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# Egg Limitation in Parasitoids: A Review of the Evidence and a Case Study

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**Life history theory predicts that a nontrivial proportion of parasitoids should exhaust their egg supply during their lifetime. We reviewed the literature on egg limitation in parasitoids and found partial support for this prediction. Most of the evidence in support of egg limitation is indirect and does not constitute absolute proof of egg limitation. However, a few direct studies in which field-collected parasitoids were dissected, gave unequivocal evidence of egg limitation. Egg limitation was detected both in proovigenic species, in which it signals the attainment of maximum fecundity, and in synovigenic species, where it is more likely to be temporary than permanent. We demonstrated substantial egg limitation in the synovigenic parasitoid *Aphytis aonidiae.* Although an unknown (and probably large) proportion of egg-limited individuals was apparently unable to mature eggs for unknown reasons, the egg load distribution indicated that even those individuals able to mature eggs could be at risk of becoming egg limited. Thus, egg limitation in this species can apparently occur through egg depletion or an inability to mature eggs. We investigated possible correlations between time of day, time of year, ambient temperature, parasitoid size, and host density on egg limitation in *A. aonidiae.* We found a slight tendency for egg load to drop during the course of the day. Although we could detect no effect of time of year or of temperature on egg load, larger parasitoids had higher egg loads than did smaller ones. Finally, we could detect no effect of host density on egg load. This result is paradoxical given recent theory predicting increased egg limitation with increased host availability. We suggest that already-documented state-dependent behavior in *A. aonidiae* may partly explain this unexpected result. Parasitoids may reduce the risk of egg limitation when the host encounter rate is high by exhibiting increasingly selective host-use patterns with declining egg load.**

## INTRODUCTION

Female parasitoids lay eggs on, in, or near host insects. Broadly speaking, lifetime reproductive success can therefore be limited by the time available for locating hosts or by the number of eggs available for oviposition. While it has traditionally been assumed that parasitoid fitness is not limited by egg supply, however (e.g., see Hassell, 1978; Godfray, 1994), a new generation of behavioral and population-level models incorporating egg limitation has been developed (e.g., Iwasa *et al.*, 1984; Lessells, 1985; Mangel, 1987, 1989; Kidd and Jervis, 1989; Briggs *et al.*, 1995; Shea *et al.*, 1996; Getz and Mills, 1996). Also, Rosenheim (1996) has recently argued that a nontrivial probability of parasitoids becoming egg-limited is likely to be the outcome of stabilizing selection on egg size and lifetime fecundity. Thus, a consensus seems to be emerging that parasitoid fitness can be limited by either egg supply or the time available for locating hosts and that females are selected to balance the risks of becoming egg- and time-limited (e.g., Godfray, 1987, 1994; Rosenheim, 1996; Rosenheim *et al.*, 1996).

The significance of egg limitation to parasitoid fitness is linked to the timing of egg maturation. Most parasitoid species can be classified within one of two groups: proovigenic species, in which the egg-storage capacity equals the maximum potential lifetime reproductive success, and synovigenic species, in which reproductive success can exceed the capacity to store eggs (Flanders, 1950; Jervis and Kidd, 1986). Egg limitation in proovigenic species is permanent and synonymous with attaining maximum fecundity, while in synovigenic species it can be temporary and is potentially decoupled from total fecundity (Fig. 1). Thus, egg limitation can impose a ceiling on potential lifetime fecundity in proovigenic species and reduce the rate of oviposition (and potentially lifetime fecundity as well) in synovigenic species.

Since parasitoid fitness is often closely tied to host quality and to the number of eggs laid per host (Godfray, 1994), egg limitation can also represent a cost in terms of the opportunity of producing higher quality offspring; i.e., egg-limited parasitoids can incur fitness costs by missing opportunities either to oviposit in higher-quality hosts or lay smaller clutches in hosts of a given quality. Also, in cases where offspring fitness is

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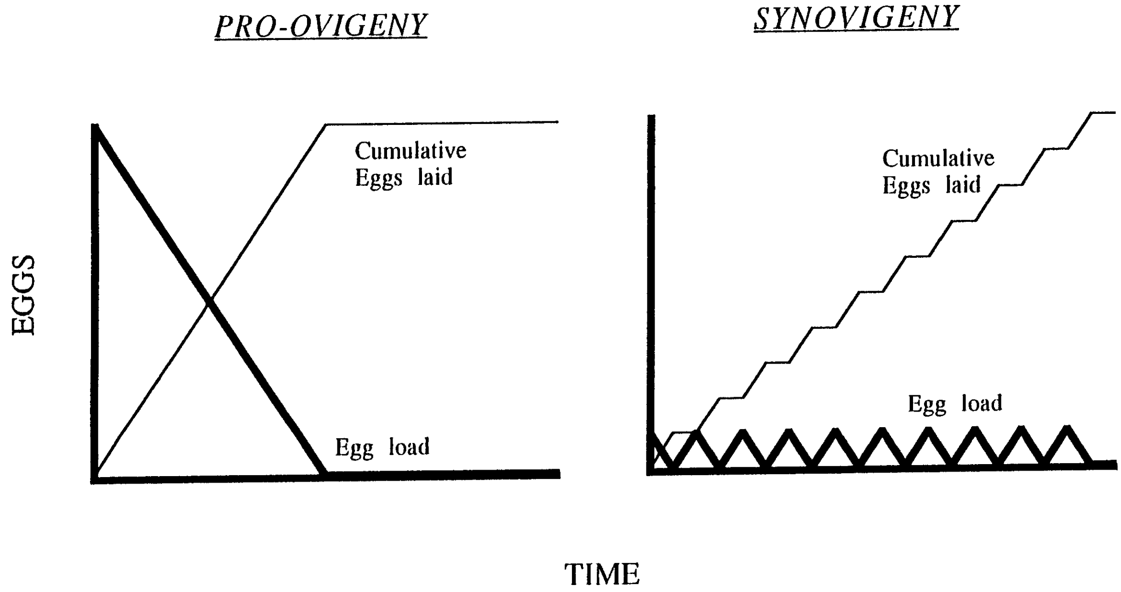

**FIG. 1.** Schematic of time-dependent cumulative numbers of eggs laid and egg loads for idealized proovigenic and synovenic parasitoids.

maximized at clutches of intermediate size, egg-limited parasitoids may be unable to produce clutches of optimal size. These and other opportunity costs have the potential to lead to selection for behaviors that minimize the risk of egg limitation. For instance, under conditions of impending egg limitation, parasitoids are predicted to be increasingly selective with respect to the hosts that they accept for oviposition and to lay smaller clutches (e.g., Iwasa *et al.*, 1984; Mangel, 1987, 1989). Analogous predictions have been made for those synovigenic species that can use hosts for oviposition or for "host feeding," which is the consumption of hosts by adult females (Jervis and Kidd, 1986; Heimpel and Collier, 1996). Like other synovigenic species, host feeders run the risk of temporary egg limitation. Unlike other synovigenic species, however, females of these species mature additional eggs by feeding on hosts. For the subset of host-feeding parasitoids that use hosts exclusively for host feeding or oviposition, the decision to host feed vs oviposit will influence the probability of becoming egg limited. As the risk of egg limitation increases, the likelihood of using a host for host feeding rather than for oviposition is predicted to rise (Heimpel and Collier, 1996).

The effects of egg limitation on parasitoid fecundity and behavior have important implications for host–parasitoid population dynamics. Some of the earliest models of host–parasitoid population dynamics assumed that the parasitism rate was limited only by the parasitoid's egg supply (Thompson, 1924; see also Klomp, 1958; Watt, 1959; Rogers, 1972; and Varley *et al.*, 1973, for discussions of Thompson's models). These models had unstable dynamics, however, and were largely rejected in favor of models in which parasitoid egg supply is unlimited (e.g., Nicholson and Bailey, 1935; Varley *et al.*, 1973; Beddington *et al.*, 1978; Hassell, 1978; Murdoch, 1990; Hassell and Godfray, 1992). A minority of contemporary models have explored the effects of egg limitation on host–parasitoid population dynamics, however. These models have shown that egg limitation can affect the form of density-dependence (Lessells, 1985) as well as equilibrium densities (Kidd and Jervis, 1989; Briggs *et al.*, 1995; Shea *et al.*, 1996; Getz and Mills, 1996) and stability properties (Kidd and Jervis, 1989; Shea *et al.*, 1996; Getz and Mills, 1996) of host–parasitoid interactions. Also, a number of authors have noted that egg limitation is one possible explanation for the documented cases of inversely density-dependent parasitism rates in the field (e.g., Morrison and Strong, 1981; Lessells, 1985; Stiling, 1987; Walde and Murdoch, 1988; Kuhlmann, 1996).

Here, we assess the evidence for and against egg limitation of parasitoids in the field. We begin by reviewing the literature for direct and indirect evidence for and against egg limitation and conclude by presenting a case study on egg limitation in the synovigenic parasitoid *Aphytis aonidiae* (Hymenoptera: Aphelinidae) in the field.

## EVIDENCE FOR AND AGAINST EGG LIMITATION IN THE FIELD

A summary of our review of egg limitation in parasitoids is presented in Table 1.

The most direct way of estimating egg limitation in the field is to dissect the ovaries of field-caught females and count the number of mature eggs that are present.

**TABLE 1**

Evidence For and Against Egg Limitation in Field Populations of Parasitoids

| Species | Mode of reproduction | Class of evidence | Evidence for egg limitation? | Source |
|---|---|---|---|---|
| *Mesochorus* sp. | ? | Direct | Yes[a] | van Emden, 1963 |
| Unidentified Braconidae and Ichneumonidae | ? | Direct | Yes[a] | Pollard, 1967 cited in Jervis *et al.*, 1993 |
| *Anagrus delicatus* | Proovigenic | Direct | Yes | Cronin, 1991 |
| *Bracon hebetor* | Synovigenic | Direct | Yes | Ode, 1994 |
| *Aphaereta minuta* | ? | Direct | No | Visser, 1994 |
| *Leptopilina clavipes* | Proovigenic | Indirect | Yes | Driessen and Hemerik, 1992 |
| *Aphytis melinus* | Synovigenic | Indirect, behavioral/evolutionary | Yes | J. Casas, pers. commun., Collier *et al.*, 1994; Heimpel and Rosenheim, 1995 |
| *Sympiesis sericeicornis* | Synovigenic | Indirect | Yes | Casas *et al.*, 1993 |
| *Encarsia pergandiella* | Synovigenic | Indirect | Yes | Hunter, 1993 |
| *Coccophagus atratus* | Synovigenic | Indirect | No | Donaldson and Walter, 1991 |
| *Aphytis lingnanensis* | Synovigenic | Behavioral/evolutionary | Yes | Rosenheim and Rosen, 1991 |
| *Diglyphus begini* | Synovigenic | Behavioral/evolutionary | Yes | Minkenberg *et al.*, 1992 |
| *Venturia canescens* | Synovigenic | Behavioral/evolutionary | Yes | Fletcher *et al.*, 1994 |
| *Comperiella bifasciata* | Synovigenic | Behavioral/evolutionary | No | Rosenheim and Hongkham, 1996 |
| *Aphytis aonidiae* | Synovigenic | Behavioral/evolutionary, direct | Yes | Heimpel *et al.*, 1996; this study |

*Note.* Direct evidence comes from dissections of field-collected individuals. Indirect evidence comes from estimates of related factors such as host encounter rate, maximum egg load, and egg maturation rate. Behavioral/evolutionary evidence comes from tests of behavioral models that predict a response to the risk of egg limitation. The order of entries corresponds to the order in which they are discussed in the text.

[a] The authors interpreted egglessness to indicate an immature state of the ovaries prior to the onset of egg maturation.

Ovary dissections of field-caught females have been conducted by a number of researchers (van Emden, 1963; Pollard, 1967, cited in Jervis *et al.*, 1993; Askew, 1974; Cronin, 1991; Ode, 1994; Visser, 1994; Heimpel *et al.*, 1996; see Table 1). Most of these studies have uncovered some degree of egg limitation. The studies by van Emden (1963) and Pollard (1967, cited in Jervis *et al.*, 1993) were designed to test the hypothesis that recently emerged parasitoids that had not yet matured eggs were more likely to feed on floral nectar than were older parasitoids that had matured eggs (van Emden, 1963, 1990; Jervis *et al.*, 1993). While their results supported the hypothesis in the sense that a higher proportion of females captured at flowers were eggless than were females captured away from flowers, it was not clear whether egglessness was due to ovaries being immature or depleted of eggs. Askew (1974) dissected females from a number of parasitoid species but reported only mean and maximum egg loads, so that the prevalence of egglessness cannot be estimated from his study. Cronin (1991) found that 6% of *Anagrus delicatus* Dozier females, which are proovigenic parasitoids of planthopper eggs, were eggless upon capture. Ode (1994) dissected females of the synovigenic parasitoid *Bracon hebetor* Say throughout the field season and found that the fractions of females that were eggless ranged between 0 and over 50% depending on sampling date. Visser (1994) dissected field-caught females of *Aphaereta minuta*, a larval endoparasitoid of certain dipteran larvae that emerges with a large number of eggs. He did not report actual egg loads of dissected females, but instead subtracted egg load from the expected number of eggs present at emergence to estimate the number of eggs laid prior to capture. It is evident from these calculations that only very few, if any, parasitoids were eggless at the time of capture.

The expected prevalence of egg limitation can also be estimated indirectly if information is available on factors such as the maximum egg load, the egg maturation rate, and the oviposition rate in the field. Driessen and Hemerik (1992) used a combination of field observations, laboratory studies, and simulation modeling to estimate levels of egg limitation in populations of the proovigenic parasitoid *Leptopilina clavipes* (Hartig). They concluded that about 13% of the females should run out of eggs under the field conditions that they found and thus that populations probably contain both egg- and time-limited individuals. Field observations of the synovigenic leaf-miner parasitoid *Sympiesis sericeicornis* Nees also revealed that, under high host availability, interhost travel times and handling times were short enough to produce egg-limitation in a few hours of foraging (Casas, 1989; Casas *et al.*, 1993). Similarly, models incorporating empirically derived egg maturation rates, maximum egg loads, and host encounter rates suggest that egg limitation should occur daily in up to 20% of *Aphytis melinus* DeBach females, which are synovigenic as well (J. Casas, pers. commun.).

The relative importance of egg- and time-limitation has also been studied indirectly for parasitoid species in which males and females develop on different host species (Hunter, 1993; Hunter and Godfray, 1995). In such heteronomous parasitoids, population sex ratios are predicted to reflect the relative abundance of the two host types when females are time-limited and approach equality when females are egg-limited (Godfray and Waage, 1990; Hunter and Godfray, 1995). In one field study, encounter rates with hosts suitable for female production by the heteronomous parasitoid *Encarsia pergandiella* Howard were an order of magnitude greater than encounter rates with hosts suitable for male production (Hunter, 1993). Under time limitation, therefore, population sex ratios were predicted to be about 0.1 (proportion males). Actual sex ratios were significantly more male biased than this prediction, however, while not reaching 0.5. This result reflected a preference for male production, and suggested that egg-limited females were present in the population (Hunter, 1993). Different results were reported, however, for another heteronomous parasitoid, *Coccophagus atratus* Compere. Donaldson and Walter (1991) found that sex ratios in the field were closely linked to the proportion of hosts suitable for female and male production. Thus, their results are consistent with sex allocation of time-limited parasitoids.

A few field studies provide circumstantial information from which the incidence of egg limitation can be inferred. For instance, Hopper and King (1986) estimated attack rates of *Microplitis croceipes* (Cresson) in large field cages and concluded that egg limitation was unlikely to occur at host densities commonly documented in the field. A subsequent study of freely foraging *M. croceipes,* however, revealed that the cages used in the initial experiments probably impeded parasitoid search rate (Hopper *et al.*, 1991). Whether the increase in attack rates found in uncaged vs caged parasitoids was sufficient to produce egg limitation during the parasitoid's lifetime was not clear. Similarly, van Dijken *et al.* (1991, 1993) argued that low host encounter rates and high rates of superparasitism in the field indicate that the mealybug parasitoid *Epidinocarsis lopezi* DeSantis evolved under conditions of time-limitation and that egg limitation was likely only under agricultural conditions. The hypothesis that *E. lopezi* females do not become egg-limited in their native habitat remains to be tested, but the low egg capacity of this species (ca. 10; van Dijken *et al.,* 1991) suggests the potential for egg limitation.

The reproductive strategy of the mymarid *Anagrus delicatus* Dozier in the field is consistent with a risk of egg limitation. This parasitoid abandons host patches after parasitizing only a small proportion of the hosts present in the patch (Cronin and Strong, 1993a). It has further been shown that females of this species are unable to discriminate between hosts which have been previously parasitized (either by themselves or conspecifics) and hosts which have not been parasitized (Cronin and Strong, 1993b). Results from a dynamic state-variable model have suggested that, when host discrimination is lacking, abandoning host patches after even depositing only one egg can be favorable under conditions of impending egg limitation (Rosenheim and Mangel, 1994).

A number of behavioral models have been constructed with the assumption that parasitoids are time-limited and not egg-limited. Predictions from some of these models have then been compared with the behavioral of parasitoids either foraging in the field, or collected in the field and brought to the laboratory. Janssen (1989), based on an assumption of time-limitation, predicted that the *Drosophila* parasitoids *Asobara tabida* (Nees) and *Leptopilina heterotoma* Thomas would oviposit in a wide variety of host species, including hosts that were of marginal quality. He tested this prediction by observing foraging parasitoids in the field, and found that, in fact, almost no hosts were rejected. Visser *et al.* (1992a) have used an ESS approach to predict superparasitism and patch-time strategies in time-limited parasitoids and tested the theory with field-caught *L. heterotoma* individuals in the laboratory (Visser *et al.*, 1992b). The behavior of these individuals ($n = 4$) was consistent with either egg- or time-limitation. The possibility of egg limitation was indicated by significantly shorter patch times and lower parasitism rates for field-caught females than laboratory-reared females (which were presumably not egg-limited). However, field-caught females did superparasitize, a behavior linked to time-limitation in dynamic models (Mangel, 1989; Rosenheim and Mangel, 1994).

Another class of evidence for or against egg limitation comes from tests of behavioral models that explicitly include the risk of egg limitation as a variable. Dynamic state variable models make predictions for parasitoid behavior based in part upon current egg load (Mangel, 1987, 1989; Mangel and Clark, 1988). These models predict that the oviposition rate should decrease as egg load decreases, with the underlying assumption that declining egg loads signal an increased risk of egg limitation. Demonstrations of egg load effects on behavior are therefore consistent with an evolutionary history of a risk of egg limitation. A number of variants of the egg load hypothesis have been tested in the laboratory with positive results (Rosenheim and Rosen, 1991; Minkenberg *et al.,* 1992; Fletcher *et al.*, 1994; Heimpel and Rosenheim, 1995; Hughes *et al.*, 1994; see Table 1). These studies lend support to the hypothesis that behavior anticipating egg limitation has evolved in these species. To date, two laboratory studies have failed to find an effect of egg load on behavior: the Rosenheim and Honkham (1996) study on clutch size in *Comperiella bifasciata* (Howard), and the Rosenheim and Rosen (1992) study on host-feeding behavior in *Aphytis lingnanensis.* Negative results such as these are difficult to interpret; they could indicate either that egg limitation is not likely in the field or that egg load is not a reliable indicator of egg limitation (Rosenheim and Heimpel, 1994). Furthermore, the lack of an effect of egg load on host-feeding decisions obtained for *A. lingnanensis* was counterbalanced with a strong effect of egg load on clutch size (Rosenheim and Rosen, 1991, 1992).

## A CASE STUDY

We conducted a study of the effect of egg load on host-feeding strategies of the synovigenic parasitoid *A. aonidiae* (Mercet) (Hymenoptera: Aphelinidae) foraging freely in the field (Heimpel *et al.*, 1996). The main results were that host feeding (rather than oviposition) was more likely to occur at lower egg loads and on smaller hosts. These results were consistent with a risk of egg limitation in the field. Here, we present a larger data set from 270 dissections of field-caught *A. aonidiae* and look for some patterns in the risk of egg limitation.

*Aphytis aonidiae* is a uniparental ectoparasitoid of the San Jose scale, *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae), and in California it appears to be the dominant natural enemy of this pest insect (Gulmahamad and DeBach, 1978; G. E. Heimpel and J. A. Rosenheim, unpublished data). We collected parasitoids from an organically managed almond orchard in Northern California that had resident populations of both *A. aonidiae* and San Jose scale during the field seasons of 1992, 1993, and 1994 by aspirating freely foraging females. These females were brought to the laboratory on ice, and we dissected their ovaries to quantify egg load (see Heimpel *et al.*, 1996).

Approximately 18% of the females captured had an egg load of zero (Fig. 2). However, some of this egg limitation may be attributable to an unknown source of variability in egg maturation capabilities in this population of parasitoids. During the summer and fall of 1994 we discovered that approximately 35% of females that emerged from pupae collected in the field did not mature any eggs under laboratory conditions that are generally optimal for egg maturation. While most females matured a full complement of eggs during the first day posteclosion when deprived of hosts, these females matured no eggs during the first 5 days of their life under identical conditions (Heimpel *et al.*, 1996). Females were not monitored after the first 5 days of life, and we did not determine whether host feeding can lead to egg maturation in these females. Until further tests are conducted, we can only speculate as to the origin of the eggless condition. We have considered three classes of possibilities. First, the eggless individuals may be infected with a pathogen that either damages the eggs directly or causes the parasitoids to direct resources away from eggs. Second, sharp differences in host quality may exist that lead to egglessness in parasitoids developing on certain hosts. For instance, some hosts may lack an essential component needed for successful vitellogenesis or have toxic properties. Last, there may be a polymorphism in the population that involves differential resource allocation. For instance, there may be a diapausing or dispersing morph, in which resources obtained during the larval stage are allocated to the fat body, hemolymph, or muscle tissue rather than to developing oocytes. In any case, it is possible that some of the egg limitation that we found is attributable to the limited egg maturation capabilities of a subset of females in the population.

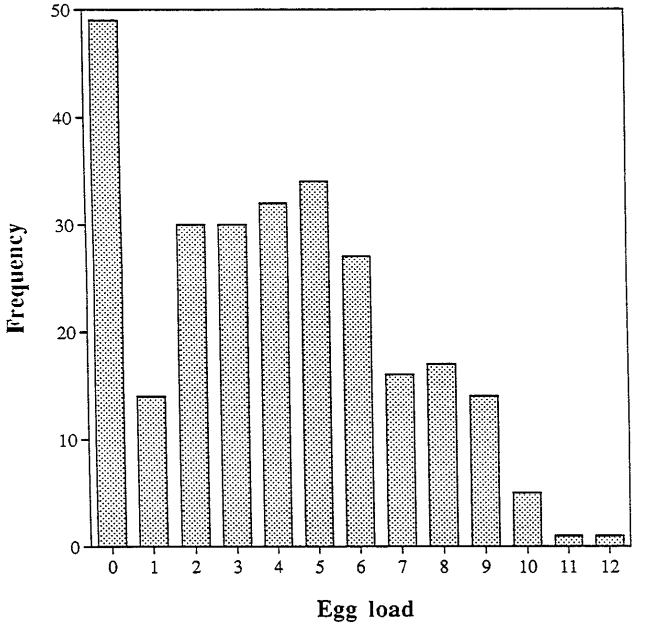

**FIG. 2.** Distribution of egg loads of field-collected *Aphytis aonidiae*. Adult female parasitoids were captured in the field and brought to the laboratory for ovary dissection.

However, even if we ignore the entire class of parasitoids with zero eggs, the risk of egg limitation is demonstrated by the large number of parasitoids carrying very few eggs (Fig. 2). Host encounter rates for this species are on average one host per hour, and handling times range from 5 to 25 minutes (Heimpel *et al.*, submitted for publication). Thus, unless the egg maturation rate is extremely rapid, *A. aonidiae* females with egg loads of 1–3 are likely to face a considerable risk of becoming egg limited. The egg maturation rate of *A. melinus* DeBach (Collier, 1995) is much lower than the host encounter rate experienced by *A. aonidiae* in the field (Heimpel *et al.*, submitted for publication).

Next, we evaluate possible trends in egg load distribution associated with time of day, time of year, temperature, parasitoid size, and host density. For each parasitoid collected, we scored the date and time collected and the temperature (in the shade) at the time of collection.

We also obtained the high and low temperatures for that 24-h period from a weather station data base for a site located approximately 15 km from our field site. Parasitoid size was estimated by measuring both hind tibiae and averaging their lengths (Heimpel *et al.*, 1996). Host density was estimated by randomly sampling four 1- to 2-year-old almond twig sections (approx. 20 cm long) per tree from the tree where the parasitoid was captured. The samples were brought to the laboratory where the covers of all San Jose scale insects attached to the twigs were removed and the condition of the scale insect was noted. Only records of scale deemed to be susceptible to parasitism (i.e., 2nd or 3rd instar females that seemed to be healthy) were used in the analysis presented here (see Heimpel *et al.*, 1996). Twig dimensions (length and circumference) were used to calculate the number of hosts per square centimeter. Host density data were not available for each individual parasitoid sampled.

Time of day had no effect on egg load when eggless females were included in the analysis (linear regression, $P > 0.30$) and a slight yet significant effect on egg load with eggless females removed (Fig. 3; linear regression; $R^2 = 0.024$; $P = 0.033$). Although the relationship was highly variable, each hour in the day between approximately 10 AM and 8 PM corresponded to an average decrease in egg load of 0.19 eggs for females with one or more eggs (Fig. 3). Thus, there appears to be a very slight increase in the risk of egg limitation as the day goes on. This trend is obscured, however, by including the eggless class of females, a portion of which may be presumably eggless all day due to the unknown reason(s) discussed above.

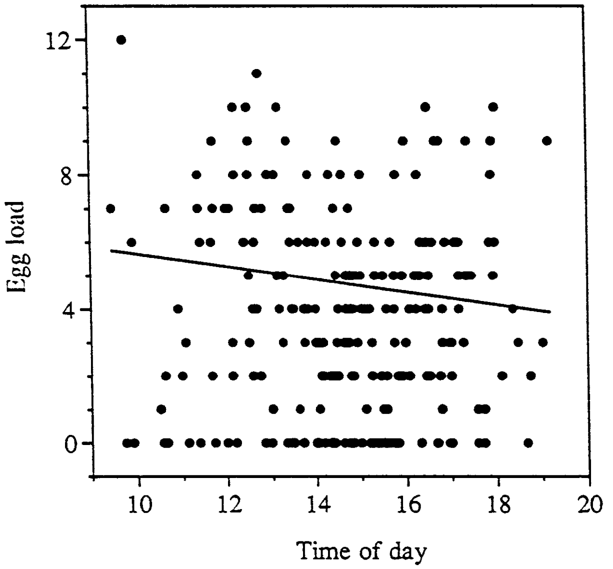

**FIG. 3.** Effect of egg time of day on egg load of field-collected *Aphytis aonidiae* females. The regression line incorporates nonzero egg loads only: Egg load = −0.19 (time of day) +7.56.

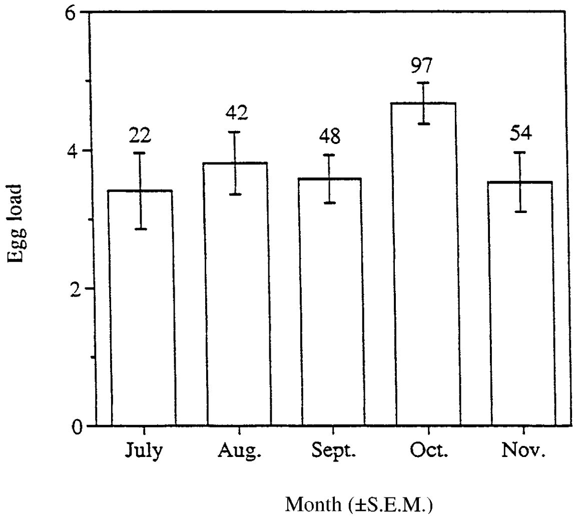

**FIG. 4.** Month-specific mean egg loads of *Aphytis aonidiae* collected from July through November (years pooled), including eggless females.

There was a slight but marginally nonsignificant effect of month (years pooled) on egg load (Fig. 4; ANOVA; $F = 2.2$; $P = 0.067$) when eggless females were included in the data set. The significance of this relationship was increased by not including eggless females (ANOVA; $F = 3.2$; $P = 0.013$). In 1993 and 1994, the month of October corresponded with peak abundance of *A. aonidiae* adults and a relatively high risk of predation on *A. aonidiae* adults by generalist predators (Heimpel *et al.*, 1997). Life expectancy, as calculated from the predation rate alone, was between 1 and 3 days during these periods (Heimpel *et al.*, 1997). Thus, it is conceivable that predation pressure during October imposed a measure of time-limitation not observed during other times of the year.

Neither temperature at collection nor low or high temperatures during the 24-h period including the collection time had a significant effect on egg load whether eggless females were included in the analyses or not ($P > 0.10$ for all six linear regressions).

Parasitoid hind tibia length, however, had a strong, significant effect on egg load whether eggless females were included (linear regression; $R^2 = 0.23$; $P < 0.0001$; Fig. 5) or not (linear regression; $R^2 = 0.31$; $P < 0.0001$).

Finally, host density had no detectable effect on egg load whether eggless females were included in the analysis or not (Fig. 6; $P > 0.5$ for both linear regressions). This result is at odds with Rosenheim's (1996) prediction that the fraction of parasitoids that become egg limited should be a positive function of host availability. To the extent that host density in our data set is a reasonable proxy for host availability, one possible explanation for this negative result could be state-dependent behavior. We showed previously for this population of parasitoids that host use is more selective at lower egg loads (Heimpel *et al.*, 1996). As egg loads declined, higher quality hosts were used for oviposition, and lower quality hosts were used for host feeding. Could this process provide a "buffer" to egg load in such a way that egg limitation is avoided when hosts are abundant? We would argue that just such a dynamic is implicitly predicted by dynamic state-variable theory for parasitoid oviposition decisions (e.g., Mangel, 1987, 1989). At high rates of host encounter, when the risk of egg limitation is high, egg load-dependent behavior decreases the oviposition rate and therefore the risk of egg limitation.

## CONCLUSIONS

During the past decade, a consensus has started to emerge that parasitoids can be limited by egg supply as well as by the time available to locate and parasitize hosts (e.g., Godfray, 1987, 1994; Driessen and Hemerik, 1992; Hunter, 1993; Briggs *et al.*, 1995; Hunter and Godfray, 1995; Getz and Mills, 1996; Rosenheim, 1996; Rosenheim *et al.*, 1996; Shea *et al.*, 1996; van Alphen and Jervis, 1996). This view has been spurred in large part by the development of dynamic state-variable models of insect reproductive behavior which explicitly incorporated the risk of egg limitation into the prediction-making process (e.g., Iwasa *et al.*, 1984; Mangel, 1987, 1989; Mangel and Clark, 1988). More recently, the idea that dying with mature eggs in the ovaries is likely to be a waste of resources has led to the argument that some degree of egg limitation should be expected in parasitoid populations (Rosenheim, 1996). It should therefore be no great surprise that egg limitation does in fact occur in field populations of parasitoids, as we document in the review portion of this paper. Although much of the modeling concerning egg limitation has focused on proovigenic species, in which egg limitation is by definition permanent, the insights apply to synovigenic species as well. In synovigenic species, egg limitation is usually temporary, but the same opportunity costs apply as do for proovigenic species. Again not surprisingly, egg limitation has been found in both pro- and synovigenic species.

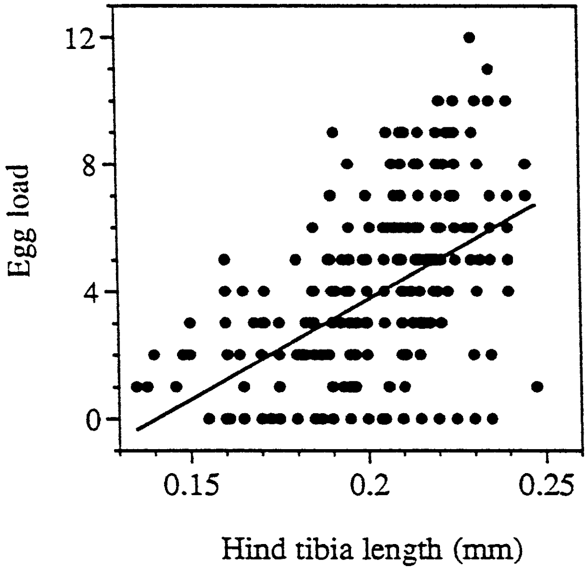

**FIG. 5.** Influence of mean hind tibia length on egg load of *Aphytis aonidiae* females collected in the field. The regression line incorporates eggless females: Egg load = 62.8 (hind tibia length) −8.8. $N$ = 264.

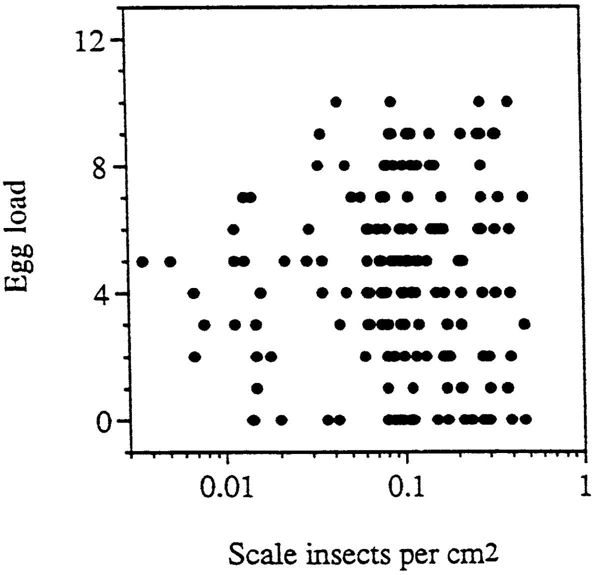

**FIG. 6.** Influence of host density (susceptible San Jose scale insects per square cm or almond twig) on egg load of *Aphytis aonidiae* females. $N$ = 201.

The recognition that parasitoids become egg limited in the field has broad implications for our understanding of host–parasitoid interactions within the context of biological control. It has traditionally been assumed that parasitoid fecundity is limited primarily by the number of hosts encountered (e.g., Hassell, 1978; Godfray, 1994). When models are constructed in which parasitoid fecundity can be limited by egg- or host-limitation, however, the ability of parasitoids to depress host populations decreases with increasing egg limitation (Getz and Mills, 1996; Shea *et al.*, 1996). Thus, egg limitation can in principle lead to higher equilibrium host densities and could potentially interfere with biological control. Furthermore, van Dijken *et al.* (1991, 1993) have argued that egg limitation is more likely to occur in agricultural systems, where host encounter rates may be especially high.

Rosenheim (1996) also predicted that egg limitation would be more pronounced at high rather than low host encounter rates. In our field study of *A. aonidiae*, however, the risk of egg limitation was found to be independent of host density. Assuming that our measure of host density was a reasonable proxy for host availability, this result is unexpected. However, in a previous study done on the same population of parasitoids, we showed that host use patterns in *A. aonidiae* are dependent on egg load and host quality (Heimpel *et al.*, 1996). At high egg loads, relatively low quality hosts are used for oviposition, while only the poorest-quality hosts are used for destructive host feeding. As egg load declines, however, host use becomes more selective; higher quality hosts are used for oviposition and a broader range of hosts are used for host feeding. We argue that state-dependent behavior of this kind could contribute to a "buffering" of egg load with respect to host availability. When host availability is high, the oviposition rate is decreased by increased selectivity, and when host availability is low, the oviposition rate is increased by decreased selectivity. The result could be an attenuation of the opportunity costs associated with egg limitation.

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