Retrospective: In Memory of John Maynard Smith (1920-2004)

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the behavior of the small amount of iron in the protolunar disk. Ideally, the results should be verified with complementary simulations using different hydrodynamic methods (*12*).

Nonetheless, the detailed predictions now possible with the new calculations and further improvements, together with the refinement in analytical tools and the corresponding progress in stable and radiogenic isotope analyses, offer a wealth of new possibilities for testing models of lunar origin.

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RETROSPECTIVE: EVOLUTION

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When John Maynard Smith died on 19 April at the age of 84, one of the last grand evolutionary theorists of the 20th century passed. The example of Charles Darwin has induced intellectually ambitious biologists, many of them in Britain, to search for general formulations by which evolution as a whole, or large domains of evolutionary phenomena, can be understood and explained. One thinks of R. A. Fisher's self-consciously named "Fundamental Theorem of Natural Selection" (which turned out not to be quite so fundamental or general as Fisher thought), or W. D. Hamilton's theory of kin selection, the chief theoretical tool used to explain the origin of cooperative, social, and apparently altruistic behavior in a world supposedly dominated by the struggle for existence.

Maynard Smith saw that a major remaining problem in evolutionary theory was to explain the evolution of characteristics whose reproductive advantage or disadvantage to an individual depended on the response of other individuals. So, for example, is it reproductively advantageous for an animal to engage in threatening aggressive behavior toward another animal when they are competing for a bit of food or space? If the response of the second animal is to back down, then the aggressive behavior has paid off, but if the opponent meets aggression with aggression, then an escalating conflict may leave both of them dead. Maynard Smith realized that this class of evolutionary problem could be approached through game theory. His invention of the concept of an Evolutionary Stable Strategy created a new and lively branch of theoretical studies of evolution.

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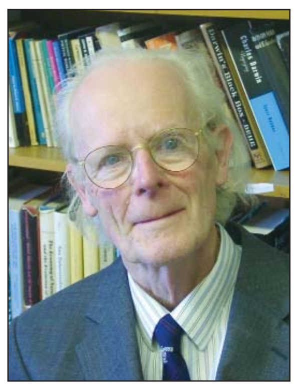
Although the concept of the evolutionary game has considerably enriched the way in which evolutionists think about the history of life, what remains unclear is the extent to which it will be possible to measure in nature the quantities that are required to turn the theory into a predictive device. It is very difficult to measure fitnesses in nature and especially the kinds of contingent fitnesses of genotypes that depend on what other interacting individuals are doing. Moreover, Evolutionary Stable Strategies only tell us whether, if a particular strategy is adopted by the entire population, an alternative strategy can invade at low frequency. They tell us nothing about the stability of the strategy after massive invasion by alternatives, as might occur from mixtures of populations with different strategies. It may turn out that game theory will serve only as a rough heuristic rather than as a precise mode of evolutionary prediction.



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The impact of evolutionary game theory has been such that Maynard Smith's earlier, largely experimental work has been unduly neglected. His demonstration that there is a trade-off between female fertility and longevity in *Drosophila* is of general importance to our understanding of the evolution of life histories. His marvelous experiments with K. C. Sondhi on changing invariant characteristics by selection is one of the best demonstrations of Waddington's claim that there is considerable hidden genetic variation underlying such constant features, variation that can be made manifest when development is disrupted. Most extraordinary was their ability to produce heritable asymmetry in a normally bilaterally symmetrical organism such as *Drosophila.* Such experiments are as important to our understanding of evolutionary processes as Maynard Smith's more seductive work on game theory.

John Maynard Smith was the child of a Harley Street surgeon, spent much of his youth on Dartmoor, attended Eton College, and went on to Trinity College, Cambridge. Like so many of his upper-middle class contemporaries at Cambridge in the 1930s, he became enamored of Marxism and joined the Communist Party. He told me he was recruited into the party by Harry Harris (who later achieved fame as a human biochemical geneticist), and that Harry was the first urban Jew he, a boy from Dartmoor, had ever laid eyes on. Like so many others he became disillusioned by Stalinism and left the Communist Party after the Hungarian uprising. This was a common pattern. I once sat in the Staff Club at the University of Sussex with Maynard Smith and a number of other faculty members trying to recall whether a particular person had been a member of the Communist Party. John said he couldn't remember and asked the man on his right, who couldn't remember either but asked the man on *his* right, and so on around the whole circle. Unlike so many Americans of a similar history, neither Maynard Smith nor his colleagues became hardened rightists, but held on to their socialist sympathies, so much so that when I told a British immigration officer that I was to spend a year at Sussex he remarked, "Ah, that Bolshie University!"

John Maynard Smith was a humane, humorous, and sensible person who did not take himself or other people more seriously than they deserved. He had a sensibly skeptical view of science and its claims, which is best encapsulated in the famous dictum of his teacher, J. B. S. Haldane, who said that a scientific idea ought to be interesting even if it is not true.