

FEMALE REPRODUCTION AND CONSPECIFIC UTILISATION IN AN EGG-CARRYING BUG

-Who carries, who cares?

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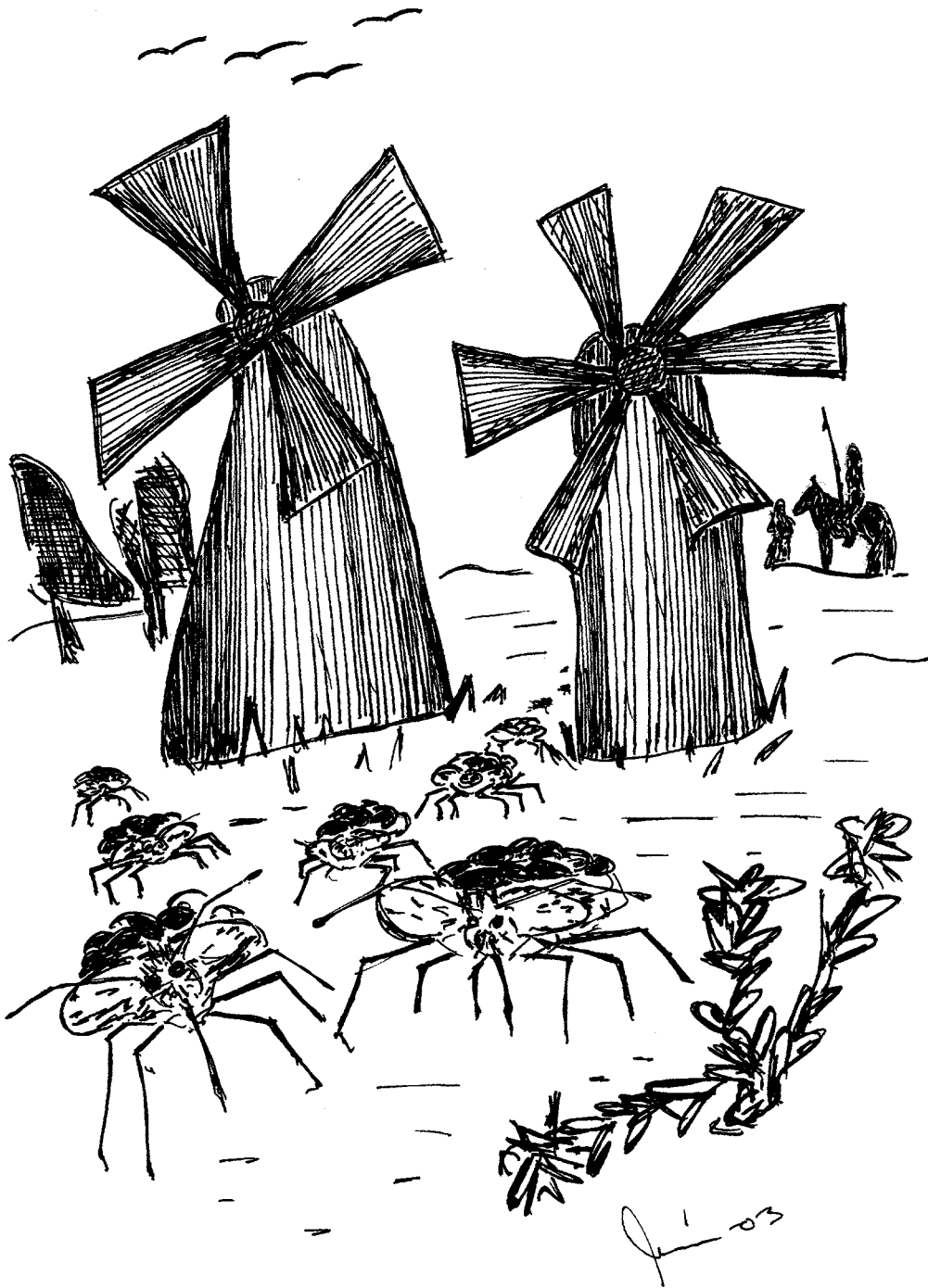
Abstract

Female ability to exploit conspecifics in reproduction may have unusual expressions. I studied the reproductive behaviour of the golden egg bug (*Phyllomorpha laciniata*; Heteroptera, Coreidae) experimentally in the field and in the laboratory. Female golden egg bugs lay their eggs mainly on the backs of conspecific males and other females. Non-parental eggs are often carried. Occasionally, the eggs are laid on the food plant (*Paronychia* spp; Polycarpea, Caryophyllaceae) of the species but typically, those eggs survive poorly due to egg parasitism and predation. I explored the dependence of female reproduction on conspecific presence and encounter rate. I also studied female current reproductive state (which depends on if she has recently oviposited) in relation to her activity as well as male choice of a female.

Female bugs preferred to oviposit on conspecifics when presented with a choice between a bug and a food plant. When alone females often did not lay eggs. Increased encounter rate with others increased female egg laying rate. Survival of carried eggs among bugs did not vary significantly although males received more eggs than females. Females with high current fecundity (mature eggs accumulated to reproductive tract) were more active than females with lower current fecundity (recently oviposited). Females with high current fecundity seemed to search for conspecifics to lay eggs on. Males also preferred to court females with high current fecundity. These females were more likely to oviposit immediately after mating, lowering the risk of female remating before oviposition.

To conclude, conspecifics are important egg-laying substrates for female golden egg bugs. Conspecific availability affects female egg laying and the rate of egg production in short term. In particular, males are necessary for egg-laying females and they typically receive unrelated eggs when they court females. Sexual interactions resulting from female polyandry are crucial factors that maintain female egg laying on the backs of males and other females in the unique reproductive system of the golden egg bug.

Keywords: egg laying, host selection, *Phyllomorpha laciniata*, polyandry



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Oulu, February 2003

Mari Katvala

List of original papers

This thesis is based on the following publications and manuscripts, which are referred to in the text by their roman numerals.

- I Katvala M & Kaitala A (2003) Conspecifics enhance egg production in an egg-carrying bug. Manuscript (accepted to Behavioral Ecology).
- II Katvala M & Kaitala A (2003) Encounter rate with conspecifics and female reproduction in an egg-carrying bug. Manuscript (submitted).
- III Katvala M & Kaitala A (2001) Egg performance on an egg-carrying bug. - Experiments in the field. *Oikos* 93: 188-193.
- IV Kaitala A, Katvala M, Ponsiluoma K & Amat A (2003) Hiders and seekers; female reproductive state and habitat choice in an egg -carrying bug. Manuscript.
- V Katvala M & Kaitala A (2001) Male choice for current female fecundity in a polyandrous egg-carrying bug. *Animal Behaviour* 62: 133–137.

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1 Introduction

1.1 Female reproduction and offspring survival

Female reproductive success is determined by the number of eggs that a female is able to produce during her lifetime and the survival rate of the offspring. However, due to trade offs among life history traits (e.g. offspring mortality, adult mortality, life span, clutch size etc.), female strategies to increase the survival of her offspring vary extensively among organisms (Roff 1992). For example, female cods (*Gadus morhua*) release millions of eggs floating into the water (Koli 1990) whereas female birds prepare a nest for their eggs that are incubated until hatching and nestlings are assisted until independence (Bennet & Owens 2002). However, irrespective of the number of offspring and parental post-natal or post-ovipositional assistance, selection of high quality nest site or egg laying substrate is a significant factor influencing female lifetime reproductive success. Sites should be safe from nest or egg predators and parasites (e.g., Lima & Dill 1990, Endler 1991, Begon *et al.* 1996). If parents desert the offspring after they are laid, as is the case in most insects, developmental needs and nutrient availability of offspring also affect a female's oviposition site selection (Thompson & Pellmyr 1991).

In nature many nest sites or oviposition substrates may be available to females but there is often considerable variation in the quality of the sites in terms of safety or nutritional value. The best sites may be limited in numbers, and there may be heterospecifics and conspecifics competing for them. For example, in open nesting birds where an average of 80% of the nests are lost due to predation (Ricklefs 1969, Martin 1992), nest sites with low predation risk may be in limited supply (Martin 1993) due to intraspecific and interspecific competition. Also, many phytophagous insects use very limited range of host plants (Janz 2002). Hence, if females have been unable to find the most suitable host plants they may be forced oviposit on plants where egg and larval performances are moderate (e.g., Minkenber *et al.* 1992, Mayhew 1997). Therefore, safe and high quality nest sites or egg-laying substrates can be considered as a resource for individuals. It is likely that there is a strong selection for female choice for safe sites and choice may be highly locally adaptive.

1.2 Interactions among conspecifics

In general, conspecifics have highly overlapping resource needs and increasing conspecific density is usually considered to reduce an individual's share of resources that are limited in supply (Milinski & Parker 1991, Begon *et al.* 1996, Sutherland 1996). Thus, conspecifics may affect each other negatively. However, when the density of conspecifics is not too high, conspecifics may also affect each other positively (see Andrewartha & Birch 1954, Sæther *et al.* 1996, Courchamp *et al.* 1999). For example, in a large group an individual's survival may be increased due to increased vigilance against predators and parasites or due to more efficient acquisition of food compared to individuals in a smaller group or alone (see Bertram 1978, Sæther *et al.* 1996 for examples). Reproductive success of both sexes may also be limited if individuals cannot find mates (see Parker 1978, Sæther *et al.* 1996). In addition, the presence of one or more conspecifics may have social effects on females present and consequently influence their reproductive output (i.e., social facilitation; Clayton 1978).

Conspecifics can also exploit each other and interaction may be asymmetrical. Acquisition of resources is often costly, and therefore individuals may be tempted to utilise or steal resources obtained by others to decrease their own costs. For example, in some kleptoparasitic solitary wasps (Vespidae), females steal prey items that are devoted to other's offspring or take over nest borrows that others have dug (Field 1989, 1992). Behavioural traits are also exploited. Providing of parental care (e.g., protect one's offspring against predators and parasites and deliver food) is a great cost for individuals (e.g., Gross & Sargent 1985, Clutton-Brock 1991). Costs of parental care include reduced possibility to produce additional offspring in the future and reduced survival due to increased predation risk or decreased foraging ability (see Clutton-Brock 1991). Hence, intraspecific cheaters are common in breeding systems with parental care (Brockman 1993). Egg dumping on conspecific's nest or egg masses is frequently described in birds (Petrie & Møller 1991, see Yom-Tov 2001 for the list of species) and in some fishes (DeWoody & Avise 2001) and insects (e.g., Tallamy 1985, Field 1992) that exhibit parental care. Raising the offspring from an unrelated individual is usually costly (but see Robertson 1998) because the host's own reproductive success is decreased (e.g., Rothstein 1990). To decrease the costs of misdirected parental care, a suite of anti-parasite mechanisms has evolved for hosts (Davies 2000). For example, parents increase their nest attentiveness when there is a risk of being parasitised (Tewksbury *et al.* 2002 for interspecific parasitism) and may also reject foreign eggs laid on their nest (Møller 1998).

1.3 Conspecifics as a resource

Conspecifics or their nests can be considered as a resource for an intraspecific parasite or when conspecifics benefit from each other (see Eggleston & Lipcius 1992). In species where females lay eggs on the bodies of conspecifics, conspecifics as such can be seen as a resource. Among insects, there are four taxonomically separate groups within Heteroptera (*Stenolemus arachniphagus*, Emesinae; Belostomatinae; *Plunentis*, Coreinae;

Phyllomorpha, Coreinae) where this is the case (Tallamy & Schaefer 1997). The best known of those groups are the giant water bugs (Belostomatinae) where only males carry the eggs on their back during egg development (Smith 1997). Eggs do not survive without aeration performed by males, and this is an example of exclusive paternal care (Smith 1979a, 1997). However, if eggs are laid on conspecifics of both sexes that are seldom parents to the eggs, intraspecific interactions are much more complicated. Egg-laying females may benefit from others by dumping eggs on their back but whether the others benefit is not clear. A female's preference of an egg laying substrate may also have consequences on her reproduction.

Female golden egg bugs (*Phyllomorpha laciniata*, Vill, Heteroptera, Coreidae) lay eggs on conspecific males and other females (Kaitala 1996). Occasionally eggs are laid on the leaves of the plants of the genus *Paronychia* (Polycarpea, Caryophyllaceae). The plants are also used for foraging. However, survival of the eggs laid on plant is poor due to high risk of predation by ants (Du Merle *et al.* 1978, Kaitala 1996) and parasitism by a wasp (*Gryon bolivari*, Hymenoptera, Scelionidae; Mineo 1984, Reguera & Gomendio 2002). Eggs laid on a conspecific's back are likely to have better survival than eggs laid on food plant (Kaitala 1996, Reguera & Gomendio 2002).

Egg carrying is costly because bugs carrying many eggs are more likely to be predated by ants and birds than individuals that do not carry eggs (Reguera & Gomendio 1999, Kaitala & Axén 2000, Kaitala *et al.* 2000). Sometimes bugs scrape off eggs laid on their body (Kaitala 1999) and they also often actively resist egg laying attempts (Miettinen & Kaitala 2000). Thus egg carrying seems to be unpleasant. Golden egg bugs commonly carry eggs that are not their own offspring. Eighty seven percent of the eggs carried by males are not sired by the carrier (Tay *et al.* 2003), and females are unable to lay eggs on their own body. Thus, it is the egg-laying female, which selects safe oviposition substrates for her eggs, and consequently utilises conspecifics to increase her offspring survival (Kaitala & Katvala 2001).

In this system, the sexes likely share a common interest to encounter each other but the motivations of the sexes to encounter are likely to be different. Males cannot force females to mate, and a female may reject a courting male and leave him only with non-parental eggs on his back. In the case of two females, they both have the selfish interest to oviposit on the back of the other one and not to accept anything in return. One goal of this thesis is to examine female egg-laying behaviour in response to the presence and availability of conspecifics and female flexibility in host use (conspecific *vs.* food plants). In many phytophagous insects, females close to oviposition accept less favourable or lower ranked hosts if the most preferred one(s) is not available (e.g., Minkenbergh *et al.* 1992). Females may also regulate their egg production according to the availability (or density) of host plants (Hopkins & Ekblom 1996, 1999). However, searching for and laying eggs on an immobile host plant (e.g., butterflies) is likely to be different than to search for and oviposit on a mobile conspecific bug. In nature, there is both inter- and intrasexual variation in the number of eggs bugs carry. This variation is examined in relation to female egg-laying by asking whether females are ovipositing on safe egg carriers. Alternative explanations are that eggs are laid equally on all available backs or eggs are laid on bugs that females happen to encounter.

The other goal of the thesis is to study female current fecundity and its effect on her behaviour and the male's response to females differing in their current fecundity. Current fecundity is defined as a categorising measure: a female has either more or less eggs in her reproductive tract that she can lay when a conspecific is encountered. In

phytophagous insects where eggs are laid on certain host plant or a range of hosts, females with high current fecundity increase their host searching efficiency (Minkenber *et al.* 1992). Host search may be costly (IV) and thus less fecund females may decrease their searching efficiency. Female behaviour may also be affected by the interest shown by males to mate and other females to lay eggs. Variation in female quality that is variation in current female fecundity may affect male's choice of a female (Parker 1983, Kirkpatrick & Ryan 1991, Owens & Thompson 1994). For males, it may be a costly option to mate with a female with low current fecundity.

1.4 The aim of the study

Specifically, in this thesis I explore the reproduction of the *Phyllomorpha laciniata* Vill from the point of view of an egg-laying female and egg recipients of both sexes. I study the dependence of egg laying and egg production on conspecific presence (I) and further egg-laying female's responses when a conspecific(s) is able to avoid the female (II). I also examine whether egg-laying females select conspecific hosts based on the best egg survival or whether alternative explanations apply (III). Female current fecundity may affect an individual's interest in encountering other bugs as well as her overall behaviour. Thus, I explore the activity and time allocation of females differing in their current fecundity both empirically and experimentally (IV). Finally, I examine egg receiving of males during courtship and the consequences of his choice of a female in terms of female egg laying after copulation (V).

2 Materials and methods

2.1 Natural history of the golden egg bug

The golden egg bug lives in the Mediterranean area, and is mainly found in dry sandy meadows with open sand growing low vegetation including food plants of the species (Jeannel 1909, Reuter 1909, Kaitala 1996). Bugs are found singly or in small groups of two or three individuals on inhabited areas during the reproductive season (Katvala M & Kaitala A, unpublished data). Usually individuals are on food plant patches. Bugs are univoltine (a single generation per season) in northern Spain but have a (partial) second generation in southern Spain (Kaitala A, Katvala M & Amat JA, unpublished data). They overwinter as adults and start to reproduce in the following spring. Female bugs lay clutches of a few eggs every 2–3 days in the laboratory (Kaitala & Miettinen 1997).

Egg laying does not follow immediately after mating but there can be hours or days between copulation and oviposition (Kaitala & Miettinen 1997). Copulations are frequent, and they are long-lasting, often more than 10 hours (Kaitala 1996, Kaitala & Miettinen 1997). In the field, females carry on average 2.5 eggs (range 1–14, $n = 378$), and males on average 5.5 eggs (range 1–28, $n = 440$) in the middle of the reproductive season (Kaitala 1996). The number of eggs and shells carried increase as the reproductive season proceeds (Reguera & Gomendio 2002). Sex roles are not reversed because males are more eager to mate than females, and females do not compete for males. Male mating attempts are also commonly rejected, and egg carrying does not increase male mating success (Kaitala 1998).

Except for carrying eggs on their back, bugs do not provide any visible care for the eggs. Eggs are white when they are laid, and developing eggs gradually turn golden before hatching (Kaitala 1996). In the laboratory, eggs develop in 10–14 days. After hatching, larvae leave the host's back but the egg shells remain on the back. One bug can carry eggs that differ in their developmental state and eggs that are laid by many females. Eggs in this species are large; one egg equals 4% of a male's and 1.2–2.0 % of a female's body weight (Miettinen M, Katvala M & Kaitala A, unpublished data). Female bugs are usually larger than males, and their body length is approximately one cm.

2.2 Study sites

Field experiments were carried out in native habitat of the golden egg bug in south western Spain in Andalusia near the city of El Puerto de Santa Maria (I, III, IV) and in north eastern Spain close to the village of Santa Clement in Catalonia (III, IV). In Andalusia, the field site was an open sandy meadow with an ample supply of the bug's food plant and several bushes of *Retama* spp. In Catalonia, the study site was an abandoned sandy vineyard with lots of *Paronychia* spp. Bugs used in the laboratory experiments were primarily collected from these sites but individuals from other Andalusian (IV) and Catalan populations were also used (V). Both field and laboratory experiments were carried out from late April to mid June when bugs are reproductively active.

2.3 Preparations for the experiments

Prior to the experiments, several procedures were repeated for all experimental bugs. All the eggs carried were gently removed, and each bug was individually marked with a paint spot for later identification. As an estimate of size, I used the length from the dorsal side from the beginning of the pronotum to the end of the abdomen. If the experiment was carried out in an enclosure (in the laboratory or in the field), wing tips were cut to prevent the bugs escaping by flying, and the walls of the enclosures were coated with flulon (polytetrafluoroethylene D) to prevent climbing out from the enclosure. In the field and in the laboratory, enclosures were uncovered. In the laboratory, bugs were kept in large containers (35 × 20 cm, 25 cm high) that contained an ample supply of planted food plant when they were not being used in experiments.

2.3.1 *Female current fecundity*

In this thesis, I define female current fecundity as a categorising measure of the number of eggs that a female has in her reproductive tract ready to be laid. Females that are expected to have more of those eggs are called gravid females, and females that have less of those eggs are called non-gravid females. Female current fecundity is easy to manipulate because they accumulate mature eggs in the reproductive tract if isolated from other bugs and will lay many of the eggs if placed with other bugs. Kaitala & Smith (2002) showed that females collected directly from the field have more mature eggs in their reproductive tract than females that have had a possibility to lay eggs. Gravid females were caught directly from the field (IV, V) or they were prepared by isolating a female from others for two or three days (IV). Non-gravid females were obtained by keeping field-caught or laboratory females in a plastic box (20 × 20 cm) for 24 hours prior to an experiment for egg laying.

2.4 Descriptions of the studies

2.4.1 *Egg laying, conspecific presence and encounter rate (I, II)*

I studied the effect of conspecific presence on female egg laying, accumulation of eggs in the reproductive tract, and egg production in the field (I). This was examined by enclosing one or two females in a netbag (20 × 25 cm) that was tied on a sprig of food plant that was naturally growing at the study site. Thus female(s) had a continuous access to fresh food and a possibility to lay eggs on the plant. The experiment lasted six days. I altered conspecific presence after three days in half of the netbags. The four treatments were as follows:

1. three days: alone → three days: alone
2. three days: paired → three days: paired
3. three days: paired → three days: alone
4. three days: alone → three days: paired

The number of eggs that females laid on a conspecific body or on a food plant was counted after both periods. After the experiment, I dissected the females to count the mature eggs in their reproductive tracts. As a measure of egg production, I used the sum of eggs laid during the experiment and the number of eggs in reproductive tract for each female.

I studied the effect of conspecific encounter rate on female egg laying in the laboratory (II). Encounter rate was manipulated by placing two individuals in different sizes of enclosures (small enclosure 7 × 17 cm and large enclosure 21 × 30 cm). In the small enclosures, bugs were unable to avoid each other, and therefore this treatment gave an estimate of how many eggs a female will lay with unlimited access to lay eggs on another bug. In the large enclosures, vegetation was complex and there was plenty of space for bugs to hide and avoided the egg-laying female. The two experiments carried out and treatments within were as follows:

- Experiment A) Two females in small enclosure
 Two females in large enclosure
- Experiment B) One female and one male in small enclosure
 One female and one male in large enclosure
 One female and two males in large enclosure
 Two females and one male in large enclosure

The two experiments lasted for eight days and I counted the number of eggs each female laid on conspecific back daily. I also monitored the number of matings, and after the experiment, I counted the eggs laid on food plant for Experiment B.

2.4.2 Egg survival and egg receiving (III)

Egg survival relative to conspecific host's sex, body size and egg receiving were studied in Andalusia and Catalonia. The number of eggs and their position on the bug's body were recorded when individuals were collected for the experiment. Experimental eggs were laid by females under controlled conditions except for one Andalusian study site (site 3) where bugs carried their original eggs. The effect of paternity on egg survival was studied in Catalonia where males carried eggs that were received before or after mating. I drew egg-maps of each bug to identify and to monitor the survival of each experimental egg since bugs may receive eggs or lose eggs during the experiment. Marked bugs were recaptured after two days in Catalonia. In Andalusia, recaptures were carried out three and six days after the initial release. The distribution of eggs on recaptured bugs was compared to the corresponding egg-maps.

2.4.3 Female current fecundity and her behaviour (IV)

The effect of female current fecundity on behaviour was studied both in the field and in the laboratory. First, I examined if females captured from different microhabitats (open, covered) varied in their current fecundity in Andalusia. Female current fecundity was estimated as the eggs laid during the 24 h immediately after capturing. Second, I examined whether differences in microhabitat choice were caused by differences in female current fecundity. In field site in Catalonia, I used a two piece enclosure and introduced gravid and non-gravid females in the inner enclosure and males in the outer enclosure. There was a bush of *Lavandula sp* in the inner enclosure to provide hiding spots for the females. Once a female had left the inner enclosure, she was unable to return due to the fence that allowed only unidirectional movement. The fence also prevented males from entering the bush area and thus affecting a female's decision whether to leave or not. I began recaptures 2.5 h after the experiments started. At recapture, it was noted whether a female had left the bush or not, the number of eggs received (for both sexes) and mating status. I also performed a manipulative experiment in the laboratory in order to follow how current fecundity affected the activity of an individual female in the presence of a male. Each enclosure consisted of one gravid and one non-gravid female and one male. They were followed for 4 h. The time (minutes) that each female spent in an open area visible for monitoring or covered under plant material was recorded. The number of male courtings and eggs laid by females were also counted.

2.4.4 Female current fecundity and males (V)

I examined whether males select females according to their current reproductive state, whether courtship is costly for males and if males gain any benefit from their choice of a female. A focal male was enclosed with a gravid and a non-gravid female. I followed the

courtships performed by a male. When a focal male began to copulate with one of the females, I removed the other female and placed it with a new male. This was done to estimate how quickly and how many eggs the focal male would have received if he had selected the other female. Once copulation was completed, I measured the time from the end of copulation to female egg laying in both boxes. I also counted the eggs laid before the second copulation, which often took place a day or two after the first one.

3 Results and discussion

Females clearly preferred to lay eggs on a conspecific back rather than on a food plant when they were able to choose, although a few eggs were laid on plant (I, II). Females laid and produced fewer eggs when they were separated from other bugs (I) or when a conspecific was able to escape an egg-laying female (II). An individual's egg laying was flexible in the sense that females ceased egg laying when isolated from others and became significantly more active when introduced with another bug (I). Therefore, egg laying of golden egg bugs depends on the presence (I) and availability of conspecific to lay eggs on (II). Thus conspecifics are an oviposition resource for reproducing females (II).

Egg survival on bugs' backs was independent of the carrier's sex and body size as well as the paternity status of the egg to the carrier (III). Males received more eggs than females. It seems that more eggs were laid on males because they were the ones that females encountered (II, IV), and not because they were "safe" egg carriers (III).

Female current fecundity affected an individual's activity as indicated by microhabitat use and time budget devoted between open and covered microhabitats (IV). Females with higher current fecundity seemed to search for conspecifics to lay eggs on where as the ones with lower current fecundity were less active although this division was not always clear (IV). Female egg laying on encountered individuals (II, III) causes a problem for males because when they court females they receive eggs fertilised by other males on their back (V). Additionally, males preferred to court females with higher current fecundity (IV, V). This is advantageous for males since females with higher current fecundity lay eggs faster after mating than do females with lower current fecundity (V). As a result, the risk of female remating before oviposition is reduced.

3.1 Egg laying on conspecifics

In insects, the female determines the developmental environment for her offspring because eggs and larvae are generally poor in dispersing (Janz 2002). Females usually desert eggs when they are laid (Tallamy & Brown 1999), and thus they should prefer sites with low predation and parasitism. The site should also provide proper

microenvironmental conditions for eggs, and after hatching, both proper nutrition and microenvironment for larvae. In general, there is a trend towards host specialisation among insects, and only a limited range of host plants or only one plant are accepted as hosts (Janz 2002). However, a scattered distribution of hosts may cause problems for reproducing females because host search may be a costly activity (Janz 2002, see IV). When the best egg laying substrates are rare, there are two hypotheses regarding the behaviour of females of phytophagous insects that seek a host plant for their eggs and desert the eggs after they are laid (e.g., Minkenberg *et al.* 1992, Hopkins & Ekbom 1996, 1999). Females will either continue egg production and accept to lay eggs on lower ranked hosts, or they will suppress egg production until better ranked hosts are encountered. In nature, individual golden egg bugs have a patchy distribution in the inhabited area. From one patch, a few bugs can be found but aggregations are seldom abundant. Bugs are never right next to each other (unless mating) and they are usually some tens of centimetres apart (Katvala M & Kaitala A, unpublished data). Female golden egg bugs' difficulties to find a conspecific host to lay eggs on are possibly different from female insects that search for an immobile host. Similarly to birds that suffer brood parasitism (Rothstein & Robinson 1998), bugs often try to prevent females from laying eggs on their back (Miettinen & Kaitala 2000). A female bug must be able to begin oviposition immediately when she encounters a conspecific or otherwise the opportunity may be lost. Thus, the problems of female bugs resemble the problems faced by parasitoids that oviposit in or on living heterospecific hosts (see Godfray 1994).

In general, increasing the number of conspecifics is suggested to have a declining effect on an individual's reproductive success or survival (Sutherland 1996). However, in species where conspecifics are resources as such, the effect of the increasing density may be positive when population density is low (*sensu* Allee effect, in Sutherland 1996). In the golden egg bug, when conspecifics are absent or infrequently encountered, female reproduction is decreased (I, II). If encounters are infrequent females lay larger proportion of their eggs on food plant. This is likely to decrease egg survival (II, see below). Thus increasing conspecific density seems to benefit both female reproduction and offspring survival. However, having too many conspecifics around may be costly if, for example, predators are attracted by dense aggregations or due to reasons related to receiving eggs (see 3.3.3).

3.1.1 Limiting resource

Conspecific males are limiting resources for females in some species. For example, females deposit eggs on the backs of males in Belostomatidae giant water bugs (Smith 1997) and males brood offspring in their body cavity or brood pouch in seahorses and pipefishes (Syngnathidae; Berglund 2000). In these taxa, female reproduction is limited by the availability of space on male's back or in the brood pouch (Berglund *et al.* 1989, Ichikawa 1989, Kraus 1989). In the golden egg bug, space on the back of a bug is not a limiting factor for egg-laying females because females choose conspecific hosts independently of the number of eggs they already carry (Kaitala 1998, see also III).

When a female bug has unlimited access to lay eggs on another bug's back, she lays approximately one egg per day independent of the partner's sex (Kaitala & Miettinen

1997, Kaitala & Smith 2002, I, II). In the laboratory, females decrease their egg laying rate when conspecifics of both sexes were able to avoid the egg-laying female (II). This indicates that conspecifics are potentially a limiting resource for females at least in the short term. The preference to lay on conspecifics may be costly in terms of limiting the number of offspring produced, and there may be a trade off between the number of eggs laid and offspring survival. Using indirect evidence Kaitala & Smith (2002) suggested that conspecific availability limits female reproduction i.e. egg laying in the field. They found that field-collected females have significantly more mature eggs in their reproductive tract than females that have been enclosed with other females for one and a half days to lay eggs. My studies (I, II) suggest that females are able to regulate their egg production according to the availability of conspecifics and they accumulate eggs in their reproductive tract when alone. Further studies to examine female lifetime reproduction and egg-laying rates in different populations would be valuable. Factors such as temporal and spatial variation of operational host density (i.e., individuals available for oviposition at the time, I) should also be taken into account.

3.1.2 Social effect

The presence of conspecifics can induce female reproduction or reproductive output. This is called social facilitation (Clayton 1978). For example, in some simultaneously hermaphrodite fresh water snails (*Biophalaria glabata* Vernon 1995, *Balea perversa* Baur & Baur 2000) females lay more eggs when reared with another snail than when reared alone. Some female fruit flies (*Ceratitis capitata*) also initiate ovipositor boring to the fruit that is already occupied by a conspecific female. In the golden egg bug, female reproduction is increased when a conspecific is present (I). Female bugs decreased the number of eggs laid when conspecifics were able to avoid them although they were at maximum within tens of centimetres apart (in large enclosure) compared to females that were in small enclosures (II). It seems that the social factor (the presence of a conspecific in an environment) is not enough to induce females to lay eggs but the most important factor for female reproduction are opportunities to oviposit on conspecifics (II).

3.1.3 Eggs laid on food plant

In the field, egg predation and parasitism are serious threats to eggs laid on a food plant. A predatory ant species *Pheidole pallidula* (Nylander, Hymenoptera, Formicidae) inhabits the same area as the golden egg bugs (Bernard 1968, Kaitala 1996, Kaitala *et al.* 2000). Workers of the ants detect and forage effectively on arthropod eggs (Du Merle *et al.* 1978) and corpses (Retana *et al.* 1991, 1992) including golden egg bugs and their eggs laid on plant (Kaitala 1996, Kaitala *et al.* 2000). Other ant species have also been observed to forage the eggs (Kaitala A, unpublished data). In an experiment by Kaitala (1996), none of the eggs deposited on food plant survived for more than one week; a time period that is not long enough for an egg to develop. A substantially large proportion of

eggs laid on food plant are also parasitised by a Scelionidae wasp (Mineo 1984, Reguera & Gomendio 2002). Thus, the survival of eggs laid on food plant appears to be poor.

Food plant was typically not an alternative egg-laying substrate for females but they did occasionally lay some eggs on plant (I, II). It is not known whether those eggs were laid on purpose or whether a female had failed to lay her eggs on a conspecific individual and after some threshold time was unable to hold an egg from being laid. In giant water bugs, Smith (1979b) suggested that females with high current fecundity dispose the oldest eggs on vegetation to be able to produce new, more viable ones. In those species, eggs laid on vegetation do not survive because eggs require continuous aeration (Smith 1997). Whether egg disposal due to increased egg viability applies to the golden egg bug is unknown. In my experiment, a smaller proportion of eggs was laid on food plant when encounter rate with conspecifics was increased (II). This suggests that frequent encounters with conspecifics may increase female egg survival.

Host preferences may vary among insect populations (e.g., Janz & Nylin 1997). In a Sicilian (Italy) golden egg bug population located approximately 1500 meters above sea level, females lay eggs mainly on plants that differ from the ones reported in Spain and Southern France (Mineo 1984). Plant species of the genus *Paronychia* that serve as food for Spanish bug populations are absent in the Sicilian population (own observation). Reguera & Gomendio (1999) also report that females are prone to lay eggs on *Paronychia* spp. in populations from central and south eastern Spain than the females from populations studied in this thesis. Variation in female golden egg bug's propensity to lay eggs on food plant rather than on a conspecific host may be due to several factors. Females may choose to lay eggs on plants instead of costly seeking for conspecific (IV) if the densities of egg enemies are low. Female propensity to lay eggs on plant may also vary during the reproductive season if there is temporal variation in the densities of the enemies. In addition, more eggs may be laid on food plant towards the end of the breeding season because the likelihood of an egg carrier dying may increase. However, it is not known whether egg survival on plants or on dead bugs is higher because the same omnivorous enemies forage both the eggs laid on plants and bug carcass (Du Merle *et al.* 1978, Retana *et al.* 1991). To conclude, these indicate that variation in female egg laying is locally adapted to prevailing ecological conditions.

3.2 Female current fecundity

The number of mature eggs in a female's reproductive tract varies depending on whether she has recently oviposited or not. Although females seem to regulate egg production according to the presence of others (I, II), they usually have some mature eggs in their reproductive tract ready to be laid. In insects, female host searching activity increases with the number of mature eggs in the reproductive tract (see Minkenber *et al.* 1992). Female golden egg bugs with high current fecundity show increased activity (IV). Those females were more often found from open microhabitats than recently oviposited females, and it seems that they were searching for an oviposition site rather than a mating partner. A female bug that has recently oviposited has several reasons to stay in a safe site until more mature eggs accumulate to her oviduct (IV). She may avoid egg-laying females because egg carrying is costly (Kaitala *et al.* 2000) or male harassment (Clutton-

Brock & Parker 1995) because it may be costly as well. A hiding female may also avoid predators (cf., waterstriders, Sih 1988). The reasons listed are not mutually exclusive. In future studies, in addition to microhabitat selection, one could explore spatial distribution of females relative to their current fecundity. A measure of female current fecundity that could be used is time interval between introduction into a small box with another bug to the first egg laying. The time interval between introduction and oviposition could better describe whether a female is in an urgent need of conspecific oviposition site or not.

For males, females that differ in current fecundity may differ in value as a mate (see 3.4). In the laboratory, males preferred to court females with higher current fecundity (IV, V). In the field, it is likely that males encounter mainly females that actively search for oviposition substrates that are females with higher current fecundity.

3.3 Egg carrying

In territorial fish, females choose both oviposition site and mating partner simultaneously because they mate with a territory-owning male (Pruett-Jones 1992, Jamieson 1995). Thus, the effects of those factors on female mate choice are difficult to separate (Jamieson 1995, Kraak 1996). Studies seem to support the hypothesis that females choose their mates according to the quality of his territory (Pruett-Jones 1992, Kraak & Weissing 1996, Forsgren 1997). In pied flycatchers (*Ficedula hypoleuca*), it is also shown that female choice is based on the quality of the territory (Alatalo *et al.* 1986, but see Siitari *et al.* 2002). However, in the golden egg bug, mating and egg laying can be separated because females lay eggs on males without mating (Kaitala & Miettinen 1997, Miettinen & Kaitala 2000, V) and eggs are laid on other females as well (I, II). In their mate choice, female bugs prefer large males (Keskinen E & Kaitala A, unpublished data) but courtship activity of males also seems to have an influence (Kaitala 1998).

Courting males and especially mating pairs are easy targets for egg laying (Kaitala & Miettinen 1997). During courtship, a male is in close body contact with a female, and therefore unable to avoid receiving eggs (V). An egg-laying female faces no resistance when dumping eggs on a mating individual that is in genitalia contact with her/his partner (Kaitala 1996). In the field, males carry more eggs than females (Kaitala 1996, III), and there is also large variation in the number of eggs carried within males ($n = 224$, range 0–20, mean \pm SE = 3.40 ± 0.22) and females ($n = 180$, range 0–6, mean \pm SE = 1.10 ± 0.10). The numbers are obtained from the data from egg survival experiments carried out in Andalusia in late April prior to manipulations of the eggs carried (III). Thus the question is whether females oviposit on bugs that are able to carry eggs safely or whether there are other factors explaining variation in the number of eggs carried.

Egg survival and egg loss did not differ significantly among bugs of different sex or size (III). Egg loss was surprisingly high: 30–80% of the bugs that carried experimental eggs had lost one or more of them after six days. However, egg loss correlated positively with the number of eggs carried. It was highest at the site where individuals carried their original clutches. This suggests that egg loss from backs may be even more common than suggested by the experiments carried out with manipulated clutch sizes. The reason for egg loss is not known but eggs can be taken by ants (Kaitala *et al.* 2000, Miettinen 2001) or bugs may scrape eggs off from their backs (Kaitala 1999, II). Thus, it seems that

factors other than female choice for safe egg carriers are needed to explain the distribution of eggs on bugs' backs.

3.3.1 Why males carry more eggs than females

The unequal distribution of eggs between the sexes is due to females ovipositing more on males, and not due to lower egg survival on female hosts (III). Three factors causing females to lay more eggs on males than on females have been identified. First, males will carry more eggs than females if eggs are laid evenly on both males and females (Kaitala *et al.* 2001). For example, in a group of two males and two females, two thirds of the eggs will be laid on males due to the fact that a female can not oviposit on herself. Although, in the field, males usually carry twice as many eggs as female, there is substantial intrasexual variation in the numbers of eggs carried (Kaitala 1996, see above).

Second, in certain conditions, females may actively select males as hosts due to better egg survival on them. Egg survival is decreased in some populations due to an egg parasitoid (Mineo 1984, Kaitala 1996, Reguera & Gomendio 2002). Eggs carried by females are relatively more often parasitised than eggs carried by males (Kaitala 1996). The bias may result if females receive their eggs more often than males in microhabitats where the parasitoid easily finds an egg-laying female (see below for the discussion when females receive their eggs). In infected populations, females may prefer to oviposit on males due to a lower proportion of parasitised eggs.

Third, females may try to lay eggs on all bugs they encounter. Therefore, males may receive more eggs if egg-laying females encounter males more often than other females. This is highly likely because males approach females with sexual intentions: courting and mating (Kaitala & Miettinen 1997, Kaitala 1998, V). In addition, females that stay at covered microhabitat may be unavailable as hosts (II, IV). If sex ratio of the population is male biased, male-male competition after mating may cause that males stay close to females after copulation or a new male is ready to court a female when she is freed from the previous copulation (see Kaitala 1998). I observed this kind of behaviour when I carried out the laboratory work for paper II. When two females were enclosed with one male in that experiment, instead of the females competing for the male, he responded to the availability of females by decreasing mating duration (II). The average number of matings per female in the treatment did not significantly differ from the other treatments even though there was only one male in the enclosure. However, in the field sex ratio is usually equal. All three factors mentioned above may act simultaneously causing females to lay more eggs on males than on other females. In the light of previous studies (Kaitala & Miettinen 1997, Kaitala 1998, Miettinen & Kaitala 2000) and this thesis (II, III, IV, V) it seems that interactions between the sexes is the most important reason why males receive and carry more eggs than females. Intrasexual variation in the number of eggs carried by males is likely to be caused by the variation in their courting activity (Kaitala 1998). Active males are the ones that receive most eggs.

3.3.2 Female egg carrying

Female egg carrying is puzzling because foreign females that are unlikely to be close relatives always carry the eggs (see Miettinen 2001). In addition, I have never seen any indication that two females would trade eggs with each other, and it seems that females avoid each other if possible (II, IV). However, if a host searching female encounters another female, she is likely to try to oviposit on her back.

The fact that eggs carried by females were better positioned than eggs laid on males indicates that females receive eggs mainly during copulation when individuals are unable to resist oviposition attempts (III). In the field, mating females have been found to carry more white, recently laid eggs than single females (Kaitala 1996). Further, there is some evidence from the laboratory that when a female oviposits on a mating pair, she lays the egg on female back more often than on male back (Kaitala A & Katvala M, unpublished data). The reason for this is unclear particularly since in parasitised populations egg survival on female back may be lower than egg survival on male back (Kaitala 1996). It is most probable that interactions between the sexes are likely to contribute to the opportunity for some eggs to be laid on females.

3.4 Egg laying, egg carrying and conspecifics

Sex ratio of the group affects female egg laying as well as egg receiving, and it would be interesting to examine this in natural circumstances. Especially, females seem to benefit from the presence of males at least in short term because they are easy targets for egg laying with their sexual intentions (Kaitala & Miettinen 1997, Kaitala 1998, II, III, IV, V). When the sex ratio is male-biased, female reproduction and egg survival may be the highest due to male courting activity. When female-biased sex ratios occur, males may be the ones that receive the most eggs but female egg laying or egg survival may be decreased because the encounter rate with conspecifics (mainly females) is decreased. In addition, whether females benefit in terms of lifetime reproduction should be examined.

Reproduction of female bugs is increased proportionally with encounter rate with conspecifics (II). Therefore, females are likely to benefit from increasing conspecific density. However, for a male the consequences of increasing group size are not necessarily only positive because they are likely to receive more non-paternal eggs to carry during courtship or copulation. This is because the proportion of females with whom they have not mated increases in the group. Increase in the number of males in the group also increases the variation in mating success of males. Hence, differing density optima of the sexes may affect their mobility patterns in the field due to their search of breeding groups of optimal sizes.

3.5 Males and polyandrous females

Mating with more than one male results in the sperm of different males competing for fertilisation in the female's reproductive tract (see Birkhead & Møller 1998), and thus males become uncertain of their paternity (e.g., Parker 1970, Eberhard 1996). In insects, it is usually the last mated male who fertilises the eggs (Simmons & Siva-Jothy 1998) but the proportion of eggs he sires will decrease in time (Parker 1998). This also seems to be the case in the golden egg bug although the data is limited (Miettinen 2001). In general, selection is predicted to favour males that can manipulate female's post-copulatory behaviour by decreasing her willingness to remate or increasing the egg laying rate temporarily after copulation (Thornhill & Alcock 1983, Simmons & Siva-Jothy 1998). In my studies, male golden egg bugs gained an immediate benefit from their mate choice by preferring females with high current fecundity that were likely to oviposit soon after copulation (V, see also IV). This reduces the risk of the female remating before oviposition. Although females with higher current fecundity laid eggs before copulation, they had eggs to be laid soon after copulation (V).

Long copulation duration may be male golden egg bug's mechanism to assure paternity. Males seem to "control" the copulation termination because male genitalia is a hook-like organ (Borgmann M, unpublished data), and a few times I have seen a female carrying a male corpses attached to her genitalia in the field (own observation). Males seem to increase copulation duration in the presence of male-male competition and correspondingly decrease the duration when competition is lacking (Niemelä T & Kaitala A, unpublished data, see also II).

Male golden egg bugs face a serious conflict because in order to avoid receiving non-paternal eggs they have to avoid encountering females (Härdling & Kaitala 2001). Females may also cheat them by refusing to mate with the recipient male after laying an egg (V). Female multiple mating seems to be the main factor maintaining egg carrying in the golden egg bug. This is because there are always courting males and mating pairs for females available to lay eggs on, although others seem to try to avoid receiving eggs if possible (Miettinen & Kaitala 2000, II) and they are reluctant to carry the eggs (Kaitala 1999).

3.6 Who carries, who cares?

The breeding system of the golden egg bug differs greatly from that of the parentally caring insect species where parent(s) care their own offspring by staying with the eggs after oviposition (Tallamy & Brown 1999, Tallamy 2000). For example, in giant water bugs (Smith 1997), females both mate and lay eggs immediately after mating on the male's back. In those species, a male always demands copulation before he allows a female to lay eggs on his back, and requires copulations repeatedly during an oviposition bout (Smith 1997). Further, caring males suffer decreased foraging possibilities (Smith 1997). In the golden egg bug, a microsatellite analysis shows that 87% of eggs carried by males are not fertilised by the carrier (Tay *et al.* 2003). In addition, females always carry eggs of other females. They carry approximately 30% of the eggs in the study populations

for this thesis (Kaitala 1996, III, IV, see 3.3). In natural populations, 90% of the eggs carried are not carrier's own eggs. There can also be a delay of hours or days between copulation and oviposition (Kaitala & Miettinen 1997, V) although males prefer females that lay eggs soon after copulation (V). In small populations, it is possible that males carry mainly their own eggs if they repeatedly encounter the same females. However, male egg carrying seems more likely to result from his effort to gain matings rather than from active care of his offspring at the cost of his future offspring. Egg-carrying individuals are unlikely to suffer from lack of nutrition because they mainly live on their food (Miettinen 2001). These main factors (also see Kaitala *et al.* 2001 for a more detailed list) suggest that the impetus to carry eggs is not the father's investment in increasing his offspring survival. Rather, it seems that accepting non-parental eggs during courtship is a male's investment to ensure mating success (see also Hårdling & Kaitala 2001). Increasing offspring survival does not explain why females carry one third of the eggs carried in the field because they are always carrying other females' eggs.

Host choice and search of an egg-laying female can be considered as a form of maternal care (definition of parental care by Clutton-Brock 1990: "*Any form of parental behaviour that appears likely to increase the fitness of the parent's offspring*") where she counterbalances low oviposition rate by selecting safe hosts for her eggs (see Janz 2002). In the golden egg bug, an egg-laying female prefers to lay her eggs on safe hosts (i.e., conspecifics) Bugs seem to try to avoid receiving eggs if possible (Kaitala 1999, Miettinen & Kaitala 2000, II, IV) most probably because there are survival costs to carry the eggs (Reguera & Gomendio 1999, Kaitala & Axén 2000, Kaitala *et al.* 2000). Thus, egg carrying can be considered as a form of intraspecific parasitism where mothers increase their offspring survival by utilising conspecifics (Kaitala & Kaitala 2001, Kaitala & Katvala 2001).

4 Concluding remarks

In nature, females employ numerous strategies to increase the survival of their offspring. For example, by covering their eggs with some substance to ensure protection, remaining with the eggs and/or larvae and expelling predators and parasites, or letting the father take care of the offspring. A convenient way to increase offspring survival is to utilise conspecifics by cheating them so that they perform a service that increases the survival of the offspring. Conspecifics, particularly males, are important egg-laying resources for female golden egg bugs because the survival of eggs laid on conspecifics is likely to be higher than that of the eggs laid on a food plant. Female bugs lay and produce more eggs when they are able to lay on conspecifics (I, II). In addition, when given a choice they will preferentially lay on a conspecific as opposed to the food plant. If alone, they predominantly stop laying eggs. The opportunities to oviposit on conspecifics induces female egg laying more than conspecific presence only. However, the preference of female bugs to lay eggs on conspecifics may be costly in terms of reduced reproduction at least in short term (II). Female lifetime reproduction was not studied here. Studies indicate that, in the field, conspecifics may be in limited supply (Kaitala & Smith 2002, II) although it is not clear how this is related to female current fecundity and her egg production. If conspecifics are unavailable for a few days, eggs accumulate in the female reproductive tract but if unavailability continues for longer, egg production seems to cease. Egg survival on the backs of males did not differ significantly from egg survival on female backs so other factors are likely to explain why males carry more eggs than females in the field (III). Encounter rate with the others affects female egg laying (II), and further sexual interactions seem to determine which bugs receive eggs (Kaitala & Miettinen 1997, Kaitala 1998, III, IV, V).

This thesis sheds some light to the peculiar reproductive system of the golden egg bug by providing data on egg-laying behaviour from both field and laboratory experiments. However, further research to study the effect of conspecific density and natural enemies (egg predators and parasites) on female lifetime reproductive success and her choice of an oviposition substrate would be valuable in further understanding the evolution of this unique system.

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