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EVOLUTION OF HOST SELECTION IN PARASITOIDS: DOES THE STATE OF THE PARASITOID MATTER?

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Insects foraging for oviposition sites face many of the same problems that are addressed in optimal-foraging theory: hosts are often encountered randomly, differ in contributions to lifetime fitness, and require different handling times. A number of authors (Iwasa et al. 1984; Mangel 1987_{a,b}; Charnov and Stephens 1988) have recently suggested that the most insight into insect oviposition decisions will be gained through the computation of trade-offs in lifetime fitness (essentially an "economic" rather than a genetic approach). In that vein, Charnov and Stephens (1988) treated the oviposition-selection problem by the methods of "optimal-foraging theory" (Stephens and Krebs 1986), producing results analogous to those in the theory of optimal-diet selection. (The theory of Charnov and Stephens is summarized in the next section.) This paper is, in a broad sense, a reply to their modeling effort and a direct response to the challenge that they put forth: "How do the results derived here compare with those that would emerge from an explicit dynamic-state-variable approach to the same questions. . . ?" (Charnov and Stephens 1988, p. 719).

The main issue in this paper is not the comparison of the theory of Charnov and Stephens, which I call a rate-maximization theory, with experimental data. Since rate-maximization theories are inherently static (see below), many phenomena cannot be predicted by a theory of oviposition decision making based on rate maximization, for example, the dynamics of host acceptance (Singer 1982) and the response to host deprivation or marking pheromones (Mangel 1987_{a,b}). The major thrust is a comparison of theoretical predictions of rate-maximization and dynamic state-variable approaches for the computation of fitness functions. Although this paper is written with insect parasitoids in mind, the general question actually applies to many phytophagous insects (Dethier 1982; Miller and Strickler 1984).

Parasitoids are classified into one of two broad reproductive groups: those born with a full or nearly full complement of eggs, and those that mature eggs throughout their lives. The approach taken by Charnov and Stephens (1988) and here is to assess trade-offs in fitness. Parasitoids born with all their eggs face an obvious trade-off: an egg used now is not available later. That is, a parasitoid trades

current reproduction directly for future reproduction (such parasitoids have been modeled in Iwasa et al. 1984; Parker and Courtney 1984; Mangel 1987*a,b*). For the case of parasitoids that mature eggs sequentially, Charnov and Stephens assumed that egg production increases mortality. Thus, the trade-off is current reproduction versus future survival (and thus expected future reproduction). This assumption—that egg production increases mortality—is essential to the argument of Charnov and Stephens, and I maintain this assumption throughout the paper.

In the next section, I summarize the “randomly distributed” host model of Charnov and Stephens and the predictions that they derived from the theory. The third section contains a brief discussion of the hypotheses underlying the use of rate maximization in behavioral ecology. The fourth section contains analytic results using a state-variable approach to exactly the same problem as formulated by Charnov and Stephens, and the fifth section contains numerical results. On the one hand, a limitation of the dynamic state-variable approach is that it is difficult to obtain simple formulas as summaries of phenomena. On the other hand, numerical results are easily obtained, and in the fifth section I show how insight can be gained from such numerical results. The sixth section contains a discussion and conclusions.

THE MODEL OF CHARNOV AND STEPHENS

Charnov and Stephens considered the following situation. A parasitoid may encounter H different hosts. Encounters with hosts occur randomly and are characterized by encounter rate λ_i , defined as follows:

$$\begin{aligned} \Pr\{\text{parasitoid encounters a host of type } i \text{ in an interval of length } dt\} \\ = \lambda_i dt + o(dt). \end{aligned} \quad (1)$$

Here, $o(dt)$ denotes terms that go to 0 faster than dt as dt approaches 0. That is, $o(dt)/dt \rightarrow 0$ as $dt \rightarrow 0$. (See the Appendix for a fuller discussion.) If a host of type i is encountered, then the parasitoid may choose to oviposit. Oviposition requires a “handling time” h_i and provides an increment in lifetime fitness E_i . (Charnov and Skinner [1984, 1985] discussed ways in which the increments in fitness can be computed; see also Mangel 1987*a,b*.) The fitness increment E_i from a host of type i is a function of the biology of the host (e.g., volume, growth rate, defenses) and of the parasitoid (e.g., chance for superparasitism). Here, it is taken as fixed.

The parasitoid considered here produces eggs during the course of her life, with mortality affected by the rate at which her eggs mature. In particular, assume that

$$\begin{aligned} \Pr\{\text{parasitoid dies in the next } dt \text{ units of time, given that} \\ \text{her egg production rate is } r\} = z_0(1 + \varphi r)dt. \end{aligned} \quad (2)$$

That is, the “base” mortality rate of the parasitoid is z_0 , in the sense that, when $r = 0$, she will survive to time t with the probability $\exp(-z_0 t)$. Egg production introduces an additional mortality factor, measured by φ .

Charnov and Stephens argued as follows. Represent the lifetime fitness of the

parasitoid as

$$W = \int \frac{w_f}{\tau} \exp(-Zt) dt, \quad (3)$$

where w_f is the "fitness gained from the offspring on a single average host" and τ is the "time required to find (search for) and handle a single average host" (p. 708). A somewhat better interpretation would be to replace w_f/τ by $\omega(t)$, the rate at which fitness is gained through oviposition at time t . Note that, in principle, the mortality rate Z is also a function of time. It actually does not affect the analysis because the next step by Charnov and Stephens (going from their eq. 1 to their eq. 2) is to assume that w_f , τ , and Z are not functions of time (although Z , since it is a decision variable, must in some sense depend on time). Then, the lifetime fitness is simply $W = w_f/\tau Z$. This assumption is equivalent to assuming that both the rate of fitness gain and the rate of mortality are constant throughout the life of the parasitoid; hence, it is an assumption that the behavior is static. *If this assumption is accepted*, the procedure for the computation of lifetime fitness is relatively straightforward.

Step 1.—Apply standard renewal theory to compute w_f/τ . This gives $w_f/\tau = \sum \lambda_i E_i \mathcal{P}_i / (1 + \sum \lambda_i h_i \mathcal{P}_i)$, where $\mathcal{P}_i = 1$ if the i th host type is accepted and 0 otherwise.

Step 2.—Observe that the rate of egg production is the rate at which eggs are used. That is, the rate of egg production is simply $\sum \lambda_i \mathcal{P}_i / (1 + \sum \lambda_i h_i \mathcal{P}_i)$.

Step 3.—Use the formulas $W = w_f/\tau Z$ and $Z = z_0[1 + \varphi(\text{rate of egg production})]$. Simplifying gives $W \propto \sum \lambda_i E_i \mathcal{P}_i / [1 + \sum \lambda_i (h_i + \varphi) \mathcal{P}_i]$.

The "optimal" rule for host acceptance is now determined by choosing the set $\{\mathcal{P}_i\}$ that maximizes W . This is formally a problem in classical diet-selection theory in which $h_i + \varphi$ plays the role of handling time. Application of that theory leads to three predictions. First, by a zero/one rule, hosts are either always accepted or always rejected by the insect. Second, hosts are ranked by $E_i/(h_i + \varphi)$. And third, under the inclusion rule, the acceptance of a given host type does not depend on its own encounter rate. (The derivation of these comes straight from optimal-diet theory; see, e.g., Stephens and Krebs 1986.)

These three rules show why rate maximization is so popular in behavioral ecology—it is easy to use. Yet, the assumption that all elements of the integral in equation (3) are constant is a great leap of faith. In the next three sections, I study the consequences of not making that leap. Even so, at this point notice some of the troublesome features of the rate-maximization approach.

1. *Lack of time dependence.*—By the way in which it is formulated, the rate-maximization approach is independent of physical time. Old insects and young insects, in this formulation, should behave in the same way. Host deprivation can be treated only in an ad hoc manner (e.g., by changing the λ_i after the period of deprivation).

2. *Egg production never appears.*—The model of Charnov and Stephens explicitly incorporates egg production into mortality; but in the end, decisions are completely independent of optimal egg production, which is buried in the mortality factor through encounter rates.

3. *Basic mortality never appears.*—The result of rate maximization is that

decisions are independent of z_0 , the basic mortality rate. Insects with lifetimes of 2 days should, according to the theory of rate maximization, make the same decisions as insects with lifetimes of 2 months.

4. *Closeness of rankings*.—The prediction of rate maximization is that decisions should be binary (i.e., either always or never accept a certain type of host), regardless of how close the members of the actual set of rankings $[E_i/(h_i + \varphi)]$ are to each other. One response would be that when rankings are close, of course, the binary decisions will be smoothed. The problem is that rate maximization provides no means for assessing when parameter sets are “close” to each other.

The fourth and fifth sections contain a state-variable model for this problem. Clearly, the decisions based on rate maximization and the decisions based on state-variable approaches overlap for some parameter ranges. The question is, then, if rate maximization is a special case of the state-variable approach (as it must be), what is the range of its validity? Before addressing the oviposition problem, it is worth considering the general assumptions underlying rate maximization.

RATE MAXIMIZATION IN A STOCHASTIC SETTING AND ITS UNDERLYING ASSUMPTIONS

The use of rate maximization is common in behavioral ecology because of its conceptual clarity and remarkable success (although its success is often disputed). It is based on an application of the renewal theorem to behavioral processes (Paloheimo 1971; Charnov 1973). A careful examination of the premises (Charnov 1973; Stephens and Krebs 1986; Charnov and Stephens 1988) reveals four implicit assumptions about rate maximization.

1. An organism is assumed to behave in a way that maximizes its fitness over an interval $[0, T]$.

2. The fitness, assessed at time T , is assumed to be given by the product of T and the rate at which fitness accumulates.

3. T is sufficiently large that the renewal theorem can be used to compute the rate at which fitness accumulates, and only the first term in the renewal theorem (i.e., the mean) is used. (The actual renewal theorem provides an asymptotic expansion—in powers of $1/T$ —of the rate at which fitness accumulates. That is, the rate of gain in fitness is the sum of the mean and $\sum_i \psi_i/T^i$, where the ψ_i 's are asymptotically normally distributed random variables. Thus, as T increases, only the mean matters; but for finite T , correction terms always exist. See Karlin and Taylor 1977 for further details.)

4. Behavior is fixed over the interval $[0, T]$, determined at the beginning and not changed regardless of what happens for intermediate times.

The conflicting assumptions are 3 and 4, that the interval is sufficiently long for only means to matter and that behavior is fixed over this interval. In light of these assumptions, the truly remarkable feature of rate maximization in behavioral ecology is that it works as well as it does, for example, with energy-budget rules (see Houston and McNamara 1985). It may be that there is an intermediate time scale on which both assumptions are valid, or it may be that the decisions obtained using rate maximization are the same as decisions obtained using more-complete models. What happens if these assumptions are dropped?

FORMULATION, DERIVATION, AND ANALYSIS OF THE STATE-VARIABLE MODEL

The insect-oviposition problem studied in this paper is a problem in stochastic-optimization theory. In particular, methods of stochastic-dynamic programming (Mangel and Clark 1986, 1988; McNamara and Houston 1986) can be used to obtain optimal decisions. In this section, I show how to derive the appropriate dynamic-programming equations and describe certain analytic results. The model developed in this section is the exact analogue of the model of Charnov and Stephens (1985). Such dynamic-programming equations are not hard to derive, once one sees the logic of the procedure. Since understanding the origin of the equation is so important for ensuing discussions, I ask the reader to bear with me during the derivation.

To begin, introduce a state variable $X(t)$, which is the insect's egg complement at time t . Let r denote the rate of egg production and c denote the rate at which eggs are laid. Then, the dynamics of the state variable are

$$X(t + dt) = \min\{X(t) + (r - c)dt, \text{cap}\}, \quad (4)$$

where cap denotes the insect's egg-load capacity, that is, the maximum number of eggs that she can hold.

Next, use the assumptions embodied in equations (1) and (2). In particular, the exponential form for the mortality function implies that

$$\Pr\{\text{insect is alive at time } t + h | \text{alive at time } t\} = \exp(-Zh). \quad (5)$$

(This is simply the memoryless property of the exponential distribution.)

Introduce a lifetime-fitness function $W(x, t)$ defined as

$$W(x, t) = \max \mathcal{E}\{\text{fitness obtained through oviposition decisions} \\ \text{from time } t \text{ onward, given that } X(t) = x\}. \quad (6)$$

In this equation, the maximum is taken over all behavioral decisions: these are the rate of egg production and oviposition decisions upon encountering a host. \mathcal{E} denotes the expectation over stochastic host encounters.

The dynamic-programming equation characterizes the dynamics of the lifetime-fitness function $W(x, t)$. It is based on two premises: (1) with probability 1, something will happen (in this case, the insect either does not encounter any host or encounters one of the hosts in the interval of time dt); and (2) whatever happens, act optimally (in this case, make the optimal oviposition decisions).

The only remaining assumption concerns the interplay of host encounters and the rate of egg production. Charnov and Stephens implicitly assumed that the rate of egg production is determined before host encounter occurs, and I do the same. Thus, $W(x, t)$ satisfies the equation

$$W(x, t) = \max_r \{ ((1 - \sum \lambda_i dt) \exp[-z_0(1 + \varphi r)dt] W(x', t + dt) \\ + \sum \lambda_i dt \max\{\exp[-z_0(1 + \varphi r)dt] W(x', t + dt); \\ E_i + \exp[-z_0(1 + \varphi r)(h_i + dt)] W(x'_i, t + h_i + dt)\}) \}. \quad (7)$$

In this equation, $x' = \min(x + rdt, \text{cap})$ and $x'_i = \min[x + r(h_i + dt) - 1, \text{cap}]$. The terms on the right-hand side of equation (7) have the following interpretations. The expression \max_r denotes that the maximum is taken over all biologically possible choices of the rate of egg production. The first term on the right-hand side is the expected lifetime fitness if no host is encountered during the interval from t to $t + dt$; this occurs with probability $1 - \sum \lambda_i dt$. When no host is encountered, the parasitoid survives from time t to time $t + dt$ with probability $\exp[-z_0(1 + \phi r)dt]$ and holds $x + rdt$ eggs at time $t + dt$. The second term represents the expected fitness if a host is encountered. A host of type i is encountered with probability $\lambda_i dt$. The terms inside the second \max compare lifetime fitnesses if the host is rejected and if the host is accepted. If the host is rejected, then fitness is identical to the situation in which no host is encountered. If the host is accepted, the parasitoid receives an immediate increment in fitness, E_i , but uses up an additional h_i units of time handling the host. The probability that she survives $h_i + dt$ units of time into the future is $\exp[-z_0(1 + \phi r)(h_i + dt)]$. If she does survive, she starts time $t + h_i + dt$ with egg complement $x + r(h_i + dt) - 1$; the -1 comes from using an egg.

The remainder of the derivation of the continuous-time dynamic-programming equation is given in the Appendix. The final equation is (the subscripts on W denote partial derivatives):

$$-W_t = \max_r (rW_x - [\sum \lambda_i + z_0(1 + \phi r)]W(x, t) + \sum \lambda_i \max\{W(x, t); E_i + \exp[-z_0(1 + \phi r)h_i]W(x + rh_i - 1, t + h_i)\}). \quad (8)$$

The solution of this equation, and corresponding decisions, are functions of both state and time and are thus dynamic. As t increases, however, the solution of equation (8) often approaches a stationary or steady-state solution, in which fitness and decisions are functions of state only. It is these stationary decisions that should be compared with the decisions derived from the rate-maximizing approach. In the steady state, the left-hand side of the equation is 0. Then, fitness is a function of x only and satisfies the equation

$$0 = \max_r (rW_x - [\sum \lambda_i + z_0(1 + \phi r)]W(x) + \sum \lambda_i \max\{W(x); E_i + \exp[-z_0(1 + \phi r)h_i]W(x + rh_i - 1)\}). \quad (9)$$

Note the following properties of this equation (which can be compared to and contrasted with the properties of the rate-maximization approach).

1. The rate of egg production explicitly enters into the determination of $W(x)$. In principle, this can be "removed" by solving for the r that maximizes the right-hand side of equation (9). This gives an optimal egg production rate, $r^* = R(W, W_x)$. The optimal rate can then be substituted back into equation (9), leading to a nonlinear partial differential-difference equation (Mangel 1985 contains some worked examples of this procedure). In this particular case, the resulting equation is quite intractable.

2. Hosts are no longer ranked according to the simple procedure described in the preceding sections. Instead, the decision to accept a host requires that

$$E_i + \exp[-z_0(1 + \phi r)h_i]W(x + rh_i - 1) > W(x). \quad (10)$$

Note that host acceptance now depends not only on E_i , ϕ , and h_i but also on the basic mortality rate (z_0), the current egg complement (x), and the egg production rate (r). This is encouraging and makes good biological sense. Iwasa et al. presented a similar acceptance rule (1984, p. 214, eq. 16).

Equation (10) can be interpreted as a marginal-value rule as well. The easiest way to see this is to use the Taylor expansion of $W(x + rh_i - 1)$ around x and keep just the first and second terms of the expansion. This gives the acceptance rule:

$$E_i + \exp[-z_0(1 + \phi r)h_i](rh_i - 1)W_x > W(x)\{1 - \exp[-z_0(1 + \phi r)h_i]\}. \quad (11)$$

Rearranging terms yields

$$\exp[-z_0(1 + \phi r)h_i](rh_i - 1)W_x > W(x)\{1 - \exp[-z_0(1 + \phi r)h_i]\} - E_i.$$

Note the nice interpretation of this equation: the left-hand side is the marginal rate of gain in fitness when the host is accepted times the net number of eggs produced during the handling period. The right-hand side is a measure of the difference in fitnesses if the host is rejected or accepted.

3. The decision rule (10) indicates that acceptance or rejection of a host does not explicitly depend on its encounter rate; this is similar to the conclusion based on rate maximization. The reason is easy to see from the full state-variable formulation: host-acceptance decisions are made only after the parasitoid encounters the host. At that point, the encounter rate enters the decision only implicitly in the determination of fitness $W(x)$. (See also the Discussion and Conclusions.)

The dynamic-programming equation is analytically complicated and difficult to solve. However, much can be learned by considering careful numerical comparisons, which is done in the next section.

NUMERICAL RESULTS

The numerical solution of the dynamic-programming equation allows one to study the effects of a variety of biological parameters on host-acceptance decisions. In this section, I derive the dynamic-programming equation using discrete time and the state space and then study the effects of capacity, basic mortality rate, closeness of rankings, egg production rate, host-encounter rate, and approach to stationary decisions for host acceptance.

The limitation of numerical studies is that specific parameter values must be used in computations, but the objective of the study is obtaining general conclusions. Here, I present numerical results and then a relatively general conclusion. The stated conclusion has been tested over a wide range of parameter values.

It is possible to obtain the numerical solution of the dynamic-programming equation (7) directly, by choosing appropriate discrete values of time and the state variable. It is easier, however, to simply recast the equation in a discrete-time setting from the outset. This is done simply by setting $dt = 1$ in equation (7) if no host is found or if a host is encountered but rejected and $dt = 0$ if a host is encountered and accepted. It also helps to think of fitness as a function of egg complement and the time that the insect has left to live, denoted by s and called the time to go (to the end of life). If $W(x, s)$ denotes its lifetime fitness from time s , then using one unit of time reduces its future time to live by 1. The discrete-time

dynamic-programming equation is thus

$$W(x, s) = \max_r((1 - \sum \lambda_i) \exp[-z_0(1 + \varphi r)] W(x', s - 1) + \sum \lambda_i \max\{\exp[-z_0(1 + \varphi r)] W(x', s - 1); E_i + \exp[-z_0(1 + \varphi r)h_i] W(x'_i, s - h_i)\}). \quad (12)$$

Again, $x' = \min(x + r, \text{cap})$ and $x'_i = \min(x + rh_i - 1, \text{cap})$; if $s - h_i < 0$, then it is set equal to 0. Note that the encounter rates λ_i may require some reinterpretation, since $\sum \lambda_i \leq 1$.

In order to solve this equation, an initial condition (which corresponds to the end of the insect's life; see Mangel and Clark 1986, 1988) is needed. Since any eggs remaining at the end of the parasitoid's life are valueless, we impose $W(x, 0) = 0$ and solve the equation forward in time (i.e., for increasing s).

The solution of the dynamic-programming equation is thus obtained by iterating until some stopping criterion is reached. A suitable stopping rule is that $\sum_x |W(x, s) - W(x, s - 1)| < \epsilon$, where ϵ is an appropriately chosen "cutoff parameter." The interpretation of this condition is that the total difference between $W(x, s)$ and $W(x, s - 1)$ is less than the cutoff. This corresponds, when ϵ is small, to an approximately stationary solution of the dynamic-programming equation. In the numerical results reported below, the value of ϵ was chosen such that behavioral decisions are essentially constant by the time of the cutoff. Most of these results involve comparisons of stationary decisions.

An alternative approach is to consider the stationary version of the dynamic-programming equation. This stationary version is

$$W(x) = \max_r((1 - \sum \lambda_i) \exp[-z_0(1 + \varphi r)] W(x') + \sum \lambda_i \max\{\exp[-z_0(1 + \varphi r)] W(x'); E_i + \exp[-z_0(1 + \varphi r)h_i] W(x'_i)\}). \quad (13)$$

Its solution can be found by a process of iteration. We begin with a guess $W^0(x)$ and then iterate for $k \geq 1$ according to

$$W^k(x) = \max_r((1 - \sum \lambda_i) \exp[-z_0(1 + \varphi r)] W^{k-1}(x') + \sum \lambda_i \max\{\exp[-z_0(1 + \varphi r)] W^{k-1}(x'); E_i + \exp[-z_0(1 + \varphi r)h_i] W^{k-1}(x'_i)\}). \quad (14)$$

The iteration procedure is followed until a predetermined stopping rule is reached. An effective rule, as in the truly dynamic version, is that $\sum_x |W^k(x) - W^{k-1}(x)| < \epsilon$. If all handling times are equal to one period, then the iteration of the stationary version of the equation and the solution of the time-dependent version are identical procedures. If some handling times are greater than one period, the procedures differ, although the solutions should be nearly identical for cutoff parameters that are small enough. In the results reported here, I used the iterative solution of the stationary equation for all computations except for the computations in which the approach to stationary decisions was studied. This has the effect of ignoring any time dependences in the lifetime-fitness function from the outset and letting time introduce itself only into the survival functions.

The number of iterations needed to reach stationary decisions, as defined by the condition after equation (14), depends on the value of ϵ . When this parameter is small, the number of iterations to stationary decisions often greatly exceed the expected lifetime of the parasitoid. Stationary decisions, however, are often achieved in just a few periods (see below). The fairest comparisons with rate maximization are ones in which decisions associated with the stationary fitness functions are used.

For the results that follow, three host types are used, and parameter values are changed according to the effect being studied. In general, only two values of egg production rate are allowed: $r = 0$ (no eggs produced during the next interval), and $r > 0$. In general, this is written $r = \{0, r_+\}$, where r_+ is the positive rate of egg production.

The objective of the analysis that follows is to understand when the rate-maximization approach is valid. This understanding is summarized in terms of predictions about biological conditions and rate maximization.

Effects of Capacity

The capacity constraint affects the number of eggs that the parasitoid can hold, and thus egg production rate, and thus mortality. The following parameter values were used:

| Host type | λ | E | h |
|-----------|-----------|-----|-----|
| 1 | 0.45 | 1.0 | 1 |
| 2 | 0.25 | 0.5 | 2 |
| 3 | 0.25 | 0.1 | 2 |

and $z_0 = 0.05$, $\phi = 2$, $r = \{0, 1\}$. According to rate maximization, only the first host should be taken. Three values of capacity were used: $\text{cap} = 5, 10, 20$. The following results emerge. When $\text{cap} = 5$ or 10, the stationary decisions correspond to rate maximization. When $\text{cap} = 20$, the stationary decision is to accept host 1 only if $x < 13$ but to accept both hosts 1 and 2 if $x \geq 13$. This makes intuitive sense: insects with a smaller holding capacity for eggs cannot take into account the effects of state variables.

Conclusion 1.—Parasitoids with small holding capacities are more likely to function as rate maximizers than are parasitoids with large capabilities for holding mature eggs.

Effects of Basic Mortality

In this case, a value of $\text{cap} = 5$ was used, along with encounter and egg-production parameters given above. A number of different host parameters were used and the basic mortality rate varied. With the host parameters given above, the following results emerge:

| Basic mortality rate, z_0 | Decision | $W(\text{cap})/W(1)$ |
|-----------------------------|---------------------------------|----------------------|
| 0.05 | Type 1 only | 1.32 |
| 0.15 | Type 1; type 2 if $x = 1, 4, 5$ | 1.68 |
| 0.25 | Types 1 and 2 | 1.79 |
| 0.50 | Types 1 and 2 | 1.71. |

A second set of encounter parameters was also used:

| Host type | λ | E | h |
|-----------|-----------|-----|-----|
| 1 | 0.45 | 1.0 | 1 |
| 2 | 0.25 | 0.8 | 2 |
| 3 | 0.25 | 0.6 | 2 |

According to rate maximization, hosts 1 and 2 should be accepted. For $z_0 = 0.01$ or 0.05, this is indeed the case; but for $z_0 = 0.15$, all hosts are accepted in the stationary regime except that when $x = 2$ only types 1 and 2 are accepted.

Another result emerging from these computations is that as z_0 decreases, $W(\text{cap})/W(1)$ approaches one; that is, there is little difference in lifetime fitness for a full or nearly depleted initial egg complement.

Conclusion 2.—Long-lived parasitoids, with a low basic mortality rate, are more likely to be rate maximizers than are short-lived parasitoids, with a high basic mortality rate.

Closeness of Rankings

The closeness of rankings, measured by the effect on the overall rate of accumulation of fitness, does not enter into the rate-maximization decisions. Consequently, rate maximization provides no systematic way of assessing the effects of closeness of rankings on deviations from rate-maximizing behavior.

For example, for the first set of host-encounter parameters given above, the rate of fitness increase is 0.19 if only host type 1 is accepted and 0.17 if host types 1 and 2 are accepted. For $z_0 = 0.05$, $r = \{0, 1\}$, $\varphi = 2$, and $\text{cap} = 5$, the state-variable model gives the same decisions. But consider a small change in handling times:

| Host type | λ | E | h |
|-----------|-----------|-----|-----|
| 1 | 0.45 | 1.0 | 1 |
| 2 | 0.25 | 0.5 | 1 |
| 3 | 0.25 | 0.1 | 1 |

and let all other parameters remain the same. In this case, the rates of fitness increase are 0.1915 if only host type 1 is accepted and 0.1855 if both host types 1 and 2 are accepted. Thus, the method of rate maximization leads to the prediction that only host type 1 will be accepted. Solution of the dynamic-programming equation shows that, in the regime of stationary decisions, both host types 1 and 2 are accepted. If parameters are changed slightly, such that the rates of gain in fitness are 0.19 and 0.17, then the stationary decision is to accept host type 1 always and type 2 when $x = 5$. (Note that this is also an example of "partial preferences"; see below.)

Conclusion 3.—If rankings are close, rate maximization may fail as a predictor of oviposition decisions. In addition, the formalism of rate maximization does not allow one to determine when the decisions based on rate maximization will optimize accumulated lifetime fitness from ovipositions. The state-variable approach allows this determination.

Effect of Egg Production Rate

The egg production rate affects the decisions through mortality. Since the rate of egg production enters into mortality as the factor φr , it is not necessary to

consider the effects of r and ϕ separately. Thus, only the effects of r are discussed. Higher egg production implies higher mortality rates. Consider the following host parameters:

| Host type | λ | E | h |
|-----------|-----------|-----|-----|
| 1 | 0.45 | 1.0 | 1 |
| 2 | 0.25 | 0.5 | 1 |
| 3 | 0.25 | 0.1 | 1 |

with $z_0 = 0.05$, $\phi = 2$, $\text{cap} = 5$, and varying values of nonzero egg production. The decision based on rate maximization is to accept only host type 1.

What does the stationary version of the dynamic-programming equation lead to? When $r = \{0, 1\}$, the stationary decision is to accept host types 1 and 2 and produce eggs when $x \leq 1$. When $r = \{0, 0.5\}$, the stationary decision is to accept host type 1 always and host type 2 when $x \geq 3$ and to produce eggs when $x < 3$. When $r = \{0, 0.2\}$, the stationary decision is to accept host type 1 always and host type 2 when $x = 5$ and to produce eggs when $x \leq 4$.

Conclusion 4.—If egg production increases mortality, then insects with low egg production rates are more likely to be rate maximizers. The effects of decreasing egg production rates or decreasing basic mortality rates are fundamentally the same.

Dependence on Encounter Rates

The approach based on rate maximization predicts that the acceptance of a host is independent of its encounter rate. The state-variable approach predicts that acceptance of a host depends only implicitly on the encounter rate with that host, through the value of the fitness function. Numerical experimentation confirms this. The following host parameters were used:

| Host type | E | h |
|-----------|-----|-----|
| 1 | 1.2 | 1.0 |
| 2 | 0.9 | 2.0 |
| 3 | 0.6 | 2.5 |

The values of λ_1 and λ_2 were both fixed at 0.2. According to rate maximization, host types 1 and 2 should be accepted. As the value of λ_3 varies from 0.05 to 0.6, the stationary decisions do not change at all and are to take types 1 and 2 always and to take type 3 if $x = 1$.

Approach to Stationary Decisions

Since the approach based on rate maximization is a static theory, it can shed little insight into the dynamics of host acceptance and the rate at which stationary decisions are approached. The full dynamic model is ideal for the study of this property. For example, consider the following host-encounter parameters:

| Host type | λ | E | h |
|-----------|-----------|-----|-----|
| 1 | 0.45 | 1.0 | 1 |
| 2 | 0.25 | 0.5 | 2 |
| 3 | 0.25 | 0.1 | 2 |

with $z_0 = 0.05$, $r = \{0, 1\}$, and $\varphi = 2$. According to rate maximization, only host type 1 should be accepted. The following computational results emerge when $\text{cap} = 10$ (recall that s is the number of periods remaining in the parasitoid's life):

at $s = 1$, accept all hosts;

at $s = 2$, accept only type 1;

as s increases from $s = 3$ to $s = 35$, accept types 1 and 2 depending on the value of x ;

for $s > 35$, the stationary decision is the same as for the case of rate maximization.

How are these results interpreted? When $s = 1$, the insect is at the last period of her life and should accept any host that she encounters. When $s = 2$, the parasitoid appears to maximize rate; but what is happening is that hosts 2 and 3 are rejected. Since they have a two-period handling time, accepting them precludes the chance of encountering a host of type 1 in the last period, and they are therefore rejected. As s ranges from 3 to 35, host types 1 and 2 are accepted, with the acceptance of host type 2 depending on both time and the value of the egg complement (as suggested in eq. 12).

Similar results emerge for other parameter values. For example, if the host parameters are

| Host type | λ | E | h |
|-----------|-----------|-----|-----|
| 1 | 0.45 | 1.0 | 1 |
| 2 | 0.25 | 0.3 | 1 |
| 3 | 0.25 | 0.1 | 1 |

and $z_0 = 0.05$, $r = \{0, 1\}$, and $\varphi = 2$, then according to rate maximization only host type 1 should be taken. For $\text{cap} = 5$, the following results emerge from the solution of the dynamic-programming equation:

for $1 \leq s < 4$, accept all hosts, regardless of x ;

for $4 \leq s \leq 8$, accept hosts 1 and 2 for all values of x and host 3 depending on x ;

for $9 \leq s \leq 13$, accept hosts 1 and 2 only, for all values of x ;

for $14 \leq s \leq 24$, accept host 1 for all values of x and host 2 depending on x ;

for $s \geq 25$, the stationary-decision regime is reached. In this limit, host type 1 is always accepted and host type 2 is accepted if $x = 5$.

Finally, consider a slight variation of the last parameter set in which E_2 is increased from 0.3 to 0.5. The decision according to rate maximization is to take only host type 1. The following results emerge from the dynamic-programming equation:

for $1 \leq s \leq 4$, accept all three hosts;

for $5 \leq s \leq 8$, accept types 1 and 2 and type 3 depending on the value of x ;

from period 9 on, stationary decisions are reached, in which host types 1 and 2 are accepted for all values of x .

Conclusion 5.—Host-acceptance decisions based on the premise of maximizing accumulated lifetime fitness are truly dynamic phenomena, in which the approach to stationary decisions depends on time, encounter and fitness parameters, and basic mortality rate. The analysis of rate maximization cannot be used to assess the approach to stationary decisions.

This conclusion is noteworthy because of considerable empirical evidence that

host-acceptance decisions by ovipositing insects change over time (see the examples of boll weevils attacking cotton, Cate et al. 1979; apple maggot flies attacking apples and hawthorn, Stanek et al. 1987). The approach based on rate maximization predicts that such time dependence does not occur.

Partial Preferences

According to the theory of rate maximization, host acceptance follows a "zero/one" rule: hosts are either always accepted by the parasitoid or never accepted by the parasitoid. With the full dynamic, state-variable model, however, "partial preferences" may occur, in which hosts are sometimes accepted and, at other times, not accepted. The simplest—and most easily understood—example follows from the dynamic results just presented. In that case, depending on time (i.e., age of the parasitoid), a host is sometimes accepted and sometimes not. This is a simple time effect: when s is small (the parasitoid is close to the end of her life), it is optimal to accept hosts (and thus gain fitness) that would be unacceptable if her expected future lifetime were large.

A more interesting case arises when the stationary decisions appear to exhibit partial preferences in the sense that, by ignoring the state of the parasitoid, one would observe partial preferences. (Naturally, in the full state-variable model, decisions are still binary but in a larger space encompassing both host parameters and parasitoid state; for a discussion of partial preferences in diet selection, see McNamara and Houston 1987.) Some examples of apparent partial preferences have already appeared. Another is the following. For the parameters

| Host type | λ | E | h |
|-----------|-----------|-----|-----|
| 1 | 0.45 | 1.0 | 1 |
| 2 | 0.25 | 0.5 | 2 |
| 3 | 0.25 | 0.1 | 2 |

and $z_0 = 0.05$, $r = \{0, 1\}$, $\varphi = 2$, and $\text{cap} = 20$, the optimal decision based on rate maximization is to accept only host type 1. The stationary decision for the state-variable model, however, is to accept host type 2 as well, as long as $x \geq 13$. Thus, a stationary partial preference exists. This is due to the capacity effect. When the value of x is large, the parasitoid should accept host type 2 because she has a large number of eggs, which will provide some fitness, certainly more than the zero fitness provided by not accepting the second host. The interplay of capacity and survival probability causes partial preferences. Partial preferences are also observed for many other values of host encounter and biological parameters.

Stephens (1985) has argued that absolute preferences are most likely not observable, even if they occur. However, the existence of absolute preferences is usually cited as one of the main predictions of theories based on rate maximization. The state-variable approach shows that such simple absolute preferences need not occur.

Does Any of This Matter? A Comparison of Fitness Functions

The preceding comparisons all involve the differences between behavioral decisions, but evolutionary pressure is determined by the values of the fitness

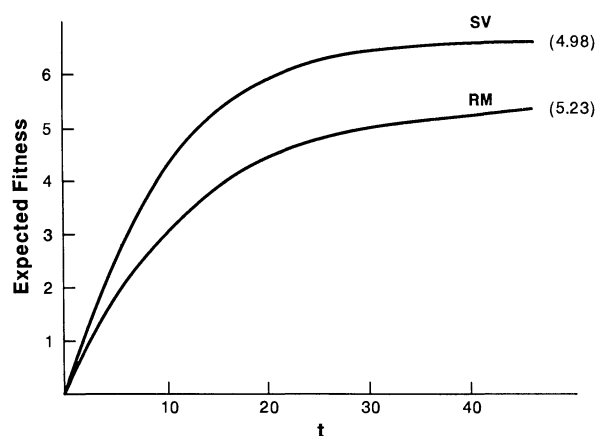


FIG. 1.—Expected fitnesses (and variances in parentheses) for simulated parasitoids following the optimal decisions of rate-maximization (RM) and state-variable (SV) approaches. Parameters are the last set of values in the text (subsection “*Does Any of This Matter?*”). Parasitoids using RM decisions have an expected fitness of about 80% that of parasitoids using SV decisions.

functions. It might be, for example, that although oviposition decisions differ, the actual fitness functions do not. For example, consider the following parameter set:

| Host type | λ | E | h |
|-----------|-----------|-----|-----|
| 1 | 0.45 | 1.0 | 1 |
| 2 | 0.25 | 0.5 | 1 |
| 3 | 0.25 | 0.1 | 1 |

and $z_0 = 0.05$, $r = \{0, 1\}$, $\text{cap} = 5$, and $\varphi = 2$. In this case, the optimal decision according to rate maximization is to accept only host type 1, whereas the optimal stationary decision from the dynamic model is to accept host types 1 and 2.

The expected fitness associated with either the rate-maximizing or state-variable decisions can be computed by the method of forward iteration (Mangel and Clark 1988) or by a Monte Carlo simulation. Figure 1 shows the expected fitnesses obtained by the simulation of 5000 parasitoids following either rate-maximization or state-variable decisions. The ultimate, steady-state values of fitness are 5.4 (for the rate-maximizing decisions) and 6.7 (for the state-variable decisions), a factor of $5.4/6.7 = 0.81$, which suggests that there are strong evolutionary pressures to follow the optimal state-variable decisions.

DISCUSSION AND CONCLUSIONS

The comparison of rate-maximization and dynamic state-variable approaches to parasitoid oviposition decisions allows us to ascertain when the approach of rate maximization is valid and when its predictions should apply. In summary, the following results emerge. Insects with small holding capacities for mature eggs or low basic mortality rate, z_0 , are more likely to follow the predictions of rate

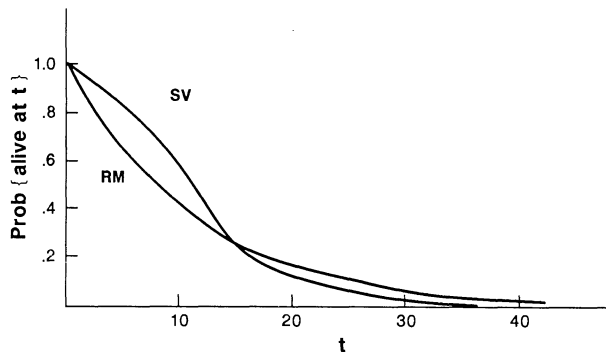


FIG. 2.—Expected survivorship curves for the situations depicted in figure 1.

maximization. When the rankings used in the rate-maximization approach are close to each other or the egg production rate of the insect is low, the decisions based on rate maximization are likely to differ from the ones based on the state-variable approach. The decision to accept a host for oviposition, based on either approach, depends only weakly on the encounter rate with that host. (For gregarious or clutch-laying parasitoids, this may not be the case; see Mangel 1987a for an example.) Host-acceptance decisions based on rate maximization are stationary and independent of time, but those based on the state-variable approach may be truly dynamic. Partial preferences may occur in decisions based on the state-variable approach. The total lifetime fitnesses computed using the rate-maximization approach and the state-variable approach may differ considerably. Finally, in some situations, the decisions based on the rate-maximizing approach and the decisions based on the state-variable approach agree. Thus, the predictions from the rate-maximizing approach of both the all-or-none acceptance decision and the ranking by $E_i/(h_i + \phi)$ are not well borne out, but the prediction of inclusion of a host independent of its own encounter rate is generally upheld. In addition, the results presented here show the importance of basic mortality, capacity, and actual rate of egg production in the optimal oviposition decisions.

Part of the underlying difference between the two approaches involves survival probabilities. The rate-maximization approach assumes that a steady state is reached instantaneously and that, in this steady state, eggs are produced at a constant rate (about 0.31 eggs per period for the last set of parameters given above). The state-variable approach, however, assumes that eggs are produced only when needed. This has the effect of providing greater survival for considerable amounts of time. Figure 2 shows the expected survivorship curves for each of the decisions for the last set of parameters given. Under rate maximization, the egg production rate leads to a single-period survival of 0.92; the probability of being alive after t periods is thus 0.92^t . With the state-variable approach, eggs are produced only when needed. An insect starting her life with a full egg complement will thus not produce eggs until the expected number of eggs used exceeds its initial complement, approximately when t satisfies $(\lambda_1 + \lambda_2)t > 5$.

The corresponding survival values are 0.95 when no eggs are produced and 0.86 when one egg is produced per period. Thus, if $t < 5/(\lambda_1 + \lambda_2)$, survival is 0.95^t . If $t > 5/(\lambda_1 + \lambda_2)$, survival is $(0.95)^{5/(\lambda_1 + \lambda_2)}(0.86)^{t - 5/(\lambda_1 + \lambda_2)}$. The results shown in figure 2 indicate that the state-variable decisions lead to considerably higher survival (and thus expected fitness) for the first 12 periods; the crossover point is at about 30% survival. The state-variable approach is "optimal" because the parasitoid produces eggs only when she needs them, rather than at a lower but constant rate.

Other factors could have been included in the state-variable models. For example, encounter rates and mortality might be functions of the egg complement, x , with encounter rates decreasing as the egg complement increases and mortality rate increasing as the egg complement increases. The effect of each of these would be to drive the state-variable decisions away from the rate-maximizing decisions.

Unlike the approach of rate maximization, a full dynamic, state-variable model allows us to understand the effects of biological parameters that are "averaged out" of the rate-maximization approach. For this particular problem, the biological parameters of the parasitoid that do not appear in the rate-maximization approach include effects of capacity constraints, basic mortality rates, closeness of rankings of hosts in the rate of fitness computation, and actual rate of egg production. The state-variable approach also allows us to compute the rate of approach to stationary decisions. The state-variable approach, to paraphrase Wellington, puts the parasitoid back into parasitoid decision making. Similar kinds of understanding have been obtained by a state-variable analysis of diet-selection problems (Houston and McNamara 1985), whereby it is optimal to accept any food type when energy reserves are low, because otherwise starvation is more likely. In the present situation, it is optimal to accept inferior hosts when egg complements are high, since inferior hosts provide at least some fitness to the parasitoid.

The main disadvantages of the dynamic state-variable approach are that the analytic results are typically complicated and that numerical work is often required to obtain biological insights. The main advantage is that much more biological realism can be added and understanding gained. It appears that the trade-off is well worth it and that the state of the parasitoid is indeed important for parasitoid decisions.

SUMMARY

A state-variable theory for parasitoid host-acceptance decisions is developed. In this theory, the state variable is the egg complement at any particular time. Decisions are determined by the maximization of Darwinian fitness, which involves both survival and reproduction in a stochastic world. The state-variable theory is compared with simpler theories based on rate maximization. In some circumstances, both theories predict the same host-acceptance patterns; but for wide ranges of biologically meaningful parameters, the predictions of the two theories differ.

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APPENDIX

In this appendix, I complete the derivation from equation (7) to equation (8). The starting point is equation (7), which is reproduced here, assuming that the capacity constraint is not binding:

$$\begin{aligned} W(x, t) &= \max_r \{ (1 - \sum \lambda_i dt) \exp[-z_0(1 + \varphi r)dt] W(x + rdt, t + dt) \\ &\quad + \sum \lambda_i dt \max\{\exp[-z_0(1 + \varphi r)dt] W(x + rdt, t + dt); \\ &\quad E_i + \exp[-z_0(1 + \varphi r)(h_i + dt)] W[x + r(h_i + dt) - 1, t + h_i + dt] \} \}. \end{aligned} \quad (A1)$$

Assume that $W(x, t)$ is smooth enough to be differentiated, and use the expansion $\exp(x) = 1 + x + (x^2/2)$. Finally, introduce the notation $O(dt)$ and $o(dt)$: $O(dt)$ denotes a term proportional to dt , such that $O(dt)/dt$ approaches a constant as dt approaches zero; $o(dt)$ denotes a term proportional to a power of dt greater than one, such that $o(dt)/dt$ approaches zero as dt approaches zero. In particular, this shorthand allows us to write $dtO(dt) = o(dt)$.

A Taylor expansion of the right-hand side of equation (A1) and using subscripts on $W(x, t)$ to denote partial derivatives leads to

$$\begin{aligned} W(x, t) &= \max_r \{ (1 - \sum \lambda_i dt) [1 - z_0(1 + \varphi r)dt + o(dt)] [W(x, t) + rW_x dt + W_t dt + o(dt)] \\ &\quad + \sum \lambda_i dt \max\{ [1 + O(dt)] [W(x, t) + O(dt)]; \\ &\quad E_i + \exp[-z_0(1 + \varphi r)h_i] [1 + O(dt)] [W(x + rh_i - 1, t + h_i) + O(dt)] \} \}. \end{aligned} \quad (A2)$$

On the right-hand side, now collect terms according to powers of dt : dt^0 , dt , and $o(dt)$. This gives

$$\begin{aligned} W(x, t) &= \max_r [W(x, t) + dt(rW_x + W_t - [\sum \lambda_i + z_0(1 + \varphi r)] W(x, t) + \sum \lambda_i dt \max\{W(x, t); \\ &\quad E_i + \exp[-z_0(1 + \varphi r)h_i] W(x + rh_i - 1, t + h_i)\}) + o(dt)]. \end{aligned} \quad (A3)$$

Now subtract $W(x, t)$ from both sides, divide by dt , and let dt approach zero. Since $o(dt)/dt \rightarrow 0$ as $dt \rightarrow 0$, equation (A3) becomes

$$\begin{aligned} -W_t &= \max_r (rW_x - [\sum \lambda_i + z_0(1 + \varphi r)] W(x, t) + \sum \lambda_i \max\{W(x, t); \\ &\quad E_i + \exp[-z_0(1 + \varphi r)h_i] W(x + rh_i - 1, t + h_i)\}), \end{aligned} \quad (A4)$$

and this is equation (8) in the body of the text.

The situation analyzed by Charnov and Stephens (1988), and most often considered in the literature, includes two hosts, with host 1 superior to host 2 in the ranking based on rate maximization. It is worthwhile considering equation (A4) in that case. The first type of host will always be accepted. In addition, there will exist a switching or boundary curve $x_b(t)$ such that the plane of egg complement (x) versus time (t) is divided into two regions. In region \mathcal{A} , hosts of type 2 are also accepted for oviposition; and in region \mathcal{R} , hosts of type 2 are rejected. The analytic problem then becomes one of determining the boundary curve, $x_b(t)$, such that in region \mathcal{A} equation (A4) is satisfied, that in region \mathcal{R}

$$-W_t = \max_r (rW_x - [\lambda_1 + z_0(1 + \varphi r)]W(x, t) + \lambda_1 \max\{W(x, t); E_1 + \exp[-z_0(1 + \varphi r)h_1]W(x + rh_1 - 1, t + h_1)\}) \quad (\text{A5})$$

is satisfied, and that on the boundary of the two regions $W_{\mathcal{R}}[x_b(t), t] = W_{\mathcal{A}}[x_b(t), t]$, where $W_{\mathcal{G}}(x, t)$ denotes the solution of the appropriate equation (eq. A4 or eq. A5) in region \mathcal{G} .

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