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ALTRUISM: THE UNRECOGNIZED SELFISH TRAITS

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Unlike Sober and Wilson, I suggest that in all cases of benefits conferred on others the direct fitness of the altruist increases. The benefit to others (group, kin, etc.) created by the altruistic act is only a consequence of the altruistic adaptation, and not the evolutionary mechanism that created it. In many cases the investment in the altruistic act, like handicaps required for signalling in general, attests to the social prestige of the altruist and thus increases its fitness. In other cases the 'altruist' is a phenotype that has only minute chances to reproduce, and what seems to be an altruistic act actually increases somewhat these meagre chances. It is easy to overlook this marginal benefit to the 'altruist'. Still, if that selfish benefit to the altruist — i.e., an increase in its direct fitness — did not exist, the altruistic acts that benefit the group could not have evolved.

Introduction

I restrict my remarks on the book *Unto Others* by Sober and Wilson (1998) to the first part of the work, which deals with the ultimate causation of altruism; I shall not address psychological altruism, which deals with mechanisms that have evolved to promote altruism — i.e., the proximate causation.

I congratulate Sober and Wilson for their clear presentation of the history of the Group Selection (GS) controversy and agree with their conclusions that models of Reciprocity and Kin Selection are special cases of the GS theory (Zahavi, 1995). However, I disagree with their conclusion that GS is important for the evolution of altruism. Although they have discussed GS in its relationship to reciprocity and kin selection, they have not even mentioned yet another alternative, namely my view on altruism as a Handicap, published over the last twenty years. A substantial part of my comment will discuss my theory as an alternative to their GS theory for resolving the problem of altruism.

My theory claims that what has been considered as altruism are phenomena that conferred benefit upon others, but were wrongly believed to decrease the fitness of the altruist. I suggest that in all these cases the direct fitness (as distinguished from indirect fitness, which includes kin selection and GS) of the altruist increases. The benefit of the altruistic act to others is merely a secondary consequence of its direct benefit to the altruist.

The main reason for the development of GS models was an attempt to resolve the evolution of altruism — i.e., the evolution of characters that seemed to decrease the fitness of their bearers. But if, as I suggest, altruism in that sense does not exist,

because these acts confer direct advantage on the altruist rather than decrease its fitness, then GS models are no longer required.

In the following I show how the exertion for a marginal increase in fitness by a desperate phenotype can drive the evolution of traits that have important consequences to the phenotype's associates. Later I present evidence from my studies on the babblers indicating that the altruistic act increases the social prestige, and thereby the fitness, of the altruist.

'Altruism' of Slime Moulds

Slime moulds, unicellular amoebae, have been described as cooperative unicellular organisms that display altruistic behaviour, because about 20 per cent of the group perish while serving the survival of the rest of the group. Unrelated slime moulds are equally 'altruistic', and obviously there is no room for reciprocity to a dead individual; thus, GS seemed to be the only model able to explain their social adaptations.

Looking for an alternative solution, we found that the doomed cells were inferior phenotypes. After studying the detailed behaviour of the doomed individuals (the 'altruists'), we suggested (Atzmony *et al.*, 1997) that these inferior phenotypes are doing the best they can to survive, and that the better phenotypes benefit from their struggle for survival. We found evidence that the inferior individuals are forced to move to the front of the migrating population by pressure from the better phenotypes. However, it has also been shown that some of these individuals may in fact escape death by following that path, which is probably their best chance to survive, meagre as that chance may be.

Babblers Competing to Serve

I became interested in the problem of altruism as a consequence of my research on the Arabian babbler, a group territory bird that I have been studying over the last 30 years. Large groups of babblers have an advantage over very small groups. One could easily suggest that a babbler that invests in augmenting the size of a particular group does so in order to serve its own individual interests as a member of that group, as suggested by Wright (1997). Wright and many others believe that this would be a model of individual selection, since the individual ends up serving its own individual interests. However, I agree with Sober and Wilson that such interpretations are based on GS.

The solution became apparent through our study of the details of babblers' social behaviour. We soon found that babblers do not merely serve their groups; they actually compete with one another to serve their group. They often take on sentinel duties when another babbler is already serving as a sentinel and is clearly willing to continue in that role. They try to feed adult babblers that are not interested in taking the food. More than that, they are often aggressive toward the individual that rejects their 'altruistic' activities: they may push a sentinel from its position; they may attack individuals that do not accept food or may attack individuals that come to help them when they are fighting their external enemies. Such social interactions could not have been selected by GS. They suggest that the 'altruist' gains, not just from the collective gain of the group, but rather directly, from its own investment in its group — i.e., from the fact that the investment in the welfare of the group is provided by itself and not by another member of the group.

Data we collected showed further that the dominant individuals inhibited subordinates from acting as altruists. Hence we suggested that babblers increase their social status (prestige) by acting as altruists. The benefit to the group from the 'altruistic' act is a consequence, and not the cause, of that act. Important though that consequence may be to the group, and consequently to the 'altruistic' individual, it is that individual's quest for social status that selected for the 'altruistic' behaviour. In other words, I suggested (Zahavi, 1977) that the 'altruism' of babblers is a selfish adaptation: the altruist gains directly from its actions. The 'cost' of the altruistic act is an investment (Handicap), similar to the investment of a peacock in its long and heavy tail. It is important also to realize that, like the peacock's tail, high prestige (reputation) also serves as a threat, to intimidate rivals within the group.

People in voluntary army units compete to risk their lives to save others, or to perform risky missions. These people are aware (pers. comm.) that their altruistic acts win them a high social status. Not all altruists are successful: some pay the ultimate price and are killed while helping others. But people also risk their lives by climbing Mount Everest, or engaging in risky sports — deeds that cannot be construed as altruistic — in their quest for social recognition. I therefore suggest that in babblers and in humans the investment in altruism is a Handicap, advertising reliably the altruist's claim to social status (Zahavi, 1977; Zahavi and Zahavi, 1997). In both cases, the individual signals his ability in a manner that would be prohibitively costly to a less able individual - that is, the war hero, the rescuer, and the mountain climber each assume a Handicap that ensures the reliability of their claim to fame.

Discussion

It is impossible on grounds of pure logic to exclude models of group selection as a potential selection mechanism. However, conditions under which GS can replace individual selection are so stringent that very good reasons should be presented why, in any particular case, GS is to be considered as the mechanism responsible for the selection process. I suggest that in every case where GS seems to solve the problem, a more thorough investigation of the facts will eventually expose the 'selfish' adaptations that have led to the apparent altruistic behaviour — as were here described for the cases of the apparent altruism in slime moulds, babblers and humans. More instances of self-interested 'altruism' can be found in our book (Zahavi and Zahavi, 1997).

Sober and Wilson describe the distribution of meat in hunters' societies as an altruistic act but agree that the hunter who offers meat may increase his reputation with women. They also refer (pp. 140–2) to inspection of predators by guppy fish as a form of altruism and suggest that the inspecting individual invests in the welfare of its group. They cite experiments in which guppies preferred to associate with conspecifics that approached a predator while inspecting it. In subsequent experiments, Godin and Dugatkin (1997) found that female guppies preferred to mate with those males that dared to come closest to the predator — that is, approaching the predator increased the fitness of the male guppy fish. Why, then, do Sober and Wilson continue to refer to these selfish investments in advertisement as 'altruism' and discuss them as cases of GS phenomena?

It is the consequence of the altruistic act — the benefit to others — that has placed altruism in a special class of adaptations; but the selection mechanism is not different from that of any other adaptation. Evidence that a group composed of altruists is doing better than a group composed of selfish individuals is no evidence that altruism evolved by GS. The group effect may enhance the rate at which altruism evolves. But I suggest that if the direct advantage to the altruistic individual should disappear, altruism will be selected out of the population. However, this will be difficult to determine experimentally, since the group effect cannot easily be separated from the direct advantage to the individual.

The fact that altruism has been selected by individual selection does not mean that altruists are cynical. It only means that the deep personal motivation for moral behaviour, as well as that of love, and of the readiness to invest and sacrifice for the sake of one's offspring, have evolved for the individual's ultimate advantage. But that takes us to the level of psychological — that is, proximate, rather than ultimate — causation.

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