

## William D. Hamilton Remembered.

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*A revolutionary thinker, Hamilton gave biologists the tools for understanding sociality in all organisms.*

William D. Hamilton died of malaria in England on March 7 at the age of 63. Although he had pondered the evolutionary impact of diseases for much of his professional life, he died because he had traveled to damp equatorial Africa unfortified by malaria-fighting drugs. Some may see this as indicating a paucity of common sense. Bill's forte was, indeed, not common sense but an astonishing fund of uncommon sense. Perhaps if he'd had much more common sense, he might not have provided the rest of us with the insights that have caused him to be described as the greatest evolutionary biologist of his generation.

Bill's extensive field meanderings, especially in the New World and Old World tropics, and his breadth of curiosity about natural history appear to have been--for him as for Darwin--a source of ideas richer than most of us can imagine. He ranged similarly across the literature of biology, seeing it, too, as a flood of significant anecdotes. Except for his own amazing internal logic and the "maths" with which he backed it up, he relied on others to test his theories and was delighted when any such effort succeeded.

Bill's originality of mind often turned the barely articulated ideas of distinguished predecessors--ideas overlooked or neglected by all the rest of us--into magnificent theoretical edifices affecting our view of all life. He expanded Charles Darwin's explanation of the existence of sterile castes in insects and combined it with Ronald Fisher's hint about quantifying altruism in caterpillars toward siblings, creating a comprehensive theory accounting for underlying patterns of sociality in all organisms. Similarly, Hamilton converted a maddeningly cryptic question about territory and sex ratios (the proportions of males and females in populations), posed by Fisher in 1930, into a broadly enlightening explanation of why the females of thousands of insect species have so many daughters and so few sons. Such females mate with a brother (who provides no parental care) and determine the sex of each egg as it is laid (a determination made possible because males derive from unfertilized eggs). Bill argued that for such females to make more or harder males than are sufficient merely to fertilize the eggs would be an unnecessary cost. His logic on these and other seemingly parochial topics affected the way biologists approached far broader issues, such as our views of the levels at which natural selection has operated--from genes to individuals and species, as well as from families to tribes and nations--and thus the basic reasons for organisms acting as they do.

Bill also contributed extensively to the development of many other theories, such as George Williams's now widely accepted pleiotropic theory of senescence (the idea that because selection is less powerful later in life, incidental deleterious effects late in life can persist if they are

accidental consequences of reproductively beneficial effects of the same genes early in life); the so-called Red Queen hypothesis, including the idea that the costly process of sexual (as opposed to asexual) re-production pays for itself by enabling organisms to outrace rapidly multiplying pathogens and parasites; and Robert Trivers's theory of reciprocal altruism among even unrelated individuals. One of my favorite Hamilton essays is "Geometry for the Selfish Herd," in which he explains how even the seemingly random stollings and mergings of individuals, as in a foraging bird flock or mammal herd, are almost certainly strategies that involve continual trade-offs between such alternatives as obtaining the best food and placing other individuals between the strategist and possible predators.

I once heard Bill assert that he avoided applying his theories to humans because he thought such extrapolation was too difficult and too subject to misinterpretation (a reluctance he later overcame). Yet only his theory of nepotism accounts for the universal human ability to respond to differing degrees of relatedness among relatives and for the varied patterning of human kinship systems in hundreds of societies in different situations worldwide. Extensive differential nepotism (meaning assistance to a wide variety of relatives, meted out so as to take into account the degree of genetic relatedness to oneself) is the crowning glory of Hamilton's theory, yet it is still known only in humans.

It is curious that Bill, who received an unprecedented array of international honors, was never made a foreign associate of the U.S. National Academy of Sciences and that one still hears even some prominent biologists dismissing his work. I see this startling attitude which all evolutionary biologists are now and then required to endure--as a reflection of the difficulty that even thoughtful and educated people often have in fairly evaluating findings in the field of evolutionary history that purport to account for day-to-day human behavior. Bill Hamilton, as much as or more than any other twentieth-century biologist, provided the basic tools for understanding and modifying such resistance. It is now up to the rest of us to use and develop all such glimpses into the human condition to generate a self-understanding adequate to the task of significantly reducing human misery and strife across the globe.

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