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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 1976), 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. Furthermore, 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 eighteen-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 the 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 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 in the 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 sixty-four 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 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 twenty-five years later. Nash wrote:

`We shall now take up he `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, ten 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 intra-species 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 PhD 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, 1985), and 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. He had no patience with those (such as Huxley or Lorenz) who argued, for instance, that escalated contests would militate against the survival of the species.

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 three 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 we published a joint paper in which the concept of an evolutionarily stable strategy was applied to animal contests.´

Three aspects of that joint paper (Maynard Smith and Price, 1973) proved seminal. One was the emergence of the mathematical concept of an ESS, leading ultimately to the marriage of game theory and population dynamics. The second was the use of agent-based computer simulations. The third, of course, was the application of game theory to conflicts between animals, and more generally to non-rational players.

There is little to say here on the mathematical concept of an ESS, since the following article by a foremost expert will investigate this aspect in depth (see also Lessard, 1990). Suffice it to say, here, that an ESS is a behavioural program such that, if all individuals adopt it, no minority using another strategy can invade. In retrospect, this notion was found to be one of a great variety of related refinements of the concept of a Nash equilibrium, based on an underlying dynamics describing the potential invasion. In spite of owning a copy of Luce and Raiffa (1958), John Maynard Smith was not familiar with the vast literature on Nash equilibria and equilibrium selection which already existed. Peter Hammerstein, a PhD student which JMS shared with the eminent game theorist Reinhard Selten, put this to right, eventually. In the preface of his book on `Evolution and the Theory of Games' (Maynard Smith 1982), Maynard Smith writes that he owes a special debt to `Peter Hammerstein, who has helped [me] to understand some theoretical questions more clearly'. Nevertheless, he unabashedly kept confusing the concept of an ESS with that (more general) of a Nash equilibrium, or with that (more special) of an unbeatable strategy, which had been defined, although implicitly, by William Hamilton. His interest in the diverse ramifications of the concept remained limited, except when it had to be adapted to new biological situations, for instance asymmetric games, finite populations, games among relatives, transmission by learning, or by Mendelian heredity. On each of these issues, he wrote short, basic papers setting the matter straight (Maynard Smith and Parker, 1976, Maynard Smith 1988, Hines and Maynard 1979, Maynard Smith 1981a, Maynard Smith 1981b) and left it to others to elaborate the issues.

For John Maynard Smith, mathematics was a tool. He was (like his mentor JBS Haldane) a vigorous defender of what detractors called beanbag genetics, and never tired to stress that `mathematics is crucial for further progress in evolutionary biology´ (Maynard Smith 1982, reprinted 1988). His introductory textbooks played a pioneering role in teaching theoretical biologists not to be afraid of mathematics, and additionally in captivating mathematicians by biological problems (as I can testify). As John Maynard Smith wrote,

But mathematics was, in his hands, essentially a way of secure the results of his biological intuition: `If the mathematical analysis of some system predicts that it will behave in a particular way, one usually tries to gain some insight into why it should do so… If I cannot gain such an insight, I check the algebra, or the computer program, and expect to find a mistake.´ He added: `mathematics without natural history is sterile, but natural history without mathematics is muddled´ (Maynard Smith 1988).

Within the habitat of a biological faculty, it is relatively easy to acquire a reputation as mathematician. John Maynard Smith never tried to do so (although he gleefully boasted with the elliptic integrals occurring in Maynard Smith and Hofbauer, 1987). But he was well aware that the ideas which he developed could offer points of departure for mathematical theory, and viewed himself without false modesty as a gold mine for mathematicians.

John Maynard Smith liked to say that in his next life, he would want to be a programmer. He greatly enjoyed testing and developing simple programs, not necessarily of a biological nature. In fact, his paper with Price (Maynard Smith and Price, 1973) is one of the most successful early examples of agent-based modelling. In the intervening thirty years, this technique has been established as a tool for methodological individualism for the social sciences, due to no small part to the progress in programming languages, for instance Java. Maynard Smith (who always stuck to Fortran) followed the development in this field with keen interest and his usual passion for debate. Some of the most visible work in the area was performed in the Santa Fé Institute, and he commented it with a mixture of enthusiasm and irritation. The irritation arose whenever he felt that the biological background was not suitably analysed – he had little inclination to analyse phase transitions in cellular automata per se, for instance, removed from scientific motivations. But he was highly appreciative of all attempts aiming to view evolution in its broadest sense, including chemical evolution, or the evolution of genetic algorithms in artificial cyber-worlds, and not to restrict attention to the one evolving system which we are familiar with (Maynard Smith 1992).

Many of the evolutionary questions arising in his joint book with Eörs Szathmary, the `Major Transitions of Evolution´ (Maynard Smith and Szathmary, 1995), were social questions, dealing with the issue of units of selection (genes, organelles, cells, organisms) ganging up to form higher units of selection (genomes, cells, organisms, societies). Maynard Smith was fascinated by these issues. In the debate between group selection versus individual selection, he had been one of the most vocal participants. He viewed both game theory and agent-based simulations as equally useful tools for methodological individualism.

A few years after his Nature paper with Price, the applications of game theory to animal behaviour came in hard and fast, first in the form of studies of asymmetric conflicts (as between owner and intruder of a territory), and different forms of `wars of attrition´ and ritualised display behaviour. Soon it was understood that the same issues were presents in conflicts between plants (concerning tree height, for instance, or root shape) and of micro-organisms. Other applications concerned sex ratio, parental investment, mating behaviour, dispersal rates, alarm calls, or life histories. By now, the number of papers applying game theory to animal behaviour is in the thousands (see Dugatkin, 1997).

Inevitably, this scientific success story influenced the application of game theory to human interactions. The current boom of experimental games and learning theories is greatly influenced by evolutionary game theory. In addition to

economic interactions, the evolution of morals or of language was studied by means of game theoretical models (Ohtsuki and Iwasa, 2004, Nowak et al, 2001). This had a substantial impact on early forms of sociobiology and evolutionary psychology, but Maynard Smith kept his distance to these debates, possibly because they were so freighted with ideology. He deplored the `controversies…of that singularly useless type which take place when people do not understand each other`, and confessed:
`I find myself disagreeing most strongly with whichever I side I talked to last…´ (Maynard Smith, 1995)

He added: `For me, the applications of socio-biology to humans are peripheral´. This aloofness may seem strange in a person who was so eminently sociable, but it was completely natural to him. I well remember how gleefully he greeted the discovery that male lizards of the species *Uta stansburia* were engaged in a game with rock-paper-scissors structure (Maynard Smith 1998): `They have read my book!´

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