

W. D. Hamilton

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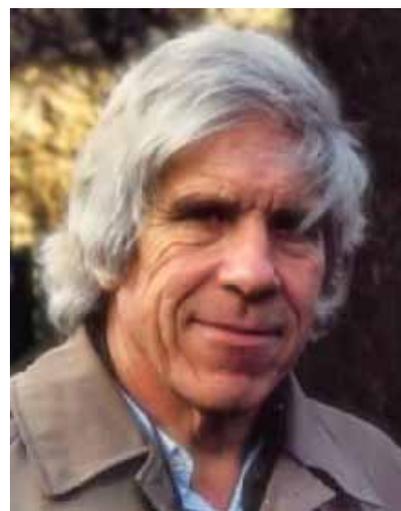
William Donald "Bill" Hamilton, FRS (1 August 1936 – 7 March 2000) was an English evolutionary biologist, widely recognised as one of the greatest evolutionary theorists of the 20th century.^{[1][2]}

Hamilton became famous through his theoretical work expounding a rigorous genetic basis for the existence of kin selection and altruism, an insight that was a key part of the development of a gene-centric view of evolution. He is considered one of the forerunners of sociobiology, as popularized by E. O. Wilson. Hamilton also published important work on sex ratios and the evolution of sex. From 1984 to his death in 2000, he was a Royal Society Research Professor at Oxford University.

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W. D. Hamilton



W. D. Hamilton, 1996

Born	William Donald Hamilton 1 August 1936 Cairo, Egypt
Died	7 March 2000 (aged 63) Fitzrovia, London, United Kingdom
Nationality	British
Fields	Evolutionary biology
Alma mater	University College London London School of Economics St. John's College, Cambridge
Academic advisors	John Hajnal Cedric Smith
Doctoral students	Laurence Hurst Olivia Judson
Known for	Kin selection, Hamilton's rule
Influences	Ronald Fisher
Influenced	Richard Dawkins

Early life

Hamilton was born in 1936 in Cairo, Egypt, the second of seven children. His father A. M. Hamilton was a New Zealand-born engineer. His mother B. M. Hamilton was a medical doctor, also from New Zealand.

The Hamilton family settled in Kent. During the Second World War, the young Hamilton was evacuated to Edinburgh. He had an interest in natural history from an early age and would spend his spare time collecting butterflies and other insects. In 1946 he discovered E.B. Ford's *New Naturalist* book *Butterflies*, which introduced him to the principles of evolution by natural selection, genetics and population genetics.

He was educated at Tonbridge School, where he was in Smythe House. As a 12-year old he was seriously injured while playing with explosives his father had. These were left over from his making hand grenades for

the Home Guard during World War II; the accident might have killed him if his mother had not been a doctor. The boy had to have a thoracotomy in King's College Hospital to save his life, but fingers on his right hand had to be amputated and he was left with scarring on his body. He needed six months to recover.

Hamilton stayed on an extra term at Tonbridge to complete the Cambridge entrance examinations, and then travelled in France. He completed two years of national service. As an undergraduate at St. John's College, he was uninspired by the "many biologists [who] hardly seemed to believe in evolution". He was intrigued by Ronald Fisher's book *The Genetical Theory of Natural Selection*; but Fisher lacked standing at Cambridge as he was viewed as only a statistician. Hamilton was excited by Fisher's chapters on eugenics. In earlier chapters, Fisher provided a mathematical basis for the genetics of evolution. Working through the stodgy prose, Hamilton later blamed Fisher's book for his getting only a 2:1 degree.

Hamilton's rule

Main article: Hamilton's rule

Hamilton enrolled in an MSc course in demography at the London School of Economics (LSE), under Norman Carrier, who helped secure various grants for his studies. Later, when his work became more mathematical and genetical, he had his supervision transferred to John Hajnal of the LSE and Cedric Smith of University College London (UCL).

Both Fisher and J. B. S. Haldane had seen a problem in how organisms could increase the fitness of their own genes by aiding their close relatives, but not recognised its significance or properly formulated it. Hamilton worked through several examples, and eventually realised that the number that kept falling out of his calculations was Sewall Wright's coefficient of relationship. This became Hamilton's rule: in each behaviour-evoking situation, the individual assesses his neighbour's fitness against his own according to the coefficients of relationship appropriate to the situation. Algebraically, the rule posits that a costly action should be performed if:

C < *r* × *B* Where *C* is the cost in fitness to the actor, *r* the genetic relatedness between the actor and the recipient, and *B* is the fitness benefit to the recipient. Fitness costs and benefits are measured in fecundity. His two 1964 papers entitled *The Genetical Evolution of Social Behavior* are now widely referenced.

The proof and discussion of its consequences, however, involved detailed mathematics, and two reviewers passed over the paper. The third, John Maynard Smith, did not completely understand it either, but recognised its significance. Having his work passed over later led to friction between Hamilton and Maynard Smith, as Hamilton thought Smith had held his work back to claim credit for the idea (during the review period Maynard Smith published a paper that referred briefly to similar ideas). The Hamilton paper was printed in the *Journal of Theoretical Biology* and, when first published, was largely ignored. Recognition of its significance gradually increased to the point that it is now routinely cited in biology books.

Much of the discussion relates to the evolution of eusociality in insects of the order Hymenoptera (ants, bees and wasps) based on their unusual haplodiploid sex-determination system. This system means that females are more closely related to their sisters than to their own (potential) offspring. Thus, Hamilton reasoned, a "costly action" would be better spent in helping to raise their sisters, rather than reproducing themselves.

Spiteful behaviour

Main article: Hamiltonian spite

In his 1970 paper *Selfish and Spiteful Behaviour in an Evolutionary Model* Hamilton considers the question of whether harm inflicted upon an organism must inevitably be a byproduct of adaptations for survival. What

of possible cases where an organism is deliberately harming others without apparent benefit to the self? Such behaviour Hamilton calls spiteful. It can be explained as the increase in the chance of an organism's genetic alleles to be passed to the next generations by harming those that are less closely related than relationship by chance.

Spite, however, is unlikely ever to be elaborated into any complex forms of adaptation. Targets of aggression are likely to act in revenge, and the majority of pairs of individuals (assuming a panmictic species) exhibit a roughly average level of genetic relatedness, making the selection of targets of spite problematic.

Extraordinary sex ratios

Between 1964 and 1978 Hamilton was a lecturer at University College London. Whilst there he published a paper in *Science* on "extraordinary sex ratios". Fisher (1930) had proposed a model as to why "ordinary" sex ratios were nearly always 1:1 (but see Edwards 1998), and likewise extraordinary sex ratios, particularly in wasps, needed explanations. Hamilton had been introduced to the idea and formulated its solution in 1960 when he had been assigned to help Fisher's pupil A.W.F. Edwards test the Fisherian sex ratio hypothesis. Hamilton combined his extensive knowledge of natural history with deep insight into the problem, opening up a whole new area of research.

The paper was also notable for introducing the concept of the "unbeatable strategy", which John Maynard Smith and George R. Price were to develop into the evolutionarily stable strategy (ESS), a concept in game theory not limited to evolutionary biology. Price had originally come to Hamilton after deriving the Price equation, and thus rederiving Hamilton's rule. Maynard Smith later peer reviewed one of Price's papers, and drew inspiration from it. The paper was not published but Maynard Smith offered to make Price a co-author of his ESS paper, which helped to improve relations between the men. Price committed suicide in 1975, and Hamilton and Maynard Smith were among the few present at the funeral.^[3]

Hamilton was regarded as a poor lecturer. This shortcoming would not affect the popularity of his work, however, as it was popularised by Richard Dawkins in Dawkins' 1976 book *The Selfish Gene*.

In 1966 he married Christine Friess and they were to have three daughters, Helen, Ruth and Rowena. 26 years later they amicably separated.

Hamilton was a visiting professor at Harvard University and later spent nine months with the Royal Society's and the Royal Geographical Society's Xavantina-Cachimbo Expedition as a visiting professor at the University of São Paulo.

From 1978 Hamilton was Professor of Evolutionary Biology at the University of Michigan. Simultaneously, he was elected a Foreign Honorary Member of American Academy of Arts and Sciences. His arrival sparked protests and sit-ins from students who did not like his association with sociobiology. There he worked with the political scientist Robert Axelrod on the prisoner's dilemma, and was a member of the BACH group with original members Arthur Burks, Robert Axelrod, Michael Cohen and John Holland.

Chasing the Red Queen

Hamilton was an early proponent of the Red Queen theory of the evolution of sex,^[4] first proposed by Leigh Van Valen. This was named for a character in Lewis Carroll's *Through the Looking-Glass*, who is continuously running but never actually travels any distance:

"Well, in our country," said Alice, still panting a little, "you'd generally get to somewhere else—if you ran very fast for a long time, as we've been doing."

"A slow sort of country!" said the Queen. "Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!"

(Carroll, pp. 46) (<http://etext.lib.virginia.edu/etcbin/toccer-new2?id=CarGlas.sgm&images=images/modeng&data=/texts/english/modeng/parsed&tag=public&part=2&division=div1>)

This theory hypothesizes that sex evolved because new and unfamiliar combinations of genes could be presented to parasites, preventing the parasite from preying on that organism: species with sex were able to continuously "run away" from their parasites. Likewise, parasites were able to evolve mechanisms to get around the organism's new set of genes, thus perpetuating an endless race.

Return to Britain

In 1980 he was elected a Fellow of the Royal Society, and in 1984 he was invited by Richard Southwood to be the Royal Society Research Professor in the Department of Zoology at Oxford, and a Fellow of New College, where he remained until his death.

From 1994 Hamilton found companionship with Maria Luisa Bozzi, an Italian science journalist and author.

His collected papers, entitled *Narrow Roads of Gene Land*, began to be published in 1996. The first volume was entitled *Evolution of Social Behaviour*.

Social evolution

The field of social evolution, of which Hamilton's rule has central importance, is broadly defined as being the study of the evolution of social behaviours, i.e. those that impact on the fitness of individuals other than the actor. Social behaviours can be categorized according to the fitness consequences they entail for the actor and recipient. A behaviour that increases the direct fitness of the actor is mutually beneficial if the recipient also benefits, and selfish if the recipient suffers a loss. A behaviour that reduces the fitness of the actor is altruistic if the recipient benefits, and spiteful if the recipient suffers a loss. This classification was first proposed by Hamilton in 1964.^[*citation needed*]

Through his collaboration with Hugh N. Comins and Bob May on evolutionarily stable dispersal strategies, Hamilton acquired an Erdős number of 5.^[5]

Hamilton also proposed the coevolution theory of autumn leaf color as an example of evolutionary signalling theory.^[6]

Expedition to the Congo

During the 1990s Hamilton became increasingly interested in the controversial argument that the origin of HIV lay in oral polio vaccines trials conducted by Hilary Koprowski in Africa during the 1950s. Letters by Hamilton on the topic to the major peer-reviewed journals were rejected. To look for indirect evidence of the OPV hypothesis by assessing natural levels of simian immunodeficiency virus, in primates, in early 2000 he and two others ventured on a field trip to the war-torn Democratic Republic of the Congo.

Death

He returned to London from Africa on 29 Jan 2000. He was admitted to University College Hospital London on 30 Jan 2000. He was transferred to Middlesex Hospital London on 5 Feb 2000 and died there on 7 Mar 2000. An inquest was held on 10 May 2000 at Westminster Coroner's Court to inquire into rumours about the cause of his death. The coroner concluded that his death was due to "Multi-organ failure due to upper gastrointestinal haemorrhage due to a duodenal diverticulum and arterial bleed through a mucosal ulcer". ECU's investigation established that he contracted malaria during his final African expedition. However, the

pathologist had suggested the possibility that the ulceration and consequent haemorrhage had resulted from a pill (which might have been taken because of malarial symptoms) lodging in the diverticulum; but, even if this suggestion were correct, the link between malaria and the observed causes of death would be entirely indirect.^[7]

A secular memorial service (he was an atheist) was held at the Chapel of New College, Oxford on Saturday 1 July 2000, organised by Richard Dawkins. He was buried near Wytham Woods. He, however, had written an essay on *My intended burial and why* in which he wrote:^[8]

“ 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 in the dusk like a huge bumble bee. I will be many, buzz even as a swarm of motorbikes, be borne, body by flying body out into the Brazilian wilderness beneath the stars, lofted under those beautiful and un-fused elytra which we will all hold over our backs. So finally I too will shine like a violet ground beetle under a stone. ”

The second volume of his collected papers, *Evolution of Sex*, was published in 2002, and the third and final volume, *Last Words*, in 2005.

Awards

- 1978 Foreign Honorary Member of American Academy of Arts and Sciences
- 1980 Fellow of the Royal Society of London^[9]
- 1982 Newcomb Cleveland Prize of the American Association for the Advancement of Science
- 1988 Darwin Medal of the Royal Society of London
- 1989 Scientific Medal of the Linnean Society
- 1991 Frink Medal of Zoological Society of London
- 1992/3 Wander Prize of the University of Bern
- 1993 Crafoord Prize of the Royal Swedish Academy of Sciences
- 1993 Kyoto Prize of the Inamori Foundation
- 1995 Fyssen Prize of the Fyssen Foundation

Biographies

- Alan Grafen has written a biographical memoir for the Royal Society.^[9]
- A book is also in press: Segerstråle, U. 2007 *Nature's oracle: an intellectual biography of evolutionist W. D. Hamilton*. Oxford University Press (<http://www.oup.com/us/catalog/general/subject/BiographyLettersMemoirs/?ci=9780198607274>).

Works

Collected papers

Hamilton started to publish his collected papers starting in 1996, along the lines of Fisher's collected papers, with short essays giving each paper context. He died after the preparation of the second volume, so the essays for the third volume come from his coauthors.

- Hamilton W.D. (1996) *Narrow Roads of Gene Land vol. 1: Evolution of Social Behaviour* Oxford University Press,Oxford. ISBN 0-7167-4530-5

- Hamilton W.D. (2002) *Narrow Roads of Gene Land vol. 2: Evolution of Sex* Oxford University Press, Oxford. ISBN 0-19-850336-9
- Hamilton W.D. (2005) *Narrow roads of Gene Land, vol. 3: Last Words* (with essays by coauthors, ed. M. Ridley). Oxford University Press, Oxford. ISBN 0-19-856690-5

Significant papers

- Hamilton, W. (1964). "The genetical evolution of social behaviour. I". *Journal of Theoretical Biology* **7** (1): 1–16. doi:10.1016/0022-5193(64)90038-4 (<http://dx.doi.org/10.1016%2F0022-5193%2864%2990038-4>). PMID 5875341 ([//www.ncbi.nlm.nih.gov/pubmed/5875341](http://www.ncbi.nlm.nih.gov/pubmed/5875341)).
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- Axelrod, R.; Hamilton, W. (1981). "The evolution of cooperation". *Science* **211** (4489): 1390–1396. doi:10.1126/science.7466396 (<http://dx.doi.org/10.1126%2Fscience.7466396>). PMID 7466396 ([//www.ncbi.nlm.nih.gov/pubmed/7466396](http://www.ncbi.nlm.nih.gov/pubmed/7466396)). with Robert Axelrod
- Hamilton, W.; Zuk, M. (1982). "Heritable true fitness and bright birds: A role for parasites?". *Science* **218** (4570): 384–387. doi:10.1126/science.7123238 (<http://dx.doi.org/10.1126%2Fscience.7123238>). PMID 7123238 ([//www.ncbi.nlm.nih.gov/pubmed/7123238](http://www.ncbi.nlm.nih.gov/pubmed/7123238)).

Notes

- [^] Obituary by Richard Dawkins - *The Independent* - 10 March 2000 (http://www.edge.org/3rd_culture/hamilton/hamilton_index.html)
- [^] BBC Radio 4 - *Great Lives* - 2 Feb 2010 (<http://www.bbc.co.uk/iplayer/console/b00qc2hn>)
- [^] Brown, Andrew (2000). *The Darwin Wars: The Scientific Battle for the Soul of Man*. London: Touchstone. ISBN 0-684-85145-8.
- [^] The Red Queen Hypothesis (http://www.indiana.edu/~curtweb/Research/Red_Queen%20hyp.html) at Indiana University. Quote: "*W.D. Hamilton and John Jaenike were among the earliest pioneers of the idea.*"
- [^] His path to Erdős: William D. Hamilton coauthored with Robert M. May, Robert M. May coauthored with Yoh Iwasa, Yoh Iwasa coauthored with Eugene Seneta, Eugene Seneta coauthored with Janos Galambos, Janos Galambos coauthored with Paul Erdős.
- [^] Hamilton and Brown, WD; Brown, SP (Jul 2001). "Autumn tree colours as a handicap signal" (<http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1088768>). *Proc. R. Soc. B* **268** (1475): 1489–1493. doi:10.1098/rspb.2001.1672 (<http://dx.doi.org/10.1098%2Frsbp.2001.1672>). ISSN 0962-8452 ([//www.worldcat.org/issn/0962-8452](http://www.worldcat.org/issn/0962-8452)). PMC 1088768 ([//www.ncbi.nlm.nih.gov/pmc/articles/PMC1088768](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1088768)). PMID 11454293 ([//www.ncbi.nlm.nih.gov/pubmed/11454293](http://www.ncbi.nlm.nih.gov/pubmed/11454293)). More than one of |last1= and |author= specified (help)

7. ^ "ECU Ruling: Great Lives, BBC Radio 4, 2 February 2010" (http://www.bbc.co.uk/complaints/content/ecu/ecu_greatlives_wdhamilton). BBC. Retrieved 24 June 2011.
8. ^ Hamilton, W.D. (2000) My intended burial and why, *Ethology Ecology and Evolution* **12** 111-122 PDF (<http://ejour-fup.cilea.it/index.php/eee/article/viewFile/859/805>)
9. ^ ^a ^b Grafen, A. (2004). "William Donald Hamilton. 1 August 1936 -- 7 March 2000" (http://users.ox.ac.uk/~grafen/cv/WDH_memoir.pdf). *Biographical Memoirs of Fellows of the Royal Society* **50**: 109–108. doi:10.1098/rsbm.2004.0009 (<http://dx.doi.org/10.1098/rsbm.2004.0009>).

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External links

- Obituaries and reminiscences (<http://www.unifr.ch/biol/ecology/hamilton/hamilton.html>)
- Royal Society citation (<http://www.royalsoc.ac.uk/DServe/dserve.exe?dsqIni=Dserve.ini&dsqApp=Archive&dsqCmd=Show.tcl&dsqSearch=RefNo=='EC/1980/12'&dsqDb=Catalog>)
- Truth and Science: Bill Hamilton's legacy (<http://www.uow.edu.au/~bmartin/dissent/documents/AIDS/Bozzi03.pdf>)
- Centro Itinerante de Educação Ambiental e Científica Bill Hamilton (The Bill Hamilton Itinerant Centre for Environmental and Scientific Education) (in Portuguese) (<http://www.mamiraua.org.br/4-2-1.html>)
- Non-mathematical excerpts from Hamilton 1964 (<http://www.serpentfd.org/a/hamilton1964.html>)
- "If you have a simple idea, state it simply" a 1996 interview with Hamilton (<http://www.froes.dds.nl/HAMILTON.htm>)
- London Review of Books book review (<http://www.lrb.co.uk/v25/n03/andrew-berry/reasons-for-being-nice-and-having-sex>)
- W.D. Hamilton's work in game theory (<http://www.iiasa.ac.at/Publications/Documents/IR-02-019.pdf>)

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Categories: 1936 births | 2000 deaths | Alumni of St John's College, Cambridge

| Alumni of the London School of Economics | British atheists | British zoologists | Evolutionary biologists | Evolutionary psychologists | Fellows of the Royal Society | Fellows of New College, Oxford | People educated at Tonbridge School | Population geneticists | Recipients of the National Order of Scientific Merit (Brazil) | University of São Paulo faculty

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