while you continue to prepare for War.

Ignore or take away what hinders her

Make sacrifices for the sake of her

It is a great part of peace
from the heart to will peace

Gentleness breeds gentleness

This is the way of love, the way
that pleases God
and makes for joy.

I've said my say.

Altruism's Evolution

Michael J. Reiss

What can recent theories in evolutionary biology about the problem of altruism contribute to a Christian perspective on the nature of humanity?

Altruism is considered a 'problem' because Darwin's theory of natural selection[1] leads us to expect all organisms, including humans, to be selfish. According to the theory of natural selection those traits which we expect to see in the natural world are the ones which have conferred on their bearers the greatest reproductive success. As altruism means the giving of aid, a preliminary reading of Darwinism suggests that altruism poses a challenge to the whole theory of adaptation by natural selection. Sociobiology has a great deal to say about the evolution of altruism in non-humans. How far does the study of altruism in non-humans help us to understand altruism in us?

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Sociobiological theories for the evolution of altruism

Sociobiology, the systematic study of the biological basis of all social behaviour[2], dates as a named discipline from only 1975, when E.O. Wilson's now much-discussed book, *Sociobiology: The New Synthesis,* was published. As altruism manifestly requires social behaviour—an organism cannot be altruistic on its own!—theories for the evolution of altruism lie at the centre of sociobiology.

The first biological explanation for altruism was, however, proposed by none other than Darwin himself. Having developed the theory of natural selection, Darwin went on to consider how the sterile castes in many social insects could have evolved. He realised that it might be argued that such castes could not have evolved by natural selection because the bearers of traits associated with sterility leave, by definition, no offspring, but he proposed that sterility in such circumstances could evolve by a process he termed 'family selection'. For example, he pointed out that 'breeders of cattle wish the flesh and fat to be well marbled together; the animal has been slaughtered, but the breeder goes with confidence to the same family'[3] So sterility might, under certain circumstances, be favoured if an individual's sterility was compensated by the extra number of descendants surviving to his or her relatives. This is the kind of altruism now called kin selection.[4]

The first steps in the determination of just how much benefit relatives have to receive to compensate an individual's altruism were taken separately by the geneticists J.B.S. Haldane and R.A. Fisher. Fisher was concerned with the evolution of distastefulness, the process by which nauseous flavours have evolved as a means of defence. The problem is that predators frequently only realise that an individual prey is distasteful once they have killed the prey and begun eating it. If predators learn to avoid such distasteful prey, then the prey species clearly benefits, but the individual eaten evidently does not. The problem is enhanced when aposematism occurs, that is, when distastefulness is associated with striking colouration, as in many butterflies. It has been demonstrated that such colourations sometimes *attract* predators. Fisher realised that the gregarious habits of many aposematic prey supplies the possible answer:

> For, although with the (solitary) adult insect the effect of increased distastefulness upon the actions of the predator will be merely to make that individual predator avoid all members of the persecuted species, and so, unless the individual attacked possibly survives, to confer no advantage upon its genotype, with gregarious larvae the effect will certainly be to give the increased protection especially to one particular group of larvae, probably brothers and sisters of the individual attacked. The selective potency of the avoidance of

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> brothers will of course be only half as great as if the individual itself were protected; against this is to be set the fact that it applies to the whole of a possibly numerous brood.[5]

Here Fisher, in his usual abrupt prose, mentions that kin selection directed towards full sibs has only half the strength of individual selection. Similarly Haldane once remarked that he was prepared to lay down his life for two of his brothers or eight of his cousins! A full quantitative treatment of kin selection came only with the publication in 1964 of W.D. Hamilton's seminal pair of papers *The Genetical Evolution of Social Behaviour I & II*[6], widely regarded as the founding papers of sociobiology. Hamilton was able to show that the condition for the spread of altruism through kin selection could succinctly be expressed in a simple equation:

$$b/c > 1/r$$

where b is the benefit (in terms of Darwinian individual fitness) that accrues to the beneficiary of the altruism, c is the cost (again in terms of Darwinian individual fitness) that the altruist suffers, and r is the degree of relatedness between the two individuals. For example, in an outbred population of a sexually reproducing diploid species the degree of relatedness between a parent and his or her offspring is a half, between an uncle or aunt and a niece or nephew is a quarter, and between two first cousins, as Haldane knew, is an eighth.

Since then there has been an enormous number of papers and books dealing with the precise quantitative predictions of kin selection theory, and minor modifications of Hamilton's simple rule are now known to apply under certain conditions.[7] However, at worst, Hamilton's formula still provides an extremely accurate approximation to the conditions under which kin selection operates.

A second way in which altruism can evolve is by reciprocal altruism. The mechanism for this was first explicitly described by R.L. Trivers in 1971. Essentially reciprocal altruism consists of 'You scratch my back, I'll scratch yours.' Trivers illustrates his theory with a hypothetical example:

> One human being saving another, who is not closely related and is about to drown, is an instance of altruism. Assume that the chance of the drowning man dying is one-half if no one leaps in to save him, but that the chance that his potential rescuer will drown if he leaps in to save him is much smaller, say, one in twenty. Assume that the drowning man always drowns when his rescuer does and that he is always saved when the rescuer survives the rescue attempt. Also assume

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> that the energy costs involved in rescuing are trivial compared to the survival probabilities. Were this an isolated event, it is clear that the rescuer should not bother to save the drowning man. But if the drowning man reciprocates at some future time and if the survival chances are then exactly reversed, it will have been to the benefit of each participant to have risked his life for the other. Each participant will have traded a one-half chance of dying for about a one-tenth chance.[8]

As Trivers notes, the value of reciprocation depends on the benefit to the recipient of the altruism exceeding the cost to the altruist. In the hypothetical example considered here, this might be the case if the drowning person is drowning because of cramp, or if the rescue can be effected by throwing a rope.

The third way in which altruism can theoretically evolve is by group selection. The first really detailed arguments in favour of group selection were put forward by V.C. Wynne-Edwards in 1962. Wynne-Edwards was primarily concerned with attempting to explain how population density is regulated. Populations, he argued, should not over-exploit their food supplies, for such over-exploitation would lead to reduced food yields and thus to lower reproductive success. As an example he described how the potential yield of many fisheries became drastically reduced when they were overfished, but could recover when catches were voluntarily restricted. Similar processes should apply, he argued, to animal populations, which should restrict their population density and rate of reproduction rather than endanger their food supply.

As Wynne-Edwards' theory depends on the assumption that individuals do *not* always maximize their own reproductive success, it was necessary to extend evolutionary theory to account for this. Wynne-Edwards argued that groups containing individuals who reproduce too fast, so that the recruitment rate persistently tends to exceed the death rate, must repeatedly exterminate themselves by overtaxing and progressively destroying their food sources. Prudent groups, where altruistic individuals restrain their reproduction, would outlive more selfish groups and so come to predominate.[9]

How has altruism evolved in non-humans?

What are the relative importances of these three theories in nature?

Most biologists, with some notable exceptions, have accorded Wynne-Edwards' theory of group selection an unenthusiastic welcome. Group selection faces a fundamental theoretical problem, as pointed out by John Maynard Smith.[10] Consider a prudent group whose members are reproducing submaximally due to group selection. Suppose that a mutation arises which causes its holder to reproduce normally. Even if the whole group now became more prone to extinction, as group

selection requires, the altruistic individuals within it would, by definition, produce fewer surviving descendants than the other members bearing the new mutations. Consequently, selection *within* the group would tend to eradicate the altruistic trait. Group selection only becomes important when two conditions are fulfilled: first, that selfish groups go extinct much more quickly than prudent groups, and, secondly, that little migration takes place within groups. If migration is common, selfish individuals tend to move between groups before groups go extinct. The available data on animal migration and demography suggest that group selection is usually likely to be outweighed by the opposing pressures of individual selection.[11]

Reciprocal altruism is on a firmer footing but appears comparatively rare within species. As Trivers realised, a fundamental problem with reciprocal altruism is the problem of cheating: 'You scratch my back, but then I run away.' Perhaps the most convincing non-human example occurs in male olive baboons, *Papio anubis*.[12] Craig Packer studied eighteen adult males in three troops at Gombe National Park, Tanzania, for more than 1100 hours. All males leave the troops in which they are born and transfer to other troops before they reproduce. This means that each troop contains a number of males usually unrelated to each other. Coalitions between males are sometimes formed in attempts to separate an opponent from an oestrous female—olive baboons form exclusive consort pairs, while a female is in oestrus, lasting for up to several days. If a pair of males does succeed in obtaining a female in this manner, only one of the two coalition partners mates with her. Attempts at enlisting a coalition partner can unambiguously be recognized: one individual, an enlisting animal, repeatedly and rapidly turns his head from a second individual, the solicited individual, towards a third individual, the opponent, while continually threatening the third.

Packer saw twenty occasions of coalitions forming when the opponent was consorting with an oestrous female. In six of these cases the formation of a coalition directed against the consorting male resulted in the loss of the female to the single opponent. In all six cases the female ended up with the enlisting male of the coalition; the solicited male generally continued to fight the opponent while the enlisting male gained access to the oestrous female. In each case the solicited male evidently risked injury from fighting the opponent while the enlisting male gained access to an oestrous female.

The crucial fact that Packer discovered was that males sometimes reciprocated in joining coalitions at each other's requests. Individual males that gave the most aid were those that received the most aid. Furthermore, males have preferences for particular coalition partners based at least partly on reciprocation.

Even in Packer's study of olive baboons, it is possible that at least

some of the males may have been related, which would implicate kin selection. The preconditions for the evolution of reciprocal altruism are similar for the operation of kin selection: long lifetime, low dispersal rate, individual recognition and mutual dependence. These common factors make it difficult to distinguish in any one case between the alternatives of kin selection and reciprocal altruism. In his original paper Trivers gave as examples of reciprocal altruism the convincing cases of so-called interspecific cleaning symbioses. These cannot have evolved by kin selection, as cleaning (the altruistic act) is performed by members of one species for the benefit of members of another.

In such cleaning symbioses one organism cleans another organism of ectoparasites, sometimes entering into the gill-chambers and mouth of the host to do so. About fifty species of fish, as well as six species of shrimp, are known to be cleaners. Innumerable species of fish serve as hosts. Cleaning habits have apparently evolved independently many times. One remarkable feature is that the host fish almost never eat their cleaners. Why, asks Trivers, does a large fish not end a cleaning bout by swallowing the cleaner—thus earning an easy meal? Trivers argues that cleaners are worth more to the hosts alive than dead. If a host eats a cleaner it may have difficulty finding another when it needs to be cleaned again. Just how important cleaners are to their hosts has been demonstrated in experiments where cleaners are removed.[13] Within a few days the number of fish in the area is drastically reduced. Within a couple of weeks almost all except territorial fish disappear and many of these develop white fuzzy blotches, ulcerated sores and frayed fins.

In the animal kingdom as a whole, it is kin selection that appears to be the most important selective force maintaining altruism. In a very large number of social species convincing data exist to show that closer relatives receive correspondingly greater aid[14] and in a few cases Hamilton's predicative equation for the evolution of kin selection has been tested and at least partially verified.[15] A particularly elegant manifestation of kin selection was revealed in a study of saturniid moths by Blest.[16] Consider two types of insect, one cryptic (difficult therefore for a predator to find) and palatable, the other aposematic (easy for a predator to find) and distasteful, and both subject to predation. The longer that a cryptic insect survives after reproducing, the greater the chances that it will be found by a predator who will *learn* to recognise and find other individuals of the species. Post-reproductive survival evidently prejudices the survival of the other members of the species, including close relatives. The contrary argument applies to the aposematic insect. Predators will learn to *avoid* such prey. The post-reproductive survival of an aposematic insect, then, should favour the survival of its siblings. Blest's predictions were fulfilled by the data he collected on Barro Colorado Island in the Panama Canal Zone. The

aposematic species had post-reproductive lifespans several times those of the cryptic species.

Kin selection is perhaps most impressive in the huge colonies of the many thousands of species of social insects. In a honeybee colony, for example, the sterile female workers are the sisters of the few fertile bees (males and females) that will give rise to future colonies. In a colony with tens of thousands of individuals, the loss of a few workers through the altruistic stinging of potential predators hardly matters. The safety and protection of the future reproductives is the paramount consideration.

Altruism in humans

So much for nonhumans. What about altruism in men and women? It is difficult to know whether group selection has been, or is, important. Many examples of apparent group selection may be due to the pressures of kin selection or reciprocal altruism, as discussed below. Nevertheless, it would probably be premature to assert that group selection definitely is unimportant in the determination of human behaviour. As Darwin himself wrote:

> A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.[17]

All of us know that kinship is important in humans. This does not necessarily implicate kin selection. It would theoretically be possible, for example, for altruism between relatives to be mediated entirely by reciprocal altruism. Not surprisingly, however, there are some convincing examples of kin selection in humans. In a few societies, for instance, fathers take little or no interest in their wives' children but direct their paternal interest towards their sisters' children. As one's sisters' children are less closely related to one than one's own offspring, this practice appears paradoxical. Consider, however, what happens when there is a good deal of uncertainty about paternity. One's sisters may only be half-sisters, but they and their children are indubitably one's true kin. On the other hand one's wife's children may often be unrelated to one, if adultery is rife. A review of the ethnographic literature provides some support for the prediction that it is in precisely those societies in which there is the greatest uncertainty about paternity that men divert a substantial part of their parental care to their nephews and nieces.[18]

While some kin selection evidently operates on humans, reciprocal altruism is probably of particular importance.[19] Reciprocation among distantly related individuals is the key to much of human society. Each of

us knows how much of the altruism we give to others we expect to receive back again. We keep a close record, for example, of who has invited us to dinner, so that we remember to reciprocate. Babysitting circles flourish best when a rigorous tally is kept. How hard we find it to forgive our brother seven times seventy times.

Some may object to the above apparently cynical view of human nature. What about, for example, the million people who give blood each year in this country with no payment beyond a biscuit, a cup of tea and the option of sporting a 'Be nice to me — I gave blood today' badge? What about the many tens of thousands of people who write Amnesty International letters on behalf of prisoners whom they will almost certainly never meet? What about all the little kindnesses most of us manage without ever expecting reciprocation?

There are some sociobiologists who would deny even these examples of apparent magnanimity. Alexander[20] has argued that in large complex societies what he terms *indiscriminate altruism* may be adaptive. The willingness to risk relatively small expenses in certain kinds of social donations to whoever may be needy may be selected because of the benefits to individuals of being *viewed* as altruists. Failure to show such indiscriminate social investment may be judged harshly.

It should be emphasised that this sociobiological interpretation of human altruism is clearly unable to explain every facet of helping behaviour in humans. For example, arguably members of a society are consciously or unconsciously motivated to practise 'indiscriminate altruism' partly because they have notions of what are the desirable norms in their society to conform to or promote; they are confirming the social values which they favour. There has been some stout resistance to Wilson's claim—to be found more explicitly in his later writings, like for example *On Human Nature* (1978) and *Genes, Mind and Culture* (1981)—that the new scientific discipline which he was introducing would successfully subsume under human biology social organization and all human culture (including religion and morals).

Nevertheless, I find that sociobiological theorising on altruism does promote in one a little more humility. To say the least, it encourages one to congratulate oneself less on one's munificence. It is important for Christians to realise that much of our behaviour which we consider altruistic can be construed to be in fact ultimately selfish. As Wilson writes:

> The 'altruist' expects reciprocation from society for himself or for his closest relatives. His good behaviour is calculating, often in a wholly conscious way, and his maneuvers are orchestrated by the excruciatingly intricate sanctions and demands of society. The capacity for (reciprocal) altruism can be expected to have evolved primarily by selection of

> individuals and to be deeply influenced by the vagaries of cultural evolution. Its psychological vehicles are lying, pretense, and deceit, including self-deceit, because the actor is most convincing who believes that his performance is real.[21]

The contribution, therefore, that sociobiology makes to theology is to prompt one, by considering how altruism may have evolved by natural selection, to realise how much of human behaviour is really selfish even when the behaviour appears to obey the injunction 'You shall love your neighbour as yourself' (Lev. 19.18). Any theology which makes complacent assumptions about a natural benevolence of human nature will be thought by those accepting even the framework of sociobiology, let alone the details of its argument, to be fatally flawed.

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A Symbolic Theology

Bede Griffiths

Professor Michael Dummett, in the article in *New Blackfriars* which has stirred up so much controversy, 'A Remarkable Consensus' (October 1987, pp. 424—431), seems to have taken as a criterion of Catholic faith what Avery Dulles, calls in his book *Models of Revelation* a propositional model of revelation. Professor Dummett is a distinguished logician. No doubt, then, he is accustomed to think of abstract logical thought as a norm of human discourse. But, if it is religious discourse we are considering, this is an assumption which can be extremely misleading. As Avery Dulles says, it tends to 'reduce meaning and intelligibility to the narrow confines of conceptual logic'. In place of this Dulles suggests a symbolic model of revelation, which seems to me to give much more meaning to faith and to present a much more convincing model of the Church.

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