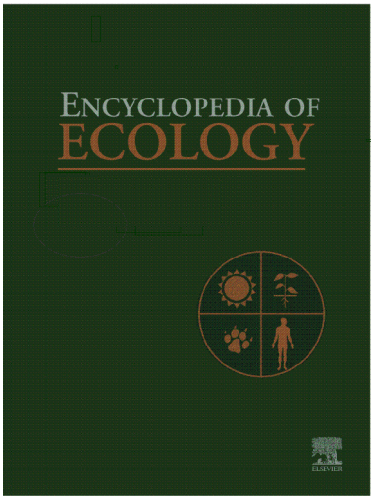




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# Cooperation

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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 D. S. 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. The most significant advance in explaining the evolution of cooperation came from Hamilton's inclusive fitness theory (see Social Behavior and Mutualism). 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 one example, 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.

But kin selection is indeed inadequate when cooperation is directed toward nonrelatives, as it often is in human societies. 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.

## Conclusion

A recent attempt at forging a synthetic view of all these myriad ideas argues that all existing models can be classified into four categories: (1) those that propose direct benefits to the cooperator, (2) those that facilitate reciprocity, (3) those that involve kin selection, and finally (4) those that invoke the so-called greenbeard effect. The last class of models is valid in a scenario where genuine cooperators can recognize each other by some phenotypic traits such as a green beard, for example, which co-occurs with the propensity to cooperate. While much more needs to be done on the theoretical front, empirical studies compatible with testing modern theoretical models are now the rate-limiting step in furthering our understanding of the evolution of cooperation.

*See also:* Altruism; Kin Selection; Mutualism; Social Behavior.

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