W.D. Hamilton, 1936–2000

William Donald Hamilton was one of the leading evolutionary biologists of our time. His theory of inclusive fitness ('kin selection') transformed the study of social behavior by demonstrating how altruistic and selfish tendencies are expected to be modulated by genetic relatedness. This theory, along with other contributions by Hamilton, also broadened the concept of social behavior to include interactions among genes and genomes. His ideas directly inform much current thought about 'genetic conflicts' and their possible involvement in aspects of development and disease.

From childhood, Hamilton immersed himself in natural history. A passion for insects led to undergraduate study in genetics at Cambridge and then to graduate study at University College London and the London School of Economics, where he developed the inclusive-fitness theory. He worked first as lecturer at Imperial College (from 1964), then as professor and curator in the Museum of Zoology at the University of Michigan (from 1977), and finally as Royal Society research professor in zoology at Oxford (from 1984). After the 1964 paper on inclusive fitness, his other early works addressed problems in the evolution of sex ratios and meiotic drive, insect sociality, group formation by unrelated individuals, senescence and dispersal. These and his later theoretical projects were all stimulated by his extensive knowledge of animals and plants, and by his gift for recognizing patterns that demand explanation.

Photo: Jeffrey Joy

Like many evolutionists in the late 1970s and 1980s, Hamilton became fascinated by the problem of sex: Why should it be so common, given the twofold reproductive advantage of asexual reproduction? He championed and further elaborated the hypothesis that species with long generation times may need regular genetic recombination to keep their defenses (and their health) one step ahead of fast-evolving pathogens and parasites. With Marlene Zuk (then his graduate student), he advanced and tested the hypothesis that showy male plumage in birds may often signal resistance to parasites, and that females may evaluate potential mates on the basis of this evidence of health. Like several of Hamilton's earlier contributions, this gave rise to an entire field of research that continues to generate surprises.

By the mid-1970s, Hamilton was recognized as a major contributor to the renaissance in evolutionary theory that was then in full swing. For example, his work was celebrated (along with work by George Williams, Robert Trivers, John Maynard Smith and others) in Edward O. Wilson's *Sociobiology* (1975) and Richard Dawkins' *The Selfish Gene* (1976). By the early 1980s, he had received the first of what would become a long string of high honors and accolades, including election to the Royal Society, the Darwin Medal, the Kyoto Prize and the Crafoord Prize (awarded by the Swedish Academy for biological research outside the bounds of physiology or medicine).

Hamilton always thought of himself as a naturalist. In an essay published in a Japanese entomological journal in 1992, he says of his audience and himself, "We are turners over of junk in waste places, pullers of loose bark from rotting logs." And indeed, those who walked in the woods with Bill Hamilton usually found themselves flipping stones and prying under bark, to see who was home and what they were up to, in the world of dark cavities that has spawned more than its fair share of insect innovations (as Hamilton argued in a paper of 1978). On such outings, the talk would move in sudden but oddly seamless leaps, first to the contemplation of general theories; then to a recitation of the particular names and habits of startled arthropods that suddenly found themselves brightly lit and closely inspected by admiring humans; and then, once the stone or log was returned to its former position, back to theory. These conjunctions were not accidental. Hamilton's theories are now applied to a wide range of biological phenomena, from human social behavior to molecular cell biology and genetics, but they began as attempts to make sense of what he saw going on, first-hand, among wasps, mites and other creatures.

Hamilton's insights into host–parasite co-evolution led to deep concern about the potential public health risks of xenotransplantation, and thereby to an interest in the hypothesis that HIV-1 may have arisen from accidental contamination of early oral polio vaccines by SIV from chimpanzees used in vaccine development. He was troubled by the biomedical establishment's dismissal of the oral polio vaccine hypothesis, which seemed plausible to him and of considerable importance, given his more general belief that xenotransplants could pose serious long-term dangers. In January of this year, Hamilton and two young associates set out to test the prediction that chimpanzees from the population used in early polio vaccine testing might harbor strains of SIV closely related to the inferred ancestor of HIV-1. With help from local guides near Kisangani in the Congo, they collected feces from adults in several troops of *Pan troglodytes* (chimpanzees) and *Pan paniscus* (bonobos). From these samples, they hoped later to recover viral RNA for sequence analysis. During these travels, Hamilton contracted malaria and was rushed back to London. He subsequently developed severe complications, fell into a coma, and died on 7 March. The exact cause of death is still under investigation.

Bill Hamilton leaves three daughters and many other heartbroken family members and friends. He will be deeply missed by all who knew him, for his intellectual courage, his inventiveness and his personal warmth. The 'gene's-eye view' of adaptation that he did so much to develop will continue for a long time to inspire productive hypotheses about the forces and events that shape genomes and the rich diversity of cellular and organismal behaviors that they animate.

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