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Dedicated to the memory of William Donald Hamilton

Sexual interactions and conspecific exploitation in an egg-carrying bug

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Female ability to exploit conspecifics may have unusual expressions. Golden egg bug (*Phyllomorpha laciniata,* Heteroptera, Coreidae) females lay eggs on the backs of conspecifics. Eggs are only attached on bugs and no active care is given. Egg carrying is costly due to increased predation risk. Females do not choose any particular "back" but lay eggs on all conspecifics available. Females carry one third of the eggs, and they never carry their own eggs. The majority of the eggs carried by males in the field are not fathered by the carrier. Females commonly dump eggs during reproductive activities on courting males or on (other) copulating females and males. In most habitats, eggs do not survive unless carried. Thus, females are dependent on the availability of conspecifics to lay eggs. Here, we review current knowledge on egg carrying and explore the costs of carrying eggs, how eggs are received and who carries the eggs. We also compare this system with that of arthropods which have exclusive paternal care. The main conclusion is that the system is a special form of intraspecific parasitism. It is maintained by high fitness benefits to an egg-dumping female and probably by rather low costs to an egg-carrying bug. Reproductive activities provide egg-laying opportunities for a female, and thus sexual interactions resulting from female polyandry are necessary for female egg dumping.

Introduction

Individuals are expected to help conspecifics if the benefits of helping are larger than costs or if individuals reciprocate in helping. If the receiver is a relative, costly helping should depend on the level of relatedness between the helper and the receiver (Hamilton 1963). If the costs of the behavior are larger than the benefits and if the receiver is not a close relative, the system is manipulative and labeled as intraspecific parasitism. Intraspecific parasitism occurs, for example, when individuals avoid the costs of parental care by exploiting the time and energy of unre-

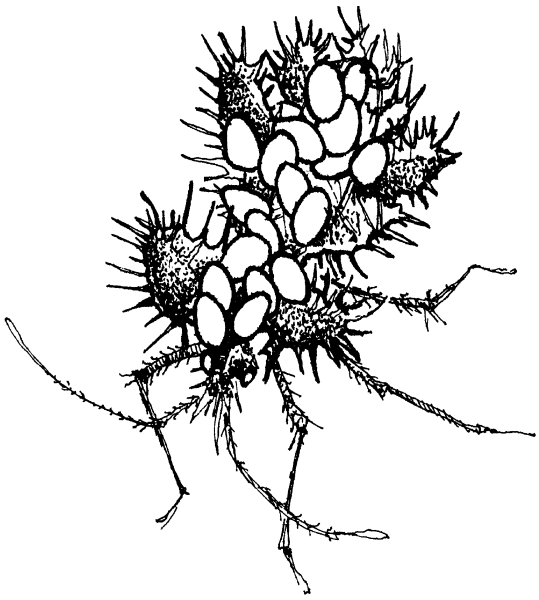

Fig. 1. The golden egg bug carrying eggs. The bug is about 1 cm long.

lated conspecifics (Field 1992). It has evolved in species that actively care for their young, and it is well described in several animal groups (e.g. for reviews *see* Field 1992, Brockman 1993).

The golden egg bug (*Phyllomorpha laciniata,* Heteroptera, Coreidae) females lay eggs on the bodies of conspecifics, mainly on their backs (Fig. 1). By definition, egg carrying by the bugs is intraspecific parasitism if it is costly for the carrier, and if bugs carry non-parental eggs. In the following, we show that the distinction between helping and parasitism is not always that clear. Using the data gathered on the species, we present a new type of behavioral strategy adopted by females. For the first time, we review the known aspects of the biology of the species, show results from laboratory and field studies on how eggs are received and who carries the eggs. We also explore the costs of carrying eggs. Finally, we give an explanation of the possible mechanism that maintains egg carrying in the species.

Natural history

The golden egg bug is found in the Mediterranean area where its host plants belong to *Paronychia* species (Polycarpea, Caryophyllaceae) (Jeannel 1909, Reuter 1909, Kaitala 1996). Bugs overwinter as adults and start breeding in spring. In southern Spain, they seem to have at least a partial second generation (J. A. Amat & A. Kaitala unpubl. data). Bugs are iteroparous and, in the laboratory, females lay eggs for more than two months but lay only one clutch of a few eggs about every third day (Kaitala & Miettinen 1997). In the field, in the middle of the reproductive period, males carry on average 5.5 eggs (range 1–28, $n = 440$) and females on average 2.5 eggs (1–14, $n = 378$) when only the number of developing eggs are counted and empty egg shells are excluded (Kaitala 1996). The number of eggs carried increases as the season progresses. Eggs are tightly attached to their carrier, and they are hard to remove without injuring the bug. Eggs change in color as they develop: recently laid eggs are white, then they turn more yellow and finally golden (Kaitala 1996). Most eggs are laid on backs, but they are also found on other parts of the body such as legs, heads and antennae. After hatching, larvae leave the carrier's back but egg shells remain on the back. In the laboratory eggs develop in 10–14 days.

The bugs have an unusual body form with an irregular contour and extension (Fig. 1). They are covered by small spikes, looking like a piece of spiky dead leaf, and are very cryptic and hard to distinguish against their natural background (Cott 1940). However, when carrying golden eggs, bugs are very visible at least to human eyes.

An egg-carrying bug does not give any visible care to eggs, and eggs survive and hatch well in the laboratory if removed from a bug. In some populations, many eggs are parasitized by the scelionid wasp (Kaitala 1996). The presence of egg parasitoids is easy to understand if bugs do not carry their own offspring. Why should an individual defend unrelated eggs against parasitism? In general, egg parasitism may be one explanation as to why laying eggs on conspecifics is uncommon in nature.

Bugs are highly polyandrous; they have long and frequent copulations. During the mating season 16%–30% of the bugs are found in copula (Kaitala 1996), and copulations often last more than ten hours (Kaitala & Miettinen 1997). A female can store sperm for more than several

weeks, and thus, females mate more frequently than necessary for fertilizing eggs (A. Kaitala unpubl. data). Egg laying does not necessary follow copulation, but a female may mate repeatedly (with different males) before laying a clutch (Kaitala & Miettinen 1997, Miettinen & Kaitala 2000). Despite egg carrying, sex roles are not reversed; males commonly court females, and females often reject male mating attempts (Kaitala & Miettinen 1997).

Female strategy for offspring survival

Laying eggs on the bodies of conspecifics is a female strategy for offspring survival because in most habitats eggs do not survive if laid on a host plant due to intense ant predation. This has been demonstrated by attaching the golden egg bug eggs to the flowers of the host plant and following their disappearance (Kaitala 1996). At least several ant species forage on bug eggs. For example, *Cataglyphis piliscapus* (Forel) (Hymenoptera, Formicidae) and *Pheidole pallidula* (Nylander) (Hymenoptera, Formicidae) ants have been noted to eat the eggs laid on the host plant (A. Kaitala unpubl. data). Experiments with the Mediterranean flour moth (*Anagasta kuehniella* Zeller, Lepidoptera, Pyralidae) eggs as "traps" showed that the eggs do not survive due to ant predation (mainly by *P. pallidula*; Du Merle *et al.* 1978). Other studies have shown that *P. pallidula* workers are able to detect arthropod corpses in less than five minutes (Retana *et al.* 1991). *P. pallidula* is extremely common in the Mediterranean region, inhabiting dry, open habitats and borders of woods (Bernard 1968), and it has been present in all habitats where we have found the golden egg bug (A. Kaitala & M. Katvala unpubl. data).

Eggs are rarely laid on the host plant, in populations consisting of hundreds of egg carrying bugs, only a few eggs are discovered on the host plant after intensive searching (A. Kaitala unpubl. data). In the laboratory, if conspecifics are available, eggs are almost exclusively laid on conspecifics; if deprived of conspecifics, females stop laying eggs within a day or two (A. Kaitala & R. L. Smith unpubl. data). In the field, when single females are enclosed in a net wrapped around the host plant, only a very few eggs are laid on the plant (A. Kaitala, M. Katvala & J. A. Amat unpubl. data). Thus, laying eggs on conspecifics is the main reproductive strategy of the bug. The only known exception where the eggs are not commonly laid on backs but on several plant species is a mountain population in Sicily (Mineo 1984). The bug's preferred host plant *Paronychia* sp. is absent in that area, and also the ant fauna is likely to differ from that of Spain (M. Katvala unpubl. data).

Paternal care or egg dumping?

The golden egg bug has been referred to as an example of parental care, especially paternal care (Reuter 1909, Wilson 1971, Reguera & Gomendio 1999, but *see* Jeannel 1909, Tallamy 1994). However, there are accumulating data showing that egg carrying cannot in general be explained as paternal care (for review *see* Kaitala *et al.* 2001). One third of the eggs in the field are carried by (non-parent) females, and DNA microsatellite data show that only a minority of the eggs (12%, $n = 40$ males) in the field carried by males are paternal (Miettinen 2001). When males have been released into natural habitats, they commonly receive eggs without copulating with the egg-donating female (Katvala & Kaitala 2001a). In the laboratory, most (60%) males receive eggs during courting (Katvala & Kaitala 2001b).

Males do not trade (non-paternal) eggs for matings because female precopulatory egg laying does not depend on whether or not a female accepts a male as a mating partner (Katvala & Kaitala 2001b). A copulating pair cannot resist egg dumping, and foreign females often dump eggs on them. A laboratory study suggests that male-male competition over matings may increase the number of paternal eggs carried because the previous mating partner stays close to a female after mating if there are no other females but only males around (Kaitala & Miettinen 1997). There is no indication that a male actively promotes eggs to be laid on his back after mating with the female.

In natural situations, females seem to receive

eggs mainly when they cannot act against eggs being laid on them, that is when they are mating themselves. In the laboratory studies when two females are reared in a large (21 × 30 cm) container consisting of hiding places like bushes, they do not commonly lay eggs on each other's back. However if enclosed in a small enclosure without possibilities to escape, they immediately lay eggs on each other's backs whether a female resists eggs or not (M. Katvala, A. Kaitala & J. A. Amat unpubl.).

The golden egg bugs can be compared to arthropods with exclusive paternal care (Zeh & Smith 1985, Tallamy 2000). Exclusive paternal care has evolved in eight independent lineages. The biggest difference between the golden egg bugs and paternally caring arthropods is that in the golden egg bug both sexes carry eggs and most eggs carried by males are not fertilized by the carrier and that females never carry their own eggs. In all paternally caring species only males care for eggs, their foraging ability is reduced due to care and most eggs are fertilized by the caring male. In the golden egg bug, eggs are only attached to the backs, and not actively guarded or looked after. It is also unknown if eggs carried by males lower their fitness by hampering foraging. The predation risk may be avoided by foraging at a safe time and in a safe place (Kaitala *et al*. 2000).

The only other taxon in which eggs are also attached on backs is the giant water bug (Belastomatids). However, in Belostomatids only males carry and actively care for eggs (Smith 1997), which otherwise cannot survive. The water bugs have a complicated courtship and egg-laying behavior. Males assure paternity by repeated matings between ovipositions. In contrast, in the golden egg bug, most eggs laid by non-mating females are received by carriers prior to or during copulation (Kaitala & Miettinen 1997, Katvala & Kaitala 2001b). In the golden egg bug, most eggs carried are unrelated to the carrier and thus egg carrying is driven by female interest while in paternally caring arthropods egg carrying increases the fitness of both the sexes (Zeh & Smith 1985, Tallamy 2000).

Kin selection?

Another often proposed hypothesis is that bugs carry relative's eggs, and the behavior can be explained via kin selection. DNA data do not support that the eggs carried are those laid by close relatives, also eggs carried by males are laid by different mothers (Miettinen 2001).

Bugs overwinter as aggregations and in spring they distribute widely. We have found bugs from > 50 meters apart from their overwintering bush during the reproductive season, and individual bugs have been noted to move tens of meters in a day (J. A. Amat, X. G. Espadaler, A. Kaitala & M. Katvala unpubl. data). During more than one month, a female lays a few eggs at a time on any bugs encountered. The likelihood that a larvae ends up on the same host plant as its sister/brother is very small.

The bugs are not territorial, and they do not defend any area such as host plant, for instance. Even large distance dispersal is possible if bugs fly after overwintering before starting to reproduce as suggested by their flight propensity in the laboratory.

Costs and benefits of carrying eggs

Crucial for the maintenance of egg carrying are the costs and benefits for a carrying bug. Ant predation is high in habitats occupied by the golden egg bug, and egg carrying increases predation risk (Kaitala & Axén 2000, Kaitala *et al*. 2000). The ant *P. pallidula* seems to be the main enemy not only for the eggs but also for the adult golden egg bugs. In the experiments when golden egg bugs were placed in enclosures that *P. pallidula* could visit (enclosures were placed around a tunnel entrance of *P. pallidula)*, ants foraged on bugs (Kaitala *et al*. 2000). In those experiments, as well as in the experiments with *Formica rufa* sp. as predators, bugs carrying eggs were attacked more often than those not carrying eggs (Kaitala & Axén 2000). This means that bugs carrying eggs are either more attractive to ants or less capable of escaping them. In the laboratory,

chicks attack bugs carrying eggs but not the bugs without eggs (A. Kaitala & G. Gamberale-Stille unpubl. data), and also bugs with eggs disappear faster than those not carrying eggs when exposed to captive great tits *Parus major* (Reguera & Gomendio 1999). However, the ants seem to be the most important predators, and we have often seen ants, especially *P. pallidula,* attacking bugs in natural situations. *P. pallidula* is active early in the morning and in the evening (Delalande 1985, Cammaerts *et al.* 1993) when *P. laciniata* is inactive (Kaitala *et al.* 2000). Thus the fact that bugs are active during the hottest time of the day when most ants and birds are inactive may be a mechanism of reducing the costs of carrying eggs.

The bugs actively reject eggs and scrape eggs off, which may be considered as indirect evidence of the costs of carrying eggs. Sometimes the bugs brush their backs against a branch of a plant until some eggs drop off. Egg scraping increases with the number of eggs carried (Kaitala 1999). However, 30%–80% of bugs lost eggs in the field either due to egg scraping or due to predation (Katvala & Kaitala 2001a). Bugs also actively resist receiving eggs, and they resist eggs irrespective of paternity (Miettinen & Kaitala 2000). Laboratory conditions may underestimate the bugs' ability to resist eggs because they lack possibilities to escape.

When encumbered with eggs, flying is impossible (Kaitala 1998) indicating additional costs of carrying eggs. Even a few eggs deposited on the wings may prevent flying. Bugs seem to fly, especially at the beginning of the reproductive period when disturbed or enclosed in a container (Kaitala *et al.* 2000).

To date, we have no evidence suggesting that carrying eggs is beneficial for the bugs bearing the eggs. Egg carrying does not increase male mating success (Kaitala 1998) as one could expect if eggs function as costly ornaments (Zahavi 1975). On the other hand, females do not avoid mating with males carrying many eggs. Actually, attractive males receive more eggs because they mate so often (dumped by females before or during mating), even if females do not select the male by eggs (Kaitala 1998).

What maintains egg carrying?

In general parasite behavior will spread if the fitness of parasites exceeds that of non-parasites (Field 1992). Females that lay eggs on conspecifics have evidently higher fitness in most habitats studied than those that lay eggs on host plants (Kaitala 1996, Kaitala *et al.* 2000). However, it is unclear how costly egg carrying really is and to what extent a bug can avoid receiving eggs. An egg-carrying bug seems to minimize the costs by behavioral adaptations, i.e. by being active while the enemies are inactive (Kaitala *et al.* 2000).

Data from laboratory experiments and from field studies show that most eggs are received during reproductive activities (Kaitala & Miettinen 1997, Kaitala 1998, Miettinen & Kaitala 2000, Katvala & Kaitala 2001b). Therefore, the mating activities, courting, copulation and intrasexual competition over matings, are necessary conditions for giving egg-laying opportunities to females. Thus, the only thing a bug can do to avoid eggs is to avoid matings. This is what females seem to do. In the field, when gravid and recently oviposited females were released together with males, gravid females were actively "hunting" for males in order to lay eggs. In contrast, recently oviposited females hid in bushes and avoided conspecifics. Female behavior is, thus, characterized by her propensity to lay eggs on one hand and to avoid receiving them on the other (M. Katvala, A. Kaitala & J. A. Amat unpubl. data).

Males may have no choice if a female copulation depends on his propensity to accept foreign eggs as shown in a theoretical model (Härdling & Kaitala 2001). In order to mate, they need to stay close to a female, and thus are exposed to female egg dumping.

It is evident that egg carrying is beneficial to an egg-laying female. Individuals of the golden egg bug suffer at least some fitness costs from egg carrying, and egg carrying can be regarded as intraspecific parasitism. However, the kind of intraspecific parasitism, in which parasitism occurs independently of parental care, and where eggs are attached to bugs and carried passively by

conspecifics, has not been previously described.

Parasitism is not the whole explanation for male egg carrying because males seem to "accept" precopulatory eggs. A female mating propensity and a male acceptance of eggs seem to be crucial for egg carrying. The interplay between the sexes may result in evolutionarily stable solutions if a courting male acceptance of non-paternal eggs "relatively" often results in successful mating as shown by an ESS model (Härdling & Kaitala 2001). Thus, costly helping may evolve without reciprocity, or relatedness as a "best of bad job" — strategy as seems to be the case in the golden egg bug.

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