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Can a simple equation explain the development of altruism?

The Altruism Equation: Seven Scientists Search for the Origins of Goodness

by Lee Alan Dugatkin

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The evolutionary explanation of altruism will surely come to be seen as one of the major breakthroughs of twentieth-century science. At first, the problem of altruism seemed insurmountable: how could natural selection favour the tendency to help others? Surely the ruthless, competitive process of evolution could give rise only to ruthless, competitive individuals. Altruism, morality and goodness must come from somewhere other than biology.

Enter 'selfish gene' theory — the recognition that genes, not individuals, are the units of selection. This at once both clarified and helped to solve the problem. It became clear that although genes must be 'selfish', in the sense of promoting their own replication, individuals need not be. On the contrary, genes can sometimes get themselves replicated by building social, cooperative and altruistic individuals.

How? Well, genes for altruism can spread if they help copies of themselves that reside in other individuals — hence that oasis of altruism we call the family (this is kin altruism). They can spread if they build organisms that team up with others to form mutually beneficial partnerships (mutualism), or that exchange benefits over time (reciprocal altruism). They can spread by building organisms that settle disputes over status and resources not by fighting but by conceding to prior ownership, or by deferring to the victors of ritual contests (conflict resolution). And genes for altruism can spread if altruism serves to attract mates (sexual selection).

These theoretical advances led to an avalanche of empirical work on the biological basis of social behaviour; this was 'sociobiology', and it laid the foundations for the scientific investigation of human behaviour. In *The Altruism Equation*, Lee Alan Dugatkin tells the story of this scientific revolution through mini-biographies of the chief protagonists.

We learn that Charles Darwin regarded altruism — in the form of sterile castes of worker bees that forgo their own reproduction and sacrifice their lives for the hive — as a "special difficulty, which at first appeared to me to be insuperable, and actually fatal to the whole theory". But we also discover he had an inkling that the problem might be solved by 'family selection'. We learn that T. H. Huxley regarded the family as the sole haven of altruism, and viewed the rest of nature as a bloody, gladiatorial arena. We learn that Petr Kropotkin thought that evolution penalized individuals who fought each other, but that it favoured those who combined to combat harsh environments. We learn that each of the triumvirate of the modern synthesis — J. B. S. Haldane, Ronald Fisher and Sewall Wright — came tantalizingly close to cracking the secret of kin altruism but, inexplicably, neglected to formulate their insights mathematically. We learn that W. D. Hamilton — an alumnus of my own institute, the London School of Economics — toiled alone to arrive at the $E=mc^2$ of evolutionary biology, $rB > C$ (where r is the coefficient of relatedness, B is the benefit and C is the cost). And we see how his elegant theory sheds light on phenomena as diverse as coloration in butterflies, helpers at the nest, alarm calls in ground squirrels, and parental care in human stepfamilies.

These biographies help to put the theories in their historical context, and bring warmth and colour to the story. Unfortunately, however, this device can also obscure the science.

First, *The Altruism Equation* focuses on kin altruism at the expense of other theories of cooperation. The theory of mutualism is never fully explained; reciprocal altruism, which is thought to be responsible for trust, gratitude, guilt and revenge in humans, gets half a chapter; ritual contests get just half a page; and the recognition of property, costly signalling and sexual selection are not mentioned at all, even in the index. There is no discussion of conflict and cooperation between genes in the same individual, the evolution of fairness, coalition formation, or recent research on cooperation in humans. This is all the more puzzling because Dugatkin's previous work shows that he is familiar with, and has indeed contributed to, the development of these theories.

Second, the logic of kin selection struggles to be heard over the din of its imprecise historical precursors. For example, kin selection depends on the chance of a particular gene for altruism being present in another individual, and not merely with the overall proportion of genes that individuals share. But readers could easily miss this point. The logic is further obfuscated by Dugatkin's folksy way of referring to kin altruism as occurring between 'blood relatives', rather than genetic relatives. This is particularly unfortunate because kin altruism can occur between organisms that have no blood at all, such as plants and bacteria.

Third, some of the early players in the story contribute little to the modern theory, with the result that the chapters devoted to them are somewhat repetitive. So, for example, Kropotkin and Huxley's 'good cop–bad cop' routine is needlessly iterated, and we are told of W. C. Allee's interest in establishing the notion of altruism as divorced from kinship more than 25 times in a 23-page chapter.

Still, you can't keep a good theory down. And if the book inspires readers to explore the area further, it will have been a success.