

Francisco García-González · Montserrat Gomendio

Oviposition site selection and oviposition stimulation by conspecifics in the golden egg bug (*Phyllomorpha laciniata*): implications for female fitness

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Abstract *Phyllomorpha laciniata* Vill. (Heteroptera, Coreidae) females lay eggs on the host plant and on the backs of conspecifics. Since egg survival is greater when eggs develop on the backs of conspecifics than when laid on plants, we predict that females should prefer to lay eggs on conspecifics. In addition, because conspecifics are a high-quality site that represents a limiting resource, females should experience oviposition stimulation upon an encounter with a conspecific. Our results reveal that, when both the host plant and conspecifics are available simultaneously, females lay eggs preferentially on conspecifics. The results also support the second prediction, since females housed with conspecifics lay more than twice the number of eggs than isolated females. Isolated females do not seem to retain eggs, suggesting that oviposition stimulation is the result of an acceleration of egg-maturation rates. Other studies have found oviposition stimulation by mating and have suggested that it is the result of male strategies to increase short-term male reproductive success at some cost to females. The evolutionary scenario of our model organism seems to be quite different since females benefit greatly from increasing egg laying when there are conspecifics, because the advantages in terms of offspring survival are likely to translate into substantial increases in female reproductive success.

Keywords Oviposition · Site selection · Ovarian dynamics · Female reproductive success · *Phyllomorpha laciniata*

Introduction

Evolutionary theory predicts that selection favours the expression of traits that maximize individual fitness (Clutton-Brock 1988; Parker and Maynard Smith 1990; Rose and Lauder 1996). Among females, offspring survival is one of the most important components of lifetime reproductive success, given the large differences in offspring survival rates between females (Clutton-Brock 1988). In organisms with rudimentary forms of parental care or with no parental care, oviposition site selection should have a considerable impact on female fitness since it often determines to a great extent the chances of survival for offspring. In these species, oviposition site preferences should evolve in order to maximize offspring survival. Available evidence shows that females of phytophagous insects and parasitoids place their eggs in sites where their offspring will find enough food resources, high-quality food resources or enemy-free spaces (Jaenike 1978, 1990; Mangel 1989; Thompson and Pellmyr 1991; Godfray 1994; Papaj and Messing 1996; Papaj 2000).

In those cases in which preferred oviposition sites are rare or difficult to find, it would be in the females' interest to adjust reproductive cycles so that oviposition is stimulated upon an encounter with a preferred site. Strong evidence suggests that ovarian dynamics in insects respond to variability in host quality and availability in adaptive ways (Papaj 2000). It is well known that female reproductive cycles are influenced by a number of environmental and social factors (Engelman 1970; Wallen and Schneider 2000). Among the latter, the presence of conspecifics and mating are known to have strong effects. The presence of conspecifics may influence the timing of reproductive events in mammals (Bronson and Maruniak 1975; Signoret 1980; Bronson 1989; Maina and Katz 1999; Schiml et al. 2000). On the one hand, inhibition of reproduction by conspecific presence is usually related to dominance relationships in group-living mammals such as primates and carnivores (Bronson 1989) whereas, on the other hand, ovarian-cycle stimulation by the presence of

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F. García-González · M. Gomendio (✉)
Departamento de Ecología Evolutiva,
Museo Nacional de Ciencias Naturales (C.S.I.C.),
José Gutiérrez Abascal 2, 28006 Madrid, Spain
e-mail: montseg@mncn.csic.es
Tel.: +34-91-4111328
Fax: +34-91-5645078

males seems widespread (Lindsay et al. 1975; Signoret 1980; Chemineau 1983; Martin et al. 1986; McComb 1987; Bronson 1989; Wallen and Schneider 2000). Among insects, the effects of mating on the stimulation of egg production and oviposition are well known (Wigglesworth 1965; Engelman 1970; Leopold 1976; Thornhill and Alcock 1983; Choe and Crespi 1997). In some insects, gonadotropic substances transferred by the male during copulation enhance egg maturation or egg laying (Leopold 1976; Loher et al. 1981; Chen et al. 1988; Kubli 1992; Chapman et al. 1993, 1998). The presence of conspecific females or conspecific eggs also stimulates oviposition in some species, mainly because females (and their eggs) obtain benefits derived from grouping eggs (Prokopy and Roitberg 2001). However, oviposition stimulation by male presence has only been reported, to our knowledge, in *Drosophila melanogaster* (Hoffmann and Harshman 1985), where it has been suggested that a “male factor” affects female fecundity in the absence of contact between the sexes, although the mechanisms involved are still unclear.

Benefits resulting from the stimulation of female reproductive cycles by conspecific males have been generally examined from a male perspective. In *D. melanogaster* and other dipteran species, the effects of mating upon female reproductive performance seem to enhance male reproductive output, while imposing a reproductive cost on females (Partridge et al. 1987; Chapman et al. 1995, 1998; Rice 1996; Holland and Rice 1999; Wolfner 2002). Thus, stimulation of female reproduction by males has usually been interpreted as benefiting almost exclusively males, who manipulate females so as to increase their own reproductive success. Such conflicts of interest between the two sexes have been regarded as being widespread (Rice and Holland 1997; Johnstone and Keller 2000). It is unclear, however, why female physiology should be influenced by males, if females derive no benefits from such manipulation. One of the few studies to investigate potential benefits to females has suggested that fallow-deer females adjust the timing of oestrus to the availability of preferred males, and delay ovulation when only undesired males are available (Komers et al. 1999); however, further evidence is needed to test this hypothesis.

The golden egg bug (*Phyllomorpha laciniata* Vill.) provides a unique opportunity to study the evolutionary implications of different oviposition strategies since females may choose among three alternatives: females can lay their eggs on host plants (*Paronychia argentea*) where they develop unattended, or on the body of conspecific males and females where they are carried until hatching (Bolivar 1894; Kaitala 1996; Reguera 1999; Gomendio and Reguera 2001). This species, together with the giant waterbugs, are the only insects in which females glue eggs on the backs of conspecifics (Ridley 1978; Zeh and Smith 1985; Clutton-Brock 1991; Smith 1997). While giant waterbugs only lay eggs on males, female golden egg bugs may lay eggs both on males and on other females. This species is an excellent

model organism because it is possible to study oviposition choice at intra-specific and intra-individual levels since all females have the option to adopt three laying strategies (eggs on plant, on males and on females) during their reproductive lives.

Eggs of *Phyllomorpha laciniata* carried by an adult have a greater probability of survival than those laid on plants (Kaitala 1996; Gomendio and Reguera 2001; Reguera and Gomendio 2002), and thus females should oviposit preferentially on conspecifics in order to maximize offspring survival rates. In addition, we predict that females should undergo oviposition stimulation in the presence of conspecific individuals so as to maximize the number of eggs laid on conspecifics. We have explored in the golden egg bug both the existence of oviposition choice and conspecific non-mating oviposition stimulation. Because we were interested in finding out the responses and preferences shown by laying females, and not the willingness of conspecifics to accept or reject the laying attempts, experiments were designed in such a way that recipients did not have the opportunity to reject egg-laying attempts because they could not move far away from the laying females as they often do in the field.

Methods

We collected 128 individuals of *Phyllomorpha laciniata* on a specific date in 2 localities in central Spain: Robledo de Chavela (4 June 1999; 39 males and 34 females collected) and El Espinar (15 June 1999; 33 males and 22 females collected) because at that time both populations were at the peak of their reproductive activity. Monitoring of both populations from the beginning of their reproductive cycles allowed us to determine this particular stage. Individuals were placed in small petri containers (5.5 cm diameter) and kept in constant conditions from then until the end of the experiment (25°C, light from 0800 hours to 2100 hours). Prior to the experiment, eggs were removed from carrying males as well as from carrying females. Throughout the experimental period, individuals were provided daily with fresh branches of the host plant, *Paronychia argentea*.

Females can exhibit different oviposition rates, i. e. number of eggs laid during a given period of time, depending on the time since their last copulation (García-González 2002, and this study). Thus, to minimize variation in female oviposition rates, we forced all the females included in the sample into a similar physiological state by placing each female with a male and allowing her to mate once in the laboratory (from now on “pre-experimental copulation”). After the pre-experimental copulation, each female was randomly assigned to four treatments: female with the male she previously copulated with (group B, $n=7$), female with a male other than the one she had copulated with (C, $n=7$), female with another female (D, $n=6$), and female with the male she had copulated with and with another male (E, $n=4$), and over 5 days we monitored the oviposition rate, as well as oviposition-site selection (plant vs conspecific) of each female. Controls consisted of a female maintained under identical conditions but with no other individuals being present at any time (group A, $n=11$). Some individuals died during the experiment, and thus the final number of replicates of each experimental group was lower (see Results).

Fecundity may depend on other factors, such as female size, female body condition and the existence of previous egg batches. In order to control for these variables, we monitored the oviposition rate of each female prior to the beginning of the experiment (number of eggs laid/number of days between their capture and the pre-experimental copulation), and measured female body size and

female body condition. Body size was estimated from three length measurements of the right hind tibia using NIH Image 1.60 software (National Institutes of Health, U.S.A.). Repeatability of these three lengths is 0.99 ($P < 0.001$) (Falconer and Mackay 1996). Females were weighed to the nearest 10^{-4} g on a Sartorius BP 110 S balance (Sartorius, Goettingen, Germany), and body condition was inferred as the residuals of body weight regressed on body size. There were no differences among treatments in female oviposition rate prior to the establishment of the experiment (ANOVA: $F_{4,20}=0.7$, $P=0.61$; mean number of eggs=1.05, SE=0.24, $n=25$), and there were no differences in female weight (ANOVA: $F_{4,23}=0.53$, $P=0.72$) or female body condition (ANOVA: $F_{4,21}=1.1$, $P=0.4$) between the experimental groups.

We also considered the possibility that differences in the number of eggs laid by females could be influenced by the occurrence or lack of copulations in the different experimental groups. To control for this variable in the analyses, we checked for copulations three times per day between 0900 hours and 2100 hours with maximum intervals of 6 h. Copulation in this insect lasts, on average, for more than 20 h (Kaitala 1998; Reguera 1999), so it is unlikely that copulations went unnoticed.

Groups were provided with a surface area of the host plant (*Paronychia argentea*) at least 20 times greater than that represented by conspecific individuals to make sure that plant availability was not a limiting factor.

In group D (female with other female), it was not possible to distinguish the eggs laid by each female. For this particular group, we have used two approaches to estimate oviposition on plants by subject females: (1) estimating number of eggs that the subject female laid on plant (P_1) according to the proportion of eggs that this same female laid on the recipient female (C_1) out of the total number of laid eggs on conspecific backs, i.e. correcting by fecundity of each female measured as eggs deposited over conspecific: $P_1 = (C_1 / [C_1 + C_2]) P_{1+2}$, where C_2 is the number of eggs deposited by the recipient female on the subject female and P_{1+2} is the total number of eggs laid on plants by both females, and (2) estimating P_1 as 1/2 of the total egg number deposited on plants by the two females. There were no differences in the use of approach (1) or (2) in the analyses, but we think that the first approach is more realistic and, thus, it has been used in all analyses.

We checked for possible "egg-retention" in the female reproductive tract by dissecting the females at the end of the experiment. We counted full-size developed eggs, as well as those that had developed to at least half the size of a full-grown egg.

We checked that all eggs on plants were firmly glued to the branches or flowers to ensure that they were willingly deposited there and not lost by egg-carrying bugs.

Dependent variables were transformed when using parametric statistics using logarithmic or Box-Cox transformations. Homocedasticity was confirmed by using Levene's test (Statsoft 1996). When parametric assumptions were not fulfilled, we used non-parametric statistics (Sokal and Rohlf 1981). All tests were two-tailed.

Results

Oviposition site selection

Females housed with conspecifics laid more eggs on adult bugs (66.6%) than on plants (33.3%) (t -test for dependent samples: $t_{19} = -2.87$, $P = 0.01$). Fig. 1a shows that the preference to oviposit on conspecifics emerges in all groups. No differences in the percentage of eggs laid on plants versus conspecifics were found between the experimental groups in which females were housed with different types of conspecifics (i.e. B, C, D and E) (chi-square test: $\chi^2 = 4.92$, $df = 3$, $P = 0.18$).

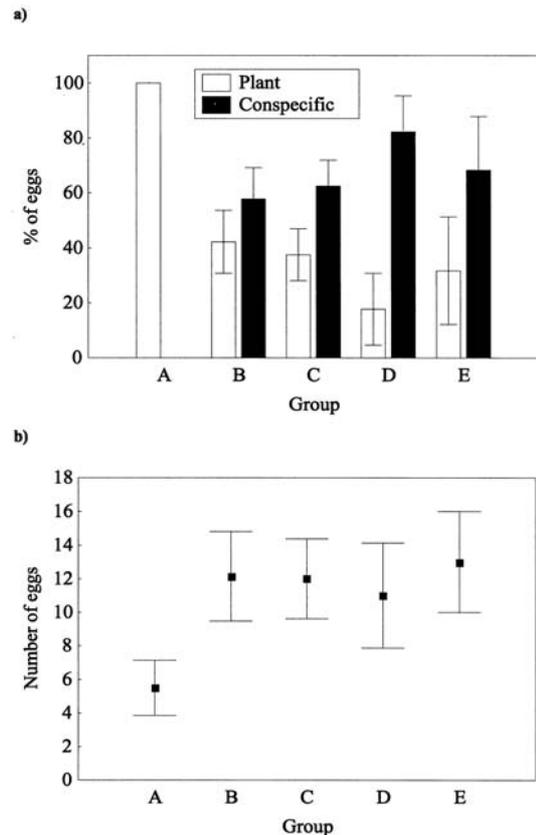


Fig. 1 a Egg allocation of females in the different treatments. A isolated females; B females with the male they copulated with; C females with a male other than the one they copulated with; D females with another female; E females with the male they copulated with and with another male. The mean values and standard errors of individual percentages are shown. b Mean number of eggs (and standard errors) laid by females in the experimental treatments

Oviposition stimulation

The total number of eggs laid in the experimental period differs depending on whether females were isolated or housed with conspecifics. Isolated females laid on average 5.5 eggs (SE=1.6, $n=8$) during the experimental period, obviously all on plants, whereas non-isolated females laid on average 12 eggs (SE=1.3, $n=20$) (ANOVA: $F_{1,26}=10.20$, $P=0.004$) (test 1). The mean number of eggs (\pm standard errors) laid by females in the groups established can be seen in Fig. 1b.

There were significant differences in daily oviposition rates between females in conspecific presence and isolated females when oviposition rate throughout the 5 days is considered for each female (repeated measures ANOVA: $F_{1,26}=6.75$, $P=0.015$) (test 2) (Fig. 2). Oviposition rate decreased with time in both groups ($F_{4,104}=4.53$, $P < 0.002$). As can be seen in Fig. 2, differences lie mainly in the number of eggs laid the first day ($F_{1,26}=12.5$, $P < 0.002$).

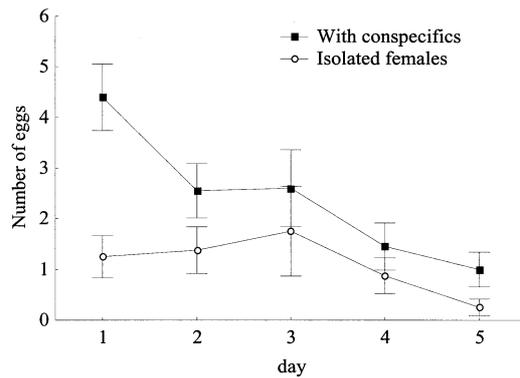


Fig. 2 Daily oviposition rates (mean and standard error) of isolated females and females with conspecifics during the experimental period

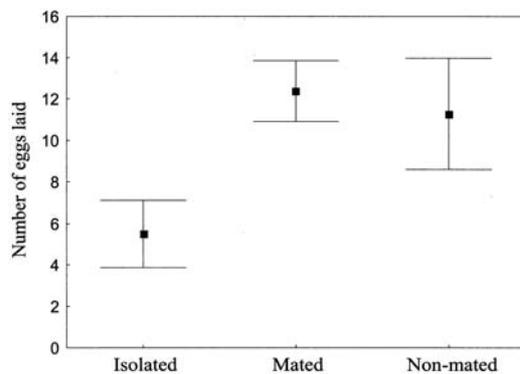


Fig. 3 Mean number of eggs (and standard errors) of isolated females ($n=8$) and females grouped according to whether they copulated (*Mated*, $n=13$) or not (*Non-mated*, $n=7$) during the experiment

Since there is no evidence suggesting that females are “worse” egg-carriers than males (in terms of survival of offspring), we can predict that oviposition stimulation in this species should occur in the presence of both males and females. To test this hypothesis, we carried out a planned comparison ANOVA (Statsoft 1996), in which we used a coefficient of -4 for the group of isolated females and coefficient $+1$ for the other groups. In doing this, we predicted no differences in the output for groups B, C, D and E, and significant differences between these groups and group A. We detected differences between females in conspecific presence (groups B, C, D and E) and isolated females (group A) (planned comparison ANOVA: $F_{1,23}=9.11$, $P<0.001$) (test 3), and no differences between groups in which females were housed with conspecifics irrespective of whether they were male or female (Fig. 1b).

If oviposition stimulation by conspecific presence is a female strategy aimed at increasing egg survival, there should be no need for mating to take place, at least not in freshly mated females. To test this prediction, we grouped females housed with conspecifics according to whether they had copulated or not (i.e. females housed with

females were grouped with females housed with males who had not copulated and this group was labelled “non-mated females”). We found significant differences among isolated females, females housed with males who had copulated and “non-mated females” (ANOVA: $F_{2,25}=5.18$, $P=0.013$) (test 4) (Fig. 3). Significant differences in the number of eggs laid during the experimental period were found between isolated females and “non-mated females” who were housed with conspecifics (Student-Newman-Keuls test, $P=0.027$). This result shows that oviposition stimulation is taking place in the absence of mating. No differences were found between females in the presence of conspecifics according to whether they had copulated or not (Student-Newman-Keuls test, $P=0.54$). Tests 1–4 retain statistical significance after sequential Bonferroni correction (Rice 1989).

Egg retention

There were no significant differences among treatments in the number of fully developed or developing eggs inside the female reproductive tract (Kruskal-Wallis ANOVA by ranks: $H=2.23$, $df=4$, $n=25$, $P=0.7$). The mean number of mature oocytes (\pm SE) were as follows: group A, 4.29 ± 1.6 ; group B, 2.14 ± 0.6 ; group C, 4.0 ± 1.3 ; group D, 3.0 ± 1.2 ; group E, 2.0 ± 1.5 . In addition, there were no significant differences between females that mated again during the experimental period and females that did not mate after the pre-experimental copulation (Mann-Whitney U -test: $U=69.5$, $P=0.64$; mating females: mean= 3.59 ± 0.9 , $n=12$; non-mating females: mean= 2.26 ± 0.7 , $n=13$).

Discussion

The results of this study show that female *Phyllomorpha laciniata* have a strong preference to oviposit on conspecifics. This preference has important consequences for female reproductive success because eggs carried by conspecifics have higher survival rates than eggs laid on plants. Because eggs are equally likely to survive on males and females, laying females do not show a preference towards males. Thus, the higher proportion of eggs carried by males in natural populations are probably the consequence of a greater willingness of males to accept eggs. Finally, *Phyllomorpha laciniata* females lay one egg at a time in sequence over several months, and because encounter rates with conspecifics are infrequent in natural populations, females enhance egg production when a conspecific is available in order to maximize the number of eggs laid on adults.

Phyllomorpha laciniata is an ideal model organism to study the evolutionary consequences of oviposition-site selection because it shows a unique pattern: females can choose between two radically different oviposition sites, the host plant or conspecifics' backs. The host plant represents an unlimited substratum of “low quality”, since eggs suffer high mortality rates, whereas conspecifics

represent a rare “high-quality” alternative, i.e. eggs enjoy higher survival rates (Reguera and Gomendio 2002). From the point of view of a laying golden egg bug female, oviposition on the back of other individuals has important benefits since eggs carried by conspecifics are less vulnerable to egg predation (mainly by ants) and to a scelionid parasitoid (Kaitala 1996; Reguera 1999; Reguera and Gomendio 2002). Thus, it is in the females’ interest to lay eggs on conspecifics since this will enhance female reproductive success. The importance of oviposition choice has been established for many species of insects and other animals (Resetarits and Wilbur 1989; Thompson and Pellmyr 1991; Godfray 1994; Resetarits 1996), but in these cases the choice is restricted to the quality of specific hosts or oviposition sites and females do not have the opportunity to choose a conspecific as a laying site.

The reason why females also lay eggs on plants, despite the low survival rates, is partly related to the likelihood of encountering a conspecific, and to its willingness to accept eggs. In natural populations, densities are low, ranging from 0.005 individuals per square meter to a maximum of 0.265 indiv./m² (data gathered from adults found in an area of 400 m² in 44 different days throughout 3 reproductive periods, see García-González 2002), and a willing individual is unlikely to be available every time a female lays an egg. When densities are increased under experimental conditions, females lay a greater proportion of eggs on conspecifics as encounter rates increase (Reguera 1999).

Because female *Phyllomorpha laciniata* lay between 0 and 12 eggs every day during the whole reproductive season (from March until July), in natural populations encounter rates may not occur as often as females have eggs ready to be laid, and several lines of evidence suggest that females may not be able to store eggs for long periods of time. *Phyllomorpha laciniata* is a synovigenic insect (that is, females continue to mature oocytes during the adult stage), with physical limitations to store a large egg load (eggs are large in relation to abdomen size, see below). This could force females to oviposit on plants when recipient individuals are difficult to locate or when conspecifics are reluctant to accept eggs. A similar situation takes place in the giant water bug *Abedus herberti*, where female egg production continues uninterrupted regardless of whether or not the female encounters a receptive male to mate and to receive her eggs (Smith 1979), even though in this species eggs do not hatch unless brooded by males.

In addition, eggs are laid one by one continuously over the whole breeding season, and each egg represents a small proportion of female lifetime reproductive success. Thus, each decision about where to lay an egg must be balanced against the costs of looking for an optimal site (i.e. a willing conspecific) and the consequent decrease in fecundity (Rosenheim 1999; Rosenheim et al. 2000). Given that eggs do have a small probability of surviving on plants, it seems to pay females to lay a proportion of their eggs on plants when conspecifics are not available.

In golden egg bug populations, finding a conspecific on which to oviposit seems to be a limiting factor for female fitness, and thus females would benefit from increasing egg output upon an encounter with a conspecific. Our findings support this prediction since females housed with conspecifics laid, on average, more than twice the number of eggs laid by isolated females. Our results indicate that the first day of exposure to conspecifics has an immediate effect on oviposition output in females. A more delayed response would be ineffective for female fitness, since individuals do not move in a coordinated way and are unlikely to remain in proximity for long periods of time. From a comparative perspective, it is well known that the availability and quality of the host for parasitoids and phytophagous insects often determine the number of eggs laid (Engelman 1970; Papaj and Messing 1996; Papaj 2000; Fournet et al. 2001), and it seems reasonable to predict that oviposition stimulation has evolved when preferred oviposition sites are rare or difficult to encounter.

Stimulation of ovarian dynamics or conspecific stimulation of oviposition by males is widespread, but it is generally the consequence of mating. In mammals, the presence of males or mating may induce ovulation (Bronson and Maruniak 1975; Lindsay et al. 1975; Signoret 1980; Chemineau 1983; Cohen-Tannoudji et al. 1986; Martin et al. 1986; McComb 1987; Bronson 1989; Schiml et al. 2000). In some spontaneous ovulators, the luteal phase (preparation of the uterus for implantation) is induced by mating (Dewsbury 1984; Schiml et al. 2000). In insects such as grasshoppers, cockroaches, crickets, locusts, fruit flies, and many others, one consequence of mating is the stimulation of oviposition (Davey 1967; Engelman 1970; Leopold 1976; Loher et al. 1981; Lange and Loughton 1985; Eberhard 1996). However, non-mating conspecific stimulation is known in very few cases in mammals (Cohen-Tannoudji et al. 1986; McComb 1987). In nonsocial insects, conspecific stimulation in the absence of mating has been rarely reported, except in those cases in which females respond to the presence of conspecifics of the same sex or conspecific eggs because they obtain benefits derived from grouping eggs, including dilution effects, increased thermoregulatory ability or increased ability to overcome host-plant physical or chemical defences (see review by Prokopy and Roitberg 2001; and Srinivasan et al. 1995; Monaco et al. 1998). In social insects, the only documented cases are those in which the presence of cocoons, brood stages, or the worker/brood ratio regulates the queen’s egg laying (Wilson 1971; Gibson and Scott 1990), or in which workers lay more eggs when there are conspecifics present (Salzemann and Plateaux 1988).

Most of the studies that have looked at the benefits of the stimulation of female reproductive cycles by male presence or mating, have adopted the perspective of the male and have concluded that it is a male strategy aimed at maximizing reproductive success, often at some cost to females (Chapman et al. 1995; Rice 1996; Rice and Holland 1997; Holland and Rice 1999; Johnstone and

Keller 2000). The evolutionary scenario of our model organism seems to be quite different since females benefit greatly from increasing egg laying when there are conspecifics on which to lay eggs. Our results show that such stimulation does not require mating.

In addition, we show that oviposition stimulation is not greater when females are in the presence of males than when they are in the presence of females, which fits nicely with field data showing that there are no differences in egg survival depending on whether they are carried by males or females. This is because once the eggs are glued to a conspecific back, there are no differences in the quality of care provided by different individuals, probably because the decrease in predation and parasitic pressure is a consequence of the fact that they are placed on a moving target, and not the consequence of elaborated behaviours to protect the eggs. Thus, females do not discriminate between potential egg carriers because they benefit from laying as many eggs as possible on other individuals irrespective of sex or paternity. However, field data show that most eggs are carried by males (Gomendio and Reguera 2001). The lack of sex-related preferences shown by laying females strongly suggests that the reason why more eggs are carried by males than females in natural populations is more a consequence of the rate of rejection of egg-laying attempts by potential recipients, than a choice made by laying females. So, under natural conditions, males are more likely to accept eggs than females, but such differences are not found when individuals are placed in a very restricted space such as in the experiments presented here, because it is impossible for recipients to reject eggs by just moving away as they do under natural conditions. Thus, our experiments were designed to reveal the choices made by egg-laying females while removing the effects of different rates of rejection of egg-laying attempts on the part of recipients.

The last question that we addressed in this study is whether oviposition stimulation in *Phyllomorpha laciniata* is the result of (1) an increase in ovulation or egg-maturation rate, or (2) an increase in the rate of laying of eggs that are already mature. Such alternatives are possible because, in insects, ovulation and oviposition may not take place simultaneously. Some insect females can store a batch of mature eggs until they discover the most suitable place for the eggs (Engelman 1970; Hoffmann et al. 1990). We dissected females at the end of the experiments and found that isolated females did not retain eggs, suggesting that conspecific presence stimulates egg maturation. It is worth mentioning that we discarded the possibility that differential egg loads of females at the start of the experiment was a confounding factor, because there were no differences among females in body weight or body condition, and it is therefore reasonable to assume that females started the experiment with similar egg loads. These variables explain egg load to a large extent because a female usually contains several eggs in her reproductive tract, and each fully developed egg represents approximately between 2% and 4% of

female body weight. In the experiments, females always had a large surface of plant available as a laying substrate, but only some of them were placed with a conspecific, which represents a high-quality host. Thus, they all had ample opportunities to lay eggs, as demonstrated by the fact that females with no conspecifics continued to lay eggs on plants. Thus, our results are in agreement with the findings by Hopkins and Ekblom (1999), showing that when a high-quality host is available, females increase oviposition rate.

The broad picture emerging from the long-term field data, as well as from the experiments carried out under controlled conditions, is that female golden egg bugs benefit greatly from laying eggs on other individuals. However, a proportion of eggs are laid on plants probably because a willing conspecific is not available every time a female lays an egg, an event that takes place almost continuously over several months. Given the marked differences in survival rates between eggs laid on conspecifics and eggs laid on plants, females increase laying rates immediately as a response to the encounter of a conspecific, irrespective of whether it is a male or a female. This response is likely to increase the chances of laying eggs on conspecifics and thus increase female reproductive success.

From the point of view of the egg recipient, the picture is more complex (see Gomendio and Reguera 2001). Carrying eggs is costly for golden egg bugs because it increases predation rates, either because individuals become easier to detect or because they are less likely to escape (Reguera and Gomendio 1999; Kaitala et al. 2000). Why, then, do individuals accept eggs? In natural populations, a low proportion of females carry eggs, and those that do carry very few eggs. We know that females always carry other females' eggs, so this seems a case of low frequency intraspecific parasitism. Males follow a different trend since all males in natural populations end up carrying eggs, and they carry more eggs than females do. The prevalence of male egg-carrying demands an adaptive explanation, since conspecifics have the choice of accepting or rejecting eggs. The available evidence supports the view that males are more likely to accept eggs to improve the survival of their own offspring. Thus, although males have an intermediate confidence of paternity (F. García-González et al. 2003), they accept eggs because the chances that they will survive on the plant are very low (3%) (Reguera and Gomendio 2002), and they suffer no costs in terms of further matings when they carry eggs.

In summary, females prefer to lay eggs on conspecifics irrespective of sex, because in this way they improve their reproductive success by enhancing offspring survival. Because conspecifics represent a high-quality host that is scarce, oviposition is stimulated by the presence of conspecifics. However, under natural conditions, males are more likely to accept eggs because the proportion of eggs fertilized by them is sufficiently high to ensure that the benefits, in terms of offspring survival, are higher than the costs of carrying eggs.

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