Is egg carrying attractive? Mate choice in the golden egg bug (Coreidae, Heteroptera)

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In several species of fish, females select males that are already guarding eggs in their nests. It is a matter of debate as to whether a female selects a good nest site for her offspring (natural selection) or a male for his attractiveness (sexual selection). The golden egg bug, *Phyllomorpha laciniata* Vill, resembles fish in the sense that mating males carry more eggs than single males, but in the bugs, female mate choice is decoupled from egg site choice. The sexual selection hypothesis predicts that if females select males using male egg load as a cue for male quality, they should not mate with a male when eggs are removed, regardless of his mating attempts. When individual females were enclosed with an egg-loaded male and an unloaded male, they mated equally often with both males, although the loaded males courted more. In addition, when only successful males were used, females mated equally often with the loaded male and the unloaded male irrespective of sex ratio. Male choice rather than female choice affected mating frequency when sex ratio was equal. Therefore, females do not select the male by the eggs he carries, but successful males may receive many eggs due to egg dumping by alien females while they mate or as a consequence of mate guarding.

Keywords: Coreidae; egg carrying; golden egg bug; mate choice; paternal care; *Phyllomorpha laciniata*; sex ratio

1. INTRODUCTION

A female is expected to choose a mate in order to get direct or indirect benefits for herself or her offspring (reviewed in Andersson 1994). In species where males carry out some, or all, of the parental care, females may choose males on the basis of their capacity to do so (Halliday 1978). In a variety of fish species where males care for eggs in nests, females show a strong preference for males that have accumulated many eggs (Ridley & Rechten 1981; Constanz 1985; Marconato & Bisazza 1986; Knapp & Sargent 1989; Ungern & Sargent 1988; Kraak & Videler 1991; Kraak & Groothuis 1994; Kraak & Weissing 1996). Since these species exhibit external fertilization, it is difficult to test what choice a female is making because the choice of oviposition site cannot be separated from the choice of mate.

There are several (although not mutually exclusive) hypotheses explaining why females choose to lay eggs in nests that already have eggs. According to sexual selection hypotheses, the presence of eggs in the nest could signify that other females have found the male attractive. This has been referred to as 'copying' (but see Pruett-Jones 1992; Jamieson 1995), although this is not copying *sensu strictu* in which females directly observe other females' choice (Dugatkin 1992; Kraak 1996a). Females are expected to copy other females' decisions, if choosing a male is costly (Gibson & Höglund 1992). Females may also select males with eggs if sites with many eggs have lower offspring mortality (the natural selection hypothesis): the presence of eggs dilutes the risk of newly laid eggs being eaten by the father (Rohwer 1978; Sargent 1988). Moreover, a female may secure greater paternal

investment in her eggs since males are expected to increase their level of care with the size of the brood (Sargent 1988). Finally, a male guarding many eggs may indicate he is a father of proven 'good parental quality' (Ridley 1978). Whether it is a safe oviposition site or male attractiveness that affects a female's choice of mate has been debated (Jamieson 1995; Kraak 1996a).

The golden egg bug, *Phyllomorpha laciniata* Vill (Heteroptera: Coreidae), provides an opportunity to separate mate choice from oviposition site choice. Females oviposit on the backs of both male and female conspecifics. Males carry, on average, twice as many eggs (1–28) as females (1–14; Kaitala 1996). The number of eggs carried increases as the reproductive season progresses. This situation differs from that found in fish with paternal care, in that female oviposition is not associated with mating, but occurs often more than a day after the termination of copulation (Kaitala & Miettinen 1997).

In the bugs, egg carrying may indicate a male's quality, and eggs might be referred to as costly ornaments (Andersson 1994) functioning as handicaps (Zahavi 1975): a male has survived despite the egg load. A female may also assess a male's egg carrying ability because she might detect directly how many eggs a male is carrying, and how many eggs have successfully hatched from his back thus far. This is because eggs can be aged by their colour, and the egg shells remain on the back after hatching (Kaitala 1996). Males can conceivably determine how many eggs they carry because they are able to scrape off eggs from their backs (A. Kaitala, unpublished data).

In the laboratory, most individuals do not resist receiving eggs from a female without mating with her (Kaitala & Miettinen 1997). This is unexpected because

egg carrying is costly due to increased predation risk (A. Kaitala & X. Espadaler, unpublished data). Also, when mating, a pair cannot resist a non-mating female laying eggs on their backs. If egg-loaded males have a mating advantage, it could be advantageous for a male to accept unrelated eggs even if carrying is costly.

In the field, males found in copula carry more eggs than non-coupled males (Kaitala 1996). Mating males were also found to carry more recently laid white eggs than non-coupled males. This may be due to males receiving eggs from non-mating females whilst mating themselves (Kaitala 1996). However, if mating males also carry more old eggs (that are laid at least four days before), females may use egg load as an indication of males' quality.

In this paper, I investigate in the field whether mating males carry more previously laid old eggs and egg shells than non-coupled males. This would indicate that females prefer to mate with males carrying more eggs (and that the eggs are not laid during the current mating). Secondly, I test whether females select a male by the eggs he carries by manipulating the egg load on a male's back. If females select a male by his egg load, they should not mate with a male when eggs are removed, regardless of a male's courting. However, if female choice depends on other male characters, mating decision should not be affected by the male's egg load. In two experiments I controlled male 'quality' by using only males that previously had had good mating success.

(a) *Female reproductive behaviour*

The reproductive period lasts at least 1–2 months, but females lay, on average, only one clutch (of 1–3 eggs) every third day. They lay eggs on all backs available, including those of other females. Most females lay eggs on the back of their mating partner while being guarded by him when the sex ratio is male-biased (Kaitala & Miettinen 1997). When there is male–male competition, the male is likely to guard the female, and therefore his back is likely to be the first suitable oviposition site around when the female oviposits (Kaitala & Miettinen 1997). Even in these cases there is often a day between copulation and egg laying. Also, females often mate with several males before laying a clutch. The cost of choosing a male is likely to be low because male bugs are constantly looking for and courting females, and females often reject mating attempts. Mating often lasts more than 20 hours (median 23 hours, range 3–53, $n=80$; A. Kaitala & M. Miettinen, unpublished data), and a female may mate repeatedly before laying a clutch (Kaitala & Miettinen 1997).

2. METHODS

(a) *Field data*

The field data were collected from three localities in southern France and two localities in Northern Spain on the slopes of the Pyrenees. Altogether 392 males were collected during 9–11 June 1994. The two field sites in France are close to Banyuls-sur-Mer and are the same as those described by Jeannel (1909). The third site in France is along the highway about 10 km from Banyuls-sur-Mer to Cerbere. The two field sites in Spain are 3 km from Campmany towards Sant Climent.

(b) *Laboratory experiments*

In all laboratory experiments, field-collected reproductively active bugs were kept in large cages with the sexes separated for at least 3 d prior to the experiments. They were provided with fresh branches of the host plant *Paronychia argentea* (Caryophyllaceae). During the experiments observations were made daily between 09.00 and 18.00, after which the bugs were placed in a dark, cool (16 °C) environmental cabinet.

In the first experiment, 40 males and 20 females were enclosed in a (40 cm × 21 cm) container, and all matings were recorded during the first two days. Prior to the release of the females and the males, eggs were either totally or partially removed from 20 randomly selected males to generate variation in males' egg load.

Because the behaviour of all bugs was difficult to follow in the above experiment, additional experiments were carried out, in which individual females ($n=70$) were enclosed in small containers (9 cm × 17 cm) together with a male whose eggs were removed and a male carrying 7–10 eggs. Experiments were carried out for 1–2 days during which time only some of the females mated. The bugs were checked every half hour, and their egg-laying and mating behaviour were recorded. Most matings last for more than 10 h, so it is likely that I detected all matings. Sometimes a female seemingly tried to avoid mating with a courting male (that was stridulating; Moulet 1995). She rejected the mating by turning and twisting her body, and sometimes by kicking the male off her back. Unsuccessful oviposition trials were also recorded to investigate the importance of male courtship behaviour for his mating success.

(c) *Male quality controlled experiments*

In these experiments only the males that had proven good mating ability (or males that were generally preferred by females) were used. This was done by picking the first males to mate (during the first day) in large mating containers (40 cm × 21 cm), each containing 20 females and 20 males.

The experiments were carried out at two female/male ratios: 1:2 and 2:2. In the male-biased sex ratio a female was enclosed with a loaded male and an unloaded male, with whom she had not mated before. The eggs were removed from the back of the female and one of the randomly selected males (unloaded male); 6–10 eggs were left on the back of the other male (loaded male). In the experiment that used an equal sex ratio, two mating pairs were enclosed and the eggs were removed as above while the loaded male had five eggs on his back. Once they had separated, female remating and rejected mating attempts were recorded by following them continuously during the first two days or until a male tried to mate. Thus, both the females had access to both the males. However, when one of the females was mating, the matings of the other female (or rejected mating attempts) were not included because then the other female had only one male to choose from. Egg laying between the first and second matings was also recorded. The total number of matings was recorded over a week.

3. RESULTS

(a) *Do males that carry more old eggs have better mating success?*

In the field, mating males carried more previously laid old eggs (yellow eggs and egg shells, mean = 6.1, range of the means among sites was 4.0–9.7) than single males (4.7, range 3.7–6.2) when adjusted for the effect of site (table 1).

Table 1. *Two-way ANOVA of the number of previously laid eggs (yellow eggs and egg shells) on the backs of males using site and mating status as predictor variables*

source	d.f.	<i>F</i>	<i>p</i>
mating status	1	5.94	0.015
site	4	5.22	<0.001
mating status × site	4	1.25	0.288
error	382	—	—

Table 2. *Male mating success and egg load in the three different experiments and two different sex ratios*

(Only a male's first mating is counted. The differences among the experiments were not significant: likelihood ratio test; $G=0.52$, d.f.=2, $p=0.77$.)

experiment	unloaded	loaded
1 female, 2 males ^a	26	21
1 female, 2 males ^b	15	16
2 females, 2 males ^b	12	13

^a male quality was not controlled for before the experiment.

^b male quality was controlled for before the experiment.

Thus, bigger egg load of mating individuals is not due to them having received eggs during the current mating.

(b) *Do females prefer males that already carry eggs?*

When the sex ratio was male-biased, a female was expected to mate with the male carrying more eggs. When individuals were allowed to mate freely in a large rearing cage, mated males carried fewer eggs (developing eggs+hatched egg shells, mean $\pm$ s.e., 6.7 ± 1.7) than single males (11.0 ± 1.3), but the difference was not statistically significant (t -test, $t=1.77$, $p=0.08$).

In all the experiments carried out in small enclosures with one female or two females enclosed with a loaded and an unloaded male, females mated equally often with the loaded male and the unloaded one (table 2). Most females rejected at least one mating attempt before mating. Considering a male's first mating attempt, and whether a female accepted a male or not, unloaded males were more successful (figure 1*a*) in the experiment in which male quality was not controlled. In that experiment, loaded males had a lower relative mating success (only 48% of the loaded males succeeded in their first copulation trial while 77% of the unloaded males were successful at the first trial).

In the male quality-controlled experiments, the unloaded males did not differ in mating success (figure 1*b,c*). When all of the females' matings were observed for a week, they did not mate more often with the loaded male compared to the unloaded one (pairwise t -test, $t=0.25$, d.f.=31, $p=0.80$, when sex ratio was male-biased; and $t=0.13$, d.f.=24, $p=0.90$, when sex ratio was equal). Females did not reject the loaded males relatively more often than the unloaded ones. However, when the sex ratio was equal, a female's first remating was more likely to be with the original partner (figure 2) irrespective of his egg load. Also, during a week, a female mated

Figure 1. Number of mating trials (rejected and successful) and a male's egg load in the male-biased experiment in which male quality was not controlled (*a*), in which male quality was controlled (*b*) and in the experiment with equal sex ratio (*c*). There was a significant difference in the relative mating success between the two males in the uncontrolled experiment ($G=4.88$, d.f.=1, $p=0.027$), but not in the male quality controlled experiments (male-biased sex ratio, $G=0.004$, d.f.=1, $p=0.95$; equal sex ratio, $G=0.24$, d.f.=1, $p=0.62$). Only the male's first trial was counted.

relatively more often with her original mating partner (pairwise t -test; $t=2.12$, d.f.=24, $p=0.04$). Thus, females were consistent in their mating decisions irrespective of male egg load. However, males did not court females randomly and courted their previous mating partner more often than the other female (figure 2). Females rarely laid eggs on their mate's back after mating. Only in 13 out of 25 cases did females lay eggs between the first and second mating. When they mated repeatedly with the same male, they never laid a clutch on his back between

Figure 2. Males' first mating trial with respect to their previous mating partner and egg load in the experiment in which the sex ratio was equal. Both the males tried to mate with their previous mating partner significantly more often than with the other female ($G = 12.51$, d.f. = 2, $p < 0.001$).

the first and second mating. Nine females laid a clutch on the back of an alien individual (a female or a male with whom they did not mate before or after egg laying). One female laid a clutch on the back of her first mating partner and then mated with the other male, and three females laid a clutch on the back of their next mating partner.

4. DISCUSSION

In the golden egg bug, mate preference is likely to be uncoupled from preference for oviposition site, in contrast to fish that exhibit paternal care. In these fish, a female simultaneously selects both her mating partner and an oviposition site (Jamieson 1995; Kraak 1996a). Thus, it is not evident whether females are selecting a good site for their offspring to develop (the natural selection hypothesis) or an attractive male with good genes (the sexual selection hypothesis; Jamieson 1995). In the golden egg bug, there is no evidence that females select their mating partner in order to lay eggs on his back. In the laboratory, females lay eggs randomly on all backs available, irrespective of paternity of the eggs laid (Kaitala & Miettinen 1997). Only when the sex ratio is male-biased are females more likely to lay eggs on their mates' backs (Kaitala & Miettinen 1997). However, this is probably because the male guards the female after mating, and is likely to offer the first available oviposition site. Furthermore, when given a choice, females do not show a preference for laying eggs on the back of a loaded male over laying on the back of an unloaded one (A. Kaitala, unpublished data).

In many fish, offspring survival is increased when eggs are laid in nests with many eggs (Sargent 1988; Kraak 1996b). In the golden egg bug there is no evidence that eggs do better if laid on the back of an already loaded individual. The only well-reported mortality factor in the field is caused by an egg parasitoid, a scelionid wasp, *Gryon bolivari* (Kaitala 1996). The wasp attacks only recently laid white eggs, but one could expect it to find the eggs more easily if the bug carries many eggs. However, contrary to expectation, eggs laid on the back of an individual that carries many eggs are equally likely to be parasitized as

the eggs laid on the back of an unloaded individual (Kaitala 1996).

Due to the relative independence between mating and offspring environment, the females of the golden egg bug are not likely to select a mating partner because his back would be a good site for the eggs to develop. Thus, the sexual selection hypothesis is more appropriate in the case of the golden egg bug, and the egg load could indicate a male's quality.

Contrary to expectations, my experiments suggest that females do not mate more often with males that carry more eggs. In one of the experiments carried out in small enclosures, females rejected mating attempts of the loaded males relatively more often than those of the unloaded males, although they mated equally often with both the males. When male 'quality' was controlled, females did not reject loaded males more often than unloaded males. However, at least when sex ratio was equal, male courting intensity seemed to be the main determinant of their mating frequency, as has been previously noted in some fish (Jamieson & Colgan 1989; Knapp & Kovach 1991) and a butterfly species (Kaitala & Wiklund 1995). In those cases, the evidence of active female choice may be lacking or be undetectable (Jamieson & Colgan 1989; Andersson 1994). In the case of the golden egg bug, a male's egg load did not affect his courting intensity when male 'quality' was controlled, but a male's previous mating success had a significant effect on which female he courted, with males preferring their previous mate.

If females do not choose on the basis of egg load, this raises the question as to why mated males, in nature, carry more eggs than single males. This behaviour held true when the effect of recently laid eggs was removed. Males carrying many eggs may be more successful due to other reasons than their egg-carrying ability. They might acquire more eggs *because* they have mated so often (the eggs being dumped by alien females while they mate), or as a consequence of mate guarding when sex ratio is male-biased (Kaitala & Miettinen 1997).

To conclude, sexual selection with respect to male brooding is well-studied among fish, including cases in which females commonly select the male on the basis of the number of eggs in the male's nest (reviewed in Pruett-Jones 1992). The golden egg bug is a good model to investigate whether females use egg load as an indicator of male quality when choosing their mates, because it is possible to separate the sexual selection from the natural selection hypothesis (Jamieson 1995). However, females did not select males carrying more eggs. Thus, the hypothesis that females use egg load as an indicator of the male's quality is not supported.

Finally, egg carrying in the golden egg bug has been debated for years (Jeannel 1909; Reuter 1909; Wilson 1971; Ridley 1978; Zeh & Smith 1985; Tallamy 1994; Kaitala 1996). It is now evident that females often lay eggs on the backs of males with whom they have not mated (Kaitala & Miettinen 1997). There is also evidence that egg carrying is costly since it increases the risk of predation (A. Kaitala & X. Espadaler, unpublished data). The present study shows that females do not choose males according to the presence of eggs. Therefore, the evolutionary explanation for why males do not resist receiving eggs they have not fertilized remains to be solved.

Thanks are due to Anders Berglund, Penny Cook, Tim Halliday, Sarah Kraak, Risa Rosenberg, Nina Wedell, Christer Wiklund, and an anonymous referee for valuable comments on the earlier version of the manuscript. I also thank John Reynolds and Birgitta Tullberg for giving the common name for the bug. This study was supported by the Swedish Natural Science Research Council.

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