polymerase from the DNA. Time course experiments should allow putative intermediates in the termination pathway to be characterized (*13*).

Similar studies performed at the initiation of transcription reveal that proteins regulating transcription have two functions: to accelerate formation of the elongation complex, and to interact with and guide the complex along the DNA. Now it appears that at certain terminator sequences some regulatory proteins cause all of the RNA polymerases to behave in a similar way (*11*).

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RETROSPECTIVE

William Hamilton (1936–2000)

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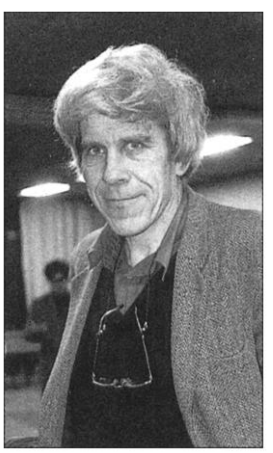
Bill Hamilton, one of the foremost evolutionary theorists of the 20th century, has died at the age of 63 from complications following malaria.

Bill is best known for the concept of inclusive fitness that he developed as a Ph.D. student at the London School of Economics. Hamilton's Rule, as it is known, is a form of genetic accounting that weights the fitness effects of an individual's actions on relatives according to their degree of kinship. Thus, from the perspective of the individual's genes, a benefit conferred on a sibling is four times the value of the same benefit conferred on a cousin but only half the value of the benefit conferred on the individual. This deceptively simple idea has revolutionized the way biologists think about the evolution of social behaviors.

Because he packed so much into each one, Bill's output of papers was small, but many have become foundation documents for new subdisciplines of evolutionary biology. The special quality of his papers was their unusual combination of a deep theoretical insight and a first-hand, encyclopedic knowledge of natural history. His article on extraordinary sex ratios proposed that many insects produce far more female than male offspring to reduce competition among brothers for mates. He introduced the idea of an unbeatable strategy and showed that this strategy differed for sex-linked and autosomal genes. Not only did this paper establish modern theoretical approaches to the evolution of sex ratios, but it also included early recognition of the potential for conflict among different elements of the genome.

Bill made significant contributions to understanding the evolution of senescence, dispersal, and cooperation among nonrelatives. The latter part of his career was devoted to exploring how parasites are involved in the maintenance of sexual reproduction. There is no better introduction to Bill's idiosyncratic world-view than his collected papers, published with autobiographical annotations under the title *Narrow Roads of Gene Land*. Bill had an enduring interest in Japan, and his title pays homage to Basho's *Narrow Roads of Oku*. In Basho's work, the traveling artist uses his experience to make poignant observations about human nature; in Hamilton's version, it is the wandering scientist who uses genetic and analytical reasoning to discover insights into animal behavior and evolution.



Bill was a lecturer at Imperial College, London, from 1964 to 1977; a Museum Professor at the University of Michigan from 1978 until 1984; then he returned to England as a Royal Society Research Professor at Oxford University. He received many honors, including the Darwin Medal, Kyoto Prize, and Crafoord Prize. The affection for him of those who knew him reflected his extraordinary humility, humor, and endless curiosity. He rarely came away from a seminar, no matter how poor, without a kind remark about an intriguing piece of natural history sometimes accidentally stumbled upon by the speaker.

Bill's interests ranged widely across disciplines, but natural history was his true passion. An Oxford boat trip would bring a stream of information, as he expertly wielded the punting pole, about the mating behavior of the midges buzzing overhead, the life history of the rust fungus infecting the nettles along the banks, or the diversity of brood parasites in the nests of bumblebees. But Bill would have been equally at home on the Amazon, discussing the aquatic caterpillars drifting by the gunwales, or the fruit-eating fishes foraging among the submerged crowns of rainforest trees in a seasonally flooded forest.

Bill constantly set himself challenges, such as learning to speak fluent Portuguese while working in Brazil, or cycling faster than any car encountered on the road between Wytham and Oxford. Personally, he regarded himself as "a lumbering dinosaur of the romantic movement," and spent several years writing a novel. It is a swashbuckling tale of intrigue, romance, diamond smuggling, gun-running, and exotic flora and fauna, not to mention a chapter in which the protagonist changes sex. His disregard for personal safety led to his last, fatal trip to the Congo in search of the origins of AIDS. Seniority and success never mellowed his fierce integrity and quest for truth. The parasites, which he believed played such an important part in evolution, at last brought an end to a life that had contributed so much.

Above all else, Bill loved insects. His letters and papers abound with tales of gall wasps, fighting stag beetles, Pharaoh's ants, and scarlet tiger moths. He once expressed a desire that when he died his body should be laid out in the Brazilian forest (adequately secured against larger scavengers such as possums and vultures) so that it could be buried by the great *Coprophanaeus* beetle. His poetic vision is a fitting epitaph (*1*): "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 or sordid fly, I will buzz in the dusk like a huge bumblebee. I will be many, buzz even as a swarm of motorbikes, be bourne, body by flying body out into the Brazilian wilderness beneath the stars, lofted under those beautiful and unfused elytra which we will all hold over our backs. So finally I too will shine like a violet ground beetle under a stone."

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