John Maynard Smith

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Abstract

John Maynard Smith was one of the most original thinkers in evolutionary biology of the post neo-Darwinian synthesis age. He was able to define new problems with clarity and by doing so open up new research directions. He did this in a number of areas including game theory and evolution, the evolution of sex, animal behavior, evolutionary transitions and molecular evolution. Although he is best known for his research and his ideas, he was a great expositor and wrote many books, including introductory texts in the areas of evolution and genetics, ecology and mathematical modeling, as well as advanced expositions of research problems.

John Maynard Smith was one of the most original thinkers in evolutionary biology of the post neo-Darwinian synthesis age. He was able to define new problems with clarity and by doing so open up new research directions. He was able to solve problems and then move on to new problems. He was a free spirit in the world of ideas, and he pursued his ideas wherever they led even if they conflicted with his personal views (as was sometimes the case with sociobiology). He believed in an objective world and science's capacity to approach it. His life was a celebration of what it means to be curious about this world and to understand it on its own terms. He was highly creative and made rational discovery an art form. Simple mathematical models and concepts were his tools (some concepts, such as the evolutionarily stable strategy or ESS, he invented). An ESS is a strategy or population state in which rare mutant phenotypes are at a fitness disadvantage relative to the common phenotype (an important point is that the fitnesses of both rare and common phenotypes are evaluated using the ecological properties determined by the common phenotype). His subjects were organisms and their phenotypes, which under his analysis revealed general characteristics of the evolutionary process. He generated a large number of deeply penetrating ideas on a wide range of topics.

Although he is best known for his research and his ideas, he was a great expositor and wrote many books, including introductory texts in the areas of evolution and genetics (20, 26, 40) and ecology and mathematical modeling (24, 27), as well as advanced expositions of research problems, such as the evolution of sex (31), game theory and evolution (33), and evolutionary transitions (48). Three collections of papers already exist in his honor (1, 2, 8) and at least two are currently in preparation (*Journals of Theoretical Biology* and *Biology and Philosophy*). He was active and productive in research until he died; his last book on the evolution of animal signals appeared in 2003 (44). He lived a long and fulfilling life and was a happy man.

He did not go in for the usual accolades of academic distinction; for example, he did not cultivate a following of dedicated students nor did he seek large sums of funding for his work; he was approached for consideration for knighthood, but he would not allow his name to go forward. Those who admire him do so out of a deep respect for his ideas and his science, not out of a shared intellectual pedigree or training. Still, he was a very social man; if he was in attendance at a conference it was sure to be a success! He had an active group at Sussex (where he spent most of his career) attracting scholars and students from all around the world.

John Maynard Smith was born in London in 1920 and died quietly at his home last year in Lewes, England. His early education was at Eton College where he read works of his future mentor, J.B.S. Haldane (one of the founding fathers of the neo-Darwinian theory of evolution, with S. Wright and R.A. Fisher). In 1947, John began studying with Haldane at University College, London, after studying engineering at Trinity College, Cambridge and working in aircraft design during the Second World War. At Cambridge he met his wife and life-long companion and some-time collaborator Sheila. He practiced Haldane's approach to science, which John characterized as a "combination of the abstract and the particular" (34), and like Haldane, Maynard Smith used simple mathematical models to clarify concrete biological problems. While studying with Haldane, John began an academic position at University College and never actually took his Ph.D. During the years 1939–1946 he was active in the British Communist Party; he left the party in 1956 following a period of progressive disenchantment; in particular he was troubled with the Communist Party's behavior during the Lysenko affair and with the Russian invasion of Hungary (34). In 1965 he became the founding Dean of the School of Biological Sciences at the University of Sussex, where he remained for the rest of his life.

Maynard Smith was awarded many prizes including the Crafoord Prize in 1999 (along with Ernst Mayr and George C. Williams) for his "fundamental contributions to the conceptual development of evolutionary biology," and in 2001 the Kyoto Prize in Basic Sciences for his application of game theory to biology and his idea of the evolutionarily stable strategy. The awarding foundation pointed out that the ESS idea has not only revolutionized evolutionary biology but also such diverse fields as economics, business sciences, and politics. He was a Fellow of the Royal Society in Great Britain and a Foreign Associate of the National Academy of Sciences in the United States.

Maynard Smith made his way in the world of science by the force of his ideas and the clarity of his thought. There was no misty profundity in his work or writings. Throughout his life, he sought to understand fitness; what it means in concrete terms for organisms, how it can be used to understand their phenotypes, and how new levels of fitness are created during evolutionary transitions in individuality (transitions that create new kinds of evolutionary units, for example, genes, cells, multicellular organisms, etc.). He said (34), "my pleasure comes from seeing the same mathematical structures emerging from such diverse problems as the evolution of behavior and the origin of life." His early work during the 1950s and 1960s involved experimental genetics on inbreeding and aging in *Drosophila subobscura* (e.g., 5, 18, 19, 21). Among his results during that period was the demonstration of a trade-off between the basic fitness components, longevity and fecundity (21), results that anticipated much of the recent work on aging and life history evolution.

Maynard Smith's work then became progressively more theoretical. He explained this shift as an outcome of his taking on administrative roles at Sussex in 1965 and also to the fact that, when his mentor Haldane departed for India, John became more confident in his own theoretical work (34). Although his mathematical techniques were basic, he had an uncanny ability to ask important biological questions and to use simple mathematical models to clarify the issues involved. He was also a good naturalist. He stuck with a problem until it yielded to his analysis, and then he moved on to a new problem. He was not big on multitasking (unless by "multitasking" we include talking science while drinking!) and he was not big on technology (I couldn't imagine him with a cell phone or a Palm Pilot), although he did move from slide rules to computers when they became available. At about that time, I remember him saying that he had stopped writing computer code or doing "sums" (as he called mathematical modeling) in the afternoon, as he would usually have a few pints at lunch and this often led to faulty programs and analyses. As a result, he usually wrote papers or worked on administrative tasks after lunch.

In his theoretical work, Maynard Smith was especially interested in the levels at which natural selection acted; for example, for the benefit of what unit, the individual or the group, may a trait be best explained (22, 28). And although he argued decisively for individual selection in most cases, say for the evolution of sex (23, 29–35) or for ritualized animal conflict (33, 45), two problems that were previously explained by group selection (as being good for the species), he was equally interested in how groups become individuals during evolutionary transitions. He viewed the major events in evolution as a series of transformations in the way in which information is coded and transferred—genes, chromosomes, networks of genes, genes in cells, cells-in-cells (eukaryotic cells), cells in groups (multicellular organisms), kin groups, societies, and language (36, 39, 48, 52, 53).

Maynard Smith developed game theory as a tool in evolutionary biology and with G. Price, the concept of an evolutionarily stable strategy (45). An ESS is characterized by the situation in which rare mutant phenotypes are at a fitness disadvantage relative to the common phenotype (an important point is that the fitnesses of both rare and common phenotypes are evaluated using the ecological properties determined by the common phenotype). The ESS tool is in wide use today to study evolution in situations in which an organism's fitness is a frequency-dependent function of other organisms in the population. The ESS approach is a kind of short cut for predicting the outcome of natural selection in situations involving frequency-dependent selection and avoids writing down explicit gene frequency equations for the underlying traits, many of which, like animal behaviors, have unknown genetics anyway. Although approaches similar to the ESS had been used on occasion by R.A Fisher and W.D. Hamilton, Maynard Smith generalized the ESS approach and studied systematically how natural selection could replace rational human decision making in predicting phenotypes in conflictual situations (33).

Maynard Smith was the grand master of the evolution of sex problem; he clarified the many costs of sex and defined the problem of sex in an especially clear and compelling way so that other biologists could both appreciate its fundamental importance and contribute to its solution. Sex is everywhere, yet what is most obvious about the trait is the high cost it imposes on the parents. What are the benefits of sex that offset these costs? The evolution of sex interested John because sexual reproduction was often interpreted as a trait that evolved because it benefited the species, by increasing the species' rate of adaptation to its environment. He showed how incomplete this good-for-the-species explanation was, by showing how hard it was to make this argument formal (indeed, under some conditions models show the argument is false) and by demonstrating in quantitative form the advantages of asexual reproduction. He also classified and studied the various kinds of benefits that could possibly overcome the intrinsic advantage of asexual reproduction to increase in sexual populations (this intrinsic advantage comes from their avoiding the so-called twofold cost of sex). His book on the evolution of sex (31) is a classic and still one of the best treatments of the problem even though an immense amount of work has been done since it was published 27 years ago (indeed, much of this work was done because of the book). In reading his book today, we see an especially clear example of how John was able to identify the essential elements of a problem area in a rather complete way and by so doing, invite others into the area to help solve the problem.

Maynard Smith did pioneering work on sex and recombination in bacterial populations and showed that recombination has been more significant in prokaryotes than many had suspected (38, 41, 42, 46, 47, 51). This was his major research interest late in life. He also anticipated and contributed to developments in the theory of molecular evolution. For example, he pioneered the notion of natural selection in protein sequence space (25) and discovered genetic hitchhiking and its effect on linked variation (9, 43), something that is fundamental to our understanding of molecular variation today. In addition, he created the only clear mathematical model of epigenetic gene regulation that I am aware of (37).

Maynard Smith is known for his recognition and development of evolutionary transitions as a problem in evolutionary biology. Transforming our understanding of life is the realization that evolution occurs not only through mutational change in populations but also during evolutionary transitions in individuality (ETIs)—when groups become so integrated that they evolve into a new higher-level individual. The major landmarks in the diversification of life and the hierarchical organization of the living world are consequences of a series of ETIs: from nonlife to life, from networks of cooperating genes to the first prokaryotic-like cell, from prokaryotic to eukaryotic cells, from unicellular to multicellular organisms, from asexual to sexual populations, and from solitary to social organisms. It is a major challenge to understand why (environmental selective pressures) and how (underlying genetics, physiology, and development) the basic features of an evolutionary individual, such as fitness heritability, indivisibility, and evolvability, shift their reference from the old to the new level. This is the ETI problem that Maynard Smith more than anyone else helped to define.

What is special about the ETI problem for evolutionary biology is that cooperation plays a central role. Maynard Smith was always interested in the evolution of altruism and cooperation, because at first glance such behaviors seem counter to what organisms should do to maximize their fitness. Throughout most of the development of ecology and evolution, the study of cooperation received much less attention than other forms of ecological interaction, such as competition and predation. Scholars generally viewed cooperation to be of limited interest, of special relevance to certain groups of organisms to be sure, as in the social insects, birds, our own species, and our primate relatives, but not of general significance to life on earth. All that has changed with the study of ETIs. What began as the study of animal social behavior some 40 years ago has now embraced the study of interactions at all biological levels. Instead of being seen as a special characteristic clustered in certain groups of social animals, cooperation is now seen as the primary creative force behind ever-greater levels of complexity and organization in all of biology. Cooperation plays this central role in ETIs because it exports fitness from the lower level (its costs) to the new higher level (its benefits).

Recognizing the importance of cooperation in the history of life on earth has taken some time, especially for neo-Darwinians and population biologists. Darwin (6), Wilson (56), and Hamilton (10, 11, 13) all understood the importance of cooperation for social organisms. There was pioneering work done as early as 1902 on the importance of cooperation in the struggle for existence (14), and there was the now widely accepted theory of Margulis (15, 16) and others on the endosymbiotic origins of mitochondria and chloroplasts in the eukaryotic cell. However, cooperation was also viewed as a destabilizing force in ecological communities and likely of limited significance because of the positive feedback loops it creates (17). Sociobiology had defined altruism as its core problem (56), but the altruism problem was not viewed as general to life on Earth until others began applying cooperation thinking to the evolution of interactions at other levels in the hierarchy of life in addition to social organisms, such as to the level of genes within gene groups (e.g., 7) and to the level of cells within cell groups (e.g., 3). Concomitant with the generalization of the cooperation problem was the development of multilevel selection theory (e.g., 12, 22, 49, 50, 54, 55). The ETI problem grew out of these two developments that, in effect, extended the sociobiology revolution to all kinds of replicating units in the hierarchy of life.

What Maynard Smith did was to synthesize a diverse body of work into a comprehensive framework for ETIs; in addition, he mapped out the problem area with a clarity that only he could produce. He did this initially in two papers (36, 39) and later in a much more systematic and complete way in his book with E. Szathmáry (48). While not single-handedly defining the ETI problem, nor solving it, Maynard Smith and Szathmáry have mapped out the important issues, and this has stimulated an increasing number of biologists to enter this area. This is yet another example of how he was able to define a problem area with clarity so that others could contribute to it.

Maynard Smith was a lot of fun to be around. He treated all people with equal respect, but he was quick to expose sloppy thinking and unreceptive to pomposity. As a result, he was a feared debater of creationists. He had a child-like wonder about him—this was my first impression of him, as a second-year graduate student visiting his group at Sussex in 1975. I have many memories of JMS (as he was often called)—unkempt appearance (the hair!), that sparkle in his eyes, the pub crawls over the South Downs, and the many long discussions over tea and beer. As a young student I wanted to be just like him, and in many ways, I still do. Now years later as I sit and reflect on this wonderful human being and what his life and work means for the rest of us, I still think mainly of how much fun he was to do science with. I miss him very much.

There are many resources available for those who want to know more about this extraordinary man. JMS was asked to write a short autobiographical sketch emphasizing his work in animal behavior (34). There is also a perspective in *Genetics* (4). A good place to begin browsing for material is the JMS web site maintained by the Center for the Study of Evolution at the University of Sussex (**http://www.lifesci.sussex.ac.uk/CSE/members/jms/jms.htm**). I have used this resource extensively in preparing this biography and have also benefited from feedback on the manuscript and insights into the man from Paul Harvey, Brian Charlesworth and Joel Peck. Matt Herron and David Harper also provided helpful comments on the manuscript.

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