

Chapter 12

**EVOLUTION AND THE PROBLEM OF ALTRUISM:
CURRENT AND HISTORICAL PERSPECTIVES**

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INTRODUCTION

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 (McAndrew, 2002). 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, who study altruism from the perspective of evolutionary theory. Before diving into the intricacies of evolutionary debates about altruism, a bit of background about evolutionary perspectives on social behavior is in order.

**THE “LEVELS OF SELECTION”
DEBATE IN EVOLUTIONARY THEORY**

Group Selection

There has always been a controversy about exactly what the “unit of selection” is in evolutionary theory. Throughout most of the 20th century, it was common for biologists to believe that evolution was primarily a struggle for survival between different species or

groups, and they freely talked about animals doing things for the “good of the species” (Segerstrale, 2000). In this case, the unit of selection was the “group” and individual survival and reproduction was only important insofar as it contributed to the fitness and well-being of the group as a whole. This position came to be known over time as “group selection.” It dominated evolutionary thinking for quite some time, reaching its peak of influence with the work of Vero Wynne-Edwards in the early 1960s (Wynne-Edwards, 1962, 1963). However, during the 1960s and 1970s there was a revolution in evolutionary thinking. The exciting work of many pioneering sociobiologists (e.g., Bill Hamilton, George Williams, Richard Dawkins, John Maynard Smith, George Price, Robert Trivers) turned the common wisdom upside down and decisively turned the focus of research away from the group and fixed it firmly on the individual organism, or even more specifically, on the gene, as the proper unit of selection. By the 1980s, group selection had been dismissed as an outdated idea and there was little serious discussion of it as an important force in evolutionary change. The critics of group selection theory had effectively 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; Dawkins, 1994; Dennett, 1994; Maynard Smith, 1989).

Inclusive Fitness and Kin Selection

Group selection remained popular for so long because there were many social behaviors that could not be easily explained in any other way. Clearly, the thorniest issue was the problem of altruism (Krebs, 1987). After all, the idea of an organism engaging in a behavior that came at a great personal cost and which only seemed to benefit other individuals was difficult for natural selection operating at the level of the individual to explain. What eventually replaced group selection as the unifying principle in evolutionary theory was the concept of *inclusive fitness*, sometimes referred to as *kin selection*. Throughout the rest of this chapter, these two terms will be used interchangeably. The concept of Inclusive fitness (or kin selection) has been so successful because it has been able to explain difficult social behaviors such as altruism without abandoning the focus on individual selection, which has been so important in evolutionary theory.

The dynamics of inclusive fitness were worked out by the evolutionary biologist Bill Hamilton and published in a now classic paper in 1964. His inclusive fitness theory has had profound implications for the study of family relationships and social behavior in general. The concept of inclusive fitness/kin selection has become the foundation upon which evolutionary explanations for many social behaviors have been built. In fact, some researchers believe that Hamilton’s inclusive fitness theory is the single most important development in evolutionary theory since Darwin’s original work was published in the 19th century (Buss, 1999).

What is “Inclusive Fitness” and “Kin Selection?”

When one moves from thinking about natural selection at the group level to thinking about it at the level of the individual, the shift in thinking that has occurred is from a larger to a more specific unit of selection. The shift in focus required for thinking about kin selection is even greater, for now the unit of selection goes beyond the individual organism all the way

down to the gene. Low (2000) has observed that people often have difficulty understanding kin selection because they have trouble distinguishing *apparently* costly behavior from *genetically* costly behavior. This distinction is essential for thinking of natural selection at such a specific level. No longer can we think solely in terms of what is good for the survival of individual organisms, but rather about what is best for the survival and perpetuation of individual genes. The reason this perspective is often referred to as “kin selection” is because natural selection may favor behaviors that benefit others who share our genes, especially closely related kin. In the words of Richard Dawkins (1976, 1989), genes assist replicas of themselves that are sitting in other bodies. Hence, the individual who sacrifices her life so that her children may 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.

Hamilton’s Rule

The great beauty of Hamilton’s inclusive fitness theory is that it also provides a mathematical formula that has successfully predicted the frequency of altruistic behaviors in species ranging from social insects to human beings. Specifically, his formula proposes that the genes responsible for a behavior will be successful whenever $rb > c$, where “r” represents something called the “coefficient of relatedness,” “b” represents the benefit to the recipient of that behavior, and “c” represents the cost of the behavior to the donor. A behavior that is costly (even fatal!) to an organism may still be adaptive if the recipient of the benefits of that behavior is a very close relative *and* if the benefit is substantial. Until the development of Hamilton’s Rule, the heroic, self-sacrificial behaviors that can be observed throughout the animal kingdom were something of an enigma, explainable only in vague “for the good of the group” language. In fact, when Hamilton’s theory was first proposed, many assumed that it was just another form of group selection. Strictly speaking, kin selection is *not* a form of group selection; at its core, it is still a matter of a selfish gene looking out for its own interests (Dawkins, 1976, 1989).

The “benefits to the recipient” and “costs to the donor” represented in Hamilton’s Rule will be clear to most readers. However, the “coefficient of relatedness” needs a bit more explanation. This concept, represented by the letter “r” in Hamilton’s formula, is an estimate of the number of genes that we are likely to share with another individual. In other words, it represents the probability that a gene present in one individual is also present in another. The probability that someone else shares a particular gene of yours depends largely on how closely he or she is related to you. This can be determined mathematically. An identical twin shares *all* of our genes, so the coefficient of relatedness for an identical twin would be as high as it would be for one’s own self. A parent or a sibling shares half of your genes and will be higher in relatedness than a grandparent who only shares 25% of the same genes. Uncles, great-grandparents, and first cousins will only share 1/8 of your genes. Hamilton’s Rule allows very specific testable predictions about how much cost an individual will be willing to bear to help others who differ in their degree of kinship. Haldane (1955) made the often repeated (at least in evolutionary circles) observation that although he would not give his life for one brother, he might do so for *two* brothers or for eight cousins.

Hamilton’s Rule revolutionized the way we think about social relationships, and the predictions that it makes have generally been borne out by research. For example, Burnstein, Crandall, & Kitayama (1994) found that an individual’s willingness to help someone else in a

life-threatening situation (rushing into a burning house to save them) could be predicted almost perfectly by the degree of relatedness of the person in the burning building. Helping in less pressing situations where the cost to the donor was very low was not as dependent upon the donor's relationship to the recipient. Similarly, many studies have shown that the likelihood that one will receive an inheritance from someone else can be predicted by the degree of genetic relatedness to that individual (Bossong, 2001; Judge, 1995; Smith, Kish, & Crawford, 1987).

Kin Recognition

Kin selection would not be a very useful idea if individuals were unable to distinguish others who are related to them from those who are not. It should not be surprising, therefore, to find that animals of all kinds have a remarkably good ability to distinguish kin from non-kin. The variety of kin recognition mechanisms have been described by several authors (Cartwright, 2000; Porter, 1987; Reeve, 1998). The most common kin recognition mechanisms would include the following:

- 1) Spatial Location – For most species, the chances that another individual living nearby will be a relative of some sort is fairly high, so these neighbors will be more likely to be treated as kin.
- 2) Familiarity/Degree of Association – Other individuals with whom an individual has spent a great deal of time early in life are likely to be kin, so the familiarity of other individuals can serve as a cue to kinship.
- 3) Phenotypic Resemblance – Others who resemble us physically in some way will likely be perceived as kin. Hence, anything that makes us seem similar to others will be likely to elicit more altruistic behavior from them. Many studies have indicated that olfactory cues are an important means of kin recognition for many species of mammals, and there is evidence that humans are also able to detect kin by odor (Cernoch & Porter, 1985; MacFarlane, 1975; Porter, Cernoch, & McLaughlin, 1983; Russell, 1976; Russell, Mendelson, & Peeke, 1983). It has even been suggested that the ease with which people develop regional dialects and accents may have evolved as a way of facilitating kin recognition.
- 4) Recognition Alleles – It may be possible that genes carry some sort of distinctive “tag” that would allow them to recognize copies of themselves in others who also have altruistic tendencies. Dawkins (1976) likened these distinctive tags to a “green beard.” An individual carrying a green beard gene will be predisposed to behave altruistically toward others who have green beards, as the odds are that this altruistic behavior will be reciprocated whether the other green bearded individual is kin or not. This predisposition to behave altruistically toward similar other has come to be known as the “Green Beard Effect.”

Of course, kin recognition is important for reasons other than directing altruism toward the “right” individuals. It will also be important for facilitating parental care and steering mate choice away from inappropriate others.

Multilevel Selection Theory (MST)

A belief that it is generally inappropriate to talk about natural selection occurring at any level larger than that of the individual organism still dominates the field at this time. This perspective fits most of the evidence. Nevertheless, it appears that group selection is not yet dead, nor has it been buried as deeply as many would have liked. In recent years the unit-of-selection debate has been rekindled by a growing number of researchers who now believe that the concept of natural selection can be meaningfully applied at the group level, and they also believe that group selection may be more common and more important than previously thought (Boehm, 1999; Fehr, Fischbacher, & Gächter, 2002; Hamilton, 1996; Wilson, 1997a, 1997b; Wilson & Kniffin, 1999). This new, more flexible perspective proposes that natural selection can occur at many levels, from genes through social groups and even multispecies communities. This new perspective is called *Multilevel Selection Theory (MST)*, and its primary spokesperson has been evolutionary biologist David Sloan Wilson. Rather than insisting that natural selection only operates on genes or species, MST allows for the possibility that selection can be occurring simultaneously at different levels.

According to David Sloan Wilson (1997c), adaptation at different levels of the biological hierarchy requires flexible thinking about natural selection. For Wilson, it is crucial to distinguish between the competition going on between individuals within the same group and the competition that occurs between individuals in different groups. Within-group selection follows the more accepted idea that individual organisms (or collections of genes) are in direct selfish competition with each other. Group-level adaptations, on the other hand, require thinking in terms of between-group selection in which groups can be thought of as adaptive units in their own right, and not just as by-products of individual self-interest (Wilson, Wilczynski, Wells, & Weiser, 2000). According to Multiple Level Selection Theorists, groups do not evolve into adaptive units for *all* traits, but only for those that are adaptive in a group but not in an individual context. In other words, "group selection favors traits that increase the fitness of groups relative to other groups" (Wilson, 1997c, p. S122). 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). Nevertheless, the MST perspective has been an especially useful way of thinking about traits such as altruism which may appear to decrease the fitness of individual altruists, but may work because groups of altruists will be more fit than groups of non-altruists under the right conditions (Wilson, 1997c). At first glance, it would appear that altruism would not be a good evolutionary strategy and that altruistic individuals will be mercilessly exploited by selfish individuals who will leave them far behind in the race for evolutionary success. While this would certainly be true in a situation in which individuals are competing directly with other individuals, it may not be true if the competition is primarily between two different *groups*. Sober and Wilson (1998) described how altruism might evolve at a group level of selection, and much of what follows is derived from their work.

According to Sober and Wilson, traits like altruism only evolve through group selection when more than one group is present, when natural selection will favor any behavior that increases the relative fitness of the group. 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 advantages on all of 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 the 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 exploited by selfish individuals.

Critics of MST believe that traits such as altruism can be better explained through kin selection (favoring those who share our genes) or through reciprocal altruism with unrelated others when an act of altruism is likely to induce a return benefit (Dawkins, 1989; Trivers, 1971, 1985). In either case, the belief is that the trait of altruism would be selected because it is ultimately adaptive to individuals, NOT just because it contributes to the fitness of the group as a whole.

Although MST is not inherently incompatible with more traditional evolutionary viewpoints, it is often presented as if this was the case. The issue can be confusing because at this time it is not even clear which theoretical perspective is the more parsimonious. It will not be the goal of this chapter to take sides in the levels-of-selection debate. Although explanations based upon kin selection and inclusive fitness will undoubtedly remain more influential, we should try to keep an open mind and consider a variety of levels of selection in an attempt to make sense of altruism and other social behaviors.

THE PROBLEM OF ALTRUISM REVISITED

Earlier in this chapter, we discussed the problems that altruism posed for evolutionary theory. Prior to the introduction of the concepts of multilevel selection theory, inclusive fitness, and kin selection, it was very difficult to explain how natural selection could favor behaviors that appeared costly to the giver and beneficial only to the receiver of those behaviors. Kin selection provided a clear framework for understanding how such behaviors may still be adaptive insofar as they benefit relatives who share genes with the altruist. Hamilton's Rule provided even more specific predictions linking the likelihood of an altruistic act with the degree of relatedness between the altruist and the beneficiaries of his or her act. The perspective provided by kin selection has been invaluable for advancing our understanding of altruism. However, it 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, and more traditional social psychological models based upon socialization processes have not been any more helpful in this regard. (For a summary of these social psychological models, see Batson, 1998; Clark, 1991, Grusec, 1991, or Schroeder, Penner, Dovidio, & Piliavin, 1995). To understand this type of altruism, we must turn to other theoretical explanations.

Reciprocal Altruism

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. Any theory of altruism that depends entirely upon the notion of kin selection cannot account for behaviors such as these. Fortunately, an alternative form of altruism, *reciprocal altruism*, explains why these important and socially necessary behaviors occur frequently in our lives.

The concept of reciprocal altruism was pioneered by Robert Trivers (1971) and extended by several other evolutionary theorists (Axelrod, 1984; Axelrod & Hamilton, 1981). Reciprocal altruism is defined as cooperative behavior among unrelated individuals which benefits everyone involved (Cosmides & Tooby, 1992; Trivers, 1971). Much of the laboratory research on reciprocal altruism has made use of two-person games in which the participants can adopt a cooperative or competitive strategy. In these games, the most beneficial strategy for both players in the long run is a strategy called "tit-for-tat" in which players reciprocate the strategy of their opponents (Axelrod & Hamilton, 1981). In tit-for-tat, if an opponent adopts a cooperative strategy, he or she receives cooperation in return. If opponents adopt a competitive strategy, that is also what they get in return. Dawkins (1989) provided a colorful example of how tit-for-tat strategies might ultimately lead to an evolutionarily stable behavior that would be favored by natural selection. Imagine a population of creatures that has three varieties of individuals: suckers, cheats, and grudgers. At first all of these individuals co-exist in equal numbers, but eventually the number of grudgers will increase until they dominate the population. This occurs for a number of reasons. Suckers end up helping everyone indiscriminately and they end up being exploited shamelessly by others. Cheats take as much as they can get from everyone and rarely reciprocate anything. The "cheat" strategy is profitable for a while, but as the number of suckers diminish and as the cheats are found out, they become less successful. The hardest survivors are the grudgers, who continue to help those who help them but refuse to cooperate with cheats. The cheats first eliminate the suckers, but they in turn are then eliminated by the grudgers. Hence, even though an altruistic behavior being performed in the present may prove beneficial to only one of the individuals involved, under a system of reciprocal altruism the other person will eventually be repaid in kind. Given this harsh fact of life, it is not surprising that "mental scorekeeping" in our relationships with others has become a finely-honed human skill (Brosnan & de Waal, 2002).

Trivers (1983) has described three conditions that will favor the evolution of reciprocal altruism. First of all, there must be a social living arrangement in which individuals cannot remain anonymous. It has been well documented that reciprocity works best in small groups where "free-riders" are quickly detected. The research showing that people in small towns and rural areas are more helpful than city dwellers in a wide range of situations undoubtedly reflects this reality (Hedge & Yousif, 1992; Steblay, 1987). Secondly, there must be a high level of mutual dependence among the individuals in the group. That is, it must be necessary for each individual to seek help from others from time to time in order to be successful. Finally, there cannot be a rigid dominance hierarchy, which would prevent some individuals from having the power to help others.

If the aforementioned criteria are present, conditions will be ripe for a social system of reciprocal altruism to develop. Before that can occur, however, the individuals in the group

must have the cognitive abilities necessary to make the most of the opportunity. Several researchers have described the cognitive capacities required to form the social contracts that would make it all work (Cosmides & Tooby, 1992; de Vos & Zeggelink, 1997; Reeve, 1998). Each person must have the ability to recognize different individuals *and* the capacity to easily store and retrieve memories of past interactions with these people. There must be “cheater detector” and “reciprocator recognition” mechanisms that can effectively identify those who are good and bad credit risks. When possible, we are well served by favoring relationships with familiar exchange partners with whom we have had successful dealings in the past (de Vos & Zeggelink, 1997). To successfully maintain mutually gratifying reciprocal relationships, we must also be able to easily think in terms of costs and benefits, and we must be able to understand the needs and desires of others while also effectively communicating our own (Cosmides & Tooby, 1992).

The concept of reciprocal altruism has been an important piece in the challenging puzzle of altruism. It has also provided a useful framework for understanding the evolution of a wide range of emotional reactions such as empathy, guilt, shame, and moralistic anger. It would appear that emotions such as these have been shaped by the need to effectively manage reciprocal altruism in our relationships with others (Trivers, 1971; Weisfeld, 1999).

Costly Signaling Theory

Together, kin selection and reciprocal altruism explain a great deal of the altruistic behaviors that one observes in everyday life. Yet, there are still instances of altruism that do not fit neatly into either of these boxes. For example, how can we explain large philanthropic gifts to non-kin or even handouts to beggars that will never be reciprocated? Another view of altruism known as *Costly Signaling Theory* (CST) has been developed to help account for these interesting charitable acts (Grafen, 1990; Zahavi, 1975, 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. The information that is transmitted can benefit *both* the signaler and the observer of the behavior. The behavior 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 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 of all, the behavior must be easily observable by others. Secondly, the behavior in question must be costly to the actor in resources, energy, or in 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.

Costly Signaling Theory 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 one's self 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 magnanimous do

get rewarded by others when times get tough (Gurven, Allen-Areve, Hill, & Hurtado, 2000). Apparently, having everyone owe you for past unselfishness can be a good hedge against future calamities.

Anthropological studies provide numerous examples of the strategic advantage afforded by exaggerated displays of public generosity. In the Ifaluk Atoll of Micronesia, males will sometimes do things the hard way to signal something about their strengths. Specifically, they will 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) describe a form of costly signaling among the Meriam, a Melanesian society located on an island off the coast of Australia. Two to five 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 will be 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 since 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 honest 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.

A study by Goldberg (1995) indicates that altruism on a more modest scale can also be motivated by the need to enhance one's status in the eyes of observers. In this study, males who were alone were observed to donate more to female panhandlers than to male panhandlers (an attempt to attract mates?). Interestingly, if males were with a female companion they were relatively *unlikely* to donate money to a female panhandler, although the tendency to give to other males did not seem to be affected.

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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