

## New Evolutionary Perspectives on Altruism: Multilevel-Selection and Costly-Signaling Theories

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### Abstract

Social psychological theories tend to be primarily concerned with the immediate causes of altruism, whereas evolutionary explanations focus more on the origins and ultimate functions of altruistic behavior. Recent developments in the evolutionary psychology of altruism promise an even richer understanding of this important category of social behaviors. Specifically, new perspectives offered by multilevel-selection theory and costly-signaling theory may help to shed light on some of the more problematic issues in the study of altruism.

### Keywords

altruism; evolutionary theory; multilevel selection; costly signaling

When defining altruism, social psychologists usually focus on the intentions of the altruist (i.e., the act as a voluntary attempt to benefit other individuals), and their research has traditionally attempted to isolate the situational factors that determine when people will behave altruistically. Four decades of research have identified the importance of such factors as empathy, rewards, emotional states, social norms, and number of bystanders in influencing helping behavior.

However, social psychological models of altruism do not address the question of why basic motives such as empathy and various situational factors came to be so important. In fact, social psychologists continue to study altruism and other social behaviors with little reference to the origins and ultimate functions of altruism, which have been the primary concerns of sociobiologists.

Altruism has always been a thorny issue for evolutionary theorists; the idea of an organism engaging in a behavior that comes at a great personal cost and seems to benefit only other individuals was difficult for natural selection to explain. It was not until the concept of inclusive fitness was introduced by Hamilton (1964) that evolutionists had a satisfactory theoretical framework for discussing altruism. Inclusive fitness is often referred to as “kin selection,” because according to this concept, natural selection favors behaviors that benefit others who share our genes, especially closely related kin. Hence, the mother who sacrifices her life so that her children survive may actually be engaging in a behavior

that is genetically very adaptive, as the copies of her genes that reside in her children will in the long run lead to greater genetic fitness than if she alone had survived.

The concept of kin selection is somewhat limited in that it cannot explain the whole range of altruistic behaviors observed in humans and other animals. For example, it cannot account for altruistic acts aimed at other individuals known not to be genetic kin. Obviously, there are many situations in which we help others who are not related to us: We loan money and personal belongings to friends, we give rides to strangers who are hitchhiking, and we go out of our way to do favors for acquaintances who ask us for help. Fortunately, an alternative form of altruism, *reciprocal altruism* (Trivers, 1971), explains why these important and socially necessary behaviors occur frequently in our lives. Reciprocal altruism is defined as cooperative behavior among unrelated individuals that benefits everyone involved. Individual success at reciprocal altruism depends greatly on the ability to quickly identify others who will be good exchange partners and those who are cheaters.

Because humans are a supremely social species, the selection pressures faced by early humans in this regard must have been profound. It would have been evolutionary suicide to consistently behave in a selfless, altruistic manner toward unrelated individuals who took as much as they could get while offering little in return. Consequently, it should not be surprising that people do seem to have skill in identifying cheaters. For example, they recognize photographs of other individuals better if the people in the photographs have been identified as "untrustworthy" the first time they were seen than if they had been described by other adjectives (Mealey, Daood, & Krage, 1996). Simi-

larly, people are hesitant to enter into interpersonal relationships with other individuals who are known to be highly manipulative (Wilson, Near, & Miller, 1998). Just as we are primed to detect cheaters, we also seem to be primed to quickly recognize true altruists who will be trustworthy partners in social exchange (Brown & Moore, 2000).

### MULTILEVEL-SELECTION THEORY

The concepts of kin selection and reciprocal altruism are the foundations of most evolutionary explanations of altruism, and a belief that it is generally inappropriate to talk about natural selection occurring at any level larger than that of the individual organism dominates the field at this time. However, in recent years, a growing number of researchers have come to believe that the concept of natural selection can be meaningfully applied at the group level, and they maintain that group selection may be more common and more important than previously thought (Boehm, 1999; Wilson, 1997).

This new perspective is called *multilevel-selection theory* (MST), and its primary spokesperson has been evolutionary biologist David Sloan Wilson. For Wilson, it is crucial to distinguish between the competition between individuals within the same group and the competition between individuals in different groups. Within-group selection follows the generally accepted idea that individual organisms (or collections of genes) are in direct selfish competition with each other. Group-level adaptations, in contrast, require thinking in terms of selection in which groups can be thought of as adaptive units in their own right. According to MST, groups do not evolve into adaptive

units for all traits, but only for those traits that increase the fitness of some groups relative to other groups (Wilson, 1997). In a highly social species such as humans, an altruistic predisposition toward other group members independent of past reciprocal interactions with these individuals may have been just such a trait. Although such "knee jerk" altruism may appear to decrease the fitness of individual altruists, it may sometimes become adaptive because groups of altruists will be more fit than groups of non-altruists under the right conditions (Wilson, 1997).

Consider what might happen if two groups that are in direct competition with each other have different concentrations of altruists and nonaltruists. If one group has a high concentration of altruists, the cooperation among the altruists might increase the success of the group, bestowing significant adaptive advantages on all the individuals within the group. If the rival group is dominated by nonaltruists, it might be at a disadvantage relative to the group dominated by altruists, which would diminish the fitness of all the individuals in the less altruistic group. Because the cooperative group would prosper at the expense of the selfish group, the net result would be an overall increase in the number of altruists in the population as a whole. Hence, MST offers a compelling explanation for how altruistic tendencies would evolve in situations in which the main selection pressure derives from intense competition between two or more competing groups, when the fortunes of each individual are closely tied to the success of his or her group. However, if groups are permanently isolated from each other and the competition that exists is entirely within the group, natural selection would eliminate the altruists from the groups in short order as they would be mercilessly ex-

plotted by selfish individuals. In this scenario, the evolution of altruism is better explained by a more discriminating brand of reciprocal altruism.

Some critics of MST have argued that although selection at the group level may have been theoretically possible, the conditions that would be necessary for it to occur almost never exist in the real world (Cronk, 1994). The validity of this criticism awaits the results of research designed specifically with this issue in mind. However, the more common attacks leveled against MST stem from a basic misunderstanding of what the theory is saying. Although MST is not inherently incompatible with more traditional evolutionary viewpoints, it is often presented as if this were the case. For example, many writers equate MST with long-discredited naive theories of group selection based on organisms acting for "the good of the species," and think that MST discounts the importance of natural selection that occurs in units smaller than groups. MST does not deny that selection at lower levels of organization is vitally important; on the contrary, MST maintains that selection at the individual level occurs at a faster pace than selection at the group level (Boehm, 1997). In fact, MST maintains that traits such as altruism are selected at the group level precisely because they are ultimately adaptive to individuals. The confusion apparently arises over the fact that it is the individual's membership in a group faced with particular selection pressures that causes the group to become the vehicle for behaviors that benefit each individual.

### COSTLY-SIGNALING THEORY

How might one explain large philanthropic gifts to nonkin or even

handouts to beggars that will never be reciprocated? None of the aforementioned explanations of altruism offer a ready answer. *Costly-signaling theory* (CST) has been developed to help account for these interesting charitable acts (Grafen, 1990; Zahavi, 1977). In some respects, CST is about truth in advertising. It proposes that individuals often engage in behaviors that are very costly as a way of signaling honest information about themselves. Such behaviors can benefit the signaler by increasing the likelihood that he or she will be chosen as a mate or an ally or that he or she will later be deferred to as dominant by would-be rivals. Costly signals can also benefit observers simply because they provide useful social information. Smith and Bird (2000) have described the four qualities that a behavior must have to qualify as a costly signal. First, the behavior must be easily observable by others. Second, it must be costly to the actor in resources, energy, or some other significant domain. Third, the signal must be a reliable indicator of some trait or characteristic of the signaler, such as health, intelligence, or access to resources. Finally, the behavior in question must lead to some advantage for the signaler.

CST suggests that extreme forms of philanthropy and altruism are conspicuous displays of resources that serve to reinforce one's status. After all, if one can afford to expend a great deal of money, energy, or time in a manner that seems to be irrelevant to one's selfish interests, then the resources that one has in reserve must be very great indeed. This type of "competitive altruism" can be a way of positioning oneself for access to resources during unforeseen future times of need (Boone, 1998). There is, in fact, evidence to support the belief that individuals who have a history of being mag-

nanimous are rewarded by others when times get tough. Among the Ache of Paraguay, for example, individuals who shared more than average with others in good times received more food from more people when they were sick or injured than did those who had been less generous (Gurven, Allen-Arave, Hill, & Hurtado, 2000). Apparently, having everyone owe you for past unselfishness can be a good hedge against future calamities, and costly signaling may be an effective strategy for inducing reciprocal altruism.

Anthropological studies provide numerous examples of exaggerated displays of public generosity, but these studies have yet to follow through on verifying the advantages that accrue to the displayers. For example, on Ifaluk Atoll in Micronesia, males sometimes engage in torch fishing (luring flying fish into nets at night with torches) when other fishing techniques would actually be more efficient. Torch fishing is a difficult, time-intensive activity, but also a highly visible activity that serves to advertise a man's work ethic (Sosis, 2000). Similarly, Smith and Bird (2000) described a form of costly signaling among the Meriam, a Melanesian society located on an island off the coast of Australia. Two to 5 years after a death, the family of the deceased puts on an elaborate feast to coincide with the erection of an expensive and showy permanent tombstone. Gifts are given to all guests, along with prodigious amounts of food. Ideally, one of the main courses is turtle meat obtained through a dangerous, time-consuming turtle hunt. Successful turtle hunting requires careful coordination of effort and great physical agility, strength, and diving abilities because the turtle hunters have to jump from a boat onto moving turtles in open water. The ability to supply many turtles for the funeral feast serves as an hon-

est signal of the physical quality of the males in the family. Everyone in the village is invited to the feast, and no reciprocation of any kind is expected.

## CONCLUSIONS

The antagonism between experimental social psychology studies of altruism and evolutionary thinking is counterproductive and misplaced. The paradigms are not inherently adversarial, and each provides a valuable piece of the puzzle. The difference between traditional psychological explanations of altruism and evolutionary explanations is a matter of focus. Social psychological theories tend to be primarily concerned with the immediate causes of altruism, whereas evolutionary explanations focus more on the origins of altruistic behavior. Social psychological theories have effectively identified many of the emotional and situational factors associated with altruistic behaviors, and evolutionary perspectives have been more effective at providing a theoretical framework for understanding the origins and ultimate functions of altruistic behavior. The concepts of inclusive fitness, reciprocal altruism, costly signaling, and multilevel selection can provide new, rich frameworks from which experimental social psychologists can launch more theoretically based investigations of altruism.

A union of these two rich traditions can provide both the hypotheses and the methods needed to study some currently unresolved issues. For example, MST suggests

that competition between groups added a new evolutionary dimension that would have changed the course of evolution for traits such as altruism. Anthropologists might explore the degree to which this appears to have occurred in early human groups, and social psychologists might use this idea as a springboard for studying the behavior of individuals in a variety of social and work groups. Similarly, anecdotal accounts of costly signaling are interesting, but more rigorous research is needed to determine if the outcomes of such behavior fall in line with what evolutionists would predict. In short, open-mindedness regarding different perspectives within evolutionary thinking and a willingness to combine an evolutionary perspective with the traditions of social psychology promise much for our understanding of the nature of human altruism.

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## Note

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