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John Maynard Smith and evolutionary game theory

When John Maynard Smith passed away on April 19, 2004, most obituaries expressed the view that among the amazing wealth of his contributions to theoretical biology, the most significant was the introduction of game theoretical methods for the analysis of evolutionary problems. JMS would probably have agreed with this. In an essay entitled 'Evolution and the Theory of Games' (Maynard Smith, 1976a), he set out to trace the history of this idea. With his characteristic blend of generosity and objectivity, he made it clear that he was not the first to discover the usefulness of game theory in evolutionary biology. Nevertheless, it is right to view him as the father of evolutionary game theory.

A quip, which is widespread in mathematical circles says that theorems are usually named, not after the first, but after the last person who discovered them. It highlights the fact that the history of science can be quite unjust in her attributions. But a discovery which remains widely unknown, or neglected, is of little use for the march of science. The last discoverer is often the one who moves the idea into public awareness, making it impossible for anyone, after that, to discover the idea anew.

John Maynard Smith certainly made sure that no one, henceforth, could ignore the power of game theoretical thinking for all aspects of population biology. What Ernst Mayr called 'the greatest conceptual revolution in biology', namely, 'the replacement of typological thinking by population thinking' (Mayr, 1970), was transferred by John Maynard Smith into game theory.

The fact that John Maynard Smith was initially trained as an engineer had a significant impact on his biological work. In 1938, as an 18-year old graduate from Eton, he had visited his uncle, a British military attaché in Berlin, and witnessed a speech by Adolf Hitler. There was no need to know German to understand that war was imminent. Young Maynard Smith decided that the most useful thing to do was to become an aircraft engineer.

In 1947, he left his engineering job to enrol as a student of biology at University College, London—aircraft were too noisy for his taste, and he vastly preferred birds—but his training in applied mathematics would prove of great help for his postgraduate work with J.B.S. Haldane. More importantly even, John Maynard Smith had learnt what it meant to work on design, and could appreciate the arguments from intelligent design, and all related issues of evolution, from the other side of the hill, as it were. Thus he could write on 'birds as aeroplanes' (Maynard Smith, 1953), and even on 'Machines that play games' (Maynard Smith and Michie, 1964). Many years later, he was to write (Maynard Smith, 1995):

> Of course when thinking about the V2 rocket I was thinking about a product of human design, whereas a few years later, when I was thinking about the shapes of mammalian teeth, I was asking why mammals were better at chewing, and so left more descendants. But this difference had no effect on the way I thought about the two problems. Indeed, I have become increasingly convinced that there is no way of telling the difference between an evolved organism and an artefact designed by an intelligent being.

Designers have routinely to face the task of optimising structure, or function. Optimisation arguments are widespread in physics, for instance as principle of the least action, and have led to an elaborate mathematical theory, including variational calculus and dynamic programming. These tools are also used in economy, for instance to decide on an optimal bundle of goods. Some questions, including NP-hard problems like finding the shortest path joining 64 towns, can be extremely difficult to solve, but it is clear what is meant by a solution. This changes when economists have to consider the interaction of several decision-makers, all trying to maximise their income. Even the concept of a solution becomes problematic. The interdependence of the agents raises different questions needing new techniques.

In 1944, John von Neumann and Oskar Morgenstern introduced these techniques in their book 'The Theory of Games and Economic Behaviour' (von Neumann and Morgenstern, 1944) which met with a huge success in spite of being not exactly user-friendly. Originally, the authors had another title in mind: 'Theory of Rational

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Behaviour'. It seems clear that this would have had less appeal with potential buyers. But more importantly, it would have nailed down the rationality axiom, and therefore obstructed applications of the theory in other, patently non-rational contexts. As it was, already in the 1949 thesis of John Nash, one finds a portend of the population dynamical approach which would be characteristic of evolutionary games, some 25 years later. Nash wrote:

> We shall now take up the 'mass action' interpretation of equilibrium points…It is unnecessary to assume that the participants have full knowledge of the total structure of the game, or the ability or inclination to go through any complex reasoning process. But the participants are supposed to accumulate empirical information…Then the assumptions we made in this 'mass action interpretation' lead to the conclusion that the mixed strategies representing the average behaviour in each of the populations form an equilibrium point.

Unfortunately, this part of the thesis was not published, in its time (but see Nash, 1996).

Nevertheless, several scientists soon saw opportunities for applying game theory in evolution. The first to do so may have been R.A. Fisher (I own this remark to Olof Leimar, personal communication). In a little known paper (Fisher, 1958) Fisher wrote:

> The relation between species, or among the whole assemblage of an ecology, may be immensely complex; and at Dr Cavalli's invitation I propose to suggest that one way of making this intricate system intelligible to the human mind is by the analogy of games of skill, or to speak somewhat more pretentiously, of the Theory of Games.

Fisher goes on to relate that in 1934, he had shown that an ancient card game known as Le Her had a solution in terms of randomized strategies (Fisher, 1934). Fisher then describes how, 10 years later, von Neumann and Morgenstern had developed a general minimax principle, adding: '…to which, indeed, von Neumann had earlier drawn attention in one of the German mathematical journals.' (In fact, von Neumann had proved the minimax theorem in 1928 already, and Fisher had been unaware of it when he studied his card game.)

What Fisher suggested was not evolutionary game theory, yet. The players he had in mind were species, not individuals. A similar suggestion was proposed, in 1960, by Richard Lewontin, who discussed populations playing 'against Nature', with the survival of the species as payoff, and 'hedging their bets' against worst-case scenarios (Lewontin, 1960). In both cases, the essential ingredient was still missing: the local competition within a population, and the fact that a strategy's success depends on its frequency. The same applies to a paper by Verner (Verner, 1965) on sex ratios.

The first to explicitly use game theory to model intraspecies competition and frequency-dependent fitness values was William D. Hamilton, in his theory of extraordinary sex-ratios (Hamilton 1967). In fact, he considered both 'a play of the individual against the population', and pairwise competition (of two parasitoids within the same host). Maynard Smith had been familiar with that work since 1963, having been the external examiner in Hamilton's Ph.D. examination. He also understood that RA Fisher had used similar types of arguments in 1930 already, in order to explain the prevalence of 1:1 sex ratios, of course without couching his idea into the language of game theory (Fisher, 1930). A similar approach was taken up in 1965 by MacArthur (MacArthur, 1965).

In 1970, a maverick scientist from the US, George Price, submitted to *Nature* a paper explaining how animals using a strategy of retaliation could have a selective advantage in intraspecific conflicts. This allowed to understand the prevalence of ritualised behaviour in animal contests without recurring to explanations in terms of group selection. Maynard Smith was quick to see the merits of this approach. He had always been a fervent 'adaptationist' using optimisation arguments to explain the outcomes of natural selection. But he was impatient with all those who used such arguments in a muddle-headed way and thereby offered easy targets to the opponents of adaptationism. In particular, John Maynard Smith militated against all those using what Haldane had called Pangloss's Theorem (cf Maynard Smith, 1964; Maynard Smith, 1985). He had no patience with those (such as Julian Huxley or Konrad Lorenz) who argued that escalated contests would militate against the survival of the species. He kept pointing out the possibility of evolutionary traps, or Red Queen types of evolution. In particular, this was one of the reasons for his intense interest in sexual selection, and signalling theory (Maynard Smith, 1991).

In spite of the merits of the manuscript by Price, John Maynard Smith could not recommend publication, as it was far too long for *Nature*. He suggested either to publish it somewhere else, or to re-submit a shorter version, and then went for 3 months to Chicago, where he developed a formal definition of evolutionarily stable strategies, and applied this to study the 'Hawk-Dove-Retaliator' game and the 'War of Attrition'. He wrote later (Maynard Smith, 1976):

> When I came to write up this work, it was clearly necessary to quote Price. I was somewhat taken aback to discover that he had never published his idea and was now working on something else. When I returned to London I contacted him, and ultimately