John Maynard Smith (1920-2004)

"One of the Last Grand Evolutionary Theorists of the 20th Century"

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There is virtually no area of evolutionary biology to which John Maynard Smith did not make a significant contribution. In this essay I try to present a flavour of his accomplishments.

Background

Modern biology is made up of highly specialized sub-fields: molecular biology, cell biology, biochemistry, structural biology, ecology, behavioural biology, genetics and evolutionary biology, to name a few. Among these, the role of genetics is both fundamental and unique. Fundamental, because it concerns itself with heredity, the single most characteristic feature of the living world. Also, genetics is unique among the life sciences, because the principles of heredity can be expressed as statistical regularities or laws. First discovered by Mendel in the late 19th century, these laws make it natural to use mathematical reasoning in genetics to an extent that is almost unthinkable in other areas of biology (except, for example, when the problem at hand allows a more or less direct application of physics or chemistry).

In the beginning of the 20th century, fairly soon after the rediscovery of the laws of Mendel, mathematicians and mathematically-minded biologists began an ambitious research programme. They tried to see whether, by combining Mendel's laws with the Darwinian theory of natural selection, they could throw light on the deepest of all biological problems, evolution. The foundations of this quest were laid by R A Fisher and J B S Haldane in Britain, S Wright in the USA and S S Chetverikov in the USSR. John Maynard Smith was trained as an engineer and later went on to study under Haldane. He was among the earliest investigators of the role played by genes in embryonic development. All

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through the second half of the 20th century he was also one of the leading contributors to the field of evolutionary genetics.

Why do we grow old?

But Maynard Smith was much else besides. My aim is to illustrate the breadth of his interest in evolutionary phenomena by choosing a small number of examples from his published work; I should stress that this is not meant to be a comprehensive survey. In what follows, I will first state the general question or questions that lie behind an article or book by Maynard Smith and then give a brief description of the particular aspect that he addressed, often with collaborators.

Articles

1. *J Maynard Smith, A Theory of Aging, Nature, Vol.184, pp.956-958, 1959.*

Why do we grow old? Is senescence a consequence of chemistry (like the rusting of iron), genetics (because mutations keep accumulating and cause a subset of critical genes to malfunction) or evolution (because the strength of selection on an individual must inevitably decline with the passage of time, thereby predisposing living creatures to a progressive 'systems failure')? The question of senescence or growing old is quite different from the question of the life span; individuals can never grow old but have short life spans. However, under controlled conditions, one can plausibly say that a measurement of life span in a population conveys information about the rate of aging.

The physicist Leo Szilard had postulated that the reason why animals age could be that many of their genes are present, right from birth, in just one functional copy. The other copy would carry an inherited defect, a 'fault'. In that case, said Szilard, as time passed, the gradual accumulation of randomly occurring mutations might make both copies of more and more genes non-functional. This would lead to a steady deterioration of the individual: it would show signs of aging. (In a modified version, the argument has been resurrected recently and is popularly known as the 'two-hit' hypothesis for cancer). Maynard Smith

Are there limits to what evolution can achieve?

used simple reasoning to show that what Szilard said could not always be right. Male flies have a single X-chromosome – unlike females, which have two. The males were sometimes shorter-lived than their female sisters, as Szilard would have predicted; but there were also strains in which, contrary to expectation, males lived longer than females. Also, Maynard Smith pointed out that within the same strain, flies aged differently at different temperatures. If this were due to differences in the rates at which their genes accumulated hits at the two temperatures, a fly raised at one temperature and then transferred to a second temperature would carry with it all the hits that it had accumulated earlier. This would show up as an effect on its subsequent life span. But the observations said otherwise: either the temperature-shift had no effect, or, in some cases, had an effect opposite in direction to what was expected. Today, the theory of aging continues to be in a state of ferment; all we can say is that chemistry, gene activity during the life of an individual *and* evolution appear to have something to do with it.

2. J Maynard Smith and K C Sondhi, The Genetics of a Pattern, Genetics, Vol.45, pp.1039-1050, 1960.

Are there limits to what evolution can achieve? Or is the range of evolutionary possibilities significantly limited by constraints – which may originate from physics, chemistry or the past history of evolution itself? The issue goes all the way back to Galileo, who is believed to have wondered whether there could ever be ants as big as elephants (the answer is no). The question investigated by Maynard Smith and Sondhi concerned the fruit fly Drosophila. This fly has three 'false eyes' or occelli on the top of its head: one in the middle and, behind it, one each on either side. Sometimes, by chance, a mutant fly arises that has one or the other occellus absent. Maynard Smith and Sondhi tried to breed selectively from such flies, the aim being to raise flies that were exclusively 'left handed' or 'right-handed'. They failed consistently, even though they managed to get populations in which flies had the two lateral occelli only, and also populations in which one or the other lateral occellus was missing. But in the latter case, the population was made up of some 'left-handed' flies and about the same number of 'right-handed' flies. It proved impossible to breed for a race of asymmetric flies – in spite of the fact that at the individual level, a fly of either handedness could exist. It appeared that the requirement of bilateral symmetry in the population as a whole (normally seen as bilateral symmetry in the individual, of course) was a strong constraint on evolution. The origin of bilateral symmetry during embryonic development remains a much-studied topic. As for the evolution of symmetry, ample evidence has accumulated to show that in one way or another, asymmetric plants and animals do poorly in comparison with their symmetric counterparts.

Can evolution work beyond the level of the individual?

3. *J Maynard Smith, Group Selection and Kin Selection, Nature Vol.200, pp.1145-1147, 1964.*

Can evolution work beyond the level of the individual? A popular way of looking at evolution is that it leads to improvements in those traits that are for the 'good of the species'. However, in general, this view is incorrect. Darwin first pointed out, and R A Fisher and G C Williams reiterated much later, that the level at which natural selection is most likely to act is the level of the individual. The reason is simple: it is the individual that exhibits heritable traits, it is the individual that differs from other individuals, and it is the individual that reproduces. Therefore the differential propagation of genes (that lies behind evolution) must reflect properties that distinguish one individual from another. In 1962, V C Wynne-Edwards wrote a book (*Animal Dispersion in Relation to Social Behaviour*) in which he tried to say that behaviours that were advantageous at the level of the group but disadvantageous at the level of the individual – commonly termed 'altruistic' – could be found in nature and were proofs of group-selection. For example, according to Wynne-Edwards, animals commonly practiced birth control – because, he said, if the population grew too large, it could outstrip the food supply and put the survival of the entire group at risk.

In this article, Maynard Smith carefully went over the special

Why do so many conflicts between individuals of the same species involve restraint rather than all-out attack?

circumstances under which traits could spread when they were favourable to groups but unfavourable to individuals. The two exceptional circumstances that he treated had been invoked earlier by Haldane and Wright, but the issue was not pursued very much by either of them. In one situation ('kin selection'), a group might consist of close relatives, meaning individuals who shared genes on account of common descent. In such a group, an individual who behaved altruistically would, by means of such behaviour, tend to favour other individuals whose genetic interests overlapped with its own. Thus 'altruism' at the individual level would mask 'selfishness' at the genetic level. In another situation ('group selection'), the population could be divided into small groups, each group being so small that there was an appreciable probability for an 'altrustic' trait to spread within the group purely by chance. Once that happened, the group consisting of altruists alone would do better than other groups and so the altruistic trait would also spread in the population as a whole. The importance of this paper lies in the careful distinction between kin and group selection drawn by Maynard Smith and in his pointing out that many cases of supposedly altruistic behaviour could in fact be accounted for without invoking either kin or group selection. The paper was written at about the same time that the scope of kin selection was detailed in two path-breaking articles by W D Hamilton. It is due to Hamilton and Trivers, more than Maynard Smith, that the study of the evolution of social behaviour (the field known as sociobiology) gained momentum subsequently.

4. *J Maynard Smith and G R Price, The Logic of Animal Conflict, Nature, Vol.246, pp.15-18, 1973.*

Why do so many conflicts between individuals of the same species involve restraint rather than all-out attack? Here Maynard Smith and Price addressed the puzzle of seemingly ritualized warfare: threat displays or feints that settle, without either party risking serious injury, the issue of who gets a resource (e.g., food or a mate). An easy explanation would be to say that by avoiding injury, the survival of the species is promoted. Indeed, Julian

Huxley, a leading evolutionary biologist who was well known for his work on courtship behaviour, had suggested just that. But, as we have seen, 'the good of the species' is a bad hypothesis. Instead, there had to be a way of looking at animal conflicts *from the standpoint of the individual* which would show why behavioural restraint might be favoured.

The essence of the explanation advanced by Maynard Smith and Price was that the best thing for an individual to do when it encountered another individual depended on what the second individual did. In short, the optimum behaviour of an individual depended on the course of action that every other individual was likely to adopt. The reasoning appears circular, but is not. The stable evolutionary outcome (assuming that it existed) would be one in which there was a simultaneous optimization of every individual's behaviour. This way of describing the problem automatically leads itself to a mathematical formation known as Game Theory. First developed by J von Neumann and O Morgenstern, Game Theory came into its own thanks to the work of John Nash (whose life is the basis of the book *A Beautiful Mind*). The initial applications of the theory were in economics and for the modeling of conflicts between the USA and USSR during the Cold War. The theory depends on the assumptions that everyone knows what options are available to everyone, and everyone knows what the consequences are of exercising one or the other option. If the assumptions are valid, Game Theory enables one to calculate an individual behaviourial strategy that can not be bettered when everyone else too uses his or her optimum strategy. Hamilton had shown that the choice of sex-ratio of offspring, namely the choice of how many sons vis-à-vis daughters to have (assuming such a choice to be possible), could be modeled on game theoretic grounds. Maynard Smith and Price adopted a more general line of reasoning and developed the concept of an ESS or evolutionarily stable strategy – basically, an unbeatable strategy. Their arguments showed that restraint and ritualized conflict could well be an ESS. For example, if an individual had a high probability of encountering

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an aggressive individual, behaving aggressively itself could leave it seriously injured. ESS-based reasoning continued to be developed by Maynard Smith in a series of publications including a widely acclaimed book, *Evolution and the Theory of Games*. His work stimulated many others to extend the basic idea, and it may well be the most influential contribution that he made to evolutionary theory. However, the ESS way of analyzing animal conflicts has not remained unchallenged. The most interesting, as also provocative, alternative is something known as the Handicap Principle, which was advanced in 1975 by Amotz Zahavi.

Books

In most areas of science, including biology, it is no longer the fashion to publish original findings or ideas in a book. The research article is the favoured medium for telling others what you have done. In this regard – and fortunately for us – the field of evolutionary studies has remained an exception. Besides publishing in scientific journals, Maynard Smith wrote a great many books. They deserve consideration in their own right. *The Theory of Evolution* (1958), his first book, lays claim also to be the best. To this day it serves as a comprehensive study of various aspects of evolution. As popular writing, it comes close to approaching J B S Haldane's pieces in style and clarity. *Mathematical Ideas in Biology* (1968) is a little (and little-known) gem. Among other topics, it contains one of the earliest descriptions of a mathematical theory of pattern formation that Alan Turing had proposed in 1952 (this goes to show how little Turing's ideas were picked up by biologists). *The Evolution of Sex* (1978) is a research monograph. It contains a detailed survey of a fundamental problem in evolutionary biology: why do essentially all 'higher' organisms scramble their genes and then pass on only one-half of the total to their children? More than anyone else, Maynard Smith hammered home the seriousness of the problem: a potential drop in fitness of 50% for an organism that reproduces sexually, as opposed to reproducing asexually. *The Problems of Biology* (1986) is a wide-ranging look at what biology is all about and is the best such work known to me. Contrary to

John Maynard Smith: A Personal Reminiscence

John Maynard Smith and M K Chandrashekaran during the 1979 Mahabaleshwar Seminar. (Photo courtesy Dr K Usman)

I first saw Maynard Smith in 1970 or 1971. At the time I was studying physics at the University of Chicago; he had come over for a longish stay, among other reasons to visit R C Lewontin. We used to meet regularly over lunch, which was eaten in a place that seemed to be popular with the three of us (he was accompanied by his wife Sheila) but not many others. He was a vivid conversationalist and intensely curious about my research – which, thanks to the interests of my supervisor, Morrel Cohen, carried a whiff of mathematical biology. However, my work was getting nowhere; looking back, this was a recurring feature of my PhD career. The problem was that this made me feel awkward to tell people what I was up to. Fortunately, Maynard Smith picked up the signals right away, and as early as our second encounter, began by saying brightly, "Do you *mind* if we talk about Indian politics? There is so much I don't know about it", and all was well. He was developing his ideas on using game theory at the time, but the one seminar by him that I remember dealt with Marxism, the possible parallels between it and Darwinism, and Darwin's successful attempts to keep Marx and Engels at a distance. Almost ten years later, I was able to cash in on our acquaintance and managed to persuade John and Sheila Maynard Smith to take part in the 1979 Mahabaleshwar Seminar. The Seminar, organized by Madhav Gadgil, was on the theme of sociobiology – a topic in some ferment during those days. It was a memorable meeting, not least for Maynard Smith's vigorous attack on Wynne-Edwards and the group selectionist point of view. He wore a shabby green pullover, his spectacles seemed to be so dirty as to be practically opaque, his trousers kept falling down, and he held the audience spellbound. He said something that cheered up many of us: he said that if you discovered something that could also be found in the works of Haldane, Fisher or Wright, you were allowed to publish it as an original finding; if not, no work would get done in evolutionary genetics. But he did mention that he felt odd lecturing in a chapel, and from a lectern at that. Raghavendra Gadagkar has written about this meeting in two places: *Journal of Scientific and Industrial Research*, Vol. 39, pp.298-301, June 1980, and *Journal of Biosciences*, Vol. 29, No. 2, 139-141, June 2004. The condition of the spectacles appears to have influenced Richard Dawkins to conclude – in *The Blind Watchmaker* – that even terrible vision must be better than none, and therefore the eye could have evolved in small steps after all. We had a long car ride after the meeting, and what I remember most from that ride is that Maynard Smith praised W D Hamilton to the skies and said what a shame it was that he had not been given the recognition that he deserved.

what one might imagine, subsequent discoveries at the molecular level have not dated it. *The Major Transitions in Evolution* (1997, with E Szathmáry) tackles a subject which is the most fascinating of all in evolution, but which is also among the most difficult to tackle. Namely, what may have been the origin of life? How did the first cell come about? What favoured the appearance of creatures made up of many cells? What led to the evolution of cooperation? To the evolution of language? Maynard Smith and Szathmáry offered two unifying principles that might help in understanding these major evolutionary advances. First, that each step involved a new way of transferring information from one generation to the next (in the case of language, the information would be cultural, not biological). Second, each transition involved a new form of cooperation, thanks to which selection at a higher level was able to override selection at the (lower) level of the components that made up the higher level – in a manner reminiscent of the working of group selection.

Rounding up

As I have said, this is merely a sample of John Maynard Smith's large output. In whatever he wrote, either he had something new and interesting to say or, equally importantly, he discussed an old problem with a greater degree of clarity than before. The issues that he dealt with were never trivial. He was as interested in applying the principles of genetics as in asking what might account for those principles in the first place. In his writings, mathematics always took a second place to biology; and he tended to rely on a combination of mathematics and verbal reasoning. Though he laid great stress on precise models, he stayed away from the intricacies of the mathematical approach favoured by Fisher or Wright or even, occasionally, his own teacher Haldane. For all that, modeling let him down badly when he asserted that Zahavi's Handicap Principle could not work. But in this, as in other matters, he seems to have been guided by Haldane's dictum that it was better to be wrong then uninteresting. In the long run, he will be remembered for his contributions to the evolution of sex and for his game-theoretic approach to animal behaviour, and most of all, for showing how illuminating the study of evolution can be. Lewontin's appraisal is an apt one: Maynard Smith was one of the last grand evolutionary theorists of the 20th century.

Suggested Reading

[1] Richard Dawkins's Foreword to The Theory of Evolution. http://www.edge.org/3rd_culture/maynard_smith04/maynard_smith04_index.html

[2] John Maynard Smith, The Problems of Biology, Oxford University Press, 1986.

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