

Introduction

The evolution of society

Although the social mechanisms responsible for the development and maintenance of societies in animals and man have fascinated and intrigued philosophers and scientists since classical times, the first systematic consideration of their evolution appears in the *Origin of species* (Darwin 1859/1958). Much of Darwin's thinking about the evolution of societies in animals and humans has a distinctly modern feel about it and he commonly anticipates theoretical developments that only occurred 100 years later. Although he did not confront the problem of altruistic behaviour directly, he was aware of the challenge to his theory posed by the evolution of sterile castes in some social insects (Darwin 1859/1958). In Chapter VIII of the '*Origin of species*', he describes how he thought, at first, that this was fatal to his whole theory of natural selection. Then, in a paragraph that presages Hamilton's subsequent extension of evolutionary theory, he describes how he realised that 'the problem is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end.' (Darwin 1859, p. 230).

In *The descent of man* (1871), Darwin turned to the evolution of human societies. In Chapter VI, he stresses the contrast between humans and other animals 'I fully subscribe to the judgement of those writers who maintain that of all the differences between man and the lesser animals, the moral sense or conscience is by far the most important' (*The descent of man*, p. 97). He then goes on to argue that the evolution of mutual assistance and the moral senses in humans and other animals are maintained by benefits shared by members of cooperative groups, a suggestion that clearly parallels modern theories of social evolution (Boyd & Richerson 1996; Clutton-Brock 2002). He goes on to point out that many animals live in groups and cooperate with each other and describes how 'wolves and some other beasts of prey hunt in packs, and aid one another in attacking their victims', how 'pelicans fish in concert' and 'social animals mutually defend each other'. He describes how vervet monkeys stretch out and groom each others coats and ends by telling a story illustrating the benefits of cooperation:

'an eagle seizes a young *Cercopithecus*, which by clinging to a branch, was not at once carried off; it cried

loudly for assistance, upon which the other members of the troop, with much uproar, rushed to the rescue, surrounded the eagle, and pulled out so many feathers, that he no longer thought of his prey, but only how to escape. This eagle as Brehm [the source of the story] remarks, assuredly would never again attack a single monkey of a troop' (p. 101, 102).

For nearly a 100 years from Darwin's death, scientific attention was focussed on mechanistic and developmental questions rather than functional ones and Darwin's interest in social evolution and his holistic view of biological adaptation were eclipsed by the growth of other biological subdisciplines. A continuing interest in social behaviour was maintained though the research and writings of naturalists like Henri Fabre, Eugene Marais, the Keatons, Edmund Selous and Eliot Howard. However, although they were experienced naturalists and observers, they lacked Darwin's theoretical structure, his compelling interest in principles and his readiness to confront exceptions and difficulties.

Not until the late 1930s did a substantial number of professional biologists start to work on the social behaviour of animals. They fell into three main groups. First, there were the founding fathers of animal behaviour, including Julian Huxley (1934, 1938), Konrad Lorenz (1927, 1931, 1935), Niko Tinbergen (1931, 1935, 1936, 1937), Karl von Frisch (1938), Frank Fraser Darling (1937, 1938), Solly Zuckerman (1929, 1932) and Clarence Ray Carpenter (1934, 1935, 1940). Their primary focus was usually on questions concerning the control and development of behaviour, though their research sometimes encompassed functional or comparative aspects of reproductive behaviour. Second, there were a number of animal ecologists, including David Lack (1932, 1933, 1935, 1939, 1943) and A. F. Skutch (1935, 1945, 1960) whose primary interests were the regulation of population density and the evolution of reproductive parameters, including egg size and clutch size. And third, there were the population geneticists, including Ronald Fisher (1930) and J. B. S. Haldane (1932) and later, G. C. Williams (1957) whose principal focus was on the operation of natural selection and the evolution of genetic systems, but whose interests also encompassed the evolution of life histories and social behaviour. Unlike the first two groups, they were well aware of the problems raised by social and altruistic behaviour, though these were tangential to their main interest and usually attracted only passing comments.

One contribution of 16 to a Discussion Meeting Issue 'The evolution of society'.

These three distinct lines of thinking persisted into the 1950s and they were still largely separate by the end of that decade. For example, neither of Niko Tinbergen's two synthetic books, *Social behaviour in animals* (1953) and *The study of instinct* (1955) cite either Darwin or Fisher. However, by 1960, both theoretical and empirical research was beginning to turn to topics that overlapped all three areas of interest. Comparative studies of social behaviour (especially studies of birds by Gordon Orians (1961, 1962) and John Crook (1962, 1964, 1965) revealed that the size and structure of social groups and the form of mating systems were closely related to variation in habitat and diet, stimulating interest in functional interpretations of social behaviour and providing detailed examples both of selfish and altruistic behaviour. In addition, research on population dynamics in birds showed that territoriality played an important part in regulating population density, focusing the interests of ecologists and ethologists on its evolution and function (Lack 1954, 1966). Finally, the development of a theoretical framework accounting for the evolution of life histories (Medawar 1952; Cole 1954; Williams 1957) led to a growing interest in the adaptive significance of apparently altruistic behaviour.

Two specific developments acted as catalysts for the rapid changes that followed. The first was the publication of Wynne Edwards' monumental book *Animal dispersion in relation to social behaviour* (1962). Wynne Edwards claimed that many animals adaptively limited their numbers in advance of resource shortage to improve the probability that the group or population would survive. Group displays had evolved, he suggested, to allow their members to assess population density and to adjust their reproductive output accordingly. Other aspects of social behaviour, including territoriality and dominance hierarchies, were closely involved in the regulation of animal numbers and had evolved for this purpose. Wynne Edwards' theory was directly contrary both to Darwin's persistent emphasis on individual variation in reproduction as the keystone of evolution as well as to the perception of many ecologists that animal populations were limited directly by the availability of resources (Lack 1954, 1966) so neither population geneticists nor ecologists could ignore the challenge. The general application of Wynne Edwards' theory was attacked and refuted (Hamilton 1963; Maynard Smith 1964; Lack 1966; Williams 1966*a,b*) and the ensuing controversy drew attention to the fact that many functional explanations of social and reproductive behaviour relied on putative benefits to groups or populations. This eventually led to a critical reevaluation of many of these ideas, culminating in G. C. Williams' influential review of adaptation (1966).

The second development was the explanation of altruism and sterility in Hymenoptera by W. D. Hamilton. In 1963, Hamilton published a brief paper arguing that altruism could evolve if it increased the fitness of relatives and, the following year, introduced the concept of inclusive fitness to account for the evolution of worker sterility in Hymenoptera and of alarm calls in vertebrates (Hamilton 1964). Subsequently,

Maynard Smith (1964) named Hamilton's process 'kin selection' to distinguish it from group selection and used it to produce a formal model of the evolution of alarm calls (Maynard Smith 1965). In contrast to many of his contemporaries working on the evolution of vertebrate-breeding systems (see above), Hamilton's thinking owed much to Fisher. He describes how his interest in the evolution of animal societies and altruism.

'began for me while I was an undergraduate reading natural sciences at the University of Cambridge in 1958. I discovered R. A. Fisher's *The genetical theory of natural selection* in the St John's College Library and immediately realised that this was the key to the understanding of evolution that I had long wanted. I became a Fisher freak and neglected whole courses in my efforts to grasp the book's extremely compressed style and reasoning. I quickly noticed, however, that Fisher's arguments implied a basically different interpretation of adaptation from what I was hearing from most of my lecturers and reading in other books. Was adaptation mainly for the benefit of species (the lecturers' view) or for the benefit of individuals (Fisher's view)? Clearly it was Fisher who had thought out his Darwinism properly; where interpretations differed, therefore, he must be right—but were the others *always* wrong? I started on what seemed the key theme in this puzzle—*altruism*. Did it exist? Could one evolve it in a model?

(Hamilton 1988, p. 15)

Hamilton's theory of kin selection (Hamilton 1964) provided the basis for adaptive interpretations of many forms of altruistic and cooperative behaviour. However, there were some types of cooperation that could not be explained in this way. In particular, why should members of different *species* (who could not possibly be closely related) cooperate with each other? And why should unrelated conspecifics sometimes assist each other? One possible explanation was that, as Darwin had suggested, cooperating individuals gained shared mutualistic benefits but explanations of this kind smacked of group selection and had difficulty in explaining why cooperation was not replaced by cheating strategies. An alternative explanation of apparently altruistic actions involving unrelated individuals was produced by R. L. Trivers in 1971. Trivers argued that if individuals assisted each other in turn and the costs of assistance were relatively low to donors while the benefits were high to recipients, reciprocal assistance (reciprocity) could evolve among individuals that were unrelated to each other. Cheats (individuals who accepted favours but did not return them) might initially be at an advantage but selection would subsequently favour individuals that discriminated against them and cooperated selectively with individuals that had assisted them in the past. This form of cooperation was originally referred to as 'reciprocal' altruism but this can lead to confusion since cooperation of this kind is mutually beneficial in the long term rather than altruistic (Dugatkin 1997; West *et al.* 2007; Clutton-Brock *in press*).

The theoretical basis of much of our current understanding of the evolution of breeding systems was laid during the decade following the publication of

Hamilton's theory of kin selection (Hamilton 1964). Hamilton's (1971) 'selfish herd' theory showed that sociality itself could confer benefits to individuals without benefiting the entire group if the chance that an individual would be selected by a predator was diluted as the number of individuals close to it increased. He subsequently examined the conditions favouring selfish and spiteful behaviour within social groups (Hamilton 1964, 1971, 1972). Maynard Smith (1974) and Parker (1974) introduced game theory models to explain why competitors did not always seek to maximize damage to their opponents and to account for 'ritualization' of aggressive behaviour. Trivers (1974) explored conflicts of interest between parents and their offspring arguing that, in sexually reproducing organisms, the genetic interests of parents will commonly differ from those of their progeny, who should often favour higher levels of parental expenditure higher than their parents' optima. Darwin's writing on sexual selection was re-examined and extended. Trivers (1972) argued that the reasons why males typically compete more intensely for mates than do females was linked to their lower expenditure on progeny, coining the term 'parental investment' to cover all forms of parental expenditure associated with rearing offspring. Fisher's (1930) explanation of the equality of most vertebrate sex ratios was re-assessed and Hamilton (1967) showed that the strongly female-biased sex ratios could be favoured where competing males were close relatives. Trivers & Willard (1973) argued that, in sexually dimorphic vertebrates where sons were more costly to rear than daughters, females who conceived sons but could not afford to rear them should prematurely terminate investment in their progeny—and suggested that this might account for the common trend for mortality to be higher in juvenile males than females. Adaptive explanations of life histories developed in a less dramatic fashion. A number of important reviews laid the basis of what is now known as life-history theory (Gadgil & Bossert 1970; Wilson & Bossert 1971; Pianka 1974; Stearns 1976; Charlesworth 1980). Over the same period, empirical studies of animal breeding systems began to proliferate, focusing more and more on issues of theoretical interest (Lack 1968; Wilson 1971; Clutton-Brock 1974; Jarman 1974).

This period of rapid development of theory culminated in a second monumental book. E. O. Wilson's *Sociobiology, the new synthesis* (Wilson 1974) contained relatively few new developments but provided comprehensive reviews of relevant areas of population genetics, demography, life-history theory and animal behaviour. Wilson stressed their inter-relatedness and defined a new sub-discipline, sociobiology, whose principal goal should be 'an ability to predict features of social organization from a knowledge of population parameters combined with information on the behavioural constraints imposed by the genetic constitution of the species'. He argued that an understanding of the evolution of population parameters (including life history variables) should be one of the principal aims of evolutionary ecology and population biology and predicted that, by the year 2000, sociobiology and behavioural ecology would

have become closely allied with population biology and genetics, while traditional ethology and comparative psychology would have been progressively integrated with neurophysiology. The first component of his prediction came about more rapidly than he had anticipated for the theoretical issues raised by the papers of Hamilton, Trivers and Maynard Smith rapidly became the focus of attention in behavioural biology and soon led to the development of an integrated conceptual framework for explaining the ecology and evolution of social behaviour (Krebs & Davies 1978).

After the publication of Wilson's (1975) review, research on social evolution expanded rapidly. The ideas of Hamilton, Trivers, Maynard Smith and Parker were explored, extended and tested (Krebs & Davies 1984; Krebs & Davies 1991, 1997). A combination of theoretical and empirical studies investigated the contrasts and parallels between cooperative and competitive interactions at different levels—between genes on the same chromosome, between cells and groups of cells, between individuals, families, groups and populations (Wilson 1980; Maynard Smith & Szathmary 1995; Michod & Roze 2001; Hoekstra 2003; Okasha 2006). Building on research on the development of social relationships (Hinde 1974, 1983), research on social vertebrates (and primates in particular) explored the development and maintenance of relationships and the ways by which individuals attempt to manipulate the behaviour of others to their own advantage (Clutton-Brock & Parker 1995*a,b*; Whiten & Byrne 1997), and the tactics they use to resolve conflicts (de Waal 1993; Aureli & de Waal 2000). New fields of research developed round the evolution of signalling systems (Zahavi 1975; Grafen 1990), cooperation between non-relatives (Axelrod 1984; Sachs *et al.* 2004; Bergmüller *et al.* 2007*a*), the evolution of cooperative breeding (Brown 1987), the extent and causes of reproductive suppression (Vehrencamp 1983*a,b*) and the resolution of conflicts within social groups (Trivers & Hare 1976; Ratnieks 1988; Boomsma & Grafen 1990; Ratnieks *et al.* 2006). The adaptive significance of life-history parameters was explored and examined and new theories were developed to account for variation in fecundity (Stearns 1976; Alexander 1991; Bourke 1999), mate choice (Lande 1980; Lande & Arnold 1983), sex allocation (Charnov 1982; Bull 1983; Frank 1990; West 2009), parental care (Clutton-Brock 1991; Godfray 1995*a,b*) and longevity (Bourke 2007). Following the development of genetic techniques capable of identifying paternity (Jeffreys *et al.* 1985) it soon came to be appreciated that competition between males extended beyond mating (Birkhead & Møller 1992). These empirical advances were associated with theoretical developments that clarified the links between inclusive fitness and other branches of evolutionary theory, including population and quantitative genetics (Grafen 1985; Frank 1986; Taylor 1990; Queller 1992; Taylor 1996; Wolf *et al.* 1999; Rousset & Ronce 2004; Gardner *et al.* 2007), making it easier to develop more general models (Taylor & Frank 1996; Frank 1998) and allowing the biology to lead the maths, rather than vice versa.

Over the same period, long-term studies of recognizable individuals provided novel insights into animal societies as well as the information necessary to explore new questions (Clutton-Brock *et al.* 1982; Woolfenden & Fitzpatrick 1984; Koenig & Mumme 1987; Betzig *et al.* 1988; Hoogland 1995). In addition, the increasing range of societies that had been examined in detail generated reviews of social behaviour and breeding systems in insects (Wilson 1971; Bourke & Franks 1995; Choe & Crespi 1997), fishes (Thresher 1984), birds (Brown 1987; Koenig & Dickinson 2004) and non-human mammals (Jarman 1974; Smuts 1986*a,b*; Gittleman 1989; Mann *et al.* 2000; Wolff & Sherman 2007). Quantitative comparisons of interspecific data were used to test evolutionary hypotheses and to explore relationships between social behaviour, life histories and ecological parameters (Clutton-Brock 1974; Clutton-Brock & Harvey 1978, 1979; Harvey & Pagel 1991). The framework of evolutionary thinking was also extended to the analysis of human behaviour, relationships and societies (Daly & Wilson 1983; Betzig *et al.* 1988; Barrett *et al.* 2002; Hrdy 2009). Theoretical studies investigated the evolution of the unusual characteristics of humans, including the development of culturally acquired adaptations (Boyd & Richerson 1996). In parallel, empirical studies of tribal societies generated quantitative data on behaviour, energetics, life-history parameters and demography that could be used to test ecological and evolutionary theories and predictions (Betzig *et al.* 1988; Borgerhoff Mulder 1988; Hill & Hurtado 1996).

Today, we understand more about the evolution of society than Darwin did. Nevertheless, the field of social evolution continues to develop rapidly and there are still many unresolved problems and many contentious areas. There is an ongoing debate as to whether social systems should be regarded as superorganisms with adaptive characteristics of their own or whether they are best interpreted as byproducts of the adaptive strategies of individuals (Okasha 2006; Wilson & Wilson 2007). There is still disagreement about the distinction between kin selection and group selection as well as about the relative importance of selection operating at different levels (West *et al.* 2007, 2008; Wilson & Wilson 2007) and the relative importance of mutualism, reciprocity and coercion in maintaining cooperative behaviour is contentious (Clutton-Brock 2002, *in press*; West *et al.* *in press*). Evolutionary explanations of sex differences have recently been the target of criticism (Gowaty 2004; Tang-Martinez & Ryder 2005) and some would even like to see the theory of sexual selection abandoned altogether (Roughgarden *et al.* 2006; Roughgarden 2009). Contrasting models of variation in reproductive skew and the proximate mechanisms responsible for reproductive suppression in cooperative societies are still widely debated (Vehrencamp 1983*a,b*; Reeve & Keller 1995; Clutton-Brock 1998; Clutton-Brock *et al.* 2001*b*; Creel & Creel 2001; Magrath *et al.* 2004). Finally, there is little agreement over the origins of human society; the sequence in which human characteristics developed or the relevance of studies of animal societies to understanding those of humans (Rodseth *et al.* 1991; Wrangham *et al.* 1999; Zhou *et al.* 2004; Hrdy 2009).

This issue of *Philosophical Transactions* brings together papers presented at a Discussion Meeting in January 2009 where 15 scientists were invited to review important issues relevant to our understanding of the evolution of society in animals and man. Our aim was to explore similarities and contrasts in evolutionary mechanisms in different groups of organisms and the relevance of studies of animal societies to humans. In the opening chapter, Grafen examines the current status of inclusive fitness theory, while Queller compares the cooperative interactions between different types of units to identify the level at which selection and adaptation occur. West explores the evolution of cooperative and cheating strategies in bacteria and suggests that an understanding of these processes may provide novel ways of controlling populations. Social insects provide many examples of the most highly developed and best studied animal societies and four subsequent chapters explore the origins of eusociality (Boomsma), the distribution of reproductive success and cooperative behaviour within groups (Field & Cant), the evolutionary mechanisms maintaining extreme altruism and reproductive inequality (Ratnieks & Helanterä) and the genetic mechanisms controlling behaviour on which selection operates (Keller). The four subsequent chapters examine the less specialized societies of non-human vertebrates. Hatchwell reviews the distribution of cooperative breeding in birds, while Clutton-Brock reviews our understanding of mammalian societies and their consequences for the evolution of life histories. Silk subsequently investigates the extent of nepotism in primates, while Hauser assesses the importance of reciprocity and spite in relationships between non-relatives. The last four chapters examine the evolution of human societies. Foley & Gamble review our current understanding of the societies of hominids and early humans; Boyd & Richerson explore the role of cultural adaptation and gene-culture coevolution in the development of pro-sociality in humans; Kaplan assesses the importance of ecological benefits and energetic constraints on the evolution of human societies; and Dasgupta explores the role of trust in the development and maintenance of cooperation between economic units. By the end of the meeting, there was a general consensus that the integration of different approaches to investigating the evolution of society and of studies of contrasting organisms was overdue and should be an important component of future research. Our hope is that this issue will contribute to this process.

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