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[The Narrow Road Taken. Review of Nature's Oracle: The Life and Work of W. D. Hamilton by Ullica Segerstrale. Oxford: Oxford University Press. 2013.](#)

Journal of Evolutionary Psychology 2014, 12(2-4), 149-152.

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DOI link to article:

<http://dx.doi.org/10.1556/JEP-BR-20014-00001>

Date deposited:

24/06/2016



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Journal of Evolutionary Psychology

The Narrow Road Taken

Ullica Segerstrale (2013) *Nature's Oracle: The Life and Work of W. D. Hamilton*. Oxford: Oxford University Press

Review by John Lazarus

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Evolutionary behavioural science is not blessed with opportunities for concrete discoveries – a new planet, or the shape of a potentially interesting molecule, for example. Its empirical advance is driven instead by new ideas, and the 1960s and 1970s saw a revolution in the theoretical armoury of those working on the evolution of behaviour. Optimality theory, borrowed from economics, provided tools for testing the adaptiveness of non-social behaviour, and John Maynard Smith showed that to understand the evolution of social behaviours stable, rather than optimal, solutions must be sought. These methods helped to drag evolutionary thinking away from a naive species level, group selectionist, viewpoint and back to the individual and the gene as the units of importance. Crucially at stake here was the understanding of altruism and it was W. D. Hamilton who put the gene centre stage as the unit of selection with the concept of inclusive fitness, and who showed how to analyse the evolution of interactions between relatives. The concept of inclusive fitness was Hamilton's greatest achievement but he went on to make a number of strikingly original contributions to evolutionary biology before his untimely death in 2000 at the age of 63.

In her biography Ullica Segerstrale gives us both the man and his work. With sympathy and intelligence she seeks to understand how his evolutionary and genetic approaches to altruism, and other questions of pressing human concern, arose from his own personality and world view. Her account is enriched by letters to family and friends, and Hamilton's own commentary on his work as published in his collected papers, *Narrow Roads of Gene Land*.

William Donald Hamilton was born in Cairo in 1936, of New Zealand parents, and grew up in Kent, not far from Darwin's home, the second oldest of six children. He was a passionate naturalist from a young age, with an interest both biological and aesthetic that was to remain with him for life. His parents' influence seems to have been formative: Bill and his siblings were encouraged to be creative and self-sufficient; books and ideas were discussed; and physical risk-taking tolerated to a degree. His childhood experience of the war and its aftermath, Segerstrale suggests, made Hamilton an individualist and anti-totalitarian, and – as an example of the influence of his life on his work – coloured his attitude to group selection.

After school and national service Bill studied zoology at Cambridge and here discovered Fisher's great book *The Genetical Theory of Natural Selection*, finding it "intensely provocative". It was the stimulus for his lifelong project, started during his undergraduate years, to understand the genetic basis of social behaviour; he was already writing of "my theories of ethics". But how did this deep interest in the origins of self-sacrifice emerge, with its intellectual allure and moral imperative? Segerstrale finds answers to this question, convincingly, in Hamilton's personality – already argued to be a function of parental influence – and the early moral teaching of his mother. Of course parental traits can be inherited as well as imitated, and adopting, rather than rejecting, parental guidance may rely on a secure family life, which Hamilton certainly enjoyed.

Hamilton pursued the problem of altruism as a postgraduate student at the London School of Economics and the Galton Institute, University College, London. Working largely independently he developed his inclusive fitness theory, and published it in 1963 and 1964. His less than purist mathematical techniques drew critical responses from mainstream population geneticists, but his conclusions were, eventually, vindicated. As is well known he went on to make major contributions to theory in several fundamental areas of social evolution: sex ratios; the role of parasites in sexual selection and the maintenance of sexual reproduction; senescence; gregariousness; dispersal; and cooperation between non-relatives. Late in his career he pursued some innovative hypotheses: leaf colours as a handicap signal, for example, and the controversial theory that human HIV may have been transmitted from non-human primates. He was collecting data to test this theory on his last field expedition.

Perhaps less well known to evolutionary psychologists is his fieldwork in Brazil; he was a formidable naturalist and returned many times to the Amazon to work on the adaptations of individual species and on larger questions of macroevolution. Hamilton's feeling for the natural world, and particularly the Amazon rainforest, was profound. As Segerstrale writes: "Bill Hamilton was more than a naturalist. He had an organic connection with the living world, which could sometimes take extreme forms. He wanted to understand how nature worked, . . . to become one with her" (pp. 286-7). These "extreme forms" exemplified his risk-taking personality, and included inviting wasps to sting him as a means of capturing them, and plunging his arm into rotting wood cavities to feel what he could find.

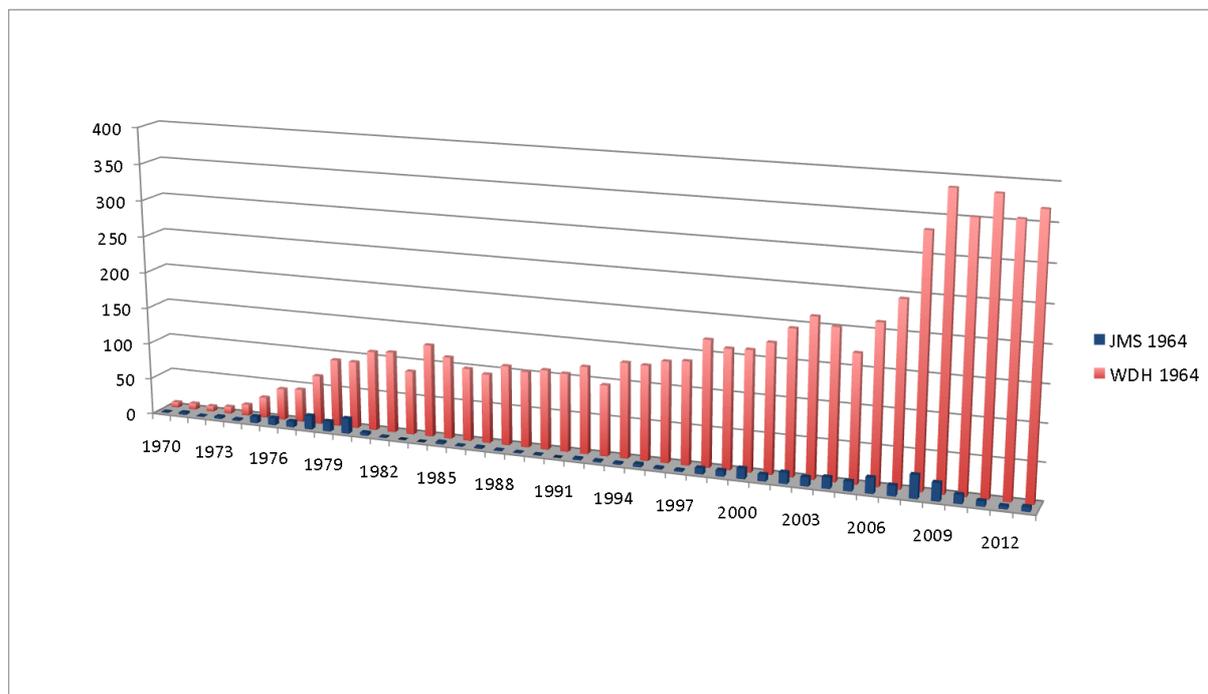
Bill Hamilton's personality was caring, romantic and fearless; his outlook scientifically rational and idealist – he did not hesitate to speak out for what he saw was the truth. His

strong egalitarian streak, concern for proper behaviour that gave due weight to the rights of others, for precedence in science, and for not letting wrongs go unchallenged, all played into the major academic falling out of his career, that with John Maynard Smith. Returning from Brazil following publication of his landmark inclusive fitness papers in *Journal of Theoretical Biology* in 1964 he discovered Maynard Smith's paper published in *Nature* four months earlier, in which he coined the term 'kin selection'. Hamilton felt that Maynard Smith (who had been Hamilton's PhD external examiner) had not given his ideas sufficient recognition in that paper, although Maynard Smith had cited his 'Hamilton's Rule' paper of the previous year. Conflict between the two was ignited again more than a decade later, in 1976, when Hamilton, again back from fieldwork in Brazil, read Maynard Smith's review of Edward Wilson's *Sociobiology*, in which he related the now famous back-of-an-envelope calculation by J. B. S. Haldane that "he was prepared to lay down his life for eight cousins or two brothers". Now Hamilton felt that Maynard Smith had robbed him of the priority of inclusive fitness theory. Segerstrale tells this story very well, analysing the motives of the two men and including the correspondence that passed between them and that appeared in *New Scientist*.

Hamilton felt deeply that his priority for inclusive fitness theory was being unfairly undermined by Maynard Smith's 'kin selection' and an anecdote about Haldane's pub calculations. However, it must have become clear to Hamilton, as time passed, that his inclusive fitness papers eclipsed Maynard Smith's and Haldane's contributions in their impact on the study of social evolution. A Web of Science analysis of the citation history of the 1964 papers by the two authors bears this out. By the end of 2013 Hamilton's paper I of 1964 had been cited 6429 times, dwarfing the 341 citations for Maynard Smith's paper. The latter had a modest record in the 16 years following publication but was then seldom cited

until the end of the century, since when it enjoyed a 10 year resurgence to its earlier modest level. In contrast, citations for Hamilton’s paper rose exponentially up to 1981 (as Richard Dawkins shows in the second edition of *The Selfish Gene*), then plateaued up to the early 1990s, before rising steadily again and then flattening out over the last five years (Figure 1). The increase in citation rates for both papers over the last 20 years or so is paralleled by the publication frequency for all papers published with the topic term ‘altruism’, and therefore probably reflects the growth of interest in cooperation and altruism over that period (although it doesn’t explain the recent decline in citations of Maynard Smith’s paper). Hamilton’s papers of 1964 are rightly recognised as foundational to the study of social evolution.

Figure 1



Ullica Segerstrale has written a wonderfully rich book with clarity and care. The account of Bill Hamilton’s life and career is detailed in its particulars, and in describing his research Segerstrale is able to explain the big questions that Hamilton was tackling, and to set them in

the context of the scientific understanding – or ignorance – of their day. And time after time in reading this book, when you find yourself wondering why Hamilton acted as he did, Segerstrale digs deep to explore and explain both his motives and their origin.

Figure Legend

Figure 1. Annual citation counts from 1970 to 2013 for the first of Hamilton's pair of 1964 papers in *Journal of Theoretical Biology* (WDH 1964) and Maynard Smith's 1964 paper in *Nature*, 'Group Selection and Kin Selection' (JMS 1964). The second of Hamilton's 1964 papers received a total of 1472 citations over the same period and adding citations to this paper to those for paper I produces a very similar pattern.