Hamilton's Rule

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The first American Naturalist *appeared in March 1867. In a countdown to the 150th anniversary, the editors have solicited short commentaries on articles from the past that deserve a second look.*

The purpose of this series of commentaries is to celebrate long-forgotten or underappreciated articles from the archive. So it feels a little odd to be providing an appreciation of W. D. Hamilton's 1963 work "The Evolution of Altruistic Behavior," which the Web of Knowledge suggests has been cited more than 700 times. By Hamilton's standards, however, that does constitute obscurity. And, in particular, these citations are dwarfed by those of his monumental article "The Genetical Evolution of Social Behaviour" (*Journal of Theoretical Biology* 7:1–52), published a year later, by nearly 20 to 1. Some of this imbalance is warranted, as the latter article covers much of the same ground in more detail and makes a number of additional contributions. But Hamilton's "little-read first paper" (W. D. Hamilton, 1996, *Narrow Roads of Gene Land, Volume 1: Evolution of Social Behaviour*, Oxford University Press, Oxford, p. 5) manages, in barely more than two pages of text, to cover the core principles of inclusive fitness theory. So I believe it deserves a second look.

What is the story behind this article? Hamilton's genetical work on altruism was a reaction against the stultifying "for the good of the species" thinking and concomitant pseudoexplanation of social behaviors that he encountered as an undergraduate at Cambridge University. Building on foundations laid by R. A. Fisher, he developed, while enrolled as a PhD student at the London School of Economics, a mathematical account of how natural selection acts on genes underpinning social behaviors. The 1964 article was written first, but its publication was slowed by the request of a reviewer (later revealed to be John Maynard Smith) that the manuscript be rewritten as two separate articles. Eager to speed his ideas into print while the longer

article languished in review, Hamilton composed a short overview of his main results and fired it off to *Nature*. It was immediately rejected, with the suggestion that the author might try a "psychological or socialogical [sic] journal" (Hamilton 1996, p. 3); instead, Hamilton submitted it to *The American Naturalist* as a Letter to the Editor. It was accepted at the end of 1962 and published the following year—narrowly ahead of Maynard Smith's own treatment of "kin selection" in *Nature*. U. Segerstrale provides an excellent account of Hamilton's life and work during that time (2013, *Nature's Oracle: The Life and Work of W. D. Hamilton*, Oxford University Press, Oxford).

What are the main contributions of "The Evolution of Altruistic Behavior"? First, Hamilton introduces the gene's-eye view of natural selection, noting that—irrespective of the fitness effects experienced by individuals—the ultimate criterion for a gene to be evolutionarily successful is that it leaves more copies of itself to future generations. This gives him a conceptual entry point into the problem of altruism and places the work within a rigorous, population-genetical framework. Second, Hamilton points out that a gene encoding altruism can leave more copies of itself to the future, despite reducing the altruist's reproductive success, if the recipient also carries copies of the altruist's genes. This pinpoints, in a qualitative way, the source of altruism's selective advantage.

Third, getting quantitative and using the language of "concentration" and "dilution," Hamilton explains that it is the "regression" of the altruist's genotype in the recipient that determines how well the recipient transmits the altruist's genes. He points out that this regression coefficient will be well approximated by Sewall Wright's correlation coefficient of relationship: that is, one-half for full siblings, one-quarter for half-siblings, and so on, in typical scenarios. This regression approach to relatedness measures genetic similarity relative to the population average, rather than in absolute terms, and it is in this sense that we can be related to our siblings by only one-half despite sharing 99% of our genes with chimpanzees.

Fourth, Hamilton brings these insights together into a single inequality, describing the necessary and sufficient condition for the gene to be favored by natural selection: $k > 1/r$, where k denotes the ratio of the fitness benefit

to the recipient and the fitness cost to the actor, and *r* denotes the degree of relatedness. This simple result now forms the centerpiece of the theory of social evolution, and in its various forms, it is referred to as "Hamilton's rule" (coined by E. L. Charnov, 1977, "An Elementary Treatment of the Genetical Theory of Kin Selection," *Journal of Theoretical Biology* 66:541–550).

Fifth, setting aside genes and returning his attention to individual organisms, Hamilton extracts a normative rule from the evolutionary dynamics, noting that "an animal acting on this principle would sacrifice its life if it could thereby save more than two brothers, but not for less" (p. 355). This represents a fundamental shake-up of Darwinian understanding, as it demonstrates that natural selection need not lead individuals to behave as if striving to maximize their personal reproductive success and that—at least in some circumstances—they should value the lives of their kin. Sixth, Hamilton clarifies that, in addition to nepotistic behavior directed toward recognized kin, natural selection may favor even indiscriminate altruism, such as the warning cries of birds, as neighboring individuals will tend to be genetically related in viscous populations.

What is not in this article? In addition to expanding on all the above points, Hamilton's subsequent "The Genetical Evolution of Social Behaviour" would make a number of further contributions. Chief among these are: a classification of social behaviors according their impact on the reproductive success of actor and recipient, incorporating not only altruism but also what would later be termed selfishness, mutual benefit, and spite; the expansion of Hamilton's rule to accommodate multiple recipients with different degrees of relationship to the actor; the identification of inclusive fitness as the coherent design objective underpinning all of an organism's adaptations, not just those involving altruism; a third mechanism for kin selection—in addition to kin discrimination and population viscosity—that would later become known as the "green-beard effect"; and the "haplodiploidy hypothesis" for the evolution of insect eusociality (which is now largely discredited—while inclusive fitness remains central to our understanding of eusociality, haplodiploidy appears to have been a red herring).

Rereading "The Evolution of Altruistic Behavior," I'm struck by how directly relevant it is to current social-evolutionary discourse. For example, Hamilton preempts the misconception that kin selection requires kin discrimination and neatly clarifies why this is incorrect. This particular misconception is strangely entrenched in the literature and continues to underpin spurious claims about altruism being favored in the absence of kin selection. Also, Hamilton breezily remarks that his rule readily accommodates multifactorial inheritance with arbitrary dominance and epistatic interactions, though without providing any further details. A proper understanding of how such complexities fit into the theory of kin selection—if, indeed, they do at all—is the focus of intense, ongoing debate.

Most of all, however, I am struck by the article's remarkable lucidity and its economy with words. Hamilton's lengthy exposition of inclusive fitness theory in "The Genetical Evolution of Social Behaviour" is rather daunting, and it is clear that many researchers are citing that article without properly reading it, instead relying on secondary, error-prone sources to bring them up to speed. So I suggest that readers take a look at the short and snappy "The Evolution of Altruistic Behavior" and that lecturers consider putting it on their reading lists, as it remains among the clearest of introductions to the topic and a real pleasure to read.

In *The American Naturalist*

Hamilton, W. D. 1963. The evolution of altruistic behavior. American Naturalist 97:354–356.