ORIGINAL ARTICLE

Factors shaping life history traits of two proovigenic parasitoids

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Abstract

What shapes the relative investment in reproduction versus survival of organisms is among the key questions in life history. Proovigenic insects mature all their eggs prior to emergence and are short lived, providing a unique opportunity to quantify their lifetime investments in the different functions. We investigated the initial eggloads and longevity of 2 proovigenic parasitoid wasps: *Anagrus erythroneurae* and *Anagrus daanei*, (Hymenoptera: Mymaridae) that develop within leafhopper eggs in both agricultural vineyards and natural riparian habitats in Northern California. We collected *Vitis* spp. leaves containing developing parasitoids from 3 natural sites (Knight Landing, American River and Putah Creek) and 3 agricultural vineyards (Solano Farm, Davis Campus and Village Homes). We recorded eggloads at parasitoid emergence and female parasitoid longevity with or without honey-feeding. Theory predicts that parasitoids from vineyards (where hosts are abundant) would have higher initial eggloads and lower longevity compared with parasitoids from riparian habitats (where hosts are scarce). Although host density and parasitoid eggloads were, indeed, higher in vineyards than in riparian habitats, parasitoid longevity did not follow the predicted pattern. Longevity without feeding differed among field sites, but it was not affected by habitat type (natural *vs* agricultural), whereas longevity with feeding was not significantly affected by any of the examined factors. Moreover, longevity was positively, rather than negatively, correlated with eggloads at the individual level, even after correcting for parasitoid body size. The combined results suggest a more complex allocation mechanism than initially predicted, and the possibility of variation in host quality that is independent of size.

Key words: *Anagrus* parasitoids, eggload, leafhoppers, life-history tradeoffs, longevity

INTRODUCTION

Life history theory seeks to explain optimal allocation of resources to different developmental, physiological and reproductive functions of the organism. While the approach of "one solution per species" is tempting, it is widely acknowledged that environmental conditions are likely to alter optimal life-history traits, either at the phenotypic (i.e. plastic responses) or genotypic

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(i.e. evolutionary responses) level (Stearns 1992; Roff 2002).

Parasitoids are insects (mostly wasps) that lay their eggs in or on the body of another organism (mostly another insect) and whose offspring develop while feeding on the host, eventually killing it. Parasitoids have long been used for life history studies due to their varied strategies, relative ease of rearing and manipulating in the laboratory, and high responsiveness to environmental conditions (Godfray 1994). The reproductive success of parasitoids is considered to be limited mostly by the availability of mature eggs, or by the availability of suitable hosts in the environment (Rosenheim 1999). Hence, what shapes the relative investment in egg production versus longevity is a key question in parasitoid life history.

Despite early opinions that female parasitoids rarely deplete their eggs in nature (van Alphen *et al.* 1992; Visser *et al.* 1992; Sevenster *et al.* 1998), recent empirical data combined with theoretical developments suggest that egg limitation in parasitoids, as well as in other insects, is likely to occur under field conditions (Heimpel & Rosenheim 1998; Casas *et al.* 2000; Rosenheim *et al.* 2008; Segoli & Rosenheim 2013; Phillips & Kean 2017). Moreover, even in cases where egg limitation is rare, it may impose strong selection on female reproductive traits, due the disproportionately high reproductive contribution of egg-limited females (i.e. those that lay all of their eggs) to the next generation (Rosenheim 2011). Hence, the risk of egg limitation may lead to higher investment in egg production in environments with many oviposition opportunities. In contrast, in environments with limited host availability, higher investment in longevity, at the expense of egg production, is expected, as parasitoids need an extended amount of time to search for scarce hosts (Rosenheim 1996; Ellers *et al.* 2000; Gandon *et al.* 2009).

The majority of parasitoids are synovigenic; that is, they continue to mature eggs throughout their adult life (Godfray 1994; Jervis *et al.* 2001). Hence, decisions regarding the relative investment in survival versus egg production may change during the lifetime of the parasitoid, making it difficult to quantify. In contrast, strictly proovigenic parasitoids emerge with their full egg complement and do not mature additional eggs following emergence. In this case, the relative investment in egg production is a "one-time decision" that is made during parasitoid development inside the host, prior to its emergence. This provides a unique opportunity to study intraspecific variation in lifetime investment of parasit-

oids. Nevertheless, very few studies have investigated life history responses in proovigenic parasitoids in relation to environmental conditions. Part of the reason could be difficulties in handling and dissecting proovigenic parasitoids due to their small size.

We studied egg load and longevity of 2 strictly proovigenic parasitoids of the genus *Anagrus* (*A. erythroneurae* S. Trjapitzin & Chiappini, 1994 and *A. daanei* Triapitsyn, 1998). These parasitoids attack the eggs of leafhoppers that are considered major pests in vineyards in Northern California. Both the parasitoids and the leafhoppers occur also on wild grapes in riparian habitats in California. This provides an excellent opportunity to study the life history traits of parasitoids originating from contrasting habitats. Previous work demonstrated higher initial eggloads for parasitoids from vineyards (approximately 25 eggs) compared to their congeners from riparian habitats (fewer than 20 eggs) (Segoli & Rosenheim 2013). This is consistent with theory, as leafhoppers are more abundant and may reach very high densities in agricultural vineyards. In this study we extended this work to compare parasitoid longevity among these different habitats. Based on theory, we predicted higher longevity for parasitoids from riparian habitats (where hosts are scarce) compared to those from vineyards (where hosts are abundant). Longevity was quantified either with or without feeding the parasitoids with a sugar source (honey). Sugar supplementation was previously shown to extend parasitoid lifespan from less than a day to few days (Segoli & Rosenheim 2013). We predicted that differences in longevity would be more pronounced under starvation conditions, where the parasitoid needs to rely on teneral reserves (Jervis *et al.* 2008), than when provided with honey.

MATERIALS AND METHODS

Study species

Anagrus spp. parasitoid wasps are among the most important natural enemies of *Erythroneura* and *Erasmoneura* spp. leafhoppers in California (Doutt & Nakata 1973; Daane & Costello 2000; Bentley 2009). They complete their entire development (egg to adult) inside the leafhopper egg, consuming the egg as they develop. These parasitoids 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 *et al.* 2007). *Anagrus* are short lived, even under the most benign laboratory conditions (English-Loeb *et al.* 2003).

Erythroneura and *Erasmoneura* spp. leafhoppers deposit eggs singly or in clusters under the epidermal tissue or along the veins of *Vitis* spp. leaves. Each egg is approximately 0.8 mm long. The freshly deposited egg is colorless and transparent. When eggs are parasitized, they become brown or red. The leafhoppers complete approximately 3 generations per growing season (June to September) and may reach very high densities in vineyards towards the end of the season (Daane & Costello 2000).

Collection of parasitoids

Grapevine leaves with apparent leafhopper damage were collected from 3 riparian habitats and 3 vineyards located in Yolo, Solano and Sacramento counties in California, during August 2016. Some of the leaves were put immediately in emergence cages (approximately 10 cages per agricultural site and 20 per natural site; approximately 40 leaves per cage) and kept at room temperature for one week. The cages were empty paper carton containers with a transparent funnel and a vial on top. Parasitoids emerging from leafhopper eggs on the leaves were attracted to the light and collected from the vials. The remaining leaves were kept in the refrigerator (4 °C) and were used to replenish the emergence cages throughout the week. Emergence cages were monitored hourly between 07:00 and 20:00 hours.

Longevity without feeding

Newly emerged parasitoids were put in individual glass vials, kept in an incubator (29 °C, 12:12 h light : dark cycle) and checked hourly during 12 h. Experimental temperature reflected temperatures in the field during this season. Following death, parasitoid sex was determined and females were used for egg load and body size estimates (see below). Longevity was calculated as the number of hours that passed from parasitoid emergence until its death. Only parasitoids that emerged between 0700 and 1000 hours were used for this estimate. This is because it was impossible to determine the timing of emergence for parasitoids that were already emerged at 0700 hours, and it was sometimes impossible to record the time of death for parasitoids emerging after 1000 hours (they sometimes survived beyond the observation period).

Longevity with sugar feeding

Newly emerged parasitoids were put into individual vials with a small piece of filter paper soaked with honey solution. Parasitoids were kept in an incubator (29

°C, 12:12 h light : dark cycle) and checked daily until all died. Longevity was calculated as the number of days from parasitoid emergence until its death. Parasitoids that were found stuck in honey were excluded from the sample as this might have expedited their death. Following death, each parasitoid was sexed, females were identified to species (Triapitsyn *et al.* 2010), and the length of a hind tibia was measured.

Eggload estimates

Females were then dissected to determine their eggloads. Dissection was done under a dissecting microscope using Minuten insect pins (Fine Science Tools, USA, Inc.). The number of eggs upon death was assumed to represent the number of eggs upon emergence. This is because these parasitoids do not resorb eggs, did not have oviposition opportunities in the vials and were never observed to lay eggs outside a host. Males were not used in this study.

Sample sizes

Sample sizes (Table 1) were highly unequal across sites because of strong inter-site variation in leafhopper and parasitoid abundance, and despite the higher intensity of sampling (larger number of emergence cages) in low-density sites.
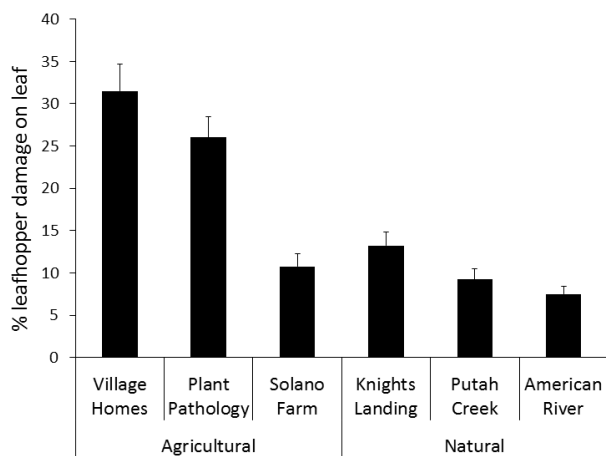
Host density estimates

To test the assumption of higher host density in agricultural fields we examined 20 of the leaves collected from each site. The percentage of leaf area that was damaged by leafhopper feeding (visible as white stipling on the leaves) was estimated. Host density estimates differed significantly among field sites and were higher in agricultural sites (Fig. 1, GLM, habitat type $F_{1,119} = 64.91$, $P < 0.001$; field site $F_{4,119} = 16.34$, $P < 0.001$), although based on the Tukey post-hoc test, one of the agricultural sites (Solano Farm) did not differ significantly from the natural sites.

Statistical analysis

Host density and parasitoid body size were compared using general linear models with habitat type (agricultural vs. natural), field site (nested within habitat type) and parasitoid species (only for body size) as independent factors. Eggloads were compared using general linear models with habitat type, field site (nested within habitat type), feeding treatment (feeding vs. no feeding), parasitoid species and tibia length as independent factors. Because longevity with or without feeding was es-

Table 1 Sample sizes of females of the different field sites

Habitat type	Field site	Eggloads *Anagrus daanei* *Anagrus erythroneurae*	Longevity (hr) without feeding *Anagrus daanei* *Anagrus erythroneurae*	Longevity (d) with feeding *Anagrus daanei* *Anagrus erythroneurae*
Agricultural	Village Homes	4 29	4 21	0 8
	Davis Campus	4 43	4 28	0 15
	Solano Farm	24 2	12 1	12 1
Natural	Knights Landing	11 3	5 0	6 3
	Putah Creek	21 3	9 2	12 1
	American River	37 7	27 2	9 5

Figure 1 Means ± SE leafhopper density estimated as % leafhopper damage on the leaf at the different field sites (*n* = 20 leaves per site).

timated using different units (hour *vs* days), it was analyzed separately using the same model as for eggload (excluding the feeding-treatment factor). To test the relationship between longevity and eggloads at the individual level, we regressed longevity (with or without feeding) against the residuals of eggloads, based on the model above. Data that were not distributed normally were log or square root transformed to meet model assumptions. Means are reported ± SE throughout.

RESULTS

Body size

Hind tibia length of female parasitoids did not differ among habitat types, field sites or parasitoid species (GLM, habitat type $F_{1,187} = 0.02$, $P = 0.88$; field site $F_{4,187} = 0.88$, $P = 0.47$; Species $F_{1,187} = 0.34$, $P = 0.56$, $N = 188$ females).

Eggloads

Mean eggloads of females varied among sites and were higher in agricultural vineyards (Fig. 2, GLM, field site $F_{4,187} = 2.39$, $P = 0.05$; habitat type $F_{1,187} = 20.46$, $P < 0.001$). In addition, eggload variation among females was positively correlated with tibia length ($F_{1,187} = 41.36$, $P < 0.001$), although it explained a small portion of the variation ($R^2 = 0.29$ for *A. erythroneurae* and $R^2 = 0.21$ for *A. daanei*). Eggloads were not affected by either the parasitoid species ($F_{1,187} = 0.20$, $P = 0.66$) or by the feeding treatment ($F_{1,187} = 3.28$, $P = 0.07$, $N = 188$). Residual eggloads based on this model were used for the regression between longevity and eggload (see below).

Effect of feeding

As expected, feeding increased female lifespan from less than a day (mean = 5.44 ± 2.36 hours, *n* = 115) to several days (mean = 4.08 ± 0.33 days, *n* = 72).

Longevity without feeding

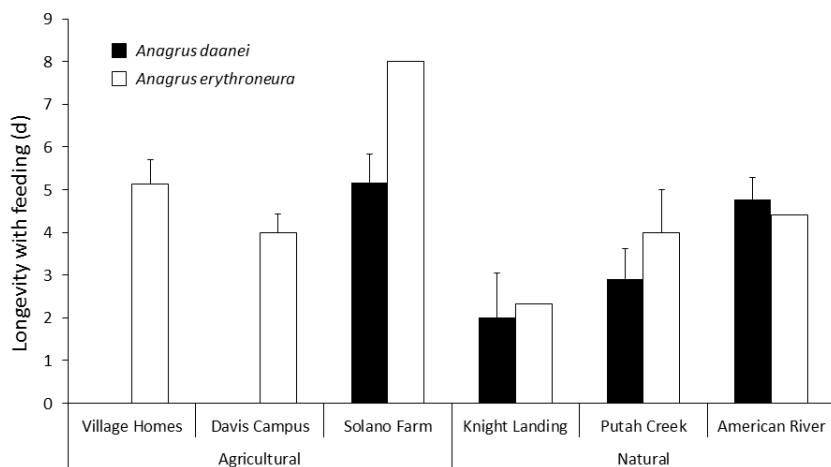Longevity without feeding differed significantly among field sites but was not affected by habitat type, by tibia length or by parasitoid species (Fig. 3, GLM, habitat type $F_{1,114} = 1.07$, $P = 0.30$; Field site- $F_{4,114} = 3.41$, $P = 0.01$; tibia length- $F_{1,114} = 0.01$, $P = 0.93$; Species- $F_{1,114} = 0.44$, $P = 0.51$). The main variation was
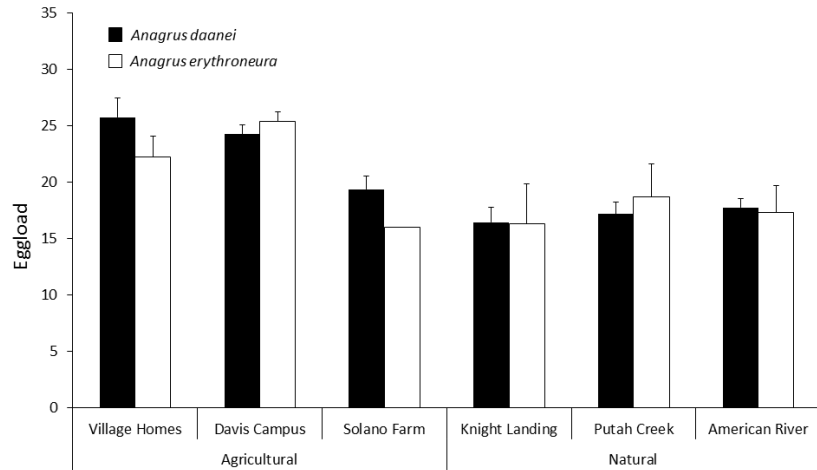
Figure 2 Means ± SE eggloads of female parasitoids of the different field sites.
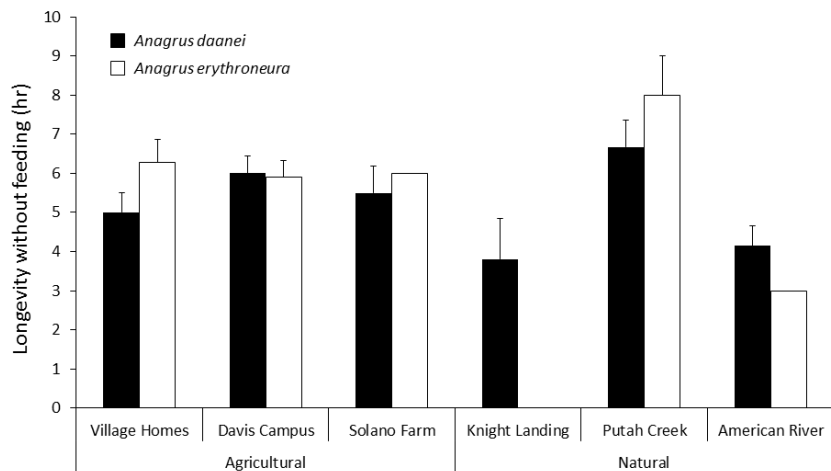
Figure 3 Means ± SE longevity (h) of unfed female parasitoids of the different field sites.

Figure 4 Means ± SE longevity (days) of fed female parasitoids of the different field sites.

among the different natural sites, while the agricultural sites had similar values.

Longevity with feeding

Longevity with feeding was not significantly affected by any of the independent factors (Fig. 4, GLM, habitat type $F_{1,71} = 2.15$, $P = 0.09$; field site $F_{4,71} = 2.75$, $P = 0.10$; tibia length $F_{1,71} = 0.75$, $P = 0.39$; species $F_{1,71} = 0.27$, $P = 0.6$). This may partly be due to the small sample size for some of the species/site combinations.

Relationship between eggload and longevity

We found a weak positive, rather than a negative, relationship between longevity without feeding and residual eggload (controlling for tibia length, habitat type, field site and species [see above]; linear regression, $P = 0.01$, $R^2 = 0.06$; Fig. 5). Longevity with feeding was not related to residual eggload (linear regression, $P = 0.37$, $R^2 = 0.01$).

DISCUSSION

Variation in eggloads

We studied life history traits of 2 species of proovigenic parasitoid wasps originating from either natural riparian habitats or agricultural vineyards. Consistent with our predictions, parasitoids from agricultural habitats emerged with more eggs, and, hence, were prepared for the plentiful oviposition opportunities in their environment. This is consistent with previous results (Segoli & Rosenheim 2013), further confirming the robustness of this observation. To our knowledge, this is the only example of inter-population variation in initial eggloads in a strictly proovigenic parasitoid. Given that eggloads are determined prior to parasitoid emergence, variation in eggloads cannot be explained as an immediate plastic response to host availability experienced by adult females in the environment. Alternative explanations include variability in host quality among the different habitats, transgenerational phenotypic plasticity (maternal effects) or genetic differences among parasitoids of the different populations. We will next discuss these possibilities.

Host size is one of the most basic aspects of host quality and in other host-parasitoid systems has often been shown to affect both the number and quality of emerging parasitoids (Godfray 1994). For example, in the parasitoid *Uscana lariophaga*, which parasitizes eggs of bruchid beetles, females reared in small host eggs developed slower, were smaller and produced fewer eggs compared to those reared in large host eggs (Spitzen & van Huis 2005). Previous work in the *Anagrus*-leafhopper-grapes system found no consistent differences in leafhopper egg size on leaves collected from vineyards or from wild grapes, suggesting the lack of differential host quality between these habitats (Segoli & Rosenheim 2013). This conclusion is strengthened by the lack of difference in mean parasitoid body size between these habitats, as demonstrated in the current
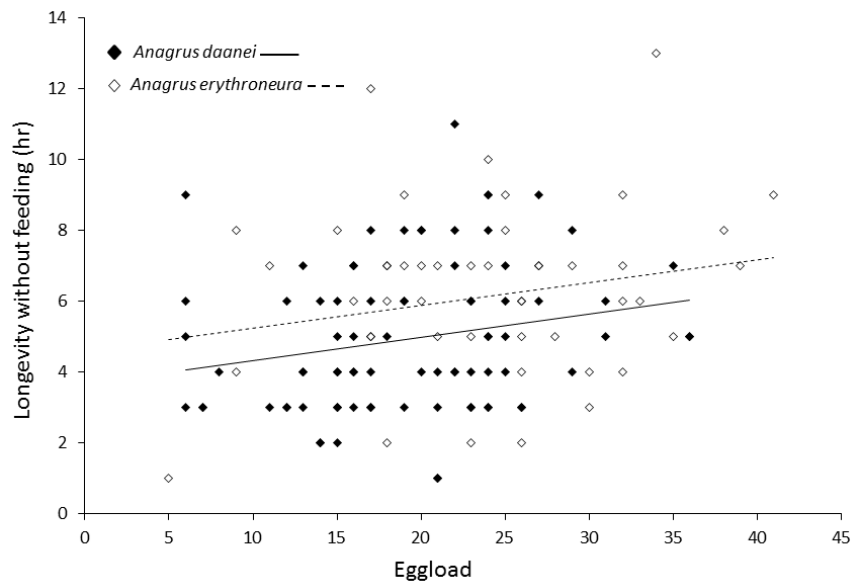
Figure 5 Relationship between longevity of unfed female parasitoids and their eggload.

study. Nevertheless, other aspects of host quality may also be of importance. For example, fertilization and irrigation in vineyards may affect the nutritional composition of leafhopper eggs, independent of their size, subsequently affecting parasitoid traits. This hypothesis is yet to be examined.

Transgenerational plasticity of reproductive traits in relation to environmental conditions experienced by ovipositing females has been demonstrated in many insects (Mousseau & Dingle 1991; Mousseau & Fox 1998), including parasitoids (Morag *et al.* 2011). The possibility of transgenerational response to host availability in *Anagrus* parasitoids was previously tested by exposing *A. erythroneurae* females to either high or low host densities and examining the eggloads of their daughters (Andreazza & Rosenheim 2015). However, no differences across host density treatments were found, arguing against the operation of transgenerational phenotypic plasticity.

Initial fecundity has been found to be heritable in many insects, including *Anagrus* parasitoids (Cronin & Strong 1996; Andreazza & Rosenheim 2015). Although the observed inter-population variation in *Anagrus* is likely to be at least partially genetic, the relative contribution of genetic variation is currently unknown. Future work will aim to conduct common garden experiments (in which parasitoids of different origins are reared on the same host cohort), transplant experiments (in which parasitoids originating of one habitat are reared on hosts of another habitat and vice versa) and evolutionary experiments (in which parasitoids are reared at high or low host densities over multiple generations) to address this question.

Tradeoff between eggload and longevity

Higher investment in egg production is likely to come at the expense of other functions. Indeed, studies have demonstrated both phenotypic and genetic tradeoffs between reproduction and longevity in many insects (Miyatake 1997; Tatar 2001; Roff 2002; Edward & Chapman 2011). In parasitoids, such tradeoffs were demonstrated at the species level (i.e. long-lived species emerge with relatively fewer eggs; Jervis *et al.* 2001, 2003) and the individual level (i.e. individuals investing more in egg production die sooner; Ellers *et al.* 2000; Zhang *et al.* 2011; Segoli & Rosenheim 2013). Tradeoffs at the population level were also suggested, but these were either confounded with parasitoid reproductive mode (sexual *vs* asexual; Pelosse *et al.* 2007; Ameri *et al.* 2015), or were more likely to represent dif-

ferences in the timing of allocation than in total investment (Ellers & van Alphen 1997).

Here we examined the potential tradeoff between eggload and longevity for proovigenic species, at both the population and individual level. Because longevity of parasitoids that do not feed is dependent exclusively on their teneral reserves (Jervis *et al.* 2008), we expected that variation in longevity will be more pronounced in food deprived females. Indeed, the longevity of females fed with honey was substantially greater (up to 10-fold) and was not dependent on the specific site or habitat of origin. The longevity of starved females, however, differed significantly among field sites, suggesting inter-population variation in parasitoid energy reserves. Nevertheless, in contrast to our predictions, longevity was not consistently higher for parasitoids originating from natural habitats. Moreover, longevity was positively, rather than negatively, correlated with eggload at the individual level, even after correcting for parasitoid body size and site of origin. This contradicted previous results that instead suggested a negative relationship between female eggload and longevity at the individual level (Segoli & Rosenheim 2013).

There are several general explanations for the absence of an expected tradeoff in life history traits (Stearns 1992; Agrawal *et al.* 2010). One possible explanation is that a tradeoff may not be expressed under certain environmental conditions. For example, parasitoids from natural habitats could perhaps have the ability to survive longer in the field, but this ability might not be expressed under the artificial conditions experienced in the lab. In particular, confining parasitoids in a vial could substantially alter their movement behavior (van den Assem 1996), thereby affecting their energy expenditure. However, documenting the realized longevity of such small insects in the field, or quantifying their energy reserves at emergence (Ellers 1996), may be extremely challenging.

Another potential reason is that allocation patterns and selection pressures may be more complex or simply different than initially assumed. For example, higher investment in egg production could come at the expense of energy reserves, but could also potentially trade off with egg quality, female mobility, immune function or stress tolerance. Hence, certain functions may not always directly compete for resources (Agrawal *et al.* 2010). In particular, the tradeoff between egg number and size was suggested to be of high importance (Berrigan 1991; Rosenheim 1996). Indeed, previous results suggest that *Anagrus* eggs in agricultural sites in Cali-

fornia are smaller (Segoli & Rosenheim 2013). Hence, the tradeoff between egg number and size may be more pronounced than that of eggload and longevity in this system. Moreover, additional environmental factors, such as food availability, habitat complexity, predation and competition, may impose stronger or even opposing selection on longevity, leading to inter-site variation that is independent of host density. For example, higher competition among females at higher densities may compromise their oviposition rates, as was shown for another *Anagrus* species (Cronin & Strong 1993).

Finally, the expectation for a tradeoff is based on the assumption of a resource pool whose size is constant across individuals. If instead there is individual variation in total resource availability, individuals with larger total resource pools may have both greater fecundity and longevity, thus masking the occurrence of a tradeoff. This does not mean that these functions do not trade off; rather, that in order to detect the tradeoff there is a need to control for individual quality, either statistically or experimentally (Stearns 1992). Although we statistically controlled for female body size, as mentioned above, this may not be a reliable measure of the quality of resource available for parasitoid development. In particular in egg parasitoids, body size may be constrained by the size of the host egg, which could be relatively constant. Hence, parasitoid traits may be dependent on the composition of nutrients inside the host, which, in turn, may depend on the nutritional value of the plant (Turlings & Benrey 1998; Sarfraz *et al.* 2009). Such effects may lead to positive correlations between different life history components as observed in this study. This may also explain the previously documented tradeoff (Segoli & Rosenheim 2013) that was observed in a small sample of parasitoids of a uniform origin (parasitoids of the same site, emerging on the same day).

In conclusion, parasitoid life history traits varied among field sites, and although we confirmed the greater fecundity of parasitoids originating in agricultural sites, we found no evidence of a tradeoff with parasitoid longevity at either the population or individual level. The lack of apparent tradeoff between eggload and longevity may be due to inappropriate experimental conditions, complex allocation patterns or variation in host quality that is independent of host size.

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