

# The link between host density and egg production in a parasitoid insect: comparison between agricultural and natural habitats

Michal Segoli\* and Jay A. Rosenheim

Department of Entomology, University of California, 1 Shields Avenue, Davis, CA, 95616 USA

## Summary

1. Theory predicts that organisms should invest more heavily in overcoming factors that more frequently emerge as the primary constraints to fitness, and especially, those factors that constrain the fitness of the most highly reproductive members of the population.

2. We tested the hypothesis that the fecundity of a pro-ovigenic parasitoid (where females emerge with their full egg load) should be positively correlated with the mean expectation for oviposition opportunities in the environment. More specifically, we tested whether females from agricultural systems, where hosts are often relatively abundant, emerge with more eggs than those from natural habitats.

3. We studied the pro-ovigenic parasitoid wasp *Anagrus daanei*, which parasitizes eggs of leafhoppers of the genus *Erythroneura*. *Erythroneura* spp. leafhoppers feed on *Vitis* spp. (grapes) and are major pests of commercial vineyards as well as common herbivores of wild *Vitis californica*, which grows in riparian habitats. We sampled leafhoppers and parasitoids from eight vineyards and eight riparian habitats in central California.

4. We found that leafhopper density was higher at vineyards than in riparian habitats, whereas leafhopper egg volume and parasitoid body size did not differ among these habitat types. Parasitoids from vineyards had higher egg loads than parasitoids from wild grapes, and fecundity was positively related to host density across field sites. Parasitoid egg volume was larger in natural sites; however, this variation was not significantly correlated with host density across field sites. Within a single population of parasitoids collected from a vineyard, parasitoid egg load was negatively correlated with longevity, suggesting a trade-off between reproduction and life span.

5. The results may be explained by a rapid evolution of reproductive traits in response to oviposition opportunities; or alternatively, by the occurrence of maternal effects on the fecundity of daughters based on the foraging experience of their mothers.

6. The ability of parasitoid fecundity to track mean host availability is likely to modulate the likelihood that parasitoid fitness will be constrained by a shortage of eggs and strengthen the ability of parasitoids to suppress the population densities of their hosts.

**Key-words:** fecundity, longevity, egg size, trade-off, *Anagrus*, *Erythroneura*, *Vitis*

## Introduction

The lifetime reproductive success of organisms may be limited by many factors such as food availability, mate availability, competition, predation, parasites and pathogens. Organisms can potentially invest in reducing the impact of a particular limiting factor, but the ability to overcome

one factor is often traded off against the ability to overcome another (Stearns 1992). Theory predicts that organisms should invest more heavily in overcoming factors that more frequently emerge as the primary constraints to fitness (Rosenheim, Alon & Shinar 2010). However, this prediction is difficult to test, because the relative importance of different limiting factors may change over the course of an organism's lifetime, and the relative investment in overcoming these factors is often plastic. Moreover, data on

\*Correspondence author. E-mail: msegoli@ucdavis.edu

the relative importance of factors that limit the reproductive success of organisms in nature are scarce; yet, these are likely to be the factors that shape the evolution of life-history traits.

Parasitoids have long been used as model organisms to test ecological and evolutionary theory. The lifetime reproductive success of a female parasitoid is considered to be limited by two main factors: (i) the finite number of hosts available to a female for oviposition during her lifetime (termed host or time limitation); and (ii) the finite supply of mature eggs (termed egg limitation; Godfray 1994). Under a perfectly balanced life history, a female parasitoid would die immediately after laying her last egg, without spending time or energy on activities that do not contribute to fitness. However, due to environmental stochasticity, host availability in the environment cannot be predicted accurately. Thus, many females will die before they are able to lay all of their eggs (i.e. host limited females). This is likely to impose selection on females to increase longevity and to decrease fecundity, given that the 'excess' eggs make no contribution to fitness, and egg production may trade off with other fitness components. In contrast, some females will entirely exhaust their egg supply while hosts are still available (i.e. egg-limited females). This is likely to impose selection on females to increase egg production at the expense of other fitness-correlated traits (Rosenheim 1996). Hence, female fecundity is predicted to reflect the balance between these two opposing risks.

In accordance, it has been suggested that fecundity should increase as host availability and hence, oviposition opportunities increase (Rosenheim 1996; Sevenster, Ellers & Driessen 1998; Ellers, Sevenster & Driessen 2000). Some indirect support for this prediction comes from interspecific comparisons. In seminal work, Price (1973, 1974) demonstrated that parasitoids in the family Ichneumonidae attacking younger host stages, which are more abundant in the environment, are more fecund than those targeting later host stages. Jervis, Moe & Heimpel (2012) validated Price's results while controlling for phylogeny, although they found no support for the hypothesis in a taxonomically broader data set. Additional evidence comes from synovigenic parasitoids, where females continue producing eggs throughout their adult lives. Synovigenic females have been shown to adjust their egg production rate in response to host availability (Papaj 2000). For example, in the parasitoid *Eupelmus vuilleti*, brief antennal contact with a single host individual initiates a hormonal cascade leading to egg maturation (Casas *et al.* 2009), and in the aphid parasitoid *Aphelinus albipodus*, females mature eggs faster when in the presence of preferred hosts (Wu & Heimpel 2007).

These two lines of evidence demonstrate a match between egg production and host availability that is either (i) found within a species and is based entirely on phenotypic plasticity (physiological responses by individual females) or (ii) found between species. In this study, we ask whether there might additionally be ecologically important intraspecific, between-population variation in

fecundity that matches local variation in expected host availability that is not based on adjustments in egg maturation by the adult parasitoids. To date, evidence for such intraspecific variation in parasitoid fecundity is scarce and equivocal. In the parasitoid *Venturia canescens*, thelytokous (asexual) wasps are mostly found in grain storage facilities, where host caterpillars are aggregated, and females emerge with more eggs than arrhenotokous (sexual) wasps that are exclusively found in natural habitats, where hosts are scattered (Pelosse, Bernstein & Desouhant 2007). However, the interaction of egg load with reproductive mode in this system makes this observation difficult to interpret. In the species *Asobara tabida*, females from southern European populations, where host availability is higher, have a larger initial egg load than females from northern populations (Kraaijeveld & van Derwel 1994). However, populations do not differ in their lifetime fecundity, and hence, this appears to represent a shift in the timing of egg maturation rather than an actual increase in total reproductive effort (Jervis, Ellers & Harvey 2008).

The potential for a microevolutionary response in fecundity to host availability likely depends on the relative risks of egg limitation and host limitation under field conditions. For example, if females never deplete their eggs, we would expect little or no selection to increase egg production, even under higher than average host densities. However, the actual occurrence of egg depletion in the field is rarely known (Heimpel & Rosenheim 1998). Moreover, egg limitation has sometimes been considered to be negligible and as a consequence has often been omitted from mathematical models predicting parasitoid population dynamics, life history and behavioural traits (Charnov & Skinner 1985; Visser, van Alphen & Nell 1992; Murdoch, Briggs & Nisbet 2003).

We studied the link between fecundity and host availability across populations of the parasitoid *Anagrus daanei* Triapitsyn (Hymenoptera, Mymaridae). *A. daanei* is a proovigenic parasitoid, that is, females emerge with their full egg load and do not mature eggs as adults. Thus, the complete investment in egg production is fixed by the time the adult female emerges and cannot respond plastically to environmental variation in host availability. *A. daanei* parasitize eggs of leafhoppers of the genus *Erythroneura* (Homoptera: Cicadellidae), major pests in vineyards throughout California. Both leafhoppers and parasitoids occur also on the native wild grape *Vitis californica* in riparian habitats. This provides a unique opportunity to test changes in parasitoid life-history traits over a large range of host densities, within the same plant herbivore-parasitoid complex. A previous study indicated that more than 10% of *A. daanei* females become egg-limited during their lifetime in the field (Segoli & Rosenheim, in press), suggesting that there is an actual risk of egg limitation in this system.

We predicted that egg loads would be higher in females from agricultural vineyards than in females from natural riparian habitats. Modern agriculture has simplified the

agricultural landscape, increased the field size of crops, reduced the amount of noncrop habitat and often increased plant quality for herbivores by supplying plants with abundant water and mineral nutrients. Furthermore, the process of crop plant domestication may, in many cases, entail a diminution or loss of antiherbivore defensive traits. It has been suggested that, collectively, these changes often contribute to an increase in herbivore densities (Bianchi, Booij & Tschardt 2006). Hence, parasitoids foraging in agricultural systems are likely to be exposed to higher host densities relative to those foraging in natural habitats.

We further predicted that the hypothesized increase in egg production would entail trade-offs in the form of reduced allocations to other life-history traits. We examined two trade-offs that seemed particularly plausible. First, increasing the number of eggs produced might trade off with producing smaller eggs (Berrigan 1991; Fox & Czesak 2000). Egg size has been shown to affect developmental success, developmental rate, offspring size and offspring fecundity in insects (Tauber, Tauber & Tauber 1991; Fox & Czesak 2000). In parasitoids, egg size has been suggested to increase survival and larval competitive ability, although evidence is scarce (Kraaijeveld & van Alphen 1994; Boivin & Gauvin 2009). Second, increasing the number of eggs produced might trade off with a reduced investment in somatic maintenance or nutrient reserves, thereby decreasing longevity. Studies have demonstrated both phenotypic and genetic trade-offs between reproduction and longevity in insects (Miyatake 1997; Tatar 2001) and specifically in parasitoids (Blackburn 1991; Ellers, Driessen & Sevenster 2000; Jervis, Ferns & Heimpel 2003).

In an earlier study, we found that *A. daanei* egg loads at emergence across a small series of vineyards appeared to be positively correlated with leafhopper density. A single parasitoid population associated with wild grapes had the lowest fecundity of all (Segoli & Rosenheim, in press), an observation that motivated the current study. Here, we conducted a replicated comparison of parasitoids collected from agricultural and natural fields. First, we tested the assumption that host density is consistently higher in vineyards compared with riparian habitats. Second, we examined the possibility that leafhopper egg size, a measure of host resources available to individual developing *Anagrus* spp. parasitoids, might vary between vineyards and riparian habitats. Third, we tested the prediction that initial egg loads of parasitoid females are higher in agricultural compared with natural populations. Finally, we tested for possible trade-offs between initial parasitoid egg load, egg size and longevity.

## Materials and methods

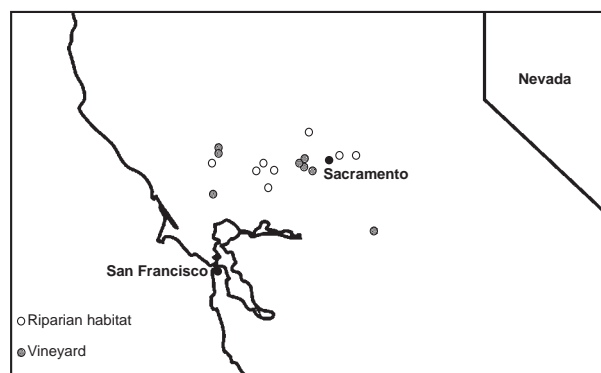
### STUDY ORGANISMS

*Anagrus daanei* wasps are among the most important natural enemies of *Erythroneura* spp. leafhoppers in Cali-

fornia (Doutt & Nakata 1973; Bentley 2009). *Anagrus* spp. complete their entire development (egg to adult) inside the host egg, consuming the egg as they develop. These wasps are solitary (develop singly inside the host), pro-ovigenic (emerge with their full lifetime complement of eggs already matured) and do not resorb eggs (Jepsen, Rosenheim & Matthews 2007). Emergence of wasps occurs mainly during the early morning hours (M. Segoli, pers. obs.). *A. daanei* wasps are short lived, even under the most benign laboratory conditions (English-Loeb *et al.* 2003). Three or more *Anagrus* generations are completed during each leafhopper generation (Daane & Costello 2000), with more than 10 parasitoid generations per growing season (June to October). *Erythroneura* spp. leafhoppers deposit eggs singly or in clusters under the leaf epidermal tissue or along the veins of *Vitis* spp. leaves, depending on the species. Each egg is minute, about 0.8 mm long. The freshly deposited egg is colourless and transparent. When eggs are parasitized, they become brown or red.

### FIELD SITES

We sampled from eight vineyards and eight natural sites in riparian habitats (Fig. 1) between July–September 2011. The distance between field sites was at least 2.5 km. The mean  $\pm$  SD distance from a vineyard site to the nearest riparian habitat (as estimated by the use of Google Maps) was  $1.1 \pm 1.0$  km (range, 0.1–5 km) and from a riparian habitat site to the nearest vineyard was  $2.3 \pm 2.0$  km (range, 0.2–5 km). We worked in fields that had not been treated with sulphur, which has been shown to be harmful to the wasps (Jepsen, Rosenheim & Bench 2007). We found three species of leafhoppers in our field sites: (i) the Virginia creeper leafhopper *Erythroneura ziczac*, which had not been documented from California previously; (ii) the variegated leafhopper *Erythroneura variabilis*, which invaded from the south over the past several decades (Settle & Wilson 1990); and (iii) the western grape leafhopper *Erythroneura elegantula* Osborn, which is native to California and considered to be the



**Fig. 1.** The locations of vineyards and riparian field sites in central California.

most important leafhopper host for *Anagrus* parasitoids (Daane & Costello 2000).

#### LEAFHOPPER DENSITY

To quantify leafhopper density, we collected 30 leaves from each site. To get estimates that are relevant to what is experienced by the foraging parasitoids, we sampled the leaves from the same sections of the field from which parasitoids were sampled. We counted the number of leafhopper eggs (both hatched and unhatched) on half of each leaf (top and bottom) under a dissecting microscope. We distinguished among eggs of the three leafhopper species based on their distribution pattern and location on the leaf (western grape leafhoppers lay their eggs singly under the leaf epidermis, variegated leafhoppers lay their eggs singly along the veins, and Virginia creeper leafhoppers lay their eggs in clusters under the leaf epidermis). We identified parasitized eggs according to their darker colour (although this inevitably excluded some recently parasitized eggs that had not yet changed colour), or the emergence holes left by the parasitoids (a round exit hole, easily distinguished from the slit in the leaf epidermis left by an emerging leafhopper nymph). To estimate leafhopper density, we averaged the total number of leafhopper eggs (hatched and unhatched) per half a leaf, for each of the field sites. We considered two additional estimates of host density: (i) the density of unparasitized eggs (this would reflect host availability if parasitoids completely avoid laying eggs in already parasitized hosts); and (ii) the density of western grape leafhopper eggs only. The western grape leafhopper was the only leafhopper species that was found in all field sites. It accounted for 54% of all leafhopper eggs, compared with 7% for the variegated leafhopper and 40% for the Virginia creeper leafhopper ( $N = 9089$ ). Eggs of the western grape leafhopper were more often parasitized than those of the other leafhopper species (40% of the western grape leafhopper eggs, compared with 7% for the variegated leafhopper and 2% for the Virginia creeper leafhopper), suggesting that it is preferred by *A. daanei* parasitoids, or that parasitoids more often develop successfully within eggs of this host species.

#### LEAFHOPPER EGG VOLUME

Due to the higher abundance and higher parasitism rate of the western grape leafhopper compared with the other two host species, we used eggs of this species to explore differences in leafhopper egg size among habitat types. We measured 10–30 leafhopper eggs from each of six vineyards and seven riparian habitats under a dissecting microscope. We measured maximal length and maximal width and estimated egg volume as a spheroid using the equation: volume =  $\pi/6 \times \text{width}^2 \times \text{length}$ . Parasitoids fully consume the leafhopper egg during their development; thus, host egg volume represents the total quantity of host resources available to the parasitoids.

#### PARASITOID SAMPLING

To quantify initial egg loads of newly emerged females, we brought fresh leaves with apparent leafhopper damage from each field site to the laboratory and placed them inside emergence cages. The cages were empty carton containers with a transparent funnel and a vial on top. The emerging wasps were attracted to the light and collected from the vials daily. Females were held at  $-30^\circ\text{C}$  and later dissected in a drop of water under a dissecting microscope to count eggs. As females do not mature additional eggs as adults, this initial egg load represents the maximum potential fecundity of females. For most samples, we also measured the dimensions of parasitoid eggs. *Anagrus* eggs are 'hydropic', that is, they expand as soon as they contact the host's haemolymph or when placed in water. To avoid measuring partially expanded eggs, we measured the largest fully expanded egg for each female (ovum maximal width and length). We estimated egg volume as a spheroid using the equation: volume =  $\pi/6 \times \text{width}^2 \times \text{length}$ . We then slide-mounted females in Hoyer's solution and measured the length of a hind tibia as an estimate of body size. We distinguished *A. daanei* from other species of *Anagrus* that emerge from leafhopper eggs using a phase-contrast microscope (Triapitsyn *et al.* 2010). In addition, we extracted DNA and sequenced a section of 28s rDNA for 20 wasps collected from different sites (Triapitsyn *et al.* 2010). The DNA sequence data confirmed our morphologically based identifications for 18 of the 20 sampled parasitoids. In two cases, we mistakenly identified *A. tretiakovae* as *A. daanei*. One of these wasps originated from a vineyard and the other from a riparian site, suggesting that *A. tretiakovae* occur in both habitat types, and thus, their occasional presence is not likely to bias our results. Sample sizes (Table 1) were highly unequal across sites because of strong inter-site variation in leafhopper and parasitoid abundance and despite increased sampling intensity at low-density sites. In addition, we failed to measure eggs for some collections; thus, the number of sites for this analysis is reduced.

#### PARASITOID LONGEVITY

Preliminary results suggested that most parasitoids emerge during the morning hours and survive <12 h without feeding. Similar patterns were observed in the field, where parasitoids were often abundant during the morning but were rarely captured after 16:00 h (M. Segoli, pers. obs.). To learn about possible trade-offs between parasitoid egg loads and longevity, we placed female parasitoids from a single vineyard (West UC Davis) that emerged during 10–20 July in individual glass vials. We used females that were already in the emergence cages at 08:00 h ( $n = 10$ ) or that emerged between 08:00–09:00 h ( $n = 5$  females). The glass vials were kept in a growth chamber at  $29^\circ\text{C}$  and were checked hourly for wasp survival until 20:00 h, by which time all individuals had died. Once dead, a female was



**Table 1.** Sample size for egg loads and egg volumes of *Anagrus daaneii* wasps from the different field sites and habitat types

Field site	Type of field	N for wasp egg load	N for wasp egg volume
Sonoma Valley	Agricultural	11	8
Solano County	Agricultural	28	27
West UC Davis	Agricultural	17	15
Pope Valley	Agricultural	15	11
South UC Davis	Agricultural	4	4
Santa Helena	Agricultural	7	8
Lodi	Agricultural	16	2
Davis	Agricultural	9	9
Sacramento	Natural	33	17
Bothe State Park	Natural	1	0
Putah Creek	Natural	25	15
Cold Canyon	Natural	13	7
Gates Canyon	Natural	4	4
Winters	Natural	4	4
Rancho Cordova	Natural	18	15
Woodland	Natural	12	1

immediately placed in the freezer and later dissected and slide-mounted to obtain egg counts and body size estimates. We were not able to obtain data on longevity for wasps from riparian habitats, as their densities were too low to obtain a suitably large sample of females emerging in the laboratory during a narrow time window.

#### STATISTICAL ANALYSIS

We used *t*-tests to compare leafhopper density, leafhopper egg volume, parasitoid tibia length, parasitoid egg load and parasitoid egg volume, all averaged per field site, among the two habitat types (natural vs. agricultural). Both egg loads and egg volume of newly emerged female parasitoids were positively related to hind tibia length (linear regression for females from all sites,  $R^2 = 0.31$ ,  $P < 0.001$ ,  $N = 208$  for egg load;  $R^2 = 0.04$ ,  $P = 0.013$ ,  $N = 131$  for egg volume). Thus, we compared the residuals from regressions of egg load and parasitoid egg volume vs. tibia length among the two habitat types. For each variable, we included only fields for which we had data from at least five females. Some data did not satisfy the assumptions of homogeneity of variance (Levene's test,  $P < 0.05$ ) and therefore were rank-transformed. In addition, we used a nonparametric multiple regression based on ranks (Conover 1999) to test the effects of leafhopper density and habitat type simultaneously on mean residual parasitoid egg load and egg volume. We used two-tailed tests to compare leafhopper density, egg volume and parasitoid size between the two habitat types. The results confirmed our expectation for higher leafhopper density in vineyards and no difference in leafhopper egg volume or parasitoid size (see Results section), and therefore, we used a one-tailed test for subsequent comparisons, where we had clear predictions regarding the directionality of the results. Finally, we used linear regression to learn about the relationships between egg load and longevity. Parasitoid longevity was

not affected by tibia length (linear regression,  $R^2 = 0.047$ ,  $P = 0.43$ ,  $N = 15$ ); thus, we did not include this factor in the model.

## Results

### LEAFHOPPER DENSITY

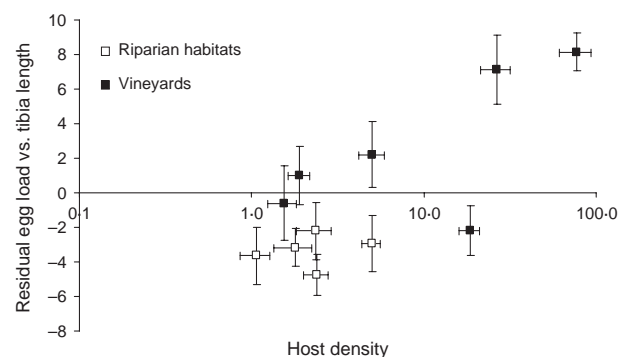
Leafhopper density was higher in vineyards than in natural riparian habitats with wild grapes (*t*-test based on ranks,  $T_{1,14} = 2.98$ ,  $P = 0.009$ ). Natural sites had consistently lower leafhopper densities [range 0.37–4.97,  $n = 8$ ], whereas vineyards showed a much greater range of densities [range 1.53–77.40,  $n = 8$ ] (Levene's test for homogeneity of variances,  $F = 6.1$ ,  $P = 0.027$ ). Similar results were obtained when considering only unparasitized host eggs or only eggs of the preferred leafhopper host species.

### LEAFHOPPER EGG VOLUME AND PARASITOID BODY SIZE

Mean leafhopper egg volume, representing the amount of resources available to the developing parasitoid, did not differ between vineyards and riparian habitats (*t*-test,  $T_{1,11} = 0.98$ ,  $P = 0.346$ ,  $n = 6$  vineyards and 7 riparian habitats). In accordance, parasitoid mean hind tibia length, representing parasitoid body size, did not differ among habitat types (*t*-test based on ranks,  $T_{1,10} = 0.23$ ,  $P = 0.821$ ,  $n = 7$  vineyards and 5 riparian habitats).

### PARASITOID EGG LOAD

Mean parasitoid egg load was consistently low for natural sites [range 16.9–17.8,  $n = 5$ ], whereas vineyards showed a much greater range of mean egg loads [15.4–33.5,  $n = 7$ ] (Levene's test for homogeneity of variances,  $F = 18.3$ ,  $P = 0.002$ ). Mean residuals of parasitoid egg load vs. tibia length were larger for vineyards than for riparian habitats (*t*-test based on ranks,  $T_{1,10} = 5.26$ ,  $P < 0.001$ ). A non-



**Fig. 2.** Residuals of parasitoid egg load (mean = 21.55) vs. hind tibia length ( $\mu\text{m}$ ) in vineyards (solid squares,  $n = 7$ ) and riparian habitats (empty squares,  $n = 5$ ), against host density (on a log scale). Bars represent standard errors of residual egg loads and host density within each field site.

parametric multiple regression suggested that both habitat type and leafhopper density have significant influences on mean parasitoid egg load, after correcting for parasitoid size (Fig. 2,  $P = 0.036$  for leafhopper density and  $P < 0.001$  for habitat type). Considering only unparasitized leafhopper egg density yielded similar results, but a significant effect of host density was lost if density estimates included only eggs of the preferred leafhopper host.

#### PARASITOID EGG VOLUME

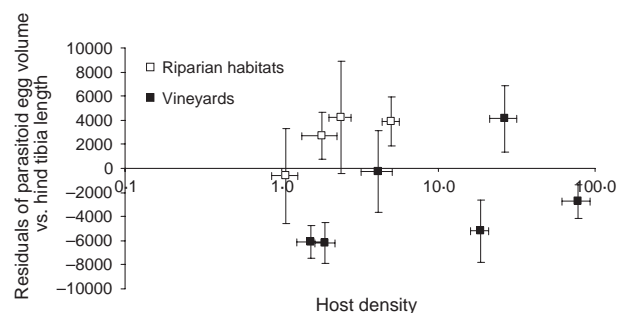
Residuals of parasitoid egg volume vs. tibia length were larger for riparian habitats compared with vineyards ( $t$ -test based on ranks,  $T_{1,8} = 1.96$ ,  $P = 0.043$ ,  $n = 6$  for vineyards and 4 for sites with wild grapes). The nonparametric multiple regression also indicated a significant effect of habitat type on mean residual parasitoid egg volume; however, this effect was independent of leafhopper density (Fig. 3,  $P = 0.31$  for leafhopper density and  $P = 0.05$  for habitat type). Similar results were obtained using the two alternate measures of leafhopper density.

#### PARASITOID LONGEVITY

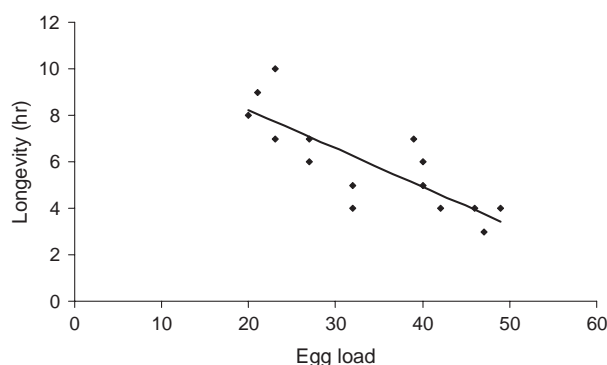
Parasitoid longevity was negatively related to egg load (Fig. 4, linear regression,  $R^2 = 0.65$ ,  $P < 0.001$ ,  $N = 15$ ). Despite the small sample size, the results were also significant when considering only females that emerged between 08:00–09:00 h, for which emergence time was determined with certainty ( $n = 5$ ), or only females that emerged before 08:00 h, for which exact emergence time was unknown ( $n = 10$ ).

### Discussion

We tested the hypothesis that the fecundity of a pro-ovigenic insect is positively correlated with the mean expectation for oviposition opportunities in the environment in which it was collected. In support of our predictions, parasitoids from agricultural habitats (vineyards), where hosts



**Fig. 3.** Residuals of parasitoid egg volume (mean =  $25\ 183\ \mu\text{m}^3$ ) vs. hind tibia length ( $\mu\text{m}$ ) in vineyards (solid squares,  $n = 6$ ) and riparian habitats (empty squares,  $n = 4$ ), against host density (on a log scale). Bars represent standard errors of residual egg loads and host density within each field site.



**Fig. 4.** Relationship between parasitoid egg load and longevity.

are more abundant, emerged with more eggs than those from natural riparian habitats (wild grapes), and egg loads were positively associated with host density across field sites. As pro-ovigenic females emerge with their full egg load and do not mature more eggs as adults, this intraspecific variation is not likely to represent a direct plastic response in egg maturation rate to host availability; rather, it is likely to represent an allocation strategy to egg production expressed during parasitoid development inside the host.

Parasitoids traditionally have been considered to be host rather than egg-limited (Godfray 1994). However, a growing body of theoretical and empirical work suggests that the risk of egg limitation is of importance, especially because it is likely to affect the most productive females in the population (i.e. those that had laid many eggs). Hence, parasitoids are probably adapted to balance their investment in overcoming these two opposing risks simultaneously (Heimpel & Rosenheim 1998; Ellers, Sevenster & Driessen 2000; Rosenheim 2011). The link between parasitoid egg load and leafhopper density across field sites documented here may represent an adaptive response to variation in the relative importance of host vs. egg limitation: that is, when oviposition opportunities are plentiful, females are selected to invest more in egg production to reduce the risk of egg limitation, and when oviposition opportunities are scarce, females invest less in egg production and possibly more in survival, to reduce the risk of host limitation. This may suggest a rapid evolution of fecundity and related traits following the recent transition of the host–parasitoid complex from natural to agricultural systems that began around 200 years ago with the establishment of commercial grape production (Doutt & Nakata 1973).

Alternatively, egg loads of parasitoids may differ among habitat types due to differential host quality (i.e. due to environmental rather than genetic effects). High vine vigour in commercial vineyards may provide better nutrition to the leafhoppers and hence to the developing parasitoids. The difference in grape plant species (*Vitis vinifera* in vineyards vs. *V. californica* in riparian habitats) and leafhopper species composition could also potentially affect parasitoid characteristics. We find this hypothesis less com-

elling as an explanation for the differences in parasitoid egg loads for several reasons. First, leafhopper egg size and parasitoid body size did not differ between vineyards and riparian habitats, suggesting that the amount of resources available to the developing parasitoids and the resulting ability of immature parasitoids to build adult biomass were similar in the two habitat types. Moreover, observed differences in parasitoid egg loads were significant after controlling statistically for variation in parasitoid body size. Second, we found possible evidence for trade-offs between fecundity and other life-history traits. This suggests that the increase in egg load is not simply due to a larger amount of resources available to the developing offspring; rather, it may represent an adjustment in an adaptive strategy of resource allocation. Finally, fecundity was found to be strongly heritable in another *Anagrus* species (Cronin & Strong 1996), as well as in other parasitoids, suggesting that sufficient additive genetic variation exists in reproductive traits for them to respond quickly to selection (Jervis, Ellers & Harvey 2008). Nevertheless, we cannot rule out the possibility of phenotypic plasticity in egg production via maternal effects (Mousseau & Fox 1998). Females encountering many hosts are likely to become more selective (Minkenber, Tatar & Rosenheim 1992; Roitberg *et al.* 1993; Heimpel & Rosenheim 1998; Jervis, Ellers & Harvey 2008) and hence to produce better quality and possibly more fecund offspring or may induce increased allocation to egg production in their daughters through epigenetic transgenerational effects (Jablonka & Raz 2009). Additional work is required to distinguish between these options and the possibility of purely genetic evolutionary changes in egg loads.

The feasibility of local adaptation depends on some degree of genetic isolation among populations (Nunney 2001). The level of genetic differentiation among *Anagrus* populations in grape systems is yet to be determined and is difficult to predict. On the one hand, *Anagrus* wasps have been shown to disperse upwind over moderate distances, for example, hundreds of metres (Corbett *et al.* 1996), within the distance range between some of the field sites and adjacent *Vitis* habitats. In addition, *Anagrus* wasps that forage in vineyards must overwinter inside the eggs of an alternate host species that is found in adjacent habitats (Murphy *et al.* 1998). Thus, at least one generation of parasitoids per year must disperse out of the vineyards and may mix with other populations. On the other hand, other field sites were relatively isolated (a few kilometres from adjacent *Vitis* habitats), providing an opportunity for some degree of genetic isolation. Moreover, the small size and short life span of *Anagrus* wasps may suggest that most wasps forage over modest distances during their lifetime. Finally, *Anagrus* complete multiple generations from May to October. This may allow some degree of local adaptation even within a single reproductive season, as was shown in another minute insect (Rhombert, Joseph & Singh 1985). Asymmetrical dispersal among habitat types should also be considered. For example, females from

riparian habitats with lower egg loads and possibly higher life expectancies may have a larger probability of dispersing. On the other hand, the larger populations in vineyards provide a larger source of individuals that could potentially disperse to adjacent riparian habitats.

We found possible evidence for trade-offs between life-history traits at both the population and individual level. Females from vineyards had higher egg loads, but smaller egg sizes than those from riparian habitats. This result suggests an adaptive shift in response to increased oviposition opportunities in vineyards. Mean egg size was not related directly to host density; however, host density likely fluctuates substantially in both agricultural and natural sites, making it more difficult to resolve a relationship between a snapshot view of host density and parasitoid egg volume when comparing a small number of sites, as was performed here. If, as appears to be the case, mean host density over the long term is lower in natural sites in comparison with agricultural sites, then a clearer signal of site type on parasitoid egg volume may not be unexpected.

Possible evidence for a trade-off was also obtained from the negative relationship between egg load and adult longevity among wasps from a single population. Although phenotypic correlations do not provide a definite proof for an evolutionary trade-off, they are more likely to mask existing trade-offs rather than to generate a spurious negative relationship (Reznick 1985). Thus, the negative relationship observed here may represent a trade-off that is mediated by differential allocation of reserves to egg production, at the expense of somatic maintenance (Jervis, Ellers & Harvey 2008). For example, in the synovigenic parasitoid *A. tabida*, females from southern European populations, where host availability is high, emerge with more eggs but fewer fat reserves than females from northern populations. In addition, females of both populations invest more in egg production at the expense of fat reserves and hence longevity, when exposed to high host densities (Ellers & van Alphen 1997). To our knowledge, we provide the first test for a possible trade-off between egg production and longevity for a pro-ovigenic parasitoid. The strength of this negative relationship is somewhat surprising, given that parasitoids were collected from the same habitat type. We hypothesize that this trade-off may represent a bet-hedging strategy in reproductive effort, in which some offspring invest more in reproduction, while others invest more in body maintenance. Such a strategy may be adaptive for pro-ovigenic parasitoids that lack the ability to respond plastically to current host encounter rate in a temporally fluctuating environment. This may be especially important in vineyards where variation in leafhopper densities was higher. It is yet to be determined whether mean egg load is traded off against longevity also within natural sites and at the population level.

Although insect herbivores are commonly assumed to reach higher densities in agricultural compared with natural habitats, this assumption has been challenged recently (Normark & Johnson 2011) and has rarely been tested

explicitly by comparing field populations of herbivores on domesticated plants and their wild ancestors (Chen & Welter 2002). Our results generally support this basic assumption. However, higher host densities were only observed in some of the vineyards, while others had leafhopper densities as low as those found in riparian natural sites. The larger variation in host densities in vineyards may represent a large effect of the specific conditions and cultivation practices at each site. Indeed, management practices such as supplemental irrigation, fertilization and suppression of competing plants have been shown to affect leafhopper densities in vineyards (Daane & Costello 2000). The high variation of leafhopper densities in vineyards could have potentially generated the observed higher variation in egg loads of parasitoids across agricultural field sites.

In conclusion, our study provides the first direct evidence for an interpopulation positive relationship between oviposition opportunities and lifetime fecundity in parasitoids. This may be explained by the occurrence of maternal effects on the egg loads of daughters based on the foraging experience of their mothers, but may also suggest the possibility of a rapid evolutionary change in parasitoid reproductive traits in response to variation in oviposition opportunities. In either case, the ability of parasitoid fecundity to track mean host availability is likely to modulate the likelihood that parasitoid fitness will be constrained by a shortage of eggs and also to strengthen the ability of parasitoids to suppress the population densities of their hosts. Hence, it may suggest the exciting possibility of an important ecological or eco-evolutionary feedback.

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