

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

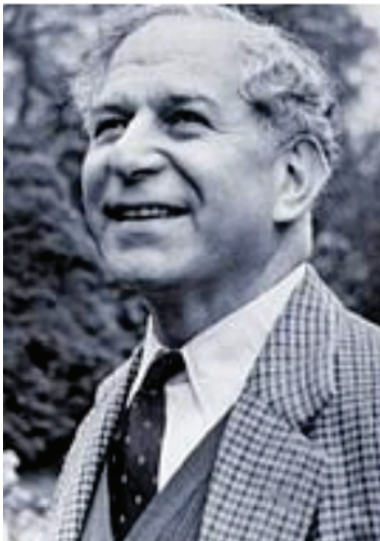
life-history parameters and who faced the need to explore the role of territoriality and competition between breeding pairs. Finally, there were the population geneticists, including Ronald Fisher and J.B.S. Haldane, whose principal focus was on the operation of natural selection and the evolution of 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

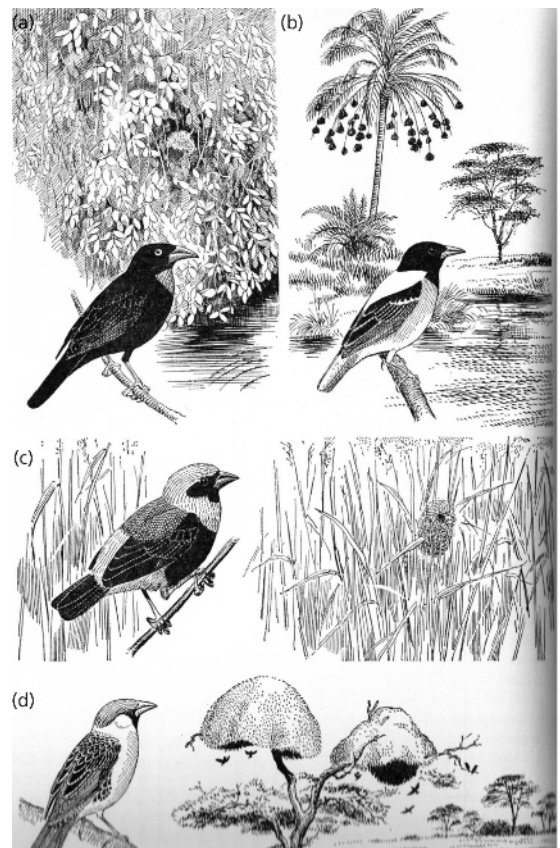


Figure 1.3 (a–d) In one of the first systematic comparative studies of vertebrate social behaviour, Crook (1964) showed that there were consistent relationships between the size and structure of the colonies of African weaver birds and the type of habitat they lived in: forest-dwelling species mostly 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).

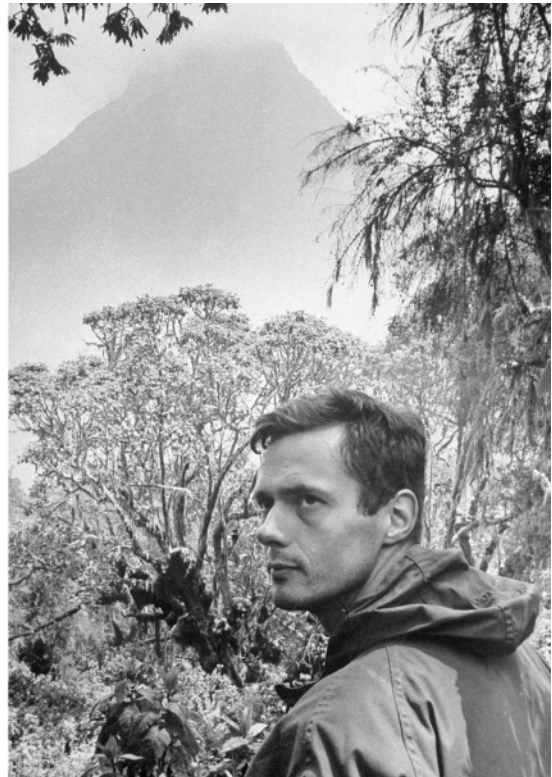
Over the following decade, similar studies began to investigate social behaviour in other groups of mammals, including carnivores (Kruuk 1972; Schaller 1972), rodents (Armitage 1962), ungulates (Walther 1964; Leuthold 1966; Geist 1971), marsupials (Kaufmann 1975; Russell 1984) and cetaceans (Norris 1966; 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.

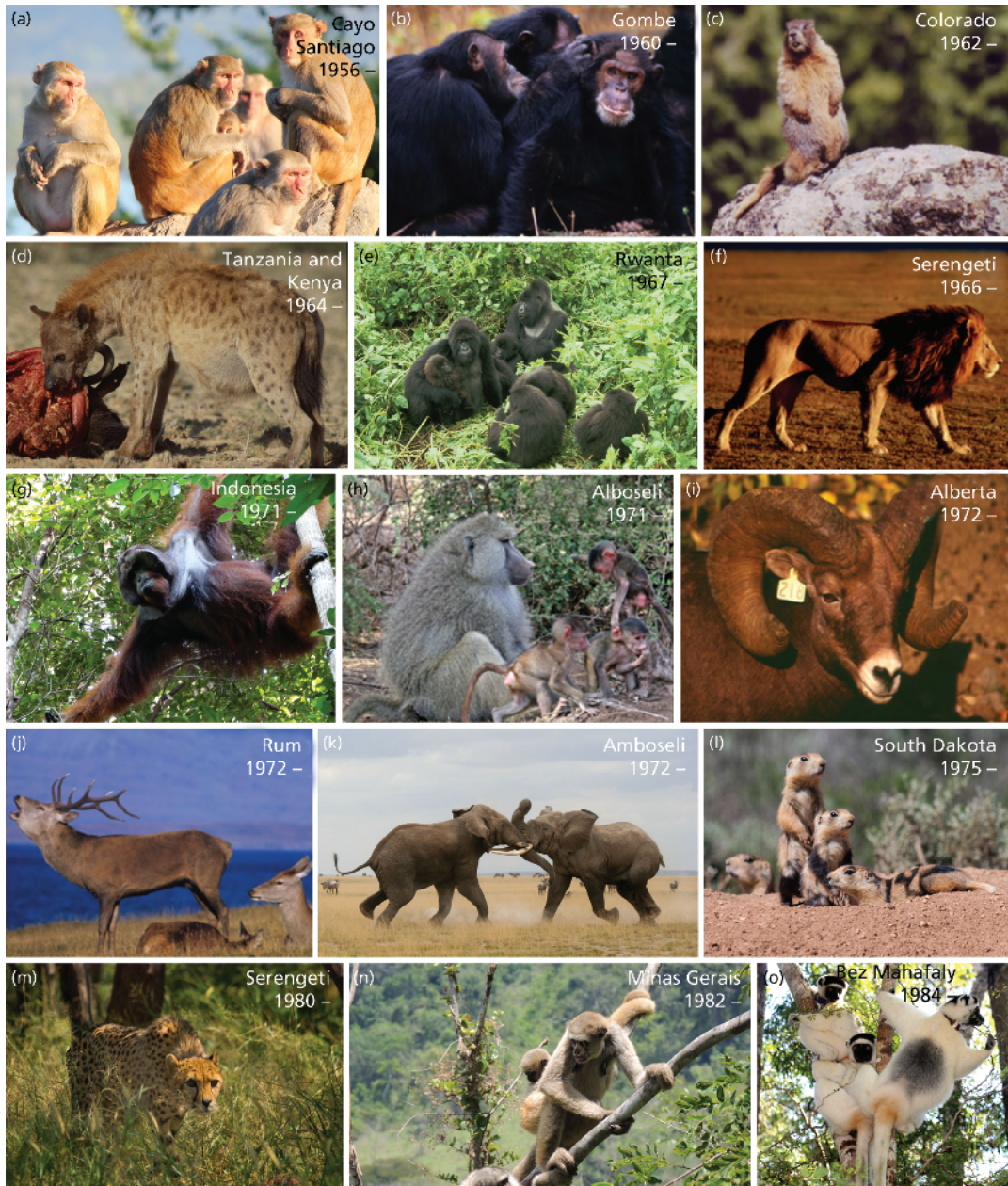


Figure 1.5 A selection of mammals that are the subject of continuing long-term, individual-based field studies: (a) rhesus macaques, Puerto Rico (© Alexander Georgiev); (b) chimpanzees, Tanzania (© Ian Gilby); (c) yellow-bellied marmots, USA (© Kenneth Armitage); (d) spotted hyenas, Tanzania and Kenya (© 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. 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

to discourage opponents from pursuing challenges by signalling their superior strength or commitment to winning (Maynard Smith 1982, 1991). They raised questions about the ‘honesty’ and reliability of signals (Johnstone 1997) which led to a substantial field of theory dealing with the evolution of competitive signalling systems (Maynard Smith and Harper 2003; Searcy and Nowicki 2005) (see Chapter 7).

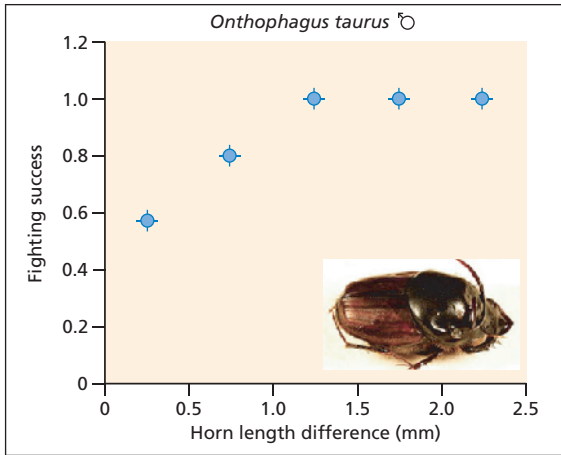
As empirical studies of reproductive behaviour in natural populations proliferated, the diversity and complexity of male reproductive strategies became apparent. In some societies, dominant males allow one or more subordinate males to remain in the group and subordinates may assist dominants in repelling neighbouring groups or potential rivals (see Chapter 11). Where female groups are large and include several adult breeding males, individual males often form alliances to compete with each other, and may attempt to disrupt the formation of alliances by rivals (see Chapter 14). In many species, males use force, harassing tactics, or intimidation to coerce females to mate with them, generating arms races between the sexes and, in some species, males frequently attempt to kill dependent infants fathered by their competitors (see Chapter 15). In some species, particular males form ‘friendships’ with particular females, providing them and their infants with some protection from attacks by rival males and benefiting from this by increased reproductive access to their female ‘friends’.

Moreover, competition between males does not end at copulation. Where females commonly mate with more than one male per breeding attempt, sperm from more than one male compete within the reproductive tracts of females and adaptations in males that increase the probability that their sperm will inseminate females or reduce the probability of successful fertilisation by subsequent mating partners are common (Parker 1970, 1984, 1998; Simmons 2001). Early studies of mating competition often assumed that the sperm supplies of individual males were virtually unlimited, but more recent work has shown that this is often not the case and that males may limit their allocation of sperm to different mating partners so as to maximise their breeding success (Parker *et al.* 1997; Parker 1998, 2000; Wedell *et al.* 2002). The risk of sperm competition and associated male tactics often affects the intensity and duration of mate guarding bonds between the sexes and the form and duration of competition for mating opportunities (Birkhead and Møller 1992; Tregenza and Wedell 1998; Simmons 2001; Bjork and Pitnick 2006).

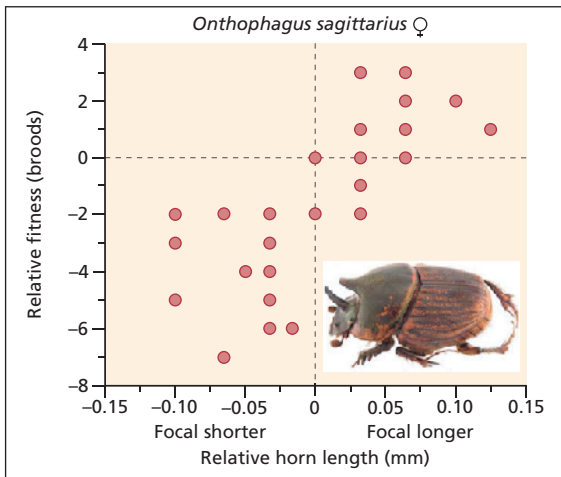
Between females

Partly because interactions between females less frequently involve escalated fights and partly because females rarely possess such elaborate weaponry or ornaments, research on reproductive competition initially focused principally on males. However, in many animal societies, females also compete intensely between themselves for rank, access to breeding territories or other resources necessary for conception or rearing offspring and are commonly aggressive towards each other’s offspring, sometimes with lethal consequences (Clutton-Brock 2007; Rosvall 2011; Stockley and Bro-Jørgensen 2011; Clutton-Brock and Huchard 2013a). Like males, females may also compete for access to mates and, in some cases, reproductive competition is more intense between females than between males. For example, in polyandrous birds where males care for eggs or offspring and single females can monopolise access to multiple males, OSRs can be biased towards females and females can be more competitive and more ornamented than males (Figure 1.10) (Emlen and Oring 1977; Oring *et al.* 1991a,b). Where males produce unusually large sperm, this too can lead to competition between females for mates (Bjork and Pitnick 2006). In other cases, males may bring nuptial gifts to females that increase their fecundity and females gain direct benefits by mating with multiple partners and so compete for mating partners (Simmons and Gwynne 1993; Simmons 1995; Kvarnemo and Simmons 1999). Similar reversals in the usual pattern of sex differences in reproductive competition also occur in some singular cooperative breeders where variance in female breeding success is larger in females than in males (see Chapter 17).

While sex differences in parental care sometimes mean that the OSR is consistently biased towards one sex, in some species the direction of biases in the OSR changes throughout the breeding season and the relative intensity of reproductive competition in males and females also varies (Forsgren *et al.* 2004; Gowaty and Hubbell 2005). For example, in two-spotted gobies, the relative intensity of competition for mating partners in the two sexes varies throughout the breeding cycle as the relative number of receptive females and males changes (Amundsen and Forsgren 2001; Forsgren *et al.* 2004). It is also important to appreciate that intrasexual competition between females is not confined to cases where OSRs are



(a)



(b)

Figure 1.10 Horn length and fighting success in male and female *Onthophagus* beetles. (a) Relationship between male fighting success and horn length in *Onthophagus taurus*. Graph adapted from Moczek and Emlen (2000). (b) Relationship between relative horn length and relative fitness of competing females in *O. sagittarius*. Positive values on the *x*- and *y*-axes represent cases where, in pairs of competing individuals matched for body size, the focal animal had a larger horn and produced more broods relative to her competitor. Source: Graph from Watson and Simmons (2010), reproduced with permission from the Royal Society. Photo source: (a) © Tim Murray; (b) © Udo Smidt.

male biased and can occur wherever females can increase their fitness by competing for access to particular males, multiple mating partners or resources necessary for breeding.

While there are fundamental similarities in reproductive competition in males and females, there are also general differences. Where females compete for resources while males compete for access to breeding partners, the fitness benefits of winning particular contests are often likely to be lower in females than in males. In addition, the relative intensity of intrasexual competition (and the development of traits that increase their competitive success) may be more strongly influenced by variation in resource distribution and less by variation in the form of mating systems than in males. The costs of competition are often likely to be higher to females if agonistic interactions endanger the survival of fetuses or dependent infants. As a result, females are often likely to invest less in attempts to win competitive contests than males, though research on singular cooperative breeders shows that this is not always the case (see Chapter 17).

One consequence of the common tendency for females to invest less in winning contests than males is that the survival costs of traits associated with competitive success are seldom as large in females as in males. For example, while the evolution of increased body size in males is often associated with higher juvenile mortality and reduced longevity in adult males compared to females (Clutton-Brock *et al.* 1985; Clutton-Brock and Coulson 2002), there is little evidence that sex differences in survival are reversed in species where reproductive competition is more intense or secondary sexual characters are more highly developed in females (Clutton-Brock 2007). An additional reason for this difference may be that the costs of expenditure on reproductive competition or ornamentation by females depress fecundity or parental investment, constraining the development of secondary sexual characters below the level at which they have measurable costs to female survival (LeBas 2006). For example, elevated levels of testosterone may have adverse effects on the fecundity of females or on the development of their offspring which constrain the evolution of further increases in female competitiveness (Drea *et al.* 2002; Knickmeyer and Baron-Cohen 2006).

As in males, the characteristics that affect the ability of individual females to acquire breeding opportunities, high status or mates and to rear young successfully include the individual's age, weight and hormonal status (see Chapter 8). Maternal status and support in social interactions can also be important, as can the number

and identity of allies (Hrdy 1981; Chapais 1992; Walters and Seyfarth 1997). For example, in some social primates, where females from the same matriline support each other in competitive interactions with members of other matriline, the social rank of individuals as well as their reproductive success depends on the rank of their matriline (see Chapter 8). Where similar characteristics determine competitive ability in the two sexes, selection often favours the development of similar secondary sexual characters in males and females. For example, in *Onthophagus* beetles, selection operating through the effective fighting success on reproduction has led to the evolution of horns in both sexes (Watson and Simmons 2010) (see Figure 1.10). Similarly, intrasexual reproductive competition has led to similar behavioural strategies adapted to the acquisition of rank in both sexes in some primates (see Chapters 8 and 13).

Evidence that reproductive competition can lead to the evolution of secondary sexual characters in females as well as in males has sparked a debate over whether or not this should be regarded as a form of sexual selection. Research on sexual selection and secondary sexual characters has focused principally on males and sexual selection has come to be defined as operating exclusively through competition for mates, mating opportunities or access to gametes produced by the opposite sex (Andersson 1994; Kokko and Jennions 2008). This generates a semantic difficulty in describing the evolution of secondary sexual characters in females, since they typically compete for breeding opportunities rather than mating opportunities. If sexual selection is confined to selection operating through variation in mating opportunities, many examples of selection operating through reproductive competition between females (and the adaptations it generates) would have to be excluded and fundamentally similar evolutionary processes operating in males and females would have to be ascribed to different evolutionary processes (Clutton-Brock and Huchard 2013b). For example, if a narrow definition of sexual selection is adopted, the evolution of horns in male and female *Onthophagus* beetles (Figure 1.10) would have to be attributed to different evolutionary processes. Similarly, selection operating through competition for dominance status in male primates would be regarded as an example of sexual selection (because it enhances mating success) while selection operating through competition for dominance status in females would have to be treated as a consequence of some

other form of selection (because it improves opportunities to breed but may not influence the chance of mating).

Several ways out of this dilemma have been suggested. One possible solution is to recognise some additional category of selection operating through intrasexual competition for resources other than mates, such as ‘social selection’ (Crook 1972; West-Eberhard 1979, 1983) and this has been advocated in some recent reviews (Roughgarden *et al.* 2006; Lyon and Montgomerie 2012; Tobias *et al.* 2012). However, in social species, distinguishing between ‘social’ selection and ‘sexual’ selection is difficult since virtually all selection pressures are affected by social interactions and relationships (Clutton-Brock and Huchard 2013b). Another approach is to abandon the attempt to distinguish between sexual and natural selection and to categorise selection pressures on the basis of whether or not they differ between the sexes (Carranza 2009, 2010), although few selection pressures are unaffected by sex. A third is to broaden the current definition of sexual selection to include all selection processes operating through intrasexual competition for breeding opportunities in either sex (Clutton-Brock 2007; Cornwallis and Uller 2010), although this can lead to problems in distinguishing between sexual selection and natural selection (Shuker 2010). A final approach is to abandon any formal attempt to distinguish between natural and sexual selection and to concentrate instead on comparisons of the relative intensity of selection operating through different components of fitness and on different phenotypic characters (Clutton-Brock 1983, 2004). Whichever solution to these semantic problems is adopted, this discussion underlines the qualitative similarity in the evolutionary mechanisms operating in the two sexes.

1.4 Mate choice

In *The Descent of Man*, Darwin (1871) described examples of female mating preferences and argued that sexual selection operating through consistent preferences for males with particular characteristics or ornaments could lead to the evolution of male secondary sexual characters. However, he did not explain the origins of female choice in any detail and his idea attracted criticism (Wallace 1889; Huxley 1938a,b). ‘Shall we assume’, wrote T.H. Morgan in 1903,

that still another process of selection is going on, that those females whose taste has soared a little higher than that of the average (a variation of this sort having appeared) select males to correspond, and thus the two continue heaping up the ornaments on one side and the appreciation of these ornaments on the other? No doubt an interesting fiction could be built up along these lines, but would anyone believe it, and, if he did, could he prove it?

Today, Morgan's scepticism appears wonderfully dated, for the process he describes was shown to be feasible by Fisher (1930) and empirical studies have confirmed the presence and benefits of consistent female preferences for mating with partners with a variety of anatomical, physiological, behavioural and genetic traits in a wide variety of animals (Andersson 1994). One of the earliest studies that provided clear evidence of female mating preferences based on male ornaments was Andersson's study of long-tailed widowbirds where he showed that he could increase (or decrease) the attractiveness and mating success of males by altering the length of their tail feathers (Andersson 1982), but there are now several other examples where experimental studies have demonstrated female mating preferences based on the characteristics of male ornaments (Andersson 1994; Wilkinson and Reillo 1994; Ryan 1997).

Female mating preferences may provide direct fitness benefits if their choice of mating partner affects their own survival, fecundity or rearing success. Direct benefits of mate choice are widespread and include reduced risks of predation, harassment or disease transmission while mating, improved access to resources defended by males and increased paternal investment (Danchin and Cézilly 2008; Pizzari and Bonduriansky 2010) (see Chapter 4). They can lead to the evolution of signals or ornaments in males that advertise their fertility or their ability to invest (Andersson 1994) (see Chapters 13 and 18).

Alternatively (or additionally), female mating preferences can generate indirect fitness benefits that affect the fitness of their offspring. Several different mechanisms for the evolution of mating preferences through indirect benefits have been suggested. Fisher (1930) argued that, if heritable choice variation in male ornaments associated with fitness arises by chance, females preferring ornamented males will produce sons with superior mating success and alleles favouring female discrimination and those controlling the development of male ornaments will spread together (Fisher 1930; O'Donald 1962, 1967).

Subsequent models confirmed that female preferences and male traits can coevolve in a runaway fashion leading to the evolution of exaggerated male characteristics and strong female mating preferences even if they have substantial costs to survival (Lande 1980, 1987; Kirkpatrick 1982; Lande and Arnold 1985). Empirical studies have confirmed the presence of these costs: for example, in guppies, there is a negative genetic correlation between male attractiveness and the survival of their offspring (Brooks 2000). A second possibility is that conspicuous, costly male traits indicate the overall fitness of their carriers and that females mating with males bearing these traits produce offspring of both sexes that have relatively high fitness. Models of this kind have come to be known as 'good genes' models and are currently regarded as providing the most plausible explanation of the benefits of female mate choice and the evolution of male ornaments through female choice (Andersson 1994; Ryan 1997; Danchin and Cézilly 2008).

The expression of secondary sexual traits is usually strongly condition-dependent and so may allow males to signal their genetic quality to females (see Chapter 4). One suggestion is that females may be selected to favour males with conspicuous ornaments because the high costs of ornaments guarantee the genetic quality of their mates (Zahavi 1975, 1977; Johnstone and Grafen 1993). Although this idea was initially regarded with scepticism (Kirkpatrick 1986), later modelling that combined heritable differences in viability with mating advantages showed that this process might contribute to the evolution of male ornaments, especially if their size depends on the individual's phenotypic condition (Grafen 1990; Andersson 1994).

Where females select partners on the basis of genetic differences, it is necessary to explain why heritable variation in male quality persists (Kirkpatrick and Ryan 1991). One of the first suggestions was that this is a result of continuing coevolution between parasites and their hosts (Hamilton and Zuk 1982), though attempts to test this possibility have produced mixed results (Danchin and Cézilly 2008). Alternatively, variation in male quality may be maintained by the accumulation of deleterious mutations, interactions between selection at different loci, fluctuating selection pressures and variation in the degree of inbreeding (Danchin and Cézilly 2008).

Recent research on female mating preferences has also explored the possibility that females preferentially mate with males whose genotype complements their own (Mays and Hill 2004). Laboratory studies of a variety of organisms suggest that heterozygosity at specific loci can improve individual fitness and that the degree of male ornamentation is sometimes correlated with levels of heterozygosity (von Schantz *et al.* 1997). The best examples of effects of this kind come from studies of the effects of heterozygosity at the major histocompatibility complex (MHC) locus, which is involved in immune function (Jordan and Bruford 1998). Genes at this locus are extremely variable, both within and across species (Zinkernagel and Doherty 1974; Klein 1986; Potts and Wakeland 1990), and individuals which are heterozygous at particular MHC loci are often more resistant to infections and diseases (Gabriel *et al.* 1994; Comings and MacMurray 2000; Penn *et al.* 2002). They can also show high levels of ornamentation, display or social status (Yamaguchi *et al.* 1981; Roberts and Gosling 2003) and several studies have produced empirical evidence of disassortative mating for MHC genotype (see Chapter 4).

As well as selecting particular partners, females may gain both direct and indirect fitness benefits by mating with more than one male (Andersson 1994; Zeh and Zeh 1996). Direct benefits include improved fecundity arising from the avoidance of monopolisation by infertile males or by access to multiple 'nuptial' gifts, as well as improved survival of offspring as a consequence of improved protection and reduced rates of infanticide (see Chapter 4). Indirect benefits include improved viability of offspring caused by avoidance of the negative consequences of genetic incompatibility or selfish genetic elements (Trogenza and Wedell 2002; Price *et al.* 2008).

In some animals, females can also control the probability that their eggs will be fertilised by different males through post-copulatory mate choice. In insects and birds, which commonly store sperm, females can control the paternity of their offspring by storing sperm at different sites and subsequently varying its release (Birkhead and Møller 1992; Ward 1993; Andersson 1994; Simmons 2001). In some mammals, females also store sperm (Birkhead and Møller 1993), but a more common way by which they can manipulate paternity is by controlling the number and identity of males they mate with (see Chapter 4). Females

commonly mate with more than one male. Potential benefits include direct fitness benefits, such as confusing paternity and reducing the risk of infanticide, and indirect benefits associated with increases in genetic variability within litters (Simmons 2001).

While theoretical research tends to contrast different mechanisms maintaining female mating preferences, in reality, several evolutionary mechanisms may often be involved in maintaining the same ornament (Kokko 2003; Kokko *et al.* 2003). For example, where females select males on the basis of direct benefits, their choice may also have indirect benefits, and where females select males on the basis of indirect benefits, their decisions may also benefit their own fitness directly. Indirect benefits may commonly include benefits to survival as well as to attractiveness, and selection pressures outside the context of mate choice may often affect both male traits and female preferences (see Chapter 4).

Where OSRs are biased towards males, mate choice is typically more highly developed in females than males (Trivers 1972; Emlen and Oring 1977). However, this does not preclude the evolution of mating preferences in males and an increasing number of empirical studies have found evidence of mate choice in both sexes (Edward and Chapman 2011). Like female competition for males, the relative choosiness of males varies with the availability of partners and can differ between local populations (Simmons and Gwynne 1993) as well as between stages of the breeding cycle (Amundsen and Forsgren 2001).

Like female preferences, male preferences vary qualitatively and quantitatively. In some species, males prefer familiar partners, while in others they prefer novel partners (Orrell and Jennsen 2002). In some cases, males prefer older, larger or more dominant partners, while in others they prefer younger partners (Werner and Lotem 2003; Wong and Jennions 2003; Herdman *et al.* 2004; Kvarnemo *et al.* 2007). In several species, males also show consistent preferences for partners that have not mated recently (see Chapter 15). Where females are ornamented or brightly coloured, males often show a preference for brighter or more highly ornamented females (Andersson 1994). In addition, males, like females, sometimes copy each other's choice of partners, reinforcing the effects of individual choice (Dugatkin 1992; Widemo 2006).

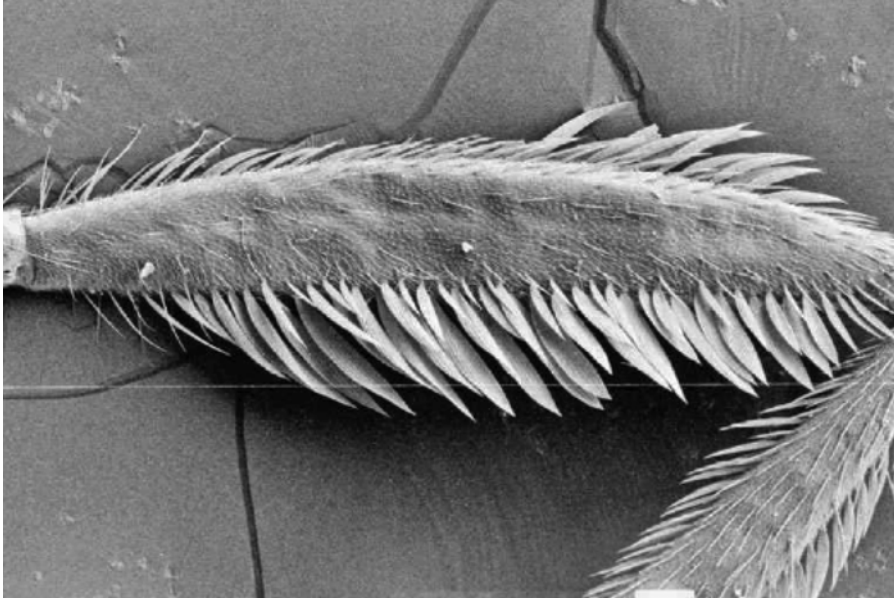


Figure 1.11 Sexually selected ornaments in females. Scanning electron micrograph of pinnate leg scales on the leg of a female empidid dance fly (*Rhamphomyia longipes*). In most dance fly species, males bring nuptial gifts to females, who compete for suitors; the size of scales on the legs of females is related in some species to their fecundity, and males mate preferentially with females with large leg scales. *Source:* From LeBas *et al.* (2003). Reproduced with permission from the Royal Society.

Individual differences in fecundity between females caused by intrasexual competition for resources are likely to strengthen selection on males to identify and prefer superior partners and, on females, to signal changes and individual differences in fecundity (Berger 1989; Reinbold *et al.* 2002; Clutton-Brock 2007). Male preferences often appear to favour female characteristics associated with fecundity, suggesting that they may generate direct fitness benefits (see Chapter 15). For example, in empidid dance flies, where females are ornamented with large pinnate leg scales whose size reflects their fecundity, males preferentially mate with highly ornamented partners (Cumming 1994; LeBas *et al.* 2003) (Figure 1.11), while sexual swellings in female primates (Figure 1.12) appear to advertise temporal changes in their fertility (see Chapter 7).

1.5 Parental care

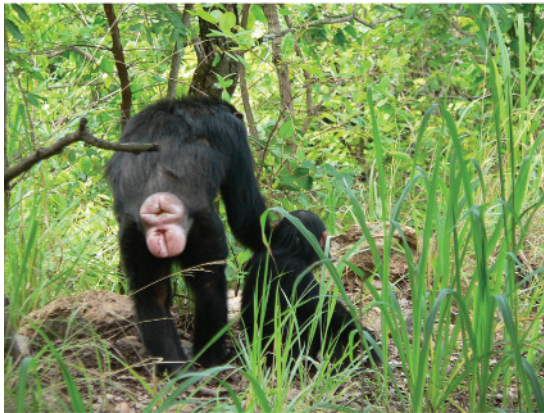
Males and females

The extent of parental care in animal societies ranges from species where parents abandon eggs shortly after they are laid to species where they associate with and

protect their offspring throughout much of their lives (Clutton-Brock 1991). The first attempts to account for these differences focused not on the evolution of care but on the evolution of egg size and clutch size (Perrins 1965; Lack 1968; Smith and Fretwell 1974). Theoretical treatments argued that the survival of individual embryos should increase rapidly with egg size before approaching an asymptote and used the marginal value theorem to identify the egg size that would provide parents with the greatest fitness return per unit of egg weight or investment (Smith and Fretwell 1974; see also Chapter 5). In most cases, this is likely to be lower than the egg size at which offspring fitness is maximised, favouring parents that produce intermediate-sized eggs. In addition, the evolution of egg size is also likely to be modified by trade-offs between egg size and clutch size or fecundity (Charnov and Krebs 1974). The same model can be used to predict the amount or duration of parental care, leading to the general prediction that, where neonates and juveniles face adverse physical or social environments, the benefits of extended parental care are likely to increase. Empirical studies of a wide range of animals confirm that this is often the case (Clutton-Brock 1991).



(a)



(b)

Figure 1.12 Sexually selected ornaments in female primates: (a) female baboon and (b) female chimpanzee at mid-cycle. Source: (a) © Phyllis Lee; (b) © Michael Wilson.

Among vertebrates that care for their offspring, patterns of care vary from groups where care is usually restricted to females (including many mammals), through groups where biparental care is normal (as in most birds and a few mammals, including titi monkeys; see Figure 1.13), to groups where exclusive male care is common (as in some fish and amphibia). One obvious question is why patterns of parental care vary so widely? The first theoretical explanations of the evolution of parental care focused on the benefits that each sex would gain by deserting mating partners after copulation, and predicted that uniparental care should be most likely to evolve in whichever sex benefits most from caring for its offspring when the costs of care and the response of the other sex to desertion are taken into account (Maynard Smith 1977; Houston



Figure 1.13 The South American titi monkey is monogamous and produces single young. In contrast to other monogamous, monogamous species, males carry dependent infants for a larger proportion of daytime than females. Source: © Kathy West.

et al. 2013). Trivers (1972) originally argued that because anisogamy generates male-biased OSRs and more intense mating competition among males than among females, it predisposes females to care and males to invest in competition for mates, and this argument was subsequently accepted as a general explanation of the prevalence of female care (Emlen and Oring 1977; Maynard Smith 1977). However, the prevalence of uniparental male care in some groups suggests that other factors must be involved. Recent models of the initial evolution of parental care have pointed out that where males routinely desert partners after mating, the OSR will become strongly male-biased and the probability that deserting fathers will find additional mates is likely to fall, increasing the relative benefits to males of guarding mates and contributing to parental care (Queller 1997; Houston and McNamara 2002; Kokko and Jennions 2008; Houston *et al.* 2013). Under these conditions, anisogamy may still favour the evolution of care by males rather than females, though contrasts in ecology, life histories and the structure of breeding systems are also likely to have important effects and have the potential to reverse this bias in particular cases (Kokko and Jennions 2008).

Comparisons of patterns of care in different animal groups support the suggestion that ecological factors play an important role in the evolution of sex differences in parental care. For example, in many demersal-breeding fish, intrasexual competition between males

has led to the defence of preferred breeding sites. As the presence of eggs attracts further mating partners and males can care for multiple clutches simultaneously, the marginal costs of care may often be lower and the marginal benefits may be higher for males than for females, leading to the evolution of male care (Clutton-Brock and Vincent 1991). Since parents do not usually need to maintain the temperature of eggs and rarely provision young directly, biparental care is relatively rare in fish. In contrast, in birds, the need to brood and feed young with scarce high-energy foods generates strong selection for biparental care and female fecundity is often constrained by the number of eggs that can be brooded. In mammals, the commitment of females to gestation and lactation constrains female opportunities for increasing fecundity even further and (in most species) reduces the marginal benefits of contributing to parental care in males, while the relatively high density of females and their tendency to form groups favours the evolution of polygyny (Clutton-Brock 2009a). While interspecific contrasts in ecology appear to be responsible for major contrasts in patterns of care, the relative costs and benefits of care to the two sexes also vary and, in some cases, can generate changes in the sex responsible for care within or between populations (Alonzo and Klug 2012).

A related question is how partners in biparental species would be expected to divide the workload associated with raising young. Where both parents are involved in care, reductions in the level of contributions by one partner are likely to cause its mate to increase their contributions, though rising costs of care may prevent them from compensating fully (Houston and Davies 1985; Parker *et al.* 2002; Johnstone and Hinde 2006). Situations of this kind can generate conflicts of interest between partners, and may lead to a process of 'negotiation' over their contributions to care, which may occur both within particular breeding seasons and over evolutionary time (see Chapter 16). As long as individuals do not overcompensate for reductions in their partner's contributions, a stable equilibrium is reached when the reaction curves of the partners intersect and neither partner can improve its fitness by altering its contributions (Parker 1985; Westneat and Sargent 1996; McNamara *et al.* 2003). In many birds and mammals, males have greater opportunities than females to increase their fitness by extra-pair mating, so that contributions to care

have higher fitness costs to males than females which may explain why females contribute more to parental care than males in many biparental species (Clutton-Brock 1991).

Parent-offspring conflict

Early theories explaining the evolution of parental care usually assumed that parents were free to allocate the resources at their disposal among offspring so as to maximise their own fitness. However, in sexually reproducing animals, offspring will often be selected to extract more care from parents than the amount that would maximise the parent's fitness, generating conflicts of interest between parents and offspring over the level of parental investment (Trivers 1974). For example, where parents are related to their offspring by 0.5, they would be likely to 'disagree' with their offspring over the continuation of parental care from the point when the benefit–cost ratio equals 1.0 to the point when it equals 0.5 (see Chapter 5). Depending on the rate at which the benefit–cost ratio declines with increasing offspring age, this may either be a relatively short period or a relatively long one. In a subsequent model, Trivers also showed that parents and offspring are likely to disagree over the amount of care at particular stages of development. Trivers' argument was subsequently challenged by Alexander (1974) on the grounds that the evolution of strategies in offspring that reduced their parents' fitness would be selected against when the offspring themselves became parents and were similarly exploited by their own offspring. However, subsequent models of parent–offspring conflict showed that, in sexual organisms, 'conflictor' genes are able to spread, though this can be inhibited if their cost to parental fitness is high or parents are able to control the distribution of care (Parker and MacNair 1979; Parker 1985).

Conflicts of interest between parents and offspring are likely to affect all aspects of parental investment, but testing predictions is often complex because of the difficulty of identifying separate optima for parents and offspring. Some of the most convincing evidence that parent–offspring conflict affects patterns of investment comes from studies of the sex ratio in eusocial insects (Trivers and Hare 1976; Charnov 1982; Boomsma and Grafen 1991; West 2009) or from cases where conflicts between offspring reduce brood size below the parent's optimum (Godfray

1994; Mock and Parker 1997). In many cases, conflicts of interest have been settled long ago and the current situation is a consequence of past conflict but there are some interactions where overt behavioural conflicts are played out in real time over the course of each breeding cycle (see Chapter 5). Some of the best examples are of interactions between offspring and parents in nidicolous birds and insects, where young signal or beg for food and parents commonly adjust both their frequency of feeding and the distribution of food in relation to begging frequency (Kilner and Johnstone 1997; Smiseth and Moore 2002; Hinde *et al.* 2009). Though it has been suggested that begging could represent a way of blackmailing parents to supply food in order to reduce wasteful solicitation or the risk of predation (Zahavi 1977; Parker and MacNair 1979), most of the available evidence suggests that it is often an honest signal of need with tangible costs to chicks which maintain its reliability as a signal and prevents exploitation of parents by manipulative offspring (Kilner 2002).

Offspring sex ratios

Especially in polygynous or promiscuous species where males compete intensely for breeding opportunities, parental investment is often likely to affect the fitness of sons more than daughters. In an early paper, Trivers and Willard (1973) argued that this should often cause parents to invest more heavily in individual sons than daughters and that phenotypically superior mothers that can afford the expenditure of energy necessary to rear a son might be expected to specialise in producing male offspring while inferior females would be expected to produce females. Other aspects of parental phenotype that affect the fitness of offspring of one sex more than that of the other (such as their social status or their attractiveness to the opposite sex) would also be expected to affect the sex ratio of progeny, as should temporal fluctuations in the resources necessary for parental care (Clutton-Brock 1991; Leimar 1996) (see Chapter 18). While a number of studies have demonstrated trends in the expected direction, these are often inconsistent and there is still disagreement over the extent to which empirical studies support theoretical predictions (Charnov 1982; Lessells 2002; West 2009).

Trivers and Willard's predictions concern variation in the relative numbers of sons and daughters that different

mothers should produce rather than the overall (or average) ratio of males to females. In many insects, average sex ratios vary widely, though in birds and mammals most species produce approximately equal numbers of male and female offspring (Williams 1979; Clutton-Brock 1991). This puzzled some early advocates of group selection, who argued that selection would be expected to favour female-biased sex ratios that maximised the productivity of groups or populations. However, the problem had already been discussed by Darwin (1871, p. 316) and solved independently by Düsing (1883, 1884a,b) and Fisher (1930). Fisher pointed out that because all individuals require a mother and father, if parents (on average) produced a preponderance of one sex, this would increase the average fitness of individuals of the other sex, generating frequency-dependent selection to increase the number of offspring of the rarer sex. Eventually, he argued, this would lead to offspring sex ratios close to parity, unless there are sex differences in survival of juveniles before the end of parental care, in which case sex ratios at the beginning of parental care should be biased towards the less viable sex and biases should be reversed by the end of the period of parental care so as to maintain equal (total) investment in the two sexes (Fisher 1930; Shaw and Mohler 1953; Leigh 1970).

More recently, a range of other factors that can affect the average sex ratio have been identified (West 2009). These include sex differences in parental investment of the kind predicted by Trivers and Willard (1973) and sex differences in the intensity of competition or cooperation between relatives that influence the relative costs of producing sons and daughters to the parents' fitness (Malcolm and Marten 1982; Gowaty and Lenartz 1985; Griffin *et al.* 2005). A range of other mechanisms, including trade-offs between the sex ratio and potential litter size and conflicts of interest between parents or between parents and offspring, may also affect the average sex ratio (Frank 1987; Seger and Stubblefield 2002). In addition, sex determining mechanisms may generate deviations from Fisher's principle and may themselves be affected by selection operating on the sex ratio (Kraak and Pen 2002; Pen and Weissing 2002). Unfortunately, the diversity of evolutionary theories concerning sex ratios means that it is often difficult to attribute the presence or absence of observed deviations from Fisher's principle to particular mechanisms

with confidence and there is still disagreement over their relative importance (Cockburn *et al.* 2002).

1.6 Cooperation

Definitions

The evolution of cooperation presents evolutionary biologists with the intriguing problem of explaining why individuals should assist other animals at some cost to their own fitness (Gardner and Foster 2008). To explain cooperation, it is important to be clear about how it is defined. Evolutionary biologists view interactions between individuals as having four potential outcomes for the direct fitness of the participants (Figure 1.14): they can be mutually beneficial or ‘mutualistic’ if both partners assist each other and both gain ‘direct’ fitness benefits that increase their survival or breeding success (+/+); altruistic, if one partner assists another at some net cost to its own direct fitness (-/+); selfish, if one partner increases its own direct fitness at some cost to that of its partner (+/-); or spiteful, if one individual’s actions reduce both its own fitness and that of its partner (-/-).

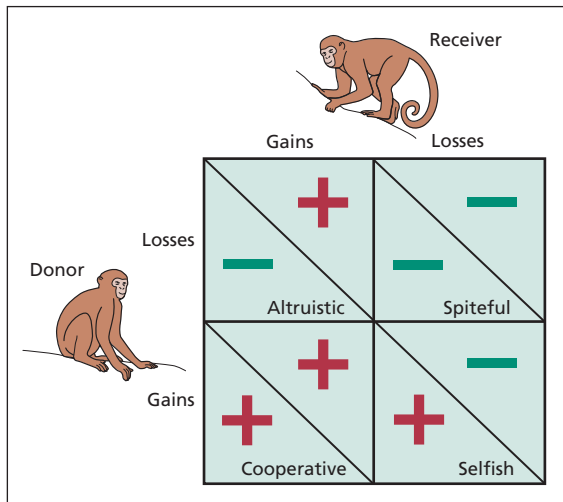


Figure 1.14 Interactions between group members can be allocated to four categories: selfish (+/-); mutually beneficial or mutualistic (+/+); altruistic (-/+); and spiteful (-/-) Source: From Hauser *et al.* (2009). Reproduced with permission from the Royal Society.

Cooperation is usually taken to include behaviour that generates direct fitness benefits to cooperators through its benefits to others as well as altruistic behaviour that is maintained by indirect benefits (West *et al.* 2007). The inclusion of a requirement that the effects of cooperative behaviour on recipients affect selection operating on the cooperator is necessary because there are many cases where the actions of individuals generate coincidental, unselected benefits to others, which are usually referred to as ‘by-product mutualisms’ (Brown 1987). For example, individuals that react to approaching predators may alert other group members but their behaviour may be adapted only to maximising their own chances of survival. Although interactions of this kind are sometimes regarded as examples of cooperation, this is misleading since selection is not operating through behaviour that provides benefits to others.

If by-product mutualisms are excluded, explanations of cooperative behaviour in non-human animals fall into six main categories, described in the following sections.

Prestige

Some models of cooperation suggest that cooperative activities represent costly displays or ‘handicaps’ that increase the ‘prestige’ of individuals and attract mates or intimidate rivals (Zahavi and Zahavi 1997). While this is feasible, there is little empirical evidence that cooperative behaviour in non-human animals operates in this way (Wright *et al.* 2001; Nomano *et al.* 2013); individuals seldom compete to perform cooperative activities; dominants seldom contribute consistently more than subordinates; and this explanation does not coincide with our current understanding of the causal basis of cooperative behaviour (see Chapter 17).

Induced assistance

In some cases, the selfish behaviour of one (or more) individual induces others into providing assistance at some cost to their own net fitness. For example, stronger or more powerful individuals may coerce other individuals to assist them, using either direct force or the threat of punishment, or needy individuals may harass other group members until they provide assistance (Clutton-Brock and Parker 1995; Cant and Johnstone 2006).

Pseudo-reciprocity

In other cases, individuals may derive direct fitness benefits by assisting or stimulating others, whose

responses are purely selfish (Connor 1995). Some inter-specific interactions provide examples of this kind of cooperative behaviour. For example, some ants provide food for fungus colonies whose growth provides food and so contributes to the ants' breeding success, but is not (necessarily) adapted to provide benefits to ants (Hölldobler and Wilson 1990). In other cases, individuals may modify their behaviour to take advantage of the generalised responses of conspecifics: for example, by regularly associating with dominant individuals and grooming them repeatedly, subordinates may habituate them to their presence, gaining shelter from competition and interference by rank neighbours as a consequence (Barrett *et al.* 2002; Watts 2002; Cheney and Seyfarth 2008). Cases of this kind are referred to as 'pseudo-reciprocity' (Connor 1995; Leimar and Connor 2003) since the behaviour of one partner is adapted to providing benefits while its partner's responses are purely selfish.

Shared benefits

Both the *Origin of Species* and *The Descent of Man* show that Darwin was aware that social animals commonly cooperate with each other. In *The Descent of Man*, he 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'. Subsequent studies show that there are a number of birds and mammals where several breeding females pool their young and care for them together (Figure 1.15) and gain benefits by doing so (see Chapter 17).

Mutually beneficial interactions of this kind are common in social animals and are modelled in 'collective goods' or 'public goods' games (Hawkes 1992; Mesterton-Gibbons and Dugatkin 1992; Sandler 1992; Dugatkin 1998; Nunn and Lewis 2001; Johnstone and Rodrigues 2016). The simplest models consider two unrelated players and only differ from Prisoner's Dilemma games in their pay-off structure while, in N-person games, all individuals have access to collective goods. Utilisation of collective goods can either have no effect on their availability or can reduce it, leading to competition between contributors; situations of the first kind are described as *non-rival* while those of the second are described as *rival* (Nunn and Lewis 2001).

Models seek to identify the conditions where cooperative behaviour is maintained and is not eroded by exploitative 'free-riding' strategies or other collective

action problems (CAPs) (Ostrom 1990, 2003; Nunn and Lewis 2001). The exploitative strategies that they consider vary and include cases where free-riders contribute nothing to the creation of collective goods as well as cases where they contribute less than the benefits they receive (Marwell and Ames 1980; Sandler 1992). While cooperative behaviour involving non-kin that generates shared mutualistic benefits can be viewed as being maintained through selection operating on individuals, it is also possible to argue that it reduces the fitness of individuals relative to other group members but increases the fitness of groups of cooperators and so is maintained by group selection (Wilson 1975, 1977).

Cooperators may be able to reduce the risk of exploitation in 'public goods' games in a number of different ways. For example, they may associate selectively with each other or they may assist other group members only if they have previously received assistance from any other member of their group, a scenario known as *generalised reciprocity or contingent cooperation* (Pfeiffer *et al.* 2005; Rankin and Taborsky 2009; Taborsky *et al.* 2009 a,b). Alternatively, group members might monitor the frequency of cooperation between third parties (Nowak and Sigmund 1998a,b) or might punish defectors by reducing their own level of investment (Houston and Davies 1985) or by imposing some penalty on them (Clutton-Brock and Parker 1995; Andreoni *et al.* 2003).

In non-human animals, cooperation maintained by shared benefits is most likely to be evolutionarily stable if group size is small (Sandler 1992; Nunn and Lewis 2001) and synergistic effects of the presence of other individuals are strong (Kokko *et al.* 2001). For example, the relative importance of shared benefits may increase if there is some degree of labour division or role complementarity which helps to increase the efficiency of individuals working together (Olson 1965; Nunn and Lewis 2001). In addition, cooperation can be maintained in 'public goods' games if group members police each other's activities and punish individuals that fail to cooperate (Boyd and Richerson 1992; Frank 1995; Ruxton and van der Meer 1997; Fehr and Gächter 2002), though individuals might also be expected to avoid contributing to punishing defectors and to free-ride on the efforts of others (Heckathorn 1989; Henrich and Boyd 2001) and empirical studies suggest that 'policing' behaviour in non-human animals is largely confined to groups consisting of close relatives or breeding partners.



(a)



(b)

Figure 1.15 Two communal breeders: in both (a) acorn woodpeckers and (b) African lions, several breeding females jointly provide care for their young. Sources: (a) © Bruce Lyon; (b) © Dave Hamman.

Reciprocity

In ‘public goods’ games, cooperating group members derive immediate benefits from assisting each other. However, in many animal societies, individuals assist each other at different times, sometimes giving assistance and sometimes receiving it. Where there are time delays between giving and receiving assistance, individuals might be expected to attempt to minimise their investment in assisting their partners while maximising the amount of assistance they receive, leading to selection for ‘free riding’. This will, in turn, favour the evolution of strategies that minimise the risk that cooperation will be exploited by their partners.

One way for cooperators to avoid being exploited is to adjust the amount of assistance they give to particular partners the amount they receive from them. In 1971, Trivers published a classic paper arguing that cooperation between non-kin could be maintained where individuals that give assistance to others at some cost to their own fitness receive assistance from them in turn, so that although giving assistance has temporary costs, these are exceeded by subsequent benefits and both (or all) partners gain when net fitness benefits are calculated across several interactions. Trivers referred to this process as *reciprocal altruism* and used it to explain the evolution of interspecific cooperation as well as of intraspecific cooperation between unrelated individuals. Today, it is usually referred to as ‘direct’ or ‘cost-counting’ reciprocity.

As Trivers pointed out, reciprocal altruism is analogous to theoretical games devised by economists called the Prisoner’s Dilemma (von Neumann and Morgenstein 1953). In these games, two individuals that cooperate both gain higher pay-offs than if they refuse to assist each other (defect), but the highest pay-off is gained by individuals that defect when their partners cooperate, while the lowest pay-off is to individuals that cooperate when their partners defect (Box 1.1 and Figure 1.16). In ‘one-shot’ encounters, these conditions always favour defection but, where partners interact repeatedly (as in iterated Prisoner’s Dilemma, or IPD, games), strategies that involve copying each other’s responses (such as tit-for-tat or TFT) can be stable.

Following the publication of Trivers’ paper, the evolution of cooperation in Prisoner’s Dilemma games was widely investigated (Axelrod 1984; Dugatkin 1997). Several models showed that the most successful versions of TFT strategies are slightly ‘generous’ ones, where individuals copy the previous behaviour of their

		Player 2	
		Cooperate	Cheat (defect)
Player 1	Cooperate	R 1-year prison term	S 5-year prison term
	Cheat (defect)	T 0-year prison term	P 3-year prison term

Figure 1.16 Pay-offs for Player 1 in the original Prisoner’s Dilemma game. If neither prisoner snitches on his mate (‘cooperate’), they both get 1-year prison terms; if both snitch, they both get 3-year terms (‘defect’). However, if one prisoner defects while the other cooperates, the defector goes free while the cooperator gets 5 years. The game is defined by the inequalities $T > R > P > S$ and $2R > T + S$. Source: From Dugatkin (1997). Reproduced with permission of Oxford University Press, USA.

partners, cooperating when they do and forgiving occasional lapses but eventually responding to defection by ceasing to provide assistance (Nowak 2006). In general, direct reciprocity is most likely to be stable where the costs of assistance are low; where there is a high certainty of repayment; where the potential benefits of the exchange are high; and where the interval between exchanges is short (Trivers 1971, 2006; Wilkinson 1984).

A number of additional tactics that individuals involved in Prisoner’s Dilemma type situations might use have been suggested. One way of reducing the chance of assisting non-cooperators is to monitor interactions between third parties, and cooperate selectively with frequent cooperators (Sugden 1986; Boyd and Richerson 1989; Nowak and Sigmund 1998a,b, 2005; Riolo *et al.* 2001; Wedekind and Braithwaite 2002). Cooperation maintained by third party effects (including models of ‘reputation’ and ‘image scoring’) is sometimes referred to as *indirect reciprocity* and has been the focus of recent experiments with humans (Milinski *et al.* 2002; McElreath 2003). Although indirect reciprocity will usually strengthen the benefits of cooperating (Nowak and

Box 1.1 Reciprocity and the Prisoner's Dilemma

The Prisoner's Dilemma game envisages a situation where two or more players can choose to cooperate with each other or can refuse to do so (von Neumann and Morgenstein 1953; Axelrod and Hamilton 1981; Dugatkin 1997; Trivers 2006). Refusals to cooperate are usually referred to as 'defecting' or 'cheating'. The example originally used to illustrate this situation is one where two suspects of a crime are interviewed by the police in separate rooms. If both suspects cooperate and keep silent, the police only have enough evidence to send them to prison for 1 year each but if both snitch on their partners or 'defect', the police can send them both down for 3 years (see Figure 1.17). However, if one snitches (defects) but the other doesn't (cooperates), the snitch walks free while the cooperator gets 5 years (Dugatkin 1997).

What is the best strategy trade-off under these conditions? In 'one-shot' encounters where the two players interact once, defection is the best strategy, but in repeated (iterated) versions of the same game, cooperative strategies can generate higher pay-offs than purely selfish ones (Axelrod and Hamilton 1981). A conditionally cooperative strategy, where individuals initially cooperate and subsequently imitate the response of their partner (tit-for-tat or TFT), is sometimes the best solution. TFT is successful because it combines three characteristics (Axelrod 1984): it is never the first to defect; it is swift to retaliate; and it is forgiving of past defection, in the sense that its memory does not extend back beyond the previous move.

Axelrod and Hamilton's initial work led to a spate of papers exploring factors affecting the outcome of different strategies in the Prisoner's Dilemma game (Trivers 2006). While many of them confirm that TFT is the most successful strategy under a range of conditions, some have shown that simple TFT can be beaten by TFT-like strategies that are slightly more forgiving (Boyd and Richerson 1989; Nowak and Sigmund 1992, 1993) or that a mixture of TFT and defecting strategies can be the stable outcome of iterated games (Peck and Feldman 1986; Dugatkin and Wilson 1991; Pollock and Dugatkin 1992). Others show that where TFT-like strategies predominate, a policy of 'win-stay, lose-shift' which repeats successful strategies and abandons less successful ones is favoured (Nowak and Sigmund 1993).

Theoretical studies have also explored a range of factors affecting the outcome of Prisoner's Dilemma games (Dugatkin 1997) and have shown the following.

- Increasing group size may hinder the evolution of cooperation (Boyd and Richerson 1988; Trivers 2006).
- Subdivisions within populations can increase the chance that cooperative strategies will resist invasion by defectors (Pollock 1989).
- Stochastic variation in responses can lead to cycles of cooperation and defection (Nowak and Sigmund 1993).
- Individual variation in behaviour can help to maintain cooperation (McNamara *et al.* 2004).
- Where players alternate between donor and recipient roles, this favours generous TFT over win-stay, lose-shift strategies (Nowak and Sigmund 1994).
- Kinship between players is likely to promote cooperative strategies (Queller 1985).
- Dispersing or 'roving' defectors will hinder the evolution of cooperation (Dugatkin and Wilson 1991).
- Punishment of defectors promotes cooperation (Boyd and Richerson 1992).
- Stochastic 'mistakes' in the responses of players can affect the outcome of games, sometimes hindering the evolution of cooperative strategies (Hirshleifer and Coll 1988; Boyd and Richerson 1989; Stephens *et al.* 1997).
- Monitoring the responses of other group members in reactions with third parties and adjusting responses to them on the basis of their 'reputation' ('observer TFT') can invade populations of individuals playing simple TFT (Pollock and Dugatkin 1992).
- Competition for cooperative partners can help to maintain and increase cooperative behaviour (Roberts 1998).

Related work has explored the effects of more fundamental changes in the assumptions underlying models of the Prisoner's Dilemma (see Trivers 2006). Strategies that can vary between individuals may replace fixed inflexible ones (Johnstone and Godfray 2002). Similarly, strategies that initially invest little in cooperative behaviour but increase their investment after they interact with other cooperators are often favoured (Roberts and Sherratt 1998). The division of investment in cooperative behaviour into small units can limit the potential costs of defectors and favour the evolution of prolonged exchanges of small acts of assistance (Fischer 1988; Trivers 2006). Finally, some recent models envisage situations intermediate between those considered by traditional Prisoner's Dilemma models and models of generalised reciprocity or group augmentation. For example, if purely selfish actions by one individual generate independent, coincidental benefits to another, selection can favour coordinated cooperative investment (Hauert *et al.* 2002; Hauert and Doebeli 2004).

Sigmund 1998a), minor differences in assumptions can lead to different outcomes (Leimar and Hammerstein 2001; Leimar and Connor 2003). For example, the presence of individuals that cannot afford to contribute to cooperative activities broadens the range of conditions under which cooperation is maintained as a result of selection against both defectors and unconditional assistance.

Examples of direct reciprocity are common in humans (see Chapter 20) but are rare in non-human animals and there is a growing perception that the situation considered by IPD models ignores many important features of cooperative interactions and relationships among animals (Noë and Hammerstein 1994; Clutton-Brock 2002, 2009b; Hammerstein 2003; Trivers 2006). These include communication between partners concerning their intentions (Smuts and Watanabe 1990), the capacity of individuals to modify their behaviour in the course of repeated interactions (McNamara *et al.* 1999), variation in partner quality (Noë 1992), the ability of individuals to choose between several alternative partners (Enquist and Leimar 1993) and the effects of different tactics on the individual's subsequent ability to attract or retain partners (Smuts and Watanabe 1990; McNamara *et al.* 1999).

Moreover, it is questionable how often cooperative interactions between animal partners involve an alternation of costs and benefits since fitness benefits should be accounted prospectively and it is frequently unclear that there really are delays between incurring costs and gaining benefits, as models of reciprocal cooperation based on IPD assume. Many cooperative interactions between non-kin occur in the context of well-established supportive relationships that benefit both parties (see Chapter 9) and repeated failure to provide assistance to a regular ally may cause them to engage in punishing tactics or lead to supportive relationships unravelling. Not only may defectors subsequently have difficulty in finding new partners and establishing cooperative relationships with them (Hirshleifer and Rasmusen 1989; Pollock and Dugatkin 1992) but previous partners may form new alliances and re-emerge as competitors. Where providing assistance reduces these dangers, it may be more realistic to account it as providing immediate net benefits rather than net costs that are subsequently offset by greater net benefits. Arguments of this kind suggest that many interaction that have been interpreted as examples of reciprocity may, in practice, represent cases where interacting individuals gain

immediate shared benefits from their actions and may be more realistically modelled as restricted 'public goods' games (see Chapter 9).

The direct benefits of cooperating with particular individuals (whether they are kin or non-kin) are likely to be affected both by the partner's ability to contribute to cooperative activities and by their intrinsic skill or power. For example, where individuals provide each other with support in competitive interactions with other group members, alliances with dominant partners are likely to yield larger benefits than alliances with subordinates (see Chapters 9 and 14). Since the availability of desirable partners will usually be limited, individuals might be expected to compete for the best allies and that they appear to do so in several social mammals (Noë and Hammerstein 1994, 1995; Roberts 1998; Noë *et al.* 2001). Some of the most detailed evidence of competition comes from studies of social primates where group members use grooming to establish alliances and tolerate larger asymmetries in grooming when interacting with higher ranking animals (Harcourt 1988, 1989, 1992; Cords 2000).

Cases where competition for social partners generates asymmetries in the provision of assistance are often referred to as 'market effects' to emphasise their similarity to exchanges of services between humans, where the amount that individuals will pay for a resource depends on its availability relative to the number of individuals that need it (Noë and Hammerstein 1994, 1995). Although the presence of market effects is sometimes presented as a prediction of models of cooperation based on reciprocity, they are likely to be common wherever the productivity of different potential partners varies or opportunities for cooperation are limited by the supply of partners. For example, individuals might be expected to compete to form mutualistic relationships with powerful individuals or to coerce individuals whose behaviour is most likely to influence their fitness. As a result, the presence of market effects provides no strong evidence that direct reciprocity is involved or that interactions between individuals resemble the exchanges that occur in human markets.

Altruistic assistance

In some animal societies, a single female in each group monopolises reproduction and her offspring are reared by non-breeding helpers of either or both sexes. Cooperative breeding systems of this kind occur in insects, birds and mammals (Figures 1.15, 1.17 and 1.18). In



Figure 1.17 In some birds, like pied babblers, social groups consist of a single breeding female and her mate, that are assisted in raising young by non-breeding helpers of both sexes. In this photograph, an adult helper brings food to a dependent juvenile. *Source:* © Alex Thompson.

some cooperative vertebrates, like naked mole rats, and many social insects, breeding females and subordinate helpers differ in size and shape as well as in physiology and behaviour (Figure 1.19), while in some social insects (which live in far larger colonies than any cooperative vertebrate), workers are obligately sterile (Figure 1.20). Some authorities refer to species where breeders and helpers differ in morphology as ‘eusocial’ while others only use the term for species where helpers are obligately sterile. On the first definition, a number of mammals that breed cooperatively would be classed as eusocial while, on the second, no vertebrates would be eusocial (see Chapter 17).

Although most of the examples of cooperative behaviour that Darwin discusses in *The Descent of Man* are examples of shared benefits (see above), he also recognised the existence of cases where individuals provide assistance but do not receive it and appreciated that these represented a serious problem for the theory of natural selection. In the *Origin of Species* (Chapter VIII, p. 228) he describes how the problem of the evolution of sterile females in social insects initially appeared to be ‘insuperable, and actually fatal to my whole theory’, but then goes on to explain how the problem ‘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’ (p. 230), presaging developments in our understanding of social evolution that did not occur for another 100 years.

Just over 100 years later, W.D. Hamilton produced the first formal models of animal altruism, laying one of the cornerstones of our current understanding of animal societies. In contrast to many of his contemporaries working on vertebrates, Hamilton was familiar with formal evolutionary theory and population genetics and his thinking owed much to Fisher. In an account of his early work (Hamilton 1988), he describes how his interest in the evolution of insect societies

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



Figure 1.18 In Kalahari meerkats, most groups consist of a single breeding pair of adults and a variable number of non-breeding helpers of both sexes. *Source:* © Tim Clutton-Brock.

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?



Figure 1.19 Some of the more specialised cooperative breeders, like naked mole rats live in large colonies; breeding females ('queens') and helpers differ in size and shape, as well as in physiology and behaviour. *Source:* © Lorna Ellen Faulkes.

In 1963, Hamilton published a brief paper arguing that altruism could evolve if it benefited the fitness of relatives and the following year published more formal models of this process (Hamilton 1964). To account for the evolution of cooperation between relatives, he introduced the concept of 'inclusive' fitness, consisting of the 'direct' fitness individuals derive from producing descendants and the 'indirect' fitness that they derive from helping non-descendant relatives minus any benefits received from them. Subsequently Maynard Smith (1964) named the process by which indirect benefits accrue as *kin selection* to distinguish it from group selection. The mathematics incorporated in Hamilton's original papers are complex, but the kernel of his theory can be presented as a simple equation (usually referred to as Hamilton's Rule) which states that a gene will increase in frequency whenever $B/C > 1/r$ where B represents the benefit of the trait that the gene codes for derived by the recipient of assistance, C the costs of assistance to the 'donor' and r Wright's coefficient of relatedness. Mechanisms capable of generating increased levels of r and important indirect fitness benefits include limited dispersal (Hamilton 1964; West *et al.* 2002) and kin discrimination based either on environmental cues (such as prior association) or on genetic mechanisms (such as the recognition of shared



Figure 1.20 Much larger breeding groups occur in social insects, where sterile workers rear the offspring of one or more breeding females, as in yellow meadow ants. The large size of colonies has led to the evolution of specialised workers and larger, specialised queens that are able to produce large numbers of eggs. *Source:* © Tom Houslay.

heritable odours or other characteristics) (Mateo 2002; West *et al.* 2007).

Hamilton's Rule makes intuitive sense. Under most conditions, relatives should be most likely to assist each other where coefficients of relatedness are high, the costs of providing assistance are low and the potential benefits of assistance to recipients are large (Wilson 1974; Dugatkin 1997). However, there are difficulties in incorporating inclusive fitness in formal models of population genetics, especially where natural selection is strong (Cavalli-Sforza and Feldman 1978; Uyenoyama 1984; Mueller and Feldman 1988; Dugatkin 1997). Measuring the indirect benefits and costs of cooperation is also more difficult than it might initially appear since actions that are likely to increase the fitness of non-descendant kin may also contribute to the helper's own fitness or to the fitness of its descendants (Brown 1987; Creel 1990). For example, estimating the costs of cooperation to resident workers or helpers in cooperative societies makes it necessary to decide whether individuals delay dispersal in order to assist relatives (in which case costs may be large) or whether they remain in their natal group to

maximise their survival and their chance of breeding and costs should be measured as the marginal costs of helping per se (in which case costs may be small) (see Chapter 17). In many cooperative species, helpers are the parents of some of the offspring being raised, so that helping may also increase the helper's direct fitness. Finally, assistance may affect the fitness of donors and recipients throughout their entire lifespans, so that estimates of B based only on short-term effects (such as the survival of nestlings) are likely to underestimate their real magnitude. Despite these problems, the components of Hamilton's equation have now been measured successfully in several natural systems and its predictions have been tested and verified (Bourke 2014; Hatchwell *et al.* 2014).

Theoretical research since 1964 has clarified the measurement of inclusive fitness and its assumptions (Queller 1996; Frank 2013; West and Gardner 2013) and explored its links to other branches of evolutionary theory (Taylor 1996; Gardner *et al.* 2007), though some theoreticians continue to be critical of its assumptions and argue that inclusive fitness will only be maximised by

selection under limited circumstances (Nowak *et al.* 2010; Allen *et al.* 2013). However, the large number of cases where inclusive fitness theory has generated testable predictions about the evolution of social or reproductive strategies that have subsequently been verified by empirical research provides substantial evidence of the insights that it has provided (Abbot *et al.* 2011).

The central importance of kinship in understanding the evolution of animal societies has been recognised in a wide range of empirical studies and emphasised by many reviews (Trivers and Hare 1976; Grafen 1984; Bourke and Franks 1995; Silk 2009; West and Gardner 2013). Across animal species, costly forms of cooperative behaviour are largely confined to species where group members are, on average, closely related, and even in species where members of one sex live in groups consisting of relatives while members of the other sex associate with unrelated individuals, the sex that usually associates with relatives typically shows a greater development of cooperative behaviour (Boomsma 2009; Clutton-Brock 2009b). In addition, where non-breeding individuals have opportunities to choose between joining and assisting close relatives, distant relatives or unrelated individuals, they typically show a strong preference for joining close relatives (Emlen and Wrege 1988; Hatchwell *et al.* 2001; Hatchwell 2007), and where groups include a mixture of related and unrelated animals, individuals are often more cooperative to close kin than to non-kin or distant relatives (Boncoraglio and Saino 2008; Hatchwell 2009; Silk 2009).

Cheats and defectors

Cooperative behaviour invites exploitation and selection is often likely to favour the evolution of strategies that are adapted to exploit cooperative behaviour in other animals (Brembs 1996; West *et al.* 2007). The existence of cheating strategies that exploit the behaviour of cooperators has been demonstrated in bacterial populations (West *et al.* 2006). For example, in the pathogenic bacterium *Pseudomonas aeruginosa*, some individuals produce iron-scavenging agents (siderophores) that benefit local populations at a cost to their own fitness while others do not (Griffin *et al.* 2004).

As the frequency of cheats increases in populations, the density of individuals that can be exploited falls and selection is likely to strengthen the defences of

cooperators so that the benefits of cheating strategies are likely to be negatively frequency dependent. If this eventually leads to a situation where the fitness of cheats is lower than that of cooperators, a stable equilibrium may develop; however, if the relative fitness of cheats continues to exceed that of cooperators as their frequency rises, cooperation will become extinct (Ross-Gillespie *et al.* 2007; Ghoul *et al.* 2014). Consequently, where cheating strategies and cooperators both persist in the same populations, we can expect the fitness of cheats to show negative frequency dependence and several studies support this prediction (Ghoul *et al.* 2014).

Large individual differences in contributions to cooperative behaviours are also common in many cooperative vertebrates. However, in most cases, these do not appear to be associated with contrasts in development or reproductive strategies and they are commonly related to contrasts in age, size, sex, reproductive status or nutrition. Many of them probably reflect variation in the costs and benefits of providing assistance (see Chapter 17). For example, in many cooperative breeders, hungry helpers that are in relatively poor condition give a smaller proportion of the food they find to dependent young and the fitness costs they incur for the amount of provisioning they do are not necessarily lower than those of better-fed individuals that contribute more and could be similar or even higher.

Unfortunately, variation in cooperative behaviour is often interpreted as evidence of cheating and individuals that contribute relatively little are often referred to as 'cheats' or 'defectors' when their behaviour may be a result of individual differences in the costs or benefits of contributing to cooperative activities, so that the incidence of cheating in natural populations is likely to be overestimated. So how common is cheating in cooperative societies? Few studies of non-human mammals have yet produced unequivocal evidence of cheating strategies and several which explored behaviour that initially looked like examples of cheating have concluded that the behaviour is a consequence of tactical decisions based on last-minute assessments of the needs of juveniles rather than of cheating strategies (see Chapter 17). One possible explanation is that, where cooperation is highly developed, cooperative behaviour usually provides net benefits that are sufficiently large that cheating is not favoured, while another is that cooperative species

have evolved mechanisms that safeguard individuals against potential cheats.

1.7 Loaded labels

Like ‘cheating’ strategies, many descriptions of social strategies derived from theoretical models carry implications about the intentions of the individuals involved and the functions of their behaviour: examples include teaching, exchanges, punishment, policing, reconciliation and consolation. The use of these labels provides a convenient shorthand description of strategies and can indicate the way in which evolutionary processes are likely to operate (West *et al.* 2007; Ghoul *et al.* 2014) but also has disadvantages. The implication that strategies are intentional has led to arguments between biologists and psychologists (see Chapter 6), though evolutionary biologists are

usually aware of this problem and avoid it by adopting functional definitions of strategies that avoid implications about intentions. A more serious problem is that strategy labels (like many of those described) carry implications about the functions of behaviour. As a result, their application to empirical examples often assumes answers to precisely the questions that need to be asked. ‘Cheating’ is an obvious case where the uncritical application of a strategy label to observed behaviour is often likely to be misleading. Similarly, it can be misleading to refer to examples of mutual assistance as exchanges unless there is real evidence of reciprocity and an alternation of costs and benefits (see Chapter 9). There are many other examples and it is not possible to avoid using strategy labels altogether, but it is important to question the reality of their implications and to find less misleading labels for observed behaviour where possible.

SUMMARY

1. The structure of animal societies and breeding systems exerts profound effects on almost all evolutionary and ecological processes so that an understanding of their diversity and distribution is of central importance in research on virtually all aspects of organismal biology.
2. Although the existence of animal societies has been recognised since classical times, systematic descriptions of animal societies and social behaviour were uncommon before 1960. However, during the 1960s and the 1970s, long-term field studies that were able to recognise individuals and track their life histories began to provide detailed insight into the diversity of social behaviour and social organisation and its causes and consequences.
3. While early explanations of contrasts in social behaviour among animals frequently suggested that they served to increase the survival of groups or populations, theoretical research between 1960 and 1980 demonstrated the extent to which the interests of individuals differ and laid the basis for our current understanding of social evolution based on selection operating at the level of individuals or genes.
4. Research on breeding competition between individuals shows that individual differences in breeding success are often large in both sexes and that individuals compete intensely for breeding opportunities, though individuals may benefit by avoiding fights and settling competitive interactions in other ways where the costs of escalated fights are high. Empirical studies have shown how the factors affecting breeding success commonly differ between the sexes, with female breeding success often depending primarily on access to resources and male success depending principally on access to females.
5. A combination of theoretical and empirical research (which continues to be extended) now provides a framework for explaining the evolution of mate choice and parental care. Early studies showed how the sex that invests most heavily in individual offspring is often more selective in its choice of mating partners than the sex that invests less heavily, while the latter competes more intensely for access to mates than the former. More recent research has refined this generalisation and shown how both sexes frequently compete for mates and are selective of mating partners and how sex differences in competitiveness and choosiness can vary between and within populations and individuals.
6. A combination of theoretical and empirical research has also provided a basis for understanding the evolution of animal cooperation. While several evolutionary mechanisms have the capacity to favour the evolution of cooperative behaviour, most examples of animal cooperation are either cases where both (or all) cooperating individuals gain net fitness benefits from assisting each other or cases where individuals provide assistance to descendent or

non-descendent relatives and so gain net benefits to indirect components of their fitness or (in many cases) a combination of both processes. Most examples of animal cooperation involving the provision of assistance that has substantial costs involve interactions between relatives, while cooperation between non-relatives seldom involves costly actions.

7. Strategy labels generated by theoretical studies are commonly used to describe observed differences in behaviour. While this can stimulate thinking and lead to novel lines of research, it frequently assumes answers to the precise functional questions that need to be asked. It is also important to remember that different theoretical models commonly generate similar predictions, so that a match between the general predictions of a model and empirical results does not necessarily indicate that the model is realistic or that evolution has operated in the way that it suggests.

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