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Dedicated to the memory of William Donald Hamilton

Altruism, intraspecific parasitism and reciprocity: egg carrying in the golden egg bug

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The evolutionary theories of helping assume reciprocity, genetic relatedness or group selection. The evolution of an altruistic act, that is, a costly act by an individual that benefits another unrelated individual, often requires reciprocal interactions. Therefore, models of evolutionary stability (ESS) have been successful in studying the evolution of altruistic behavior. Nevertheless, altruistic behavior may evolve without reciprocity. Such a situation may arise when altruistic behavior is costly but other behavioral alternatives lead to more costly outcomes. However, this setting may closely resemble intraspecific parasitism where one individual exploits the resources, behavior or actions of another. Egg carrying behavior in the golden egg bug (*Phyllomorpha laciniata* Vill, Heteroptera, Coreidae) exemplifies the close and problematic relation between altruism and parasitism. The golden egg bug females lay eggs on the backs of female and male conspecifics. Egg carrying in the golden egg bug can be understood as intraspecific parasitism, altruistic behavior, reciprocity, or paternal care depending on which individual is receiving the eggs, from whom, and when. In this paper, we discuss the alternative theories in order to understand the unique reproductive behavior in the golden egg bug.

Introduction

Social behavior, expressed as cooperation and helping, is frequently observed in mammals, birds and fish, and it is also reported in invertebrates, in particular in social insects (Hamilton 1964a, 1964b, Dugatkin 1997). Helping and cooperation may occur in a number of different forms, such as anti-predation vigilance, inspection and warning behavior, non-parental offspring raising, cleaning behavior and cooperative hunting. Help can also be received by stealing or by force: intraspecific parasitism may sometimes be difficult to tell apart from helping.

Individuals acting for the benefit of another or other individuals, such that the actor suffers costs from the action, are referred to as being altruistic. Despite a long history of research, the evolution of altruistic acts has remained a challenge for behavioral ecologists. The evolutionary theories of helping and cooperation, where altruistic actions are usually involved, assume reciprocity, genetic relatedness or group selection (Connor 1995, Dugatkin 1997). The use of evolutionary stability (ESS, Maynard Smith 1982) also has its merits in unraveling the evolution of altruistic behavior (Connor 1995, Dugatkin 1997). Altruistic behavior may, nevertheless, evolve without reciprocity. Such a situation may arise when altruistic behavior is costly but other behavioral alternatives lead to more costly outcomes, a case often referred to as the best of a bad job. However, this setting may closely resemble intraspecific parasitism where one individual exploits the resources or actions of another.

Egg carrying in the golden egg bug (*Phyllomorpha laciniata* Vill, Heteroptera, Coreidae) exemplifies a close relation between altruism and parasitism. The golden egg bug females lay eggs on the backs of female and male conspecifics (Kaitala 1996, Kaitala & Miettinen 1997). Eggs do not survive unless carried by bugs. Egg carrying bears predation costs for adults (Kaitala & Axén 2000, Kaitala *et al*. 2000). Females do not base their mating decision according to the egg load of the male (Kaitala 1998). Individuals of both sexes receive eggs involuntarily (Kaitala & Miettinen 1997). When mating, they cannot resist close-by non-mating females laying eggs on their backs. Additionally, males receive eggs while courting and after mating. Most eggs received by males are received before copulation when a male courts a female (Katvala & Kaitala 2001). As a consequence, mating males receive eggs from their mating partners as well as from other females (Kaitala 1998). Theoretically, the reproductive behavior provides an unusually challenging evolutionary problem. To honor William D. Hamilton's memory we wish to combine many aspects of his work, including kin selection theory, evolutionary game theory and extraordinary phenomena, when studying the unusual reproductive behavior of the golden egg bug.

In this paper, our aim is to discuss the enigma of the reproductive behavior, in particular, the egg carrying in the golden egg bug, against different conceptual backgrounds, such as altruistic behavior, reciprocity, paternal care, group selection, kin selection, trait group selection, and intraspecific parasitism. Guided by the general mainstream in the literature of the evolution of cooperation one would be tempted to suggest that the reproductive behavior in the golden egg bug is an expression of parental care or cooperative breeding. We suggest, however, that in the golden egg bug altruism, expressed by frequent carrying of unrelated eggs (Kaitala & Miettinen 1997), may have evolved without reciprocal interactions, most probably through intraspecific parasitism.

Conceptual background

In this section we briefly review the basic concepts related to the studies of evolution of cooperation, which we feel that are the most important in addressing the exceptional breeding behavior in the golden egg bug.

An altruistic act has often been used to refer to a costly act by an individual (actor) that benefits another unrelated individual (Hamilton 1972). Noting, however, that an altruistic act may well give benefits to close kin we prefer to apply another definition proposed by Brown (1987). In reviewing "Hamiltonian altruism" and direct and indirect fitness components he defines an altruistic act as a costly act by an individual that benefits another non-descendent individual (Brown 1987). This definition rules out the actor's own offspring. The recipient can be, for example, a sister, the parent, or a completely non-related individual. The actor's help can be viewed to be voluntary. If the actor's help is involuntary we would be dealing with intraspecific parasitism (*see* below).

A single altruistic act is expected to decrease the fitness of the altruistic individual. Consequently, in order for an altruistic act to evolve, such a behavior should enjoy indirect fitness benefits. Otherwise, such a behavior will lack evolutionary stability and should not be able to spread in animals. Altruism may also be viewed as unilateral cooperative action.

Cooperation is commonly used to illustrate the behavior where individuals act so as to maximize joint benefits, e.g., reward or fitness. Cooperation is usually not evolutionarily stable since in most cases a cooperative strategy is vulnerable to cheating, or unilateral deviations from cooperative strategies, by at least one of the individuals involved in the cooperative game. Thus, when we observe cooperative behavior in nature we expect it to be supported by some mechanisms which are based on unilateral fitness maximization of the individuals.

Reciprocity is one of the mechanisms used to explain the evolution of cooperation. In reciprocal interaction, the individuals usually act in turns and, depending on the behavior of the individuals, the interaction may be cooperative or non-cooperative (Axelrod & Hamilton 1981, Dugatkin 1997). Reciprocal altruism, for example, may appear to be evolutionarily stable (ESS, Maynard Smith 1982) if the same individuals meet several times to alternate altruistic actions. If reciprocal altruism can be maintained in the long-term interaction between the individuals then these individuals may be able to enjoy extra fitness benefits as compared to "selfish" individuals.

The well-known tit-for-tat game is based on reciprocal actions (Axelrod & Hamilton 1981). Here two individuals encounter each other for an uncertain number of times and have two options: defect or cooperate. The individuals start to cooperate with each other, and then follow the opponent's last move. Such a strategy has been shown to be very successful such that an individual following it may enjoy the fitness benefits matching those derived from cooperating.

Kin selection explains the evolution of altruistic behavior such that the benefits for the individual are extracted by benefiting its own genes (Hamilton 1964a, 1964b). Here, indirect fitness benefits are derived, for example, if the individual takes care of his/her sisters and brothers. Kin selection has been used to explain the helping behavior and cooperative breeding in birds, where young birds may help their parents to raise new offspring (Brown 1987). Kin selection has been most successful in explaining the cooperative behavior in social insects (Hamilton 1964a, 1964b), as well as conflicts between individuals therein (Trivers & Hare 1976, Ratnieks & Visscher 1989).

Parental care contributes to an individual's direct fitness (individual selection) if the individual takes care of his/her own offspring. Here, the benefits from helping to raise young are delivered to the closest relatives. A common trade-off here is whether to invest in parental care or in increased number of offspring. Parental care usually increases the offspring survival and offspring quality, but may also decrease the time for future reproduction, increase parental survival and physical condition.

Trait group selection is a form of group selection where the individuals of the groups need not be relatives (Dugatgin 1997). In this setting, the individuals occur in groups and those individuals which succeed in avoiding most selfish behavior and in choosing collaborative behavior will win the evolutionary race. This is because all the members in the group will benefit from collaboration within the group and gain an advantage against the individuals of groups where cooperation has not been reached.

Intraspecific parasitism occurs in a non-reciprocal interaction when an individual (actor) utilizes another individual in increasing the actor's fitness. In contrast to the case of altruism, the actor derives benefits from its actions and the utilized individual suffers costs from being utilized. Moreover, the "helping" by the utilized individual does not occur voluntarily. A well-known example is intraspecific nest parasitism in birds where females lay eggs in the nests of unrelated birds.

We next discuss the concepts described above in the context of the egg reproductive behavior of the golden egg bug *P. laciniata*. We note, however, that no serious attempts have been made to formally apply these concepts to explain the observed behavior (but *see* Härdling & Kaitala 2001).

Altruism, reciprocity or intraspecific parasitism in the golden egg bug?

The golden egg bug *P. laciniata* occurs in the Mediterranean area where it lives on the host plant *Paronychia* sp. (Polycarpea, Caryophyllaceae; Bolivar 1894, Jeannel 1909, Reuter 1909, but *see* Mineo 1984). The natural history of the species is described by Kaitala & Katvala (2001).

Most often the golden egg bug females lay eggs on the backs of female and male conspecifics (Kaitala 1996, Kaitala & Miettinen 1997), although occasionally eggs may also be deposited on host plants. The general pattern is that, while hatching, almost all the eggs are carried by adults. In most habitats, eggs do not survive unless carried (Du Merle *et al*. 1978, Kaitala 1996). Ants, for example, forage on arthropod eggs eagerly (Du Merle *et al*. 1978, Kaitala 1996, Kaitala *et al*. 2000), egg carrying protects against predation. Egg carrying also bears predation costs for adults (Kaitala & Axen 2000, Kaitala *et al*. 2000). In this light, the egg carrying behavior could be considered as a cooperative behavior among the breeding individuals or as parental care.

Golden egg bug females look for an appropriate back for her eggs independent of the father's willingness to accept and carry eggs. Males have been observed to actively avoid accepting eggs after copulation (Miettinen & Kaitala 2000). Since only a small fraction of the eggs carried in the field by males are paternal (Kaitala & Katvala 2001, Miettinen 2001), and none carried by females are maternal, we are tempted to reject parental care as an explanation for the extraordinary breeding behavior in the golden egg bug (Kaitala *et al*. 2001). That parental care may not be present in this breeding system is also supported by the fact that egg-carrying individuals have not been observed to provide any visible care to eggs. Furthermore, the evolution of paternal care may be difficult in this system of egg carrying since it seems to be impossible for the male to differentiate the care between his own and unrelated eggs, even if the male could tell them apart. Thus, we need to consider other forces behind the evolution of this breeding behavior.

Recall that egg-carrying individuals suffer increased predation risk. Due to the predation costs from egg carrying, the males and females should avoid accepting eggs. Thus, if viewed as cooperative breeding behavior, such behavior seems to lack evolutionary stability.

Individuals of both sexes receive eggs involuntarily (Kaitala & Miettinen 1997). When mating, they cannot resist other non-mating females laying eggs on their backs. As a consequence, mating males receive eggs from their mating partners as well as from other females (Kaitala 1998). When eggs are received involuntarily, without any chance to remove them, we are dealing with intraspecific parasitism where an individual cannot escape egg carrying. The presence of intraspecific parasitism in the mating system is supported by the observation that females also carry unrelated eggs on their backs.

Occasionally, males do not resist receiving unrelated eggs to carry (Miettinen & Kaitala 2000, Katvala & Kaitala 2001). A male that courts a female is likely to receive an unrelated egg from his mating partner, but if he does not court he will not receive a mating. Thus, it is evident that males do not get matings unless they expose themselves to receiving unrelated eggs (Härdling & Kaitala 2001). Thus, in this setting, a reciprocal act appears to happen. A male accepts an egg in order to get a mating, and a female accepts mating, being able to find a host for an egg at lower cost. However, the observations do not suggest that copulating pairs will continue reciprocity such that the assumptions of repeated encounters of the tit-for-tat concept would be realized (Axelrod & Hamilton 1981, Dugatkin 1997). And if repeated encounters would continue for several matings followed by egg laying, the degree of the paternity of the males to the eggs they carry would be higher. Reciprocal cooperation is also undermined by the fact that the females seem to be actively polyandrous, leaving their mating partners soon after copulation.

In most habitats, the golden egg bugs are widely dispersed and move continuously. However, when host plants are scarce, the bugs occur in aggregations. Thus, it is possible that the individuals in the mating aggregations are related to each other, providing a mechanism for group selection to operate through kin selection. However, this option is not supported by the recent DNA analyses (Miettinen 2001) which show that egg carrying males and eggs are not close relatives.

Trait group selection (Dugatkin 1997) does not assume relatedness between the individuals in the mating pool. If we assume that cooperative behavior dominates in a group of individuals and is lacking in another group, for whatever reason, then it is obvious that the individuals in the first group have an evolutionary advantage. Thus, cooperative behavior should become more common in the population. Interestingly enough, it seems that for the golden egg bug the cooperative gain for the group is derived through intraspecific parasitism which turns out to be beneficial for the group and for all individuals. Accepting unrelated eggs to care for does not benefit an individual but may be impossible to escape. Testing the presence of trait group selection would require further data on the spatial distributions and aggregations and dispersal of the golden egg bugs among them.

Conclusions

Egg carrying in the golden egg bug can be understood as intraspecific parasitism, altruistic behavior, reciprocity, paternal care, or trait group selection, depending on which individual is receiving the eggs, from whom, and when. When a non-mating female dumps eggs on the back of a mating individual, regardless of the receiver's sex, egg carrying may be considered as intraspecific parasitism because the egg receiver is unable to resist. When individual males accept eggs during courtship prior to mating, egg receiving may be regarded as reciprocity. When males receive unrelated eggs without resistance (Kaitala 1998), egg carrying may be viewed as altruism. Finally, when males accept and carry their own eggs we are dealing with paternal care.

We suggest that in the golden egg bug, altruism, expressed by frequent carrying of unrelated eggs (Kaitala & Miettinen 1997), may have evolved without reciprocal interactions or kin selection, most probably through intraspecific parasitism.

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