ORIGINAL ARTICLE

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A field test of the intraspecific brood parasitism hypothesis in the golden egg bug (*Phyllomorpha laciniata*)

Abstract In natural populations of golden egg bugs (*Phyllomorpha laciniata*), females lay eggs on plants where they develop unattended, or on conspecifics, where they remain firmly glued until the nymphs hatch and start an independent life. Mortality rates among eggs laid on plants are higher than among eggs carried by adults. Because females cannot lay eggs on themselves, in order to improve offspring survival, they have to lay eggs on other individuals. Two hypotheses have been proposed to explain egg carrying: (1) the mating pair intraspecific brood parasitism hypothesis suggests that females dump eggs on copulating pairs, and (2) the paternal care hypothesis suggests that the system is driven mainly by males accepting eggs to improve the survival rates of their own offspring. Our data from the field show that 77% of the eggs are carried by males, because more males than females carry eggs, and because males carry a greater number of eggs. In addition, we show that mating males carry more recently laid eggs than single males. These results support the view that egg carrying is performed predominantly by males and that eggs are laid on males by their current mating partner, probably between repeated copulations. Males are likely to accept eggs, despite intermediate levels of paternity, because they cannot discriminate in favour of their own eggs, because rejected eggs will face 97% mortality rates on plants, and because they do not suffer mating costs when they carry eggs. However, females carry 23% of the eggs, but no differences in egg carrying have been found between mating and single females, suggesting that this is not the result of egg dumping while females are copulating. Egg carrying by females could reflect low levels of intraspecific parasitism, which is likely to reflect the

low rate of successful attempts by egg-laying females who try to oviposit on other conspecifics rather indiscriminately, in an effort to improve the survival of their offspring.

Introduction

Parental care evolves when the benefits in terms of offspring survival are greater than the costs to the parents' future reproduction (Williams 1966; Trivers 1972). In insects, care of eggs or young is not common, possibly because in most species adults can do little to protect or nurture the offspring (Zeh and Smith 1985; Tallamy and Wood 1986; Clutton-Brock 1991). However, in a few species in which eggs or young face high mortality risks because they live in harsh environments, or because they suffer intense predation or parasitation rates, parental care does occur because it substantially improves offspring survival (Wilson 1971; Eberhard 1975; Ridley 1978; Tallamy and Denno 1981; Zeh and Smith 1985; Tallamy and Wood 1986; Clutton-Brock 1991; Hardin and Tallamy 1992). Among terrestrial arthropods, care is most often performed by the female alone, followed by biparental care, while the least-frequent form is male care (Zeh and Smith 1985; Clutton-Brock 1991). Such interspecific differences are thought to be a consequence of the different costs experienced by both sexes when providing care. According to this view, males provide care only when the costs for them are low, and the main costs of paternal care are related to the loss of opportunities to re-mate with other females (Zeh and Smith 1985; Clutton-Brock 1991; Smith 1997).

Given that providing care entails costs, each sex would benefit from manipulating the other into caring for offspring. Thus, there will be sexual conflict in relation to which sex provides care or, in the case of biparen-

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tal care, in relation to the effort made by each partner. Male care is only expected to arise once a threshold in certainty of paternity is reached, but once this threshold is crossed, females can deceive males into providing care for offspring which they have not fathered (Westneat and Sargent 1996). As a consequence, males often care for unrelated young (Birkhead et al. 1988; Burke et al. 1989; Møller and Birkhead 1993; Dixon et al. 1994; Hughes 1998). The conditions under which males should decrease their investment are still a matter of debate (see, for example, Whittingham et al. 1992; Westneat and Sherman 1993; Wright 1998; Houston and McNamara 2002; Sheldon 2002).

When females provide care, they may also be the target of manipulation, since other conspecific females may lay eggs in their nests. In this way, unrelated females (or pairs) will rear the offspring of the parasite, and parasitic females improve the survival of their offspring while avoiding the costs of parental care. This strategy, known as intraspecific brood parasitism, can only evolve once parental care has spread in the population, and tends to be practised by a small proportion of individuals (Brown 1984; Petrie and Møller 1991; Brown and Brown 1998; Åhlund and Andersson 2001). The phenomenon is well known among birds (Yom-Tov 1980; Petrie and Møller 1991) and has also been described in insects (Müller et al. 1990; Field 1992; Brockman 1993; Zink 2000).

Females may therefore manipulate both males and unrelated females into providing care for their offspring and, in this way, they will increase their own reproductive success. However, the individuals who are the target of this deception should retaliate and minimise the chances of caring for young who are not genetically related to themselves. In the case of males, they should attempt to ensure that at least some of the offspring are their true genetic offspring, but their level of acceptance depends on other factors as well, such as the chances that the offspring will survive without care, the chances of improving certainty of paternity in future reproductive attempts, and the magnitude of the costs associated with providing care (Westneat and Sherman 1993). In the case of intraspecific brood parasitism, unrelated females should try to avoid being deceived. The levels of conflict involved between mothers and other potential caregivers may give rise to complex situations in which males care for offspring even though some of them are not their own, and some females care for other females' offspring. The conflicts of interest in relation to who provides care become particularly acute when mothers cannot care for their own offspring, and in order to improve offspring survival they have no other choice but to find other conspecifics who will provide the necessary care. Very few model systems with obligate alloparental care have been studied so far.

Female golden egg bugs (*Phyllomorpha laciniata*) face exactly this kind of situation because they cannot lay eggs on themselves, and yet egg carrying greatly improves egg survival. Females can lay eggs on plants (*Paronychia argentea*), where they develop unattended or on the backs of conspecifics, where they remain firmly glued until the nymphs emerge and start an independent life (Kaitala 1996; Reguera 1999). The survival rates of eggs laid on plants are very low as a result of high predation rates and attacks by an egg parasitoid wasp. However, when eggs are laid on conspecifics, survival rates improve considerably, mainly due to a decrease in parasitoid pressure (Reguera and Gomendio 2002). Females thus benefit from laying eggs on conspecifics and, when given the choice, have developed a preference to lay eggs on them rather than on plants (F. García-González and M. Gomendio, unpublished work). Although females would benefit equally from laying eggs on males or females, because survival rates do not differ according to the sex of the caregiver, the patterns observed in natural populations show that egg carrying is more prevalent among males (Gomendio and Reguera 2001). Carrying eggs is costly because individuals become conspicuous and are more easily detected by predators, while at the same time are less able to escape because the eggs tend to be glued on top of the wings and make flying difficult (Reguera and Gomendio 1999). Thus, it is worth asking why nearly all males in natural populations, and a small proportion of females, carry eggs.

Kaitala (1996) suggested that egg carrying is the result of intraspecific parasitism by females, which takes place while other conspecifics are engaged in copula, the so-called "mating pair intraspecific brood parasitism hypothesis" (henceforth MPIBP hypothesis). This hypothesis assumes that individuals are unable to resist laying attempts by females while in copula, and that females take advantage of this vulnerability to lay eggs on unrelated individuals. This hypothesis thus suggests that intraspecific parasitism has evolved in the absence of parental care. The formulation of the MPIBP hypothesis was based on two lines of evidence. (1) Copulation lasts many hours in *Phyllomorpha laciniata* (more than 20 h on average; see Kaitala 1998 and Reguera 1999), and some observations on captive individuals suggest that mating individuals offer little resistance to egg-laying females (for example, Kaitala and Miettinen 1997). (2) In natural populations, males in copula carry more eggs than single males (Kaitala 1996).

The main alternative hypothesis to explain egg carrying takes into account that males are the main recipients of eggs and suggests that males are more likely to accept eggs because they father enough offspring to benefit directly from the improved survival rates that egg carrying conveys, i.e. the "male parental care hypothesis" (PC hypothesis) (Gomendio and Reguera 2001). Males would be expected to try to maximise the chances that the eggs they carry are their true genetic offspring, and two of the most common strategies followed by males are long copulations (which maximise the number of sperm transferred and the likelihood that an egg will be produced at the end of the copulation), and repeated copulations with the same female (which maximise the chances that eggs laid between copulations are fathered by the male partner) (Smith 1979b; Dickinson 1986; Müller and Eggert

1989; Simmons and Siva-Jothy 1998; Simmons 2001). Thus this hypothesis is also consistent with the existence of long copulations and with the fact that mating males tend to carry more eggs than single males.

In this paper, we examine data from our longitudinal field study to discriminate between these two hypotheses by testing the following predictions:

1. The MPIBP hypothesis predicts no sex differences in egg carrying since obviously males and females should be equally vulnerable while in copula. In contrast, the PC hypothesis predicts that egg carrying will be performed mainly by males. More specifically, the two hypotheses make opposite predictions in relation to the following variables: the proportion of males and females carrying eggs, the average number of eggs carried by males and females, and the proportion of all carried eggs that are laid on males versus females.
2. Both the MPIBP and the PC hypotheses predict a higher proportion of mating males than single males carrying eggs, as well as a greater egg load on mating males. However, while the MPIBP hypothesis predicts that this should also be the case among females, the PC hypothesis predicts no differences in egg loads between mating and single females.
3. The MPIBP hypothesis predicts that a higher proportion of mating individuals than single individuals should carry recently laid eggs irrespective of sex (because of oviposition by an alien female), and that no sex differences should be observed in the number of recently laid eggs among mating individuals. In contrast, the PC hypothesis predicts that a higher proportion of mating males than single males should carry recently laid eggs (because of oviposition by current mating females between repeated copulations), but no differences should be observed between mating and single females. In addition, mating males should carry more recently laid eggs than single males, whereas no differences between mating females and single females are predicted.

Methods

Our 5-year field study has shown that adults emerge around March/April when temperatures start to rise. The bugs are very cryptic on their natural habitat, where they feed on the host plant *Paronychia argentea*. Soon after they emerge, they begin to copulate and to lay eggs. Copulation is long, lasting around 24 h (23 h on average in Kaitala 1998; 32.5 h on average in Reguera 1999; 11 h minimum in Mineo 1984). Females do not lay clutches, but instead lay one egg at a time. On any given day, they can lay around four eggs, and egg laying takes place throughout the whole active season (from March/April until August) so fecundity rates are very high. Nymphs hatch after around 12 days (depending on ambient temperature) and after 5 instars they become adults. The first adults born on any given year can be detected around June. The individuals born on that year will not copulate, nor will they accept eggs, until the following year when they emerge after the winter. Around mid-summer, the host plant becomes dry and the adults disappear until the next spring. In our study populations, sex ratio is 1:1 and remains constant throughout the entire season (see also Reguera 1999).

Field observations were conducted in five adjacent localities of central Spain: Villaviciosa de Odón, Robledo de Chavela, Colmenar del Arroyo, Valdemorillo and El Espinar. A total of 1,464 individuals were observed during the years 1998 and 1999 throughout the reproductive season (mid-April to mid-August). This sample includes 1,244 adults and 220 nymphs in different stages of development.

We did not include in the analyses (1) recaptured individuals, which could give rise to pseudoreplication (in Villaviciosa de Odón we conducted longitudinal studies during the 2 years, which involved weekly observations), and (2) individuals born during the reproductive season, because these individuals do not mate and do not accept eggs until the following year (García-González 2002). The reason why we know they have been born in that year is that we have marked them after their last nymphal stage when they were still soft and pale in colour. Once these individuals were excluded, the final sample consisted of 796 adults, and the total number of matings in which we recorded data on egg carrying was 76. No significant differences were found in patterns of egg carrying among different populations, so we pooled the data to increase the sample size.

To test the predictions of the two competing hypotheses, we registered for each individual, its sex and mating status, whether it carried eggs and, if so, the number of eggs carried, their stage of development (see below), their position, and whether they were parasitised. To assess the stage of development of the eggs, we followed the methodology used by Kaitala (1996). Eggs are white for some hours after being laid, then they turn yellow, yellow with some orange spots, golden with lots of orange spots, and finally, after about 12 days, they eclose. Parasitised eggs with scelionid parasitoids (*Gryon bolivari* Giard) are easily identified. This hymenopteran parasitises recently laid eggs, and parasitation is apparent because the eggs turn black.

Since copulation is lengthy, the developmental stage of eggs carried by mating individuals indicates roughly the time in which the egg was laid with respect to the current mating. Of particular interest to the predictions that are tested in this paper is whether eggs carried by mating individuals are white, since this would unequivocally mean that they have been recently laid (most likely during the current copula). Thus, we distinguished in the analyses recently laid eggs (white eggs) from old eggs (all the other categories), as Kaitala (1996) did. After hatching, the egg shell remains on the individual for some time. In spite of the fact that there are no differences in the number of egg shells carried by mating males or single males (Mann-Whitney $U=12650$, $P=0.66$, n mating males: 76, n single males: 344) nor between mating females and single females (Mann-Whitney $U=10810$, $P=0.37$, n mating females: 75, n single females: 299), we included also egg shells in the category of old eggs to make our results directly comparable with those of Kaitala (1996, 1998).

Non-parametric statistics were carried out because of the nature of the variables analysed (Sokal and Rohlf 1981).

Results

Prediction 1

Since females should be equally likely to lay eggs on either sex while a pair is engaged in copula, the MPIBP hypothesis predicts that there should be no sex differences in the proportion of individuals carrying eggs, nor in the average number of eggs carried. However, in natural populations a higher proportion of males than females carry eggs ($\chi^2_{\text{Yates corrected}}=35.91$, $df=1$, $P<0.001$, $n=795$) (Fig. 1a) and males carry more eggs than females, whether one considers all individuals (Mann-
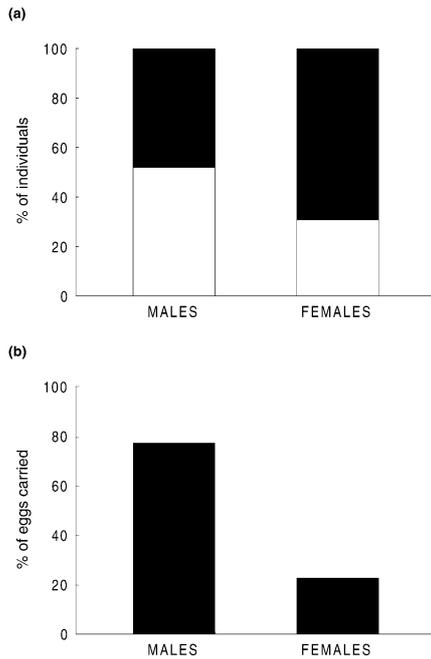
Fig. 1 Percentage of males and females without eggs (*black bar*) or carrying eggs (*white bar*) (**a**), and percentage of eggs carried by males and females out of the total number of eggs carried by individuals in the population (**b**)

Fig. 2 Percentage of males and females carrying eggs depending on whether they were mating or not (**a**), and percentage of males and females carrying recently laid eggs depending on whether they were mating or not (**b**)

Whitney *U*-test, $U=57005.5$, $P<0.001$; males $n=421$, mean±SE number of eggs=1.87±0.13, maximum number of eggs=14; females $n=374$, 0.62±0.06, maximum number of eggs=6) or only individuals that are carrying at least one egg (Mann-Whitney *U*-test, $U=7616.5$, $P<0.001$; males $n=219$, 3.6±0.17; females $n=115$, 2.02±0.11). When we take into account both the fact that a higher proportion of males carry eggs, and that males carry more eggs, by looking at the proportion of all carried eggs that are laid on each sex, we find that 77.3% of eggs are carried by males, while only 22.7% are carried by females ($\chi^2_{\text{Yates corrected}}=162.9$, $df=1$, $P<0.001$; number of eggs carried by males=789, number of eggs carried by females=232) (Fig. 1b), despite of the fact that sex ratio does not differ from 1:1. These results support the predictions of the PC hypothesis.

Prediction 2

Both the MPIBP and the PC hypotheses predict a higher proportion of mating males than single males carrying eggs, as well as a greater egg load on mating males. However, while the MPIBP hypothesis predicts that this should also be the case among females, the PC hypothesis predicts no differences between mating and single females. When we compare egg carrying among mating versus single individuals, we find that a higher proportion of mating males than single males carry eggs ($\chi^2_{\text{Yates corrected}}=5.17$, $df=1$, $P=0.023$, *n* mating males=76, *n* single males=345) (Fig. 2a), and that mating males car-
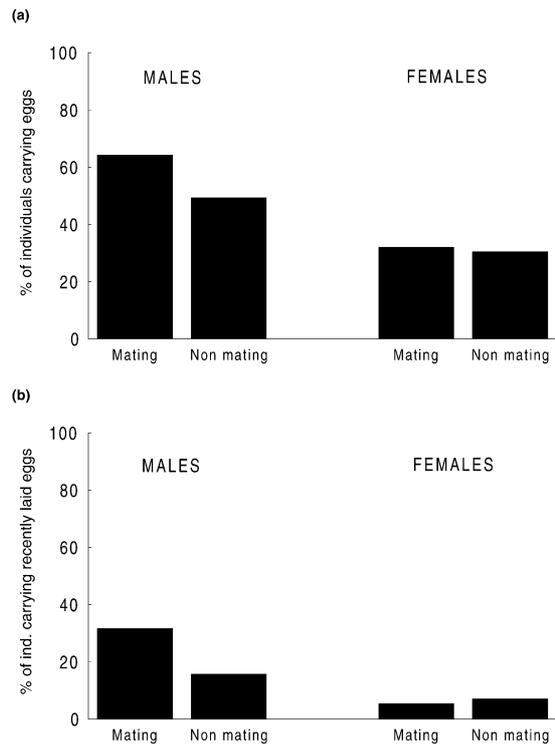
ry more eggs than single males (Mann-Whitney *U*-test, $U=10873.5$, $P=0.01$) (Fig. 3a), as predicted by both hypotheses. However, contrary to the prediction of the MPIBP hypothesis, no differences were found between mating and single females (proportion of mating vs single females carrying eggs: $\chi^2_{\text{Yates corrected}}=0.02$, $df=1$, $P=0.9$, *n* mating females=75, *n* single females=299; number of eggs carried: Mann-Whitney *U*-test, $U=10811.5$, $P=0.56$) (Figs. 2a, 3a).

Prediction 3

The MPIBP hypothesis also predicts that as a consequence of oviposition by alien females on mating pairs, a higher proportion of mating individuals than single individuals should carry recently laid eggs, irrespective of sex. However, while a higher proportion of mating males than single males carry recently laid eggs ($\chi^2_{\text{Yates corrected}}=9.36$, $df=1$, $P=0.002$, *n* mating males=76, *n* single males=344), the proportion of mating females carrying recently laid eggs does not differ from that of single females ($\chi^2_{\text{Yates corrected}}=0.07$, $df=1$, $P=0.8$, *n* mating females=75, *n* single females=299) (Fig. 2b). These results support the predictions made by the PC hypothesis. In addition, the MPIBP hypothesis predicts that no sex differences should be observed in the number of recently laid eggs among mating individuals, i. e. mating males
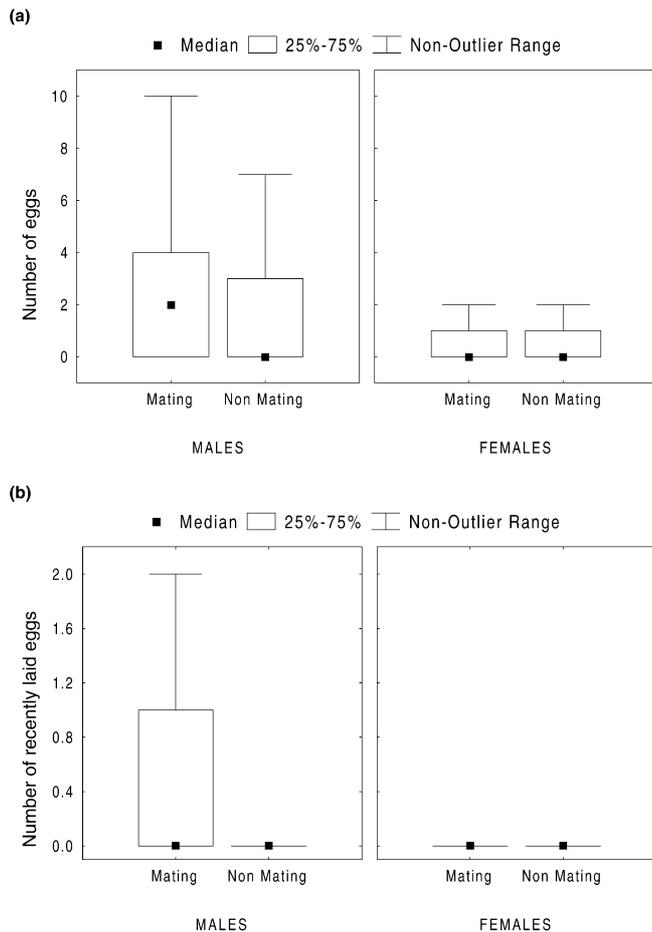
(a)

(b)

Fig. 3 Medians, quartile ranges and non-outlier ranges for the number of eggs carried by mating and non-mating individuals (**a**), and for the number of recently laid eggs carried by mating and non-mating individuals (**b**)

and mating females should carry more recently laid eggs than single males and single females, respectively. The number of recently laid eggs is greater in mating males than in single males (Mann-Whitney U-test, $U=10996.0$, $P=0.001$), whereas it does not differ between mating and non-mating females (Mann-Whitney U-test, $U=11023.0$, $P=0.82$) (Fig. 3b). Therefore, results regarding this prediction are also against the MPIBP hypothesis while strongly supporting the PC hypothesis, since only males are the recipients of the eggs laid during the mating association.

Discussion

The results from our longitudinal study in natural populations of *Phyllomorpha laciniata* do not support the hypothesis that egg carrying by adults is the result of egg dumping by females on individuals in copula, as suggested by the mating pair intraspecific brood parasitism hypothesis. This hypothesis predicts that females should be equally likely to lay eggs on males and females if

they are unable to resist egg-laying attempts while engaged in copula. Contrary to this prediction, our results show that in natural populations, more males than females carry eggs, and that males carry more eggs than do females. As a result, 77% of all carried eggs are found on males.

In addition, if females take advantage of a presumed inability to reject egg-laying attempts while in copula, mating individuals should more often receive eggs than single individuals, as a consequence of oviposition by alien females. Contrary to these predictions, we found no differences between mating and single females with respect to the proportion found to carry eggs, or in the number of eggs carried. This could be either because it is wrong to assume that individuals cannot resist laying attempts while in copula, and/or because encounter rates with copulating pairs are extremely low. Our long-term studies show that population density is very low: data gathered from adults found in an area of 400 m² in 44 different days throughout 3 reproductive periods (years 1998–2000) showed densities ranging from 0.005 individuals/m² to 0.265 individuals/m² (mean density=0.042 individuals/m², SE=0.007). Despite many hours of field work and more than 200 matings observed in the field, we have never observed a female laying eggs on copulating individuals. The assumption that alien females exploit mating pairs seems to apply only in captivity: Kaitala and Miettinen (1997) showed, in a study in which mating couples were placed with a single female, that copulating individuals could not avoid receiving eggs except by terminating the copulation. In 5 cases out of 20 (25%) copulation was terminated when a female tried to oviposit on a copulating individual; in 11 cases (55%) an egg was laid on a copulating female, and in 4 cases (20%) on a copulating male (Kaitala and Miettinen 1997). Thus, the MPIBP hypothesis could account for a significant proportion of the eggs that individuals are carrying in captivity under certain conditions, but natural conditions are not the same. In captivity, encounter rates between single females and mating pairs may be artificially elevated.

Mating males do carry eggs more frequently and in greater numbers than single males. This result could arise if females prefer to mate with males who are already carrying eggs, either because they have already proven their propensity to provide egg care or because of beneficial dilution effects with respect to egg parasitism or predation (see, for example, Ridley and Rechten 1981; Kraak and Weissing 1996; Jennions and Petrie 1997). However, this explanation can be rejected because the differences in egg load between mating and single males are due exclusively to recently laid eggs, which were almost certainly just laid on the male by his current mate. In this sense, our data are in agreement with two independent studies that examined female mate choice in this species (Kaitala 1998; Reguera 1999).

We suggest that our results are best explained if the system is driven by paternal care, and intraspecific brood parasitism arises as a low-frequency strategy that ac-

counts for a small proportion of the eggs carried. The paternal care hypothesis proposes that, although females benefit equally from laying on males or females, only males are willing to accept eggs, and that they tend to do so between repeated copulations with the same partner. This hypothesis is consistent with all the results presented here, namely that eggs are mostly carried by males, that mating males differ from single males only in the number of recently laid eggs that they carry, and that no differences in egg carrying have been found between mating and single females.

However, golden egg bug females copulate with several males, so that certainty of paternity must vary. In other species with paternal care, males ensure the paternity of the eggs they carry by demanding repeated copulations between the laying of successive eggs (Smith 1979a, 1979b, 1980; Müller and Eggert 1989). In golden egg bugs, this behaviour seems more flexible. Males do not always demand copulations between successive eggs, but instead may sometimes continue to accept eggs for some time after a single copulation has taken place. This flexibility raises the question as to whether the paternity of the eggs carried by males is high enough to favour paternal care. In a previous study, we used mating pairs from the field to estimate paternity, and found that the last male to copulate with a female fathers around 40% of the eggs laid during the following days (García-González et al. 2003). Females lay several eggs each day in sequence (minimum=0, maximum=12), and our findings suggest that paternity remains at intermediate levels for at least 5 days. These results suggest that sperm mixing is the mechanism by which sperm competition operates in this species, implying that, once the female has copulated with several males, the paternity of each egg laid will be determined randomly. From the point of view of the male, it is therefore impossible to predict when his own eggs will be produced, and once copulation has taken place he probably shares paternity with other males for a rather long period. This may explain why males do not only accept eggs just after copulation, but also for some time after it has taken place. It also means that if males cannot predict which eggs contain their true genetic offspring, the option of not accepting eggs will increase the risk of allowing their descendants to die when laid on plants. Thus, males have to balance the costs of caring for unrelated eggs against the mortality costs for their own young if no care is provided in a system in which little information is available on the chances of being the father of each egg laid. Several factors have probably favoured egg acceptance by males, including the extremely low survival rates of eggs laid on plants and the apparent lack of mating costs for males from carrying eggs (Kaitala 1998; Reguera and Gomendio 1999).

When sperm mixing takes place, the most effective way to maximise the number of eggs fertilised would be to transfer more sperm than rival males. This would explain why males often do demand repeated and long copulations. In addition, long and repeated copulations probably maximise the chances that the female will lay an egg while the male is still close to her, and therefore the likelihood that it will be laid on the male, thus substantially increasing its survival prospects. The reason why males sometimes do and sometimes do not demand repeated copulations is interesting, and may depend on the perceived risk of sperm competition at the time of mating.

However, paternal care cannot account for all egg carrying, because 23% of eggs are carried by unrelated females. The fact that mating females were not more likely to carry eggs, nor did they carry a greater number of recently laid eggs than single females, seems to suggest that those eggs were not laid while the females were mating. Data from 5 years of field work suggest that throughout the season, the proportion of females carrying eggs is always substantially lower than that of males, and never exceeds 40%, while after the first weeks of the season almost 100% of males are carrying eggs. Thus, egg carrying by females probably occurs because of the low frequency of parasitism in the population, which is likely to be the result of attempts by egg-laying females ovipositing on other conspecifics indiscriminately. In our view, the fact that females attempt to lay eggs on conspecifics, irrespective of their relatedness to the eggs, is in accordance with their reproductive interests, but has no bearing on the question of whether male egg carrying can be interpreted as a form of paternal care, as Kaitala et al. (2001) argued. Females lay eggs almost every day throughout the breeding season and, when ready to oviposit, they prefer to lay on conspecifics if available (F. García-González and M. Gomendio, unpublished work). Nevertheless, conspecifics are likely to be rarely encountered given the low population densities. When the conspecific is a male with whom they have copulated, the male is likely to accept the eggs because of the high benefit to cost ratio. Acceptance by females is probably lower because they will be unrelated to other females' eggs. Thus, the questions "why do females attempt to lay eggs on males and females" and "why are males more likely to accept eggs than females" address entirely different issues.

An alternative interpretation could be that males carry more eggs than females, and that mating males carry more recently laid eggs than females, because males search actively for females, and thus are more exposed to egg-laying attempts. This hypothesis assumes that the role of the recipient in accepting or rejecting the eggs is negligible. However, encounter rates depend on population density, so if encounter rates are crucial then differences between populations in egg carrying should be associated with differences in population density. We have studied populations in Andalucía (south of Spain) where egg carrying is less common than in populations from Madrid. Contrary to this hypothesis, such populations do not differ in density, nor do they differ in sex ratio, or female fecundity. Thus, differences in egg carrying cannot simply be explained by encounter rates. Indirect support for the notion that differences in egg-carrying rates arise due to differences in the rates at which egg-laying females are rejected by males comes from Miettinen and

Kaitala (2000) who showed that males in Andalucía rejected 70% of female laying attempts, while the rate of rejection was only 20% in populations from other regions. Such high rates of rejection cannot be ignored in explanations of egg carrying in *Phyllomorpha laciniata*.

In conclusion, patterns of egg carrying in nature suggest that females benefit from laying eggs on males and females because they are much more likely to survive when carried by conspecifics than when laid on plants. Because the benefits for the eggs seem to derive merely from the fact that they are glued to an adult's back, and not from elaborated forms of care, the "quality" of the carrying individual is irrelevant for the laying female. Experiments in the laboratory have shown that females do prefer to lay on conspecifics, but that they show no preferences for males or females, which is consistent with field data showing that egg survival is the same on both sexes (Reguera and Gomendio 2002). The fact that most eggs are carried by males and that, as the season progresses, almost all males in natural populations end up carrying eggs, can only be explained if males are more likely to accept eggs than females. This seems to be the case, because males tend to accept eggs from their current mating partner. Paternal care has evolved despite intermediate levels of paternity, because only 3% of eggs laid on plants survive, and because males continue to mate with other females while carrying eggs. Thus, male golden egg bugs avoid the main cost of paternal care, which has prevented its evolution in many other groups.

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