1998 Sewall Wright Award:

William Donald Hamilton

The Sewall Wright Award was established in 1991 to honor active investigators who have contributed in especially significant ways to the conceptual unification of the biological sciences. This year's recipient is William D. Hamilton of Oxford University. Beginning in the 1960s with his papers on the theory of inclusive fitness and the evolution of eusociality, Bill Hamilton's publications have permanently changed the landscape of ideas and interpretation surrounding a wide range of biological phenomena. His papers have clarified murky problems, generated new research agendas, and unified our understanding of many central concepts, on a truly revolutionary scale.

Hamilton developed the theory of inclusive fitness in the early 1960s, as his Ph.D. dissertation, and applied it to various problems, including the evolution of insect sociality. He made important contributions to the evolutionary theory of senescence and more generally to the analysis of life-history evolution. He developed the theory of sex-ratio evolution under local mate competition and explored other phenomena associated with highly structured populations and incestuous breeding systems, as are found in many insects living in figs or under bark. In addition to inventing the concept of local mate competition, the landmark 1967 paper on extraordinary sex ratios also presents one of the first explicit treatments of intragenomic conflict and an early application of the theory of games to an evolutionary problem.

In the 1970s, Hamilton's concept of the selfish herd provided a framework for understanding why unrelated animals would choose to live in groups, and a simple model of dispersal showed why individuals might often choose to move away from their close relatives as a fundamental consequence of population structure and ecological uncertainty. The chapter on evolution under bark (1978) evokes an explicitly Wrightian view of strongly subdivided populations as cradles of major innovation. In the 1980s, he carried out a series of influential theoretical and empirical studies into how the coevolution of hosts and parasites might shape aspects of sexual reproduction, and how cooperation could evolve among unrelated organisms. He continues to produce innovative analyses of subjects that have recently included, among others, the basis for bright colors in autumn leaves and biological aspects of the genesis of clouds.

Bill Hamilton's contributions are remarkable not only as scientific findings that have opened up new areas of inquiry but also as pioneering applications of the "gene's-eye point of view" that has proved so powerful in many other situations. In this respect his work has indirectly but profoundly influenced research on a great variety of problems in evolutionary genetics that seem to have little or nothing in common with his own immediate interests. As anyone lucky enough to have spent time with him in the field knows, his theoretical breakthroughs are grounded in keen observations of nature and in deep and broad knowledge of biological diversity. This connection between gritty fact and abstract generality is clearly demonstrated in all of his papers. In this respect, too, Hamilton's influence has gone far beyond the boundaries of his own research program, as he has shown us what can happen scientifically when a well-prepared mind lets nature do the talking.

Hamilton has also done more than almost any other living biologist to make our literature literary. Those who study his papers are always struck by his gifts for unusual but economical turns of phrase, for apt metaphors, and for wry humor. A famous example from the 1979 chapter on fighting males in fig wasps will have to stand for hundreds of others: "A male's fighting movements could be summarized thus: touch, freeze, approach slowly, strike, and recoil. Their fighting looks at once vicious and cautious—cowardly would be the word except that, on reflection, this seems unfair in a situation that can only be likened in human terms to a darkened room full of jostling people among whom, or else lurking in cupboards and recesses which open on all sides, are a dozen or so maniacal homicides armed with knives." Such art appears so regularly in Hamilton's writing as to suggest that it must be integral to his science, or at least to the vision of the world that gives rise to the science. He has also written a novel (unpublished), and a wonderful set of essays introducing his papers through 1980, which are collected in *Narrow Roads of Gene Land* (Hamilton 1996). The title of this volume alludes to a work by the seventeenth-century Japanese poet Matsuo Basho, who walked the Narrow Roads of Oku and recorded his penetrating observations in a mixture of haiku and extended prose commentaries. To learn how Bill Hamilton came to walk the roads of Gene Land, and why he still thinks that "believing in the explanatory power of evolution by natural selection is like migraine," readers may wish to consult this volume, and

the sequel, to be published soon, which will collect and annotate his papers from the 1980s and 1990s.

On hearing that he was this year's recipient of the Sewall Wright Award, Hamilton sent an e-mail message to ASN President Rob Colwell, which included the following comments about Wright.

> I left Cambridge as a graduate in 1960 with a rather mediocre opinion of SW's significance because, I am sure, I was trained in genetics in what had been R. A. Fisher's department, but I steadily increased my respect until finally I came to esteem him as the deepest thinker of all three of the great theoretical founders of neo-Darwinism. Due to Fisher's seemingly almost deliberate misunderstanding and needless criticism, he remained under-appreciated, and was definitely for a long time maligned for views he didn't hold. Happily by the time of his old age all this had changed. I as well as everyone else well understood how much he had covered and how he had seen things far in advance of his time.
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> When I was at the University of Michigan I had the great privilege to host Sewall Wright for a party at my home and came to appreciate that not only was he farthest seeing but undoubtedly he was the nicest of the three. One of my small daughters asked him at the party about the guinea-pig-board-duster story and he told her, regretfully it seemed to me, that there was no truth in it. Afterwards she (Helen) said she was disappointed: she wished it had been true. I said that, well, maybe he was such an absent-minded professor that it was true and he still didn't know it…[laughter].
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> Anyway, he was a great evolutionist and it is an immense pleasure for me to be honoured by an award bearing his name! Thanks to you all.

Literature Cited

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