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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Introduction

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Introduction

John Maynard Smith is one of the most influential evolutionary biologists of our time. This year he celebrates his 80th birthday, and it seemed appropriate to mark this occasion with a collection of papers by his former associates, and distinguished evolutionists whose work has been influenced by his example. John is noted for his breadth of interests and his ability to spot important but soluble problems, which he continues to attack by deceptively simple methods. He has published 13 books and collections of papers on an astonishing diversity of subjects. He has also published many semi-popular articles on biology, which are remarkable for their clarity and diversity. He is a widely sought-after lecturer, who is famous for his humorous and lucid presentations.

After a sojourn at University College London, as undergraduate, postgraduate and staff member, John was the founding Dean of the School of Biological Sciences at the University of Sussex, where he has remained. He rapidly built Sussex up as a leading centre for biological research, especially in evolutionary biology, neurobiology, and experimental psychology. Numerous postgraduate students, postdoctoral researchers, sabbatical visitors and junior colleagues at Sussex, several of whom are contributors to this volume, have been deeply influenced by their interactions with him. John has always gone out of his way to encourage young talents, and he continues to display an engaging enthusiasm for interacting with scientists at all levels of experience.

Our aim in this volume is to display something of the breadth of areas of research in evolutionary biology that have been stimulated by John, to many of which he made the pioneering contributions. Much of his early career was devoted to the study of ageing, using *Drosophila* as the experimental organism. He provided one of the earliest demonstrations of the survival cost of reproduction (Maynard Smith 1958). The evolution of life-history traits in general, and ageing in particular, have since become key areas of research in evolutionary biology. Penetrating experimental studies of the quantitative genetics of life-history traits have been carried out on *Drosophila*, aimed at testing alternative models of life-history evolution. This approach is now being applied to the analysis of the seeming paradox of levelling of mortality rates late in life (Rose & Mueller, this issue).

John was also an early contributor to the development of theoretical models of molecular variation and evolution, stimulated by empirical studies of protein sequence evolution and electrophoretic variation that started in the 1960s. Modern developments in this field are discussed in this issue by Ohta, Slatkin, and Wichman *et al*. John's most influential early contribution was probably the model of 'hitchhiking' (Maynard Smith & Haigh 1974), whereby the spread of an advantageous mutation reduces variation at linked neutral loci. This theory has become an important component of the interpretation of data on natural variation in DNA sequences, as a result of the discovery that DNA sequence variation is greatly reduced in regions of the *Drosophila* genome that have low frequencies of genetic recombination. Various forms of hitchhiking are currently believed to be responsible for this phenomenon (Barton, this issue).

John has devoted much of his recent research to the analysis of data on molecular variation and evolution in bacteria. This has led to the realization that there is much more exchange of genetic information among bacterial cells in nature than was formerly believed (Maynard Smith *et al*. 1993). Recent extensions of this work by John and his co-workers have generated the provocative suggestion that human mitochondrial genomes may also experience evolutionarily significant amounts of recombinational exchange (Eyre-Walker, this issue).

John's writings on the evolution of sex and genetic systems have, of course, been enormously influential, and helped to transform this field from one of loose, group-selectionist, thinking to an area in which detailed population-genetics-based models are being challenged by empirical studies (Maynard Smith 1978). Four papers in this issue, on the evolution of Y chromosomes (Charlesworth & Charlesworth), split genomes in viruses (Nee), genomic imprinting (Haig & Wilkins), and sex ratios in primates (Packer *et al*.) illustrate this theme.

Perhaps John's most significant single contribution was his introduction (with George Price) of game theoretical methods for the analysis of complex evolutionary scenarios. These are based on the concept of the evolutionarily stable strategy (ESS): the idea that a necessary condition for a population to be at a stable equilibrium under natural selection is that a rare mutant phenotype will always be at a selective disadvantage. This permits the analysis of the effects of selection when relative fitnesses are dependent on the make-up of the population, without resorting to detailed study of the ensuing complex dynamics (Maynard Smith 1982). Parker (this issue) illustrates the application of ESS theory to the problem of defining modes of competition in behaviour and ecology, while Godfray & Johnstone (this issue) use the approach to analyse

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the evolution of signalling between parents and their offspring, as do Haig & Wilkins (this issue) in their examination of genomic imprinting.

John is also noted for his numerous contributions to the discussion of general questions in evolutionary biology, and of providing an evolutionary perspective on other areas of biology, such as ecology (Harvey & Rambaut, this issue) and development. Within evolutionary biology, he was an early and vigorous advocate of the importance of kin selection (which he named), as opposed to group selection, in the evolution of altruistic characters that are disadvantageous to their carriers (Queller, this issue). He has recently been applying concepts derived from evolutionary game theory to the problem of the 'major transitions' in evolution, in which radical shifts to new levels of organization take place (Maynard Smith & Szathmáry 1995). Questions of this kind are asked in this issue in the papers by Queller, Nowak, and Szathmáry.

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