

4

Oviposition Behavior of Insect Parasitoids

Techniques used in chapter 4

- Fitness measures (4.1)
- Static optimality models (4.2)
- Rate-maximizing models (4.2)
- State-independent dynamic models (4.3)
- State-dependent dynamic models (4.4)
- Multiple state variables (4.5)
- Qualitative testing of models (4.2–4.5)

In this chapter we describe the application of dynamic state variable models to insect parasitoids (which we describe in more detail below). This has been an especially fruitful area of application, in which dynamic state variable models have yielded new insights and suggested a number of new experiments.

4.1 Parasitoid life histories

Parasitoid life styles are manifold (Godfray 1994), but for simplicity, one can envision them as follows (Price 1980). Adults (who may live just a few hours up to many weeks) are free ranging. Eggs are laid on or inside various life stages of other insects, ranging from eggs to adults. Upon hatching, the offspring use the body fluids and tissues of the host as resources for growth. Offspring may complete development in the host or may exit and pupate elsewhere (for example, in the ground); offspring development generally results in the death of the host. Thus the key notion is that offspring are “trapped” in the host, even though the adults are mobile. This makes parasitoids easier to model than moths or butterflies, in which offspring can move (e.g., Mangel

and Roitberg 1993; Roitberg and Mangel 1993). Parasitoids are often used for biological control of pest insects. However, insects with parasitoidlike life styles such as tephritid fruit flies (e.g., Mediterranean fruit fly, apple maggot) can often be pests themselves.

David Lack's ideas on clutch size and their generalization

The great evolutionary biologist David Lack introduced notions about clutch size in birds (Lack 1946, 1947, 1948a,b; Monaghan and Nager 1997) that remain influential in evolutionary biology 50 years later (e.g., Godfray et al. 1991; Risch et al. 1995). Lack's approach is based on two fundamental observations. First, individuals can generally lay more eggs than they do. Second, in general there is density-dependent competition for resources among the offspring—laying more eggs means that the share of resources per offspring is smaller because competition will be more intense. This implies that there is a trade-off between eggs laid and some measure of reproductive success (we discuss these measures in more detail later) and that there will be an “optimal clutch size.”

We illustrate these ideas for insects, using data collected by Rosenheim and Rosen (1991), who studied the parasitoid *Aphytis lingnanensis*, which attacks the armored scale insect, a worldwide pest of citrus. They found that the size of an emerging daughter, measured by hind tibia length, depends upon the clutch laid by the mother. In particular, if $S(c)$ is the average size of a daughter from a clutch of size c

$$S(c) = 0.245 - 0.0223(c - 1) \quad (4.1)$$

Furthermore, the number of eggs that a female parasitoid can lay depends upon her size and thus upon the clutch from which she emerged. If $E(S(c))$ denotes the number of eggs, Rosenheim and Rosen found that

$$E(S(c)) = \max\{181.8S(c) - 26.7, 0\} \quad (4.2)$$

where $\max\{A, 0\} = A$ if $A > 0$ and 0 otherwise. We combine these equations to create a measure of fitness, potential granddaughters, for the ovipositing mother as a function of the clutch that she lays, that is, each daughter from a clutch of size c has size $S(c)$ and the potential to lay $E(S(c))$ daughters herself, so that the potential number of grandchildren is $cE(S(c))$; fig. 4.1. In subsequent analyses, we shall use $f(c) = cE(S(c))$ as the increment in fitness obtained from oviposition of a clutch of size c in a single host. It is possible, of course, that the number of eggs also affects the survival of offspring in a host (in addition to their size at emergence). We defer discussion of that case (see Rosenheim and Rosen 1991).

Examining fig. 4.1 is instructive. Although, based on eq. 4.2, the mother can lay as many as 11 eggs and still have offspring emerge, we see that hosts that receive more than 6 eggs give rise to daughters who are so small that they are functionally infertile. There is an optimum clutch size for a single host,

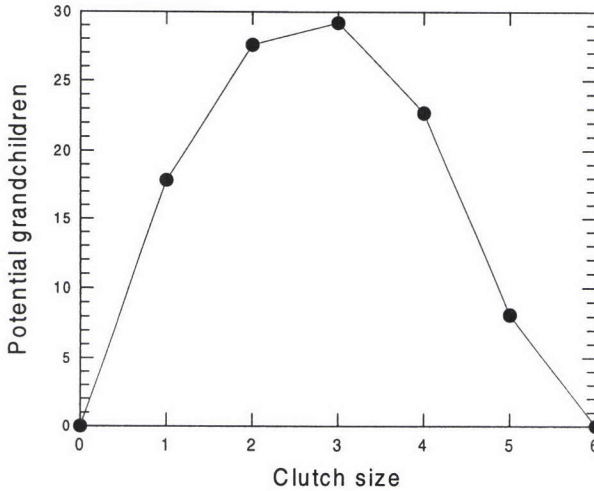


Figure 4.1 The potential number of grandchildren emerging from a host as a function of the clutch laid in the host for the data on *Aphytis* given by Rosenheim and Rosen (1991).

which we call the **single host maximum (SHM)**. Thus a clutch of 3 eggs gives fitness of 29.2 potential grandchildren, but clutches of 2 eggs give fitness 27.6 potential grandchildren, nearly as much. This simple observation leads us to recognize the need for dynamic state variable models. Imagine a female who has exactly 6 eggs left. She could put three eggs into each of two hosts and obtain fitness of 58.4 potential grandchildren. Alternatively, she could put two eggs into each of three hosts and obtain fitness of 82.8 potential grandchildren. On the other hand, if she were guaranteed to encounter six hosts, then she could put one egg into each of them and thus obtain fitness of 17.1 potential grandchildren per host, or total fitness of 102.6 potential grandchildren. Thus our predictions of what she does can depend upon the number of eggs that she currently holds (**egg complement**), the chance of encountering hosts, and the chance of mortality. It is the role of these factors that we want to sort out.

The situation might be further complicated by the presence of other females. Suppose, for example, that the focal female encounters a host that already has eggs in it. Many parasitoids mark hosts after oviposition with a pheromone, so that the second female will be able to ascertain whether or not other eggs are present. If she lays an egg, she is said to **superparasitize** the host. For many years, it was thought that superparasitism was an error in terms of reproductive success. The logic went something like this: if females mark hosts after oviposition, then they are doing it to prevent future oviposition in that host, so ovipositing in a marked host is a mistake. However, Mangel and Roitberg (1988) showed that superparasitism can be adaptive in the sense that a female who superparasitizes may achieve higher fitness than one who does not. We want to be able to predict when a female will superparasitize.

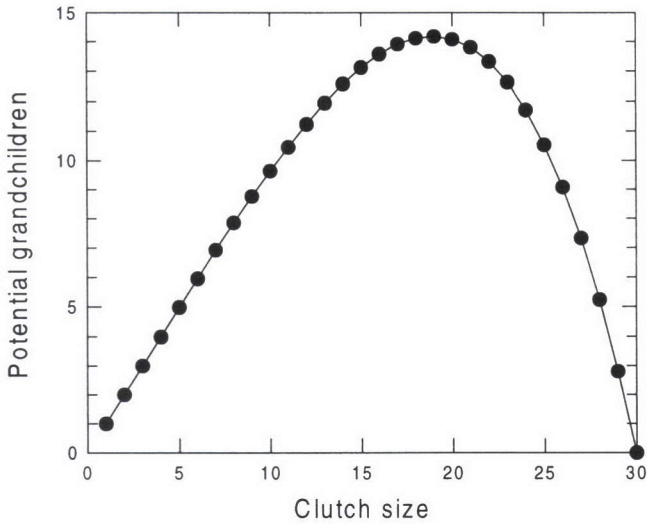


Figure 4.2 The analog of fig. 4.1, using the hypothetical fitness increment given in eq. 4.3.

Finally, some parasitoids make multiple uses of hosts. Upon encounter, a female may lay an egg in a host or feed on that host. The physiological effects of host feeding are manifold. Host-feeding may increase longevity of the parasitoid, may increase egg number, or may affect both. Consequently, we want to be able to predict when a female will feed rather than oviposit in a particular host.

In summary, we want to use dynamic state variable models to determine the ecological and physiological factors shaping (1) how many eggs are laid in a host (how often parasitoids are **egg limited** vs. **time limited**); (2) when an individual superparasitizes; and (3) when an individual host-feeds (Heimpel and Rosenheim 1995). To answer these questions, we will develop a sequence of models of increasing complexity. As described in chapter 3, we use the models to make qualitative predictions about the results of experimental manipulations; then these will be compared with the experimental results.

In the course of developing some of these models, it will be instructive to have an example with a larger range of potential clutches. Thus, in addition to $f(c) = cE(S(c))$ defined by eqs. 4.1 and 4.2, we will work with a “hypothetical parasitoid” for which the fitness increment is (fig. 4.2)

$$f_h(c) = c \left[1 - \left(\frac{c}{30} \right)^3 \right] \quad (4.3)$$

The choices of 30 and the exponent 3 in eq. 4.3 are arbitrary (we picked them to give a range of clutches and a lack of symmetry). In this case, single-host clutches of 19 are optimal. It is not uncommon for certain parasitoids to lay

Table 4.1 Single host optimum clutches for superparasitism

Data of Rosenheim and Rosen			Hypothetical parasitoid		
c_0	clutch	Optimal Fitness	c_0	clutch	Optimal Fitness
0 ^a	3	29.1	0 ^a	19	14.2
1	2	19.5	5	15	10.6
2	2	11.4	10	12	7.4
3	1	5.7	15	8	4.4
4 ^b	1	1.6	20	5	2.1
			25	8	0.7

- a. Setting $c_0 = 0$ is a check on previous calculations (always a good thing to do).
- b. This is the maximum number of other eggs that allow any fitness to the focal female.

clutches of this size (e.g., Klomp and Teernik 1967; Bai et al. 1992; Vet et al. 1993).

To conclude this section, we note that our assumption that the fitness increment from a clutch can be specified as the potential number of resulting granddaughters is not entirely consistent with the usual notion of fitness in life-history theory. To achieve consistency, we would also have to consider future generations. The method described in section 12.3 could be used for this purpose, although this would require additional information about the biology of *Aphytis*. We do not expect that this would change the qualitative predictions of the models, but this needs to be checked in future work.

4.2 Fixed clutch models

We have already described the simplest fixed-clutch model, which is the single-host maximum clutch. This model predicts that a female *Aphytis* will lay three eggs in a host that does not have any other eggs in it. If we assume that when a female encounters a previously parasitized host, she can sense the number of other eggs in it, then the fitness that she obtains from laying a clutch of size c in a host that already has c_0 eggs in it is given by

$$f_{\text{sup}}(c) = cE(S(c + c_0)) \tag{4.4}$$

In this case, we predict that the female will lay either one or two eggs, depending upon how many eggs are already in the host (table 4.1)

An analogous calculation can be done using the fitness increment for the hypothetical parasitoid, in which case we write

$$f_{\text{sup},h}(c) = c \left[1 - \left(\frac{c + c_0}{30} \right)^3 \right] \tag{4.5}$$

The SHM model predicts that clutches will be fixed, independent of physiological variables such as the parasitoid's age and egg complement and independent of ecological variables such as time of season, encounter rate with hosts, or mortality rate.

A model that involves at least one ecological variable is the **rate-maximizing** (RM) model. The notion here, lifted from classical diet choice theory (see Stephens and Krebs 1986 or the appendix to chapter 1 here), is that natural selection acts on the rate of accumulation of fitness, so that we predict individuals will behave in a manner that maximizes that rate. We focus only on hosts that are previously unparasitized. The rate of gain of fitness from oviposition of a clutch of size c is given by

$$R(c) = \frac{f(c)}{\text{search time} + \text{handling time}} \quad (4.6)$$

where the search time is the time needed to find a host and the handling time is the amount of time needed to lay a clutch of size c . Rosenheim and Rosen discovered that the first egg in a clutch took 6.5 minutes and each subsequent egg took 3.25 minutes. Thus, we define one period of time as 3.25 minutes; the handling time $h(c)$ associated with a clutch of size c is given by

$$h(c) = 2 + (c - 1) = c + 1 \quad (4.7)$$

Instead of search time, we use encounter rate ρ , which has units of hosts/time period. Thus

$$\text{Search time} = \frac{1}{\rho} \quad (4.8)$$

and eq. 4.6 becomes

$$R(c) = \frac{f(c)}{\frac{1}{\rho} + h(c)} = \frac{f(c)\rho}{1 + \rho h(c)} \quad (4.9)$$

For the hypothetical parasitoid, we assumed that a clutch of size c requires $0.1(c + 1)$ time units. The results (fig. 4.3) are instructive. First, consider *Aphytis*, for which the rate-maximizing clutch is two eggs over a very wide range of encounter rates (fig. 4.3a). In fact, it is only when encounter rates are very low (less than 0.08) that the rate-maximizing clutch shifts to three eggs, which is also the single-host maximum clutch. Thus, we predict that clutch size will decrease as the encounter rate increases, but this might be difficult to verify with *Aphytis* because (1) the shift will only be from three to two eggs and (2) to observe the shift at all, one might need to use encounter rates that are so low that they are unnatural.

The results are more dramatic with the hypothetical parasitoid (fig. 4.3b), for which the SHM clutch is 19 eggs. In this case, the clutch size drops to 10 eggs as the encounter rate increases.

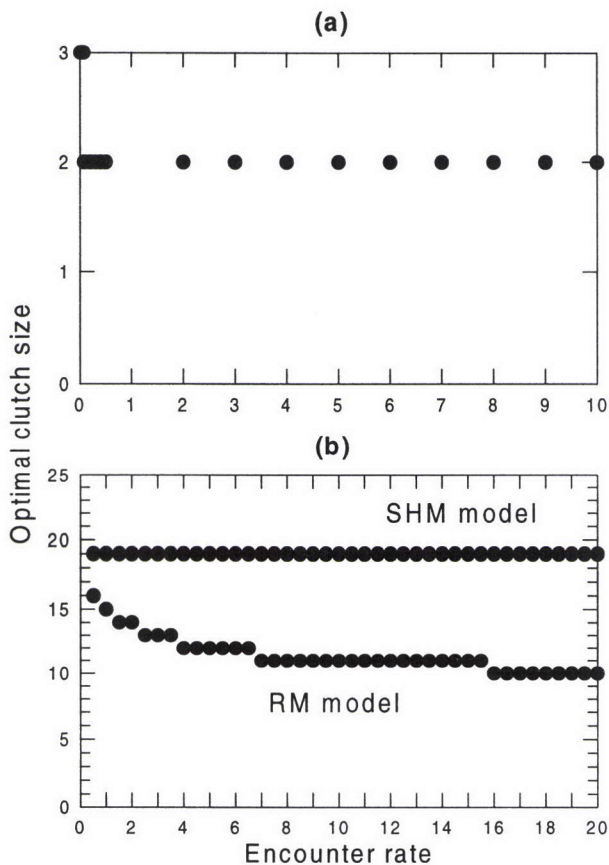


Figure 4.3 The single host maximum (SHM) and rate-maximizing (RM) models can be separated by different qualitative predictions relating encounter rate and clutch size. (a) For the *Aphytis* data, over most of the range, the RM clutch is two eggs and only approaches the SHM clutch for very low encounter rates. (b) The separation of SHM and RM models is more dramatic with the hypothetical parasitoid.

In summary, then, we conclude that SHM models are not sensitive to the encounter rate whereas rate-maximizing models are. For both models, superparasitism may occur (see below) but will be independent of time, and clutch size will not depend upon time, mortality rate, or egg complement. Wilson and Lessells (1994) and Wilson (1994) refer to both of these as examples of **static optimality models**.

Wilson (1994) tested these ideas (and many more) using the bean beetle *Callosobruchus maculatus*. Females lay their eggs on bean seeds, and the larvae burrow into the seeds on which they then feed. Pupation takes about 25 days; reproductively mature adults weigh 2–10 mg and live for 7–10 days. Females have about 80 eggs, and the clutch size varies between 1 and

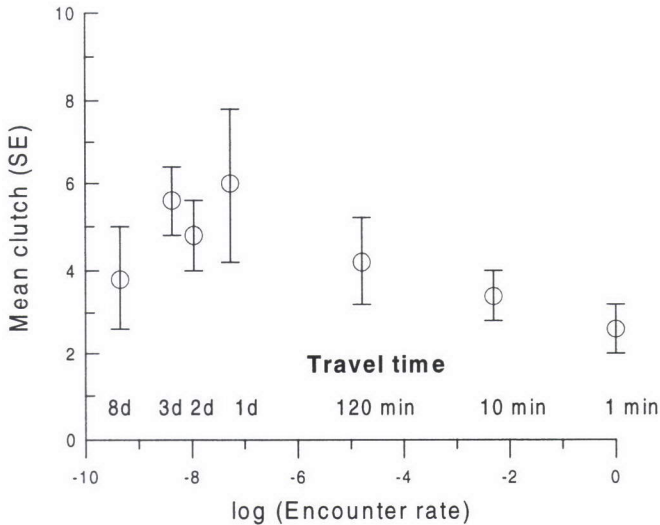


Figure 4.4 Wilson (1994) measured how clutch size depended upon encounter rate for a bean beetle. Consistent with the rate-maximizing model but not with the single host maximum model, clutch size decreased as encounter rate increased.

10 eggs per bean. Wilson found that larval competition leads to fitness increments similar to figs. 4.1 or 4.2 (Wilson 1994, fig. 4).

Wilson studied the effect of encounter rate on clutch size by mating virgin females and allowing them to lay a clutch two hours after mating. The clutch was considered complete when a female walked at least one seed length away from the bean seed. Subsequent seeds were presented to females at 1, 10, 120, or 1440 minutes after the first seed. Wilson estimated oviposition time by using the average time per seed for the first five clutches laid. First clutches did not vary with the travel time manipulation, but subsequent clutches did (fig. 4.4), qualitatively consistent with the rate-maximizing model but inconsistent with the single host maximum model. To quote Clark, “I should hope so!” Other tests of these ideas are found in Nakamura (1997) and Visser and Rosenheim (1998).

4.3 A dynamic but state-independent model

Now we turn to a dynamic but state-independent model. This allows us to consider effects of the time interval and mortality rates but not egg complement. We do this using a model involving superparasitism in a parasitoid that only lays one egg per host. In such a case, let f_u denote the average increment in fitness from oviposition in an unparasitized host. It is often true among such solitary parasitoids that only one egg emerges from a host (the offspring have a contest within the host). Thus, if a female lays an egg in a previously parasitized host, on average she will receive a smaller fitness increment than

f_u . We let f_p denote the average fitness increment from oviposition in a previously parasitized host. Both hosts require the same amount of time τ for oviposition. Finally, we assume that hosts are encountered singly; this makes the analysis easier.

Now there are two encounter rates, ρ_u and ρ_p , with unparasitized or previously parasitized hosts, respectively. Analogous to the classic rate-maximizing solution for the two-prey diet choice problem (Stephens and Krebs 1986), we focus on the rate of gain of fitness R_u if only unparasitized hosts are attacked, and on the rate of gain R_b , if both unparasitized and previously parasitized hosts are attacked.

We find R_b in the following manner (see the appendix to chapter 1). The time interval of length T can be broken into search time S and handling time H , so that $S + H = T$. Given that the search time is S , the parasitoid encounters $\rho_u S$ unparasitized hosts and $\rho_p S$ previously parasitized hosts. Since each host requires τ time units for handling, the handling time is given by

$$H = \rho_u S \tau + \rho_p S \tau = S \tau (\rho_u + \rho_p) \quad (4.10)$$

Assuming that the only activities are search and handling

$$T = S + H = S + S \tau (\rho_u + \rho_p) \quad (4.11)$$

so that

$$S = \frac{T}{1 + \tau(\rho_u + \rho_p)} \quad (4.12)$$

The gain in fitness from unparasitized hosts is $f_u \rho_u S$ and from previously parasitized hosts is $f_p \rho_p S$. Consequently the average fitness acquired over the interval 0 to T is given by

$$(f_u \rho_u + f_p \rho_p) S = (f_u \rho_u + f_p \rho_p) \frac{T}{1 + \tau(\rho_u + \rho_p)} \quad (4.13)$$

and the rate of gain of fitness is given by

$$R_b = \frac{f_u \rho_u + f_p \rho_p}{1 + \tau(\rho_u + \rho_p)} \quad (4.14)$$

Repeating this analysis shows that

$$R_u = \frac{f_u \rho_u}{1 + \tau \rho_u} \quad (4.15)$$

We predict that the parasitoid will superparasitize if $R_b > R_u$. This condition is the same as

$$\rho_u < \frac{1}{\tau} \frac{f_p}{f_u - f_p} \quad (4.16)$$

The right-hand side of eq. 4.16 is a switching value of ρ_u : if ρ_u exceeds the switching value, then it is predicted that the parasitoid will avoid superparasitizing; if ρ_u is less than the switching value, it is predicted that the parasitoid will superparasitize.

In summary, the rate-maximizing model predicts that (1) the parasitoid will always attack all unparasitized hosts; (2) if the encounter rate with unparasitized hosts is sufficiently low, the parasitoid will also attack previously parasitized hosts; (3) the encounter rate with previously parasitized hosts has no effect on the acceptance or rejection of those hosts; and (4) neither mortality nor time within the season will affect oviposition behavior. These predictions are analogous to those obtained in the theory of diet choice (Stephens and Krebs 1986). Now we develop a simple dynamic model for this situation and ignore physiological state but take time into account. Two additional variables are needed. First, we must characterize mortality. We assume that the rate of mortality while searching is m , in the sense that

$$\Pr\{\text{parasitoid survives one time unit}\} = e^{-m} \quad (4.17)$$

Similarly, we assume that mortality during oviposition is m_{ov} and survival is determined by an expression similar to eq. 4.17. Mortality is included in the rate-maximizing solution in a simple way: the expected lifetime of the parasitoid is $1/m$, so that the lifetime fitness for the rate-maximizing solution is $\frac{1}{m}R_u$ or $\frac{1}{m}R_b$, and hence m has no effect on the optimal behavior. For further discussion, see Mangel (1989).

Because the dynamic model uses discrete time rather than the continuous time implicit in the rate-maximizing solution, we need to characterize the probability of encountering a host in one time unit. Assuming that search is random, we set

$$\lambda_u = \Pr\{\text{parasitoid encounters an unparasitized host in one time unit of search}\} = (1 - e^{-\rho_u - \rho_p}) \frac{\rho_u}{\rho_u + \rho_p} \quad (4.18)$$

$$\lambda_p = \Pr\{\text{parasitoid encounters a previously parasitized host in one time unit of search}\} = (1 - e^{-\rho_u - \rho_p}) \frac{\rho_p}{\rho_u + \rho_p}$$

The logic behind eq. 4.18 is that the chance of encountering a host of either type in one time unit is $1 - e^{-\rho_u - \rho_p}$. Given that a host is encountered, the chance that it is unparasitized is $\frac{\rho_u}{\rho_u + \rho_p}$, and the chance that it is parasitized is $\frac{\rho_p}{\rho_u + \rho_p}$. Recall that when x is small, $e^{-x} \approx 1 - x$, so that when ρ_u and ρ_p are small, the encounter probabilities are approximately ρ_u and ρ_p , respectively.

The fitness measure is

$$F(t) = \text{expected accumulated fitness from oviposition from } t \text{ to } T \quad (4.19)$$

We assume that no oviposition occurs at time T , so that $F(T) = 0$. For previous times, it makes sense to assume that when an unparasitized host is encountered, it is always attacked, but that when a previously parasitized host is encountered, oviposition is chosen to maximize expected reproductive success. With these assumptions, the dynamic programming equation is

$$F(t) = (1 - \lambda_u - \lambda_p)e^{-m}F(t+1) + \lambda_u\{f_u + e^{-m_{ov}}F(t+\tau)\} \\ + \lambda_p \max\{f_p + e^{-m_{ov}}F(t+\tau), e^{-m}F(t+1)\} \quad (4.20)$$

The three terms on the right-hand side of eq. 4.20 correspond to not encountering a host, encountering an unparasitized host, or encountering a previously parasitized host during period t . When an unparasitized host is encountered, the parasitoid receives an immediate increment in current fitness f_u and future fitness $e^{-m_{ov}}F(t+\tau)$, taking into account survival. When a previously parasitized host is encountered, oviposition behavior involves the trade-off between current and future fitness.

The solution of eq. 4.20 generates a value t^* before which previously parasitized hosts will not be attacked and after which they will be attacked. The boundary depends upon the fitness increment from the two kinds of hosts, the encounter rate with each kind, and the two mortality rates. We focus on time and mortality while searching. In fig. 4.5a, we show the boundary between superparasitizing and not superparasitizing for $f_u = 1$, $f_p = 0.2$, $t = 1$, $T = 30$, $m_{ov} = 0.23$, and $\rho_u = \rho_p = 0.5$ (for which $\lambda_u = \lambda_p = 0.316$). The switching value for the rate-maximizing model is $\rho_u = 0.25$, so based on the rate-maximizing theory, we predict that the parasitoids will never superparasitize. This state-independent dynamic model, on the other hand, predicts that if time is short—that is, if t is close enough to T , the parasitoid will superparasitize. Similarly, if mortality while searching is sufficiently high, it is predicted that the parasitoid will superparasitize regardless of the value of t .

The precise location of the boundary depends upon the encounter rates. For example, we might envision two scenarios about encounter rates. In the “Good world” scenario, $\rho_u = 1.5$ and $\rho_p = 0.5$, whereas in the “Bad world” scenario, $\rho_u = 0.5$ and $\rho_p = 1.5$. The boundary between superparasitizing or not has the same shape as before (fig. 4.5b), but the location depends upon the encounter rates. In the “Good world” scenario, parasitoids wait longer or must experience a higher rate of mortality, while searching, than in the “Bad world” scenario.

Thus, a simple dynamic but state-independent model predicts that superparasitism behavior is dynamic and will respond to time within the season and mortality during search. The rate-maximizing model predicts fixed behavior, regardless of time within the season or mortality during search. Roitberg et al. (1992, 1993) and Fletcher et al. (1994) tested these ideas.

Roitberg et al. (1992) used the solitary drosophilid parasitoid *Leptopilina*

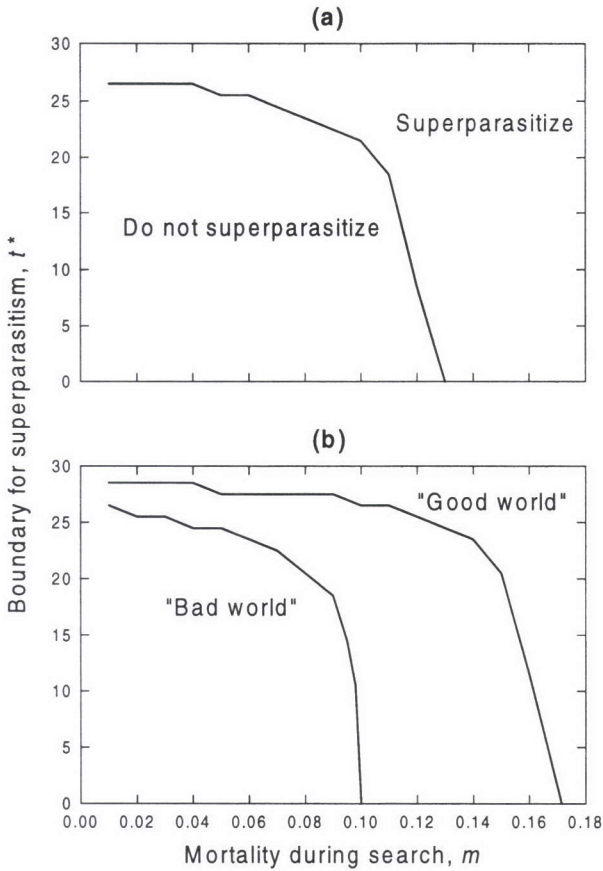


Figure 4.5 (a) The time at which the parasitoid starts accepting previously parasitized hosts depends upon the ecological and physiological factors. Here we hold all but one constant ($f_u = 1$, $f_p = 0.2$, $t = 1$, $T = 30$, $m_{ov} = 0.23$, and $\rho_u = \rho_p = 0.5$) and vary the mortality rate while searching. (b) The location of the boundary depends upon encounter rates. In the “Good world” scenario, $\rho_u = 1.5$ and $\rho_p = 0.5$, whereas in the “Bad world” scenario, $\rho_u = 0.5$ and $\rho_p = 1.5$.

heterotoma, whose larvae are solitary. This wasp has about 800 eggs upon emergence; consequently it is appropriate to assume that the effects of physiological state (egg complement) can be ignored. Females seek out host patches (rotting mushrooms) and search for hosts (*Drosophilid* larvae) by inserting their ovipositors into the patches that may contain larvae. Upon contact with larvae, a female paralyzes and parasitizes the host. Because of the venom in a previously attacked host, a female can recognize a previously parasitized host.

A Dutch (i.e., temperate zone) strain of *Leptopilina heterotoma* was reared on larvae of *D. simulans* under two sets of light to dark cycles: 16h:8h (“Summer”) and 12h:12h (“Fall”). Since many species of insects are sensitive to photoperiod, Roitberg et al. (1992) assumed that the fall photoperiod

indicates that t is approaching T , whereas the summer photoperiod indicates that t is far from T .

The protocol involved a three-day experimental period. On the first two days of the experiment, 4- and 5-day-old wasps were individually placed on a yeast patch containing thirty 48-h-old *D. simulans* larvae. Wasps reared on the 16:8 light cycle were further divided into "Good world" and "Bad world" groups. In the "Good world" treatment wasps were released on yeast patches that contained 30 unparasitized hosts, whereas wasps in "Bad world" treatments were released on patches that contained 30 already parasitized hosts. Wasps reared on the 12:12 light cycle experienced only "Good world" conditions. On the third day, all wasps were individually placed on patches containing thirty *D. simulans* larvae that had already been parasitized by other *L. heterotoma* females. Residence times and superparasitizations were observed and recorded for each wasp.

In a second set of experiments, Roitberg et al. (1992) manipulated perceived mortality by raising parasitoids under both "Good world" and "Bad world" conditions and under steady barometric pressure ("Steady"), typical of a fair summer day, or dropping barometric pressure ("Dropping"), as would occur several hours before the onset of a storm. Such summertime storms are known to be a source of mortality for small insects (Wellington 1946).

The results (fig. 4.6) are striking, and in accord with the qualitative predictions of the dynamic, state-independent model. First (fig. 4.6a), with "Summer" photoperiods, encounter rates clearly affect superparasitisms ($p < .05$ for "Summer, Good world" vs. "Summer, Bad world"). Second, when encounter rates are the same, the closeness of t to T clearly affects superparasitisms ($p < .005$ for "Summer, Good world" vs. "Fall, Good world"). Third (fig. 4.6b), when a cue indicates an imminent increase in mortality, the number of superparasitisms increases ($p < .0014$ for "Steady" vs. "Dropping"). Further intuition about these patterns can be developed by considering the third term in eq. 4.20. This term involves a trade-off between current and future reproduction. Whenever empirical manipulations make future reproduction less valuable (e.g., by increasing m or t), the balance shifts toward current reproduction and superparasitism. Fletcher et al. (1994) investigated this notion by varying the food supply of the parasitic wasp *Venturia canescens*. Some wasps were fed a 50% honey solution, whereas others were fed only water. The starved wasps had a maximum life span of three days and an average life span of about two days, whereas the fed wasps had a maximum life span of five days and an average life span of about four days ($p < .0001$). Fed and starved parasitoids did not differ in egg complement (about 50 eggs each; $p = .65$). Oviposition behavior upon encounter with hosts in a system similar to that used by Roitberg et al. was observed. The starved wasps superparasitized approximately 63% of the hosts they encountered, whereas the fed wasps superparasitized only about 43% of the hosts they encountered and this difference was highly statistically significant ($p < .001$).

Thus we conclude that oviposition behavior is more effectively described as

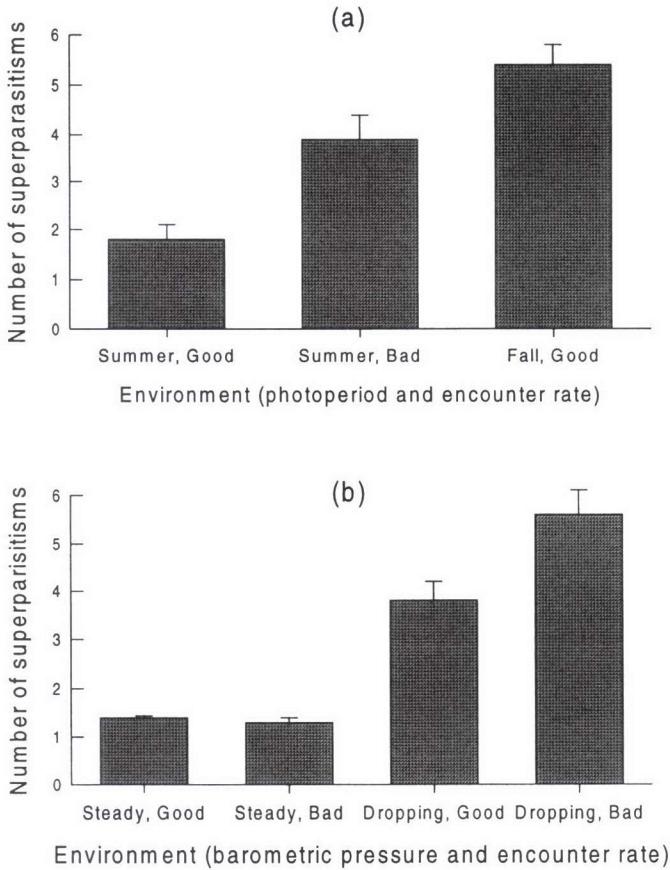


Figure 4.6 The results of experiments by Roitberg et al. (1992, 1993) clearly demonstrate that (i) encounter rates affect the tendency to superparasitize (panel a, Summer, Good world versus Summer, Bad world); (ii) when encounter rates are the same, the closeness of t to T affects the tendency to superparasitize (panel a, Summer, Good world vs. Fall, Good world); and (iii) mortality rate clearly affects the tendency to superparasitize (panel b).

a dynamic process that responds to the mortality rate and the time of the season than as a static, rate-maximizing process. Next, we consider the effect of physiological state, using a dynamic state variable model.

4.4 The proovigenic parasitoid

For parasitoids that lay clutches the simplest physiological state is the number of eggs that a parasitoid holds (i.e., the egg complement). It is clear that none of the single host maximum, rate-maximizing, or state-independent dynamic models will lead to predictions that oviposition behavior depends upon egg

complement because these models simply do not include the egg state. Next we develop a model that does and then describe experiments that tested the major predictions of such a model.

We let

$$X(t) = \text{number of eggs at the start of period } t \quad (4.21)$$

The parasitoid has a maximum number of eggs that it can physically contain; we denote this by x_{\max} . The minimum value of $X(t)$ is zero. Parasitoids can be broadly classified into those that emerge with their entire egg complement (**proovigenic**) and those that mature eggs during their lifetimes (**synovigenic**). In this section, we focus on the former, in which case the dynamics of the physiological state are given by

$$X(t+1) = X(t) - \text{clutch laid in period } t \quad (4.22)$$

Fitness, defined in terms of expected potential number of grandchildren, now depends upon time and state, with the definition

$$F(x, t) = \text{maximum expected accumulated number of potential grandoffspring from period } t \text{ to } T, \text{ given that } X(t) = x \quad (4.23)$$

For simplicity, we consider the situation in which only one host type is encountered and for which the increment in fitness from a clutch of size c is $f(c)$. We assume that laying a clutch of size c requires time $h(c)$, as described by eq. 4.7 (or some appropriate modification). If λ is the probability of encountering a host in one unit of search time and m is mortality rate during search and oviposition, we can immediately write the equation that $F(x, t)$ must satisfy:

$$F(x, t) = (1 - \lambda)e^{-m}F(x, t + 1) + \lambda \max_c \{f(c) + e^{-mh(c)}F(x - c, t + h(c))\} \quad (4.24)$$

The first term on the right-hand side of eq. 4.24 corresponds to the case in which no host is encountered. In that situation, if the parasitoid survives period t , she begins period $t + 1$ with the same number of eggs. The second term corresponds to the case in which a host is encountered. In that case, the parasitoid may trade current reproduction (larger clutches) with expected future reproduction (survival times fitness at the end of the current clutch). The solution of eq. 4.24 generates $F(x, t)$ and the optimal clutch $c^*(x, t)$ for each egg complement and time.

In fig. 4.7, we show how the first-period clutch $c^*(x, 1)$ depends upon egg complement and mortality when $\lambda = 0.5$, using the fitness increments for *Aphytis* (panel a) or for the hypothetical parasitoid (panel b). In either case, we predict a shift toward higher clutches as egg complement increases. This

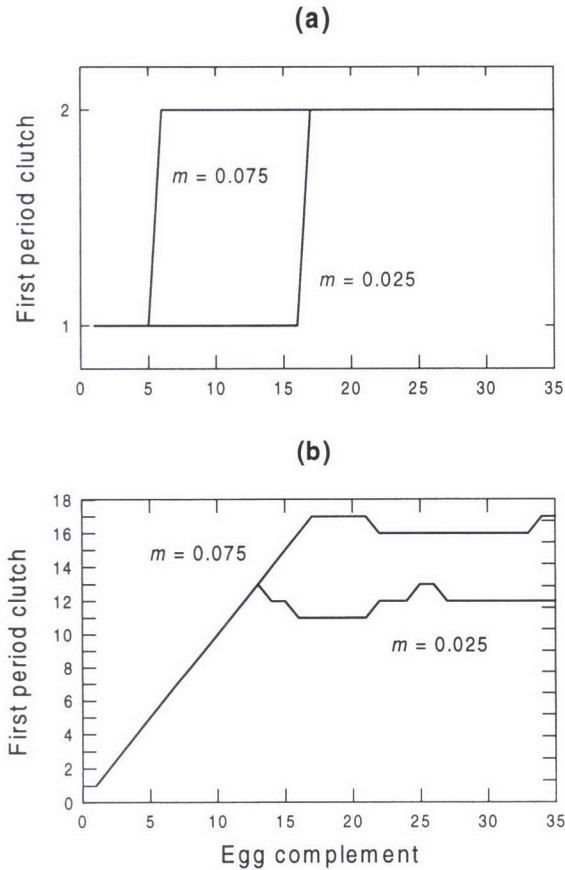


Figure 4.7 The simplest state variable model predicts that clutch size will respond to egg complement, mortality rate and encounter rate. We show the results for fitness increments associated with *Aphytis* (a) and with the hypothetical parasitoid (b) for $\lambda = 0.5$, $x_{\max} = 35$, and $T = 60$.

shift will occur sooner when mortality rates are higher or (not shown) when encounter rates are lower.

Rosenheim and Rosen (1991) tested the ideas of encounter rate and egg complement using the parasitoid *Aphytis lingnanensis*. This parasitoid is actually synovigenic and may host-feed (see the next sections), so we shall describe the protocols that Rosenheim and Rosen used to ensure that the experimental manipulations were appropriate.

The hosts used in the experiments were large virgin third instar females of the California red scale *Aonidiella aurantii*. Scales were maintained as virgins because the females develop a hard protective shell after mating.

Rosenheim and Rosen provided parasitoids with a uniform history of host encounter but with different egg complements. They manipulated egg load

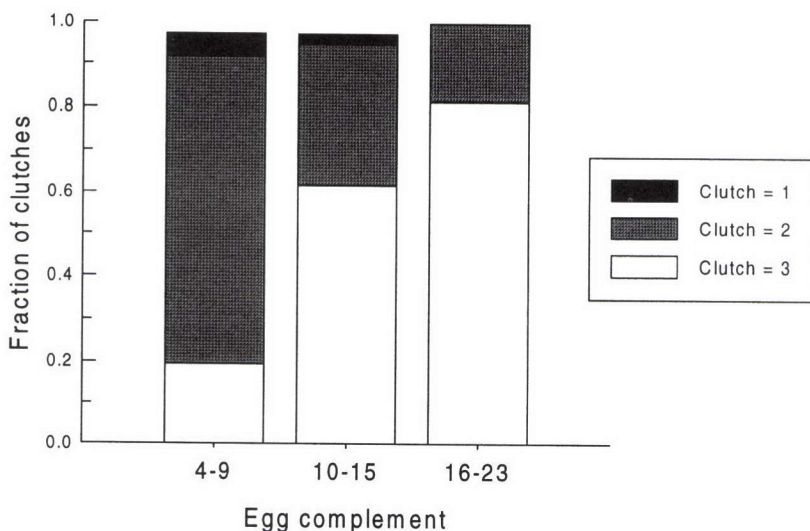


Figure 4.8 Results of the clutch size experiment conducted by Rosenheim and Rosen; details are in the text. We aggregated the egg complement and show the fraction of observations that correspond to clutches of size 1, 2, or 3. For egg complement 4–9, these values are 0.056, 0.722, and 0.194, respectively; for egg complement 10–15 they are 0.025, 0.333, and 0.615 respectively; for egg complement 16–23 they are 0.0, 0.185, and 0.812 respectively. There was one clutch of size 4 for the smaller egg complements.

by using parasitoids of different sizes (see eqs. 4.1, 4.2) or raising parasitoids at low temperature, which slows egg production.

Parasitoids were confined with a single host, and oviposition behavior was observed. After that, the parasitoid was given a second host and only parasitoids ovipositing in both hosts were used in the data collection; after the second oviposition, parasitoids were dissected to determine the egg complement. The egg complement at the start of the experiment was the sum of the eggs laid plus those counted during dissection.

We present results by aggregating the egg complement (fig. 4.8), but the raw data can be found in Hilborn and Mangel (1997, chapter 6) and other versions of the aggregated data in the paper by Rosenheim and Rosen (1991). Virtually all of the clutches were one, two, or three eggs and as egg complement increased, the likelihood of larger clutches increased. Indeed, no clutches of size 1 were observed for an individual that had more than 13 eggs.

In summary, the experiments of Rosenheim and Rosen support the conclusion that oviposition behavior is fundamentally dynamic and responds to changes in physiological state and ecological conditions (encounter rates with hosts and mortality rates). Indeed, egg complement has been suggested as a major source of variability in insect foraging and oviposition behavior (Minkenberg et al. 1992).

Now we can combine the effects of egg load and previous parasitism to extend the results in the last section by assuming that a previously parasitized host already has c_0 eggs in it. The combination of eqs. 4.20 and 4.24 that we choose is

$$\begin{aligned}
 F(x, t) = & (1 - \lambda_u - \lambda_p)e^{-m}F(x, t + 1) \\
 & + \lambda_u \max_{c_u} \{f(c_u) + e^{-mh(c_u)}F(x - c_u, t + h(c_u))\} \\
 & + \lambda_p \max_{c_p} \{f(c_0 + c_p) \frac{c_p}{c_p + c_0} + e^{-mh(c_p)}F(x - c_p, t + h(c_p))\}
 \end{aligned} \tag{4.25}$$

As before, the first term on the right-hand side corresponds to the situation in which no host is encountered in period t . The second term corresponds to the encounter with an unparasitized host, in which case the clutch laid c_u is determined by the balance between current reproduction $f(c_u)$ and future reproduction $e^{-mh(c_u)}F(x - c_u, t + h(c_u))$. When a previously parasitized host is encountered and the clutch is c_p , the current reproduction is only a fraction of what it would be were the parasitoid only putting her eggs into the host. Hence the term $\frac{c_p}{c_p + c_0}$. Thus, we assume that all offspring survive in a host with $c_p + c_0$ eggs, but the mother is credited only with her share of the associated fitness.

The solution of eq. 4.25 generates a threshold level of eggs $x_p(t)$ required for superparasitism at time t . We applied eq. 4.25 to the fitness increment for *Aphytis* with $c_0 = 1$ and considered “Good worlds” (for which $\lambda_u = 0.8$ and $\lambda_p = 0.2$) or “Bad worlds” (for which $\lambda_u = 0.2$ and $\lambda_p = 0.8$) and two values of the mortality rate (fig. 4.9).

To our knowledge, the combination of experiments of Rosenheim and Rosen and Roitberg et al. that would be needed to demonstrate the existence of the boundary in fig. 4.9 has not yet been done. In chapter 1, we discussed similar boundaries in the feeding behavior of small fish, including experiments that are consistent with the notion of a dynamic threshold, as in fig. 4.9.

There are at least some gamelike aspects to the problem of superparasitism, that is, in eq. 4.25 we assumed that other individuals do not superparasitize (hence the use of $f(c_u)$ for the fitness increment upon encounter with an unparasitized host) and have fixed c_0 . These are likely to depend upon the behavior of other individuals, and this would imply that a game is involved (see chapter 10).

4.5 The synovigenic parasitoid: Eggs and reserves

Now we turn to models that involve various complications; these models require more than one state variable. For example, in addition to looking for hosts, parasitoids may look for non-host food sources (e.g., plants that provide nectar or pollen or aphid honeydew). Consumption of non-host foods (or

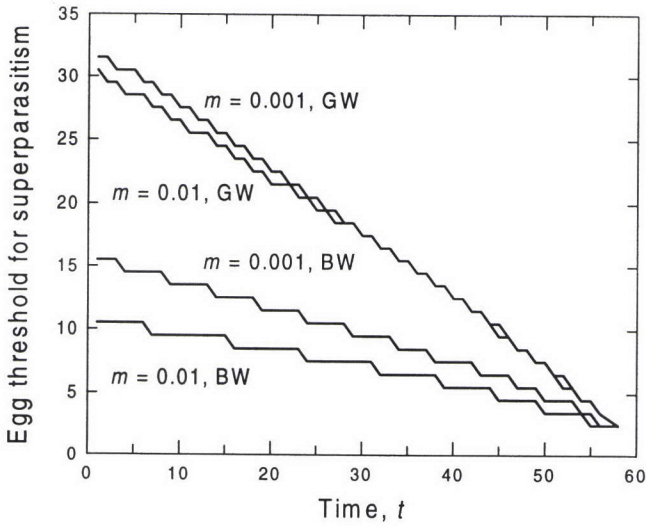


Figure 4.9 A dynamic state variable model for superparasitism generates a boundary in egg complement-time space. At a given time, if the parasitoid's egg complement is above the boundary, we predict that it will superparasitize; if its egg complement is below the boundary, we predict that it will not superparasitize. Other parameters are as in fig. 4.7.

their substitutes in the laboratory) can increase fecundity, longevity, or both (Jervis et al. 1993 and references therein; Rivero-Lynch and Godfray 1997). Alternatively, upon encounter with a host, a parasitoid may feed rather than oviposit (de Bach 1943—a classic paper; Jervis and Kidd 1986 and references therein).

To be explicit, we focus on the case in which reserves are used to “power” the parasitoid in the sense that one period of activity decreases reserves by α ; in addition, reserves may be used to increase the egg complement. As before we denote the egg complement at the start of period t by $X(t)$ and introduce

$$Y(t) = \text{amount of reserves at the start of period } t \quad (4.26)$$

We measure reserves in the same units as eggs and assume that reserves cannot exceed the maximum value y_{\max} and that if the reserves fall below a critical level y_c , the parasitoid dies. Finally, we assume that when a non-host food source is encountered, food reserves increase by an amount g . Thus, if a non-host food source is encountered in a period in which x_e eggs are made, the dynamics of $Y(t)$, subject to the constraints concerning y_{\max} and y_c , are given by

$$Y(t+1) = Y(t) - \alpha - x_e + g \quad (4.27)$$

We assume that eggs cannot be converted back into reserves.

As we go through the models, it is important to keep in mind that there are

many different ways to formulate the behavior and the physiological dynamics. Consider, for example, how one might change the model if reserves can be used to increase longevity.

Non-host-feeding parasitoids

A parasitoid that does not host-feed needs to find reserves elsewhere. Thus at a particular time, two questions arise: How much of the current reserves should be allocated to producing new eggs? and Should the parasitoid search for hosts or non-host sources of reserves? The key trade-off here is the level of reserves. Since food may not be located immediately, there is value in keeping reserves up. However, keeping reserves at a value that is too high may mean that potential reproduction is lost.

For simplicity of presentation, we assume that the parasitoid is solitary, so that upon encountering a host, she lays a single egg and obtains an increment in fitness f_o from oviposition. In any given time period, the parasitoid can search either for a non-host food source or for a host. We let

$$\begin{aligned}\lambda_f &= \text{Probability of encountering a non-host} \\ &\quad \text{food source in a single period of search} \\ \lambda_h &= \text{Probability of encountering a host in a} \\ &\quad \text{single period of search}\end{aligned}\tag{4.28}$$

and introduce fitness

$$F(x, y, t) = \text{maximum expected fitness accumulated from reproduction between } t \text{ and } T, \text{ given that } X(t) = x \text{ and } Y(t) = y\tag{4.29}$$

which satisfies the end condition $F(x, y, T) = 0$ for every value of x and y . In addition, it satisfies the boundary condition $F(x, y_c, t) = 0$ for every x and t (by measuring x and y in units of eggs, which are integers, we avoid the problems of interpolation near the critical value y_c).

We assume that eggs are matured before she seeks either hosts or food. In this case, the value of seeking a host is given by

$$\begin{aligned}V_{\text{host}}(x, y, t) &= \max_{x_e} [\lambda_h \{f_o + e^{-m} F(x - 1 + x_e, y - \alpha - x_e, t + 1)\} \\ &\quad + (1 - \lambda_h) e^{-m} F(x + x_e, y - \alpha - x_e, t + 1)]\end{aligned}\tag{4.30}$$

and the value of seeking a non-host food source is expressed by

$$\begin{aligned}V_{\text{food}}(x, y, t) &= \max_{x_e} [\lambda_f e^{-m} F(x + x_e, y - \alpha - x_e + g, t + 1)] \\ &\quad + (1 - \lambda_f) e^{-m} F(x + x_e, y - \alpha - x_e, t + 1)]\end{aligned}\tag{4.31}$$

Then fitness and the optimal behavior are determined according to

$$F(x, y, t) = \max\{V_{\text{host}}(x, y, t), V_{\text{food}}(x, y, t)\} \quad (4.32)$$

The solution of eq. 4.32 leads to a boundary value of reserves that depends upon egg complement and time (fig. 4.10). When $Y(t)$ is below the reserve boundary, we predict that the parasitoid will search for food sources; otherwise she will search for hosts.

The precise form of the boundary is of less interest to us than its existence. The general prediction is that there is separation into states that correspond to seeking hosts and states that correspond to seeking food. Experiments that demonstrate this separation were conducted by Lewis and Tasuku (1990), Wäckers and Swaans (1993), and Wäckers (1994). These workers investigated the way in which parasitoids use food and host odors, but did not explicitly test the predictions that we have derived. Wäckers and Swaans (1993) and Wäckers (1994) separated the parasitoid *Cotesia rubecula* (which attacks the cabbage butterfly *Pieris rapae*) into fed and deprived groups. The fed groups received 70% saccharose solution whereas the deprived groups were fed only water. The sugar is used to “power” the parasitoid, as in our model. Wäckers and Swaans (1993) found that deprived individuals lived an average of 1.6 days. Mated females who were inexperienced with both host and food odors were given a choice of flying toward flowers of rapeseed or flying toward leaves of rapeseed that were damaged by larvae of *P. rapae*. The results (fig. 4.11) are clearly and significantly in accord with the predictions of the theory: about 65% of the deprived parasitoids sought food sources, whereas only 25% of the fed parasitoids did.

Host-feeding parasitoids

Sometimes hosts can be used as food sources, rather than as sites for oviposition. Parasitoids that exploit hosts in this manner are said to be **host-feeding parasitoids**. Some parasitoids actually can use hosts for both oviposition and feeding; see Jervis and Kidd (1986). As in the previous case, there are different ways in which host reserves can be used (Bartlett 1964; Sandlan 1979; Jervis and Kidd 1986) and not all of them will be explored here; this subject has attracted considerable research effort recently. Excellent introductions to the primary literature are Chan (1991); Rosenheim and Rosen (1992); Collier et al. (1994); Heimpel et al. (1994); Collier (1995a,b); Heimpel and Rosenheim (1995); and McGregor 1997; reviews are found in Rosenheim and Heimpel (1994) and Heimpel and Collier (1996).

4.6 Discussion

Since models of host-feeding become complicated very rapidly (see the primary literature cited before), we have no such models in this section. However, we

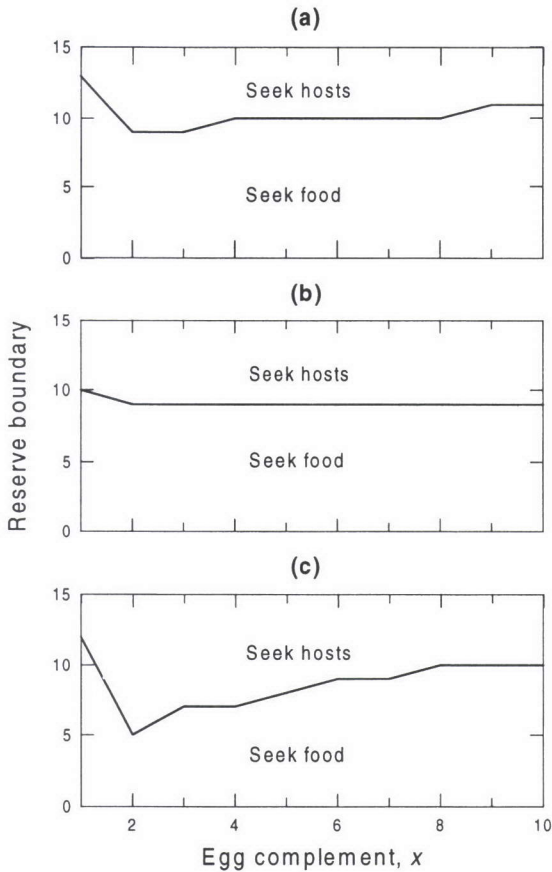


Figure 4.10 The solution of eq. 4.32 generates a boundary in the egg complement-reserve space. Above this boundary, the parasitoid is predicted to seek hosts; below the boundary it is predicted to seek food sources. The results shown used $f_0 = 1.0$, $\alpha = 1.0$, $g = 5.0$, $T = 50$, $y_{\max} = 40$, $x_{\max} = 10$, and $m = 0.01$, and we show the boundary at $t = 15$ for (a) $\lambda_h = 0.25$, $\lambda_f = 0.25$; (b) $\lambda_h = 0.75$, $\lambda_f = 0.25$; and (c) $\lambda_h = 0.5$, $\lambda_f = 0.5$.

use the intuition developed throughout the chapter to make predictions about the nature of host-feeding and then describe various experiments that have been conducted. We'll see that there is, in fact, incomplete resolution of the question of predictions about host-feeding. Host-feeding implicitly involves two states (egg complement and reserves used for making eggs), and time delays as reserves are converted into eggs. Thus, single host maximum, rate-maximizing, and one-state dynamic state variable models cannot be used to describe host-feeding. At the minimum, a two-state dynamic model is needed.

One of the difficulties in the study of host-feeding is that although egg complement can be determined (it is very tedious), the determination of reserves is still essentially impossible. Thus, one of the state variables is not observable.

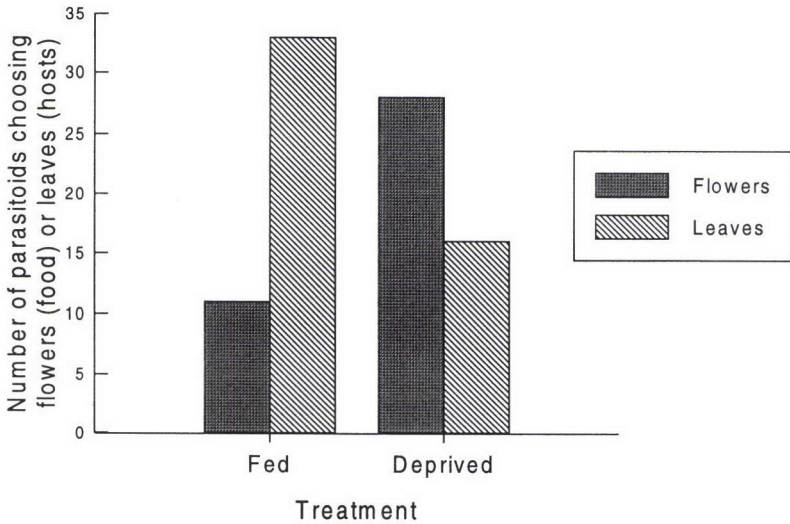


Figure 4.11 Results of the experiments of Wäckers (1994) in which parasitoids were either fed or deprived and then given a choice of seeking hosts or seeking non-host food sources. The deprived parasitoids significantly ($p < .05$, binomial test) sought food sources (flowers) rather than hosts (leaves).

However, we can begin to think about the implications of host-feeding and, based on the experience in this chapter, derive certain qualitative predictions.

Reserves are ultimately converted into eggs for future oviposition. Collier (1995b) showed that when *Aphytis melinus* (a parasitoid of California red scale *Aonidiella aurantii*) host-fed, the host meal led to two new eggs about 15 hours later. These parasitoids can live for 40 days (Collier 1995b) and encounter hosts in the field at the rate of one host every two hours or so (Heimpel et al. 1996 found that one host was encountered every 137 minutes). Thus we anticipate that a parasitoid which is far from T may host-feed when the egg complement is low, to obtain reserves that will be used as eggs in future ovipositions.

Prediction #1: Parasitoids will host-feed when egg complements are low.

Collier et al. (1994) developed a number of simple dynamic state variable models that lead to this prediction. Perhaps their most important conclusion is that there is a threshold egg level x^* , above which the parasitoid oviposits and below which it host-feeds. Furthermore, Collier et al. show that if the delay between host-feeding and having the egg available is a single period, then $x^* = 1$. However, if the delay is greater (e.g., it takes a number of physiological “stages” to convert reserves into eggs), then x^* may be greater than one. Collier (1995a) developed more complicated state variable models, which include physiological realism, that give the same qualitative feature.

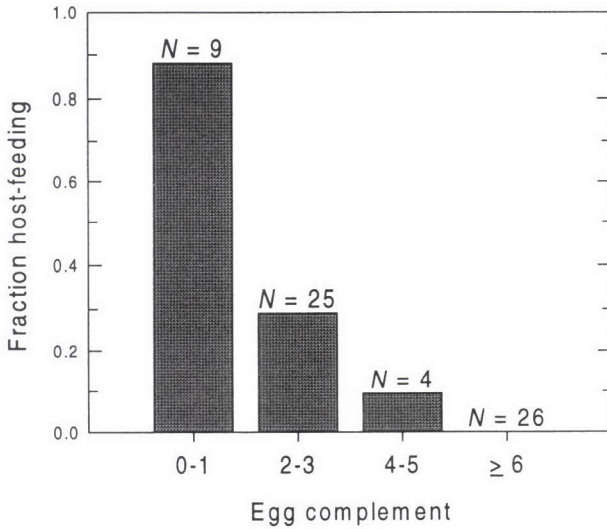


Figure 4.12 The parasitoid *Aphytis melinus* was more likely to host feed at low than at higher values of egg complement (data from Collier et al. 1994). Note, in fact, that parasitoids with more than five eggs never host-fed. The numbers above the bars indicate the number of parasitoids sampled.

Collier et al. (1994) tested these predictions using the parasitoid *Aphytis melinus*. They used newly mated, young females placed into small petri dishes containing scale insect hosts on lemon. They observed parasitoids ovipositing and host-feeding. Once the parasitoid host-fed, it was removed and dissected so that egg complement could be determined. The result (fig. 4.12) shows a clear qualitative agreement with the prediction: as egg complement increased, the likelihood that a parasitoid host-fed decreased. Heimpel and Rosenheim (1995), using *Aphytis melinus* that attacks oleander scale, found results consistent with those of Collier et al.: egg complement significantly ($p < .001$) affected whether a parasitoid host-fed or not.

The results of Collier et al. are in contrast to those of Rosenheim and Rosen (1992) who found that egg complement did not influence (in the sense of a statistically significant result) the host-feeding behavior of the parasitoid *Aphytis lingnanensis*. Collier et al. note the following differences between their work and that of Rosenheim and Rosen. First, Rosenheim and Rosen examined behavior of the parasitoid on the first host encounter whereas Collier et al. waited until the parasitoid host-fed, which usually took two or three encounters. Thus, in the experiments of Collier et al., parasitoids differed in both experience (encounters with hosts) and egg complement. Second, Rosenheim and Rosen used second instar scale insects, whereas Collier et al. used third instar scale insects; the second instar scales are poor quality for oviposition purposes, and Collier et al. suggest that host-feeding on third instar scales—which are high-quality hosts for oviposition purposes—may be

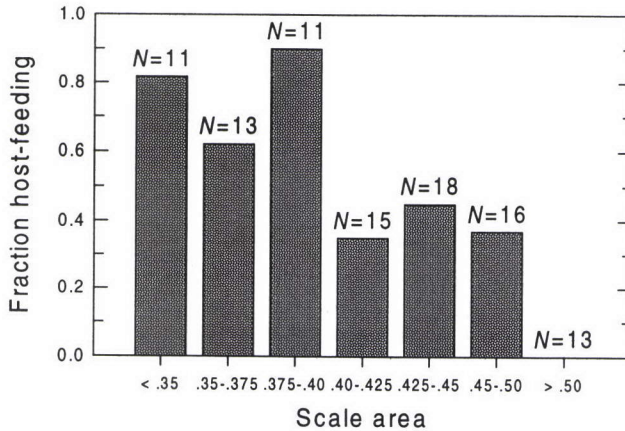


Figure 4.13 Rosenheim and Rosen (1992) found that smaller second instar hosts were used for host feeding with much higher frequency ($p < .001$) than larger hosts. Scale area is measured in mm^2 .

sensitive to egg complement, whereas host-feeding on second instar scales may not be. The question has not yet been resolved.

However, the notion that host variation may lead to different behavioral responses is valuable. For example, scale area affects the number of progeny that emerge. Heimpel et al. (1996) found that oviposition in first instar scales leads to a fitness increment (potential grandchildren) of 3 emerging, in second instar scales to a fitness increment of 9 progeny emerging, and in third instar scales to a fitness increment of 11. Thus we come to the second qualitative prediction.

Prediction #2. Smaller hosts are more likely to be used for host-feeding than for oviposition.

Rosenheim and Rosen (1992) found exactly this dependence (fig. 4.13) and used stepwise logistic regression to determine that host area was the most important variable and highly significant ($p < .001$) as a predictor of whether a parasitoid would host-feed. Rosenheim and Rosen used *A. lingnanensis*; Heimpel and Rosenheim (1995) confirmed the result with *A. melinus*.

Into the woods

All of the studies described thus far took place in the laboratory. Heimpel et al. (1996, 1998) combined predictions 1 and 2 and took them to the field. During three seasons, parasitoids were observed in an abandoned almond orchard. Once found, parasitoids were followed until a host encounter, and their behavior was observed using a handlens. After oviposition, parasitoids and the encountered host were captured and brought to the laboratory for dissection. In this manner, the egg complement of the parasitoid at the time of encounter was determined. Host area (treated as an ellipse) was an index of host size. Approximately 70 parasitoids were observed either ovipositing or host-feeding.

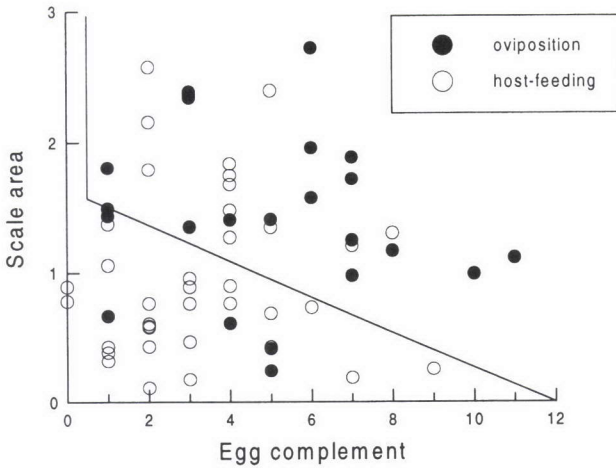


Figure 4.14 Heimpel et al. (1996) studied the oviposition and host-feeding behavior of *Aphytis melinus* in the field and found support for the predictions developed in this chapter. Filled circles denote hosts that were used for oviposition, open circles hosts that were used for host-feeding. The boundary line between oviposition and host-feeding is drawn for ease of presentation and was determined by using least squares to determine the parameters S_o and E_o that give the best fit between the data and the line $S_b(E) = S_o(1 - E/E_o)$, with the understanding it is predicted that the hosts which fall above the line are used for oviposition and hosts below the line are used for host-feeding. Oviposition is impossible when the egg complement is less than one, hence the vertical line.

The broad general prediction is that parasitoids with larger egg loads are more likely to oviposit and that smaller hosts are more likely to be used for host-feeding than oviposition. The field studies support (fig. 4.14) all of the predictions that we've developed in this chapter:

- Ovipositing parasitoids had a higher mean egg load (5.1 ± 0.51 , SEM) than host-feeding parasitoids (3.4 ± 0.32).
- Scale hosts used for oviposition were larger ($1.5 \pm 0.12 \text{ mm}^2$) than scale insects used for host-feeding ($1.0 \pm 0.11 \text{ mm}^2$).
- Both scale area and egg complement entered into a logistic regression for the probability of host-feeding versus ovipositing, and both were significant ($p = .004$ and $p = .039$, respectively).
- The interaction term (scale area) \times (egg complement) did not enter into the logistic regression significantly ($p > .5$), showing that the two variables affect behavior independently.