Introduction

JOHN MAYNARD SMITH

The papers in this volume are concerned with two main topics – the concepts of sociobiology, and the ways in which hypotheses can be tested.

Much of the discussion of concepts takes the form of arguments about the meanings of words – fitness, altruism, replicator and so on. I do not think these arguments are purely semantic. Certainly, some difficulties have arisen because words have been used in different senses by different people; for example, the phrase 'group selection' has been used in such different ways that it has become almost meaningless. However, our difficulties could not be solved merely by an agreement to use words in particular ways. The trouble is, of course, that we would not agree on appropriate meanings. The reason would not be obstinacy on our part. It would be that words are the means whereby we order our thoughts. Consequently, if two scientists see the world in different ways, they will want to use words differently to describe it.

In this introduction I want to suggest that two main concepts have dominated the study of the evolution of social behaviour during the past fifteen years, but that in the last four years a third idea, not in fact a particularly new one, has been increasingly prominent.

Of the two dominant concepts, the first, tracing back primarily to the work of John Crook, is that social systems should be seen as ecological adaptations. The second, which we owe mainly to W.D. Hamilton, is that the evolution of behaviour is influenced by the fact that the genes of relatives may be identical. The latter idea has had an extraordinary fascination for biologists. Theoreticians have been attracted by its intellectual elegance, and by the fact that it offers an explanation for what would otherwise by an anomaly – the existence of behaviour patterns which do not increase the classical fitness of the individual displaying them. Field

workers have been impressed by the observation that, far more often than not, societies do consist of relatives. There may be another reason for the fascination; students of Hamilton would not be surprised to find that scientists are obsessed by kinship.

I do not doubt that biologists have been right to be excited by these two concepts. However, I think that an interest in kinship may have blinded some of us to a third idea. This is the very obvious one that two animals may cooperate because it pays both of them to do so. This is not a new idea, and it has not been wholly missing in discussions of sociobiology, but its importance may have been underrated. The process has usually been called 'mutualism'. When writing my own chapter in this book, I had some reservations about the term, because it has usually been used by ecologists to refer to interactions between members of different species. On reflection, however, I can see little danger in its use; the term competition is used both for inter- and intraspecific interactions, so why not mutualism? It will always be possible to add a qualifying adjective when there is any possibility of confusion.

It seems likely, then, that the immediate future of sociobiology will be concerned with the joint effects of mutualism and of kin selection on the evolution of societies, subject to particular ecological constraints. This future is clearly foreshadowed in this volume.

The testing of hypotheses has become a sensitive subject among sociobiologists. Who wants to be accused of telling Just So stories? Perhaps the most promising thing that has happened – also reflected in this volume – is the recognition that the statistical analysis of comparative data calls for just as much care and sophistication as the analysis of experimental results. However, in one field that interests me – that of sex ratio – our difficulty is not that we can think up a variety of hypotheses to explain the data and are unable to decide between them, but that we are unable to think of any adequate hypothesis. This is a disturbing state of affairs, but at least it suggests that if we can formulate a hypothesis which makes quantitative predictions, we ought to be able to test it.

It is hard to think about animal societies without wondering what light they may shed on human ones. Although only one chapter in this book is specifically concerned with man, the question is certainly in the minds of several of the contributors. I cannot answer it, but I will make some comments. The first is a very general one. The explanations of animal societies offered by biologists are essentially reductionist. That is, they attempt to explain the structure of societies as a consequence of the properties of the individuals which compose them. By no means all

sociological or anthropological theories are of this kind. Theories in economics are reductionist; even Marxist theories of capitalist economic systems assume that individuals behave so as to maximise their profits, or the return on their labour, although Marxists would insist that the particular goals of individuals are socially determined. But many sociological theories are not reductionist even in this limited sense. The properties of individuals are seen as produced by society, and even as serving the purposes of that society, and not the other way round. If sociobiologists are to persuade sociologists that their ideas and methods are relevant to man, the first thing they must establish is that reductionist theories of *some* kind are relevant; it is a further, and to my mind more doubtful, step to persuade them that the concept of inclusive fitness is appropriate to human behaviour.

While reading about human sociobiology during the past few years, one thing has struck me very forcibly. The works which I have found most interesting have not been those which, whether for or against, have dealt with general or philosophical issues, but those which discuss specific societies, as do, for example, Dickeman, Irons and Chagnon. There is, however, a question which often remains unanswered by those who apply sociobiological concepts to man. What *kind* of explanation are they offering? I can think of at least two answers to this question, but I suspect that there are many more. The first would be that they are seeking an explanation of why particular social systems are associated with particular ways in which people obtain the necessities of life – i.e. with particular ecologies. This would be analogous to the first problem of sociobiology – why do particular animal social systems evolve in particular ecological circumstances?

There is, however, a second kind of explanation. One could accept the rules and customs of a society as given, and ask whether the actions of different people in that society – rich and poor, old and young, male and female – are those which would be predicted if each individual is behaving, subject to the rules, in the way which would maximise his or her inclusive fitness. In the same vein, one could also ask whether, if people do act in such a way, the results of their actions will preserve the society or transform it. It may be that few sociobiologists think that inclusive fitness can be applied in such a direct manner. If so, it would help if they told us what they do think. It cannot merely be that human behaviour is influenced by kinship, and that kinship has something to do with genetic relationship, because surely, despite some very odd remarks by anthropologists, that is uncontroversial?

I

Natural selection and sociobiology

Edited by
R.W. WRANGHAM

It is a remarkable tribute to Darwin that ideas whose seeds he planted more than a hundred years ago are still developing with enormous vigour. Sociobiology is a prime example. Since 1964 it has blossomed into a rapidly changing discipline growing along several different branches. As with any such endeavour, this process brings not only excitement but also a danger of overextension: the beauty of new ideas can obscure their proper interpretation. In acknowledgment of sociobiology's sudden growth, therefore, the essays in Section 1 are directed to taking stock of issues at the root of the discipline.

First, Dunbar examines the nature of evolutionary explanations. He takes up the familiar accusation that Darwinism is tautological, arguing that although the accusation is wrong it is useful because it draws attention to limitations in the ways evolutionary theory should be used. The intuitive appeal of sociobiological explanations hides a number of traps, and Dunbar discusses how some of them can be avoided. Among other things he calls for a more careful use of language, undoubtedly a necessary step on the path to a strong science and one which is overdue in the present instance.

The second chapter concerns altruism, a subject of central importance in the modern development of sociobiology. In 1964 Hamilton provided the first satisfactory explanation for its evolution, and here Maynard Smith discusses subsequent theoretical advances. The diversity of recent proposals concerning the evolution of altruism is more than enough to cause confusion, and we are still a long way from a coherent theory. Maynard Smith clarifies the field by identifying five mechanisms by which altruism might be favoured, and by pointing out their different assumptions and implications. Kin selection has traditionally been the most important and it

is given special attention here because two distinct methods have been proposed for analysing its effects. By outlining the merits of each Maynard Smith shows how they can be reconciled. His chapter thus points the way to an integration of the mechanisms of social evolution more sophisticated than is currently available.

The recent focus on altruism has been accompanied by extensive discussion of the level at which natural selection is supposed to act. The mid-1960s saw a solid attack on group selection theory, leading ultimately to a reconsideration of individual selection, and the concept of the selfish gene. The debate concerns the merits of groups, individuals and genes as 'units of selection'. These have sometimes been treated as similar kinds of 'unit', a view which Dawkins devotes chapter 3 to rejecting. He shows that two distinct arguments are involved in discussions of the level at which selection acts, and holds that the conflict between 'individual-selectionists' and 'gene-selectionists' is more apparent than real because the processes which they describe are complementary. Sociobiology's reductionism is therefore seen as a tool for understanding complexity rather than as a dismissal of the importance of individual characteristics. Dawkins' essay should do much to clear up a major source of misunderstanding.

In the final chapter of this section O'Donald discusses one of the most important questions in the logical structure of kin-selection theory: what is the basis for the idea that natural selection leads to the maximisation of inclusive fitness? Given the widespread acceptance of Hamilton's theory it is perhaps surprising that this needs to be asked at all. There is a variety of outstanding difficulties, however. For instance, the original proof lacks generality: the assumptions it makes about population structure mean that for many species its conclusions are invalid. Another problem concerns the use of words. Many authors use the term 'inclusive fitness' to refer to actual personal fitness plus the fitness of relatives devalued by the coefficient of relationship. Though this definition is helpful because it allows inclusive fitness to be measured easily, it is not what Hamilton showed to be maximised. O'Donald discusses a third issue. He argues that the classical methods of population genetics are inadequate for modelling the spread of genes which influence the fitness of kin. In particular, it is necessary to take gene frequencies into account in new ways when calculating subsequent changes in gene frequency. O'Donald argues that when this is done inclusive fitness values can still be regarded as independent of gene frequency. Like Maynard Smith he goes on to conclude that so long as the effects of a given behaviour are small the spread of genes responsible for it can be modelled accurately by simple methods. In other cases, however, they

cannot. His analysis brings a valuable level of precision to models of the evolution of social behaviour and illustrates how carefully sociobiology must proceed.

1

Adaptation, fitness and the evolutionary tautology

R.I.M. DUNBAR

'... for it was a kind of cloud that overshadowed knowledge for a while and blew over.'
(Francis Bacon, *De Augmentis Scientiarum*, 1623.)

Introduction

As the major unifying force in biology, Darwin's theory of evolution by natural selection remains virtually unchallenged by serious contenders after more than a century of debate. Yet, it frequently stands accused of being tautologous by both philosophers of science (Smart, 1963; Manser, 1965; Popper, 1972) and biologists (Birch & Ehrlich, 1967; Peters, 1976) alike. Although a number of philosophers (Ruse, 1973; Hull, 1974) and biologists (Maynard Smith, 1969; Thompson, 1981) have argued against this criticism, many biologists are inclined to dismiss it as either vacuous or at best irrelevant to the way in which they conduct their research. Such a response, of course, leaves the main thrust of the criticism unanswered, a fact that would be of only passing significance were it not the case that the criticism, if true, leaves evolutionary biology based on such weak foundations that its pursuit as a serious scientific discipline becomes a trivial exercise in dogmatism in the worst sense (cf. Feyerabend, 1963).

In this chapter, I will try to show that the criticism of circularity is ill-founded because it rests on a mistaken view of the structure of Darwinian explanations. I will argue that although a correct formulation of Darwinian explanations resolves the circularity without issue, it does so at the expense of placing some significant restrictions on the metaphysical framework within which most sociobiologists operate. These restrictions have more important consequences than the original criticism.

The structure of evolutionary explanations

The Darwinian formula

Darwinian explanations are conventionally conceived as involving a three-step argument (see Maynard Smith, 1969; Williams, 1970; Hull, 1974). Lewontin (1978), for example, states that three steps (or principles as he calls them) are 'necessary and sufficient to account for evolutionary change by natural selection', namely,

> 'Different individuals within a species differ from one another in physiology, morphology and behaviour (the principle of variation); the variation is in some way heritable, so that on average offspring resemble their parents more than they resemble other individuals (the principle of heredity); different variants leave different numbers of offspring either immediately or in remote generations (the principle of natural selection)'.

Unfortunately, it is this formulation that lies at the very root of the criticism of circularity, for it offers us no necessary reason why different variants should leave different numbers of offspring other than the fact that they do indeed do so.

The problem, in a nutshell, is this: if the criticism is valid, then evolutionary explanations are reduced to mere descriptions of observed fact. Statements that appear to offer explanations for the evolution of particular characters turn out on closer analysis to be no more than restatements in definitionally equivalent form of the facts that they purport to explain. More specifically, if the terms 'survival' and 'fittest' in Darwin's unfortunate catch-phrase 'the survival of the fittest' can only be defined (or at least recognised operationally) in terms of each other, then the phrase merely observes that 'the survivors survive'. Any pretence at genuine explanation dissolves away, since definitions explain nothing. A particularly lucid explanation of this difficulty has recently been given by Brady (1979).

There is a widespread belief that, because each of the three statements can be empirically verified, the formulation cannot be tautological (see for example Connolly, 1966). Unfortunately, this claim misses the point entirely. That the principles can be shown to be empirically true is not in dispute; but the argument so formulated remains a simple description of observed facts, and no amount of empirical evidence will turn it into an *explanation* of those facts (except in the trivial sense that an account of the biochemical bases of heredity is an explanation of *how* evolution is brought about – though it is not an answer to the evolutionary biologist's problem of *why* it is brought about*). The fundamental purpose of science is to

*I should stress that, in saying this, I do not mean to belittle the achievements of molecular geneticists, but merely to point out that an explanation at one logical level need not, and often will not, be an explanation at another level. This distinction is commonly blurred, and the resulting obfuscation has made nonsense of an already murky area.