

Yule and by Pearson himself in 1903 using a mendelian model. Acceptance followed later following Fisher (1918). Mendel's work was rediscovered when Galton was almost 80, but well before his death in 1911. Surely, if Galton had appreciated Mendel's results, he would have taken the quantitative genetic analysis further and would have also seen that a deficiency in his law of ancestral heredity (that it led to homogeneity) was simply met in 1908 by the Hardy–Weinberg equilibrium.

Animal and plant improvement programmes have been based successfully on statistical methods derived by Galton and used in the Mendelian genetic framework. Galton wanted to 'improve' the human population and

indeed made a financial legacy to University College London to support the study of eugenics. His work has, however, been of great significance in the study of both human and natural populations, and Bulmer has done valuable service in showing how these evolved and can be interpreted.

This book should appeal to those interested in the history of genetics, quantitative variation and applied statistics, and those wishing to understand the scientific origins of the eugenics movement.

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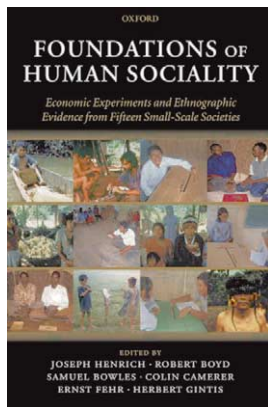
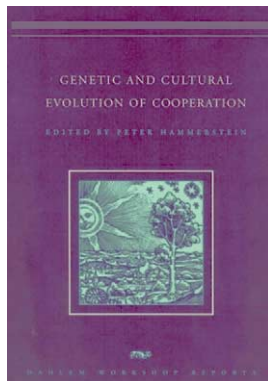
Book Review

The puzzle of cooperation

Genetic and Cultural Evolution of Cooperation edited by Peter Hammerstein. MIT Press, 2003. £29.95 hbk (xxiii + 450 pages) ISBN 0262083264. **Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies** edited by Joseph Henrich, Robert Boyd, Samuel Bowles, Colin Camerer, Ernst Fehr and Herbert Gintis. Oxford University Press, 2004. £55.00 hbk, £16.99 pbk (xiv + 320 pages) ISBN 0 19926204 7/0- 19 926205 5

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In his landmark treatise *Sociobiology* [1], E.O. Wilson predicted that, one day, neodarwinism should be able to explain all forms of social behaviour, from intercell cooperation within multicellular organisms to trade relationships in humans. At the time, Wilson's ideas appeared almost too grand. Now, 30 years on, his vision is appearing as sharp as ever.

Genetic and Cultural Evolution of Cooperation, an edited volume, presents one of the most inspiring interdisciplinary syntheses on the subject to date. The result of the 90th Dahmen Workshop, convened in Berlin in 2002, the book brings together contributions from 40 top researchers from fields as diverse as biology, anthropology, experimental economics, evolutionary psychology and mathematics. The common theme: the

evolution of conflict and cooperation, analyzed using the tools of evolutionary game theory [2].

The result of this interdisciplinary *tour de force* is a most stimulating and inspiring read. The main emphasis is on

paradoxical cases of cooperation that have proved difficult to explain theoretically. For example, there is no discussion of cooperation among kin, as kinship-based altruism is considered to be well understood [3] and extensively documented [3,4]. Instead, the focus is on other cooperation-promoting mechanisms, such as reciprocity, mutualism or cheater punishment. These processes are used to explain cooperation in a swathe of systems, from the cooperation between genes and cells in multicellular organisms to the origin of human sociality. In humans, issues such as reputation, memory of previous interactions and the establishment of social norms greatly broaden the scope for cooperation. But major challenges remain. For example, experiments consistently show that humans are more altruistic and less self-interested than theory predicts. This is perhaps the major strength of the book: it does not brush under the carpet observations that do not fit. Instead, a fair treatment of both what can be explained and what should still be investigated further is given. The book is highly readable, and formal models, when available, are just referred to in the text. This, I feel, was an excellent editorial decision.

Of course, no book is perfect. In spite of the title, cultural evolution is incompletely covered and too little attention is given to the complex details of cultural inheritance [5]. I also found it disappointing that relatedness-based theories of cooperation [3] were so under-emphasized. Although this might have been a deliberate choice, it struck me that, in several places, relatedness did appear, but disguised under different labels, such as positive assortment [6], or as group selection, which requires relatedness for it to work [3]. Even in human interactions, relatedness would often seem higher than the

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authors pretend. (When I visited a Maasai settlement earlier this year, the chief explained to me that he had 18 wives, and that all 63 people in the village were his offspring. If he was right, this would imply an average relatedness in the village of 0.25, actually not much lower than the relatedness among the bees in a beehive, 0.3.)

These criticisms do not detract from the great overall value of the book. The interdisciplinary slant on the evolution of cooperation clearly pays off, for example in the chapters where the exchange of goods in mutualisms is analysed using market theory. The result is a book that is extremely broad, making it required reading for anyone interested in the evolution of cooperation, whether they are biologists, sociologists or economists. I heartily recommend it.

In another edited book, *Foundations of Human Sociality*, the quest to explain human sociality is continued. Involving some of the same authors that contributed to *Genetic and Cultural Evolution of Cooperation*, the emphasis here is entirely on humans. The starting point is the observation that, when people are presented with simple dilemmas, they often act irrationally. The classic case is an experiment known as the Ultimatum Game. A person is given a sum of money, and he must propose a share to be given to another, anonymous, person. This person can either accept or reject the offer, but if he rejects, both get nothing. The game is played only once and confidentiality is maintained. The rational, self-interested way to play this game is for the first player to offer as little as possible and for the second player to accept: something is always better than nothing. But when groups of university students play, the most common offer is 50% of the money, much higher than what would be rational. And offers below 20% are almost always rejected, implying that humans tend to punish unfair offers, even at a cost to themselves.

Is this puzzling generosity and fairness a panhuman phenomenon, and if so, how can it be explained? That is the topic of this book. To find out, the authors repeated the above game, and other related games, in 15 small-scale societies, from Machiguenga subsistence farmers in the Peruvian rainforest, to Orma pastoralists in northern Kenya or Lamalera whale-hunters in Indonesia. The result was striking: in none of these societies, did humans act in a fully rational, self-interested way. There were, however some important cross-cultural differences. The Machiguenga, for example, made relatively 'mean' offers of only 26%, whereas the Orma were more generous, making offers of 44%. Explaining this variability is not easy, and most anthropologists come up with different explanations, based, for example, on differences in group cohesion, stability or interdependence. In some cases, people seem to

mistake the game for some situation they are more familiar with. This was evident in the Orma, who, when presented with the one-shot, anonymous Public Goods Game, likened it to a local fundraising scheme called 'harambee', where people contribute money for public goods projects, such as the building of new schools. However, unlike the Public Goods Game, a harambee is not anonymous, and social controls are quite tight. This might explain why also in the Public Goods Game, the Orma were quite generous, and contributed in proportion to their own wealth.

Disregarding these potential methodological issues, how would an evolutionary biologist explain the irrational, unselfish nature of humans? One possibility is that it reflects a problem with the conceptual basis of economic game theory itself [5]. The assumption that humans should act in a rational, self-interested way follows from the darwinian principles embodied in evolutionary game theory [5]. However, tendencies for fairness or generosity are almost certainly culturally determined. Evolutionary game theory only successfully predicts the spread of cultural beliefs or 'memes' when memes are effectively transmitted from parent to offspring or when successful memes are copied more often than others [5]. There is actually little evidence for either of these preconditions [5]. Instead, memes sometimes appear to spread at a cost to those that believe in them, akin to 'selfish genes', which can spread at a cost to an organism's fitness [7,8]. Religious beliefs, for example, tend to spread as a result of active church proselytizing, but the values that are thought (e.g. fairness, altruism, generosity, etc.) invariably are ones which do not serve individual self-interest.

Much work remains to be done to explain the exact causes of human sociality. Meanwhile, I recommend this thought-provoking book to all who would like to develop their own opinion on the important issues at stake.

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