harles Darwin once had a scholarly spat with John Stuart Mill. Mill maintained that moral feelings were acquired rather than innate. Not so, wrote Darwin in a robust footnote in *The Descent of Man* (1879): "the ignoring of all transmitted mental qualities will . . . be hereafter judged as a most serious blemish in the works of Mr Mill", about as near as the mild-mannered Darwin ever got to outright rage.

In many ways the spat has been going on ever since, though not without a lengthy hiatus during the first half of the twentieth century. Darwin at least had the advantage of operating within a partially Lamarckian framework in which the finest acquired moral sentiments could be inherited. This, coupled with his conviction that natural selection could operate at the level of the group, genes not yet being on the horizon, made it much easier to believe in the inheritance of morality. All this changed with the later demise of Lamarckianism, and then the neo-Darwinian synthesis in which natural selection was incorporated into mathematical population genetics. Now the attention shifted to random mutation and the individual as the unit of selection, and later to the selfish gene as the ultimate arbiter of evolutionary outcomes.

J. B. S. Haldane started the twentieth-century discussion with his comment, reported by the biologist Maynard Smith, that "he would jump into a river and risk his life to save two brothers, but not one, and that he would jump in to save eight cousins, but not seven". But in general the problem of the evolution of co-operation and altruism was largely neglected by biologists in the decades immediately following the construction of the neo-Darwinian synthesis in the 1920s and 30s. The leap from natural selection operating on individuals striving for reproductive success all the way to individuals seeking the good of others at a net loss to themselves seemed to involve a conceptual chasm too wide to cross.

The situation began to change with the kin-selection (or "inclusive fitness") theory of W. D. Hamilton, who followed up Haldane's observation with some rigorous maths: natural selection can favour co-operation if the donor and the recipient of an altruistic act are genetic relatives. But in practice we observe co-operation between unrelated individuals or even between members of different species. This led in turn to Robert Trivers's idea of direct reciprocity. If I co-operate now, you may co-operate later. But this relies on repeated encounters between the same two individuals. In practice most human encounters are not like that, but asymmetric and fleeting - you still jump in the river to save the drowning unrelated person though you may never see him or her again. Hence the proposal of indirect reciprocity - the person who helps gains a reputation for helping and in turn is thereby, in general, more likely to receive help.

Evolution, Games, and God is a fine collection of twenty essays bringing this discussion right up to the present day. The editors map out the relevant territory by defining co-operation as "a form of working together in which one individual pays a cost (in terms of fitness, whether genetic or cultural) and another gains a benefit as a result". Altruism is defined "as a form of (costly) cooperation in which an individual is motivated by good will or love for another (or others)". The key word here is "motivated", and this supplies fuel to the ethicists and philosophers who go out to bat in this

Not so selfish gene

DENIS ALEXANDER

Martin A. Nowak and Sarah Coakley, editors

EVOLUTION, GAMES, AND GOD The principle of cooperation 416pp. Harvard University Press. £25.95 (US \$35). 978 0 674 04797 6

volume after the historians, game theorists and evolutionary psychologists have had their say.

Evolution has always been interpreted through many different kinds of ideological filter. In the same era that J. D. Rockefeller was assuring his readers that "The growth of a large business is merely a survival of the fittest

.... The American Beauty rose can be produced in the splendor and fragrance which bring cheer to its beholder only by sacrificing the early buds which grow up around it", the late nineteenthcentury Protestant modernists were busy extolling evolution for its progressive aspirations, destined to lead to a world of perfect co-operation. As the leading American Congregationalist pastor Washington Gladden somewhat optimistically observed, the golden rule – "Thou shalt love thy neighbour as thyself" – was "incorporated into the nature of man at his creation", proclaiming "that this law ... will be perfectly obeyed in the perfect society of the future is now recognized as a scientific certainty".

The mathematical elegance of game theory, illustrated by the "prisoner's dilemma", provides the core starting point for the contemporary discussion. Building on the insights of Hamilton, Trivers and others, Martin Nowak explains the five mathematically based rules for the evolution of co-operation in a chapter which is a model of brevity and clarity, readily accessible to those allergic to equations. As Nowak suggests, "perhaps the most remarkable aspect of evolution is its ability to generate cooperation in a competitive world", even suggesting that co-operation should come alongside mutation and natural selection as a "third fundamental principle of evolution".

The "prisoner's dilemma" generates models of co-operative behaviour, it turns out, that find "surprisingly little support from empirical evidence in biological systems", according to Christopher Hauert, leading in turn to a whole range of more complex and sophisticated mathematical models, including the "snowdrift game", which seem to do a somewhat better job. Nevertheless, "the core challenge" still remains and "lies in the proper translation of biological questions into tractable mathematical models", Hauert continues. There is no doubt that the models predict co-operation, and that it is a universal characteristic of biological existence, but much work remains to be done to match mathematical theory with observation.

Game theory can equally be applied to economics. The common assumption underlying the four games described is that individuals maximize their own material payoffs according to selfish goals, as Johan Almenberg and Anna Dreber argue. But in traditional societies the results are not consistent with this assumption. Humans are stubbornly more co-operative than is recognized by those who condemn



J. B. S. Haldane, 1939

crass Western individualism

So is human co-operation hard-wired? Addressing that question entails the further question as to what is specifically distinctive about human co-operation in comparison with other animals. The human brain evolved to be part of a social matrix and its neurological structures reflect that fact, suggests Stephen Rosslyn. Dominic Johnson adds that human co-operation is unique owing to a sophisticated "theory of mind" coupled with the capacity for complex language. "The evolution of these cognitive traits made selfish behaviour more costly than at any previous point in our evolutionary history." The fear of supernatural retribution nurtured co-operative behaviours. "Even atheists tend to have a gnawing belief and expectation that people who do wrong will somehow be punished by subsequent life events." Does religion have adaptive value from an evolutionary perspective? The authors disagree, faithfully reflecting the broader disagreement within the scientific community. Marc Hauser sees human "moral grammar" as innate, with "emotions", pace Hume, "as fol*lowing* from our moral judgements". Our basic moral neuronal circuitry is impervious, claims Hauser, to cultural relativism.

It is an evolutionary biologist, Jeffrey Schloss, who first articulates a growing dissatisfaction with the idea that altruism represents simply a more sophisticated version of animal co-operation. There seem to be evolutionary trends in co-operation that are neither logically entailed by, nor at present fully accounted for, by selection or game theory, rooted as they are in "methodological individualism" – although Schloss accepts that they might be in the future. More importantly, "counterproductive sacrifice that foreshadows intentional altruism ... seems in principle not to be explicable by traditional Darwinian accounts". As Schloss points out, it is the evolutionary enthusiast Richard Dawkins who proclaims that "We, alone on earth, can rebel against the tyranny of the selfish replicators".

If the biologists have doubts about the capacity of Darwinian evolution to deliver the goods, meaning genuine altruism, then it is the philosophers and theologians in the last few chapters who seek to change the goalposts altogether. The theologian Friedrich Lohmann takes a Kantian approach in making the important distinction between morality, which is based on normative deontological claims – "obligations that have to be fulfilled for their own sake without any regard for inclinations or results in terms of success" – and behavioural descriptions of what people actually do, the descriptive approach used by behavioural scientists. Here intentionality begins to gain its proper prominence, something which sociobiological or game-theoretical approaches to morality simply ignore. Moral goodness is the lack of any pursuit of selfish gain. Games based on self-interest in which co-operation is an emergent property are of interest, but not of moral interest. "Morality does not deal with what usually happens but with what *ought* to happen", says Lohmann.

Another theologian contributor, Timothy Jackson, continues this line of thought with some useful reminders concerning the use of language. Reciprocal altruism is not really altruism, but prudence. Sacrifice for a group is tribalism, not altruism. Kin selection is a form of nepotism. If *agape* is confused with *eros*, the evolutionary adaptation that underlies game theory, then confusion is bound to follow. "Evolution does not create *agape*", suggests Jackson, "but, rather, divine *Agape* creates evolution, which in turn makes human *agape* possible."

The philosopher Alexander Pruss homes in on motivations. Normative facts contain a claim about how things ought to function. Non-normative facts tell us about how things actually are in the world. Current theories of co-operation provide non-normative facts, leaving moral altruism unexplained, non-reducible to adaptive evolutionary explanations. Dawkins is right.

It is left to Sarah Coakley to draw the threads together within the matrix of a robustly Trinitarian theology. God the divine chess-master will bring about his purposes through evolution, not by kenotically evacuating the created order of his presence, but by the reverse: infusing the whole process with his active presence: "the cooperative tendencies of evolution" therefore suggest selection "for the potential later heights of saintly human self-sacrifice". Incipient co-operativity, intrinsic within the evolutionary process from the beginning, thereby acts as a pointer to a later, bigger, theological story that transcends the language of selection and adaptation.

This is an important volume because it completely subverts the idea that the evolutionary narrative is in some profound sense antithetical to theology. Not so. The "selfish gene" as a metaphor makes no sense of biological realities. Co-operation is here to stay, as important at the level of interacting genes in genomics as it is at the level of interaction between organisms. As the nineteenth-century Oxford clerical scientist Aubrey Moore so rightly commented: "Darwinism appeared, and, under the guise of a foe, did the work of a friend".

