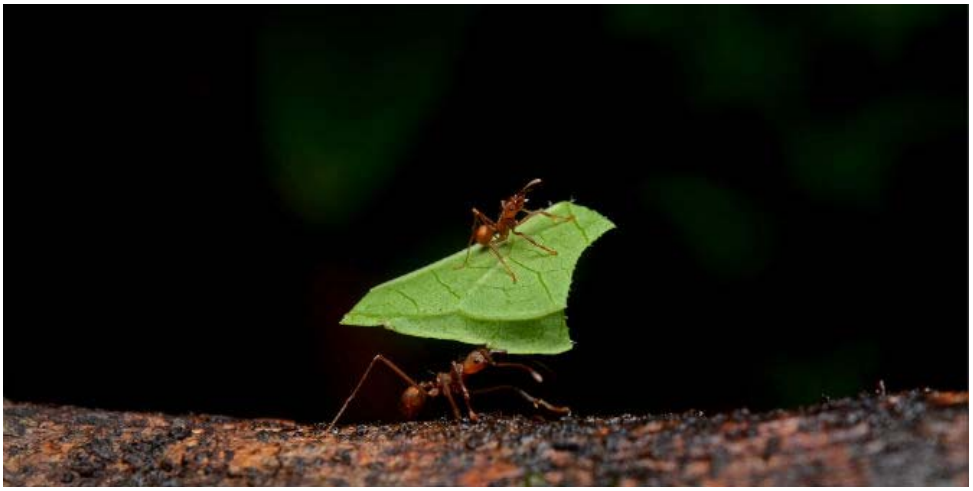
Where does altruism come from?



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Can altruism be reconciled with evolutionary theory? Philosopher of biology, Jonathan Birch (http://www.lse.ac.uk/philosophy/people/faculty/#jonathan-birch), discusses “Hamilton’s Rule”.

By Jonathan Birch (http://www.lse.ac.uk/philosophy/people/faculty/#jonathan-birch)

The natural world is full of examples of apparently “altruistic” behaviour: behaviour that detracts from an organism’s chances of survival and reproduction in order to boost the chances of another. Think of worker ants rearing the larvae of the queen, or a meerkat making an alarm call to warn others of a nearby snake. Behaviour like this used to present evolutionary biologists with a puzzle. Isn’t evolution a matter of “survival of the fittest”? If so, how come there is so much behaviour that clearly makes an organism less fit?

In the early 1960s, an LSE/UCL graduate student called Bill Hamilton (https://en.wikipedia.org/wiki/W._D._Hamilton) came up with a solution.* His basic insight was this: when interacting organisms share genes, they sometimes have an evolutionary incentive to help each other. And, crucially, the size of their incentive to help is proportional to the degree of genetic relatedness between them. It’s an insight captured pithily by the geneticist J.B.S. Haldane, who remarked that he would lay down his own life “for two brothers or eight cousins.”

But while Haldane came up with a nice quip, it was Hamilton who came up with a mathematically rigorous theory. He showed that you can derive a remarkably simple result, now known as "Hamilton's rule", that specifies the conditions in which a social trait will be favoured by natural selection. It says that a social trait will be selected when r multiplied by b is greater than c, where "c" is the fitness cost to the organism that has the trait, "b" is the fitness benefit the trait confers on another organism, and "r" is the genetic relatedness between the two organisms.

The main qualitative prediction of Hamilton's work is that, when we find an organism performing a costly helping behaviour, we should expect to see the benefit falling on its genetic relatives rather than on genetically unrelated organisms. This is indeed what we see. In social insects like ants and termites, in bacteria, in amoebae, in social mammals like wolves, chimps, gorillas, baboons, meerkats... and even, to some extent, in humans.

In recent years, however, Hamilton's theory—usually known as the theory of "kin selection"—has come under fire. For example, E. O. Wilson, the famous author of Sociobiology, was once an enthusiastic supporter but has since changed his mind. In August 2010, a strongly worded critique of kin selection by Martin Nowak, Corina Tarnita and E. O. Wilson ignited a new round of debate, which has since continued unabated. So does Hamilton's theory lie in tatters, or is it healthier than ever? It depends on whom you ask.

(http://www.lse.ac.uk/philosophy/wp-content/uploads/2015/06/meerkat.jpg)
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In a couple of recent (http://bjps.oxfordjournals.org/content/65/2/381.full) papers (http://bioscience.oxfordjournals.org/content/65/1/22.full) (both available through

Open Access), I try to make some sense of this on-going controversy. As a philosopher of science, rather than a practising biologist, I've been able to approach the issue with a certain detachment: rather than simply seeking to vindicate or debunk kin selection, my aim has been to tease out the subtle conceptual and philosophical disagreements that lie at the heart of the debate.

The key to moving things forward, in my view, is to get clear about what exactly we mean by "Hamilton's rule". There are various different versions that define cost, benefit and relatedness in subtly different ways. On some versions the rule almost never holds, whereas on other versions it almost always holds. Nowak, Tarnita and Wilson claimed it "almost never holds" because they had one of the more fragile versions in mind.

In "Hamilton's Rule and Its Discontents" (http://bjps.oxfordjournals.org/content/65/2/381.full), I discuss the different versions in more detail. While this may initially seem like a rather narrow, technical issue, it turns out to connect in interesting ways to broader philosophical debates about causation and explanation. The more general versions of Hamilton's rule buy their generality at the expense of causal detail. This leads to the accusation that they explain nothing—that all the explanatory power has gone. But it depends on what you mean by "explanation".

As I see it, the most general version of Hamilton's rule, though not very useful for generating quantitative, testable predictions, serves as a kind of "organizing principle" for social evolution research. It allows us to see what otherwise disparate models of the evolution of cooperation have in common: they are all models in which r multiplied by b is greater than c. And it allows us to distinguish three broad categories of causal process in social evolution: those that alter relatedness, those that alter benefit, and those that alter cost. So despite its limitations, the principle still has a pivotal role in the theory.

There are other issues in the mix here too. Part of the debate is about the right measure of "fitness": should we count effects on relatives, as Hamilton's notion of "inclusive fitness" does, or should we only count an organism's direct offspring? And in the background there is the spectre of 'group selection'—an idea also known as "multi-level selection"—which E. O. Wilson and his allies hold up as a viable alternative to kin selection.

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In "Kin Selection and Its Critics" (http://bioscience.oxfordjournals.org/content/65/1/22.full), Samir Okasha and I bring these strands together to provide an overview of the controversy. One of the key claims we make is that the methodologies of kin selection and group selection are formally equivalent—in the sense that gene frequency change can be accurately calculated either way—but not necessarily causally equivalent. From a causal point of view, the two approaches give us quite different pictures of what is going on when altruism evolves. We think it's worth trying to spell out their differing causal commitments, in the hope of actually testing which process is occurring in any given case.

This is one exciting direction for further work. It could even help reconcile the two camps in the current controversy over kin selection, though that may be a bit too much to hope for.

Jonathan Birch is Assistant Professor in the Department of Philosophy, Logic and Scientific Method. A selection of his work is available here (http://philpapers.org/profile/8764).

Further reading

- Birch, J. (2014) Hamilton's Rule and Its Discontents. British Journal for the Philosophy of Science 65:381-411. (http://bjps.oxfordjournals.org/content/65/2/381.full)
- Birch, J. and Okasha, S. (2015) Kin Selection and Its Critics. BioScience 65:22-32. (http://bioscience.oxfordjournals.org/content/65/1/22.full)

- Nowak, M. A., Tarnita, C. E. and Wilson, E. O. (2010) The Evolution of Eusociality. Nature 466:1057-1062.
- Segerstrale, U. (2013) Nature's Oracle: The Life and Work of W. D. Hamilton. Oxford University Press.

*Hamilton's graduate work was funded through the Department of Sociology at LSE, and his iconic first paper, "The Evolution of Altruistic Behavior" (1963), carries that address. But he was also associated with the Galton Laboratory at UCL, and he gave this as the address for his even more iconic second paper, "The Genetical Evolution of Social Behaviour" (1964).

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