

# In Memory of Bill Hamilton

## Obituary: William Donald Hamilton (1936-2000) (Nature 404: 828, 2000).

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W. D. Hamilton was one of the greatest evolutionary theorists since Darwin. Certainly, where social theory based on natural selection is concerned, he was easily our deepest and most original thinker.

His first work (1964) - his theory of inclusive fitness - was his most important, because it is the only true advance since Darwin in our understanding of natural selection. Hamilton's work is a natural and inevitable extension of Darwinian logic. In Darwin's system, natural selection refers to individual differences in reproductive success (RS) in nature, where RS is the number of surviving offspring produced. Hamilton enlarged the concept to include RS effects on other relatives; that is, not just fitness or reproductive success but inclusive fitness, defined (roughly) as an individual's RS plus effects on the RS of relatives, each devalued by the appropriate degree of relatedness ( $r$ ).

This idea had been briefly advanced by R. A. Fisher and J. B. S. Haldane, but neither took it seriously and neither provided any kind of mathematical foundation. That foundation was not as obvious as it sounds. For a rare altruistic gene, it is clear that  $B > C$  will give positive selection, where  $B$  is the benefit conferred and  $C$  the cost suffered; but the matter is not so obvious at intermediate gene frequencies. As the altruistic gene spreads, should not the criterion for positive selection be relaxed?

Hamilton showed that the answer is 'no' and that his simple rule worked for all gene frequencies. He once told the story of sitting down as a doctoral student to write to Haldane, but to formulate each question precisely he had to do additional work and after a couple of years of such work he never sent the letter because by then he had worked out all the answers himself. A noteworthy implication of Hamilton's work was that in almost all species the individual was no longer expected to have a unitary self-interest, because genetic elements are inherited according to different rules (contrast paternal transmission of the Y chromosome with maternal transmission of mitochondrial DNA).

He soon followed this work with major advances in understanding

selection acting on the sex ratio, the moulding of senescence by natural selection, the aggregation and dispersal of organisms, the evolution of the social insects, the evolution of dimorphic males, and the origin of higher taxonomic units in insects. For the latter he argued that the more-or-less closed spaces created by rotting wood imposed a system of small, inbred subpopulations in insects inhabiting it, leading to a great diversity of homozygous forms, often with arbitrary, novel characters (such as a second complete metamorphosis in many male scale insects). In 1981 with Robert Axelrod he laid the mathematical foundation for the study of reciprocal altruism, when they showed that the simple rule of tit-for-tat in playing iterated games of Prisoner's Dilemma was itself evolutionarily stable.

Twenty years ago Hamilton began to devote most of his time to the theory that parasites play a key role in generating sexual reproduction in their hosts, recombination being a defence against very rapidly and antagonistically co-evolving parasites. In his memorable phrase, sexual species are "guilds of genotypes committed to free, fair exchange of biochemical technology for parasite exclusion". He was not the first to advance this theory but he took it more seriously than others and he worked most successfully to define the form of the argument as well as its implications. Notable here was his work with Marlene Zuk on parasites as a key to mate choice. In 1982 they showed that species of birds with higher loads of blood parasites showed more colour and complex song, an unexpected finding unless parasite-rich environments favoured mate choice for these traits, thereby driving up their average value.

It is hard to capture on paper the beauty of the man and the reason that so many evolutionists felt such a deep personal connection to Bill Hamilton. He had the most subtle, multi-layered mind I have ever encountered. What he said often had double and even triple meanings so that, while the rest of us speak and think in single notes, he thought in chords. He was modest in style, with a warm sense of humour. For example, he had no illusions about the clarity of his lecturing style, and once told a class we taught at Harvard that after hearing him lecture they would wonder whether he understood even his own ideas.

His letters were laced with humorous asides. He once sent me a news clipping of a human father-to-son testicle transplant, along with the comment, "New vistas for parent-offspring conflict?". The last time I saw Bill, at Oxford in December 1998, he pointed with pride to the two, and possibly three, species of moss growing on his Volvo - indeed

on its windows - and told me that this was a clear advantage of Oxford over Cambridge, the latter climate being too dry. (He had come to Oxford University in 1984, after seven years at the University of Michigan and 13 at Imperial College, London.)

Bill Hamilton was a naturalist of legendary knowledge, especially of insects, but he was also an acute observer of human behaviour, right down to the minutiae of your own actions in his presence. Had I noticed, he asked, that lopsided facial expressions in humans are almost exclusively male? (No, but I have seen it a hundred times since then!) He was an evolutionist to the core, and was always heartened by news of fellow evolutionists enjoying some reproductive success. In a similar spirit I take joy in the lives of his three daughters, Helen, Ruth and Rowena, not to mention his many surviving siblings. But the loss of this 'gentle giant' is very great. Bill died at the age of 63 on 7 March 2000, from complications after contracting malaria during fieldwork in the Congo in January, work which was designed to locate more exactly the chimpanzee populations that donated HIV-1 to humans, as well as the mode of transmission. He had been strong in mind, body and spirit, with many new projects and thoughts under way. He will be sorely missed for many years to come.

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