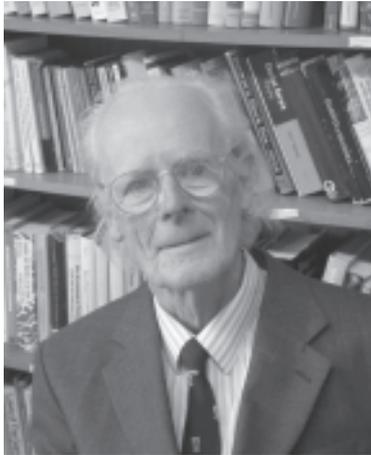


## Maynard Smith, John (1920–2004): Game is not over



Professor John Maynard Smith, one of the most renowned and influential evolutionary biologists of the modern time, passed away of lung cancer on April 19, 2004 at the age of 84. Maynard Smith, the British biologist who was commonly referred to as JMS by his colleagues, was not only a prolific researcher, but also a versatile thinker, a devoted teacher and the leading authority in the study of evolution of sexual selection and evolutionary game theory. His legendary career and influential works have always inspired generations of researchers.

Maynard Smith was born in London on January 6 1920, only after the death of his surgeon father. He graduated in 1941 from Cambridge University with a degree in engineering. From 1942 to 1947, he was involved in designing military aircraft before deciding they were “noisy and old-fashioned” and moving to University College of London to study fruit fly genetics under the famous J. B. S. Haldane. He obtained his BSc in zoology in 1951 and remained at University College of London as a lecturer in zoology. In 1965, he became the founding dean of School of Biological Sciences at University of Sussex and served as professor there until 1985, when he became emeritus professor. For nearly two decades after his retirement, Maynard Smith never stopped working until the day of his death.

Maynard Smith emerged as one of the leading theorists of the postwar era with his *Theory of Evolution* (1958), which inspired many leading researchers to become biologists. His 1966 paper on disruptive selection set the stage for the modern studies on sympatric speciation. He is probably

most widely known for applying game theory to evolutionary biology. Much influenced by W. D. Hamilton and Robert MacArthur, and using concepts originally developed by John von Neumann and Oskar Morgenstern, Maynard Smith introduced, with George Price, the idea of game theory into evolutionary research in the 1970s. By introducing mathematical models from game theory into the study of behavior, he showed that the payoff to an individual’s behavior often depends on what other individuals do. He introduced the idea of an ESS: a strategy that, once prevalent in the population, cannot be invaded by alternative strategies. The idea of ESS was described in his *Mathematical Ideas in Biology* (1968) and *Evolution and the Theory of Games* (1982). This finding has completely revolutionized the way evolutionists think about behavioral evolution. The evolutionary game theory is now one of the most commonly used tools in evolutionary research and its introduction was a clear turning point in evolutionary thinking.

Maynard Smith is also known for his work on one of the most challenging questions in evolutionary biology: why has sexual reproduction evolved? His book *The Evolution of Sex* (1978) pointed out “the twofold cost of sex,” which suggests that if an asexual individual were introduced into a sexually reproducing population, asexual individuals would soon take over. In a population of sexual individuals, it takes two individuals to produce one. However, a female capable of reproducing parthenogenetically can produce as many individuals as any pair of sexually reproducing individuals. Therefore, the asexual subpopulation will grow twice as fast as its sexual counterpart; thus the twofold cost of sex. Advantage from sexual reproduction must overcome this cost to be able to spread in a population.

Even after his retirement, Maynard Smith has continued to write on evolutionary theory in such influential works as *Evolutionary Genetics* (1989, 1998) and *The Major Transitions of Evolution* (1995) with E. Szathmary. His final book with D. Harper, *Animal Signals*, was published in 2003. In this book, Maynard Smith attempted to clarify the complex and often confusing terminology that had characterized the subject, and then challenged the widely held assumption that there is only one correct explanation for why signalers do not