Where does altruism come from?

Can altruism be reconciled with evolutionary theory? Philosopher of biology, Jonathan Birch, discusses “Hamilton's Rule”.

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 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

* See, for example, “The Genetical Analysis of Natural Selection” by William D. Hamilton (1964).
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.

In a couple of recent papers (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.

(http://www.lse.ac.uk/philosophy/wp-content/uploads/2015/06/bees1.jpg)
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.

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

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Further reading

*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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6 Comments

Steve Davis 23rd September 2016 at 2:24 am - Reply
(https://www.lse.ac.uk/philosophy/blog/2015/06/19/where-does-altruism-come-from/?replytocom=902#respond)

Jonathan, you referred in the first paragraph to the altruism of worker ants rearing larvae, but this is an example of the problems that have arisen for the Hamiltonian school by their habit of redefining terms to suit an agenda. Their definition of altruism cannot apply to the eusocial insects. When a worker bee or ant feeds the queen, or feeds pupae, she cannot lower her direct fitness as she has no direct fitness. She is sterile. She does have indirect fitness however, as she can contribute to the production of adult offspring. The act of feeding the queen or pupae contributes to the production of adult offspring of the queen. Because feeding the queen or pupae is an indirect fitness act, a contribution to the fitness of kin, it is a demonstration of fitness. As such it cannot be seen as lowering fitness, therefore such acts are not altruistic. It follows from this that parental
altruism in general, often referred to, also cannot exist.
You said, “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.” That was taken beautifully to its logical nonsensical conclusion in *The Selfish Gene* where Dawkins declared without a hint of a blush that a cake should be cut in portions proportional to the relatedness of the recipients. (*The Selfish Gene* 30th Anniv. Edition (Oxford University Press 2006) 94, 291)
You said, “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.” That which you see is an illusion, an assumption, a logical fallacy. The fallacy on which Hamilton's Rule is based is the classical “correlation is causation.” It cannot be assumed that cooperation is kinship based. In the case of humans we are more altruistic towards elderly neighbours unable to reciprocate than we are to kin. In the case of social animals, insects and bacteria, the altruism is also not based on kinship. It is also based on proximity. Cooperation assists survival so we cooperate with those most likely to be able to assist us, which in the natural world is those closest to us. Cooperation with elderly neighbours or those unable to reciprocate becomes altruism.
I'm not a mathematician, but I'd say it's highly likely that for every application of Hamilton's Rule that is alleged to support the kinship hypothesis, if the kinship factor was replaced with a proximity factor the result would be identical. And the fact is, that we often see examples of non-kin cooperation not only in human society, but throughout the natural world.

Those interested in the origins of altruism should also be aware of the shady origin of the inclusive fitness concept.
Hamilton was an unabashed eugenicist, and despite his denial that his passion for eugenics (that's not hyperbole) did not influence his development of inclusive fitness, it's clear from his *Narrow Roads of Gene Land* that eugenics was a powerful influence.
Hamilton's passion for eugenics was fuelled by his fear of overpopulation, and inclusive fitness is concerned with the production of adult offspring, so to deny a link is futile. (For a more detailed explanation see
It should also be of interest that the lack of logic at the heart of eugenics has been replicated in the inclusive fitness concept and carried through to gene-centrism in general. Just as the eugenicist assumes that poverty criminality and poor health are gene-based, (the “correlation is causation” fallacy) so the kin selectionist assumes that cooperation is gene-based by the same faulty reasoning. And all this despite this clear statement from Hamilton; “Inclusive fitness may be imagined as the personal fitness that an individual actually expresses in its production of adult offspring as it becomes after it has first been stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual’s social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm or benefit which the individual causes to the fitness of his neighbours. The fractions in question are simply the co-efficients of relationship appropriate to the neighbours he affects; unity for clonal individuals, one half for sibs, one quarter for half-sibs, one eighth for cousins…and finally zero for all neighbours whose relationship can be considered negligibly small” (Hamilton Narrow Roads of Gene Land Vol. 1, 38) By any fair reading of that statement inclusive fitness is an artificial construct not representative of actually existing phenomena. But for what purpose? To support Fisher’s General Theory which was itself intended to support eugenics. And Hamilton was not going to let facts get in the way. “My ideas about kin selection were at last written down and submitted to a journal. I was pretty sure they were right – that is, that they were correctly argued. If right in this way, it was clear that no amount of evidence from nature would make them wrong;...” (Hamilton Narrow Roads of Gene Land Vol. 3, 80) And this, “But even before this, still at Cambridge, I had made the decision that I would not even try to come abreast of the important work that was being done around me on the molecular side of genetics. This might well be marvellous in itself; I admitted the DNA story to concern life’s most fundamental executive code. But, to me, this wasn’t the same as reading life’s real plan. I was convinced that none of the DNA stuff was going to help me understand the puzzles raised by my reading of Fisher and Haldane or to fill in the gaps they left...” (Hamilton Narrow Roads of Gene Land Vol. 1, 12) This is a clear admission of a prior agenda. How did this ever gain traction?
Sorry, that should be Fisher’s Genetical Theory.

Steve Davis 26th September 2016 at 12:46 pm - Reply
(http://www.lse.ac.uk/philosophy/blog/2015/06/19/where-does-altruism-come-from/?replytocom=906#respond)

Actually Jonathan, the precise nature of the definitions of biological fitness and biological altruism creates a serious problem for kin selection. The concept claims to explain the origin of altruism, as the title of your article indicates, but when altruism is an act that lowers fitness and fitness is the capacity to produce adult offspring, we see that altruism within kinship groups is becoming difficult to explain. It simply cannot be argued that raising offspring is altruistic. Can a mother feeding a child be seen as altruistic? Feeding a child is a demonstration of fitness and therefore cannot lower fitness. Raising a child cannot be seen as reducing the capacity to raise a child. Parental altruism is therefore impossible.

The same problem exists for kin altruism. Assisting the survival of cousins is an inclusive fitness act, a demonstration of inclusive fitness, and therefore cannot lower inclusive fitness. Assisting the survival of cousins cannot be seen as reducing the capacity to assist their survival, so kin altruism is a fiction. Kin altruism also fails as it is a function carried out at the group level and there is no nett loss of group fitness.

Does assisting cousins lower the individual fitness of the actor? Yes, but only in a sense so narrow as to be meaningless. Consider Hamilton’s position that the concept of inclusive fitness is “stripped of all components which can be considered as due to the individual’s social environment”. If we accept the stripping of all social components then it must be acknowledged that we are now dealing with a concept that is separated from reality. In reality, assistance to kin is reciprocated; the loss of individual fitness is regained, so there is no nett loss of fitness for the individual therefore there is no altruism.

There is therefore no such thing as kin altruism or reciprocal altruism, as there is no loss of fitness involved in both cases. Kin selection is no more than a construct comprised of a jumble of contradictory meaningless concepts, and it certainly does not explain the origin of altruism.

Let’s go back to your discussion of proportional altruism. You said, “His basic insight was this: when interacting organisms share genes, they sometimes have an evolutionary incentive to help each other.” That is merely an assumption based on correlation implying causation. Interacting organisms can share more than genes. They share proximity. And when we see cooperation between unrelated organisms (as we do on a regular basis) we see that shared genes cannot be the determining factor. Shared genes are therefore irrelevant to cooperation. The only common factors are proximity and in some cases need. If need does not apply to one party then
This may be altruism, or it may be reciprocal cooperation. It cannot be reciprocal altruism as this, we have seen, cannot exist. So if need is not applicable to one party and we have a case of genuine altruism, this leaves the origin of altruism unresolved, with the Hamiltonian input to the question basically irrelevant.

Jonathan Birch (http://personal.lse.ac.uk/birchj1/) 18th October 2016 at 6:23 pm - Reply (http://www.lse.ac.uk/philosophy/blog/2015/06/19/where-does-altruism-come-from/?replytocom=927#respond)

Thanks for these interesting comments. I regret that I don't have time to reply at length. One quick comment though: workers in most social insect species are not fully sterile. They have ovaries and can lay unfertilised eggs, which develop into males. However, the vast majority of workers raise the queen's larvae instead of attempting to produce their own. This is a good case of biological altruism in Hamilton's sense, since rearing the queen's larvae detracts from the direct fitness of the actor. In a minority of species, such as leafcutter ants of the genus Atta, the workers are completely sterile. I agree there is potentially something a bit misleading about describing the actions of a completely sterile worker as altruistic, because its direct fitness is always zero, regardless of its behaviour. Cooperation is probably a better term than altruism in these cases.

Steve Davis 19th October 2016 at 8:18 pm - Reply (http://www.lse.ac.uk/philosophy/blog/2015/06/19/where-does-altruism-come-from/?replytocom=930#respond)

Jonathan, thanks for the reply.

You said that a worker bee can produce offspring but chooses instead to raise offspring of the queen. This raises the question as to why this is so. I'm no expert but my guess is that because hive activities are strongly influenced by pheromones, (as in re-queening a hive,) that this is not a choice made by the worker, instead the worker is influenced by pheromones to perform in a certain way. While influenced in this way she has been chemically sterilised. Being sterile, she has no fitness, so cannot lower fitness, so cannot be altruistic. Even if the influence is some form of communication other than pheromones, the worker is effectively sterile. It matters not if that influence can be turned on and off by the hive, while operating under that influence the worker has no personal fitness and so cannot be altruistic.

But let's look at the big picture. The whole intent of the inclusive fitness idea is to show that there is no loss of fitness at all – that an individual can manage its fitness activities at an alternative level. That
level of choice is now the kinship group. The fitness drive has now become a group activity. Yet Hamilton deliberately tried to exclude the group from the concept, restricting it to “the personal fitness that an individual expresses”. Arbitrary decisions like that have no place in science. The inclusive fitness concept has been so tightly defined that it does not reflect reality. Social contributions to fitness cannot simply be “stripped” as Hamilton did. A concept so distant from reality cannot give us the origin of altruism.