

ALTRUISM
OR JUST
SHOWING OFF?

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Altruism or Just Showing Off?

Among the many debates regarding the evolution of altruism are suggested theories such as group selection, kin selection, reciprocal altruism and altruism as a signal, also known as the handicap principle. The first three theories mentioned are among the more conventional models. Models of group selection were used to explain altruism by many biologists until the 1960's, but were later rejected by evolutionary biologists because the model has been shown to be vulnerable to social parasitism (Maynard Smith, 1964, as cited by Zahavi, 1995). Reciprocal altruism and kin selection are theories still used by most evolutionary biologists, with much supporting experimental evidence, and are therefore more widely accepted. Reciprocal altruism is based on the theory that if one member of a population performs an altruistic act, the recipient of the altruistic act will reciprocate the action at some time (Trivers, 1971, as cited by Zahavi, 1995). Social parasitism is not considered a problem in this model as those individuals who do not reciprocate are punished by other members of the population (Trivers, 1971, as cited by Zahavi, 1995). Kin selection, on the other hand, states that altruism is based on a model of individual selection where the gene for altruism is being selected for (Dawkins, 1989, as cited by Zahavi, 1995). In other words, the result of altruistic behavior is an increase in the frequency of the altruistic gene in a population (Zahavi, 1995). The handicap principle, first proposed by Zahavi, although a much newer model with less experimental evidence to support it thus far, is a very logical theory and usually proves itself in situations where kin theory or reciprocity fail to hold true in certain populations. The handicap principle suggests that the seemingly wasteful altruistic acts performed by an individual function to advertise their quality, fitness and social prestige (Zahavi, 1995). In other words, an individual performing an altruistic act is not doing so for the sake of being 'nice' or for the benefit of the rest of the population, but rather the

altruistic behavior is purely selfish, serving only to advertise the fitness of the individual to possible rivals, and quality and social prestige to possible mates (Zahavi, 1995). Although all of these theories claim to be the only possible explanation for the evolution of altruistic behavior in nature, I feel that none of these theories are complete alone, and not only can they all be used to explain altruistic behaviors in different situations, but in some circumstances, they can complement each other. After researching all four theories, it seems to me that none of these theories hold true for all situations or within all animal species, but rather the lifestyle of a certain animal species determines the logical use of altruism within the population.

In his paper, "Altruism as a handicap – the limitations of kin selection and reciprocity" Amotz Zahavi exposes the weaknesses of the three models previously discussed. About group selection, the paper states that it makes sense for individuals to invest in a population if the benefit to the population is greater than the loss to the individuals (Zahavi, 1995). Yet, in the context of evolutionary biology, this model is weak because as a game, it cannot have an evolutionary stable strategy because it can be invaded. For example, group selection is vulnerable to social parasites who gain as much as the other members of the group without having to incur the costs of investing in the welfare of the group (Zahavi, 1995). Even so, I feel that this model should not be rejected based only on this susceptibility because social parasitism is ever present in biology. It exists in the animal kingdom and is quite evident in the human world, so how can we reject a model that represents what goes on in real life?

Zahavi just as easily discredited the kin selection model since it is in fact a model of group selection among kin, and therefore, just as vulnerable to social parasites. A good example is Zahavi's variant of the story, attributed to J.B.S. Haldane, of two brothers walking beside the river, one falling in and the other rescuing the first. Zahavi's version with three or more brothers

describes how the second brother will jump in to save the first that fell into the river, while the third brother who does not risk anything will gain just as much as the second brother who risked his life.

Zahavi also attempts to prove reciprocal altruism to be unstable by stating that even in animal populations where altruism is enforced by punishment, it is costly to take on the role of the punisher. Therefore, those individuals who do not take part in punishing the social parasites are themselves social parasites with respect to the other individuals that take on the role of a punisher (Zahavi, 1995). Although Zahavi disclaims this theory, it seems to me that altruistic punishment somewhat resembles the tit-for-tat strategy, which is often quite effective. In a group where the majority is helping (cooperating), if an individual chooses to be a social parasite (defect), another member of the group will punish him (by also defecting) until the parasite chooses to cooperate. Therefore, if all group members cooperate, they will gain equal payoffs from their investment. If an individual chooses to be a social parasite, he might receive a higher payoff than the others who are investing their fitness in an altruistic act, but only for as long as it takes for a punisher to notice. Once a punisher notices, he will punish the parasite, thereby decreasing the parasite's overall payoff in the long run.

Zahavi's paper attempts to offer an alternative to the previous models in order to explain the interesting phenomenon of "helping at the nest", where the question, "Why would a non-breeding animal chose to invest in the fitness of breeders instead of trying to breed itself?" arises (Zahavi, 1995). The handicap principle seems like a logical way to explain the seemingly wasteful altruistic actions of individuals with respect to game theory. Game theory suggests that it is always in the individual's best interest to try to acquire as much utility as possible in all situations. That is, a rational individual will always try to maximize his utility by choosing

options that offer the highest payoff. It doesn't make game theoretic sense for an individual to invest his fitness into the welfare of a group if he isn't guaranteed to get something back.

Zahavi's alternative model is based on his studies of the cooperatively breeding Arabian Babbler. The results of the studies suggest that the motivation for an individual to invest into the welfare of the group is to advertise their own quality and to increase their "social prestige" (Zahavi, 1995). I find this concept of social prestige slightly difficult to account for or to assign a certain utility to, since other factors would also contribute to social prestige within a group and it is likely that there would exist quite a bit of overlap when trying to assign a utility for gain in social prestige. Unlike social prestige, deterring rivals, attracting mates and breeding successfully are outcomes that are much easier to assign utilities to.

An interesting point to note about this model is that unlike the previous three models, the advantage to the helper is direct. This might not only explain why babblers are so motivated to invest in the welfare of their group, but also why there are no social parasites in the population (Zahavi, 1995). In fact, it is quite common for individuals to compete with one another to be the helper, often interfering with the helping of others (Zahavi, 1995). This behavior cannot be explained by the other three models (Zahavi, 1995), as those models suggest that it is in the individual's best interest to be a social parasite, letting others help; reaping the benefits without paying the costs.

A paper entitled "From reciprocity to unconditional altruism through signaling benefits" by Lotem, Fishman and Stone support Zahavi's handicap principle. The paper acknowledges that although kin selection can account for altruism among genetically related individuals, it cannot explain unconditional altruism. Unconditional altruism, the unconditional help offered by an individual to a non-relative can be explained to an extent by reciprocity or by altruistic

punishment, but those models are unlikely to account for situations in which individuals offer unconditional help to distant and weak non-kin individuals who are unlikely to reciprocate the altruistic act, or to administer punishment for not having received help (Lotem *et al.*, 2002). An interesting recognition is that the level of help offered by an individual is dependant on the quality and fitness of that individual, which in turn advertises the level of individual quality to possible mates (Leimar, 1997 as cited by Lotem *et al.*, 2002). This idea was taken even further by suggesting that the competition for high-quality mates leads to competitive altruism between individuals in order to advertise their qualities through performance of altruistic acts (Roberts, 1998 as cited by Lotem *et al.*, 2002). An analysis of unconditional altruism has showed that for some individuals, unconditional altruism is only an evolutionary stable strategy when the cost of helping is higher than the benefit of signaling (Lotem *et al.*, 2002). This discovery might be explained by Zahavi's suggestion that if a signal of fitness was affordable to all individuals within the community, then it would become extinct (Lotem *et al.*, 2002). Therefore, the only individuals who can display this signal of fitness are those who are so fit that they can afford to suffer the costs of helping in order to reap the benefits of the signal. This means that the individual is risking to lose more of its utility than it might regain in the future. I personally feel that the theory of competitive altruism is weak in the sense that if two individuals were trying to outperform one another in order to reveal their higher level of fitness, they are ultimately reducing any difference in fitness that existed between them in the first place. In other words, if Bob was twice as fit as George, then according to the theory of competitive altruism suggested by Zahavi, the quality Bob's signal of fitness would be higher than that of George because Bob can afford to invest more into his signal. But by investing so much into his signal in order to outperform George, Bob is effectively reducing his own fitness. Over time Bob's fitness will

decrease to the level of George's fitness. As George could not afford to invest as much into his signal as Bob could, his fitness did not decrease as much as Bob's did.

An alternate view is presented in Russell and Hatchwell's paper entitled "Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate." This study is also based on observations of cooperatively breeding birds known as long-tailed tits. These birds represent an ideal model to study because initially, individuals breed independently in pairs, and only following a breeding failure would an individual choose whether or not to help another, and if so, who to help (Russell and Hatchwell, 2001). Also, individuals have the ability to distinguish between the calls of their kin and non-kin (Russell and Hatchwell, 2001). An experiment was set up in order to study whether or not helping was kin-biased within long-tailed tits. The key finding was that not all failed breeders become helpers – in fact many avoid helping unless they have kin present – and of those that do, virtually always help kin in preference to non-kin (Russell and Hatchwell, 2001).

All of these views are quite interesting in that they seem to all hold for the populations in which they were tested. This makes it very difficult to take a stance and support one argument or another because it seems to me that when kin selection fails, the handicap principle accounts for our observations, and vice versa. Another important point to note is that in Zahavi's study of the Arabian babbler, the handicap principle held true while the babblers were trying to promote their quality in order to find a mate, in other words, *before* the actual mating. In Russell and Hatchwell's study of the long-tailed tit, the kin-selection model held true *after* the individuals had mated and the initial breeding had failed. It would be interesting to know if the long-tailed tits studied by Russell and Hatchwell did use altruism as an advertisement before their initial mating. It seems that the problem here is that the altruistic acts being studied are performed in

completely different contexts. It would seem logical to think that since both Arabian Babblers and long-tailed tits are cooperatively breeding birds, they would have the same reasons for investing in altruistic actions with kin or non-kin. We can also make an argument here, in favor of the handicap principle. It is possible that the populations of failed breeding long-tailed tits that do choose to become helpers are doing so to advertise their fitness in order to attract new mates so that they may attempt to breed again. Although this is a possibility it does not explain why the helpers are choosing only to help their kin. This is a sound example of where both kin selection and the handicap principle can work together to explain altruism in a population. Just because one theory is likely to explain a phenomenon, it doesn't necessarily mean that another cannot be account for it also.

Another interesting observation I made while researching the different theories about the evolution of altruism is that some of the theories that seem to be supported by extensive credible evidence in the animal world are rejected by most evolutionary biologists simply because it seems illogical for an individual to perform an altruistic act solely for the benefit of another. I find this odd because I see people perform altruistic actions every day in the human world, and though they may seem illogical in terms of the 'every man for himself' mindset, the actions seem quite logical to the person performing the act. The problem I find with this mindset is that it fails to take into account emotions and other characteristics of animals, especially humans. I feel that ignoring these characteristics and qualities leads to theories being made that make sense if we were to consider animal instinct only, but are not quite reflective of the real world.

According to Zahavi, group selection was rejected because the system is vulnerable to parasites. As I mentioned before, it seems unreasonable to reject group selection for this reason because group selection is representative of real life. Social parasites exist in all animal species

and we see examples of it everyday in the human world. Zahavi discredited kin selection for the same reason, which again I feel is unreasonable. Zahavi's rejection of reciprocal punishment also puzzled me for reasons I mentioned previously. Again the situation in reciprocal altruism is present in real life so it seems unfair to reject it because it doesn't represent an ideal situation that cannot be invaded. I find this odd because I see these things happen every day in the human world, and though they may seem illogical in terms of the 'every man for himself' mindset, they seem quite logical to the person performing the act.

In conclusion, my research on the topic has shown that neither kin selection nor the handicap principle can explain all altruistic behaviors among animals. I feel that Zahavi's rejection of kin selection, reciprocal altruism and group selection was premature. Research has shown that all four of the theories discussed have been observed in animal behavior. Some behaviors exhibited by animals demonstrate the validity of more than one theory.

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