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Amotz Zahavi

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Point-of-View

Altruism as a handicap – the limitations of kin selection and reciprocity

Amotz Zahavi, Inst. for Nature Conservation Research, Tel-Aviv University, Tel-Aviv 69978, Israel.

The phenomenon of "helping at the nest" has exposed ornithologists to the problem of the evolution of altruism, i.e. why should a non-breeder invest in the fitness of breeders rather than trying itself to breed. Until the 1960s altruism was explained by many biologists through models of "group selection" (GS), i.e. the investment of the non-breeders in the breeding of their group members was justified by its contribution to the group. GS was later rejected by most evolutionary biologists (Maynard Smith 1964, Lack 1966, Williams 1966), and another model, that of "kin-selection" (KS) (Hamilton 1964) was suggested as an alternative solution to the problem of altruism. In KS models the investment of the altruist is justified by the benefit to its relatives. However, the many studies on group living birds which have resulted from the growing interest in the dilemma of altruism, have revealed that the helpers are in fact often not related to the breeders (Ligon and Ligon 1990, Reyer 1990, Zahavi 1990). Trivers (1971) suggested an additional model – "reciprocal altruism" (RA) – to interpret altruistic adaptations among non-relatives. This latter model suggests that the investment of the altruist is compensated by a gain from a reciprocal investment by other group members. However, data from several field studies have indicated that in many cases the act of the non-related altruist was not reciprocated. In these cases neither KS nor RA could explain helping at the nest. It was evident, however, in some of these studies (Ligon and Ligon 1990, Reyer 1990, Zahavi 1990) that many of the helpers were enhancing their own chances to breed. Helping by non-related birds, which is not reciprocated, can therefore only be interpreted as a simple selfish investment. However, these findings did not stimulate further research into the possibility that "helpers" in general gain direct advantages by their apparently altruistic investment.

Weaknesses of previous models

In the following I note the inherent instability in the models based on GS, KS or RA and propose what I consider to be a more general and stable model, in which helping is considered as a selfish behaviour, i.e. its initial presentation as an altruistic adaptation was misleading. The model also has implications for interpreting other altruistic phenomena, even among the eusocial insects, but these will not be discussed here.

Group selection. GS is not an illogical model: it pays to invest in a group, if the benefit of having a successful group exceeds the investment of the individual members in the general welfare of the group. However, at present GS is generally not used by most evolutionary biologists, because it has been shown to be vulnerable to social parasitism (Maynard Smith 1964). The reason is that, in a GS model, a member of the group that does not invest in the group's welfare (a social parasite), gains as much as the individuals that do invest in the group, without incurring the cost of helping.

Kin selection. According to KS theory, altruism is based on a model of individual selection in which the gene for altruism is the selected unit (Dawkins 1989). The theory claims that the frequency of the gene for altruism increases in the population as a result of the altruistic behaviour, even though it decreases the reproduction of the altruist itself. Is this really so? The best way to expose the fallacy of this claim is to tell a variant of a story attributed to J.B.S. Haldane, who suggested (1955) that if one of two brothers walking beside a river, were to fall into it and be in danger of drowning, it would be reasonable for the other brother to risk his life somewhat to save the drowning brother, since by taking such a risk (i.e. decreasing his fitness), he may save his brother and increase the frequency of genes similar to his own in the following generation.

The instability of the model is clearly apparent if the same story is told with three or more brothers, rather than two, walking along the river. It is obvious that if one of them jumps to the rescue, the other sibling (who does not risk himself), gains as much as the one who risks himself, but without incurring any cost. Thus, in KS models, as in GS models, the total gain of the selfish brother (the social parasite), is higher than that of the altruist. Eshel and Motro (1988), trying to untangle the problem of multiple potential rescuers, suggested an unrealistic model, in which there is no interaction or communication among the potential rescuers, and consequently, no way for the brothers to predict which of them, if any, is likely to rescue the drowning sibling.

Models of KS are in fact models of GS among kin. They are equally unstable. Although the investment and gain in GS models are not presented by gene frequencies, any investment is ultimately turned into gains or losses in fitness. Thus, because of the potential advantage to social parasites in models of KS and GS, both are equally unstable over evolutionary time.

The similarity between GS and KS has recently been discussed by Wilson and Sober (1994). They suggested that this similarity justifies the use of GS, while I consider both GS and KS to be equally inadequate to explain social evolution. It is certainly not reasonable to reject GS and accept KS.

Reciprocal altruism. It is easy to show that reciprocal altruism (RA) is also inherently unstable. Trivers (1971) suggested that RA could be stable in cases in which there are mechanisms that ensure reciprocation. He suggested that among higher animals, such as man and monkeys, the social parasite, i.e. the individual that does not reciprocate, will be punished. However, like any other character, such a mechanism is costly to the individual that possesses it (Zahavi 1981). Sigmund (1993) discussed the difficulty in enforcing reciprocation and regarded it as a major problem for models of RA. Thus, as in GS and KS models, selfish individuals that do not invest in punishing a social parasite, gain more than those that invest in maintaining reciprocation within their group.

An alternative model

Our studies of the Arabian Babbler *Turdoides squamiceps,* a group-breeding songbird, suggest a completely different interpretation for the motivation of birds to invest in helping their group: an interpretation that may provide a general solution to the problem of altruism. It suggests that the investment in the welfare of the group, or of its members, functions to advertise the quality and motivation of the helper. The advertiser gains from its investment by increasing its "social prestige". Helping may thus be considered as a simple selfish character. Earlier (Zahavi 1976, 1990) I used the term "social status" instead of "social prestige", however, "social status" is often used as a synonym for "social rank". To emphasize the difference – the rank order of babblers does not change as long as they remain members of the same group, whereas their social prestige may change (without a change in rank), i.e. other individuals may compromise with them to a greater or lesser extent, as a consequence of their performance.

Social prestige functions like a peacock's tail or the song of a songbird. It attracts collaborators and deters rivals. Prestige may be gained by investing in wasteful characters (Zahavi 1977a, 1987) as well as by investing in "altruistic" activities. The investment involved in the altruistic activities serves as an honest signal of the ability of the babbler to help its group and its quality as a collaborator; it also reflects its quality as a rivar in intragroup conflicts.

It is interesting to note that, contrary to what might be expected from all three models in which the advantage to the helper is indirect (GS, KS & RA), babblers are highly motivated to invest in their group, and the population is not infected by social parasites. On the contrary, individuals compete with each other to invest in the interests of the group, often interfering with the helping of others. Dominants interfere with the "altruistic" activities of subordinates in feeding the nestlings (Carlisle and Zahavi 1986), in allofeeding between adults, in sentinel activities (Zahavi, unpubl.obs.), in mobbing (Carmeli 1988, Anava 1992), and in the defence of the common territory (Zahavi, unpubl. obs.). Dominants often prevent subordinates from helping the group. They are most likely to interfere with older and experienced individuals, which are one rank lower than themselves, and are more tolerant towards the investment of young and inexperienced birds of lower ranks. Competition and interference among individuals acting as helpers have been observed in other studies of cooperatively breeding birds (Reyer 1990), but these phenomena were not considered by the observers as a challenge to the theories of indirect selection.

These kinds of interference cannot be explained by any model of indirect selection, according to which individuals gain more when other individuals, rather than themselves, invest in the altruistic acts. However, if, as I suggest, helping confers a direct advantage on the helper, the interference and competition for opportunities to help can easily be explained by individual selection, and there is no need for alternative models to explain the phenomenon of helping.

Investment in "altruistic" activities stabilises the social collaborations by advertising the motivation of the altruists to cooperate, hence it may erroneously be considered as a mechanism that has been selected to ensure reciprocation. Reciprocation, however, cannot explain the interference with the altruistic acts of others, or the fact that altruism can also function as threat.

The evolution of cooperation in groups of two, such as sexual mates, is no easier to explain than that of larger cooperations. Although some sexual partners do abandon their mates, or do not invest much in their offspring, frequently mates invest more than is required of them. Sexual mates, like individuals in a group of babblers, tend to compete for the investment in the cooperation: incubating birds are often reluctant to be replaced by their incoming mate, and frequently the incoming bird has to push its mate aside in order to replace it (Zahavi, unpubl. obs.). I suggest that even in collaborations of two, a large part of the investment can be explained as an advertisement of the quality of the investor and of its motivation to continue collaborating, in order to decrease the partner's tendency to cheat or desert.

It has been suggested that the solution to the "prisoner's dilemma" could explain the problem of the evolution of cooperation in general (Axelrod 1984). Hence it has attracted much attention among biologists. I suggest that neither the dilemma, nor its solutions, has much to do with the real biological world. In the real world, individuals assess the qualities and the motivations of their potential partners and invest in advertising their own qualities and motivations – before they enter into any collaboration. They continue to test each other as long as they continue to cooperate (Zahavi 1977b). In the prisoner's dilemma the collaboration is neither preceded by communication, nor are the prisoners able to talk to one another during the game. Hence, clever as the "dilemma" and its solutions are, they have very little, if any, relation with the world of biology and social behaviour.

It has often been claimed that the observations that individuals of many species tend to cooperate with their kin, support the theory of KS. However, this is not necessarily so. When a new group is formed, members invest time, energy and risk in advertising their qualities and assessing the qualities and motivations of their potential collaborators before they decide with whom to collaborate, and how much to invest in the collaboration with a particular partner. Collaboration with kin may save a large amount of this investment, because in a group of kin the individuals know each other, and their rank order and social prestige have been established long before the establishment of the new collaboration. In babblers, new groups composed of non-related individuals, take much longer to settle down to breed than groups composed of kin (Zahavi, unpubl. obs.). The fact that it is easier to collaborate with kin may have an effect on the gene frequency of the following generation. I term this 'kin effect'. However, if this effect would cause individuals to compromise their own direct fitness, in order to increase their "inclusive fitness", the path would be open for the success of social parasites and for the disintegration of the social system.

To conclude, I suggest that all three models, GS, KS and RA, sophisticated as they seem to be, are not useful for interpretating social interactions, because natural selection has evolved a much more stable solution to the problem: individuals invest in their collaboration in order to increase their social prestige. They do so by advertising their qualities and their motivation to collaborate. The benefit to the group is a consequence of, rather than the factor that selects for the investment. It is now generally accepted that a handicap involving waste, such as the peacock's tail, is a logical and stable strategy to advertise quality. Altruistic handicaps may operate equally well. Thus, the problem of altruism is solved when the investment in the altruistic phenomenon is considered as a handicap.

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