OBITUARY

John Maynard Smith

(6 January 1920 – 19 April 2004)

The evolutionary biology community has been saddened and depleted this month by the loss of Prof. John Maynard Smith who made many important contributions to evolutionary theory, including the now ubiquitous concept of an evolutionarily stable strategy (ESS). In a half-century long working career, Maynard Smith – trained originally as an aeronautical engineer and then as an evolutionary geneticist – applied his mind to a wide variety of problems in evolutionary biology, ranging from ritualized animal combat to the mechanisms of speciation. In more recent years, despite his age, he was working actively on microbial evolution, the evolution of genetic redundancy in developmental systems, and the issue of how to accurately assess recombinational rates from DNA sequence data. He had recently finished writing, along with David Harper, a book on animal communication, and was working on a new edition of his 1995 book with Eörs Szathmáry, '*The Major Transitions in Evolution*'. He had been suffering from breathing problems for the past few months but was otherwise in good health, active and interacting with friends and colleagues; he passed away peacefully at home in his chair. Prof. Maynard Smith is survived by his wife Sheila, and his three children, Anthony, Carol and Julian.

Maynard Smith was born in London, lost his father, a surgeon, at the age of eight, and the family then moved to the western British countryside near Exmoor. In an interview published in *Natural History*, Maynard Smith recalled having become an avid bird watcher at that time. At Eton, he found the atmosphere 'really anti-intellectual', 'snobbish' and 'arrogant', although he enjoyed learning mathematics there. He also recalled that the teachers at Eton had a great degree of antipathy towards J. B. S. Haldane and said in the same interview, 'I remember thinking: anyone they hate so much can't be all bad – I must go and find out about him.' After Eton, Maynard Smith studied engineering at Trinity College, Cambridge, upsetting his family who expected him to join his grandfather's stockbroking business. During World War II, he worked for a company involved in stress testing aircraft components. Once the war was over, he went back to seek a second degree in biology, studying at University College, London, with Haldane, and then worked at University College from 1952 to 1965. Like his mentor, Maynard Smith was blunt and iconoclastic, irreverent about established hierarchies, and had extremely leftist political views. Also like his mentor, he was interested in a very wide range of topics and usually had novel insights or viewpoints to offer.

In 1965 Maynard Smith moved to the University of Sussex at Brighton as founding dean of the School of Biological Sciences, and continued there as an emeritus professor after his retirement in 1985. In addition to his numerous research publications, he wrote over a dozen influential books, including basic books intended for students – such as '*Models in Ecology*' (1974), and '*Evolutionary Genetics*' (1989, 1998) – as well as more narrowly focussed technical books like '*The Evolution of Sex*' (1978) and '*Evolution and the Theory of Games*' (1982). The contribution for which Maynard Smith was perhaps most well known even beyond the community of evolutionary researchers was his application of game theoretic models and approaches to issues in animal behaviour. In particular, he introduced the concept of an ESS, a strategy that, when practiced by a majority of a population, cannot be successfully displaced by another strategy. The concept of the ESS, together with the related concept of a coevolutionarily stable strategy, has gone on to become ubiquitous in evolutionary ecology. Of course, game theory is essentially an optimization model in which the benefits tend to be frequency-dependent i.e. how 'good' a phenotype is depends on the relative numbers of other phenotypes present in the population. Maynard Smith was one of the early practitioners of optimization modelling in biology, applying this approach to a study of mammalian gaits in 1956. He was also one of the most articulate and cogent defenders of optimization approaches in ecology and evolution, approaches that have remained somewhat controversial, appearing suspect especially to many evolutionary geneticists uncomfortable with purely phenotypic models of the evolutionary process.

Over his long and very active career, Maynard Smith consistently worked on problems, often controversial, that lay at the centre of important debates in evolution. Early in his professional life, he worked on sexual selection and possible mechanisms of sympatric speciation. Along with George C. Williams, Maynard Smith was the leading figure

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in the decisive rebuttal of the notion that group selection played a major role in the evolution of animal behaviour. Around the same time, he worked on the vexatious issue of the evolutionary maintenance of sexual reproduction in the face of the apparent overwhelming efficiency of asexual reproduction, an issue that occupied several of the brightest minds in evolution during the 1970s and early 1980s. Maynard Smith first clearly articulated the cost of sex in terms of the cost of investing in male function, although this too became controversial because G. C. Williams preferred to formulate the cost of sex in terms of genome dilution, based on the reduced relatedness of a sexual mother to her offspring compared to that of an asexual mother to her offspring. Maynard Smith was also drawn into the often acerbic debate over the issue of 'selfish genes' and sociobiology. Unlike fellow leftist Richard Lewontin, however, Maynard Smith was not vehemently opposed to the very notion of sociobiology as an attempt to understand human behaviour in evolutionary terms, although he may have disagreed with specific sociobiological explanations for this or that phenomenon. In more recent years, Maynard Smith had worked with Eörs Szathmáry on the commonality between major events in the evolutionary history of life-forms, attempting an examination of the evolution of complexity from an informational viewpoint. He also contributed to thinking about developmental constraints on adaptive evolution, and the broader issue of integrating knowledge about development with our understanding of evolution as a dynamic process and also with the historical record of evolutionary transitions. Maynard Smith also worked on the population and evolutionary genetics of bacteria during the past decade, work that has contributed to our understanding of the evolutionary dynamics of pathogenic microbes and the evolution of antibiotic resistance.

Maynard Smith's many contributions to evolutionary biology were abundantly recognized: he was awarded the Crafoord Prize (1999), along with Ernst Mayr and G. C. Williams, and the Kyoto Prize (2001), among other honours. The ultimate appreciation of a teacher, however, comes from how his or her students remember him. By this yardstick, too, Maynard Smith was greatly appreciated, earning the lasting affection and regard of those who worked with him, whether students or colleagues. He was down to earth, had no pretensions, and was always approachable and willing to respond to questions and help other scientists, although he could be sharply critical and blunt about scientific arguments he felt were not cogent. As David Harper puts it, Maynard Smith was 'famous not only for the quality of the science he produced, but also for the way in which he produced it.' He will be both remembered and missed by evolutionary geneticists, not only now but well into the future too.