J Maynard Smith: From Engineering to Evolution

John Maynard Smith (1920-2004) was a very versatile evolutionary biologist who applied his mind to a number of vexatious conceptual questions in evolution, including whether the unit of selection is typically the individual or the group, the evolutionary maintenance of sexual reproduction, the evolution of social behaviours in animals, and the likelihood of sympatric speciation being driven by host or habitat specialization. In particular, Maynard Smith, along with the maverick George Price, pioneered the application of Game Theory to evolutionary questions and gave us the now ubiquitous concept of an evolutionarily stable strategy (ESS). 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. Along with David Harper, he had recently finished writing a book on animal communication, and was working on a new edition of his 1995 book with Eörs Szathmáry, *The Major Transitions in Evolution*, an extensive treatise on the important milestones in the evolution of different life forms and social systems.

Maynard Smith was born in London, the son of a surgeon. Unfortunately, his father died when he was just 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, after an aunt gifted him a book on bird-watching. He went on to school at Eton and later recalled finding the atmosphere at this famous school "really anti-intellectual", "snobbish" and "arrogant", although he enjoyed learning mathematics there. Indeed, a disdainful dislike of pomp and snobbery was a characteristic of Maynard Smith throughout his life. 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 joined Trinity College, Cambridge, to study aeronautical engineering, a move that upset his family who expected him to join his grandfather's stock-broking 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 studying at University College, London, seeking a second degree in biology. At this point, Maynard Smith was a student of Haldane, who had a tremendous influence upon him. During this phase and early in his career, Maynard Smith worked on many questions in *Drosophila* genetics. Like his mentor, Maynard Smith was not only very sharp intellectually, but was also

blunt and iconoclastic, irreverent about established hierarchies, and had liberal 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.

After finishing his studies, Maynard Smith worked as a lecturer at University College from 1952 to 1965, before moving to the University of Sussex at Brighton as founding dean of the School of Biological Sciences. He remained at Brighton till his retirement in 1985 and continued on as an emeritus professor. 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, which 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 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 (these prizes have a status similar to the Nobel for evolutionary biologists who are usually ineligible for a prize given for 'physiology or medicine'). The ultimate appreciation of a teacher, however, comes from how his or her students remember their mentor. 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 a colleague and co-author, David Harper put it in the obituary that he wrote; Maynard Smith was "famous not only for the quality of the science he produced, but also for the way in which he produced it."

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