

Bill Hamilton – The Greatest Darwinian Since Darwin

William Donald Hamilton, described by Richard Dawkins (author of *The Selfish Gene*), as the greatest Darwinian since Darwin, made many monumental contributions to evolutionary biology, but his theory for the evolution of altruism stands out as his most significant contribution. Some animals, especially social insects, display remarkable degrees of altruistic behaviour. The honeybee worker for example spends her whole life working for the welfare of her colony and helps the queen to reproduce, and dies usually without producing any of her own offspring. Indeed, she even commits suicide in an attempt to protect her colony – when she stings any marauder of her nest, she is unable to withdraw her sting. Her abdomen ruptures and she flies away leaving behind her sting, her poison gland and a portion of her intestines, only to die within a few minutes. But her poison gland continues to pump venom into the victim for some 60 seconds after the bee has flown away.

How does natural selection, which is often paraphrased as ‘survival of the fittest’, favour the evolution of such blatantly altruistic behaviour? This question bothered Darwin himself and others for a hundred years after him. Hamilton however realised that natural selection is not really about the survival or reproduction of individuals but is about the relative frequencies of different genes (alleles) in the population. Thus Hamilton argued that, rather than compute fitness as the number of offspring left behind by an individual, we should compute ‘inclusive fitness’ as the number of copies of one’s genes that are transmitted to future generations, transmitted both by producing offspring as well as by aiding genetic relatives. Hamilton proposed his theory as a simple rule, now known as Hamilton’s rule, which states that altruism can evolve by natural selection if $br - c > 0$, where b is the benefit to the recipient of altruism, c is the cost to the altruist and r is the coefficient of genetic relatedness between altruist and recipient. Hamilton’s rule has now become the cornerstone of evolutionary biology, and has helped to unify many hitherto apparently disparate areas of biology. Hamilton also made extremely significant contributions to our understanding of sex ratios, sexual selection, the evolution of sex itself, the role of disease in evolution and several other areas.

The purpose of this little essay is not to summarise Hamilton’s work but to pay tribute to the man behind the science, a year after his untimely demise. Although most of Hamilton’s papers were theoretical in nature, he was widely acknowledged as an extraordinary naturalist. His former student, Marlene Zuk says “He was the best field biologist I have ever met... If you went out with him in England, he could identify every bird, every plant, every insect, practically every microorganism he encountered”. Indeed his natural history expertise was by no means restricted to England; his knowledge of the flora and fauna of Brazil, or even of India was equally impressive. When he once visited my laboratory, he noticed that one of my students was looking at an insect under a dissection microscope and repeatedly referring to an identification manual, obviously attempting to identify the insect. Hamilton, sitting a meter away, asked “to what level are you trying to identify that insect?” When told that the student was trying to place the specimen in its family, Hamilton immediately gave the correct identification of this specimen from Western Ghats, from a meter away and of course, without the aid of microscope or manual. In his inimitable style Richard Dawkins has said “I suspect that, of all his 20th-century successors, Darwin would have enjoyed most talking to Hamilton. Partly because they could have swapped jungle tales and beetle lore, partly because both were gentle and deep, but mostly because Hamilton the theorist was responsible for clearing up so many of the very problems that had intrigued and tantalised Darwin”. Hamilton’s success was surely because of his deep knowledge of natural history but also because of the fact that his approach was theoretical and mathematical. Despite his deep interest in natural history, Hamilton’s hero was R A Fisher the author of one of the most difficult books on mathematical biology, and that too in spite of his teacher telling him that “Fisher had no credentials even to be writing on biology”.



Another ingredient in Hamilton's success was surely his belief in himself. His first, and now, landmark paper was rejected by *Nature*. Hamilton recalls, "I received the editor's decision almost by return of post. In about three lines he regretted that he had no space for my manuscript and suggested that, it might be more appropriate to a 'psychological or sociological' journal". Throughout his career Hamilton had trouble publishing his papers in peer-reviewed journals, underscoring the shortcomings of the peer-review system. Paul Harvey, head of the Department of Zoology at Oxford, where Hamilton worked, says, "Some of his ideas you thought were lunatic and some great, and it sometimes turned out that the lunatic ideas were the great ones".

Hamilton died a year ago from complications arising out of cerebral malaria that he contracted while doing field work. His former graduate student Bernie Crespi said in an email, "I expect that this is how Bill would have preferred to go, fighting malarial parasites after an expedition to the Congo to find the source of AIDS". I met Bill after his first expedition to the Congo when he told me why he had to go again (on his last fatal trip): "I wish they (the microbiologists he was collaborating with) had told me they needed more (of Chimpanzee faeces), I could easily have collected kilograms".

Hamilton was very fond of coprophagous beetles and knew that there is at least one species in the Western Ghats. Before one of his visits to my lab, I asked him what arrangements he desired? His reply was that he wanted two or three large dead rats to be kept ready for him! Knowing Bill, I kept the dead rats ready. It is only after his arrival that I realised that he was planning to use them as bait to get his favourite beetles. For Hamilton, his science was inseparable not just from his life but also from his death. He wrote a moving article entitled "My Intended Burial and Why?", in which he expresses his desire to have his body dealt with thus: "I will leave a sum in my last will for my body to be carried to Brazil and to these forests. It will be laid out in a manner secure against the possums and the vultures just as we make our chickens secure; and this great Coprophanaeus beetle will bury me. They will enter, will bury, will live on my flesh; and in the shape of their children and mine, I will escape death. No worm for me nor sordid fly, I will buzz by the dusk like a huge bumble bee". I can't help being reminded of what Albert Einstein said of Mahatma Gandhi, "Generations to come will scarce believe that such a one as this ever walked upon this earth".

Suggested Reading

R Gadagkar, *Survival Strategies – Cooperation and Conflict in Animal Societies*, Harvard University Press, USA and Universities Press, Hyderabad, 1997.

R Gadagkar, The Origin and Resolution of Conflicts in Animal Societies – The Case of the Bees and the Birds. *Resonance – journal of science education*, Vol.5, No.4, 62-73, 2000.

R Gadagkar, Genomic imprinting – some interesting implications for the evolution of social behaviour, *Resonance – journal of science education*, Vol.5, No.9, 58-68, 2000.

W D Hamilton, *The collected papers of W D Hamilton, Narrow Road of Gene Land*, Vol.1, W H Freeman, New York, 1996.

W D Hamilton, My intended burial and why, *Ethology Ecology and Evolution*, Vol.12, 111-122, 2000.

W D Hamilton, *Narrow Roads of Gene Land, The collected papers of W D Hamilton*, Volume 2, Oxford University Press, London, 2001.

Web site in memory of Hamilton: <http://www.unibas.ch/dib/zoologie/ebert/hamilton.html>

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