Obituary

John Maynard Smith (1920–2004)

John Maynard Smith, one of the greatest thinkers in evolutionary biology, died on 19 April: at the time he was sitting in his chair at home, surrounded by papers over which he had been brooding. He was a generous and extremely gifted man, whose strength was to tackle biological problems with simple mathematical models and to draw insightful conclusions from them; indeed, Maynard Smith showed an aversion to the pompous use of mathematics and the mystification of science that often goes with that. He made crucial contributions to several debates in evolutionary theory: the levels — genes, the individual organism, and so on — at which natural selection operates most effectively; the maintenance of sex as a costly mode of reproduction; the use of game theory for biological analysis of conflict and cooperation; the characteristics of major evolutionary transitions, such as the origin of multicellularity; and the logic of animal signalling.

Maynard Smith was born in 1920, into a British upper-class family with a limited interest in the scientific and cultural matters that were to become so important to him. In due course he was sent to Eton College, an establishment that features near the top of the pecking order of British 'public' (that is, private) schools. He did not have fond memories of his time at Eton. But he did receive a good grounding in mathematics there, which he found very useful for "doing his sums" in his later callings of engineering and theoretical biology. And, as he pointed out in his typically fair way, it was also to Eton's credit that the library included books by his future mentor, J. B. S. Haldane, even though this co-founder of population genetics and vocal member of the Communist Party was held in particular disregard there.

The family preference was for Maynard Smith to become a stockbroker. He firmly rejected this option, but he needed an alternative. Prompted by an earlier visit to Eton by one of the designers of Sydney Harbour Bridge, whom he thought very impressive, he decided to become an engineer, finishing a degree in the subject at Trinity College, Cambridge, in 1941. He was involved in aircraft design during the Second World War, but in 1947 left this occupation partly because his bad eyesight prevented him from pursuing his ambition of flying. He then began his second, breathtaking, career in evolutionary biology, studying at University College London under the guidance of the man who had already inspired him from a distance: the charismatic J. B. S. Haldane, a towering figure in British science at that time, and still a prominent supporter of the Communist Party.

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From Eton to Sussex, from aircraft engineer to original thinker in evolutionary biology

Both men adhered to the Communist ideology for quite some time. Maynard Smith's main motivations for joining the party were its stance on racism and sexism, its fight against social inequality, and its firm anti-Nazi position. He felt that these attributes were synergistic, but in later reflections admitted his blindness to the malign aspects of Communism — to which, for instance, the eyes of George Orwell and Arthur Koestler had been opened earlier because of their more worldly experiences. It was the detrimental influence on Soviet biology of Trofim Lysenko's politically motivated genetics theories that caused Maynard Smith to abandon his overly idealistic view of Communism. He ultimately withdrew from political activism, and left the Communist Party, when Hungary was invaded by Soviet troops in 1956.

Maynard Smith's initial scientific work, developed before Haldane's departure for India in 1957, largely involved experimental work on inbreeding and ageing of the fruitfly *Drosophila*. His most important theoretical insight into ageing was that natural selection would be expected to synchronize the ageing processes of the various subsystems of an organism. To get a feel for this insight, suppose for a moment that there was no such synchrony and that a 'lead mechanism' of ageing existed instead. Investment in the higher durability of the other subsystems would then be superfluous because they would last longer than needed. Natural selection would counteract such a waste of resources. A similar consideration must have guided Henry Ford to the junk yard of old automobiles, to decide which parts to produce in lower quality in the future, so as to synchronize the expected time at which different parts would wear out.

Maynard Smith was not keen on administrative affairs. But in 1965 he was delighted to accept a proposal, initiated by Peter Medawar, to become the founding dean of the School of Biological Sciences at the University of Sussex, where he stayed happily for the rest of his life. In his hands, Sussex became a respected centre in various branches of biology, and now boasts a John Maynard Smith Building (where the man himself would attend lectures).

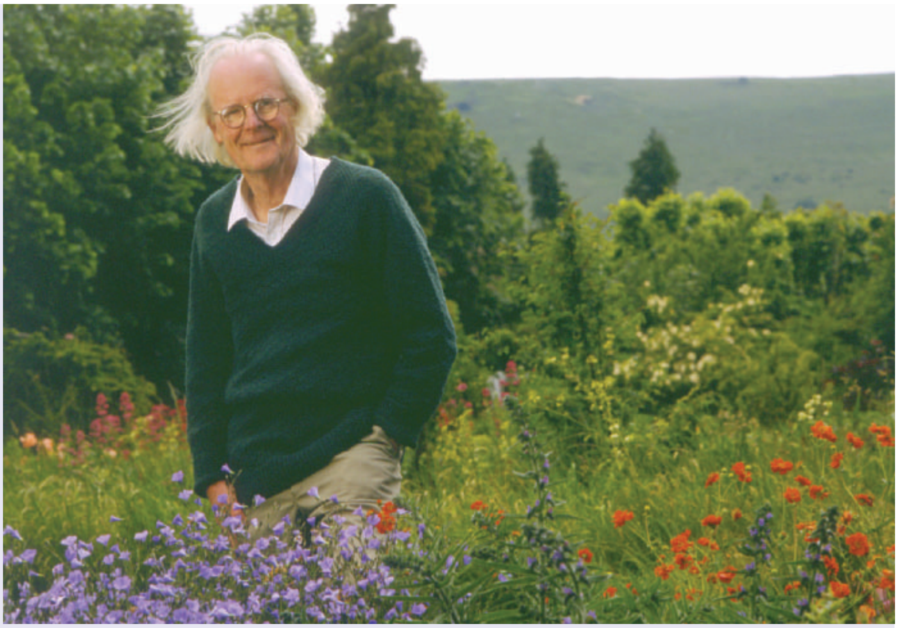
Maynard Smith often admitted that he was not a champion chemist, but he was comfortable with molecular biology, where the processing of information plays a central role. His formulation of the concept of 'sequence space' in the late 1960s was visionary. He wanted to know how natural selection could guide proteins through a highly multidimensional space (where proteins differing in only one amino acid would be nearest neighbours), to assume various distributions of functionality in that space ('continents', 'islands', and so on). He was about 20 years ahead of his time with these early considerations, which are now widely applied in molecular evolution both at the protein and the RNA level.

In 1971, he formulated a basic problem in evolutionary biology known as the 'twofold cost of sex'. It goes as follows: other things being equal, a population of parthenogenic females — females that reproduce without fertilization — should grow at a rate twice that of sexually reproducing females, because half of the offspring of the latter are males. With admirable frankness, he later called attention to the fact that the problem was seen in much the same way by the German biologist August Weismann — whom, after distancing himself from his previous prejudices against the man, he considered to have been second only to Charles Darwin as a nineteenth-century thinker about evolution. The characteristically lucid posing of the problem has stimulated much research on the evolutionary maintenance of sex — research in which both theoreticians and empiricists have asked what advantages could compensate for the twofold cost.

It is fair to wonder about the common thread behind Maynard Smith's various lines of investigation. From discussions with him, we think that it was the application of rigorous evolutionary reasoning to phenomena that at first sight seem to contradict darwinian theory. For example, if organisms should maximize their 'fitness', then why do they age? Dead organisms do not reproduce; hence their fitness does not increase any more. The cost of sex obviously poses a similar problem, and in the same vein it is a puzzle why so many antagonistic interactions between animals of the same species seem to be ritualized encounters rather than serious fights. Competing animals should try to attack and kill one another, shouldn't they? There are two proposed answers to this question. The first is that it is good for the species to avoid harmful encounters by finding ritualized ways of resolving conflict. Maynard Smith, however, argued convincingly that a second type of answer is the correct one. The idea, which he worked out together with George Price, is that ritualized contests can be advantageous to the individual by allowing an assessment of the probable outcome of fighting. This way, the weaker individual can escape or surrender before the opponent escalates the contest; the stronger individual avoids possible injury. Overly aggressive animals foregoing a ritual display would too often be harmed by opponents who fought back.

In their analysis of animal behaviour during contests, Maynard Smith and Price laid the foundation for the new field of evolutionary game theory. Traditionally, the theory of games dealt with rational human decision-making in situations where there is a conflict of interest among interacting individuals. The new branch of game theory was one in which natural selection acts instead as the decision maker. The framework of evolutionary game theory has turned out to be extremely useful, and has been generalized to plants and even to microbes and replicating molecules. At the heart of problems in evolutionary game theory lies a complex optimization problem, where an individual's best 'strategy' depends on what strategies other members of the population are using. A trivial example is driving on the left side of the road. In the population where Maynard Smith tended to use his car, it is advisable to drive on the left side — not because this is good in itself but because, as all other the drivers are doing it, it is the best strategy for avoiding an accident.

Evolutionary game theory considers genes and individuals as units among which there may be conflict. But it was also clear to Maynard Smith that there can be a problem with overemphasizing these units and their competition. In evolution, higher-level units (such as a plant or animal cell) repeatedly formed from lower-level ones (such as bacteria). If competitive evolution at the lower level had not been suppressed somehow, the higher-level units would have been disrupted. How is this possible? A thorough investigation of major transitions in evolution revealed some common themes: multi-level selection, origin of novel inheritance systems, combination of function and division of labour, and so on. We have yet to reach a full understanding of any of the major transitions, but many scientists have been stimulated to enter this field.



A. CORBIN & J. O'GRADY

Asking a new question is sometimes as useful as answering an old one. Maynard Smith observed succinctly that twentieth-century biology is more about the role of information in biology than about anything else. The terminology of molecular biology (transcription, translation, proofreading and so on), the concept of positional information in embryology, the nervous system as information processor and the questions on animal signalling (about which he published his last book just a few months ago) all confirm the validity of his point.

Although it was not always apparent, Maynard Smith had been a naturalist since his childhood. Following the tradition of the British gentleman as a keen observer of the countryside, he was convinced that science must be deeply grounded in empiricism. He would always start with a concrete problem and boil it down to the key issues. Of course, his engineering past occasionally surfaced. For example, his models of a dual inheritance system (genetics and epigenetics) have a strong engineering flavour. They were published in the *Journal of Theoretical Biology* — this was a journal close to his heart, and he served on its editorial board almost until his death.

John Maynard Smith — widely known as JMS — was an exceptionally lucid thinker and a delightful man. He would talk about science to anyone and, in the same open-minded way, treat young and established people with equal respect. This was apparent at an international meeting on evolution and systematics at Sussex in 1986 (shortly after his cancer operation), when he listened during a long break to a completely unknown foreign youngster explaining a novel model of early evolution, having chased everybody else away, including celebrities of the time. And he was willing to give up preconceptions: his reappraisal of Weismann is a case in point.

Some of us will find it difficult to live without him. He said that he always wanted to follow in the footsteps of Haldane, and in many respects he was successful in that aim. Emulating John Maynard Smith, mentor, colleague and man, will be an immense challenge. **Eörs Szathmáry and Peter Hammerstein**

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See also: www.nature.com/nature/focus/maynardsmith