BOOK REVIEW

Sex, spite, and selfish genes

Nature's oracle: the life and work of W. D. Hamilton

Ullica Segerstrale

Oxford University Press, Oxford, UK; 2013; 336 pages; ISBN13: 978-0198607274

Reviewed by J. ARVID ÅGREN*

The greatest honour that can be bestowed upon an Argentinian football player is to be named heir to Diego Maradona. In evolutionary biology, the equivalent recognition comes by being compared to Charles Darwin. The English theoretical biologist and naturalist William Donald (Bill) Hamilton (1936–2000) is, together with his hero R. A. Fisher, probably the biologist who most often receives this homage. Fisher, and the other architects of the Modern Synthesis, had solved one of the main problems left by Darwin: to reconcile gradual evolution with a functioning theory of inheritance. Hamilton is best known for providing the solution to another of Darwin's puzzles, that of altruistic behaviour, something Darwin called his 'one special problem'. In addition, he made substantial contributions to theories on the evolution of sex, senescence, sex ratios, evolutionary game theory, mate choice, and intragenomic conflict.

Nature's Oracle is the first book-length treatment of Hamilton's life. Sociologist of science Ullica Segerstrale, author of the highly acclaimed history of the sociobiology controversy *Defenders of the Truth* (2000), has done a superb job in telling the story of an incredible scientific life. Scattered insights into Hamilton's life were previously available from the three volumes of collected papers *Narrow Roads of Gene Land* (1996; 2001; 2005). Unfortunately, the books are now out of print, which means that they are difficult and expensive to get hold of. Other, less extensive, biographical treatments include Kohn (2004) and Grafen (2004). The latter remains a great resource for those who wish to have more details and context on Hamilton's scientific work. In her research, Segerstrale has been very successful in uncovering many aspects of Hamilton's life not previously covered. For example, we learn that Hamilton was a keen rugby player while a schoolboy at Tonbridge, that he seriously considered becoming a schoolteacher instead of going to graduate school, and that he spent a night in a Greek prison following a car accident. Segerstrale also sheds additional light on more well-described aspects of Hamilton's life, such as his strained relationship with John Maynard Smith, his love for the Amazon, and his (often controversial) views on human nature.

Over 24 chapters, we are taken on a tour through Hamilton's life. Though born in Cairo, Egypt, to New Zealander parents he spent his childhood in Kent in southeast England. Following school days at Tonbridge and two years of National Service with the Royal Corps of Engineers, he went on to read natural sciences at St John's College, Cambridge. It was in Cambridge that Hamilton discovered Fisher; first by finding *The Genetical Theory of Natural Selection* (Fisher 1930) in his college library and later meeting the man himself as a retired professor in the Genetics Department. Evolutionary biology played a very minor role in the Cambridge undergraduate curriculum at the time, which frustrated Hamilton. The effect that Fisher's book had on the young Hamilton is therefore hard to exaggerate. One needs only to read Hamilton's endorsement of the 1999 Complete Variorum Edition of the *Genetical Theory*:

> 'This is a book which, as a student, I weighed as of equal importance to the entire rest of my undergraduate Cambridge BA course and, through the time I spent on it, I think it notched down my degree. Most chapters took me weeks, some months; even Kafka whom I read at the same time couldn't depress me like Fisher could on say, the subject of charity, nor excite me like his theory of civilization. Terrify was even the word in some topics and it still is, so deep has been the change from all I was thinking before. (...) By the time of my ultimate graduation, will I have understood all that is true in this book

*Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario, Canada M5S 3B2
E-mail: arvid.agren@utoronto.ca

> and will I get a First? [JAÅ: the highest level of degree a UK undergraduate can receive] I doubt it. In some ways some of us have overtaken Fisher; in many, however, this brilliant, daring man is still far in front.'

Reading Fisher not only cemented his interest in evolution, but also planted the seed of what would be his obsession for the first years of his career: the genetics of altruism. Up until the Second World War, this had not been a controversial topic. But this was after the War, and the topic was not considered appropriate. He therefore struggled to attract attention from his Cambridge advisors and as a consequences seriously considered abandoning his research ambitions to become a schoolteacher. With some help from the father of a Cambridge friend, however, Hamilton eventually gained acceptance as a graduate student at the London School of Economics, and owing to his interests in genetics he was later part-registered at University College London.

His time in London has become legendary. Despite being so lonely that he often did his work at subway stations and public buses in order to receive some human interactions, this was the time when he derived his now famous models of inclusive fitness (Hamilton 1963, 1964). His inequality, now known as Hamilton's Rule, $rb > c$, where r is the relatedness between the social interactors, b is the benefit to the recipient of the action and c is the cost to the individual performing the action, is probably, together with the Hardy–Weinberg equilibrium ($p^2 + 2pq + q^2 = 1$), the most famous equation in all of biology. The generality of the inclusive fitness framework is highlighted by its prediction of phenomena that at the time were poorly studied or unknown, such as spite (behaviour that is costly both to the actor and the recipient—referred to as 'stupid' behaviour in Hamilton's early notes), deviations from the Fisherian 1:1 sex ratio, and greenbeard genes. These are all phenomena that later empirical work has found an impressive amount of support for.

Stemming partly from his study of sex ratios, Hamilton later began moving on to what has become his second major contribution to evolutionary biology: his theories on the evolution of sex. The topic was another example where the masters of the Modern Synthesis had not made it all the way. In particular, as Jim Crow and Motoo Kimura had pointed out, Fisher in his model of the evolution of sex had relied on what seemed liked a group selection argument (Crow and Kimura 1965). Hamilton, who had declared himself 'allergic' to group selection, could not resist getting involved in the debate. His engagement resulted in what is now known as the parasite, or Red Queen, theory of sex. Here, sex is maintained in the population because it aids in the coevolutionary arms race with parasites. The theory continues to inspire researchers to this day (Lively 2010).

Hamilton did not, however, have the same inspirational effect on his undergraduate students. He was a notoriously bad lecturer, and while he was a lecturer at Imperial College, Silwood Park, undergraduates used to urge the department administrators not to count their marks in Hamilton's course towards their degree marks. The popularizing of his ideas was therefore left to others. We are many who first learned about Hamilton's ideas through the writings of Richard Dawkins, in particular *The Selfish Gene* (1976). However, while Hamilton was instrumental in the development of the concept of selfish genes in the Dawkinsian sense, he also made contributions to the study of selfish genes in the stricter definition of the term, that is the study of intragenomic conflict. For example, in his 1967 sex ratio paper he discusses how X and Y chromosomes will have different fitness interests (Hamilton 1967). The paper is now considered to be one of the best demonstrations of the ability of the theory of natural selection to generate quantifiable predictions. Moreover, it also carried a special personal meaning to Hamilton himself: he thought it provided scientific consolidation for his sense of an inner split. In *Narrow Roads of Gene Land, Volume 1* he writes:

> 'Seemingly inescapable conflict within diploid organisms came to me both as a new agonizing challenge and at the same time a release from a personal problem I had had all my life. In life, what was it I really wanted? My own conscious and seemingly indivisible self was turning out far from what I had imagined and I need not be so ashamed of my self pity! (. . .) Given my realization of an eternal disquiet within, couldn't I feel better about my own inability to be consistent in what I was doing, about my indecision in matters ranging from daily trivialities up to the very nature of right and wrong?'

As Segerstrale's book reveals, struggle was not only confined to his inner self, but defined much of Hamilton's career. This was first manifested in the need to convince his senior colleagues that the genetics of altruism was a topic worth pursuing, later with mathematically trained population geneticists who thought his models too sloppy, and with journal editors (especially those of *Nature*, a journal, with which he appears to have had a love–hate relationship), who according to Hamilton failed to grasp the insight of his work. To a degree, his problems stemmed from a very idealistic view of science. He was a firm believer that scientists had responsibility to follow their thinking and data wherever they led them. This desire sometimes led him into controversial territory and he did receive criticism for his speculations on the nature and future of humanity. Perhaps partly owing to his own experience as a graduate student, he also kept a soft spot for ideas that he thought had not received a fair hearing by his scientific colleagues. Later in his career he would lend his support to a number of controversial ideas, including James Lovelock's Gaia hypothesis and the link between polio vaccine and the spread of AIDS.

Hamilton's scientific idealism was also reflected in his continuous striving for the greatest generality possible for his theories. Like Darwin, Hamilton is widely associated with a

term he did not coin himself. However, while Darwin incorporated Herbert Spencer's 'survival of the fittest' into the fifth edition of the *Origin of Species*, Hamilton resisted 'kin selection' as a way of capturing his theory of social evolution. Indeed, the origin and use of the term were one source of Hamilton's long-lasting unhappiness with John Maynard Smith, who was the first to use it in print (Maynard Smith 1964). Hamilton thought the term put too much emphasis on genealogical relatives, which was only one route for inclusive fitness to be maximized. In other words, inclusive fitness was a more general concept than kin selection. At the end of her book, Segerstrale discusses the overwhelming support inclusive fitness received from his contemporary peers in response to a recent attack (Nowak *et al*. 2010). His defenders highlight the wide variety of phenomena that inclusive fitness has provided insights into, ranging from altruism, via cannibalism, to genomic imprinting (Abbot *et al*. 2011). Although not covered by Segerstrale (which is not a weakness of the book; *Nature's Oracle*, like any scientific biography, has to strike a balance between science and the personal story of the scientist), the last few years have seen an increased interest in expanding the scope of Hamilton's inclusive-fitness framework even further. In particular, Bourke (2011) has argued that inclusive fitness provides the conceptual foundation for understanding the major transitions in evolution (sensu Maynard Smith and Szathmáry 1995). While not everyone is convinced by the argument (see discussion by Birch 2012), Bourke's thesis offers a generality for Hamilton's idea that he himself could probably not have imagined: his idea does not only explain social behaviour, but the organization of all of life.

In sum, Segerstrale has done a terrific job. *Nature's Oracle* is a biography truly worthy of a scientist of Hamilton's stature and it will be an invaluable source of insight for anyone interested in the life and science of one of the giants of twentieth-century biology.

References

Abbot P., Abe J., Alcock J., Alizon S., Alpedrinha J. A., Anderson M. *et al*. 2011 Inclusive fitness theory and eusociality. *Nature* **471**, e1–e4.

Birch J. 2012 Social revolution. *Biol. Philos*. **27**, 571–581.

Bourke A. F. G. 2011 *Principles of social evolution*. Oxford University Press, Oxford, UK.

Crow J. and Kimura M. 1965 Evolution in sexual and asexual populations. *Am. Nat*. **99**, 439–450.

Dawkins R. 1976 *The selfish gene*. Oxford University Press, Oxford, UK.

Fisher R. A. 1930 *The genetical theory of natural selection*. Clarendon Press, Oxford, UK. (Variorum edition, 1999, Oxford University Press, Oxford, UK.)

Grafen A. 2004 William Donald Hamilton. *Biogr. Mem. Fellows R. Soc*. **50**, 109–132.

Hamilton W. D. 1963 The evolution of altruistic behavior. *Am. Nat*. **97**, 354–356.

Hamilton W. D. 1964 The genetical evolution of social behaviour I & II. *J. Theor. Biol*. **7**, 1–52.

Hamilton W. D. 1967 Extraordinary sex ratios. *Science* **156**, 477–488.

Hamilton W. D. 1996 *Narrow roads of gene land*: The collected papers of W.D. Hamilton volume 1: evolution of social behaviour. Oxford University Press, Oxford, UK.

Hamilton W. D. 2001 *Narrow roads of gene land*: The collected papers of W.D. Hamilton volume 1: evolution of sex. Oxford University Press, Oxford, UK.

Hamilton W. D. 2005 *Narrow roads of gene land*: The collected papers of W.D. Hamilton volume 1: last words (with essays by co-authors, ed. M. Ridley). Oxford University Press, Oxford, UK.

Kohn M. 2004 *A reason for everything: natural selection and the English imagination*. Faber and Faber, London, UK.

Lively C. M. 2010 A review of red queen models for the persistence of obligate sexual reproduction. *J. Hered*. **101**, S13–S20.

Maynard Smith J. 1964 Group selection and kin selection. *Nature* **201**, 1145–1147.

Maynard Smith J. and Szathmáry E. 1995 *The major transitions in evolution*. Oxford University Press, Oxford, UK.

Nowak M. A., Tarnita C. E. and Wilson E. O. 2010 The evolution of eusociality. *Nature* **466**, 1057–1062.

Segerstrale U. 2000 *Defenders of the truth: the battle for science in the sociobiology debate and beyond*. Oxford University Press, Oxford, UK.