Cooperation☆

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Background

Not surprisingly, humans have displayed an absorbing fascination for examples of cooperation in the animal world, long before the evolutionary puzzle associated with them became evident. Indeed, freedom from evolutionary thinking accommodated all manner of untenable theories about cooperation, in the past. While T.H. Huxley believed that cooperation and altruism were only possible among close kin and P. Kropotkin saw "mutual aid" everywhere he looked, unconnected with any sort of kinship, both W.C. Allee and V.C. Wynne Edwards succumbed to a naive form of group selection, the notion that cooperation and self-sacrifice existed because they were good for the group and the species—never mind that they were harmful to the individuals displaying them.

Kin Selection

Modern evolutionary thinking by people such as J.B.S. Haldane, W.D. Hamilton, R.L. Trivers, J.M. Smith, and E.O. Wilson, which kept in mind the critical problem of the potential for a few cheaters to wreck any cooperative group, has given us our current theories of cooperation. These modern advances have depended in part of clear-cut demarcation and definition of different kinds of interactions possible among animals (see **Fig. 1**). The most significant advance in explaining the evolution of cooperation came from Hamilton's inclusive fitness theory. Not only does this theory provide a logical explanation for why cooperation evolves more easily among kin, it also shows why close kinship is not always essential. Kin selection or, more precisely, Hamilton's rule has three parameters, namely, cost to the actor, benefit to the recipient, and the coefficient of relatedness between actor and recipient. Given appropriately skewed cost/benefit ratios, it is easy to see that even rather low levels of relatedness can satisfy Hamilton's rule. Unfortunately, an excessive and often exclusive focus on measurement of relatedness and the neglect of the cost and benefit terms in empirical studies, has sometimes given the false impression that kin selection fails to explain cooperation.

When the cost and benefit terms have been adequately measured, Hamilton's rule has proved to be a powerful theoretical framework for understanding the evolution of cooperation and altruism in a wide variety of organisms from bacteria to man. To cite just two examples, studies on the white-fronted bee-eater in Kenya have shown that not only the presence of helpers at the nest but also the bizarre behavior of the father's harassing their sons to return and act as helpers, is consistent with the predictions of Hamilton's rule. Computation of the costs, benefits, and relatedness involved in different strategies shows that by harassing their sons and bringing them back to help rear additional offspring, fathers gain a substantial fitness advantage. In contrast, sons reap about the same fitness benefit whether they resist their father's harassment and carry on with their own family life or whether they succumb to the harassment and return to act as helpers. And in the primitively eusocial wasp *Ropalidia marginata*, Hamilton's rule correctly predicts that only about 5% of the individuals should opt for solitary life while the remaining should opt for altruistic, sterile worker roles.

In any case, kin selection is indeed inadequate when cooperation is directed toward nonrelatives, as it often is in human societies. Those who study humans use a somewhat more liberal use the word cooperation using it not only when there is cooperation, that is, both actor and recipient benefit from an interaction but also when there is altruism, that is, when the actor pays a cost and only the recipient benefits, cost and benefit being measured of course in terms of Darwinian fitness. To help explain the evolution of cooperation by natural selection in the absence of close genetic relatedness between actor and recipient, at least four additional potential mechanism of evolution have been suggested, in addition to kin selection (see **Fig. 2**). The first of these additional mechanisms is Direct Reciprocity, originally proposed by Robert Trivers as "Reciprocal Altruism." The idea here is that if a cost incurred now is retrieved at a later point in time, then both actor and recipient will benefit on the long run. As might be expected, such reciprocity will require individual recognition, long-term memory, and well developed cognitive abilities. For these reasons direct reciprocity is more likely in humans than in animals for which it was first proposed. And once we allow cognitive abilities involving recognition and memory, other more sophisticated and more subtle mechanisms can be imagined. For example, one can postulate that there is no need for the same individual who received help to reciprocate. As long as the helper received help in the future from someone, the same effect is achieved. This is possible if the act of helping someone by a helper is noticed by others in the population and the helper builds up a reputation for being a helper. Then others who may

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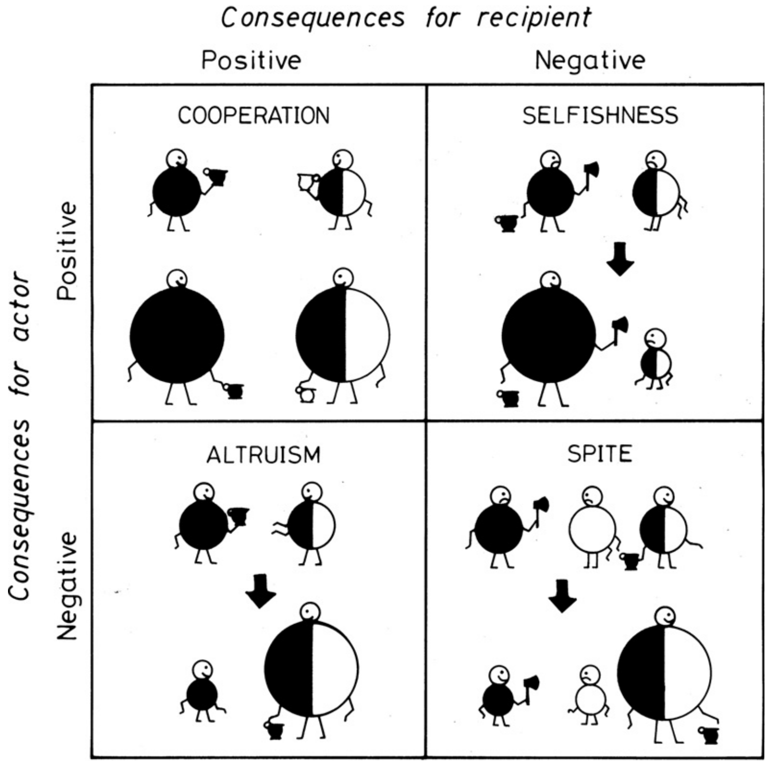

Fig. 1 The consequences of interaction between animals. The recipient here is the actor's brother and therefore shares 50% of his genes, as is indicated by the shading. Help of any kind (the offering of food or shelter, easing access to a mate, and so on) is indicated by a vessel, and harmful behavior by an ax. *Cooperation*: Both individuals benefit and such behavior will therefore evolve easily. *Altruism*: The altruist diminishes his own genetic fitness but raises his brother's fitness to the extent that the shared genes are actually increased in the next generation. *Selfishness*: The selfish individual reduces his brother's fitness but increases his own to an extent that more than equals the brother's loss. *Spite*: The spiteful individual lowers the fitness of an unrelated competitor (the unshaded figure) while reducing that of his own or at least not improving it; but the act increases the fitness of the brother to a degree that more than compensates for the actor's loss. Reproduced from Gadagkar, R. (1997). Survival strategies—Cooperation and conflict in animal societies. Cambridge, MA: Harvard University Press.

not necessarily have received help directly from this helper will also be likely to help her because she is a known helper. This kind of mechanism labeled as Indirect Reciprocity is postulated to explain why for example, people donate to charities. A more sophisticated form of indirect reciprocity may involve cooperators for spatially defined networks to keep cheaters at bay. This is labeled as Network Reciprocity and has been shown mathematically to help cooperation to evolve in populations of potentially selfish individuals. Finally there is Group Selection, a refined version that is cognizant of the problem of cheaters and postulates that although selfish individuals outcompete cooperative or altruistic individuals within groups, groups of cooperators out-compete groups of selfish individuals and the net effect depends on how fast the selfish individuals drive cooperators within group to extinction relative to how fast groups of cooperators drive to extinction groups of selfish individuals. Despite their apparent diversity, these five mechanisms for the evolution of cooperation have a rather beautiful mathematical unity (see Nowak, 2006).

Perhaps the most fascinating recent advance in the study of cooperation and altruism in humans has been due to the collaboration of evolutionary biologists, psychologists, and economists and the use of "games," such as the ultimatum game and the public goods game, to uncover patterns of human behavior. The main results of such studies are that people by and large do not behave and expect others to behave, in apparently rational, selfish ways traditionally predicted by theoretical economists. Instead, people behave in a fair manner and expect others to do the same. Even more interestingly, people appear to have an innate dislike for cheaters and are often willing to incur as cost to themselves to punish cheaters even if it yields them no direct benefit. The prevalence of such "altruistic punishment" is now thought to be the evolutionary force that maintains cooperation and altruism in human societies.

It must be mentioned that even in the context of evolution of sociality and cooperation in animals and insect societies such as those of ants, bees and wasps, kin selection itself has recently come under severe criticism. Claiming that kin selection, also known often as inclusive fitness theory or Hamilton's rule, is not sufficiently general and robust, some prominent researchers have turned back to a combination of individual and group selection to explain the evolution of cooperation, altruism, and

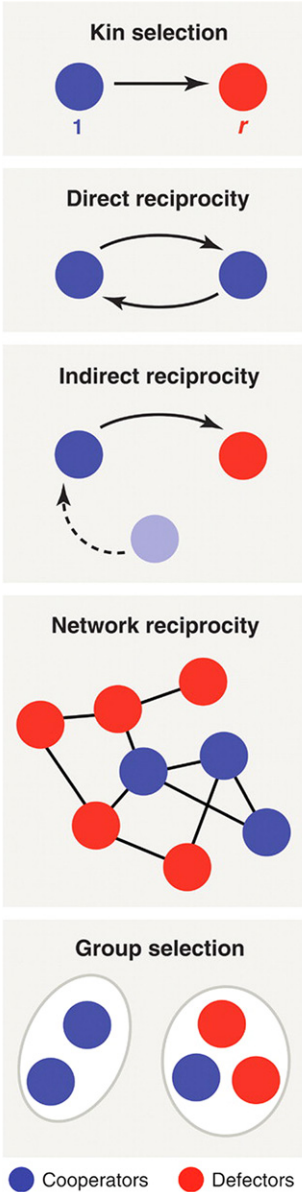

Fig. 2 Five mechanisms for the evolution of cooperation. Kin selection operates when the donor and the recipient of an altruistic act are genetic relatives. Direct reciprocity requires repeated encounters between the same two individuals. Indirect reciprocity is based on reputation; a helpful individual is more likely to receive help. Network reciprocity means that clusters of cooperators outcompete defectors. Group selection is the idea that competition is not only between individuals but also between groups. Reproduced from Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science* **314**, 1560–1563.

sociality in the animal kingdom as a whole. This effort is sometimes referred to as multilevel selection. While the defenders of kin selection have dismissed these criticism as unjustified and a rather fierce debate has ensued and deeply divided the disciple, it appears to me that the scientific study of cooperation in animals and humans is poised for even more exciting new developments, whichever way the debate for and against kin selection goes. This optimism is rooted in the current realization among biologists that although natural selection is rooted in competition it is cooperation among competing actors that is central to every major evolutionary innovation, every major transition in evolution, whether it was the origin of cells, of eukaryotes, of insect and other animal societies, or of language.

See also: Behavioral Ecology: Social Behavior and Interactions. General Ecology: Communication

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