W.D. Hamilton, 1936–2000

selection') transformed the study of social behavior by demonstrating and what they were up to, in the world of dark cavities that has how altruistic and selfish tendencies are expected to be modulated spawned more than its fair share of insect innovations (as Hamilby genetic relatedness. This theory, along with other contributions ton argued in a paper of 1978). On such outings, the talk would by Hamilton, also broadened the concept of social behavior to move in sudden but oddly seamless leaps, first to the conteminclude interactions among genes and genomes. His ideas directly plation of general theories; then to a recitation of the particular inform much current thought about 'genetic conflicts' and their pos- names and habits of startled arthropods that suddenly found themsible involvement in aspects of development and disease.

A passion for insects led to undergraduate study in genetics at Camback to theory. These conjunctions were not accidental. Hamilbridge and then to graduate study at University College London ton's theories are now applied to a wide range of biological phe-

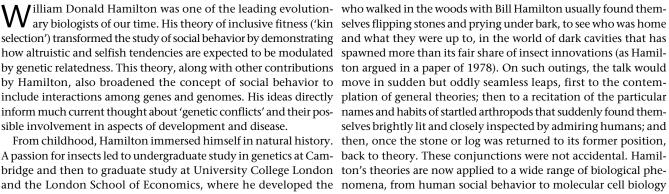
inclusive-fitness theory. He worked first as lecturer at Imperial College (from 1964), then as professor and curator in the Museum of Zoology at the University of Michigan (from 1977), and finally as Royal Society research professor in zoology at Oxford (from 1984). After the 1964 paper on inclusive 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.

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 cham- to test the prediction that chimpanzees from the population used pioned and further elaborated the hypothesis that species with long in early polio vaccine testing might harbor strains of SIV closely generation times may need regular genetic recombination to keep related to the inferred ancestor of HIV-1. With help from local their defenses (and their health) one step ahead of fast-evolving guides near Kisangani in the Congo, they collected feces from pathogens and parasites. With Marlene Zuk (then his graduate stuadults in several troops of *Pan troglodytes* (chimpanzees) and *Pan* dent), he advanced and tested the hypothesis that showy male paniscus (bonobos). From these samples, they hoped later to plumage in birds may often signal resistance to parasites, and that recover viral RNA for sequence analysis. During these travels, females may evaluate potential mates on the basis of this evidence Hamilton contracted malaria and was rushed back to London. of health. Like several of Hamilton's earlier contributions, this gave He subsequently developed severe complications, fell into a coma, rise to an entire field of research that continues to generate surprises. and died on 7 March. The exact cause of death is still under

By the mid-1970s, Hamilton was recognized as a major contribinvestigation. utor to the renaissance in evolutionary theory that was then in full swing. For example, his work was celebrated (along with work by ken family members and friends. He will be deeply missed by all George Williams, Robert Trivers, John Maynard Smith and others) who knew him, for his intellectual courage, his inventiveness and in Edward O. Wilson's Sociobiology (1975) and Richard Dawkins' The his personal warmth. The 'gene's-eye view' of adaptation that he Selfish Gene (1976). By the early 1980s, he had received the first of did so much to develop will continue for a long time to inspire what would become a long string of high honors and accolades, productive hypotheses about the forces and events that shape including election to the Royal Society, the Darwin Medal, the Kyoto genomes and the rich diversity of cellular and organismal behav-Prize and the Crafoord Prize (awarded by the Swedish Academy for iors that they animate. 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



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 ton and two young associates set out

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, Hamil-

Bill Hamilton leaves three daughters and many other heartbro-

