Predation costs associated with parental care in the golden egg bug *Phyllomorpha laciniata* (Heteroptera: Coreidae)

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Parental care will evolve when the benefits in terms of offspring survival are greater than the costs to the parents. Costs have been classified as reproductive and survival costs. Greater predation rates among adults caring for young are included among survival costs, but few studies have been able to demonstrate such a link. Among golden egg bugs (*Phyllomorpha laciniata*) females can lay eggs on plants, males, or other females; adults carry the eggs until they hatch. Using an experimental approach, we show that adults carrying eggs are more likely to be preyed upon by birds than adults without eggs. These greater predation rates may be the consequence of adults being more easily detected by predators when carrying eggs, and/or to their reduced ability to escape, as most eggs are carried over the wings, making it impossible for individuals carrying eggs to fly. Despite these survival costs to carrying adults, caring for eggs is favored by natural selection because it greatly increases the survival of offspring.

Key words: golden egg bug, Heteroptera, reproductive costs, *Phyllomorpha laciniata*, predation, parental care. [Behav Ecol 10: 541–544 (1999)]

Life-history theory predicts that parental care will evolve when the benefits in terms of offspring survival are greater than the costs to the parents. Although the benefits for offspring tend to be fairly obvious and easy to measure, the costs for parents have proven more difficult to detect. Some studies have found no evidence of reproductive costs, while others have (for a review, see Clutton-Brock, 1991; Lindén and Möller, 1989; Reznick, 1985). These contradictory results have stirred some controversy as to whether reproduction is costly (Bell, 1980; Jönsson and Tuomi, 1994; Partridge, 1992; Partridge and Harvey, 1985, 1988; Reznick, 1985, 1992). Several factors can obscure the existence of costs: (1) interindividual differences in body condition within populations, which influence the level of investment by parents; (2) differences in the availability of resources over time and between populations, which determine the magnitude of the cost; (3) the existence of costs expressed in the long-term (for a review, see Clutton-Brock, 1991). These confounding factors can be overcome by using an experimental approach.

The costs derived from parental care have been classified in two categories: (1) reproductive costs associated with a decrease in future fecundity, such as loss of mating opportunities, extended intervals between reproductive events, and reduced number of offspring in the next reproductive bout; and (2) survival costs that can be a consequence of the energetic demands associated with parental care (which can make individuals more susceptible to predators or pathogens) or due to a decrease in mobility, which can increase predation risk (Clutton-Brock, 1991; Shine, 1980).

Greater predation rates among adults caring for young are included among survival costs, but few studies have been able to demonstrate a direct link. Most studies measure predation risk indirectly in terms of a shift in habitat selection, changes in activity levels and escape tactics, or in terms of a decrease in locomotor performance (for a review, seeMagnhagen, 1991). Reduced locomotor capacity has been demonstrated in pregnant snakes and lizards (Bauwens and Thoen, 1981; Brodie, 1988; Cooper et al., 1990; Seigel et al., 1987; Shine, 1980; Sinervo et al., 1991; Tinkle, 1969) and in gravid birds (Lee et al., 1996), as well as in animals that carry either eggs (water bugs; Smith, 1976) or offspring after birth (scorpions; Shaffer and Formanowicz, 1996). These studies assume that the variables measured make individuals more vulnerable to predators, but direct evidence is lacking. Increased predation rates have been linked directly to pregnancy or egg-carrying in few taxa: ephippial *Daphnia* (Mellors, 1975), lizards (Shine, 1980), ovigerous copepods (Vuorinen et al., 1983; Winfield and Townsend, 1983), prawns (Berglund and Rosenqvist, 1980), and ventraly brooding pipefish (Swenson, 1988). However, some of these studies do not directly compare pregnant or caring females with females who do not care (for example, Mellors, 1975; Shine, 1980). Instead, they compare survival costs between pregnant or caring females with males, assuming that the other sex is equal in all other respects, which is questionable.

Among invertebrates parental care is uncommon, and, when it occurs, it is typically less extensive than in other taxa (Tallamy and Wood, 1986; Zeh and Smith, 1985). This evidence has led some authors to argue that reproductive costs may be minimal in this group (Godfray, 1987). The golden egg bug (*Phyllomorpha laciniata*) is a coreid bug with a unique pattern of oviposition behavior. Females can lay eggs on plants, males, or other females; adults carry the eggs until they hatch (Kaitala, 1996). This reproductive strategy is unique for two reasons. First, females follow a flexible strategy in their choice of oviposition site, which leads to a situation in which some offspring receive no care, while others are carried by either males or females during the egg stage. The coexistence of these three alternatives in the same population (no care, care by male, care by female) is unusual because most insect species follow one option and therefore lack such flexibility. Furthermore, most females adopt all three strategies during their reproductive lives. Second, other terrestrial arthropods...
in which there is parental care lay eggs on plants or inside burrows rather than on conspecifics, where they are cared for by the parent(s) (Zeh and Smith, 1985). Carrying eggs on the body may well influence the nature of the costs.

In this study we followed a natural population of golden egg bugs during the entire reproductive season to determine which proportion of the population carried eggs, which proportion of males and females carried eggs, and the number of eggs carried. In addition, we used an experimental approach to test whether egg-carrying adults suffer higher predation rates than non-egg-carrying adults of the same sex. As *P. laciniata* carry their eggs attached externally over their bodies and wings, this presumably makes them more visible and reduces their ability to escape from predators.

**METHODS**

**Natural population**

During 1997 we performed weekly samplings of a natural population of *Phyllomorpha laciniata* during the reproductive season (March to August) in Villaviciosa de Odón, 25 km west of Madrid, Spain. We searched for bugs in a quadrangular area, 20 × 20 m, and we marked all the bugs with unique combinations of typist’s colored correction fluid (Tippex brand). For every individual found, we recorded the identity of the bug, its spatial position (recorded as a grid reference to the nearest 1 m), whether it carried eggs, and, if so the number, the stage of development and the position of the eggs over the body.

**Predation experiment**

*Phyllomorpha laciniata* adults were collected at El Espinar (Segovia), 65 km northwest of Madrid from June to July 1997. Bugs used in the experiment were kept together in a plastic container (29 × 51 × 32 cm) with ground substrate and growing *Paronychia argentea* as a food resource. They were kept under natural conditions of light and temperature. The high adult bug density in the plastic container resulted in females laying eggs on individuals that had been captured from the field without eggs. Thus, egg laying was artificially induced for experimental purposes. However, it was not possible to remove eggs from individuals because doing so causes major damage to the wings.

We chose great tits, *Parus major*, as the predator because they forage on the ground (Gosler, 1987; Herrera, 1978; Lack, 1971) and because they occur naturally in the same habitat as *Phyllomorpha laciniata*. We used 11 adult male and female birds in pairs as predators.

The experiments were carried out in the north of Madrid at the Estación Biogeológica “El Ventorrillo” from 20 July to 17 August 1997. We kept birds together in two rooms (2 × 2 × 1.6 m) of an outdoor aviary and ran experiments in a third room of the same aviary from 1100 to 1700 h on days that the air temperature was higher than 21°C to ensure that bugs were active. *P. argentea* was present on the ground of the aviary to resemble as much as possible the natural habitat of the bug. A 75-cm high plastic barrier was placed on the walls of the aviary to prevent bugs from escaping.

Each experiment was initiated by randomly choosing two adult birds and placing them in the aviary at least 30 min before the trial started. After this settling period, we chose four potential prey of the same sex, two with eggs and two without eggs, at random from the plastic container, introduced them into the aviary, and left them alone. We entered the aviary every 20 min and looked for bugs. Whenever a bug was eaten by a bird, we recorded whether it was carrying eggs. Each trial was performed until only one prey was left alive or during a maximum of 2 h. We performed one trial per day and used a new set of four bugs in every trial. We performed 17 trials, but the type of bug that was the last one left alive in the aviary could only be determined in 11 trials.

Mean values are shown with their standard errors. Logarithmic transformations were applied when necessary (Sokal and Rohlf, 1981).

**RESULTS**

**Natural population**

In the long-term study of the natural population of *Phyllomorpha laciniata* in Villaviciosa de Odón, 40.4% of the females and 67.8% of the males carried eggs (Table 1). The proportion of females that carried eggs was significantly lower than the proportion of males that carried eggs ($n = 507$, df = 1, $\chi^2 = 57.40$, $p < .0001$; Table 1). In addition, females carried on average fewer eggs than did males (ANOVA, $F_{1,272} = 49.48$, $p < .0001$; Table 1).

**Predation experiment**

The bugs used for experimental purposes carried a higher number of eggs on average than did bugs in the natural population (Table 1), but the number of eggs carried was within the range found in the natural population. There were no significant differences between the number of eggs carried by males and females (ANOVA, $F_{1,20} = 1.09$, $p = .3$; Table 1).

The proportion of eggs carried over the wings by males was 52.0 ± 9% and by females was 55.7 ± 6%. There were no significant differences in the proportion of eggs carried over the wings by males and females (ANOVA, $F_{1,20} = .333$, $p = .57$).

When we compared all-male and all-female groups, predators did not behave differently when offered a group of males than when offered a group of females (Fisher’s Exact test, $n = 11$, df = 1, $p > .9$); thus, data from trials on males and on females were pooled.

The experiment showed that *P. laciniata* was more vulnerable to predation when carrying eggs than when not carrying any. Of the 11 replicates in which we could determine the type of bug that was the last one left alive in the aviary, 10 were bugs without eggs, and 1 was a bug carrying eggs (bi-
nominal test, $n = 11, p = .006$). This result shows that bugs without eggs are more likely to avoid predation than bugs carrying eggs.

**DISCUSSION**

Bugs carrying eggs were predated at higher rates than non-carrying bugs. In 10 out of 11 trials the last bug alive did not carry eggs. Thus, carrying eggs attached to their bodies makes *Phyllomorpha laciniata* more vulnerable to predators.

In this species females show a pattern in their oviposition behavior that is unique in its flexibility. Females can lay eggs on plants, where they are left unattended, or on conspecifics (males or females), where they develop until they hatch (Kaitala, 1991). After hatching the nymphs dismount the carrier and become independent. In our predation experiment, males and females carried on average a higher number of eggs than in the natural population, although the number of eggs carried by experimental subjects was within the natural range. Furthermore, there were no differences in the number of eggs carried by males and females. Individuals used for experimental purposes carried a higher number of eggs because they were kept together in a plastic container before the experiment started, where the high density of individuals offered greater opportunities for females to encounter other individuals upon which they could lay eggs. Because the number of eggs carried by experimental subjects was within the natural range, we can assume that at least a proportion of individuals in natural populations also incur predation costs when they carry eggs.

Why should egg-carrying make *Phyllomorpha laciniata* more susceptible to predators? *Phyllomorpha laciniata* is yellow-brownish and has a characteristic body shape with lateral prolongations which make it cryptic in the habitat where it lives (*Phyllomorpha* Phyllos, leaf; *Morphos*, shape). They resemble their host plant, *Paronychia argentea*, and the fallen leaves of the oaks where they take refuge by hiding underneath. Thus, the overall morphology of *P. laciniata* seems designed to make individuals difficult to detect by predators. However, the presence of eggs makes individuals more visible, at least to the human observer, because eggs shine under the sun. This raises the question as to why eggs are not cryptic like the individuals upon which they travel, as this would decrease the costs of carrying them and would increase the survival rates of the adults and of the eggs they carry. The answer may lie in the fact that eggs can be laid either on individuals or on plants. Egg survival on plants is much lower than on individuals (Reguera and Gomendio, unpublished data). Thus, for egg mortality, it may be a better strategy to mimic the host plant to improve survival rates when conditions are harsh than to mimic adults where egg survival is higher. This seems to be the case because eggs resemble the flower of *P. argentea*, on which they are notoriously difficult to find.

In addition, carrying eggs may decrease the locomotor performance of the individuals carrying them. More than 50% of the eggs carried by an adult are attached over its wings (see Results). In some cases the eggs cause the wings to stick to the body or to each other, while in other cases the weight of the eggs may prevent the wings from spreading. Thus, the presence of eggs over the wings may prevent adults from flying, an activity which, although rare, may be crucial when individuals are detected by predators.

Studies that look for direct predation costs associated with parental care are not common. Most of the studies assume that poor locomotor performance among pregnant females or individuals that carry eggs or young is related to a high risk of predation (Cooper et al., 1990; Seigel et al. 1987; Shaffer and Formanowicz, 1996; Shine, 1980; Sinervo, 1991; Smith, 1976). If we look at the few studies in which real predation rates were measured, we find that some of them suffer methodological problems. Shine (1980) compared pregnant female lizards with males, thus assuming that males and non-pregnant females are similar in terms of antipredatory behavior and phenotype, which may not be the case. The same approach was used by Mellors (1975), who compared ephippial (females with eggs) with nonephippial *Daphnia* (males and females). Winfield and Townesd (1983) did not directly compare ovigerous female copepods and nonovigerous females because the predator did not face the two types of prey at the same time; thus, the interpretation of the results is problematic.

In our predation experiment both types of prey, individuals carrying eggs and individuals without eggs, were presented simultaneously to the predators. This is the situation faced by predators in natural populations because during most of the reproductive season individuals with and without eggs coexist. In addition, in each trial the predators faced a group of four bugs which were all the same sex, thus avoiding any confounding factors associated with sex differences.

In other terrestrial heteropterans where there is parental care during the egg stage, eggs are left either on plants or inside burrows, and adults remain near the eggs they carry for (Zeh and Smith, 1985). In contrast, when *Phyllomorpha laciniata* females lay eggs on plants, these are left unattended, and eggs are only cared for when they are laid on adults. It remains to be explained why *P. laciniata* carries eggs over the body. This peculiar strategy could be related to the size of the clutch that a female can lay at one time, the time it takes for the eggs to hatch, and/or the density of the population. In any case, carrying eggs externally, attached to the body, may well influence the nature of the costs. Adults that carry eggs experience higher predation rates, as we show in this study. But there are clear advantages associated with carrying the eggs attached to their bodies instead of caring for eggs left on plants or inside burrows: adults can go on moving and are not restricted in their search for food and sexual partners. This mobility may also allow adults to look for the most appropriate climatic conditions (temperature or humidity) for egg development.

Given that the predation costs associated with egg carrying are considerable, it is worth asking what benefits males and females gain. Caring for eggs in *P. laciniata* greatly enhances their survival by protecting them from egg predators (such as ants) and from an egg parasitoid (Reguera and Gomendio, unpublished data). In the case of males, preliminary data suggest that a proportion of the eggs they carry are their own offspring. Thus, the benefits in terms of improved offspring survival seem to compensate for the costs in terms of predation rates. On the other hand, females never carry their own offspring. It is still unknown whether the eggs they carry are genetically related or whether this is a form of intraspecific parasitism. In any case, fewer females than males carry eggs, and those who do carry fewer eggs. These results suggest that females are minimizing the costs of egg carrying.

We thank Arancha Mendiola for assistance in the field; Eulalia Moreno and Marta Barluenga for capturing the birds and allowing us to use their facilities; and Juan Antonio Delgado for constructive comments on the manuscript. This work was supported by grants from the Ministerio de Educacion y Cultura (PB95-0186 and PB96-0880). PR enjoyed a predoctoral fellowship from the Ministerio de Educacion y Cultura (FPI 300435379).

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