THE SEVENTY GREAT MYSTERIES OF THE NATURAL WORLD

UNLOCKING THE SECRETS OF OUR PLANET

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with 368 illustrations, 338 in colour

Thames & Hudson

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Why are animals nice to each other?

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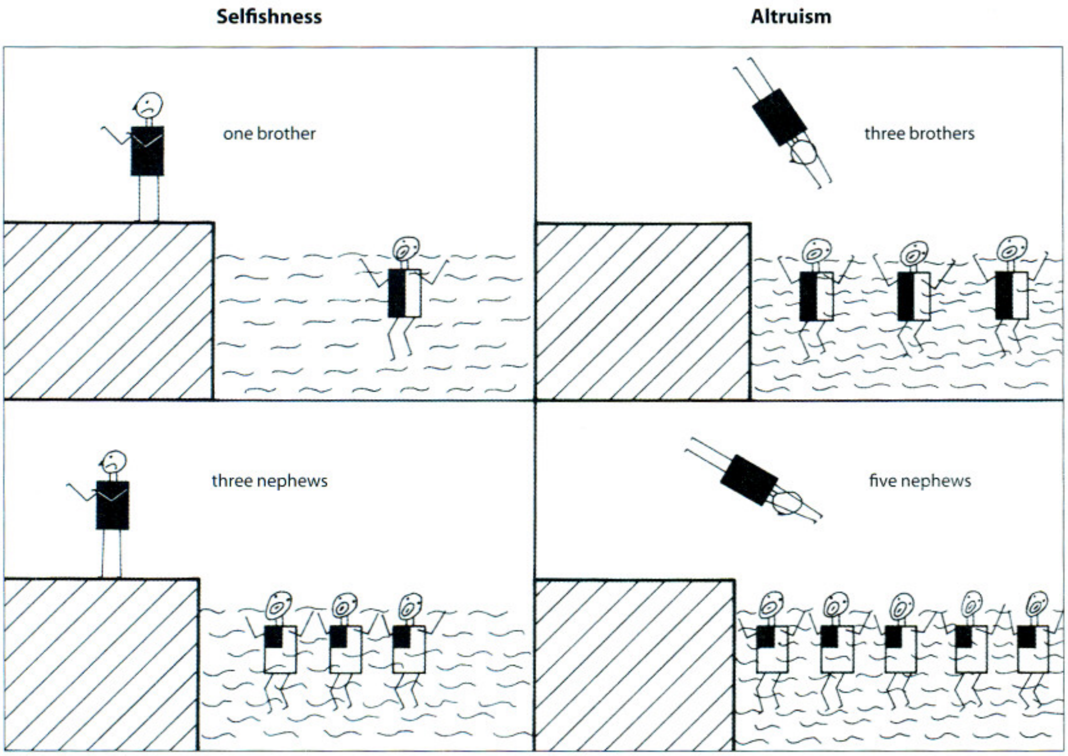
Natural selection, it should never be forgotten, can act solely through and for the advantage of each being.
CHARLES DARWIN, 1859

It may sound strange, even perhaps malicious, to label niceness as a mystery. But that's just what it is for evolutionary biologists, who like to label anything that they cannot easily explain through Darwin's theory of natural selection as a mystery. Natural selection, graphically described by Darwin's phrase 'the preservation of favoured races in the struggle for life', prepares us to expect competitive selfishness rather than cooperation and altruism. After all, how can an individual that pays a cost in helping another be expected to win the race to survive and reproduce?

And yet we find many examples of animals doing just that. Honey bee workers kill themselves in the process of stinging predators that might destroy their nest. Helpers at the nest of the bee-eater postpone rearing their own offspring and spend time and energy in assisting their parents to raise an additional brood. A ground squirrel risks attracting the attention of the predator to itself by giving an alarm call to warn its neighbours. Why aren't such individuals eliminated by virtue of lowering their chances of survival and reproduction?

Ground squirrels, which give alarm calls warning others of danger while putting themselves at a slightly greater risk of predation, provide an opportunity to investigate how such altruistic behaviours spread through natural selection.

Many birds, such as the bee-eaters seen here, show cooperative breeding, where older siblings who are reproductively mature postpone breeding and remain in their natal nests to assist their parents in raising an additional brood.



A cartoon illustrating J. B. S. Haldane's idea:. the shaded sections of the drowning individuals indicate the proportions of their genes which are also present in the altruist standing on the bank. The altruist is willing to risk his life when the number of his genes expected to be rescued is greater than the number in his body expected to be lost by his drowning.

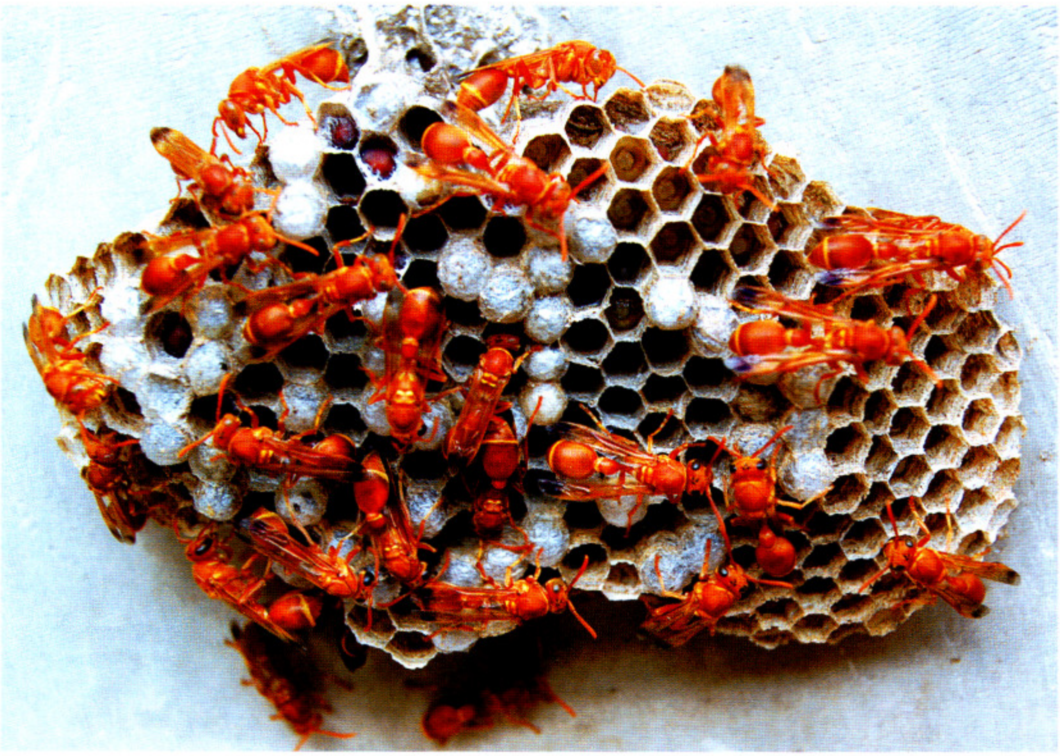
A modern evolutionary theory

Not surprisingly, humans have displayed an absorbing fascination for cases of cooperation in the animal world, long before the evolutionary puzzle associated with them became evident. Precise evolutionary thinking on this matter can be traced back to J. B. S. Haldane, who realized that risking one's life to save drowning relatives can indeed be favoured by natural selection, provided that more copies of genes that give rise to such behaviour are recovered in the saved relatives than are lost in the risk taker. W. D. Hamilton (see also p. 222) formalized essentially the same idea in what has since come to be known as Hamilton's Rule, which states that an altruistic gene will spread in a population when the benefit to the recipient, devalued by the coefficient of relatedness between altruist and recipient, is greater than the cost incurred by the altruist.

Thus the alarm-calling behaviour of the ground squirrel is no longer a mystery if the probability of saving individuals carrying genes for alarm-calling is greater than the probability of losing one copy of such a gene due to the death of the caller. Similarly, the helping behaviour of the bee-eater can be explained if its assistance at its parents' nest results in the rearing of more additional siblings than the number of offspring it might have produced instead of helping. Not only does this theory provide a logical explanation of why cooperation evolves more easily among kin, it also shows why close kinship is not always essential. If the benefit is very much greater than the cost, even low genetic relatedness will suffice.

Testing the theory

The theory is elegant indeed, but the hard part is to show that animals behave as if they obey Hamilton's Rule. Here, most observers have chosen the easy option of assuming that the cost and benefit terms are equal, and of testing the simpler prediction that altruism is more often directed towards close relatives than it is to distant relatives or non-relatives. This simpler prediction is sometimes, but not always upheld. Thus 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



Ropalidia marginata *is a tropical paper wasp abundant in South India. Each nest may contain from one to around a hundred adult female wasps, but only one – the queen – is fertile, while the others assist in raising her offspring. Because the queen is no different in size or shape from the sterile helpers, such a society is considered 'primitive'.*

impression that Hamilton's Rule is inadequate to explain altruism. Where the cost and benefit terms have been measured, Hamilton's Rule has indeed provided a powerful tool to understand altruism.

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 behaviour of a father harassing his 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 sons and bringing them back to help rear additional offspring, a father gains 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 and return to act as helpers.

In our study of the primitively social wasp *Ropalidia marginata* in South India, we have used Hamilton's Rule to compute the costs and benefits for different wasps of remaining in their mother's nests as sterile helpers versus leaving to found their own new colonies and reproduce. It turns out that for some individuals staying back is a more profitable strategy, while for others leaving brings more fitness. We have succeeded in predicting correctly the fraction of the population that should opt for a sterile helper role in a social setting rather than a reproductive role in a solitary setting.

Hamilton's Rule is, however, inadequate when cooperation is directed towards non-relatives. The theory of reciprocal altruism (which is based on the idea that favours are returned after a time lag) provides a powerful explanation for cases of cooperation among non-relatives. There is also a relatively untested but very promising radical new idea that altruism may simply be a handicap that the most successful individuals can afford to take on without paying the same cost that unsuccessful individuals would have to pay.

While more needs to be done on the theoretical front, empirical studies measuring all three terms – cost, benefit and relatedness – are now what is mostly required to clinch our understanding of the evolution of altruism. But I would hazard a guess that we are poised to demystify the evolution of niceness in the natural world.