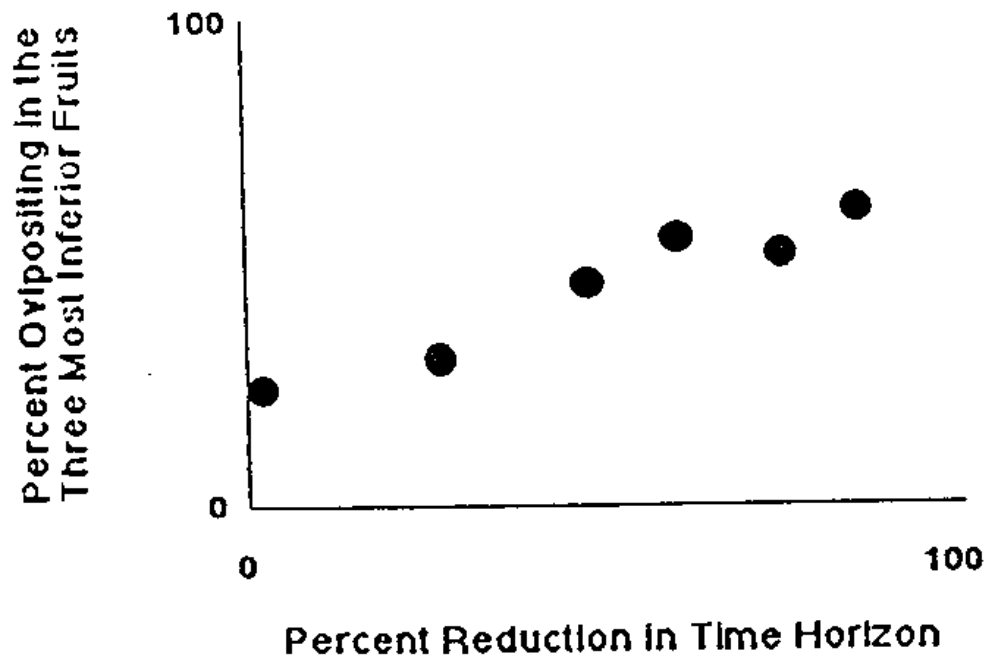
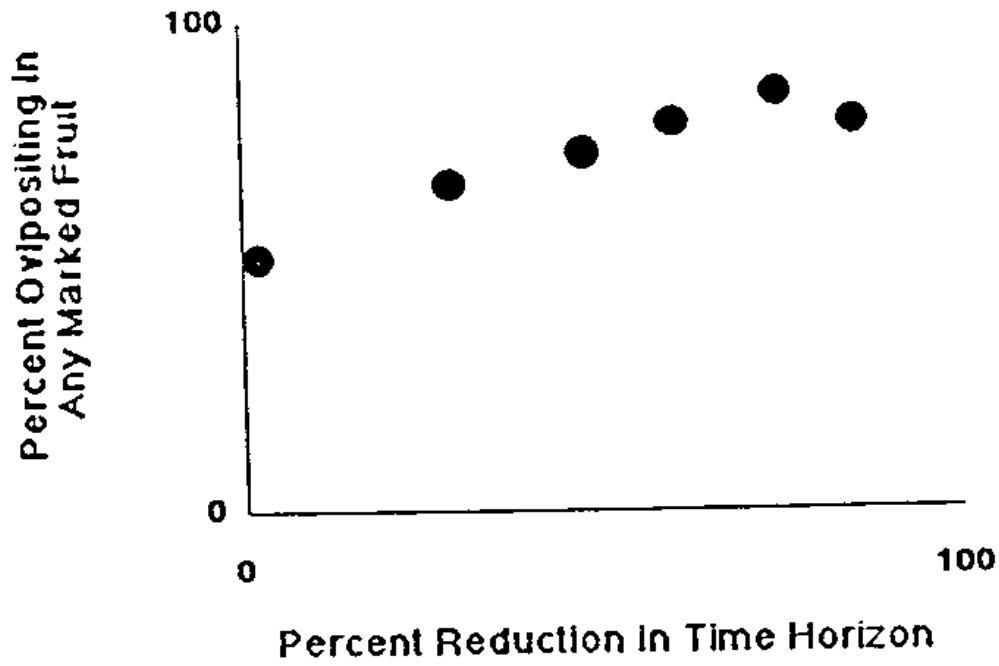


Figure 2. Results of simulation experiments on host deprivation. (a) Fraction of flies ovipositing in any marked fruit. (b) Fraction of flies ovipositing in any of the three most interior fruits.

§5. Discussion and Speculation

The two models presented in this paper provide examples of how Markov decision theory based on state variable models can be used to analyze insect behavior. Other models are possible as well. For example, one can take into account the energetic reserves of the insect and include a state variable that measures those reserves. In such a case, the insect must choose between foraging for food and foraging for oviposition sites (see Mangel 1987 for an example). Markov decision processes thus provide a method for analyzing a wide variety of behavioral activities.

I will close this paper with speculations (fitting for conference proceedings) about how insects might solve dynamic programming problems. There are at least two lines of thought about this question. The first is based on a hypothesis of R. Fox, School of Physics at Georgia Institute of Technology:

Fox's Hypothesis: If one can simulate fast enough then any stochastic optimization problem can be solved.

With this in mind, one can leap to the speculation that perhaps one reason for the evolution of molecular and chemical chaos in organisms is to provide a mechanism for simulation. Most ecologists are familiar with chaos through nonlinear population maps such as the logistic:

$$(5.1) \quad N(t+1) = N(t) + rN(t) (1 - N(t))$$

which goes through a series of bifurcations to chaos as r increases. There are, however, many chemical systems which involve continuous time reaction kinetics that also lead to dynamical chaos. Perhaps these kinetics provide the underlying "tools" by which organisms can solve dynamic programming problems.

In addition to a "chaotic simulation" approach, there is extremely exciting work currently being done by J. Hopfield and his collaborators (e.g. Hopfield 1982, Hopfield and Tank 1985, 1986) on the use of model neuron systems to solve optimization problems. They find that large, interconnected networks of model neurons can find good (if not fully optimal) solutions to hard optimization problems such as the

Travelling Salesman Problem. It is likely that their work can be adapted to deal with dynamic optimization problems such as the ones described in this paper (the Travelling Salesman Problem can, in fact, be put into a recursive dynamic form as well). Much exciting work needs to be done!

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