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EGG LIMITATION, HOST QUALITY, AND DYNAMIC BEHAVIOR BY A PARASITOID IN THE FIELD[1]

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Abstract. Patterns of host selection and host use by insects with parasitic lifestyles are predicted to be fundamentally dynamic, responding to environmental conditions and physiological states. A particularly robust prediction is that the number of mature eggs that a female carries (her "egg load") should influence behavior. As egg load decreases, females are predicted to exhibit increasingly selective host use patterns. We tested the hypothesis that egg load and host size influence the behavior of the parasitoid wasp *Aphytis aonidiae* attacking the armored scale insect *Quadraspidiotus perniciosus. Aphytis* females can use hosts either for oviposition or for adult "host feeding," which is the consumption of host material by adult parasitoids. Theory predicts that host feeding should be (i) favored by low egg loads and (ii) more prevalent on lower-quality (smaller) hosts. We conducted observations of individual females foraging freely in the field to determine whether hosts were used for oviposition or for host feeding. As predicted by theory, the likelihood that a host was used for oviposition (as opposed to host feeding) increased with both parasitoid egg load and host size. Thus, parasitoids exhibited higher host-selectivity at lower egg loads. Since egg load and a parasitoid's experience with hosts were not experimentally separated, the egg load effect could in principle have been either direct or indirect and operating through a correlation with experience. In either case, this result constitutes the first demonstration of a link between physiological state and oviposition behavior by a parasitoid in the field. Parasitoid age, as measured using a wing wear index, did not influence behavior. A laboratory study revealed that the relationship between a host's size and the size and initial egg load of the parasitoid developing on that host was positive, but that it followed a pattern of diminishing returns. No effect of host size on behavior could be detected over the range of host sizes that were within the asymptotic region of this relationship.

Key words: Aphytis; *egg load; egg limitation; host feeding; host quality; parasitoid; oviposition;* Quadraspidiotus perniciosus.

INTRODUCTION

Opportunities for reproduction in insects that reproduce by allocating eggs to discrete sites (i.e., entomophagous parasitoids and some phytophagous and fungivorous parasites) can be restricted by egg limitation or by time limitation. Egg limitation occurs if females deplete their egg supply prior to running out of oviposition opportunities, and time limitation occurs when females are unable to locate enough suitable oviposition sites in their lifetime to deposit all of their eggs. The idea that insects must balance the risks of becoming time- and egg-limited has been expressed, in various forms, by numerous authors (e.g., Price 1973, Parker and Courtney 1984, Charnov and Skinner 1984, 1985, Waage 1986, Godfray 1987, 1994, Charnov and Stephens 1988, Roitberg 1989, Driesen and Hemerik 1992, Minkenberg et al. 1992, Rosenheim 1993, Bouskila et al. 1995, Heimpel and Rosenheim 1995, Hunter and Godfray 1995), and was formalized with the application of dynamic state-variable modeling to reproductive strategies in insects (e.g., Mangel 1987*a, b,* 1989*a, b,* Houston et al. 1988, 1992, Mangel and Clark 1988, Chan and Godfray 1993, Collier et al. 1994, Heimpel et al. 1994, Mangel et al. 1994, Rosenheim and Mangel 1994, Visser 1994, Bouskila et al. 1995, Collier 1995*b*).

For insect parasitoids, which lay one or more eggs into or onto host insects, a number of behaviors are of central importance in balancing the relative risks of egg and time limitation. These include which hosts are accepted for oviposition, how many eggs to deposit per oviposition bout, and, for some species, whether hosts should be used for oviposition or for adult host feeding (Godfray 1994). In general, oviposition rates are predicted to be lowest when the risk of egg limitation is high. Thus, under impending egg limitation, parasitoids are predicted to accept only the highest quality hosts for oviposition (e.g., Mangel 1989*a, b,* Bouskila et al. 1995), lay smaller clutches (e.g., Godfray 1987, Mangel 1987a, Rosenheim and Rosen 1991), and use hosts for host

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feeding rather than for oviposition (e.g., Chan and Godfray 1993, Collier 1995*a*, Heimpel and Rosenheim 1995, Heimpel and Collier 1996).

Although a number of environmental and physiological factors influence whether a parasitoid female is likely to become egg- or time-limited, an especially reliable correlate of the risk of egg limitation is egg load (Minkenberg et al. 1992), which is defined as the number of mature oocytes that a female parasitoid carries within her ovaries at a given time. As egg load declines, the risk of becoming egg-limited increases. The potentially central role of egg load in mediating the balance between egg and time limitation has prompted a number of theoretical and empirical studies aimed at illuminating the role of egg load as a source of variability in parasitoid reproductive strategies (reviewed by Minkenberg et al. 1992). Theory predicts that declining egg loads should be associated with reduced reproductive output, and empirical studies have, for the most part, supported this prediction (but see Rosenheim and Rosen 1992 and Rosenheim and Hongkham 1996). For instance, *Venturia canescens* (Grav.) were less likely to accept already-parasitized (and therefore suboptimal) hosts when egg loads were low (Fletcher et al. 1994), *Aphytis lingnanensis* Compere laid smaller clutches at lower egg loads (Rosenheim and Rosen 1991, 1992), and *V. canescens* (Hughes et al. 1994), *A. lingnanensis* (Rosenheim and Rosen 1991), and *Diglyphus begini* (Ashmead) (Minkenberg et al. 1992) all showed elevated host-searching behavior at higher egg loads.

To date, all tests of the hypothesis that egg load influences the behavior of parasitoids have been conducted in the laboratory (but see Odendaal [1989], Odendaal and Rausher [1990], and Tatar [1991] for field studies on butterflies). A consensus is emerging among parasitoid ecologists, however, that tests of hypotheses generated by optimality analyses conducted under field conditions are desirable (Godfray 1994, Hardy et al. 1995). Studying parasitoid behavior in the field is difficult, but not impossible (see studies by Waage 1983, Thompson 1986, Rosenheim 1987, Casas 1989, Janssen 1989, Rosenheim et al. 1989, Antolin and Strand 1992, Driesen and Hemerik 1992, Völkl 1992, 1994, Adamo et al. 1995, Fauvergue et al. 1995). Here, we test predictions derived from the general hypothesis that egg load influences the reproductive strategy of parasitoids in the field. Specifically, we investigate host-feeding strategies of the parasitoid *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae).

Host feeding is the consumption of host material by adult parasitoids. Individual hosts may be used for both host feeding and oviposition ("concurrent host feeding" sensu Jervis and Kidd 1986), or for host feeding only ("non-concurrent host feeding"). The primary role of nutrients obtained by host feeding appears to be egg maturation, although host feeding also increases lifespan in a number of species (Jervis and Kidd 1986, van Lenteren et al. 1987, Collier 1995*b*, Heimpel and Collier 1996). Using a host for host feeding rather than for oviposition therefore not only diminishes a parasitoid's risk of becoming egg-limited in the short term (since eggs are not used for oviposition), it may also diminish the risk of becoming egg-limited in the future (through egg maturation). Indeed, a number of state-variable models have predicted that host feeding should be more likely at low rather than high egg loads (Chan and Godfray 1993, Collier et al. 1994, Heimpel et al. 1994, Collier 1995*a*). Higher rates of host feeding at lower egg loads have been observed in the laboratory for *A. melinus* DeBach (Collier et al. 1994, Heimpel and Rosenheim 1995).

Differences in experience may also influence host feeding strategies. As increasing numbers of hosts are encountered, a parasitoid may perceive an increase in host availability. In principle, this perception alone could signal an increased risk of egg limitation and result in a higher likelihood of host feeding (Heimpel and Rosenheim 1995). Host encounters (especially when they occur in quick succession) however, are also likely to result in declining egg loads. The effects of egg load and experience are therefore potentially confounded (e.g., see Rosenheim and Rosen 1991, Minkenberg et al. 1992). While it is possible to separate the effects of experience and egg load in laboratory studies (e.g., Rosenheim and Rosen 1991, Heimpel and Rosenheim 1995), these factors are likely to be inseparable in studies of behavior conducted in the field. Studies that do not explicitly separate egg load from experience cannot distinguish between a direct influence of egg load on behavior and an indirect effect, acting through experience.

For parasitoids that host feed non-concurrently, host feeding is often more prevalent on lower quality hosts, with higher quality hosts being reserved for oviposition (Kidd and Jervis 1991). This is probably due in large part to a steeper fitness gain with increasing host quality for oviposition than for host feeding (Kidd and Jervis 1991, Godfray 1994). The relationship between host quality and the propensity to host feed in *Aphytis* parasitoids is typical: smaller hosts, which are known to be of lower quality than large hosts for oviposition, are more likely to be used for host feeding than are larger hosts (e.g., Walde et al. 1989, Rosenheim and Rosen 1992, Heimpel and Rosenheim 1995).

In this study, we conducted direct observations of host encounters by *Aphytis aonidiae* foraging freely in the field. We tested the hypotheses that parasitoid egg load and host size affect whether hosts are used for oviposition or for host feeding. Our protocol did not distinguish effects of egg load and experience. We therefore interpret the results to include the possibility that egg load affects behavior indirectly via a correlation with experience. To adequately interpret the significance of host size, we determined the relationship between host size and some easily measured proxies of parasitoid fitness in the laboratory.

METHODS

Natural history and field site description

The parasitoid *Aphytis aonidiae* attacks the San Jose scale, *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae), which is native to eastern China and was accidentally introduced into California around 1870 (Gentile and Summers 1958). *A. aonidiae* is holarctic (Rosen and DeBach 1979), and in California it appears to be the dominant parasitoid of *Q. perniciosus* (Gulmahamad and DeBach 1978*a*; G. E. Heimpel and J. A. Rosenheim, *unpublished data*).

Aphytis females deposit eggs between the scale insect body and its waxy covering after probing the host body with the ovipositor, during which time a paralyzing venom is probably injected (van Lenteren 1994, Rosenheim and Heimpel 1994). Our observations (see below) as well as studies by Gulmahamad and DeBach (1978*b*) suggest that more than one egg is rarely, if ever, deposited per host. Reproduction is by thelytokous parthenogenesis; unfertilized females produce daughters, with males occurring only rarely (Rosen and DeBach 1979, Gulmahamad and DeBach 1978*b*; G. E. Heimpel and J. A. Rosenheim, *unpublished data*). This mode of reproduction has been linked to infection of females with sex-ratio-distorting microorganisms in a uniparental strain of *A. lingnanensis* (Zchori-Fein et al. 1994).

Because there is essentially no variability in clutch size and sex ratio among ovipositing individuals in this species, the behavioral possibilities available to an *A. aonidiae* female upon encountering a host are rejection, host feeding, and oviposition. Rejection of encountered hosts can occur before or after the host is probed with the ovipositor (van Lenteren 1994). *Aphytis* species host feed by constructing a "feeding tube" with secretions molded by the ovipositor that span the distance between the scale insect body and the scale cover. Host fluids are conducted through the feeding tube, and females feed by applying their mouthparts to the feeding tube where it contacts the scale-insect cover (Rosenheim and Heimpel 1994). The act of host feeding is readily recognizable by the posture taken by the parasitoid, but preparation for host feeding closely resembles the act of oviposition. Some *Aphytis* species may use the same host individual for both host feeding and oviposition in the laboratory (Rosenheim and Rosen 1992, Heimpel and Rosenheim 1995), but our observations of *A. aonidiae* attacking *Q. perniciosus* (see below) suggest that in the field, hosts are used exclusively for either host feeding or oviposition.

Our study was carried out in a 40-ha organically managed almond orchard (*Prunus dulcis*) in Sutter County, California, USA, 4 ha of which had resident populations of both *Q. perniciosus* and *A. aonidiae*. No releases of *A. aonidiae* (or any other parasitoids) were made prior to or during the study.

Field observations

Observations of *A. aonidiae* foraging in the field were conducted between June and November in 1992, March and November in 1993, and August and October in 1994. *A. aonidiae* adults, which forage mainly on the bark of twigs and branches, were found by scanning the branches and young twigs of the almond trees. Once found, parasitoids were followed until a host encounter occurred in which hosts were probed for >60 s. Host encounters were observed with the aid of a hand lens (16× magnification) until the host was abandoned. Conducting observations with a hand lens did not appear to influence parasitoid behavior. Although oviposition events of *Aphytis* spp. are easily discerned in the laboratory with adequate magnification and lighting as a series of pumping motions (Luck et al. 1982, Rosenheim and Rosen 1991, 1992, van Lenteren 1994, Heimpel and Rosenheim 1995), field conditions were not suitable for identifying oviposition events in *A. aonidiae*. After the completion of a host encounter, parasitoids were captured by aspiration, put on ice, and brought to the laboratory for dissection later that same day. Also, the encountered hosts were cut from the almond twigs, along with the surrounding bark, and brought to the laboratory on ice.

In the laboratory, parasitoids were dissected to determine their egg load at the time of host encounter (the sum of the number of mature eggs present in the ovaries and any eggs deposited during the host encounter). Dissections were conducted as described by Heimpel and Rosenheim (1995): parasitoids were held with the ventral side up inside a drop of distilled water with a fine probe, and the tip of the abdomen was gently pulled distally using a pair of fine forceps. This procedure exposed the ovaries, making it possible to count mature oocytes. Only oocytes that were positioned at the base of the ovaries, not associated with nurse cells, and of full size, were deemed mature. After the dissections, parasitoids were slide-mounted in Hoyer's solution as described in Rosen and DeBach (1979), and the lengths of the two hind tibiae were measured to the nearest 0.001 mm at 100× and averaged as an index of parasitoid size.

In 1993 and 1994, the number of broken forewing fringe setae was counted as an index of relative parasitoid age. *A. aonidiae* forewings have an average of 107 ± 11 fringe setae (mean ± 1 SD, $N = 12$ pairs averaged) at parasitoid emergence, and the number of these setae that are broken is easily quantified when parasitoids are slide-mounted and viewed at 400× magnification. To confirm that older parasitoids tended to have more broken forewing setae than younger parasitoids, we counted the broken forewing setae of parasitoids of known ages in the laboratory. Parasitoids that had been collected in the field as pupae were allowed to emerge in glass vials in the laboratory and provided daily with fresh undiluted honey. Parasitoids were killed (by freezing) or allowed to die without intervention and were slide-mounted to count broken forewing setae. The resulting relationship between parasitoid age and the number of broken forewing setae was not intended for use as an absolute age index. We only wished to confirm that older parasitoids tended to have more broken forewing setae than did younger parasitoids.

The size and condition of hosts that were probed by *A. aonidiae* in the field were assessed in the laboratory. Scale cover area was measured as an index of host size, and the condition of the scale insect (i.e., apparently healthy, parasitized, or dead from unknown causes) was noted. Scale cover area (as opposed to scale body area) was used as an indicator of host size so that the size of parasitized and dead scale insects could be assessed. Although the correlation between scale cover area and scale body area can be weak when measured within instars (Hare et al. 1990, Rosenheim and Rosen 1991), our study included a broad range of sizes from both immature (second) and mature (third) instars. Furthermore, scale cover area was found to be a better predictor of oviposition behavior than scale-insect body area in *Aphytis lingnanensis* (Rosenheim and Rosen 1991). The longest diameter of the scale cover (d1), as well as the perpendicular diameter bisecting d1 (d2) were measured to the nearest 0.03 mm at 40× magnification, and scale cover area was calculated using the formula for the area of an ellipse: $(p/4)(d1 \times d2)$. During the observations, behavior was scored as either host feeding or not host feeding. Hosts attacked by parasitoids that did not host feed, and that were subsequently found to have an *Aphytis* egg attached to them, were considered parasitized during the encounter. Although these hosts could in principle have been parasitized prior to the observed encounter, extensive sampling demonstrated that the frequencies of scale insects bearing *Aphytis* eggs were very low (0.008 and 0.003 in 1993 and 1994, respectively; G. E. Heimpel and J. A. Rosenheim, *unpublished data*). Hosts without *Aphytis* eggs that were not used for host feeding were scored as having been rejected. Hosts containing parasitoid larvae, pupae, or pupal remains were scored as previously parasitized, and hosts that were desiccated were scored as being dead from unknown causes.

We investigated the influences of scale cover area, egg load, and hind tibial length on whether hosts were used for host feeding or oviposition using stepwise logistic regression (Engelman 1990). This technique allowed us to separate the effects of two variables, egg load and hind tibial length, that were likely to be correlated. The year and the month during which observations took place were included in the statistical model as well. We used simple logistic regression to test for the effect of the number of parasitoid broken forewing setae on whether hosts were used for host feeding or oviposition. This latter analysis was run separately due to the lower number of observations available ($n = 31$ parasitoids); broken forewing setae were only quantified in 1993 and 1994.

Host size effects

To aid in the interpretation of the field results, we investigated influences of host size on selected components of parasitoid fitness in the laboratory. *Q. perniciosus* scale cover area was correlated with the following parameters for *A. aonidiae*: pupal survivorship, pupal length, mean hind tibial length of emerging adults, and the egg load of one-day-old females held without hosts.

Almond twigs were collected from the field, and parasitized scale containing *A. aonidiae* prepupae and pupae were chosen for analysis. Collections were made between 28 September and 28 October 1994, a time of peak abundance of *A. aonidiae* at our field site. Scale cover area was quantified as described above. The lengths of both living and dead *A. aonidiae* pupae were also measured to the nearest 0.03 mm at 40× magnification. Living pupae and prepupae were placed in 2-mL vials covered with a cotton plug, supplied with a streak of undiluted honey and held at 26.7 ± 1.5°C, 65 ± 10% R.H., and a photocycle of 14L:10D for development and emergence. Pupae were checked daily for adult emergence, and one-day-old adults (between 24 and 48 h after emergence) were frozen in preparation for dissection within the next 2 d. Dissections and hind tibial measurements were conducted as described above to determine the number of mature eggs present in the ovaries as well as the average hind tibial length.

During the course of this study, we found that ≈35% of the parasitoids dissected had no eggs. To aid in interpreting this result, we compared (1) the proportion of females that were eggless from pupal collection dates between August 1994 and January 1995, and (2) the proportion of females that were eggless at various ages. Finally, for *A. aonidiae* with non-zero egg loads, we demonstrated that egg loads at 1 d constituted a full egg complement for parasitoids fed only honey, by dissecting females within 3 h of eclosion and daily thereafter through 5 d after eclosion.

RESULTS

Field observations

In all, we observed 212 parasitoids. Of these, 131 individuals encountered and probed hosts. Of these hosts, 74 appeared to be healthy and suitable for oviposition or host feeding by *Aphytis*, and the remaining 57 were not (Table 1). All scale insects that were not in the healthy category were rejected. Of the 74 apparently healthy hosts encountered, 6 were rejected, 27 were used for oviposition, and 41 were used for host feeding (Table 1).

Parasitoids were significantly more likely to oviposit (rather than host feed) when they had higher egg loads and when they encountered larger hosts (Table 2; Fig. 1). The egg load of parasitoids ovipositing averaged 5.0 ± 0.51 eggs (mean ± 1 SE), while parasitoids host feeding had a mean load of 3.4 ± 0.32 eggs (Fig. 1). The scale cover area of hosts used for oviposition averaged 1.5 ± 0.12 mm^2 (mean ± 1 SE), and the mean scale cover area of hosts used for host feeding was 1.0 ± 0.11

TABLE 1. Condition of scale hosts (*Quadraspidiotus perniciosus*) probed by wasp *Aphytis aonidiae* during field observations, and behaviors by *A. aonidiae*.

Host condition	Number	Behavior of *A. aonidiae*
Apparently healthy	74	Oviposition: 27 Host feeding: 41 Rejection: 6
Dead from unknown causes	28	All hosts rejected
Parasitized		
A. aonidiae pupa on hosts	10	All hosts rejected
Aphytis† larvae on hosts	11	All hosts rejected
Advanced immature stages of *Encarsia perniciosi* in hosts	4	All hosts rejected
Host molting	1	Host rejected
Host producing neonate "crawlers"	3	All hosts rejected
Total	131	

† Two *Aphytis* species were present at our site that were morphologically indistinguishable in the larval stage: *A. aonidiae* and *A. vandenboschi*.

TABLE 2. Stepwise logistic regression of factors affecting whether hosts were used for oviposition or host feeding by *Aphytis aonidiae*. Scale cover area, egg load, and hind tibia length were entered as continuous variables, and year and month were entered as categorical variables.

Step number	Variables entered	Regression coefficient†	df	Improvement χ^2	P
1	Scale cover area (mm^2)	1.18	1	7.6	0.006
2	Egg load‡	0.25	1	4.2	0.040

Variables not entered	df	Approximate χ^2 to enter	P
Year	2	1.5	0.24
Month	5	0.9	0.50
Hind tibia length	1	0.4	0.50
Scale cover area × egg load	1	0.1	0.77

† The regression coefficients are used to evaluate the logistic model

$$P(\text{oviposition}) = \frac{e^{\text{constant} + b_1 (\text{scale cover area}) + b_2 (\text{egg load})}}{1 + e^{\text{constant} + b_1 (\text{scale cover area}) + b_2 (\text{egg load})}},$$

in which the constant is -2.89.

‡ Parasitoids with egg loads of zero at the time of the host encounter ($n = 2$) were excluded from the data set, since oviposition was not possible for these individuals.

mm^2 (Fig. 1). We found no evidence for a statistical interaction between scale cover area and egg load on host use (Table 2), indicating that the two factors had independent effects on behavior. In Fig. 1, we used the logistic regression model to draw isoclines of egg load and host size combinations corresponding to probabilities of oviposition (rather than host feeding) of 0.25, 0.5, and 0.75. We also used the data to create a boundary line dividing the egg load/host size matrix space into host-feeding and oviposition regions; this analysis is presented in the Appendix.

Parasitoid hind tibial length did not significantly influence behavior when included in a model containing egg load (Table 2). When egg load was withheld from the regression analysis, however, the influence of hind tibial length became marginally significant (Improvement $\chi^2 = 3.1$, $P = 0.076$). Since there was a significant positive correlation between hind tibial length and egg load ($r^2 = 0.33$, $N = 63$ parasitoids, $P < 0.0001$), this suggests that hind tibial length influenced behavior indirectly through its effect on egg load. Since stepwise regression can be sensitive to the order in which correlated variables are entered into the regression model, we reversed the order in which egg load and hind tibial length were entered as a final check on the superiority

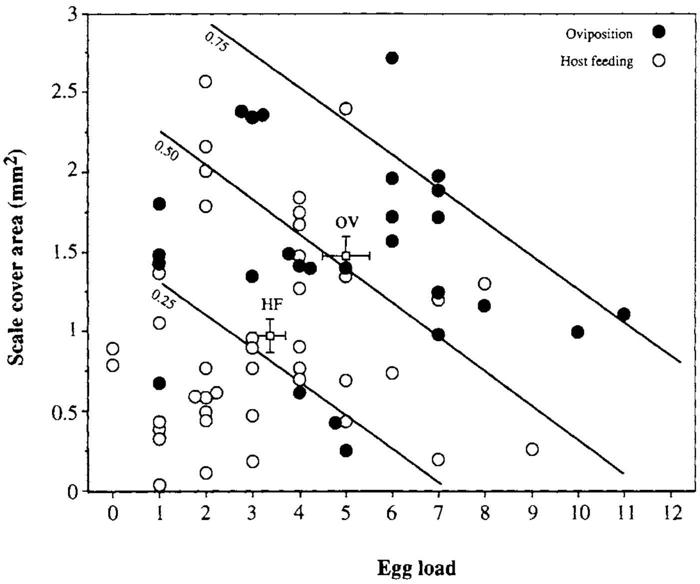

FIG. 1. Egg loads and scale cover areas of hosts encountered by parasitoids that oviposited (●) or host fed (○). The two crosses denote bivariate means (± 1 SE) of egg loads and scale cover sizes for ovipositing (OV) and host feeding (HF) parasitoids. The lines are isoclines for the probability of oviposition taken from the logistic regression model presented in Table 2. Isoclines for values of egg load and scale cover area corresponding to $P(\text{oviposition}) = 0.25$, 0.5, and 0.75 are shown. Note that $P(\text{host feeding}) = 1 - P(\text{oviposition})$.

of egg load as an explanatory variable. Indeed, when we forced hind tibial length into the model before egg load, hind tibial length was subsequently removed and replaced with egg load.

We found no evidence for yearly or monthly trends in behavior (Table 2). Furthermore, we found no effect of year or month on parasitoid egg load or the scale cover area of hosts encountered during the observations (single-factor ANOVAs produced $F < 2.3$ and $P > 0.1$ for all four relationships).

The average breakage of parasitoid forewing fringe setae observed in 1993 and 1994 was 1.00 ± 0.34 broken setae (mean ± 1 SE, range = 0 to 8, $n = 31$ cases). The laboratory study in which the number of broken forewing fringe setae was related to the age of *A. aonidiae* adults revealed that (i) essentially all setae were intact upon parasitoid emergence, and (ii) the number of broken setae increased significantly with age (linear regression: $r^2 = 0.30$, $N = 158$ parasitoids, $P < 0.0001$). The number of broken forewing setae had no significant effect on behavior, however (logistic regression: $\chi^2 = 0.15$, df = 1, 29, $P > 0.5$). Neither was there a significant difference in behavior between parasitoids with ≥1 broken forewing setae ($n = 14$ individuals), and parasitoids with zero broken forewing hairs ($n = 17$ individuals) (contingency table analysis: $\chi^2 = 0.683$, $P > 0.4$). There was no correlation between the number of broken forewing setae and egg load ($r^2 = 0.005$, $n = 31$ parasitoids, $P > 0.5$).

The six parasitoids that rejected apparently healthy hosts (see Table 1) did not have significantly different egg loads or hind tibial lengths from the parasitoids that accepted hosts (Wilcoxon's rank-sum test approximate $\chi^2 < 0.2$, and $P > 0.5$ for both factors). Also, these host encounters did not involve hosts with significantly different scale cover areas than hosts that were accepted (Wilcoxon's rank-sum test approximate $\chi^2 = 0.77$, $P = 0.38$). There were no significant differences in hind tibial length, egg load, or broken forewing setae between parasitoids probing suitable hosts ("apparently healthy" in Table 1), and unsuitable hosts (all other categories in Table 1). For these tests, hind tibial length: $t = 0.42$, df = 117, $P > 0.5$; egg load: $t = 1.25$, df = 122, $P = 0.22$; broken forewing setae: $t = 0.09$, df = 73, $P > 0.5$; degrees of freedom do not correspond exactly to sample sizes in Table 1 because all measurements were not available for each observation. Finally, we found no significant correlation between parasitoid hind tibial length and the scale cover area of hosts that were probed by parasitoids (i.e., there was no evidence that larger parasitoids visited larger hosts) ($r^2 = 0.01$, $N = 98$ parasitoids, $P = 0.32$).

Host size effects

Of 174 pupae and prepupae collected from the field, just under half (86 individuals) developed successfully into adult *A. aonidiae.* Of those that did not complete development, 32 individuals (37%) were clearly dead at the time hosts were collected, and 56 individuals appeared healthy upon collection but failed to develop in the laboratory. Pupal survivorship increased (with marginal significance) as scale cover area increased ($\chi^2_{1,\ 138} = 3.3$, $P = 0.071$). To correct for allometric differences in the growth of linear measurements (pupal length, hind tibial length) and areas (scale cover areas), we conducted regression analyses on the squared pupal and hind tibial lengths (see Fig. 2). Scale insects with greater cover areas produced significantly longer *A. aonidiae* pupae (Fig. 2A, Table 3), and longer pupae in turn developed into larger adult parasitoids (Fig. 2C, linear regression: $r^2 = 0.66$, $P < 0.0001$). This led to a positive correlation between scale cover area and adult hind tibial length (Fig. 2B, Table 3). Increases in pupal and hind tibial lengths with scale cover area appeared to follow a pattern of diminishing returns (Figs. 2A, B). Three regression models were used to explore the relationship between scale cover area and pupal and hind tibial length: linear regression, second-order polynomial regression, and a nonlinear curve-fitting procedure using a standard asymptotic function (Ralston 1990; see Table 3). For both (pupal length)^2 and (hind tibial length)^2, the polynomial and asymptotic models provided better fits than did the linear model (i.e., higher r^2 values and lower error sums of squares; Table 3). A comparison of the linear and polynomial regressions indicates that the rates of increase in these two dependent variables decrease over the larger values of the independent variable, scale cover area (i.e., the quadratic term was negative and significant in both cases). The curve-fitting procedure suggests that the relationship was asymptotic.

Of 82 parasitoids that were dissected at the age of 1 d, 29 females (35%) had egg loads of zero, and egg loads of the remaining 53 individuals ranged between 3 and 16. In eggless individuals, intact but empty ovaries were visible. For the class of parasitoids with non-zero egg loads, egg load was positively correlated with hind tibial length (Fig. 2F; linear regression: $r^2 = 0.67$, $n = 52$ parasitoids, $P < 0.0001$); pupal length (Fig. 2E; linear regression: $r^2 = 0.41$, $n = 35$ parasitoids, $P < 0.0001$), and scale cover area (Fig. 2D; Table 3). The relationship between scale cover area and egg load appeared nonlinear, and as was the case for (pupal length)^2 and (hind tibial length)^2, second-order polynomial and asymptotic models fit the data better than did a simple linear regression (Table 3), and the quadratic term was negative and significant. Thus, the rate with which egg load increased with scale cover area decreased over the larger scale cover areas.

To the extent that parasitoid size and initial egg load were correlated with parasitoid fitness in the field, an asymptotic relationship between host size and host quality suggests that behavior should be relatively insensitive to host size over the larger ranges of host sizes. This hypothesis was loosely supported by the behavioral data. The asymptotic region of scale cover area with respect to parasitoid size and egg load appears to begin

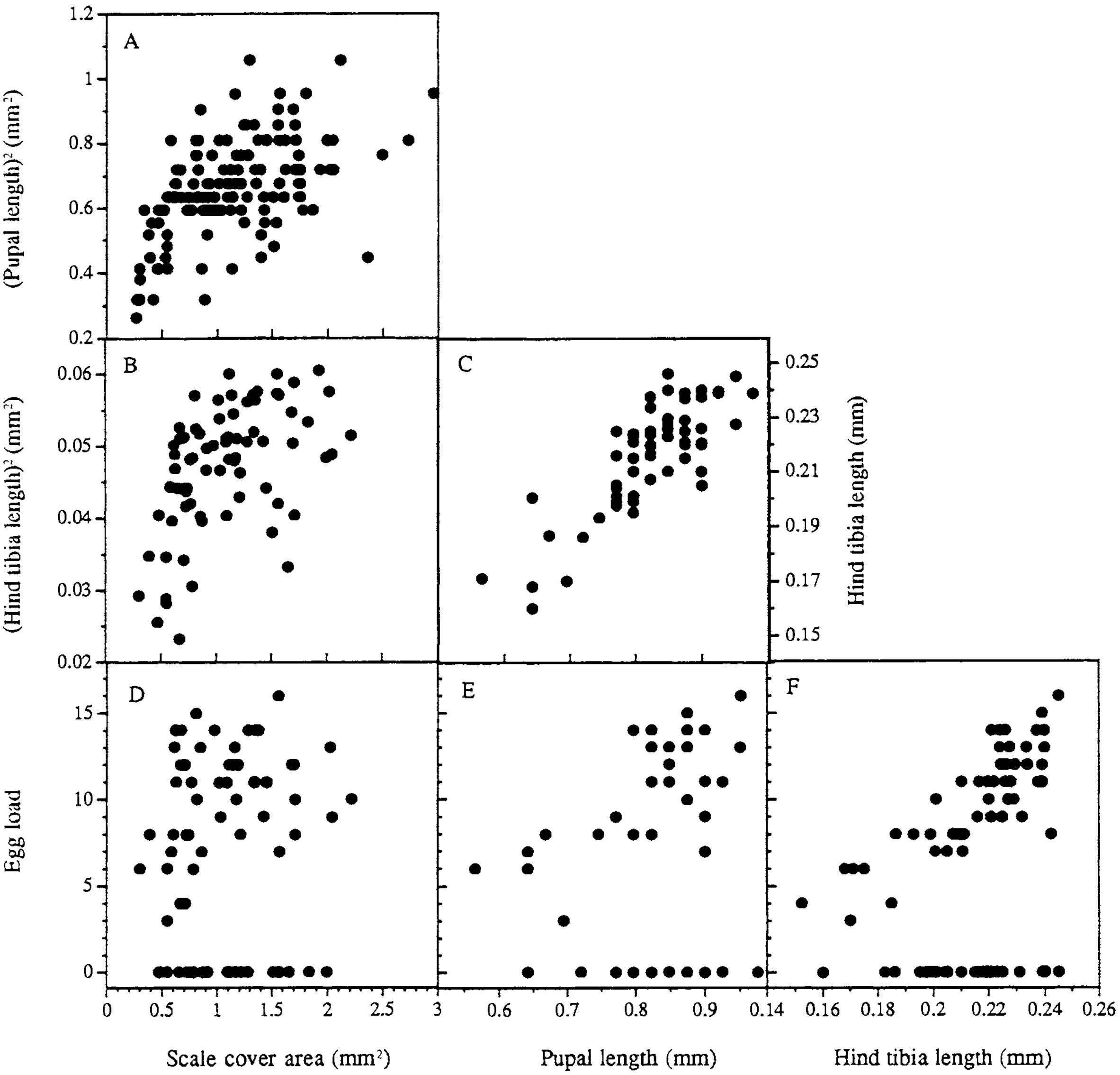

FIG. 2. Influence of *Quadraspidiotus perniciosus* scale cover area (SCA) on pupal length, hind tibia length, and egg load of *Aphytis aonidiae* parasitoids. (A) Effect of scale cover area on (pupal length)²; see Table 3 for regression analyses. (B) Effect of scale cover area on (hind tibia length)²; see Table 3 for regression analyses. (C) Effect of pupal length (PL) on hind tibia length (HTL); linear regression: HTL = 0.054 + 0.196(PL); $r^2 = 0.66$, $n = 59$ individuals, $P < 0.0001$. (D) Effect of scale cover area on egg load; see Table 3 for regression analyses. (E) Effect of pupal length on egg load; linear regression (egg loads of zero excluded): EL = −6.88 + 12.3(PL); $r^2 = 0.41$, $n = 35$ individuals, $P < 0.0001$. (F) Effect of hind tibia length on egg load; linear regression (egg loads of zero excluded): EL = −14.5 + 114(HTL); $r^2 = 0.67$, n = 52 individuals, $P < 0.0001$.

at ≈1.5 mm² (Fig. 2), and while the effect of scale cover area on parasitoid behavior was significant for data points <1.5 mm² ($\chi^2 = 9.1$, $n = 47$ parasitoids, $P < 0.01$; see Fig. 1), it was not significant above this value ($\chi^2 = 0.01$, $n = 19$ parasitoids, $P > 0.5$).

Eggless females

We are unable to explain the high frequency of eggless females. In other *Aphytis* species, egg loads of zero have been reported for the smallest individuals sampled (Opp and Luck 1986), but in this study, the hind tibial length of parasitoids with non-zero egg loads was not significantly different from that of eggless parasitoids (Fig. 2F; $\chi^2_{1,79} = 0.5$, $P > 0.4$). Dissections of females at various ages indicated that all individuals eclosed with essentially zero eggs, and that, among females 1–5 d old, the proportion that were eggless fluctuated between 0.35 and 0.60 with no apparent trend (Fig. 3). Finally, the proportion of females that were eggless at the age of 1 d did not change significantly between August 1994 and January 1995 ($\chi^2_{1,112} = 1.14$; $P > 0.25$; data not shown).

TABLE 3. Results of linear, second-order polynomial, and asymptotic regression analyses for the effect of scale cover area on (pupal length)^2, (hind tibial length)^2, and egg load. Significance of parameters: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Dependent variable	Regression equation	Parameters (mean ± 1 SE)	r^2	SSE	F	P
(Pupal length)^2 $N = 142$	Linear†	$b_1 = 0.50 \pm 0.03$*** $b_2 = 0.15 \pm 0.02$***	0.27	2.30	50.5	< 0.0001
	Polynomial‡	$b_1 = 0.39 \pm 0.05$*** $b_2 = 0.35 \pm 0.08$*** $b_3 = -0.08 \pm 0.03$**	0.31	2.16	30.9	< 0.0001
	Asymptotic‖	$a = 2.85 \pm 0.41$§ $b = 3.25 \pm 0.59$§	0.35¶	2.03		
(Tibial length)^2 $N = 74$	Linear †	$b_1 = 0.04 \pm 0.002$*** $b_2 = 0.01 \pm 0.002$***	0.25	0.0042	24.5	< 0.0001
	Polynomial‡	$b_1 = 0.02 \pm 0.005$*** $b_2 = 0.04 \pm 0.01$*** $b_3 = -0.013 \pm 0.004$**	0.36	0.0036	19.8	< 0.0001
	Asymptotic‖	$a = 0.20 \pm 0.04$§ $b = 3.22 \pm 0.77$§	0.35¶	0.0036		
Egg load# $N = 49$	Linear†	$b_1 = 8.13 \pm 1.09$*** $b_2 = 1.97 \pm 0.93$*	0.09	410.14	4.46	0.04
	Polynomial‡	$b_1 = 3.31 \pm 2.40^{NS}$ $b_2 = 11.41 \pm 4.32$* $b_3 = -3.91 \pm 1.75$*	0.18	370.00	4.92	0.012
	Asymptotic‖	$a = 45.34 \pm 18.67$§ $b = 3.39 \pm 1.77$§	0.15¶	383.89		

† Dependent variable = $b_1 + b_2$(scale cover area).

‡ Dependent variable = $b_1 + b_2$(scale cover area) + b_3([scale cover area]^2).

‖ Dependent variable = a(scale cover area)/(1 + b[scale cover area]). For the asymptotic regression, a nonlinear curve-fitting procedure was used (Ralston 1990) using a variant of Holling's (1959) disc equation as the asymptotic function. Values for F and P are not available using this procedure (Ralston 1990).

§ Standard errors for the asymptotic regression are approximate (Ralston 1990).

¶ Reported is the "Pseudo r^2"; i.e., $1 - \{\text{SSE}/([N - 1]\text{variance})\}$ (Ralston 1990).

The analyses on egg load were done using egg loads >0 exclusively.

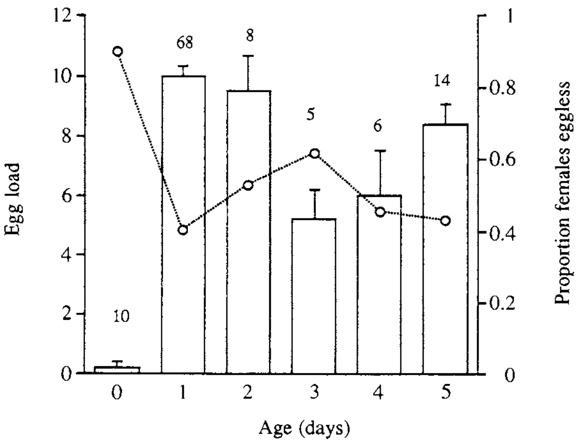

FIG. 3. Egg loads (columns; means and 1 SE) and proportions of females that were eggless (O········O) at six ages for *Aphytis aonidiae* collected in the field as pupae and reared to adulthood in the laboratory. Numbers above error bars are numbers of parasitoids in each age class. For parasitoids zero days old, values include eggless females, but for all older age classes mean egg loads do not include eggless females.

DISCUSSION

Our field observations demonstrated that *Aphytis aonidiae* with lower egg loads were more likely to host feed (rather than oviposit) than were *A. aonidiae* with higher egg loads. Also, smaller hosts were more likely to be used for host feeding than were larger hosts. These results support a body of theory that predicts oviposition strategies by parasitoids to be fundamentally dynamic, responding to environmental factors (e.g., host size) as well as physiological states of the parasitoid (e.g., egg load) (Iwasa et al. 1984, Mangel 1987*a*, *b*, 1989*b*, Houston et al. 1988, Mangel and Clark 1988, Mangel et al. 1994). Predictions that parasitoid age should influence host-feeding behavior (Heimpel and Collier 1996), however, were not supported by our study. Females with more broken forewing setae were not more likely to oviposit than were females with fewer broken forewing setae. A laboratory experiment with *A. melinus* also failed to detect an influence of age on host-feeding behavior (Heimpel and Rosenheim 1995).

Correlations among host size, parasitoid size, and initial egg load indicated that the benefits derived from ovipositing onto larger hosts followed a pattern of diminishing returns (for another example of this phenomenon, see

Mackauer 1986). Provided that parasitoid size and initial egg load are reasonable proxies of fitness in the field (Visser 1994, Kazmer and Luck 1995), this result leads to the prediction that host size effects should be weak for the uppermost ranges of host size. In support of this prediction, host size effects in our field observations were absent over the range of host sizes that showed an asymptotic relationship with parasitoid size and egg load, and were significant below the asymptotic region. Similarly, while Collier et al. (1994) failed to find an effect of scale cover area on host-feeding behavior by *A. melinus* offered third-instar (mature) hosts, other behavioral assays in which second instar hosts were offered revealed strong effects of scale cover area on behavior (Rosenheim and Rosen 1992, Heimpel and Rosenheim 1995).

The effects of egg load and experience were confounded in our study. To appreciate this, consider the behavior of *A. melinus* in the laboratory. When *A. melinus* females are offered a series of high-quality hosts, they use the first few hosts for oviposition before host feeding (Reeve 1987, Collier et al. 1994). Since egg load drops as the number of hosts encountered increases, egg load and experience are inexorably confounded when a series of hosts are encountered. Although laboratory protocols can be devised to isolate the influence of egg load from experience (Rosenheim and Rosen 1991, 1992, Minkenberg et al. 1992, Rosenheim 1993, Fletcher et al. 1994, Hughes et al. 1994, Rosenheim and Heimpel 1994, Heimpel and Rosenheim 1995), field studies like the one described here are highly susceptible to a confound between egg load and experience. The interpretational problem that arises is that either (i) decreasing egg load or (ii) a perception of increasing host availability could signal an increase in the risk of becoming egg-limited, and therefore directly favor host feeding. Although predictions for the effect of host availability on the tendency to host feed can vary at intermediate and high values of host availability, oviposition is universally predicted to be favored when host availability is very low (Jervis and Kidd 1986, Chan and Godfray 1993, Collier et al. 1994, Heimpel et al. 1994, Collier 1995*a*, Heimpel and Collier 1996). Thus, when parasitoids have high egg loads and host availability is very low, oviposition can occur as a result of either or both of these factors. The correct interpretation of our results is therefore that we observed an association between egg load and behavior, and that this association could reflect either a direct causal relationship, or an indirect effect acting through experience.

Regardless of the confound between egg load and experience, our results are consistent with parasitoids maximizing reproductive success by balancing the risks of becoming limited by eggs and time. When egg loads are high, the risk of the parasitoid's reproductive success becoming limited by the time it has to locate hosts is relatively high as well. Under these circumstances, oviposition is favored, and even relatively low-quality hosts may be used for oviposition rather than host feeding. As egg loads decline, however, the risk of becoming egg-limited (i.e., running out of eggs) rises. As the risk of egg limitation increases, parasitoids are predicted to be increasingly selective with respect to oviposition and use only the best quality hosts for oviposition. Our results demonstrate more selectivity at lower egg loads, and therefore provide evidence that the reproductive behavior of *A. aonidiae* foraging freely in the field is dynamic, responding to parasitoid egg load as well as host size.

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LITERATURE CITED

Adamo, S. A., D. Robert, J. Perez, and R. R. Hoy. 1995. The response of an insect parasitoid, *Ormia ochracea* (Tachinidae), to the uncertainty of larval success during infestation. Behavioral Ecology and Sociobiology **36**:111–118.

Antolin, M. F., and M. S. Strand. 1992. Mating system of *Bracon hebetor* (Hymenoptera: Braconidae). Ecological Entomology **17**:1–7.

Bouskila, A., I. C. Robertson, M. E. Robinson, B. D. Roitberg, B. Tenhumberg, A. J. Tyre, and E. van Randen. 1995. Submaximal oviposition rates in a mymarid parasitoid: choosiness should not be ignored. Ecology **76**:1990–1993.

Casas, J. 1989. Foraging behaviour of a leafminer parasitoid in the field. Ecological Entomology **14**:257–265.

Chan, M. S., and H. C. J. Godfray. 1993. Host-feeding strategies of parasitoid wasps. Evolutionary Ecology **7**:593–604.

Charnov, E. L., and S. W. Skinner. 1984. Evolution of host selection and clutch size in parasitoid wasps. Florida Entomologist **67**:5–21.

Charnov, E. L., and S. W. Skinner. 1985. Complementary approaches to the understanding of parasitoid oviposition decisions. Environmental Entomologist **14**:383–391.

Charnov, E. L., and D. W. Stephens. 1988. On the evolution of host selection in solitary parasitoids. American Naturalist **132**:707–732.

Collier, T. R. 1995*a*. Adding physiological realism to dynamic state variable models of parasitoid host-feeding. Evolutionary Ecology **9**:217–235.

———. 1995*b*. Host feeding, egg maturation, resorption, and longevity in the parasitoid *Aphytis melinus* (Hymenoptera: Aphelinidae). Annals of the Entomological Society of America **88**:206–214.

Collier, T. R., W. W. Murdoch, and R. M. Nisbet. 1994. Egg load and the decision to host feed in the parasitoid *Aphytis melinus*. Journal of Animal Ecology **63**:299–306.

Driesen, G., and L. Hemerik. 1992. The time and egg budget of *Leptopilina clavipes*, a parasitoid of larval *Drosophila*. Ecological Entomology **17**:17–27.

Engelman, L. 1990. Stepwise logistic regression. Pages 1013–1046 *in* W. J. Dixon, editor. BMDP Statistical Software Manual. Volume 2. University of California Press, Berkeley, California, USA.

Fauvergue, X., K. R. Hopper, and M. F. Antolin. 1995. Mate finding via a trail sex pheromone by a parasitoid wasp. Proceedings of the National Academy of Sciences, USA **92**:900–904.

Fletcher, J. P., J. P. Hughes, and I. F. Harvey. 1994. Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. Proceedings of the Royal Society of London, series B **258**:163–167.

Gentile, A. G., and F. M. Summers. 1958. The biology of San

Jose Scale on peaches with special reference to the behavior of males and juveniles. Hilgardia **27**:269–285.

Godfray, H. C. J. 1987. The evolution of clutch size in invertebrates. Pages 117–154 *in* P. H. Harvey and L. Partridge, editors. Oxford Surveys in Evolutionary Biology, Volume 4. Oxford University Press, Oxford, England.

———. 1994. Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, New Jersey, USA.

Gulmahamad, H., and P. DeBach. 1978*a*. Biological control of the San Jose scale *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae) in Southern California. Hilgardia **46**:205–238.

Gulmahamad, H., and P. DeBach. 1978*b*. Biological studies on *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae), an important parasite of the San Jose scale. Hilgardia **46**:239–256.

Hardy, I. C. W., J. J. M. van Alphen, G. E. Heimpel, and P. J. Ode. 1995. Entomophagous insects: progress in evolutionary and applied ecology. Trends in Ecology and Evolution **10**:96-97.

Hare, J. D., D. S. Yu, and R. F. Luck. 1990. Variation in life history parameters of California red scale on different citrus cultivars. Ecology **71**:1451–1460.

Heimpel, G. E., and T. R. Collier. 1996. The evolution of host feeding behaviour in parasitoids. Biological Reviews, *in press*

Heimpel, G. E., and J. A. Rosenheim. 1995. Dynamic host feeding by the parasitoid *Aphytis melinus*: the balance between current and future reproduction. Journal of Animal Ecology **64**:153–167.

Heimpel, G. E., J. A. Rosenheim, and J. M. Adams. 1994. Behavioral ecology of host feeding in *Aphytis* parasitoids. Proceedings of the Fifth European Parasitoids workshop (Biri Oppland, Norway; 24–28 May, 1994). Norwegian Journal of Agricultural Sciences, Supplement **16**:101–115.

Holling, C. S. 1959. Some characteristics of simple types o predation and parasitism. Canadian Entomologist **91**:385–398.

Houston, A., C. Clark, J. McNamara, and M. Mangel. 1988. Dynamic models in behavioural and evolutionary ecology. Nature **332**:29–34.

Houston, A. I., J. M. McNamara, and H. C. J. Godfray. 1992. The effect of variability on host feeding and reproductive success in parasitoids. Bulletin of Mathematical Biology **54**:465–476.

Hughes, J. P., I. F. Harvey, and S. F. Hubbard. 1994. Host-searching behavior of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): interference-the effect of mature egg load and prior behavior. Journal of Insect Behavior **7**:433–454.

Hunter, M. S., and H. C. J. Godfray. 1995. Ecological determinants of sex allocation in an autoparasitoid wasp. Journal of Animal Ecology **64**:95–106.

Iwasa, Y., Y. Suzuki, and H. Matsuda. 1984. Theory of oviposition strategy of parasitoids. Theoretical Population Biology **26**:205–227.

Janssen, A. 1989. Optimal host selection by *Drosophila* parasitoids in the field. Functional Ecology **3**:469–479.

Jervis, M. A., and N. A. C. Kidd. 1986. Host-feeding strategies in Hymenopteran parasitoids. Biological Reviews **61**:395–434.

Kazmer, D. J., and R. F. Luck. 1995. Field tests of the size-fitness hypothesis in the egg parasitoid *Trichogramma pretiosum*. Ecology **76**:412–425.

Kidd, N. A. C., and M. A. Jervis. 1991. Host-feeding and oviposition strategies of parasitoids in relation to host stage. Researches in Population Ecology **33**:13–28.

Luck, R. F., H. Podoler, and R. Kfir. 1982. Host selection and egg allocation behaviour by *Aphytis melinus* and *A. lingnanensis*: comparison of two facultatively gregarious parasitoids. Ecological Entomology **7**:397–408.

Mackauer, M. 1986. Growth and developmental interactions in some aphids and their hymenopteran parasites. Journal of Insect Physiology **32**:275–280.

Mangel, M. 1987*a*. Modeling behavioral decisions of insects. Lecture Notes in Biomathematics **73**:1–18.

———. 1987*b*. Oviposition site selection and clutch size in insects. Journal of Mathematical Biology **25**:1–22.

———. 1989*a*. An evolutionary interpretation of the "motivation to oviposit." Journal of Evolutionary Biology **2**:157–172.

———. 1989*b*. Evolution of host selection in parasitoids: does the state of the parasitoid matter? American Naturalist **133**:688–705.

Mangel, M., and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey, USA.

Mangel, M., J. A. Rosenheim, and F. R. Adler. 1994. Clutch size, offspring performance, and inter-generational fitness. Behavioral Ecology **5**:412–417.

Minkenberg, O. P. J. M., M. Tatar, and J. A. Rosenheim. 1992. Egg load as a major source of variability in insect oviposition behavior. Oikos **65**:134–142.

Odendaal, F. J. 1989. Mature egg number influences the behavior of *Battus philenor* butterflies. Journal of Insect Behavior **2**:15–25.

Odendaal, F. J., and M. D. Rausher. 1990. Egg load influences search intensity, host selectivity, and clutch size in *Battus philenor* butterflies. Journal of Insect Behavior **2**:15–25.

Opp, S. B., and R. F. Luck. 1986. Effects of host size on selected fitness components of *Aphytis melinus* and *A. lingnanensis* (Hymenoptera: Aphelinidae). Annals of the Entomological Society of America **79**:700–704.

Parker, G. A., and S. P. Courtney. 1984. Models of clutch size in insect oviposition. Theoretical Population Biology **26**:27–48.

Price, P. W. 1973. Reproductive strategies in parasitoid wasps. American Naturalist **107**:684–693.

Ralston, M. 1990. Derivative-free nonlinear regression. Pages 395–423 *in* W. J. Dixon, editor. BMDP Statistical Software Manual, Volume 1. University of California Press, Berkeley, California, USA.

Reeve, J. D. 1987. Foraging behavior of *Aphytis melinus*: effects of patch density and host size. Ecology **68**:530–538.

Roitberg, B. D. 1989. The cost of reproduction in rosehips flies, *Rhagoletis basiola*: eggs are time. Evolutionary Ecology **3**:183–188.

Rosen, D., and P. DeBach. 1979. Species of *Aphytis* of the world. Dr. W. Junk, The Hague, The Netherlands.

Rosenheim, J. A. 1987. Host location and exploitation by the cleptoparasitic wasp *Argochrysis armilla*: the role of learning (Hymenoptera: Chrysididae). Behavioral Ecology and Sociobiology **21**:401–406.

———. 1993. Comparative and experimental approaches to understanding insect learning. Pages 273–307 *in* D. R. Papaj and A. C. Lewis, editors. Insect learning: ecological and evolutionary perspectives. Chapman and Hall, New York, New York, USA.

———. *In press*. An evolutionary argument for egg limitation. Evolution.

Rosenheim, J. A., and G. E. Heimpel. 1994. Sources of intraspecific variation in oviposition and host-feeding behavior. Pages 41–78 *in* D. Rosen, editor. Recent advances in the study of *Aphytis*. Intercept, Andover, Hants, UK.

Rosenheim, J. A., and D. Hongkham. 1996. Clutch size in an obligately siblicidal parasitoid wasp. Animal Behaviour **51**:841–852.

Rosenheim, J. A., and M. Mangel. 1994. Patch-leaving rules of parasitoids with imperfect host discrimination. Ecological Entomology **19**:374–380.

Rosenheim, J. A., T. Meade, I. G. Powch, and S. E. Schoenig. 1989. Aggregation by foraging insect parasitoids in response to local variations in host density: determining the dimension of a host patch. Journal of Animal Ecology **58**:101–117.

Rosenheim, J. A., and D. Rosen. 1991. Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: distinguishing the influences of egg load and experience. Journal of Animal Ecology **60**:873–893.

Rosenheim, J. A., and D. Rosen. 1992. Influence of egg load and host size on host feeding behaviour by the parasitoid *Aphytis lingnanensis*. Ecological Entomology **17**:263–272.

Tatar, M. 1991. Clutch size in the swallowtail butterfly, *Battus philenor*: the role of host quality and egg load within and among seasonal flights in California. Behavioral Ecology and Sociobiology **28**:337–344.

Thompson, J. N. 1986. Oviposition behaviour and searching efficiency in a natural population of braconid parasitoid. Journal of Animal Ecology **55**:351–360.

van Lenteren, J. C. 1994. Oviposition behavior of *Aphytis*. Pages 13–40 *in* D. Rosen, editor. Advances in the study of *Aphytis*. Intercept, Andover, Hants, UK.

van Lenteren, J. C., A. van Vianen, H. F. Gast, and A. Kortenhoff. 1987. The parasite–host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). XVI. Food effects on oogenesis, life-span and fecundity of *Encarsia formosa* and other Hymenopterous parasites. Journal of Applied Entomology **103**:69–84.

Visser, M. E. 1994. The importance of being large: the relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera: Braconidae). Journal of Animal Ecology **63**:963–978.

Völkl, W. 1992. Aphids or their parasitoids: who actually benefits from ant-attendance? Journal of Animal Ecology **61**:273–281.

———. 1994. Searching at different spatial scales: the foraging behavior of the aphid parasitoid *Aphidius rosae* in rose bushes. Oecologia **100**:177–183.

Waage, J. K. 1983. Aggregation in field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera: Ichneumonidae). Ecological Entomology **8**:447–453.

———. 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. Pages 63–95 *in* J. K. Waage, and D. Greathead, editors. Insect parasitoids. Academic Press, London, UK.

Walde, S. J., R. F. Luck, D. S. Yu, and W. W. Murdoch. 1989. A refuge for red scale: the role of size-selectivity by a parasitoid wasp. Ecology **70**:1700–1706.

Zchori-Fein, E, D. Rosen, and R. T. Roush. 1994. Microorganisms associated with thelytoky in *Aphytis lingnanensis* Compere (Hymenoptera: Aphelinidae). International Journal of Insect Morphology and Embryology **23**:169–172.

APPENDIX

A BOUNDARY LINE FOR HOST FEEDING

We used data from the field observations to create a boundary dividing the host size/egg load matrix space into oviposition and host-feeding regions. We began with the premise that when a parasitoid with egg load E encounters a host with scale cover area S, she oviposits if S exceeds a critical egg load threshold, $S_t(E)$, and otherwise host feeds. A simple linear formulation for a boundary line conforming to these rules is:

$$S_t(E) = S_0\left(1 - \frac{E}{E_0}\right) \qquad \text{(A.1)}$$

with two parameters, S_0 and E_0. To consider the behavior $B(E, S)$ of parasitoids with egg load E encountering a host of size S, we set $B(E, S) = 1$ for oviposition and $B(E, S) = 0$ for host feeding. The parameters S_0 and E_0 are determined by minimization of the error sum of squares, SSE,

$$\text{SSE} = \sum_{j=1}^{N} [B(E_j, S_j) - \hat{B}(E_j, S_j)]^2 \qquad \text{(A.2)}$$

in which E_j and S_j are the egg load and scale cover area of the jth behavioral event, and $\hat{B}$ (E_j, S_j) is the predicted behavior derived using Eq. A.1. Thus, the SSE is equivalent to the number of mis-classified data points. Parameter values minimizing SSE are $S_0 = 1.5$ and $E_0 = 12$. These values were used to generate the boundary line between oviposition and host feeding regions (Fig. A1).

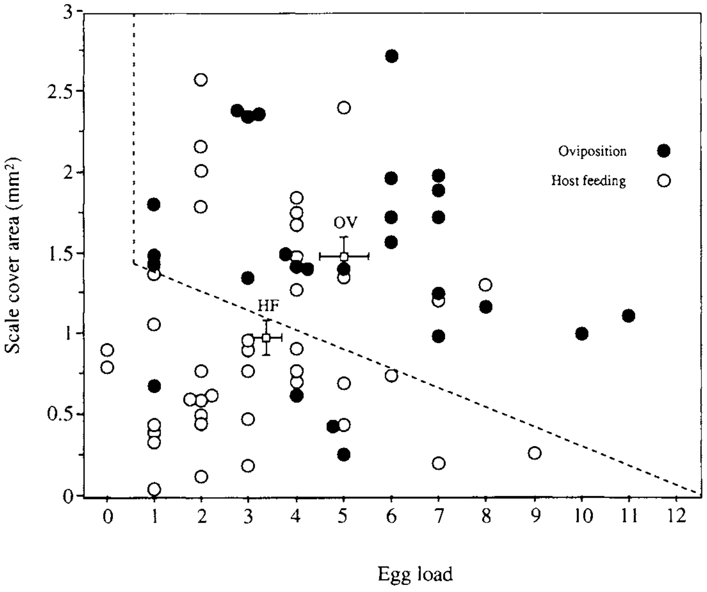

FIG. A1. Egg loads and scale cover areas of hosts encountered by parasitoids that either oviposited (●) or host fed (○) (as in Fig. 1). The dotted boundary line divides the graph into oviposition and host-feeding regions. Since oviposition is not possible at egg loads of zero, the line for the zero egg load class is vertical.