

CURRENT TRENDS IN SCIENCE

PLATINUM JUBILEE SPECIAL



Edited by
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INDIAN ACADEMY OF SCIENCES
BANGALORE

Why are animals (and humans) nice to each other?*

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1. Introduction

It usually comes as a surprise to my friends, especially to those in the humanities, that a major problem that we evolutionary biologists are obsessed with is why animals and humans are so nice, i.e., cooperative and altruistic, toward each other. Why not investigate selfishness, conflict and back-stabbing that is so widespread, they plead. It may indeed sound strange, even malicious, to label nicety as a mystery. But that's just what it is for evolutionary biologists, who like to label everything that they cannot easily explain through Darwin's theory of natural selection, as a mystery. Of course, the motivation for labelling something as a mystery is to provoke deeper study of the phenomenon and, where appropriate, a modification of the theory to fit the new facts. Darwin's theory of natural selection, graphically described by his 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 order to help another individual, 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 additional brood. Ground squirrels risk attracting the attention of the predator to themselves by giving an alarm call to warn their neighbours. How can natural selection promote such behaviour? Why don't such individuals get eliminated by virtue of their lowering their own chances of survival and reproduction?

Not surprisingly, humans have displayed an absorbing fascination for cases of cooperation and altruism in the animal world, long before the evolutionary puzzle associated with them became evident. Indeed, freedom from precise evolutionary thinking accommodated all manner of untenable theories about cooperation and altruism, in the past. While Thomas Henry Huxley believed that cooperation and altruism were only possible among close kin, Peter Kropotkin saw "mutual aid" everywhere he looked, unconnected with any sort of kinship. W C Allee and V C Wynne Edwards and many others succumbed to a naïve 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 [1]. There was unfortunately a long period during which such 'naïve group selection' and vague 'good of the species' arguments prevailed. The Nobel Laureate Konrad Lorenz wrote for example

*Expanded and modified (with permission) from Gadagkar R (2008) Why are animals nice to each other? In: *The Seventy Mysteries of the Natural World – unlocking the secrets of our planet*, (ed.) Michael J Benton, Thames and Hudson Ltd., London.

that ‘Darwin had already raised the question of the survival value of fighting, and he has given us an enlightening answer: It is always favourable to the future of a species if the stronger of two rivals takes possession either of the territory or the desired female’ [2]. Ironically such arguments were neither logically sound nor were they attributable to Darwin who was a clear individual selectionist stating unambiguously that ‘Natural selection, it should never be forgotten, can act solely through and for the advantage of each being.’ Apart from obfuscating the true significance of many biological phenomena, naïve good of the species rhetoric readily lent itself to the vindication of social Darwinism and such other evils that purported to justify such human social inequalities as racism and genocide, in the name of natural selection. Naïve group selection came to an abrupt end in the 1960s at least among evolutionary biologists due to some simple but precise thinking by a handful of people; for a brief review, see [3].

2. A modern evolutionary theory

Precise evolutionary thinking on this matter can be traced back to the famous 20th century biologist J B S Haldane who became an Indian citizen in the 1960s. Haldane appears to have been the first person to realize the arithmetic truth 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 (figure 1). The English biologist W D Hamilton formalized essentially the same idea in what has since come to be known as Hamilton’s Rule (box 1). The rule, usually written as $[b \cdot r > c]$ states that an altruistic gene will spread in a population when the benefit $[b]$ to the recipient, devalued by the coefficient of relatedness between altruist and recipient $[r]$, is greater than the cost incurred by the altruist $[c]$. In the words of Edward O Wilson, ‘How can altruism, which by definition reduces personal fitness, possibly evolve by natural selection? The answer is kinship.’ 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 behaviour 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 is no longer a mystery if its help 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 for why cooperation evolves more easily among kin, it also shows why

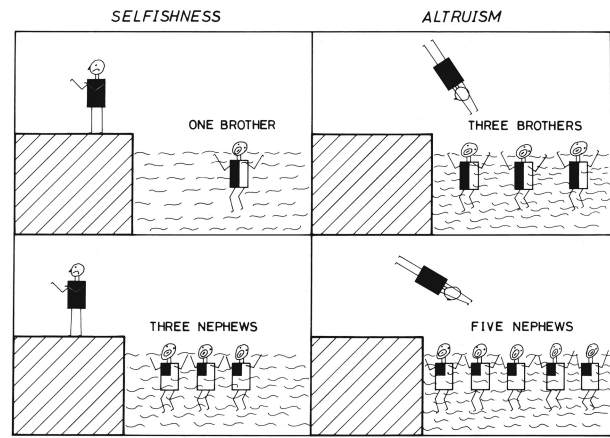


Figure 1. Cartoon illustrating the theme of J B S Haldane’s story. The shaded portions of the drowning individuals indicate the proportion of their genes which are also present in the altruist standing on the bank. Notice that the altruist is willing to risk his life when the numbers of his genes expected to be rescued is greater than the number in his body likely to be lost. (Drawing by Sudha Premnath; reprinted from [3].)

close kinship is not always essential. If the benefit is very much greater than the cost, even low genetic relatedness will do.

3. 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, i.e., whether they behave altruistically only when Hamilton’s Rule is satisfied and behave selfishly when the rule is not satisfied. Here most empiricists 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. Perhaps the most famous example of such a limited test, based merely on the measurement of relatedness, has been carried out in the honey bee. Because of their peculiar haplodiploid genetics, honey bee workers are more closely related to their nephews than they are to their brothers, as long as their mother mates with a single male. But the relatedness to nephews becomes less than that to their brothers if the queen mates with more than two males. Because honey bee queens are known to routinely mate with several males, worker bees are expected to be less related to their nephews than to their brothers and thus are expected to destroy any nephew eggs that their sister workers might sneak into the nest and rear only their brother eggs laid by the queen. There is now good evidence that worker bees undertake such policing of each other and destroy most worker laid eggs

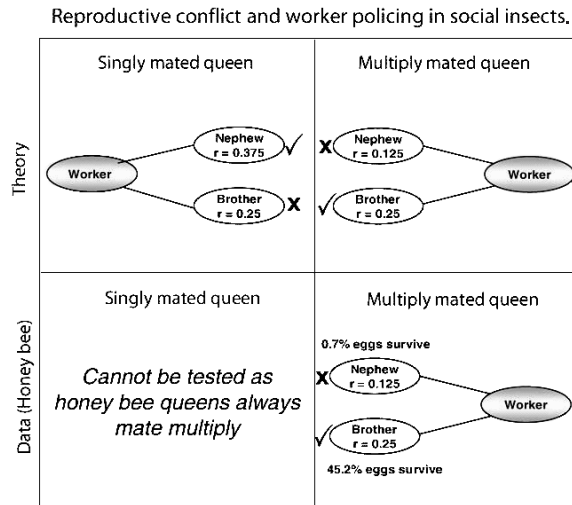


Figure 2. Because of their peculiar haplodiploid genetics, workers in hymenopteran insect societies are more closely related to their nephews than they are to their brothers, as long as their mother mates with a single male. But the relatedness to nephews becomes less than that to their brothers if the queen mates with more than two males. Thus theory predicts that workers should prefer nephews over brothers when their mother mates singly but should prefer brothers over nephews when their mothers mate multiply (upper panel). One part of this theoretical prediction is upheld in experiments with honey bees, because honey bee queens mate with multiple males. There is now good evidence that worker bees police each other and destroy most worker laid eggs; in experiments where honey bee workers were offered queen-laid haploid eggs which are normally expected to be their brothers, and worker laid eggs (which are normally expected to be their nephews), only 0.7% of the worker laid eggs survived while 42% of the queen-laid eggs survived (lower panel; see [4]). Because honey bee queens always mate with multiple males, the other part of the prediction that workers should prefer nephews over brothers cannot be tested in the honey bee.

(figure 2) [4]. Nevertheless, because the proximate cues used by the workers to distinguish worker-laid eggs from queen-laid eggs are not well understood, there is always a lingering doubt that destruction of worker eggs may have been selected for some reason other than relatedness based, indirect fitness benefits [5].

4. Measuring relatedness is not enough

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 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

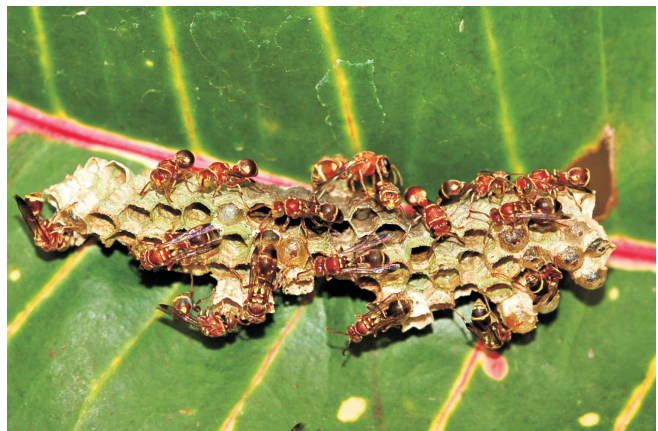


Figure 3. Typical nests of the primitively eusocial wasps *Ropalidia marginata* (upper panel) and *Ropalidia cyathiformis* (lower panel) (see text and [6]).

only the presence of helpers at the nest but also the bizarre behaviour of fathers harassing their sons to return and act as helpers, are consistent with the predictions of Hamilton's Rule. In an attempt to answer the question whether animals behave as if they obey Hamilton's Rule, I and my students have chosen the locally abundant social wasps *Ropalidia marginata* and *Ropalidia cyathiformis* (figure 3). These wasps live in relatively small colonies consisting of less than a hundred individuals among which only one individual (referred to as the queen) reproduces while the rest function as altruistic sterile workers and spend their whole lives rearing the queen's offspring. An important feature of these wasps is that they are primitively social, meaning that they can still pursue a solitary life style, i.e., a lone female wasp can build a nest, lay eggs and bring her offspring to adulthood, all by herself. The remarkable fact of course is that most wasps nevertheless prefer to nest in groups and lead the life of a sterile

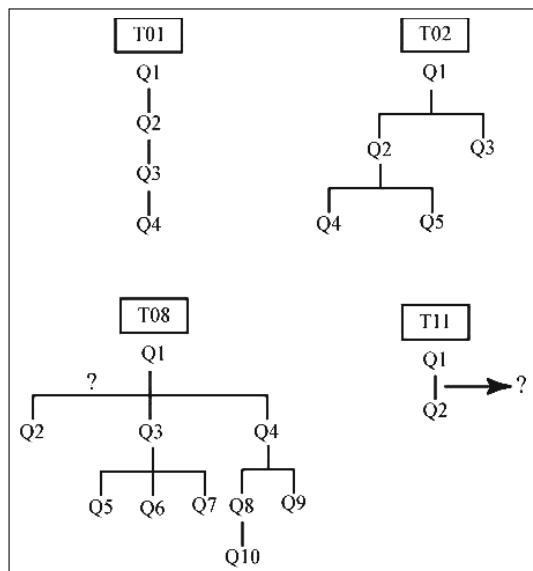


Figure 4. Pedigrees of queens in four colonies of *R. marginata*, involved in a long-term study. The relationship between queen 1 (Q1) and queen 2 (Q2) is unknown for colonies T08 and T11 because both Q1 and Q2 were among the wasps present on the nest at the time of its collection and transplantation (Reprinted from [6]).

worker, helping to rear the queen's brood. Our research has uncovered some rather remarkable facts concerning the lives of these wasps and has provided novel insights into the evolutionary forces that mould the evolution of altruism. For example, we were able to construct royal pedigrees of the queens in these wasps (figure 4) and discover to everyone's surprise, that altruism in these colonies is not merely directed towards close genetic relatives such as brothers and sisters but also directed to nieces and nephews, cousins, cousins' offspring, mother's cousins, mother's cousins' offspring and even mother's cousin's grand-offspring. I often joke that these wasps will put any Indian joint family to shame (table 1). We also find that altruism in these wasps is very context dependent – not all wasps are altruistic, the same wasp is not altruistic at all times, altruism depends on genetic relatedness to the recipient and even more importantly, altruism depends on the ecological situation the wasps find themselves in. Perhaps our most important discovery is that, contrary to conventional wisdom, altruism is not just a matter of kinship; it is shaped by complex ecological features of the environment and complex physiological and demographic features of the wasps themselves. Our research has now reached a level of sophistication that allows us to correctly predict the proportion of the population of wasps that should opt for a selfish, solitary nesting strategy and the proportion that should opt for an altruistic, worker strategy [6].

Table 1. Genetic relationships between successive queens and between workers and brood observed in the four colonies (Reprinted from reference [6]).

Relationship between queens and their immediate predecessors	Relationship between workers and brood
(a) Daughters	(1) Sisters
(b) Sisters	(2) Brothers
(c) Nieces	(3) Nieces and nephews
(d) Cousins	(4) Cousins
	(5) Cousins' offspring
	(6) Mother's cousins
	(7) Mother's cousins' offspring
	(8) Mother's cousins' grand-offspring

5. Group selection resurrected?

David Sloan Wilson has all along kept alive interest in a certain unobjectionable form of group selection, better termed as 'trait-group selection' or 'intrademic group selection' [7,8]. It is now being recognised that selection could act in principle at various levels of biological organization. Attempts are being made to develop models of multi-level selection, to address such fundamental questions as how selection at lower levels of organization such as that of individuals create higher levels of organization such as societies and, how selection at one level affects selection at other levels [9]. More recently, a different and more controversial attempt is being made to resurrect group selection. There are several reasons why this has created something of a turmoil in the field. First, group selection is being touted as an alternative to kin selection and not just as an alternative to individual selection. Second, it is being spear-headed by E O Wilson [10], the very man who created the field of sociobiology based largely on kin selection. Third, the new group selection ideas are being most forcefully applied to the evolution of insect societies, the traditional bastion of kin selection. Indeed, the claim is that '*...group selection is the strong binding force in eusocial evolution; individual selection, the strong dissolutive force; and kin selection... either a weak binding or weak dissolutive force...*' [11]. And fourth, it is being claimed that genetic relatedness is not essential for the evolution of altruism [12]. The last point is probably the most useful part of the debate because we can make precise and mutually exclusive predictions. Indeed, Foster *et al* [13] have taken up the gauntlet with the words '*...the discovery of true altruism that evolved in the absence of relatedness would be strong evidence against*

kin selection theory, paralleling Darwin's statement that altruism between species would reject natural selection...' One can therefore hope that at least this point will soon be settled one way or another, unless of course people keep changing the very definitions of altruism and relatedness.

6. Humans are a special case

Humans are indeed a special case because we often cooperate with and behave altruistically toward non-kin. Robert Trivers [14] proposed the theory of reciprocal altruism to explain altruism toward non-kin. The idea is that 'I will do you a favour today, at a cost to myself if there is a reasonable guarantee that you will return the favour tomorrow, when I am in need'. And 'if you don't, then I punish you of course by not helping you the next time you are in need'. This sounds like a good idea but it has been hard to document in animals. Cognitive abilities to recognise past helpers so as to selectively return favours and even more importantly, to remember, recognise and punish cheaters who take help and do not reciprocate, may be absent or limited in animals. Reciprocal altruism may work more effectively in humans because of our well-developed cognitive abilities and social networks but we still cannot explain many acts of altruism that are directed at strangers without a history of specifically helping the altruist. Indirect reciprocity or the idea that A helps B because B is known to have helped C, may be somewhat easier to evolve because it depends on reputations of individuals as 'altruistic, helping individuals' [15,16]. Nevertheless, human altruism remains a puzzle because we often behave altruistically not only to genetically unrelated strangers in large groups but also when reputation gains or cues are entirely absent. This is a uniquely human dimension of cooperation and altruism that appears to be absent in any other animal species.

An exciting new paradigm for investigating the evolutionary puzzle of human cooperation and altruism is beginning to develop and promises to provide what might be a uniquely human solution to a uniquely human problem [17]. There are several other most interesting and unique features of this new paradigm. One is that it is being developed as a collaborative effort between evolutionary biologists, psychologists and economists. Another is that the primary methodology in use consists of 'economic games' played with human volunteers. Many games are being used and I will mention two of the most common ones.

One game, called the *Ultimatum* game, invented by the German economist Werner Güth some three

decades ago, has become something of the 'laboratory rat' in this line of research. The game is played between two anonymous players who have to decide on how to split a sum of money given by the experimenter. One player, the *proposer* offers a certain proportion of the sum to the other player, the *responder*. If the responder, who is aware of the total sum, agrees to the proposed division of the money, the deal goes through and the game is over with money distributed between the proposer and responder as agreed. If the responder rejects the offer, nobody gets any money and the game is nevertheless over. The excitement associated with this game has to do with the fact that the results obtained when played with real people are in stark violation of the theoretical prediction made by economists. Economists have implicitly or explicitly postulated the concept of *Homo economicus*, meaning that humans behave as rational maximizers of individual selfish gains. Thus the responder is expected to accept even the smallest non-zero sum offered to him because something is better than nothing. Knowing this, as the proposer is also a member of *Homo economicus*, he ought to always offer the smallest non-zero sum and keep the rest to himself. But real people do not play that way. Generally people offer 40 to 50% of the total sum and offers below 30% are often rejected. This is a remarkably robust result that appears to be largely unaffected by the cultural background or literacy of the players and even more surprisingly, it does not seem to be affected by the magnitude of the total sum involved. Indeed researchers have had to travel to remote cultures in Africa, South America and the Pacific Islands, to detect any significant variation in the sums offered by proposers and in the sums rejected by responders. The broad conclusion is that humans do not behave as *Homo economicus*. People often reject grossly unfair offers and the proposers know this so that they offer a fair or nearly fair proportion. The world average for offers seems to be about 45%. People appear to have a sense of fairness and behave in an 'other-regarding' way.

The results of another game, the so-called *Public Goods* game are even more striking. In this game, the experimenter offers say Rs. 100 to each of 4 players. The players are anonymous to each other and each has to independently decide how much of his or her Rs. 100 to keep and how much to invest in a common pool which brings benefit to all the players. To simulate the benefits accruing from the common pool, the experimenter doubles the common pool and distributes it equally among all four players. Thus if each player invested Rs. 50 in the common pool, Rs. 200 would accumulate in the common pool and the investigator doubles this to Rs. 400 and gives Rs. 100 back to each

player. Thus everyone gets back twice what he or she had invested in the common pool. Clearly, it is good to invest in the common pool, i.e., good to cooperate. However consider the situation where one player contributes nothing to the common pool and keeps his Rs. 100 to himself. Since the other three players invest Rs. 50 each, the common pool now has Rs. 150, which the investigator doubles to Rs. 300 and gives back Rs. 75 to each player (note that the player who did not contribute to the common pool also gets an equal share of the benefit). Thus the three players who contributed to the common pool end up with Rs. $50 + 75 = 125$ each, while the player who did not contribute anything to the common pool takes home a booty of Rs. $100 + 75 = 175$. Clearly, it pays even more to be selfish, not to contribute anything to the common pool and reap the benefits of other people's generosity. Thus the *Homo economicus* model of human behaviour predicts that nobody should contribute anything to the common pool and that nobody should go home with any more than their initial Rs. 100. But again, real people do not play that way. Most people contribute nearly half their initial sum to the common pool. But why do people play this way? Why are people not as selfish as predicted by the *Homo economicus* model. Why do people cooperate and behave altruistically?

A possible answer suggests itself when the public goods game is played with an interesting twist. When players were offered the opportunity to punish their (anonymous) co-players who did not contribute enough to the common pool in previous rounds, many were eager to do so even if they had to incur a cost to themselves. For example, a player could impose a fine of Rs. 10 on a co-player but in order for this punishment to be executed the punisher had to pay say, Rs. 5 so that both the Rs. 10 and the Rs. 5 went back to the experimenter. It was remarkable the players were willing to punish their co-players at a cost to themselves even when they were unaware of the identity of the co-players and even when they were aware that they would not encounter the same players again. In games that had such an option to punish, all players seemed to fear punishment because contributions to the common pool went up. Fehr and Gächter [18] who performed these experiments conclude that people seem to derive a 'primal pleasure' in punishing free-riders and that it may be in our genes to do so. In other words they suggest that human cooperation and altruism may be maintained more because of fear of punishment rather than due to any innate tendency to cooperate. These are intriguing results and intriguing suggestions, by no means definitive, but clearly worthy of further investigation.

Taken at face value these results suggest that the evolution of human cooperation and altruism may be based on quite different forces as compared to what we have seen for other animals. Unless of course we begin to find that animals also show generalised reciprocity, other-regarding behaviour and a tendency to punish free-riders. Recent examples of very clever experiments with rats, capuchin monkeys and chimpanzees promise to engage with these questions in the near future [19–21].

7. Conclusion

While more needs to be done on the theoretical front, empirical studies compatible with testing modern theoretical predictions (arising out of Hamilton's Rule, group selection of different kinds, multilevel selection and reciprocity of various hues) are now probably the rate limiting step in clinching our understanding of the evolution of cooperation and altruism. But I would hazard a guess that we are poised to demystify the evolution of nicety in the natural world – animal and human.

Acknowledgements

My research is supported by the Department of Science and Technology, Department of Biotechnology, Ministry of Environment and Forests and Council for Scientific and Industrial Research, Government of India.

Box 1

Hamilton's Rule

$$b/c > 1/r$$

b = benefit to recipient

c = cost to donor

r = genetic relatedness between donor and recipient
or

$$n_i r_i > n_o r_o$$

n_i = No. of relatives reared

r_i = relatedness to relatives

n_o = No. of offspring reared

r_o = relatedness to offspring

Hamilton's Rule defines the condition for the evolution of altruism. The upper form is useful to predict when an individual will be selected to sacrifice its life to help others. The lower form is useful

to predict when a sterile individual who rears relatives will be selected over a fertile individual who rears offspring.

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