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Effects of Time Limitation and Egg Limitation on Lifetime Reproductive Success of a Parasitoid in the Field

George E. Heimpel,[1,*] Marc Mangel,[2,†] and Jay A. Rosenheim[1,‡]

1. Department of Entomology, University of California, Davis California 95616;
2. Department of Environmental Studies, University of California, Santa Cruz, California 95064

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ABSTRACT: We used field observations of freely foraging *Aphytis aonidiae* parasitoids in conjunction with results of laboratory studies of *A. aonidiae* and other *Aphytis* species to simulate lifetime patterns of behavior and reproduction. Field observations provided estimates of encounter rates with three classes of hosts, the mortality rate from predation on adult parasitoids, and host-handling times for oviposition and host feeding by adult wasps. A series of physiological parameters, including the egg maturation rate and the value of host-feeding meals, were estimated from previously published studies. Plasticity in parasitoid behavior was incorporated in two ways. For one set of simulations we used a behavioral rule derived empirically from observations of parasitoids made in the field, and for another we used a dynamic state-variable model to generate a set of behavioral rules that maximize lifetime reproductive success. As was expected, the empirically derived rule led to better matches with field observations than did simulations using the output of the dynamic model. Projections of lifetime reproductive success in the field ranged between three and 37 eggs within the 95% confidence intervals of the mortality rate and host encounter rate and depending on which behavioral rule was used. Lifetime reproductive success from the simulation with central estimates of the mortality and host encounter rates that incorporated the empirical rule was 6.25 eggs. Using the empirical versus the theoretical rule in the simulations led to a 10%–30% decline in projections of lifetime reproductive success, depending on mortality and host encounter rates. Regardless of the behavioral rule, the simulations underscored the observation that the host encounter rate was greater than the egg maturation rate. The overall oviposition rate was sufficiently high to lead to daily episodes of temporary egg limitation during which parasitoids must mature an egg before being able to oviposit.

Keywords: Aphytis, dynamic modeling, egg limitation, fecundity, reproductive success, parasitoids.

*To whom correspondence should be addressed. Present address: Department of Entomology, University of Minnesota, St. Paul, Minnesota 55108; E-mail: heimp001@tc.umn.edu.

†E-mail: msmangel@cats.ucsc.edu.

‡E-mail: jarosenheim@ucdavis.edu.

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The lifetime reproductive success that insect parasitoids attain in the field has important implications for both the evolution of reproductive strategies (Godfray 1994) and the demographics of host-parasitoid interactions (Hassell and Godfray 1992; Murdoch 1994). Estimates of lifetime reproductive success of any parasitoid species in the field are almost entirely lacking, however, and the factors that limit reproductive success in the field are largely unknown (Driessen and Hemerik 1992; Visser 1994; Kazmer and Luck 1995; West et al. 1996). Most estimates of reproductive success in parasitoids come from laboratory studies in which hosts and food are superabundant and parasitoids are free of predation and harsh climatic conditions. While laboratory studies are valuable for establishing relationships between various parameters and potential reproductive gain, they cannot tell us which factors are likely to limit reproductive success in the field.

Broadly speaking, the lifetime reproductive success of female parasitoids can be limited by the number of eggs that are available for oviposition or by the number of suitable hosts encountered during a parasitoid's lifetime (e.g., Mangel 1987; Driessen and Hemerik 1992; Godfray 1994; Getz and Mills 1996; Rosenheim 1996; Shea et al. 1996; Ellers and van Alphen 1997). Lifetime reproductive success of female parasitoids is therefore expected to depend on host encounter rates, life expectancy, and the timing and rate of egg maturation. Furthermore, parasitoid foraging and oviposition behavior can vary in response to a wide variety of factors that include host availability as well as the parasitoid's physiological state (Godfray 1994). The function of this behavioral plasticity is presumably to maximize lifetime reproductive success by balancing the risks of becoming time- and egg-limited (e.g., Mangel 1987, 1989; Mangel and Heimpel 1998).

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Here, we report observations of freely foraging parasitoids to estimate host availability and life expectancy for a parasitoid wasp in the field. These estimates, along with behavioral rules and data describing the dynamics of egg maturation, are used to run Monte Carlo simulations that provide projections of lifetime reproductive success and allow us to explore conditions under which parasitoids are likely to become egg- or time-limited. We contrast the effect of two classes of behavioral rules on lifetime reproductive success. First, we use a rule obtained empirically in the field that incorporates host quality and the parasitoid's egg load (Heimpel et al. 1996). Second, we parameterize a dynamic state-variable model that takes into account these factors as well as host availability and life expectancy in generating a complex set of behavioral rules that leads to the theoretical maximum lifetime reproductive success.

Linking observations of freely foraging parasitoids in the field to models that incorporate variability in oviposition behavior allows us to address two questions that have broad implications for host-parasitoid interactions. First, what is the projected lifetime reproductive success of parasitoids in the field? Second, what factors are likely to limit this lifetime reproductive success?

The Study System and Observational Protocol

Aphytis aonidiae (Mercet) (Hymenoptera: Aphelinidae) is a holarctically distributed parasitoid of the San Jose scale *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae), a pest of fruit and nut trees that was accidentally introduced into the United States from Asia around 1870 (Gulmahamad and DeBach 1978*a;* Rosen and DeBach 1979). Most stages of diaspidid scale insects ("armored scales") are sessile, feeding on their host plant and secreting a waxy, protective cover over their body (Rosen 1990). *Aphytis* parasitoids deposit one or more eggs ectoparasitically beneath the scale cover, and the developing offspring consume the scale insect body (Rosen and DeBach 1979; Rosen 1994). Hosts may also be used for "host feeding," in which adult females construct a feeding tube through which they imbibe host hemolymph (Rosenheim and Heimpel 1994; Collier 1995*b*). *Aphytis aonidiae* is a uniparental parasitoid that uses hosts to either deposit single female eggs or host feed (Gulmahamad and DeBach 1978*b;* Heimpel et al. 1996). Approximately 60% of accepted hosts are used for host feeding, and smaller hosts are more likely to be used for host feeding than are larger hosts (Heimpel et al. 1996).

Lifetime reproductive success of *Aphytis* females is determined not only by the availability of suitable hosts as oviposition sites but also by the availability of nutrients in the form of hosts used for host feeding and by the time available to mature eggs. *Aphytis* parasitoids are synovigenic, meaning that they have the capability to mature more eggs than can be held in their ovaries at one time (Collier 1995*b;* Heimpel et al. 1997*a;* Heimpel and Rosenheim 1998). An initial number of eggs is matured from material obtained during the larval stage, and additional eggs can be matured via host feeding (Heimpel et al. 1997*a*). The ovarian capacity of *Aphytis* females is limited, and egg maturation rates are relatively long (Collier 1995*b*). *Aphytis* parasitoids are therefore at risk of depleting their egg supply when the host encounter rate is high (Heimpel et al. 1996; Heimpel and Rosenheim 1998). *Aphytis* females balance the benefits of oviposition with the potential costs of impending egg limitation by adjusting clutch size and host-feeding behavior to match the perceived risk of egg limitation. As the number of mature eggs held in the ovaries ("egg load") declines, females lay smaller clutches and are more likely to use hosts for host feeding rather than oviposition (Rosenheim and Rosen 1991; Collier et al. 1994; Rosenheim and Heimpel 1994; Heimpel and Rosenheim 1995; Heimpel et al. 1996).

Maximum reproductive output requires the maturation of approximately five to 10 full complements of eggs, a process that takes between 2 and 4 wk in *Aphytis melinus* (Heimpel et al. 1997*a*). Both starvation and predation have the potential to limit severely the lifespan of *Aphytis* parasitoids in the field, however. The lifespan of *Aphytis* females held in the laboratory without a sugar source is typically less than 2 d even if host feeding takes place (DeBach and White 1960; Heimpel et al. 1994, 1997*a*), and the availability of sugar sources in the field can be highly variable (G. E. Heimpel, personal observation). Also, as we discuss in more detail below, predation rates on *A. aonidiae* females foraging in the field can be very high (Heimpel et al. 1997*b*).

Here, we use values of host availability, life expectancy, and host handling times estimated from observations of *A. aonidiae* females foraging freely in the field and documented estimates for the egg maturation rate and the relationship between host feeding and egg maturation in *Aphytis* spp. to calculate the projected lifetime reproductive success of female *A. aonidiae* in the field. We calculate two classes of projections by incorporating parasitoid behavioral plasticity in two ways: by using an empirically derived behavioral rule derived from field observations (Heimpel et al. 1996) and by parameterizing a dynamic state-variable model (Mangel and Clark 1988; Mangel and Ludwig 1992), in which behavior is allowed to vary with host quality and availability as well as the parasitoid's physiological state and life expectancy. We are

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therefore able to contrast projections of lifetime reproductive success stemming from "real" versus theoretically "optimal" behavior.

Details of the observational protocol are described elsewhere (Heimpel et al. 1996), and we summarize them briefly here. *Aphytis aonidiae* were found by scanning almond trees, and once found were followed until a host encounter occurred, they were lost to the observer, or they were preyed upon. Host encounters that resulted in more than 1 min of probing by the parasitoid were classified as rejection, host feeding, or oviposition, and parasitoids and hosts were put on ice and brought to the laboratory to quantify parasitoid egg load and host size (Heimpel et al. 1996). These observations allowed estimation of host encounter rates and rates of predation on adult parasitoids. Although observations were only done on trees that harbored host insects, host populations are perennial due to the limited capability for dispersal of scale insects. *Aphytis* activity is therefore restricted to trees and areas of the orchard harboring hosts, and it is unlikely that more than a small fraction of *A. aonidiae* searched trees that contained no hosts. Informal searches for *A. aonidiae* in sections of the orchard not harboring scale were never successful.

The Simulation Model

In this section, we describe how observations of freely foraging individuals in the field and results from laboratory studies were used to estimate host availability, handling times, the parasitoid mortality rate, the relationship between host size and parasitoid fitness, the rate of egg maturation, and the benefits derived from host feeding. We also explain how plasticity in behavior is incorporated via a simple, empirically derived rule.

Parameters estimated in this study include availability of three host size classes and handling times for the three behaviors. The relationship between host size and parasitoid egg load at eclosion and pupal mortality rate are reported in an earlier study (Heimpel et al. 1996), and an estimate of mortality rates due to predation of adult *Aphytis aonidiae* during the behavioral observations was available from data presented elsewhere (Heimpel et al. 1997*b*). Information on egg maturation rates and the rate at which resources obtained by host feeding are converted to eggs is available for *Aphytis melinus* (Collier 1995*b*), and the contribution of individual host-feeding meals to longevity of *A. melinus* and *Aphytis lingnanensis* has been investigated (Heimpel et al. 1994, 1997*a;* Collier 1995*b*). A summary of parameters used in the model is provided in table 1. The behavioral rule specifying whether hosts of a given size class are used for oviposition or host feeding is derived from field observations (Heimpel et al. 1996). The generation of a set of behavioral rules derived by dynamic modeling is discussed in the section below titled "The Dynamic Model."

Host Availability

Host availability, or the probability of encountering a host within a given time period, was estimated from field observations of foraging parasitoids that either encountered hosts or did not encounter hosts. We begin by assuming that the probability of a host encounter (λ) occurring during time interval t can be described using the Poisson process in which r is the rate of encounter:

$$\lambda = 1 - \exp(-rt). \quad (1)$$

To estimate the encounter rate, we divided the total number of encounters observed by the total time spent observing foraging parasitoids, whether the parasitoids encountered hosts or not. This estimator of the encounter rate is valid even if observations are begun at a random time between events (see Feller 1971, pp. 11–14). The total observation time was 87.3 h, and individual observation times ranged between 1 and 120 min (Heimpel et al. 1996, 1997*b*). In all, 212 *A. aonidiae* females were observed, 68 of which encountered and accepted hosts for either oviposition or host feeding (Heimpel et al. 1996). Rejections of seemingly healthy hosts were relatively rare and could not be explained by parasitoid egg load or host size (Heimpel et al. 1996). We do not regard them as encounters with healthy hosts in this study because of the possibility that the hosts were unsuitable for some unknown reason (e.g., endoparasitism by *Encarsia perniciosus* Tower; see Heimpel et al. 1996). Our estimate of the encounter rate thus measures only the rate of encounter with hosts that are ultimately accepted for either host feeding or oviposition.

Observations were conducted in 1992, 1993, and 1994. In 1992, only the total time spent observing parasitoids was recorded, but in 1993 and 1994 the time parasitoids spent resting and handling hosts was recorded as well. Total observation time during 1993 and 1994 was 36.9 h. Parasitoids spent 16% of this time resting and 22% of the time handling hosts; the remainder of the observation time (62%) was spent "foraging." By assuming that these fractions are roughly equivalent from year to year, our estimates of resting, handling, and foraging time during all of our observations become 14.0, 19.2, and 54.1 h, respectively. Since handling times are explicitly included in the simulations (see below), we base the rate of encounter on the sum of foraging and resting times.

Since the total number of host encounters that resulted

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Table 1: Description of parameters and their estimates used in the simulation and dynamic models

Parameter	*Description*	*Estimate*
Δt	Single time unit	5 min
λ_i	Probability of encountering hosts in size class i during a single time unit	$\lambda_1 = .025$; $\lambda_2 = .028$; $\lambda_3 = .027$
μ	Within-day mortality rate per time period	.0048
τ_b	Handling time for behavior b	$\tau_{\text{reject}} = 5$ min; $\tau_{\text{oviposit}} = 10$ min; $\tau_{\text{host feed}} = 25$ min
D	Number of days	8
T	Number of time periods per day	120
m	Eggs matured from nutrient reserve pool per time unit	.011
hf_b	Number of egg equivalents stored as nutrient reserves for behavior b	$hf_{\text{reject}} = 0$; $hf_{\text{oviposit}} = 0$; $hf_{\text{host feed}} = 4$
c_b	Clutch size for behavior b	$c_{\text{reject}} = 0$; $c_{\text{oviposit}} = 1$; $c_{\text{host feed}} = 0$
g_i	Grand eggs obtained per host i	$g_1 = 7$; $g_2 = 10$; $g_3 = 12$
p	Developmental mortality	.39

Note: See text and table 4 for 95% confidence limits for λ and μ.

in either oviposition or host feeding during these observations was 68, our estimate of the encounter rate is 68/68.1 = 1.00 host per hour. The time period, Δt, used in the simulations is 5 min (see below), so the encounter rate that we used was 0.083 ± 0.010 (bootstrapped standard error) hosts per 5-min period. This estimate was confirmed using maximum likelihood techniques (app. A), and confidence limits were calculated using standard bootstrapping procedures by randomly resampling the original data set with replacement 1,000 times (Efron and Tibshirani 1993). Using equation (1) to calculate the probability of encountering a host during a 5-min time period yielded 0.080, with a lower 95% confidence limit of 0.062 and an upper 95% confidence interval of 0.097. These are the host encounter rates used in the simulation and dynamic models, and in figure 1 we show the probability of host encounter as a function of time spent foraging and resting.

We used the distribution of host sizes from the observations (Heimpel et al. 1996) to assign roughly equivalent encounter rates for three host size classes. The smallest size class included hosts with scale cover areas of between 0.04 and 0.70 mm^2 and corresponded to 31% of the hosts accepted for either host feeding or oviposition. The medium size class included hosts with scale cover areas ranging from 0.71 to 1.40 mm^2 and corresponded to 35% of the hosts accepted, and the largest size class included hosts with scale cover areas ranging from 1.40 mm^2 to 2.72 mm^2, which is the largest host size, or 34% of all hosts accepted.

Handling Times

Handling times for host feeding, oviposition, and rejection were measured in the field in 1993 and 1994. Because in some cases parasitoids were found while a host encounter was in progress, and in a few cases host feeding was interrupted, complete handling times were not recorded for all encounters. The complete observations, however, demonstrated that there were significant differences in handling times for the three activities. Para-

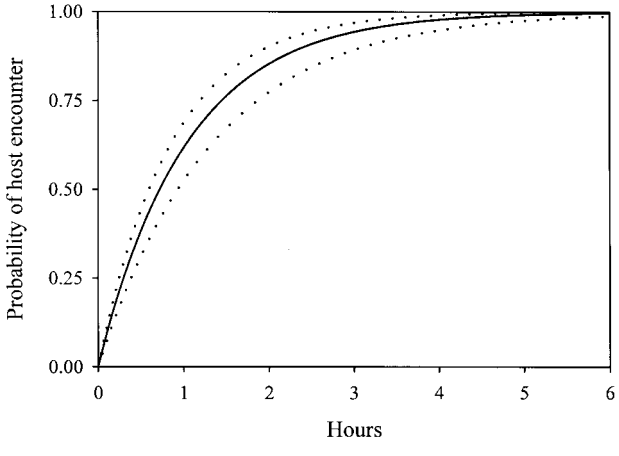

Figure 1: Probability of *Aphytis aonidiae* encountering hosts (size classes pooled) as a function of time. The solid line is calculated from the point estimate of the host encounter rate, and the dashed lines are lower and upper 95% confidence limits from bootstrapped data sets.

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Table 2: Handling times of *Aphytis aonidiae* rejecting hosts, ovipositing, and host feeding

Behavior	*Mean handling time (min) ± SEM*	*Sample size*
Rejection	4.89 ± 1.29	16
Oviposition	9.47 ± 2.07	12
Host feeding	25.18 ± 4.99	8

Note: Overall F test: $F = 15.59$, df = 2, 33; $P < .0001$.

sitoids took approximately 5 min to reject hosts, 10 min to oviposit, and 25 min to host feed (table 2). The fundamental time increment used for the model was therefore 5 min, with rejection being allocated one time unit, and oviposition and host feeding two and five time units, respectively. Rejection time refers to rejection after probing the host with the ovipositor. Rejection without probing is much more rapid (van Lenteren 1994; G. E. Heimpel, personal observations).

Survival Function and Time Horizon

We estimated the survival function from observations of predation events on *A. aonidiae* during the course of the field study. During the 87.3 h of observations, five predation events by a number of generalist predators including spiders, assassin bugs, and ants were recorded (Heimpel et al. 1997*b*). To obtain an estimate of the mortality rate attributable to predation, we divided the number of predation events observed by the total time spent observing parasitoids. This yields an overall mortality rate from predation of 0.057/h, or $\mu = 0.0048$ per 5-min time period, with a bootstrapped confidence interval of 0.0007–0.0083. The probability of survival during a 5-min time period is then $\exp(-\mu) = 0.995$, with a 95% confidence limit of 0.991–0.999 (fig. 2). This estimate was confirmed using maximum likelihood estimation (as in Heimpel et al. 1997*b*). In using this estimate, we made the simplifying assumption that predation rates are independent of parasitoid activity and we ignore adult mortality not attributable to predation. All of our observations were done during the day, and we also make the simplifying assumption that there is no risk of predation at night.

Our observations indicated that active foraging by *A. aonidiae* generally takes place between 9 A.M. and 7 P.M. (Heimpel and Rosenheim 1998), and we reflect this in the simulations by setting the within-day time horizon, T, at 10 h, or 120 time units. Since foraging does not occur at night in the model, the number of days, D,

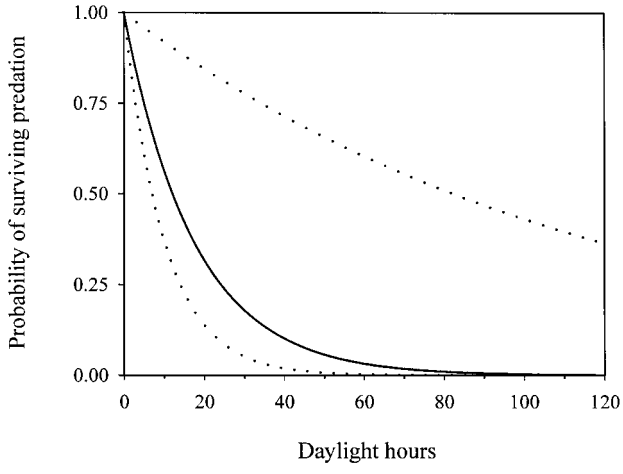

Figure 2: Probability of surviving predation for *Aphytis aonidiae* over time measured in daylight hours. The solid line was calculated from the point estimate of the mortality rate, and the dashed lines are lower and upper 95% confidence limits from bootstrapped data sets.

are simply multiples of T. For most model runs, the time horizon, $T \times D$, was set at the number of time units corresponding to a probability of 0.01 of surviving, or $(\ln 0.01)/-\mu = 960$ time units, or 8 d of foraging. For model runs using the lower 95% confidence limit of the predation rate, $T \times D$ was set at 3,600 time units, or 30 d of foraging. This time horizon corresponds to a probability of survival of approximately 0.1, and a number of laboratory studies suggest that senescence may become important by this age for *Aphytis* parasitoids (e.g., Gulmahamad and DeBach 1978*b;* Collier 1995*b;* Heimpel and Rosenheim 1995; Heimpel et al. 1997*a*).

The mortality estimate used here is lower and associated with broader confidence limits than that reported in earlier work (Heimpel et al. 1997*b*) for two reasons. First, we consider the complete observation time here instead of focusing on times of the year when predation rates were especially high, and second, we consider predation on *A. aonidiae* only and ignore observations of another parasitoid species present at our field site, *Aphytis vandenboschi* DeBach and Rosen.

Egg Load, Nutrient Reserves, and Host Feeding

Parasitoids in the simulations are described by the number of mature eggs that they carry (egg load) and the nutrients carried in reserve, also measured in units of egg load. Egg load is decremented by oviposition (only a single egg per host is allowed) and increased by egg maturation, which is dependent on availability of nutrients held

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in reserve. Nutrients can either be carried over from the larval stage or acquired in the adult stage by host feeding (Heimpel et al. 1997*a*). Collier (1995*b*) found that new eggs did not appear until 12–18 h after host feeding and that two eggs were matured during this period. Using 15 h as the maturation time for two eggs translates into a conversion rate of 0.011 eggs/5-min time period. In addition, 1.85 eggs can be matured during the 14-h inactive "night" period at this rate. Maximum egg capacity was set at 10 from the average maximum egg load of sugar-fed *A. aonidiae* females dissected 24–48 h posteclosion (Heimpel et al. 1996), and the maximum level of reserves was set at 15 based on another study (Heimpel et al. 1997*a*) showing that *A. melinus* females mature approximately 1.5 full egg complements without host feeding.

The egg load and nutrient reserves possessed by newly emerged *A. aonidiae* in the field are unknown. Although egg loads of recently eclosed *Aphytis* are close to zero when parasitoids are isolated from host scales prior to eclosion in the laboratory (Opp and Luck 1986; Collier 1995*b;* Heimpel et al. 1996), this may not reflect egg loads of adults emerging from underneath scale covers in the laboratory or the field. Eclosed adults may remain under the scale cover to mature eggs prior to emerging (G. E. Heimpel and J. A. Rosenheim, personal observation), as has been demonstrated for *Nasonia vitripennis* (Edwards 1954). Because of these ambiguities, we varied the initial egg load in the simulations. We both used fixed values for initial egg load, which ranged between 0 and 10, and randomized the initial egg load. Regardless of initial egg load, however, one full batch of eggs is matured without host feeding in all species of *Aphytis* studied to date (e.g., Opp and Luck 1986; Rosenheim and Rosen 1991; Collier 1995*b;* Heimpel et al. 1996, 1997*a*). *Aphytis melinus* females are also able to mature an additional one-half complement of eggs without host feeding. For the simulations, we assumed that reserves present before host feeding were used to mature the initial egg load by setting the initial nutrient reserves level at 1.5 × maximum egg load − initial egg load.

Laboratory studies of *A. lingnanensis* and *A. melinus* have shown that a single host-feeding meal leads to the maturation of approximately two eggs over a 2-d period (Heimpel et al. 1994; Collier 1995*b*). For *A. melinus,* the same gain was reported for second and third instar hosts (Collier 1995*b*). The overall gain in eggs per host-feeding meal averaged over the lifetime of *A. melinus* was found to be 3.9 eggs, however (Heimpel et al. 1997*a*). The value of a single host-feeding meal was therefore set at four eggs for the simulations.

Although egg resorption has been documented in laboratory studies of *Aphytis* parasitoids (Collier 1995*b;* Heimpel and Rosenheim 1995; Heimpel et al. 1997*a*), it has only been found under conditions of host deprivation (i.e., when host feeding was not allowed). We assume that egg resorption is less important when host feeding takes place (or is incorporated into documented rates of egg maturation under these conditions) and do not include it in our model for this reason.

Host Feeding and Starvation

Although the primary role of host feeding for *Aphytis* parasitoids appears to be egg maturation, host feeding can increase longevity as well. The benefits to longevity can be substantial when parasitoids are offered honey in addition to host-feeding opportunities (Collier 1995*b;* Heimpel et al. 1997*a*) or can be slight to nonexistent when parasitoids are deprived of sugar (Heimpel et al. 1994, 1997*a*). To incorporate an effect of host feeding on life span in our model, we constrained parasitoids to starve when nutrient reserves fall below a single unit of nutrient level. Parasitoids can only replenish nutrient reserves by host feeding and can therefore avoid starvation by host feeding. This rule is most applicable to parasitoids that have access to a sugar source because sugar-starved *A. melinus* cannot increase their life span by host feeding (Heimpel et al. 1997*a*). Starvation can occur during the day or at night in the simulations. Since neither host encounters nor the risk of predation operate at night, however, we did not include an explicit time structure between days. Parasitoids are therefore constrained to starve if the reserves at the end of a given day are below what is needed to survive through the 14-h inactive period given the nutrient conversion rate (i.e., starvation occurs if nutrient reserves are below 2.85 at the end of the day).

An Empirically Derived Behavioral Rule

We used a behavioral rule derived from field observations, which is presented elsewhere (Heimpel et al. 1996, app.). To derive the rule, we calculated the slope and intercept of a line dividing the parameter space containing empirically based parasitoid egg load and host size combinations into oviposition and host-feeding regions. The equation for this line gives the threshold host size, S_t, above which oviposition tended to occur and below which host feeding tended to occur, at a given parasitoid egg load, x (Heimpel et al. 1996):

$$S_t(x) = 1.5 - 0.125x. \quad (2)$$

This rule is independent of nutrient reserves, host en-

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Table 3: Egg loads at which parasitoids host feed or oviposit according to the empirically derived behavioral rule (eq. [2]) for the midpoints (in parentheses) of three host size classes

Host size class	*Host feeding*	*Oviposition*
Small (.33 mm^2)	0–9	10
Medium (1.06 mm^2)	0–3	4–10
Large (2.06 mm^2)	0*	1–10

*The behavioral rule would mandate oviposition for all parasitoids encountering large hosts, but this is not possible when egg load is zero.

counter rate, or mortality rate. The host sizes compared with $S_i(x)$ in allocating behavior were the midpoints of the three size classes discussed above. Table 3 shows the combinations of host size class and egg load that lead to host feeding and oviposition under this rule.

The Dynamic Model

In dynamic state-variable models, behaviors maximizing lifetime reproductive success are identified as a function of an organism's physiological state(s), the time an organism has left to live, and physiological and ecological parameters (Mangel and Clark 1988). Dynamic models have been constructed to analyze a wide variety of behaviors and life-history strategies in insects and other taxa (e.g., Stephens and Krebs 1986; Houston et al. 1988; Mangel and Clark 1988; Mangel and Ludwig 1992; Clark 1993; McNamara and Houston 1996).

The specific class of dynamic model that we consider generates predictions for a behavioral dichotomy faced by many species of insect parasitoids: that of using hosts for oviposition or for adult "host feeding." Females of all parasitoid species lay one or more eggs on, in, or near host insects (Godfray 1994). The adult females of some species, however, may feed upon host insects as well as parasitizing them (Jervis and Kidd 1986; Heimpel and Collier 1996). Most host-feeding models include at least two physiological state-variables (egg load and nutrient reserves) and at least two ecological variables, the host encounter rate and the risk of parasitoid mortality (e.g., Chan and Godfray 1993; Collier 1995*a;* reviewed by Heimpel and Collier 1996).

In our model, behavioral predictions over the parasitoid's lifetime are computed as a function of egg load, nutritional reserves, and host size class. As in the simulation models, the parasitoid's life is divided into D days, each of which is divided into T time units. Time is measured discretely such that one unit, Δt, corresponds to the shortest handling time for a probed host. This precludes the possibility that two or more hosts are encountered during a single time period. During each time period, a parasitoid survives with probability $\exp(-\mu)$, where μ is the mortality rate due to predation per time period, and encounters one of i host types with probability λ_i. The host types differ in size and, therefore, affect the size and the egg capacity, g_i, of parasitoids that develop on them. Parasitoids are characterized by an egg load, x, and a level of nutrient reserves, y, and nutrients are converted into eggs at a rate of m egg units per time period. For the within-day dynamics, we incorporated the conversion rate into the model using two-dimensional linear interpolation (app. B). State variable dynamics are as in the simulation model. Egg load and nutrient reserves cannot exceed x_{max} and y_{max}, respectively. Egg loads can drop to zero, but the parasitoid starves if nutrient reserves drop below y_{min}. The behaviors available to the parasitoid are rejection, oviposition, and host feeding and are specified by the subscript b. Oviposition yields a clutch of $c_{oviposit} = 1$, and host feeding yields $hf_{host\ feeding}$ nutrients, also measured in units of egg load. Handling times, τ_b, differ according to the decision.

In the dynamic model we distinguish between fitness obtained from the different host classes. Reproductive gain accrued during a given time period in which a host of type i is encountered is denoted by $W_{b,i}$, and depends on the number and egg capacity of parasitoids emerging from host type i, as well as the developmental mortality of parasitoid offspring, p:

$$W_{b,i} = c_b g_{b,i}(1 - p). \tag{3}$$

The maximum expected lifetime reproductive success of a parasitoid at time t during day d, with egg load x, and nutrient reserves level y is

$$\sum_{d=1}^{D} F(x, y, t, T, d)$$

for parasitoids with a maximum life span of $T \times D$ time units. Fitness values are calculated using backward iteration, beginning with time T from day D, for which fitness is set at 0 (no fitness can be accrued after death). Fitness for all other time steps is the sum of future fitness (fitness accumulated during $t + 1$ to T and summed over days) and fitness gained during t. The dynamic programming equation for within-day fitness gain and state-variable dynamics is as follows:

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$$F(x, y, t, T, d)$$
$$= \left(1 - \sum_{i=1}^{n} \lambda_i\right) \exp(-\mu) F(x + m, y - m, t + 1, T, d)$$
$$+ \sum_{i=1}^{n} \lambda_i \max_b (W_{b,i} + \exp(-\mu\tau_b) F(x - c_b + m\tau_b, y + hf_b - m\tau_b, t + \tau_b, T, d)). \quad (4)$$

The first term on the right-hand side of the equation represents fitness associated with not encountering a host during t_d. The second term represents the fitness associated with encountering a host. The value is calculated for each host class and each of the three behaviors, and the behavior associated with the highest value is chosen for each host type. Fitness values gained from each host type are weighted by the probability of encounter and summed to update the fitness function. The model stipulates that egg load and nutrient reserves cannot exceed a maximum capacity, and if nutrient reserves fall below a certain level, the parasitoid dies of starvation, as discussed above for the simulation model. Ten-hour daylight foraging periods are separated by 14-h nights, when eggs can be matured and reserve levels decremented, but host encounter is not possible. Mortality through starvation is possible at night, but we assume that there is no predation risk. Fitness values are updated each day as follows:

$$F(x, y, T, T, d) = F(x + m\tau_n, y - m\tau_n, 1, d + 1), \quad (5)$$

in which τ_n is the length of the night.

Parameterization of the Dynamic Model

Host encounter rates, survival rates, and physiological parameters are as described for the simulations described above. Parameters associated with the fitness of parasitoid offspring are included only in the dynamic model.

Developmental Mortality

Of 142 apparently healthy *Aphytis aonidiae* pupae collected from the field and brought into the laboratory, 56 (39%) failed to develop into adults (Heimpel et al. 1996). We use this as an estimate of developmental mortality in the field (p in eq. [3]). Biases associated with the value include potential differences in pupal mortality rates in the laboratory and the field and our omission of mortality occurring during other immature stages.

Fitness Currency

We use the expected initial egg complement of daughters (the "grand eggs") as a fitness currency and link it to host size via the relationship between host size and initial egg load of parasitoids. Since *Aphytis* parasitoids mature eggs throughout their adult life, egg loads of 1-d-old females cannot be viewed as representing lifetime fecundity. However, this value correlates with potential fecundity early in life, and larger individuals have both higher initial egg loads under laboratory conditions (Opp and Luck 1986; Rosenheim and Rosen 1991; Heimpel et al. 1996) and greater potential lifetime fecundity (Luck 1990). We use the relationship between host size and egg load of 1-d-old parasitoids to assign fitness values to the three host classes, which was found to be asymptotic (Heimpel et al. 1996):

$$\text{Egg load} = \frac{(\text{scale cover area})45.3}{1 + (\text{scale cover area})3.4}. \quad (6)$$

By applying this relationship to the midpoints of the size ranges cited above, we estimated that the number of grand eggs associated with small, medium, and large host classes was 7, 10, and 12, respectively.

Results of the Dynamic Model

We report model predictions for the time period at which one-half of the parasitoids are expected to be surviving (i.e., $(\ln 0.5)/-\mu = 144$; time period 24 on day 2; fig. 3). The predictions are in general agreement with other host-feeding models that have predicted increased likelihood of host feeding with decreasing egg load, nutrient reserves, and host size (Heimpel and Collier 1996; McGregor 1997). Also, predicted behavior was most sensitive to the state variables on the smallest host class (fig. 3). Model predictions within and between days, and using lower and upper 95% confidence limits of λ and μ, were qualitatively very similar to those presented in figure 3 but differed in exact combinations of host types and state variables resulting in host feeding, oviposition, and rejection.

Implementing the Simulations

The simulations were iterated forward in time, and for each time step, random numbers were drawn from uniform distributions to determine whether the parasitoid survived the time period, whether a host was encountered, and which host type (if any) was encountered. Initial egg loads were set at values between 0 and 10 or chosen at random from a uniform distribution among these values. Initial reserves levels were set at 15 − initial egg

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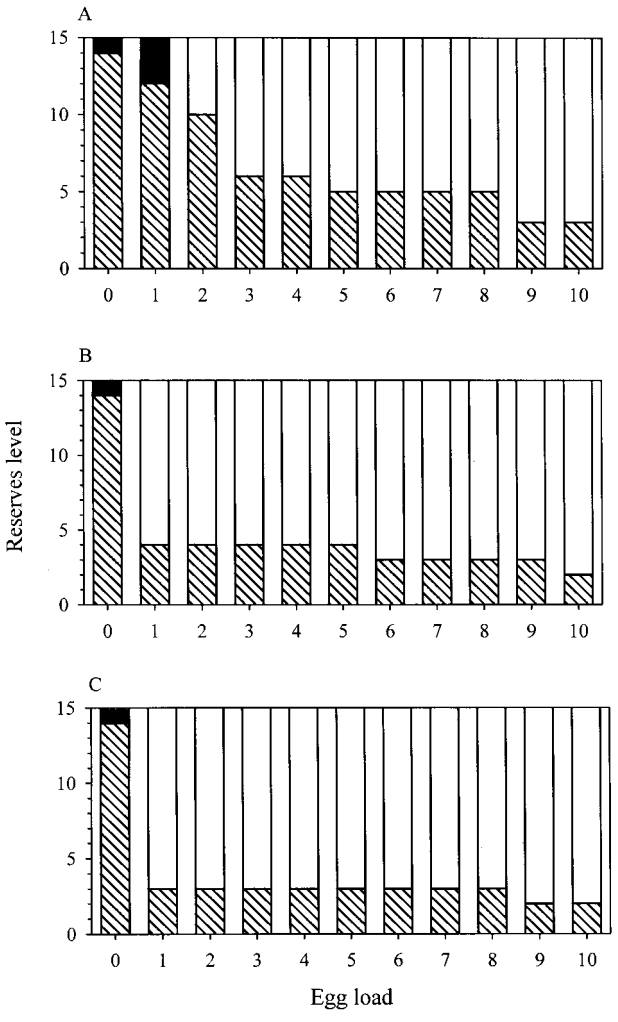

Figure 3: Predictions from the dynamic model for effect of nutrient reserves, egg load, and host size class on behavior for day 2, time period 24 (the adult parasitoid half-life). *Striped area* = host feeding; *black area* = rejection; *clear area* = oviposition. *A,* Small host; *B,* medium-sized host; *C,* large host.

load. Both of these state variables were updated according to the physiological parameters discussed above. Because state-variable changes occur as subinteger values for each time step, we truncated egg load values to the nearest integer and rounded reserve levels to the nearest integer to determine the behavior in the next available time period. We implemented the empirically derived behavioral rule by constraining parasitoids of egg load x to oviposit if the size of the host encountered was equal to or greater than $S_t(x)$ from equation (2) and to host feed otherwise. For runs using the theoretical behavioral rule, the decision matrix from the dynamic model was used to determine the behavior during each time step given the egg load, reserves level, and host type encountered. Handling times were incorporated by not allowing parasitoids to encounter hosts for τ_b time periods following a host encounter. We modeled 1,000 parasitoids for each simulation and obtained four classes of results: lifetime reproductive success (total number of eggs laid per parasitoid per lifetime); means and 95% confidence limits of egg loads and reserve levels at each time period; the proportion of hosts used for oviposition and host feeding; and the distribution of egg loads that occurred during the simulations.

Model Validation

Before discussing the estimates of lifetime reproductive success, we compare model output with parasitoid egg load distributions observed in the field. These comparisons will guide our choice of a model with which to estimate lifetime reproductive success.

We generated expected egg load distributions by summing the number of time steps that contained wasps within each egg load class and dividing these sums by the total number of parasitoid-time combinations that occurred. Since parasitoids died with probability $(1 - \exp(-\mu))$ during each time step, these distributions reflect the diminishing contribution of older parasitoids. We simulated the egg load distributions for various levels of egg load at emergence for both behavioral rules and for all combinations of the 95% confidence limits of the host encounter and mortality rates. These simulated distributions were compared to the distribution of egg loads of field-collected wasps using single-classification goodness-of-fit tests (Sokal and Rohlf 1981). Interpretation of the zero-egg class from field-collected parasitoids is problematic, however. We found that a substantial fraction of pupae collected from the field developed into adults that were unable to mature eggs within at least the first 5 d of life when deprived of hosts (Heimpel et al. 1996). This differed markedly from the majority of parasitoids that matured a full complement of eggs in 24 h when deprived of hosts (Heimpel et al. 1996). We are unable to identify the causes of this egg limitation, and because we do not know what fraction of eggless adult parasitoids captured in the field belonged to this class of females, we restrict the zero-egg class to parasitoids that were observed to lay their last egg. Thus, the field data that we use in these analyses are post-host-encounter egg loads of *Aphytis aonidiae* that had one or more eggs before encountering hosts. The zero-egg class is therefore a minimum estimate, but we are confident that it includes only females that were egg-limited due to oviposition.

In figure 4, we compare the distribution of egg loads for field-collected parasitoids and the distribution of the simulation model using both behavioral rules, randomized initial egg loads, and the central values for mortality

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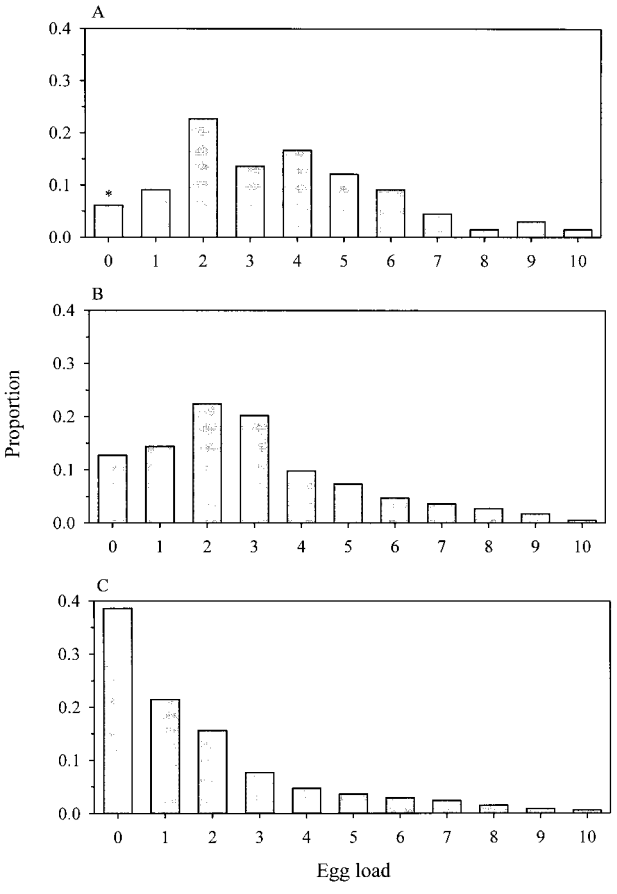

Figure 4: Egg load distribution of *Aphytis aonidiae* collected in the field that encountered and accepted hosts (*A*) and from simulations using the empirically derived behavioral rule (*B*) and the output of the dynamic model (*C*). The asterisk above the field data panel indicates that the zero egg load class is a minimum estimate because only parasitoids carrying eggs prior to the host encounter were included in the figure (see text). For both simulations, initial egg loads were randomized and the central estimates for mortality and host encounter rates were used.

and host encounter rates. The criterion for significant difference in the goodness-of-fit tests was that $G > \chi^2 = 18.3$, df = 10, $P = .05$ (Sokal and Rohlf 1981). The value of G was greater than this for all simulations using the output of the dynamic model, regardless of encounter rate, mortality rate, or initial egg load. Values of G lower than 18.3 were found, however, for some of the simulations using the empirically derived behavioral rule. Lack of significant difference was found only when the initial egg load was randomized but for various combinations of the host encounter rate and mortality rate. The mean population-wide simulated egg loads are lower in every case than those of field-collected wasps but in many cases the difference is less than half of an egg (table 4). The conditions leading to egg load distributions most closely resembling those in the field are low host encounter rates and high mortality rates; low mortality rates and high host encounter rates lead to mean egg loads that are in most cases one egg or more lower than that of field-collected wasps (table 4).

The comparison of field data on egg loads with output from the simulations suggests that our model is most successful in simulating behavior in the field when the empirically derived behavioral rule is used and when the initial egg load is randomized. Thus, we will consider these conditions most likely to give accurate estimates of lifetime reproductive success in the field. Model runs that use the output of the dynamic model to determine behavior, on the other hand, will provide a theoretical benchmark for maximum achievable lifetime reproductive success given the other constraints built into the model.

Model Results

Lifetime Reproductive Success

Projected estimates of lifetime reproductive success ranged between three and 37 eggs, depending on the value of the mortality rate, the host encounter rate, and the behavioral rule (table 5). Differences in the mortality rate, μ, had a greater effect on projected lifetime reproductive success than did differences in λ, the host encounter rate. Estimates using the empirically derived behavioral rule were consistently lower than the output of the dynamic model, with differences ranging between 10% and 30% (table 5). The differences in estimated lifetime reproductive success were greatest at high mortality rates and low host encounter rates. For the central estimates of μ and λ, the estimates were 6.25 and 7.46, respectively, for the empirical and theoretical behavioral rules.

Dynamics of Physiological States

We illustrate the dynamics of egg load and nutrient levels for parasitoids following both behavioral rules, with randomized initial egg load and with central estimates of the mortality and host encounter rates. When the empirically derived behavioral rule is followed, the mean egg load drops from approximately five to 2.5 during the first day (fig. 5*A*). Average egg loads never drop below one with this rule, but egg limitation is incorporated within the 95% confidence interval for the duration of most days. Reserve levels rise during the days and stay uniformly high throughout the life of the parasitoid. When the output of the dynamic model is used to determine behavior, the general patterns are similar, but average egg loads and

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Table 4: Means and modes of egg load distributions from simulations using the empirically derived behavioral rule and randomized initial egg load for all combinations of the 95% confidence limits and central values of μ and $\sum\lambda_i$

Mortality rate, μ	*Overall host encounter rate,* $\sum\lambda_i$	*Mean egg load*	*Mode of egg load distribution*	G
.0007	.062	2.99	3	16.3
.0007	.080	2.31	2	45.7
.0007	.097	1.90	2	75.8
.0048	.062	3.46	3	8.2
.0048	.080	2.90	2	14.4
.0048	.097	2.56	2	25.8
.0083	.062	3.48	3	8.2
.0083	.080	3.17	2	13.8
.0083	.097	2.88	2	20.0

Note: *G* values <18.3 denote lack of significant difference of egg load distribution from that of field-collected wasps at $\alpha = .05$. Mean and modes for field-collected wasps are 3.64 and 2, respectively.

reserve levels are lower with mean egg loads dropping to just below one toward the end of each day (fig. 5*B*).

Variance in both egg load and reserve levels is very high in the simulations (fig. 5), reflecting the variability in both the initial state variables and the history of host encounter among individual parasitoids. In support of these simulations, our field data show a significant but highly variable tendency for a decrease in the egg load of *Aphytis aonidiae* with time of day (Heimpel and Rosenheim 1998). An example of a similar level of variability emerging from a dynamic model are the Monte Carlo simulations done in an earlier work (Mangel and Clark 1988, chap. 4) to estimate clutch sizes produced by the parasitoid *Nasonia vitripennis* given a dynamic model and stochasticity in encounter probabilities with various host size classes. The simulations produced highly variable clutch sizes that qualitatively matched observed distributions reported by Charnov and Skinner (1984).

Host-Feeding Behavior

As we mentioned above, 60% of the accepted hosts were used for host feeding during our observations of *A. aonidiae.* As expected, this value was closely approximated in our simulations when the empirically derived behavioral rule was used and initial egg load was randomized (table 6). Under these conditions, the prevalence of host feeding increased with host encounter rate and decreased with mortality rate. When the output of the dynamic model was used to determine behavior, however, host feeding prevalence was much lower and was dependent on mortality rate but not host encounter rate (table 6).

Table 5: Projected lifetime reproductive success using the empirically derived behavioral rule and the output of the dynamic model for each combination of three values of μ and $\sum\lambda_i$

Mortality rate, μ	*Overall host encounter rate,* $\sum\lambda_i$	*Empirical rule*	*Dynamic model*
.0007	.062	32.01	35.54
.0007	.080	32.69	36.01
.0007	.097	32.89	36.96
.0048	.062	5.65	7.08
.0048	.080	6.25	7.46
.0048	.097	6.39	7.51
.0083	.062	3.06	4.40
.0083	.080	3.56	4.81
.0083	.097	3.99	5.38

Note: Initial egg load randomized for all simulations.

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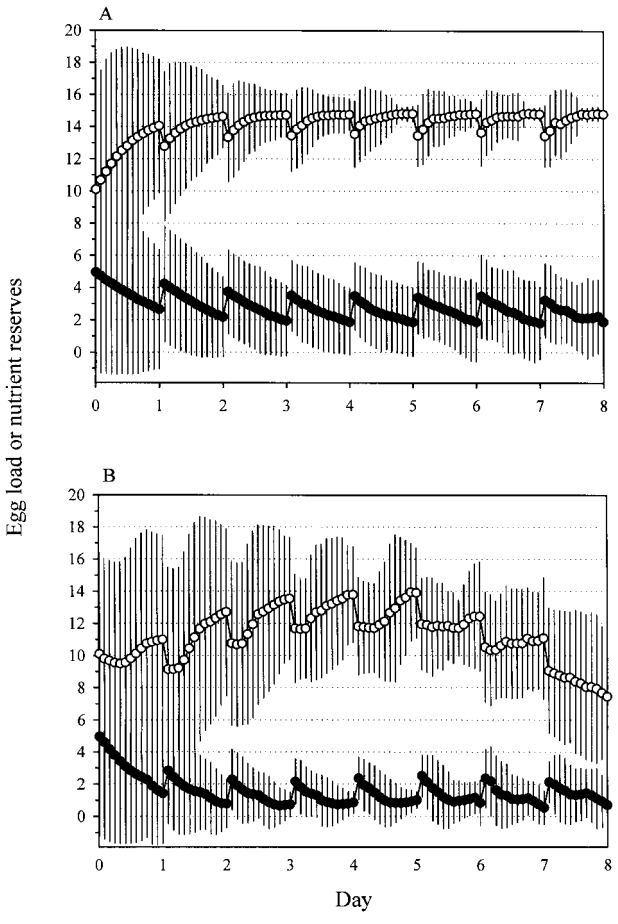

Figure 5: Time-specific means and 95% confidence intervals of egg load (*filled circles*) and nutritional reserves levels (*open circles*) from the simulations with application of the simple (*A*) and dynamic (*B*) behavioral rules. Values are shown for every 10 time periods (50 min) over 8 d. Egg loads at emergence were drawn at random from a uniform distribution between 0 and 10, and 1,000 parasitoids were simulated for each run.

Discussion

Our study supports the idea that lifetime reproductive success in *Aphytis aonidiae* can be limited both by eggs and time. We have already demonstrated that some *A. aonidiae* females become egg-limited in the field (Heimpel et al. 1996; Heimpel and Rosenheim 1998), and our simulations suggest that females may commonly cycle between zero to two and three to five eggs during the day and, thus, experience multiple episodes of temporary egg limitation. By parameterizing our simulations with high and low estimates of the predation rate on adult parasitoids, we also showed that lifetime reproductive success in the field is likely to be severely limited by constraints on longevity. Projections of lifetime reproductive success obtained using the lower 95% confidence interval for the predation rate were approximately four times as high as those obtained using the central estimate of the predation rate (see table 5). Other studies have similarly found that the mortality rate is a major determinant of lifetime reproductive success of insects in the field (e.g., Bouletreau 1978; Banks and Thompson 1987; Koenig and Albano 1987; Weisser et al. 1997).

Projections of lifetime reproductive success generated by our simulations were lower than fecundity of *A. aonidiae* reared in the laboratory. Although the mean lifetime fecundity of *A. aonidiae* in the laboratory is 85 eggs (range = 35–102; Gulmahamad and DeBach 1978*b*), our estimates ranged between approximately three and 37 eggs. With host encounter rate and mortality rate set at the central estimates, the estimated lifetime reproductive success was 6.25 eggs when the behavioral rule derived from field observations was used. As expected, the highest estimates of lifetime reproductive success were associated with model runs using the upper 95% confidence limit for the host encounter rate and the lower 95% confidence limit for mortality rate. Although the variation in projected lifetime reproductive success is due primarily to the low confidence that we have for our estimate of the predation rate (see fig. 2), the predation rate is also quite variable seasonally (Heimpel et al. 1997*b*). Thus, it is possible that natural seasonal variation in predation risk would lead to the broad range of estimated fitness values that we report. It is by no means certain, however, that *Aphytis* longevity is limited only by predation. In the laboratory, sugar-fed *Aphytis* females live between 2 and 4 wk, with most reproduction taking place during the first 2–3 wk (Heimpel et al. 1997*a*). When sugar is withheld, however, female *Aphytis melinus* and *Aphytis lingnanensis* "starve" within 2–3 d regardless of host-feeding opportunities (Heimpel et al. 1994, 1997*a*). Under conditions of sugar limitation, therefore, the central estimate of the mortality rate that we used in our simulations would probably correspond to the maximum attainable life span (see fig. 2). We suspect that the likelihood of *A. aonidiae* females becoming sugar-limited in the field may be high. In all our observations of *A. aonidiae* foraging in the field, we never observed an incident of sugar feeding.

Although lifetime reproductive success is lower in the field than in the laboratory, our central estimates of 6.25 eggs per lifetime for each female is consistent with population growth, even assuming an immature mortality rate of 0.39. The long-term population dynamics of *Aphytis*-diaspidid systems are often stable, however (Murdoch 1994), and stability implies that each individual is replaced by not more than a single reproducing adult, on average. We are not able to distinguish between the possibilities that the *Aphytis* population at our site was in a growth phase during our study and that our projected

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Table 6: Proportions of hosts used for host feeding in the simulations when the empirically derived behavioral rule or the output of the dynamic model is used for each combination of three values of μ and $\sum\lambda_i$

Mortality rate, μ	*Overall host encounter rate,* $\sum\lambda_i$	*Empirical rule*	*Dynamic model*
.0007	.062	.52	.20
.0007	.080	.59	.20
.0007	.097	.64	.20
.0048	.062	.50	.15
.0048	.080	.56	.15
.0048	.097	.59	.15
.0083	.062	.48	.11
.0083	.080	.53	.11
.0083	.097	.56	.11

Note: Initial egg load randomized for all simulations.

surplus of offspring is spurious and can be explained by overestimates of some component(s) of fitness. However, two parameters that would lead to estimates of average lifetime reproductive success that are lower than we report were not included in the model. First, our measure of developmental mortality ignored egg and larval mortality. We have no information on these parameters for our system, but even under sheltered laboratory conditions egg and larval mortality rates in *Aphytis* can range from 20% to 50% (Rosenheim and Rosen 1991, 1992; Heimpel and Rosenheim 1995). Second, our population of *A. aonidiae* contained a relatively large fraction of females that matured eggs at a much lower rate than other females, if they matured any eggs at all (Heimpel et al. 1996). Between August 1994 and January 1995 this fraction of "eggless females" fluctuated between 35% and 60% of parasitoids that were collected from the field as pupae (Heimpel et al. 1996). The potential decrements in fitness associated with prepupal developmental mortality and egglessness of daughters could therefore substantially affect recruitment of parasitoids into the population.

Parasitoid behavior can also affect the reproductive success achieved by females. We contrasted simulations that used two types of behavioral rules: a simple rule that was derived from field observations and one derived from a dynamic state-variable model that was designed to calculate the maximum theoretical lifetime reproductive success. It is not surprising that the simple rule led to better matches between egg load distributions and behaviors documented from the field than did the dynamic rule (see fig. 4, table 6). Incorporation of the dynamic model led to predictions of higher oviposition rates, which led to a decreased incidence of host feeding and lower egg loads. The potential increase in projected lifetime reproductive success associated with incorporation of the dynamic model was between 10% and 30%, depending on mortality and host encounter rates (see table 6). Our analyses therefore suggest that *A. aonidiae* could increase their lifetime reproductive success by host feeding less. This apparent anomaly could reflect constraints on the evolution of behavior maximizing lifetime reproductive success (possibly exacerbated by the fact that our study system included introduced species in an agricultural setting) and/or an underestimation on our part of the value of host feeding for *A. aonidiae.*

Our simulations showed both the pattern of state-variable changes and the variability in physiological states that can be expected given the stochastic nature of predation risk and host encounters. The patterns that emerge with respect to the dynamics of egg load appear to be driven by the fact that our estimate of the host encounter rate is higher than our estimate of the egg maturation rate. This leads to a situation in which egg loads drop monotonically during the day and increase overnight, following our assumption that egg maturation, but not oviposition, occurs at night.

In synovigenic species like *Aphytis,* the importance of time limitation is linked to the potential for temporary egg limitation. Since females emerge with relatively few eggs, and mature additional eggs relatively slowly, time limitation has an impact on lifetime reproductive success primarily by reducing time available for egg maturation. This is in contrast to pro-ovigenic species, which are unable to mature more than a single complement of eggs.

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In these species, egg limitation typically occurs only once, and it signifies the attainment of maximum lifetime reproductive success (Driessen and Hemerik 1992; Getz and Mills 1996; Shea et al. 1996). Driessen and Hemerik (1992) used an approach similar to the one in this article to support the view that both egg limitation and time limitation occur in populations of the *Drosophila* parasitoid *Leptopilina clavipes* (Hartig). Since *L. clavipes* is pro-ovigenic, individual females are either egg-limited (i.e., they die in the presence of suitable hosts having laid all their eggs) or time-limited (i.e., they die with eggs in their ovaries). In synovigenic species like *Aphytis,* however, individual females can experience both egg and time limitation by running out of eggs and the time to mature more of them.

Most traditional parasitoid-host population models make the assumption that parasitoids never become egg-limited and that reproductive success is limited primarily by the rate of host encounter (see Hassell and Godfray 1992 and Murdoch 1994 for recent reviews). The relatively recent realization, however, that parasitoid fitness can be affected by egg limitation as well, and that the likelihood of becoming egg-limited is in turn affected by a series of ecological, behavioral, and physiological factors, has motivated a new generation of models that incorporate the possibility of egg limitation and egg maturation in parasitoids (e.g., Briggs et al. 1995; Getz and Mills 1996; Shea et al. 1996; Murdoch et al. 1997). Our study has illustrated how egg and time limitation can interact in a synovigenic parasitoid and thus provides impetus for these and related efforts.

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APPENDIX A

Maximum Likelihood Estimation of the Encounter Rate

In this appendix, we describe a procedure for estimating the host encounter rate, r, which is based on the technique of maximum likelihood estimation (Edwards 1992; Hilborn and Mangel 1997). Given that our field observations included parasitoids that encountered and accepted hosts ("successful" parasitoids) and parasitoids that did not encounter or accept hosts ("unsuccessful" parasitoids), we seek the joint likelihood, L, that hosts are encountered by successful parasitoids and not encountered by unsuccessful parasitoids:

$$L = \prod_{i=1}^{N} (1 - e^{-rt_f(i)}) \prod_{k=1}^{M} e^{-rt_{nf}(k)}. \quad \text{(A1)}$$

Here, $t_f(i)$ denotes the observed search times for successful parasitoids (with $i = 1, 2, \ldots, N$), and $t_{nf}(k)$ denotes the observed search times for unsuccessful parasitoids (with $k = 1, 2, \ldots, M$). The negative log-likelihood, NLL, of equation (A1) is then

$$\text{NLL} = \sum_{i=1}^{N} \ln(1 - e^{-rt_f(i)}) + \sum_{k=1}^{M} - rt_{nf}(k). \quad \text{(A2)}$$

The parameter r was then estimated by iteration to minimize NLL and was found to be 0.018/min, or 0.09 hosts/5-min time period.

APPENDIX B

Interpolation of the State Variables

The construction of dynamic state-variable models of host-feeding strategies requires incorporation of processes that act at both behavioral and physiological timescales (Collier 1995*a*). Most important, the rate of egg maturation must be expressed in time units small enough to allow only a single behavioral event. For most parasitoid species, this means that the maturation of a single egg must occur over many behavioral time steps. One approach to obtaining realistic egg maturation delays has been the use of a large number of "pre-egg" state variables to keep track of changing nutrient levels and egg loads (Collier et al. 1994; Collier 1995*a*). This method, however, can become computationally unwieldy and may require more memory capacity than is available in many microcomputers or extremely lengthy computer runs (the "curse of dimensionality"; Mangel and Clark 1988). For example, to find solutions of the dynamic programming equation in this study (eq. [4]) using parameters from table 1 in which egg maturation is modeled using pre-egg states would require storing over 7.5×10^8 computed values.

We circumvented the curse of dimensionality by using two-dimensional linear interpolation (Mangel and Clark 1988) to estimate fitness values associated with noninteger values of the state variables of egg load (x) and nutri-

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ent reserves (y). To find $F(x, y, t)$ for noninteger values of x and y, x_i and y_j are defined as the largest integers below x and y. The actual values of x and y are then flanked by x_i and x_{i+1} and by y_j and y_{j+1}. Further, q and s are defined as the position of x and y between the two integers:

$$q = x - x_i$$

and (B1)

$$s = y - y_j.$$

Fitness values are then calculated by weighting the contribution of the fitness associated with each flanking integer value of x and y by its distance from the desired x and y. The weighted values are then summed over the four flanking integer values. For equation (4) in the main body of this study, interpolation is needed for fitness associated with not encountering a host, $F(x', y', t + 1)$, and fitness associated with host encounters, $F(x'', y'', t + t_d)$:

$$\begin{aligned} F(x', y', t+1) = {} & (qsF(x'_{i+1}, y'_{j+1}, t+1)) \\ & + [(1-q)sF(x'_i, y'_{j+1}, t+1)] \\ & + [q(1-s)F(x'_{i+1}, y'_j, t+1)] \\ & + [(1-q)(1-s)F(x'_i, y'_j, t+1)], \end{aligned} \tag{B2}$$

and

$$\begin{aligned} F(x'', y'', t+t_d) = {} & (qsF(x''_{i+1}, y''_{j+1}, t+t_d)) \\ & + [(1-q)sF(x''_i, y''_{j+1}, t+t_d)] \\ & + [q(1-s)F(x''_{i+1}, y''_j, t+t_d)] \\ & + [(1-q)(1-s)F(x''_i, y''_j, t+t_d)]. \end{aligned} \tag{B3}$$

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