Why did sex evolve?

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Narrow Roads of Gene Land Volume 2

by W.D. Hamilton

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William Donald Hamilton has been referred to as one of the greatest evolutionary theorists since Darwin. His first collection of papers, *Narrow Roads of Gene Land Volume 1*, was published in 1996; the title was inspired by *The Narrow Road of Oku*, a book written by the 17th Century Japanese poet Matsuo Basho describing a 2450 kilometer journey he undertook on foot. This first book included all his papers prior to 1981 addressing the evolution of altruism through kin selection. With this second volume, Hamilton has introduced, restyled and republished his most influential essays from 1981 to 1991, during which time his attention turned to that most important and elusive topic in evolutionary biology: the evolution of sex.

The main theme running through Hamilton's book is why sexual reproduction is so abundant, despite being so inherently inefficient. As suspected by John Maynard Smith in 1978, the advantage must presumably come from recombination, but this has been difficult to ascertain. Each of the 18 chapters is devoted to a single theoretical paper, all with a lengthy,

informative autobiographical introduction written by Hamilton. These document not only new discoveries and opinions that have emerged since the original publication, but also his thoughts on the wider background of the subject, discussed in an accessible, non-technical style.

Hamilton's major theory, first introduced in Chapter 2 with the paper 'Sex versus non-sex versus parasite' and repeatedly stressed and reviewed in later chapters, is that sexual reproduction is an adaptation to resist parasites that evolve more rapidly than their hosts. He maintains that his theory overcomes the pitfalls of previous models such as the necessity of high fecundity, intrinsic oscillations of the environment and the supposedly low frequency of parthenogenesis.

Why do the males of many species exhibit bright colours, even though this may be unfavourable for natural selection? Two hypotheses have previously been published on this principle: Fisher's 'run-away process' in 1930 and Zahavi's 'handicap principle' in 1975. Hamilton, along with co-author Marlene Zuk, added a third in 1982, the 'good gene hypothesis'. This is the subject of Chapter 6 entitled 'Heritable true fitness and bright birds: a role for parasites?' and extends this relationship between sex and disease. Based on surveys of blood parasites among wild passerine birds, Hamilton and Zuk demonstrated a negative association between incidences of blood infections and the brightness of bird plumage, particularly in males. They concluded that animals choose mates for genetic disease resistance by scrutiny of characteristics whose full expression is dependent on health and vigour.

'Kinship, recognition, disease and intelligence: constraints of social evolution' (Chapter 10) was, for me, particularly interesting since in his introduction, Hamilton describes his views on the complexity of Japanese culture and its influence on Kinji Imanishi, a leading primatologist in Japan and an anti-Darwinian philosopher. The paper was originally presented at a symposium held in 1986 in Japan and deals with altruism and sex, but its scope is intriguing. Here,

Hamilton discusses the limits of sociality. As he has already discussed at length in Volume 1, sociality is promoted if the relatedness within groups is high, a fact that may promote evolution of sterile soldiers in aphids. But eusociality in aphids has evolved only rarely and virtually no aphids have a caste system. Why has their social evolution not progressed any further? According to Hamilton, two factors, cheating and disease, may be important. As he states in this chapter, 'Soldiers cannot fight disease, but sex and genetical diversity possibly can.' Hamilton also extends the discussion to human societies and reveals his view of the 'final world organism' as a 'very self-assured, competent and, doubtless in this case, female medical student.'

Tragically, Hamilton died before the book finally went to press. On a field trip to the Democratic Republic of Congo in March 2000, he succumbed to a particularly virulent form of malaria. In his foreword to the book, Richard Dawkins not only provides an informative introduction to Hamilton's scientific contributions, but also describes his life-long sympathy for the underdog, which may explain the reason behind this fateful trip that was undertaken to test an unfashionable theory of the origin of AIDS. Dawkins also warmly recollects Hamilton's absent-mindedness and his genuine love of nature, especially insects.

In the past, measurements of genetic diversity and relatedness have been notoriously difficult. But now, the development of DNA techniques—in their widest sense—have opened up this possibility and stimulated cooperation between ecologists, geneticists and molecular biologists. All three groups of scientists would benefit greatly from reading the broad perspective offered by Hamilton's book and from the introduction to the philosophy held by one of the great evolutionary scientists of our time.

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