



# MAMMAL

# SOCIETIES

Tim Clutton-Brock



WILEY Blackwell



## **Mammal Societies**



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**WILEY**

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# Preface

The core of Darwin's theory of natural selection is the realisation (based on Malthus's demographic projections) that the rate of population increase will inevitably lead to competition between individuals for resources and reproductive opportunities, and that competition will favour individuals that are well adapted to the environments they live in, with the result that their heritable characteristics will increase in future generations. Empirical research on population ecology since Malthus has provided extensive evidence to support Darwin's argument, while research in evolutionary biology and population genetics has confirmed that favourable mutations are likely to spread.

Natural selection adapts animals to the ecological niches that they occupy. Early explorations of animal adaptation mostly examined relationships between anatomical traits and the challenges imposed on different species by their physical environments. More recently, research has documented the impact of the social environment on the selection pressures operating on both sexes and on the evolution of behavioural, physiological and anatomical adaptations. In addition, an increasing range of studies have explored the consequences of contrasts in social organisation and the adaptations they generate for ecological processes within and between species, as well as for other areas of biology, including population genetics, epidemiology and conservation biology.

While there have been excellent reviews of the social behaviour of particular Orders of mammals, there have been few attempts to integrate research across mammalian groups and more extensive reviews of social organisation are available for ants and birds than for mammals. My aim in writing this book was to produce an integrated account of the evolution of mammalian societies within the framework provided by theoretical and empirical research on social evolution. As one of the main reasons for studying animal societies is to provide a general perspective on studies of the evolution of human societies, I particularly wanted to integrate research on primates

with studies of other mammalian groups in order to explore the extent to which studies of non-human mammals (including non-primates as well as primates) provide insight into the evolution of hominin societies and human behaviour. Finally, as well as exploring the evolution of variation in the structure and organisation of mammalian societies, I wanted to examine what is known of the consequences of variation in social behaviour and breeding systems for ecological processes.

In contrast to birds, most mammals are polygamous and the structure of mating systems has important effects on the selection pressures operating on females and males and the distribution of sex differences in anatomy, physiology and behaviour. In many mammalian species, different factors determine the distribution of the two sexes: while the need to maintain access to adequate resources and to avoid predation commonly structures the distribution and behaviour of females, selection to maximise access to females often has a more important influence on the distribution and behaviour of males. As a result, although the behaviour of the two sexes coevolves, it is often useful to consider the behaviour of females and males separately. I have consequently organised the book to focus first on the behaviour and reproductive strategies of females and then on those of males. The first chapter provides a brief review of the body of theory relevant to the evolution of social behaviour that has built up over the last 40 years. Chapters 2–9 deal with different aspects of female behaviour in non-human mammals, including sociality, the kinship structure of female groups, mate choice, maternal care, social development, communication and the distribution of competition and cooperation. Subsequently, Chapters 10–16 cover similar topics in males. Chapter 17 then examines the evolution of cooperative breeding systems and Chapter 18 explores the evolution of sex differences in behaviour, physiology and anatomy. Finally, Chapters 19 and 20 provide an introduction to related research on the evolution of breeding systems and social behaviour in hominins and humans.



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Josephine Pemberton and Loeske Kruuk have also been continuously involved.

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## CHAPTER 1

# Social evolution

Nothing in biology makes sense except in the light of evolution.

*Theodosius Dobzhansky*

### 1.1 Origins

Life is full of dangers, competition for resources and reproductive opportunities is universal and all life forms need to be well adapted to the physical and social environments they occupy in order to grow, survive and breed. While an appreciation of the adaptedness of animal behaviour extends back into antiquity, the modern understanding of adaptation as a consequence of natural selection originates with the work of Darwin (1859, 1871) and Wallace (1870, 1878). In the *Origin of Species* Darwin reviews the diversity of animal adaptations for survival while in *The Descent of Man* he focuses to a greater extent on the evolution of reproductive adaptations as well as on human evolution.

The fundamental importance of Darwin's theory in explaining variation in the morphology, physiology and behaviour of animals was quickly appreciated by his contemporaries. 'If you ask whether we shall call this the century of iron, or of steam, or of electricity', wrote Ludwig Boltzman in 1886, 'then I can answer at once with complete conviction: it will be called the century of the mechanistic understanding of Nature – the century of Darwin' (Boltzman 1905).

But it wasn't. After Darwin's death, scientific attention focused on developmental questions rather than functional ones and his holistic view of biological adaptation was eclipsed by the growth of other biological sub-disciplines. As a result, the true century of Darwin was delayed for nearly 100 years, and is not yet over.

When functional questions were considered in the years following Darwin's death, they mostly related to anatomical adaptations to the physical environment. Before the 1930s, systematic studies of the behaviour and ecology of animals in natural populations were scarce and most were the work of naturalists, sociologists or philosophers who lacked Darwin's theoretical structure, his compelling interest in principles and his readiness to confront apparent exceptions. In many cases, they were satisfied with accurate descriptions of the biology of particular species coupled with ad hoc explanations of the function of particular traits. One important exception was the work of entomologists, like Fabre, who could not ignore the social behaviour of insects and who began to describe the form and structure of colonies and speculate about the mechanisms that maintained them (Fabre 1879; Cézilly 2008).

Only after 1930 did a substantial number of professional biologists start detailed studies of the behaviour and ecology of animals in their natural habitats and, when they did, their principal objective was seldom to explain their evolution or to account for their diversity. They fell into four main groups. First, there were systematists and taxonomists whose principal interest was in phylogeny and development but who found themselves confronted with the obvious diversity of animal societies. Second, there were the founding fathers of animal behaviour, including Julian Huxley, Konrad Lorenz, Niko Tinbergen, Karl von Frisch, T.C. Schneirla and Bill Thorpe. Though their research sometimes encompassed functional aspects of behaviour (especially foraging behaviour), with the exception of Niko Tinbergen, their primary focus was on questions concerning the control and development of behaviour. Third, there were animal ecologists, including Luc Tinbergen, David Lack and A.F. Skutch, whose interests included the regulation of animal populations and the evolution of

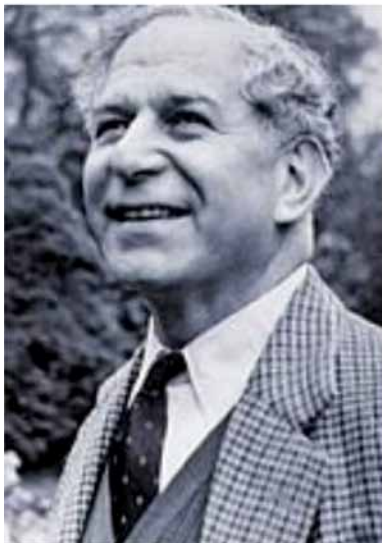
life-history parameters and who faced the need to explore the role of territoriality and competition between breeding pairs. Finally, there were the population geneticists, including Ronald Fisher and J.B.S. Haldane, whose principal focus was on the operation of natural selection and the evolution of genetic systems but whose interests inevitably included dispersal and the genetic structure of local populations as well as the evolution of demographic measures. Unlike many of the others, they were well aware of the evolutionary problems raised by social behaviour, though these were tangential to their main interests.

The development of field research after 1930 rapidly revealed the diversity of breeding systems and social behaviour and raised questions about the adaptive

significance of these differences. Many of the earliest studies involved insects or birds, since they were relatively easy to observe and their nests are often accessible (Lack 1935; Skutch 1935; Tinbergen 1935). Most birds are monogamous and biparental so that the diversity of social organisation was not a topic of immediate interest. The first professional studies of social behaviour in mammals also date from the 1930s (Figure 1.1). Zuckerman (1929, 1932) explored the social and sexual behaviour of captive baboons and related these to physiological processes, while Fraser Darling's studies of red deer and grey seals (Darling 1937a,b, 1943) and C.R. Carpenter's research on howler monkeys, macaques and gibbons (Carpenter 1934, 1935, 1942) described the size and



(a)



(b)



(c)

**Figure 1.1** Early studies of the behaviour of mammals. In the 1930s, (a) Frank Fraser Darling investigated the social and reproductive behaviour of red deer and grey seals, (b) Solly Zuckerman explored the sexual behaviour of captive baboons, and (c) Clarence Ray Carpenter established field studies of several primates, including howler monkeys, spider monkeys, rhesus macaques and gibbons. Sources: (a) © <http://littletoller.co.uk/authors/frank-fraser-darling/>; (b) Reproduced with permission of Zuckerman Archive, University of East Anglia; (c) © Smithsonian Institution Archives. Image SIA Acc. 90-105 [SIA2008-0362].

structure of groups and the reproductive behaviour of individuals and were more concerned with contrasts in ecology.

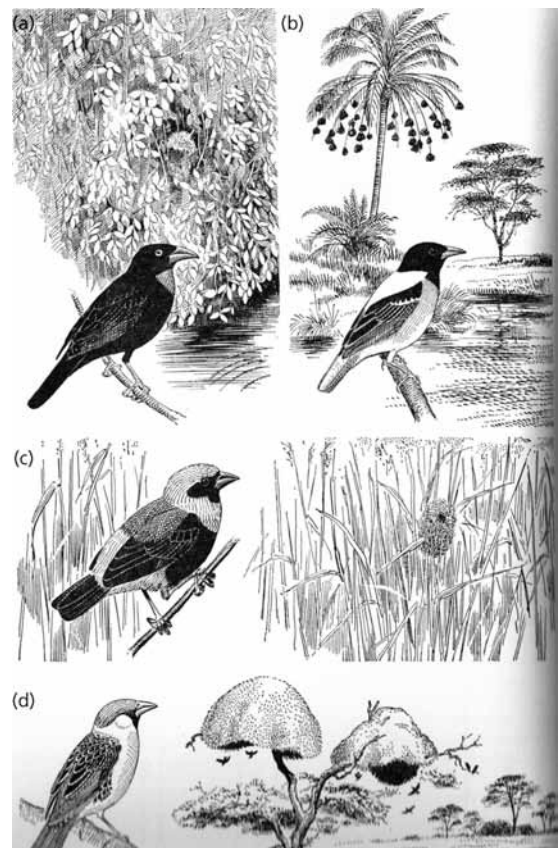
After 1945, studies of animal ecology and animal behaviour proliferated. In America, which still possessed extensive state forests and national parks, a larger proportion of ecological research was directed towards wildlife management, while in Europe the primary objectives of ecological research were more fundamental in nature. Ecological research focused on foraging behaviour, on the mechanisms regulating population density and on the proximate and ultimate factors influencing life-history parameters, including clutch size, laying data and survival (Lack 1954, 1966). While a substantial proportion of behavioural research was directed at investigating the causation and development of behaviour (Lorenz 1950; Tinbergen 1951; Hinde 1966), a substantial number of studies (mostly of birds) examined feeding behaviour, foraging strategies, territoriality and the benefits of sociality (Tinbergen 1952; Gibb 1954; Hinde 1956), laying the foundations for later work on optimal foraging behaviour (Krebs 1978). However, few studies had yet



**Figure 1.2** John Crook, founding father of socio-ecology. Source: © Simon Child.

monitored the breeding success of individuals throughout their lifespans and little was known of the extent or causes of variation in fitness in natural populations in either sex.

As field studies of birds developed and proliferated, it became obvious that there were striking contrasts in their social behaviour which were consistently related to ecological differences (Orlans 1961; Lack 1968). In particular, J.H. Crook's research on weaverbirds showed that there were systematic relationships between variation in social behaviour and contrasts in ecology: species living in open savannah or semi-arid habitats formed the



**Figure 1.3** (a–d) In one of the first systematic comparative studies of vertebrate social behaviour, Crook (1964) showed that there were consistent relationships between the size and structure of the colonies of African weaver birds and the type of habitat they lived in: forest-dwelling species mostly breed in pairs or in small colonies while the largest colonies are found in species living in arid savannahs. Source: (a–d) From Lack (1968). Reproduced with permission from Taylor & Francis.



largest breeding colonies while forest-dwelling species mostly lived in pairs or small groups (Figures 1.2 and 1.3). Crook argued that relationships between interspecific differences in social behaviour and contrasts in ecology were a consequence of adaptive responses to variation in the distribution of food resources, nesting sites and predation (Crook 1962, 1964, 1965).

Studies of social behaviour in birds stimulated similar research on mammals. Most European mammals are solitary and nocturnal, so they were less promising targets for field studies than birds but, by the early 1960s, relatively cheap air travel was opening up possibilities for research on diurnal mammals in tropical Africa and Asia. Many of them lived in stable social groups of varying size and structure and the primary aim of many studies of mammals that were established during this period was, for the first time, to describe their social behaviour and the structure of their societies. Since

one motive was to explore the biological origins of human society, many of the earliest field studies of mammals focused on primates, including macaques (Imanishi 1957; Itani 1959; Southwick *et al.* 1965), baboons (DeVore 1965), patas monkeys (Hall 1965) and the African apes (Figure 1.4).

Over the following decade, similar studies began to investigate social behaviour in other groups of mammals, including carnivores (Kruuk 1972; Schaller 1972), rodents (Armitage 1962), ungulates (Walther 1964; Leuthold 1966; Geist 1971), marsupials (Kaufmann 1975; Russell 1984) and cetaceans (Norris 1966; Whitehead 1983; Connor and Smolker 1985) (Figure 1.5). In addition, there was a large increase in field studies of other diurnal primates, including lemurs, New World monkeys and colobines while nocturnal species, which were far harder to observe, did not attract the same level of attention. To make it possible to collect regular



(a)

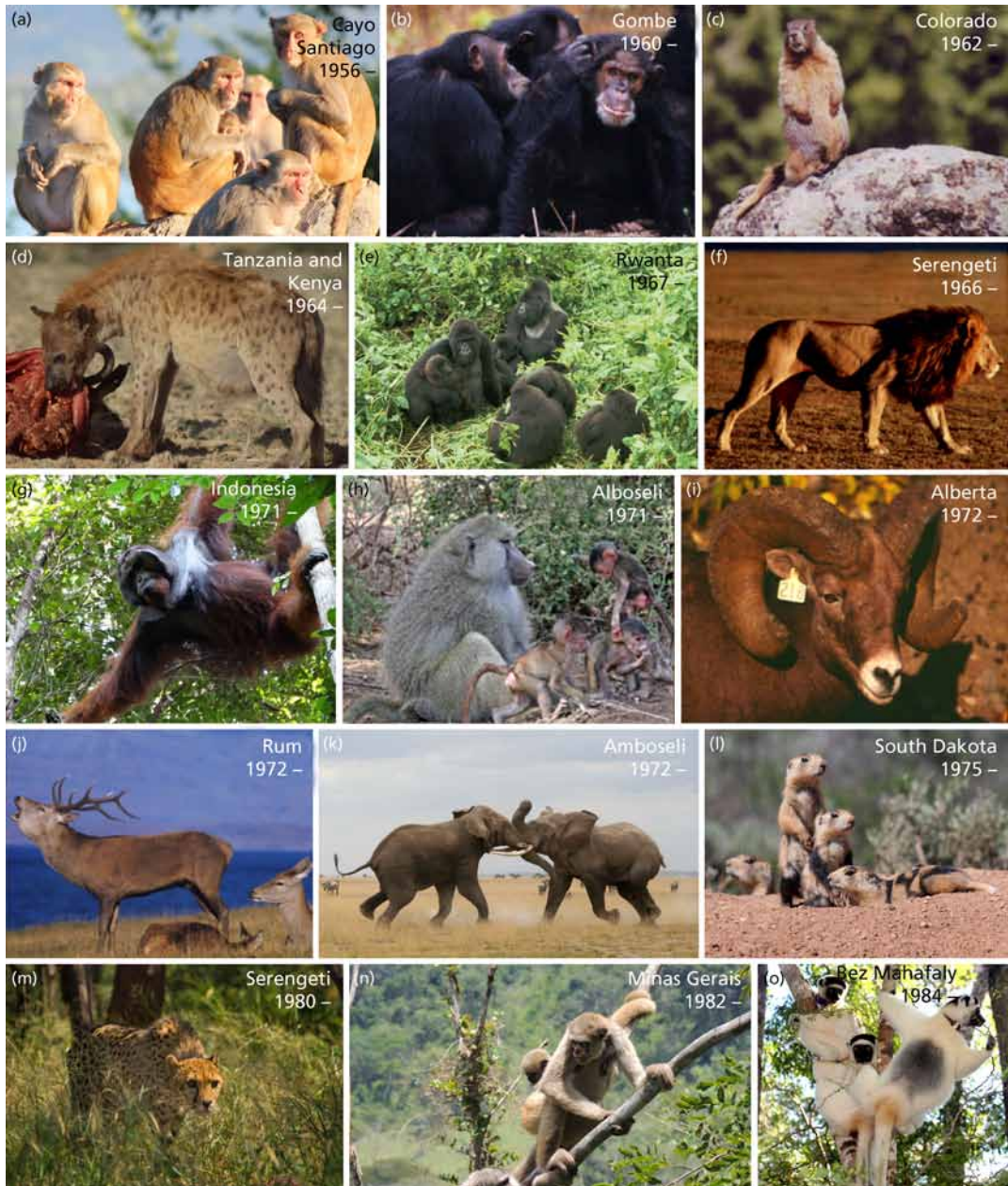


(c)



(b)

**Figure 1.4** Pioneers of long-term primate field studies: (a) Jane Goodall with alpha male Figan in Gombe National Park, Tanzania; (b) George Schaller in the Virungas; and (c) Dian Fossey with Digit in Rwanda. Sources: (a) © the Jane Goodall Institute/by Derek Bryceson; (b) © Terrence Spencer/The LIFE Images Collection/Getty Images; (c) © K.J. Stewart and A.H. Harcourt.



**Figure 1.5** A selection of mammals that are the subject of continuing long-term, individual-based field studies: (a) rhesus macaques, Puerto Rico (© Alexander Georgiev); (b) chimpanzees, Tanzania (© Ian Gilby); (c) yellow-bellied marmots, USA (© Kenneth Armitage); (d) spotted hyenas, Tanzania and Kenya (© Tim Clutton-Brock); (e) mountain gorillas, Rwanda (© K.J. Stewart and A.H. Harcourt); (f) African lions, Tanzania (© Craig Packer); (g) orangutans, Indonesia (© Anna Marzec, Tuanen Orang Research Project); (h) yellow baboons, Kenya (© Jeanne Altmann); (i) bighorn sheep, Canada (© Fanie Pelletier); (j) red deer, Scotland (© Clutton-Brock); (k) African elephants, Tanzania (© Vicki Fishlock); (l) black-tailed prairie dogs, USA (© Elaine Miller Bond); (m) cheetah, Tanzania (© Dom Cram); (n) muriquis, Brazil (© Thiago Cavalcante Ferreira); (o) sifakas, Madagascar (© Claudia Fichtel); (p) Soay sheep, Scotland (© Arpat Ozgul); (q) white-faced capuchins, Costa Rica (© Katherine MacKinnon); (r) Kalahari meerkats, South Africa (© Tim Clutton-Brock); (s) banded mongooses, Uganda (© Jennifer Sanderson); (t) red-fronted lemurs, Madagascar (© Claudia Fichtel); (u) striped mice, South Africa (© Carsten Schradin). Dates against each species show the approximate time when current long-term studies tracking the life histories of individuals began, though not all studies have maintained continuous records since they started.

(continued over)





Figure 1.5 (Continued).

observations, and to recognise individuals, it was often necessary to habituate study animals to observation by humans and, once this was done, they often became increasingly trusting, making it possible to observe them from close quarters (Figure 1.6). Techniques for quantifying behaviour in captive and field populations also improved rapidly, making it possible to compare the structure of relationships between individuals and to explore the mechanisms that controlled their development (Hinde 1970, 1973, 1983).

Until the mid 1960s, research on ecology, evolutionary biology and animal behaviour developed independently and there were limited connections between these three areas: for example, neither of Niko Tinbergen's two synthetic books, *The Study of Instinct* (Tinbergen 1951) and *Social Behaviour in Animals* (Tinbergen 1953), cite either Darwin or Fisher. But, by 1960, both theoretical and empirical research began to turn to topics which overlapped behaviour, ecology and evolutionary biology, including the evolution of life histories and social behaviour (Cole 1954; Williams 1957, 1966; Wilson 1971). In the early 1960s, two developments acted as catalysts for the rapid changes in the study of animal societies and reproductive strategies that occurred over the next decade and which are still continuing today. The first was the publication of Wynne-Edwards' monumental book *Animal Dispersion in Relation to Social Behaviour* (Wynne-Edwards 1962). Wynne-Edwards claimed that many animals cooperated to limit their numbers in advance

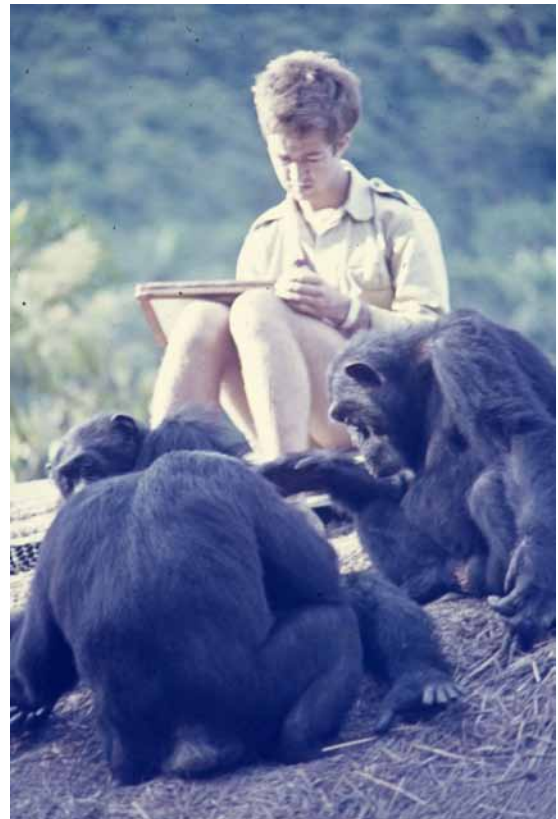


Figure 1.6 A group of male chimpanzees grooming each other in the Gombe National Park in 1969 while an observer collects data on a check sheet. Source: © Tim Clutton-Brock.

of resource shortage in order to improve the probability that groups or populations would survive. Group displays had evolved, he suggested, to allow their members to assess population density and to adjust their reproductive output so as to avoid over-exploitation of their food supplies. Other aspects of social behaviour, including territoriality and dominance hierarchies were, he argued, also involved in the regulation of animal numbers *and had evolved for this purpose*.

Wynne-Edwards' assertion that social behaviour had evolved through selection operating between groups or populations was clearly stated and was contrary to Darwin's persistent emphasis on individual competition as the keystone of evolution as well as to the view that animal populations were limited by the availability of resources (Lack 1954, 1966). Both population geneticists and ecologists rose to the challenge. Ecologists contested the view that social mechanisms regulated population density in advance of resource shortage and showed that density-dependent changes in fecundity and survival were associated with changes in resource availability, predation and disease (Lack 1966, 1968). Formal evolutionary models of Wynne-Edwards' concept of group selection showed that it would only be likely to work where all group members were genetically identical or where there was complete suppression of competition between group members (Maynard Smith 1964) and its general application was explored and refuted (Hamilton 1963; Maynard Smith 1964; Lack 1966; Williams 1966). The controversy drew attention to the fact that many functional explanations of social behaviour relied on benefits to groups or populations and led to a critical re-evaluation of these ideas, initiated by G.C. Williams' influential critique of evolutionary explanations of adaptation (Williams 1966).

The second development was the construction of a coherent body of theory capable of explaining the evolution of social behaviour, reproductive strategies and life histories and the interrelationships between them. The two most important components were the development of the concept of kin selection and inclusive fitness theory (Hamilton 1964), which provided a framework for explanations of the evolution of cooperative and eusocial breeding systems, and the introduction of game theory models to explore the competitive strategies of individuals (Maynard Smith 1974; Parker 1974). Other developments included theoretical models of the evolution of group living (Hamilton 1971) and of breeding systems (Bradbury and Vehrencamp 1977; Emlen and

Oring 1977), of reproductive competition (Trivers 1972), life-history parameters (Parker 1974; Stearns 1977), sperm competition (Parker 1970), mate choice (O'Donald 1962), parental care (Trivers 1974; Maynard Smith 1977), cooperation between unrelated individuals (Trivers 1971), communication (Zahavi 1975) and punishment (Clutton-Brock and Parker 1995).

The framework of theory, based on the theoretical papers of Hamilton, Trivers, Maynard Smith and Parker (Figure 1.7), provided the first satisfactory explanations of variation in animal social behaviour, breeding systems and life histories and emphasised the extent to which the characteristics of an individual's social environment affected its fitness and the selection pressures operating on it. One insight that emerged from this was an understanding that the evolutionary interests of individuals belonging to the same group could diverge as well as converge. While early studies of animal behaviour had seen relationships between males and females, between parents and young and between members of the same social group as harmonious interactions generating social structures that maximised benefits to all, the new framework emphasised the extent to which the interests of individuals differed, leading to conflicts between them, to the evolution of manipulative or exploitative strategies and to social structures that were the outcome of conflicts of interest and which did not necessarily maximise the fitness of all group members (Davies 1992; Arnqvist and Rowe 2005; Bourke 2011). Although they recognised that shared interests could predominate in some cases, they showed that even the most cooperative relationships contained the seeds of conflict.

Another important development was an understanding of the contrasting selection pressures operating on females and males and the role of social behaviour in causing these differences. A seminal paper by Emlen and Oring (1977) showed how the distribution of females was usually related to the distribution of resources and the risk of predation, while the distribution of males commonly depended on the distribution of females. While it came to be appreciated that there were exceptions to this generalisation and that the strategies adopted by males can influence the distribution and reproductive behaviour of females and vice versa, their argument emphasised the need to consider the reproductive strategies of the two sexes separately.

Reviewing the new field that was emerging from the integration of studies of behaviour, ecology and



**Figure 1.7** Some of the architects of social evolution theory: (a) Robert Trivers and Bill Hamilton wrestling with a problem at Harvard; (b) John Maynard Smith in his garden; (c) Geoff Parker in 1980; (d) E.O. Wilson. Sources: (a) © Sarah Hrdy; (b) © Corbin O’Grady Studio/Science Photo Library; (c) © Geoff Parker; (d) © Jim Harrison (PLoS) [https://commons.wikimedia.org/wiki/File%3APlos\\_wilson.jpg](https://commons.wikimedia.org/wiki/File%3APlos_wilson.jpg). Used under CC BY 2.5 <http://creativecommons.org/licenses/by/2.5/>.

population genetics, in 1974 E.O. Wilson had named it sociobiology and predicted that, by the year 2000, it would have become closely allied with population biology and genetics, while traditional ethology and comparative psychology would have been integrated with neurophysiology. Others disagreed: ‘I see no signs or probability of this happening and if it did, it could, I believe, be a considerable disaster for biology’ wrote W. H. Thorpe. In practice, the first part of Wilson’s prediction came about within a few years of the publication of his

book and there was a rapid expansion of research, though for studies of non-human animals, sociobiology was gradually abandoned in favour of behavioural ecology (Klopfer 1973; Krebs and Davies 1978).

Over the 40 years since 1975, a combination of theoretical and empirical research has extended and refined our understanding of animal breeding systems and social behaviour (Danchin *et al.* 2008; Székely *et al.* 2010; Davies *et al.* 2012). There has been a substantial improvement in quantitative methods (Martin and Bateson





**Figure 1.8** Kalahari meerkats can be habituated to close observation by humans, so it is possible to train them to climb onto electronic balances with small rewards of food or water. *Source:* © Tim Clutton-Brock.

1993) and a progressive refinement of experiments involving both wild and captive animals (Krebs and Davies 1981; Davies *et al.* 2012). Long-term studies that have tracked the life histories of large numbers of individual animals over decades and documented their behaviour and reproductive success have generated quantitative measures of individual differences in fecundity, rearing success and longevity and the factors that affect them, providing access to questions about the costs and benefits of variation in behaviour and reproductive strategies that were previously unavailable (MacColl 2011; Cockburn 2014). In some species, it is possible to habituate large numbers of animals to humans, making it feasible to monitor changes in weight and growth and to collect regular samples of blood, urine and faeces for hormonal and genetic analysis (Figure 1.8). The development of DNA fingerprinting and associated techniques has made it possible to measure the breeding success of males, establish pedigrees and explore the heritability of traits (Jeffreys *et al.* 1985; Charmantier *et al.* 2014). In addition, quantitative comparative studies developed from their initial use as a descriptive tool (Lack 1968) to provide quantitative tests of the generality of specific predictions concerning relationships between ecological, behavioural and anatomical traits that controlled for the effects of phylogeny (Clutton-Brock and Harvey 1977b; Harvey and Pagel 1991). More recently, the advent of gene-based phylogenetic super-trees has made it possible to document sequences of evolutionary events and to identify the ancestral states from which particular traits evolved (Pagel 1994).

Theoretical models of evolutionary processes have continued to explore the operation of selection at

different levels. Following extensive critiques of Wynne-Edwards' book, it was initially widely accepted that group selection was only likely to be an important evolutionary process under restrictive conditions (Maynard Smith 1976). However, a subsequent reformulation of the process suggested that selection could operate at multiple levels and that selection operating between groups might, after all, play an important role in the evolution of social behaviour in non-human animals (Wilson 1977; Wilson and Wilson 2007; Nowak *et al.* 2010; Nowak and Allen 2015; Akcay and Van Cleve 2016). Others disagree and have argued that the evolutionary processes described by these models do not differ substantively from Hamilton's concept of kin selection operating through variation in inclusive fitness, and that the two approaches represent alternatives ways of accounting fitness (Gardner *et al.* 2011; Marshall 2011, 2015; Frank 2013).

Recent arguments about differences between models of group and kin selection and the relative importance of these two processes have focused on whether or not high levels of relatedness between group members are necessary for the evolution of eusociality and obligate sterility in insects (Liao *et al.* 2015; Nowak and Allen 2015; Queller *et al.* 2015). While there is no final resolution to this discussion, comparative studies suggest that the initial evolution of eusocial breeding systems has been confined to groups where relatedness between group members is unusually high, though levels of average relatedness may subsequently decline (Hughes *et al.* 2008; Boomsma 2009). Further support for the suggestion that high levels of kinship are necessary for the initial evolution of extensive altruistic

cooperation comes from comparative studies of birds and mammals which show that the evolution of cooperative breeding systems has also been associated with unusually high levels of kinship between group members (see Chapters 9 and 17), though humans are an important exception (see Chapter 20). Moreover, unlike models of group selection, the theoretical framework provided by inclusive fitness theory provides a basis for a wide range of predictions about other evolutionary consequences of variation in kinship, and many of them have now been confirmed by empirical studies (Abbot *et al.* 2011).

One reason why arguments about the role of group selection and kin selection in the evolution of cooperative behaviour are important is that they can affect the way in which colony structure and individual behaviour are interpreted. Some proponents of group selection argue that social groups are ‘super-organisms’ whose size and structure are adapted to maximising survival or breeding success at the group level (Wilson and Sober 1989). Explanations of this kind are most prevalent in studies of social insects, where conflicts of interest between individuals are limited by the suppression of reproduction in other females by the queen or queens (Wilson 1971; Ghiselin 1974) and colonies can show a level of ‘functional organisation’ resembling the integrated organisation of different parts of the bodies of individual organisms (Wilson and Sober 1989). While this approach may sometimes help to generate useful hypotheses about variation in colony size and structure (Seeley 2001; Hölldobler and Wilson 2009), conflicts of interest between colony members are never eliminated entirely and functional analogies between the most specialised insect societies and individual organisms have important limitations (West-Eberhard 1975; Starr 1979; Gardner and Grafen 2009). In non-human vertebrates, where all group members are potential breeders, conflicts of interest are widespread and intense and treating groups as adapted units offers few insights and is usually misleading (Kitchen and Packer 1999; Clutton-Brock 2009a).

Two related semantic issues concerning the process of evolution need mention. While some evolutionary biologists (including many population geneticists) use ‘natural selection’ (or ‘selection’) to refer to relationships between fitness (or components of fitness) and heritable traits, others (including some population geneticists and many sociobiologists and behavioural ecologists) use

natural selection to refer to cases where there are consistent relationships between phenotypic variation and fitness (or its components), distinguishing between selection on phenotypic traits and responses to selection, which vary with their heritability. The acceptance of correlations between phenotypic variation and fitness as a measure of selection is sometimes criticised by geneticists on the grounds that selection pressures operating on phenotypic variation do not necessarily reflect those operating on genetic variation, while behavioural ecologists often respond with the argument that correlations between phenotypic variation and fitness are likely to reflect the selection pressures that operated before heritable traits reached equilibrium.

Contrasts in the usage of ‘selection’ are often associated with differences in the use of ‘adaptation’. Biologists working on the process of evolution commonly use ‘adaptation’ to refer to changes in gene frequency that increase fitness, while those interested in explaining phenotypic diversity often use it to refer to variation in phenotypic traits that increases fitness, whether or not it has been shown to have a heritable basis, and refer to fitness-enhancing strategies acquired by individuals in the course of their lives through individual or social learning as adaptive. It is particularly important to recognise the presence of differences in usage in discussions of the adaptive significance of social strategies in higher vertebrates and humans, where adaptive tactics that improve the fit of individuals to their social environment (and so increase their fitness) commonly develop as a consequence of individual or social learning, and many differences in behaviour may not be heritable. Like many other behavioural ecologists, I distinguish between selection and the evolutionary response to selection and use ‘adaptation’ to refer to phenotypic traits in non-human animals that help to fit individuals to their ecological or social environments and so increase their fitness, whether they have been shown to be heritable or not.

In the rest of this chapter, I provide a brief introduction to the development of the main areas of evolutionary theory relevant to understanding contrasts in sociality, reproductive competition, mate choice, parental care, communication and cooperation. Sections 1.2 and 1.3 examine the evolution of female sociality and its consequences for the evolution of mating systems and the form and intensity of reproductive competition in both sexes. Sections 1.4 and 1.5 review our understanding of mate choice and parental care in females and males. Section

1.6 examines the evolution of cooperation and of cooperative breeding systems. Finally, section 1.7 warns about the use of intentional language and the dangers of loaded labels.

## 1.2 Sociality and mating systems

Early field studies of social behaviour in insects, birds and mammals quickly focused attention on the reasons why many animals live in groups and showed that social behaviour could reduce the risk of predation: for example, research on colonies of black-headed gulls showed that synchronised mobbing deterred predators and that larger numbers of individuals were more effective than smaller ones (Kruuk 1964). Empirical studies led to the development of the first formal models of group-living. In a characteristically original paper, W.D. Hamilton showed that, where predators attack groups and are only likely to take a single animal per attack, individuals gain benefits by aggregating because this increases their per-capita chances of survival (Hamilton 1971). Other studies explored the effects of sociality on the probability that individuals would be detected by predators (Vine 1973; Treisman 1975) and extended the range of ways in which aggregation might reduce the per-capita risk of predation, including effects on the probability that individuals will detect dangers, confuse attackers or defend themselves (Krause and Ruxton 2002).

The potential benefits of sociality in finding and catching food were also recognised. Ward and Zahavi (1973) suggested that the aggregation of birds into flocks might allow individuals to exchange information and might facilitate the location of widely distributed food sources. In addition, comparisons of the hunting success of predators showed that they were commonly more successful when hunting in pairs or small groups than when hunting alone (Wyman 1967; Kruuk 1972; Schaller 1972). Other potential benefits included the sharing of information about the relative probability of different foods and the enhancement of exploitation efficiency.

As the range of animals studied increased, additional benefits of sociality were explored (Krause and Ruxton 2002). These included the retention of heat (especially in animals that hibernate), reductions in the risk of desiccation and improvements in efficiency of movement. In addition, it became apparent that group-living could provide a range of important social benefits, including

the ability of larger groups to displace competitors (Wrangham 1980), to limit immigration or to reduce the risk that take-overs by either sex would lead to infanticide (Packer *et al.* 1990). In cooperative breeders, where a single female monopolises reproduction, studies showed that group-living also increased the reproductive success of the breeding female and ensured the continuity of breeding groups consisting of relatives (Wilson 1971, 1974).

At the same time, the potential costs of sociality came to be recognised. Studies of birds and mammals showed that increases in group size within and across species were commonly associated with increases in territory size, home-range area and day-range length and associated energetic costs of movement (McNab 1963; Schoener 1968; Clutton-Brock and Harvey 1977a,b). In addition, a wide range of field studies showed that increasing group size was often correlated with increased rates of feeding interference or aggression and with reductions in foraging efficiency (Goss-Custard 1970; Jarman 1979; Selman and Goss-Custard 1988) and, in some cases, with increases in parasite load (Hoogland and Sherman 1976; Hoogland 1979; Brown and Brown 1986) or increased risks of detection by predators (Vine 1973; Lindström 1989). It also became apparent that, in plural breeders (species where groups contained multiple breeding females), increases in group size often raised the incidence of reproductive interference between group members and reduced fecundity and juvenile survival (Hoogland 1981; van Schaik 1983) and that relatively large groups sometimes fissioned into smaller ones (Chepko-Sade and Sade 1979).

As field studies multiplied and contrasts between species became clearer, synthetic papers examined the relationship between species differences in sociality and variation in ecological parameters. Crook and Gartlan (1966) compared the social organisation of primates living in contrasting habitats while Jarman (1974) explored the ecological correlates of variation in group size between different species of African antelope. A similar 'socio-ecological' approach was used to explore the causes of intraspecific variation in social behaviour (Richard 1974, 1978; Lott 1991). In addition, related studies began to explore interspecific associations between social behaviour and morphological and physiological adaptations, as well as life-history parameters and relative brain size (Lack 1968; Western 1979;

Clutton-Brock and Harvey 1980; Harvey and Clutton-Brock 1985).

Theoretical studies of the evolution of sociality investigated the effects of increasing group size on the costs and benefits of sociality to individuals. In particular, an important paper by Sibley argued that where the fitness of solitary individuals is lower than that of individuals living in groups, observed group size will commonly exceed the value that maximises the average fitness of group members since solitaries will keep joining groups until the average fitness of their members is equal to that of solitaries (Sibly 1983). Subsequent models examined the extent to which observed group sizes were likely to deviate from the size that optimised average fitness, and showed that variation in the relative fitness of solitaries, in the size of units that transfer between groups and in the relatedness of group members can all affect the probability that group size will deviate from optimal values (Giraldeau and Gillas 1985; Higashi and Yamamura 1993; Kramer 1995; Giraldeau and Caraco 2000; Krause and Ruxton 2002). In addition, other theoretical studies began to explore the effects of group dynamics on the distribution of group sizes (Cohen 1971, 1975).

Comparative and empirical studies also described variation in the kinship structure of groups. Contrasts in kinship between group members are partly caused by variation in fecundity and survival and partly by contrasts in dispersal. Studies of a number of mammals showed that females avoid breeding with close relatives (Packer 1979) and an influential review by Greenwood (1980) demonstrated that, in species which form stable groups, one sex usually disperses to breed elsewhere. Greenwood showed that, in mammals, males were typically the dispersing sex while, in birds, females often dispersed further than males and suggested that this contrast was related to variation in the role of males in defending breeding territories, though recent studies have shown that sex differences in dispersal are more variable and have suggested other explanations for contrasts between birds and mammals (see Chapters 3 and 12).

Most early studies of the evolution of animal sociality considered the average costs or benefits to group members and either disregarded contrasts in the effects of variation in group size on females and males or focused implicitly on females. Important reviews of mating systems in birds and mammals in the late 1970s emphasised the need to consider the separate interests of females and males (Bradbury and Vehrencamp 1977; Emlen and

Oring 1977). Empirical tests confirmed that female distributions were closely related to resources while the distribution of males was usually governed primarily by that of females (Ims 1988; Davies 1989).

The recognition that it was necessary to consider the separate interests of females and males had far-reaching consequences. First, it suggested that polygyny was associated with ecological conditions favouring the aggregation of females in stable groups defensible by males, while social monogamy was associated with conditions favouring solitary, widely distributed females (see Chapter 10). Second, it made an important contribution to explanations of the evolution of sex differences in the intensity of reproductive competition and the distribution of associated sex differences in weaponry and body size (see Chapter 18). One extension to this framework was the recognition that multi-male multi-female groups were likely to be found where group size was so large or the reproductive cycles of females were so highly synchronised that more than one female was often receptive at the same time, so that reproductive competition between males was reduced (Altmann 1962; Emlen and Oring 1977; Altmann *et al.* 1996) (see Chapter 11). Third, it led to comparisons of life histories and variation in reproductive success in the two sexes and to the recognition that intense reproductive competition between males is often associated with costs to male survival at several stages of the lifespan (Trivers 1974; Clutton-Brock 1988) (see Chapter 18). And, fourth, it showed that the interests of females and males were frequently in conflict, especially in systems where females are likely to maximise their fitness by mating with multiple males (see Chapter 4) while males are likely to maximise theirs by limiting female opportunities to mate with other partners (Davies 1985, 1989) (see Chapter 15).

Subsequent research on animal breeding systems has refined and extended these generalisations and demonstrated that there are important exceptions to these trends and that the reproductive tactics of each sex can have important consequences for selection on members of the other sex (see Chapters 10 and 15). However, the recognition that the distribution of resources plays a fundamental role in determining the distribution of females and that this, in turn, affects the distribution of males, their opportunities to monopolise multiple partners and the intensity of reproductive competition between them is still of central importance in explaining the diversity of animal societies.



### 1.3 Reproductive competition

#### Between males

In the *Origin of Species*, Darwin was principally concerned with explaining the evolution of traits that increased the survival of individuals, but he appreciated that many characteristics of animals, like the elaborate plumage of many male birds, were unlikely to increase an individual's chances of acquiring food or escaping predators (Figure 1.9). *The Descent of Man* provides an explanation of the evolution of these 'secondary' sexual characters and argues that they are adaptations that increase the chance that individuals will acquire breeding opportunities or mates. Darwin identified two ways by which individuals can compete for access to the opposite sex: by direct competition with other members of the same sex for access to mates and the resources necessary for reproduction (such as breeding territories); and by competition to attract breeding partners and induce them to mate. He realised that direct intrasexual competition for breeding opportunities was commonly more intense among males than among females and argued that this was why males commonly showed greater development of traits associated with fighting or other forms of direct competition.

Darwin's recognition of the greater intensity of competition between males (and the sex differences in size and weaponry associated with it) posed a fundamental question. Why do males compete more intensely for

females than females do for males? Part of the answer was supplied by analysis of the distribution of breeding success by males and females in fruit flies. In 1948, Bateman showed that variance in breeding success in *Drosophila* was greater in males than females and that breeding success increased more rapidly in relation to the number of mating partners in males than females (Bateman 1948). Sex differences in relationships between fitness and the number of mating partners (Bateman gradients) have now been demonstrated in a number of polygamous species (Clutton-Brock 1988, 2010; Jones *et al.* 2000, 2002) and selection for traits that influence competitive ability is often stronger in males than females (Andersson 1994; Lorch *et al.* 2008). However, the situation is more complex than Bateman appreciated and sex differences in Bateman gradients may often be smaller than was initially supposed (Sutherland 1985; Tang-Martinez and Ryder 2005; Roughgarden and Akçay 2010). In some animals (including the species of *Drosophila* that Bateman worked with) female fitness also increases with partner number (Tang-Martinez and Ryder 2005). In addition, stochastic factors commonly contribute to individual differences in breeding success in both sexes and some models predict that their influence is likely to be greater in males than in females (Sutherland 1985; Gowaty and Hubbell 2005).

But why does partner number have a stronger influence on mating success in males and why is competition for mates usually more intense among males than



(a)



(b)

**Figure 1.9** Secondary sexual characters of males include complex weaponry, for example (a) the antlers of red deer, and elaborate ornaments, for example (b) the trains of peacocks. In general, male weaponry is more highly developed in mammals while male ornamentation is more highly developed in birds, reflecting the contrasting importance of intrasexual and intersexual selection in the two groups. Sources: (a) © Tim Clutton-Brock; (b) © Roslyn Dakin.

females? In a seminal paper that built on Bateman's work, Trivers argued that it is the relative expenditure by males and females on gametes and parental care ('parental investment') that determines the relative intensity of competition for breeding partners in the two sexes (Trivers 1972). Sex differences in parental investment affect the time necessary to complete a successful breeding attempt or their 'time out' of competition for breeding partners and this limits the potential rate at which males and females can complete breeding attempts, their *potential reproductive rate* or PRR (Clutton-Brock and Parker 1992; Parker and Simmons 1996). Sex differences in 'time out' and PRR in turn affect the relative numbers of each sex that are ready to breed at any point in time (the *operational sex ratio*, or OSR) which, in many systems, is the principal factor determining the relative intensity of intrasexual competition in the two sexes (Trivers 1972; Emlen and Oring 1977; Clutton-Brock and Parker 1992). For example, among species where males care for the young, they typically compete more intensely than females for mating opportunities in species where they can care for multiple clutches of eggs simultaneously and their PRR exceeds that of females, whereas females compete more intensely than males for mates in species where males can only care for a single clutch at a time and their PRR exceeds that of males (Clutton-Brock and Vincent 1991; Ahnesjö *et al.* 2001).

While the OSR establishes the competitive arena in which both sexes compete for breeding partners, estimating the OSR and predicting the relative intensity of selection for traits that increase the competitive ability in males is not straightforward. It is frequently difficult to decide which individuals should be included in estimates of the OSR and stochastic variation in male success may increase as the OSR rises, weakening the intensity of selection for traits related to competitive ability in males (Sutherland 1985; Klug *et al.* 2010, 2012; Rios Moura and Peixoto 2013). Moreover, in multiparous species, annual breeding success often trades off against the effective breeding lifespan of males (see Chapter 13) and much of the observed variation in male success within years is often the result of age differences between individuals (Clutton-Brock 1983, 1988). As a result, standardised variance in lifetime breeding success among males does not necessarily increase with the degree of polygyny and is not always much greater in males than in females (Lukas and Clutton-Brock 2014). To predict how much members

of each sex should invest in traits that affect their competitive success (their *scope for competitive investment*, or SCI), it is necessary to consider both the OSR and Bateman gradients, as well as the social and ecological factors affecting the costs and benefits of investment in breeding competition. An integrative model constructed by Kokko and her collaborators incorporates these different factors and shows how variation in the OSR can affect Bateman gradients and why contrasts in the OSR do not always predict sex differences in competitive behaviour (Kokko *et al.* 2012).

One general conclusion emerging from research on sexual selection is that species differences in the development of male secondary sexual characters associated with competitive success and the extent of sex differences in these traits may be more closely related to variation in the frequency of fighting and the competitive tactics of the two sexes than to sex differences in reproductive variance or to differences in the OSR. While variation in the frequency of fights and the competitive tactics of the two sexes may be loosely related to differences in the OSR as well as to variance in male breeding success, these relationships may not be close.

Studies of male competition also raise important questions about the evolution of fighting tactics. Why are all-out fights often uncommon? How long and hard should individuals fight? And how might individuals minimise the costs of fighting? Empirical studies of competition show that fighting often has substantial costs to survival in males and is likely to reduce the duration of effective breeding (Geist 1971; Clutton-Brock *et al.* 1979, 1982). Maynard Smith and Parker introduced game theory models to explore the evolution of fighting tactics and showed that high levels of aggression would not necessarily be the most successful tactic (Maynard Smith 1974; Parker 1974): as more aggressive individuals ('hawks') come to predominate, more pacific strategies ('doves') may be favoured, so that both tactics persist. Subsequently, they examined different ways in which individuals might minimise the costs of fighting. Where fights consist of prolonged contests which end when one party is exhausted ('wars of attrition'), they showed that individuals should give up as soon as it becomes clear that they are unlikely to win, so that fights between disparate opponents should be relatively short while those between well-matched ones should be relatively long (Parker 1974; Maynard Smith and Parker 1976). Subsequent models argued that an even better course would be