

Obituary

John Maynard Smith (1920–2004)

Brian Charlesworth

John Maynard Smith, who died of lung cancer last month at the age of 84, was one of the most influential evolutionary biologists of his generation. He grew up in rural Somerset and was educated at Eton College. There he was stimulated by the writings of J.B.S. Haldane, a life-long influence. As he explained in the introduction to his collection of Haldane's writings *On Being the Right Size*, "I found that he was the person my schoolmasters most hated. Feeling that anyone they hated could not be all bad, I went to seek his books in the school library".

After Eton, he went on to study engineering at Cambridge, and worked on aircraft design during the war. During this period, he was an active member of the Communist Party, but later became a critic of Marxism while retaining mildly left-wing sympathies. In 1947, he enrolled at University College London, to study zoology at a time when the Department of Zoology was populated by towering figures like Haldane and Medawar. He went on to do post-graduate work with Haldane, but never took a PhD, as he was offered a lectureship before completing his studies.

His early work was mostly on the experimental genetics and biology of *Drosophila subobscura*; during the late 1950s and early 1960s he conducted some pioneering experiments on ageing with this species. In particular, his use of genetic and experimental manipulations to show that reduced reproductive effort in female *Drosophila* causes greatly extended life-span anticipated much contemporary research on ageing.

In the 1960s, he turned increasingly to theoretical research, mainly on evolution and population genetics, especially after becoming the founding Dean of the School of Biological Sciences at the University of Sussex, where he remained for the rest of his life. He is best-known for this research, which spans a very broad range.

Perhaps his most significant single contribution was the introduction (with George Price) of game theoretical methods for the analysis of evolutionary problems. These are based on the concept of the 'evolutionarily stable strategy' (ESS): this states that a necessary condition for a population to be at a stable equilibrium under natural selection is that a rare mutant phenotype is always at a selective disadvantage. This permits an elegantly simple analysis of the effects of selection when relative fitnesses are dependent on the make-up of the population. While this method was foreshadowed by work of Fisher and Hamilton on the evolution of sex ratios, John developed it into a general framework for thinking about a wide range of evolutionary problems, and it is now a standard tool of the theoreticians.

His work on the evolution of sex and genetic systems was also very influential, aiding the transformation of this field from one of loose, group-selectionist thinking to an area in which detailed population-genetics based models could be tested by empirical studies.

He was also an early contributor to the development of theoretical models of molecular variation and evolution. His 1970 paper on the concept of a 'protein space' is still much cited, and his 1974 paper with John Haigh on the hitch-hiking effect of a selectively favourable mutation has had an enormous influence on contemporary studies of DNA sequence variation in natural and human populations.

After retirement in 1985 (and a brush with colon cancer), John



John Maynard Smith (right) talking to Sewall Wright when Wright visited Sussex University in 1980 after receiving the Darwin Medal from the Royal Society.

started a very fruitful collaboration with Brian Spratt's group, on the analysis of molecular variation in pathogenic bacteria. This showed that there can be a good deal of exchange of genetic information among bacterial cells in nature. His work on bacterial population genetics continued to the end of his life, despite his suffering a long terminal illness, and John was responsible for a number of important innovations in the methods of data analysis in this field.

John was also noted for his numerous contributions to the discussion of general questions in evolutionary biology, and for providing an evolutionary perspective on other areas of biology, such as ecology and development. He was a persistent critic of group-selectionist thinking and of the theory of punctuated equilibrium. He published fourteen books and collections of papers on an astonishing diversity of subjects, as well as many lucid semi-popular articles on biology.

Numerous postgraduate students, postdoctoral researchers, sabbatical visitors and junior colleagues at Sussex were greatly influenced and encouraged by him. John was an entertaining conversationalist, with a fund of amusing stories about Haldane and other prominent figures. His friends and colleagues will remember him with deep affection.

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