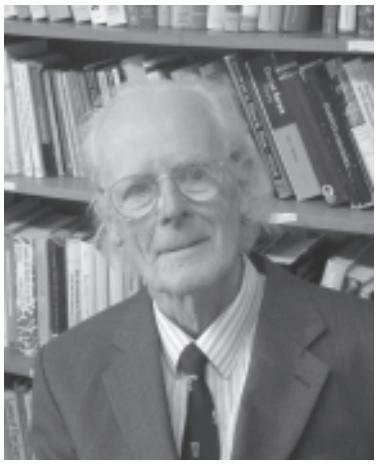
Maynard Smith, John (1920–2004): Game is not over



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 Morgentern, 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

"cheat" or what makes them "honest."

His most recent primary research was concentrated on the population structure and evolution of pathogenic bacteria. He revolutionized the field with an early publication, How Clonal Are Bacteria? (1993) and contributed to the understanding of a number of pathogens, including the bacterium causing tuberculosis.

For his achievements and advancement in science, Maynard Smith was awarded with many honors. These include the 1999 Crafoord Prize (awarded by the Swedish Academy of Sciences to scientists in fields not eligible for Nobel prizes and he shared this prize with Ernst Mayr and G. C. Williams) and the 2001 Kyoto Prize, Japan's highest private award for lifetime achievement.

While scientific communities all over the world are mourning the loss of one of the greatest minds in science, the whole new approaches he started are playing a major role in understanding how evolution works. John Maynard Smith's name is forever tied with familiar terms that he coined: kin selection, haystack model, evolutionary game theory, evolutionarily stable strategy (ESS), hawk/dove game, twofold cost of sex or the cost of meiosis and so on. He will always be known as the founder of evolutionary game theory and the defender of neo-Darwinism against group selectionists. Many "games" he started are being and will be played by generations of evolutionists. A farewell ceremony was held in Lewes on May 4. A celebration of his life and work will take place at the University of Sussex on June 26, 2004.

There is no better time to acquaint and re-acquaint Maynard Smith's work to Mongolian biologists and recommend learning more about it. For this purpose, I have included here a list of some of Maynard Smith's highly influential publications.

Most influential articles by John Maynard Smith:

Maynard Smith, J. 1964. Group selection and kin selection. *Nature* **200**:1145-1147.

Maynard Smith, J. 1966. Sympatric speciation. *Am Nat* **100**:637-650.

Maynard Smith, J. 1968. Evolution in sexual and asexual populations. *Am Nat* **102**:469-473.

Maynard Smith, J., and G. R. Price. 1973. Logic of animal conflict. *Nature* **246**:15-18.

Maynard Smith, J., and M. Slatkin. 1973. Stability of predator-prey systems. *Ecology* **54**:384-391.

Maynard Smith, J. 1974. Theory of games and evolution of animal conflicts. *J Theor Biol* **47**:209-221.

Maynard Smith, J., and J. Haigh. 1974. Hitch-hiking effect of a favorable gene. *Gen Res* **23**:23-35.

Maynard Smith, J. 1976. Short-term advantage for sex and recombination through sib-competition. *J Theor Biol* **63**:245-258.

Maynard Smith, J. 1976. Comment on Red Queen. *Am Nat* **110**:325-330.

Maynard Smith, J. 1976. Commentary - group selection. *Quart Rev Biol* **51**:277-283.

Maynard Smith, J. 1976. Sexual selection and handicap principle. *J Theor Biology* **57**:239-242.

Maynard Smith, J., and G. A. Parker. 1976. Logic of asymmetric contests. *Anim Behav* **24**:159-175.

Maynard Smith, J. 1976. Evolution and theory of games. *Am Sci* **64**:41-45.

Maynard Smith, J. 1977. Parental investment - prospective analysis. *Anim Behav* **25**:1-9.

Maynard Smith, J. 1978. Optimization theory in evolution. *Annu Rev Ecol Syst* **9**:31-56.

Maynard Smith, J. 1979. Game theory and the evolution of behavior. *Proc Royal Soc Lond B* **205**:475-488.

Maynard Smith, J. 1980. Selection for recombination in a polygenic model. *Gen Res* **35**:269-277.

Maynard Smith, J., and R. Hoekstra. 1980. Polymorphism in a varied environment - How robust are the models. *Gen Res* **35**:45-57.

Maynard Smith, J. 1981. Will a sexual population evolve to an ESS. *Am Nat* **117**:1015-1018.

Maynard Smith, J. 1982. Do animals convey information about their intentions. *J Theor Biol* **97**:1-5.

Maynard Smith, J. 1983. The genetics of stasis and punctuation. *Annu Rev Gen* **17**:11-25.

Maynard Smith, J. 1983. Models of evolution. *Proc Royal Soc Lond B* **219**:315-325.

Maynard Smith, J. 1984. Game theory and the evolution of behavior. *Behav Brain Sci* **7**:95-101.

Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert. 1985. Developmental constraints and evolution. *Quart Rev Biol* **60**:265-287.

Maynard Smith, J. 1985. Sexual selection,

handicaps and true fitness. *J Theor Biol* **115**:1-8.
Maynard Smith, J., and R. L. W. Brown. 1986. Competition and body size. *Theor Pop Biol* **30**:166-179.
Maynard Smith, J., and D. G. C. Harper. 1988. The evolution of aggression - Can selection generate variability. *Proc Royal Soc Lond B* **319**:557-570.
Maynard Smith, J. 1988. Selection for recombination in a polygenic model - the mechanism. *Gen Res* **51**:59-63.
Maynard Smith, J. 1989. Evolution - generating novelty by symbiosis. *Nature* **341**:284-285.
Maynard Smith, J. 1990. Models of a dual inheritance system. *J Theor Biol* **143**:41-53.
Maynard Smith, J. 1991. Honest signaling - the Philip Sidney game. *Anim Behav* **42**:1034-1035.
Maynard Smith, J. 1991. The population genetics of bacteria. *Proc Royal Soc Lond B* **245**:37-41.
Maynard Smith, J. 1991. Theories of sexual selection. *TREE* **6**:146-151.
Maynard Smith, J., C. G. Dowson, and B. G. Spratt. 1991. Localized sex in bacteria. *Nature* **349**:29-31.
Maynard Smith, J. 1992. Analyzing the mosaic structure of genes. *J Mol Evol* **34**:126-129.
Maynard Smith, J., and E. Szathmary. 1993. The origin of chromosomes. 1. Selection for linkage. *J Theor Biol* **164**:437-446.
Maynard Smith, J., N. H. Smith, M. Orourke, and B. G. Spratt. 1993. How clonal are bacteria. *Proc Nat Acad Sci* **90**:4384-4388.
Maynard Smith, J. 1994. Must reliable signals always be costly. *Anim Behav* **47**:1115-1120.
Maynard Smith, J., and D. G. C. Harper. 1995. Animal signals: models and terminology. *J Theor Biol* **177**:305-311.
Maynard Smith, J., and N. H. Smith. 1998. Detecting recombination from gene trees. *Mol Biol Evol* **15**:590-599.
Maynard Smith, J. 1999. The detection and measurement of recombination from sequence data. *Genetics* **153**:1021-1027.
Maynard Smith, J., E. J. Feil, and N. H. Smith. 2000. Population structure and evolutionary dynamics of pathogenic bacteria. *Bioessays* **22**:1115-1122.
Maynard Smith, J. 2000. The concept of information in biology. *Philosophy of Science* **67**:177-194.
Maynard Smith, J., and N. H. Smith. 2002. Recombination in animal mitochondrial DNA. *Mol Biol Evol* **19**:2330-2332.
Maynard Smith, J. 2003. Games and theories. *New Scientist* **178**:48-51.

Books by John Maynard Smith:

Maynard Smith, J. (1958, 1966, 1975, 1993). *The Theory of Evolution*. Penguin Books, London
Maynard Smith, J. (1968). *Mathematical Ideas in Biology*. Cambridge University Press, Cambridge.
Maynard Smith, J. (1972). *Models in Ecology*. Cambridge University Press, Cambridge.
Maynard Smith, J. (1978). *The Evolution of Sex*. Cambridge University Press, Cambridge.
Maynard Smith, J. (1982). *Evolution and Theory of Games*. Cambridge University Press, Cambridge.
Maynard Smith, J. (1986). *The Problems of Biology*. Oxford University Press, Oxford.
Maynard Smith, J. (1988). *Did Darwin Get It Right? Essays on Games, Sex and Evolution*. Chapman & Hall, London.
Maynard Smith, J. (1989, 1998). *Evolutionary Genetics*. Oxford University Press, Oxford.
Maynard Smith, J. and E. Szathmary. (1995). *The Major Transitions In Evolution*. Oxford University Press, New York.
Maynard Smith, J. and E. Szathmary. (1999). *The Origins of Life: From the Birth of Life to the Origin of Language*. Oxford University Press, Oxford.
Maynard Smith, J. and D. Harper (2003). *Animal Signals*. Oxford University Press, Oxford.

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