

Social life

The last chapter concerned relationships between parents and offspring, and grandparents and grandoffspring. We also have important relationships with others who are not our descendants or ancestors, such as our mates, our colleagues, and our friends. This chapter concerns those social relationships and the evolutionary pressures which affect them. In section 8.1 we consider the question of why (some) animals live in groups at all and section 8.2 describes the various types of social group that occur amongst non-human mammals. In section 8.3 we look at the consequences of group living and section 8.4 asks how human groups fit into this scheme. Section 8.5 then takes on a key question for understanding human behaviour, namely how does social cooperation between unrelated individuals evolve?

8.1 Why live in groups?

We humans are such strongly social creatures that we forget that not all animals belong to social groups. Leopards, for example, live solitary lives, each one patrolling a discrete territory

Figure 8.1 Leopards are solitary, whereas lions live in prides. Both sociality and non-sociality have evolved multiple times in animals. Photos © Digital Vision.



(Figure 8.1). Male–female interaction is limited to brief mating, and male–male interaction to fighting each other in territorial disputes. Cubs remain with their mothers for up to 2 years, but then disperse to find territories of their own. In contrast to leopards, lions live in prides comprising several adult females, one or two adult males, and their cubs. The adult females usually sleep, move, hunt, and feed as a group.

The leopard/lion contrast is mirrored across many groups of animals. There are solitary rodents and social rodents, solitary whales and social whales, solitary bats and social bats, and solitary fish and social fish. Thus, it is clear that both non-social and social forms of living can evolve, and have done so many times. The question is, then, under what circumstances sociality versus non-sociality is favoured. As ever, the general evolutionary expectation is that we should expect sociality to be found wherever the benefits exceed the costs and to be absent wherever the costs exceed the benefits. However, what are the benefits and costs of sociality?

8.1.1 Benefits of group living

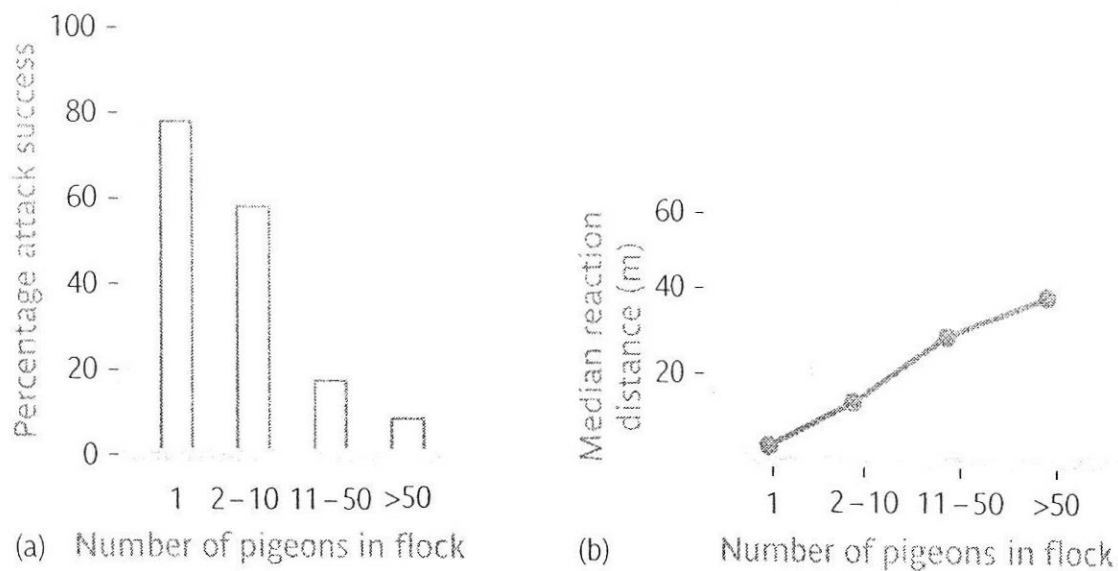
A number of different benefits of sociality have been proposed and tested. Which ones are important for a particular animal—and there might be several—will obviously depend on its ecological niche. Here, we review some of the most important.

Predation

A key benefit of group living for many social species is a reduction in the risk from predators. Being in a group reduces the risk of predation for two main reasons. One is simple dilution. A sparrowhawk can only carry off one sparrow at a time. If a sparrow lives in a flock of 100 individuals, then if the sparrowhawk strikes, the chance of being the victim is just 1% on average, whereas for a solitary sparrow the chance of being the victim in a strike is 100%. The advantage of flocking together might be diminished by the large flock being more visible to sparrowhawks and thus suffering more attacks, but the number of attacks is unlikely to be 100 times greater and so the risk of predation is still lower overall in the flock.

In addition to this effect, predators may be less effective when they attack grouped prey animals than when they attack solitary ones. One reason for this is that the larger the group, the greater the chance of someone spotting the predator early and beginning evasive action. In fact, the

Figure 8.2 (a) Attacks by goshawks (*Accipiter gentilis*) on wood pigeons (*Columba palumbus*) are less likely to be successful when the pigeons are in larger flocks. (b) Larger flocks take flight at greater distance from the approaching hawk. Data from Kenward (1978).



larger the group, the smaller the proportion of time any individual needs to spend scanning around for predators in order for constant vigilance to be maintained at the group level.

Kenward (1978) demonstrated this effect in action in attacks by goshawks on wood pigeons (Figure 8.2). The larger the flock, the smaller the proportion of attacks that ended in a kill. This was because larger flocks tended to take flight when the predator was further away, presumably because with so many eyes the probability of at least one individual detecting the hawk early was increased.

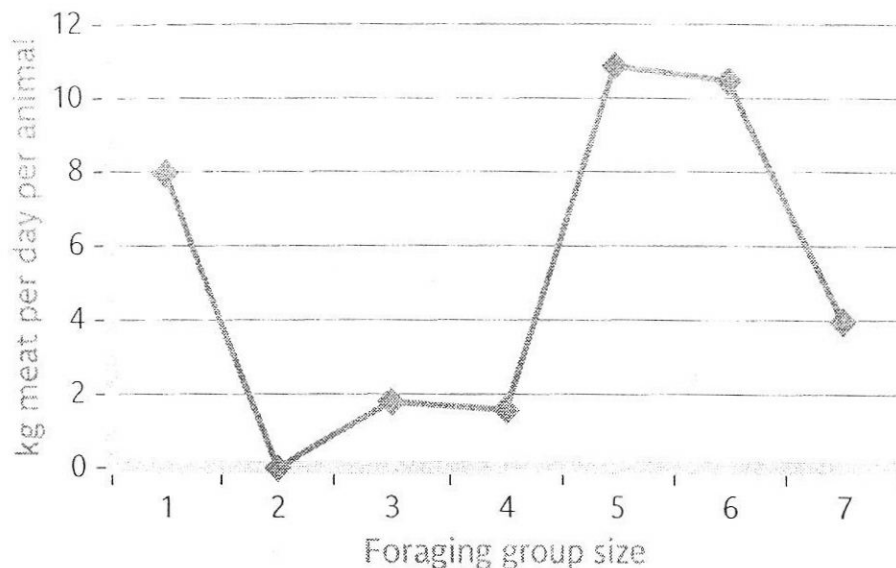
In addition to fleeing predators, larger groups of animals may also have advantages in other types of anti-predator action, such as attacking back and confusing predators with massed movement.

Joint foraging

Animals in groups may also enjoy advantages of taking on joint ventures, for example joint hunting. Pack hunters can take larger prey together than any one individual could and predatory fish derive advantages from being able to surround a shoal of prey. Note that these kinds of joint ventures are favoured not when the total return from the hunt is greater in a pack than alone, but when the return *per individual* is greater in a pack than alone. This means that social hunting has to be very much more fruitful than solitary hunting to offset the greater number of mouths at the kill. For example, hunting in pairs is only favoured if it yields overall more than twice the calories of hunting alone, hunting in groups of six if it yields six times the calories, and so on. In addition, social hunting raises problems of cooperation. It is always better for each individual to let someone else do the dangerous bit of actually killing the prey and just feed from the results. We return to these problems of cooperation in section 8.5.

Note that animals hunting in a pack does not mean that the pack has formed because of its advantages in hunting. In African lions, *Panthera leo*, for example, Packer et al. (1990) showed

Figure 8.3 Returns from foraging (kilos of meat per animal per day) for lionesses foraging in groups of different sizes during periods of prey scarcity. These data suggest that lionesses would be better off foraging alone or in groups of five or six, but in fact they often forage in twos, threes, and fours. *Data from Packer et al. (1990).*



that when food was scarce the return of meat per day was high for females hunting alone or for females hunting as a group of five or more, but low when hunting in twos, threes, or fours (Figure 8.3). This is because twos, threes, and fours seek the same prey species as a solo huntress would but are less successful and have to share it out when they do succeed. Groups of five or more can target larger prey (or larger carcasses, since lions actually scavenge a significant part of their diet).

Despite these clear advantages of foraging either alone or in a large group, the most common lioness party sizes observed were twos, threes, and fours. This suggests that the efficiency of group hunting is not the benefit driving the social aggregation of these animals, and some other factors must be relevant.

Defence of territory

A different type of joint venture is the defence of a territory. It can be advantageous for an individual to control a territory containing sources of food and water, but this means that it will have to be able to repel others of the same species trying to come in. A pair or group of animals may be able to defend a territory where a single animal could not. Indeed, if some members of a population have become social, this exerts pressure on others to follow suit, on the basis that a group can only be repelled by another group of at least equal size. A limit on such defensive group formation is imposed by the number of mouths that the territory can feed, and thus territory-defence sociality is particularly likely where there are resource-rich patches such as fruit trees or waterholes which are defensible but can support more than one animal.

Resource defence appears to be important for lionesses. Packer *et al.* (1990) observed a number of inter-group encounters between lionesses and these usually ended with an intense chase, which the larger group won. Several prides of one or two females lost their territories, which did not happen to larger prides.

Another type of joint venture that may make grouping beneficial is joint care of offspring. If a parent is to provide care, then it must remain with the offspring for a period of time, and if both parents are to provide care they must remain with each other. Thus, where there is biparental care, species have to be social, at least for the reproductive period, with a minimal group of two parents and the young. Where the parental relationship extends over several reproductive episodes, a form of social group centred around the monogamous couple and their current and recent offspring is found. This kind of social organization is found, for example, in the night monkey (see section 7.3.3).

Biparental care is not the only kind of joint care. To return to the African savannah, lionesses of the same pride pool their cubs together into a 'crèche' from the age of about 6 weeks to 2 years. The greater the number of females who have cubs in the crèche, the higher the proportion of cubs that survive. The main source of this benefit appears to be defence of the cubs against infanticidal males, who accounted for 27% of cub deaths in Packer and colleagues' 1990 study. Where there were aggressive encounters between the pride and male strangers, all the cubs died in five of six cases where there was just one mother with cubs, but some cubs always survived where there was a crèche of more than one female. Thus, lionesses have good reasons for sticking together.

Information transfer

Another potential benefit of living in a group is that seeing the behaviour of others allows access to useful information. This idea has been best developed for colony-living animals that forage separately and return to a base, such as birds or bats. There is good evidence that individuals can identify others who have foraged successfully and follow them to find resources the next time. More generally, observing other members of the same species can provide cheap information about behaviours that are suitable for the current environment (see Chapter 9).

8.1.2 Costs of group living

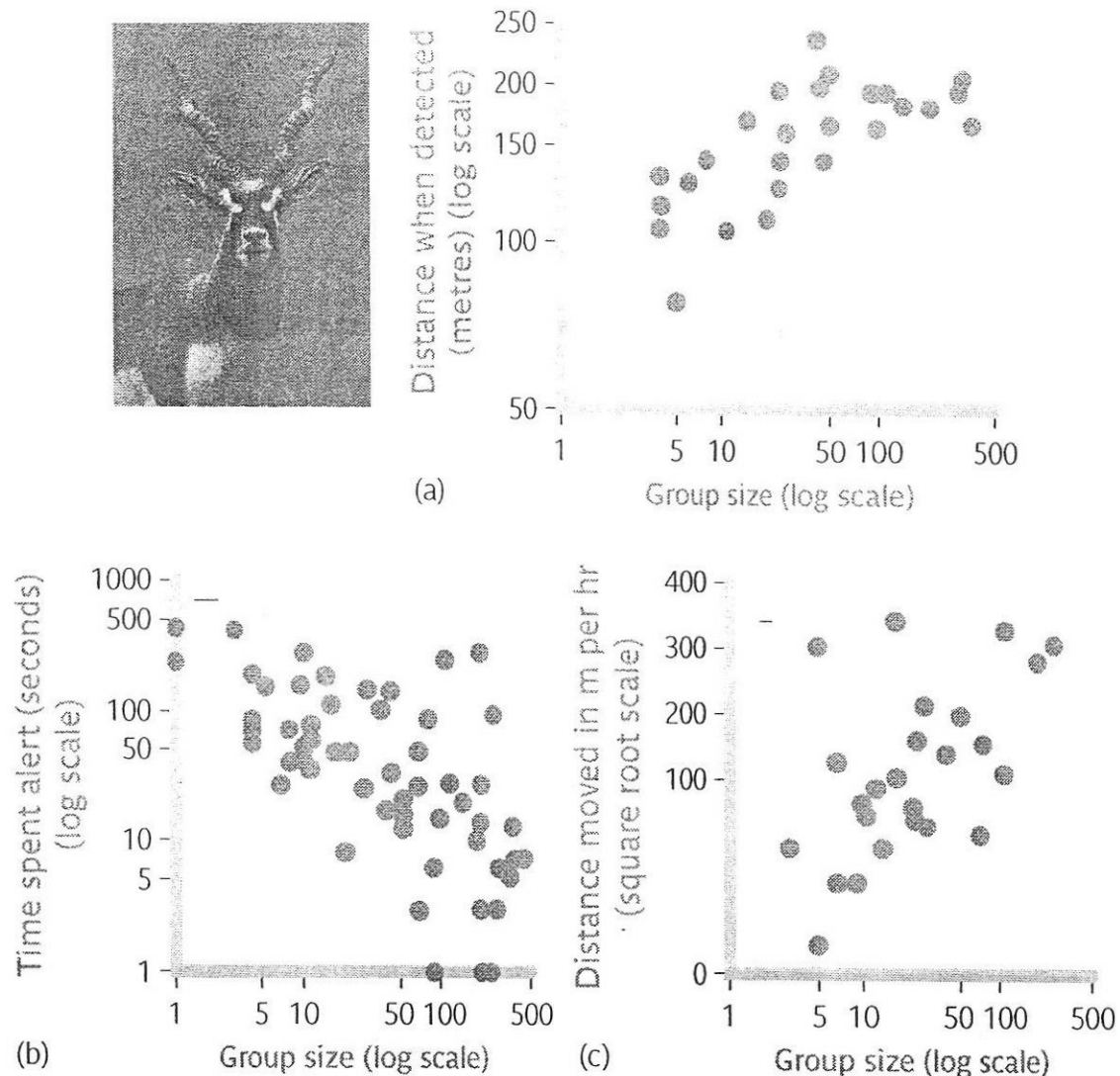
We have examined a number of benefits to group living. However, if there were only benefits then we should expect all animals to live socially, which they do not, so there must be costs as well. Although there are a number of likely costs to sociality, for example the increased transmission of infectious disease in more social animals, the best documented cost is feeding competition. The more mouths there are to feed, the quicker local resources will run out.

There would seem to be two responses to feeding competition within a group. Some animals disperse temporarily to forage independently, but return to group together the rest of the time. Colony-roosting bats or birds would be good examples. The anti-predator advantages of being in a group are thus enjoyed whilst the animals are at their most vulnerable, such as when they are resting, and the competition for food is attenuated by their temporary dispersal. However, the advantages of being in a group are lost while foraging.

The second strategy is to retain the integrity of the group the whole time. This has the effect of depleting food sources rapidly and so, the larger the group, the more quickly it has to move from patch to patch in order to get enough to eat. Thus, a cost of being in a larger group is increasing travel around in order to acquire enough food.

The costs and benefits of sociality are well demonstrated in a recent study of a number of groups of blackbuck antelope, *Antilope cervicapra*, in India (Isvaran 2007). The larger the group, the more quickly an approaching 'predator' (the researcher himself) was detected (Figure 8.4a),

Figure 8.4 In blackbuck antelope (*Antilope cervicapra*), (a) the distance at which an approach is detected increases with group size, (b) the proportion of time individuals devote to vigilance decreases with group size, and (c) the distance travelled per hour increases. Data such as these shed light on the benefits and costs of living in a group. From Isvaran (2007). Photo © tephenn Bonneau/istock.com.

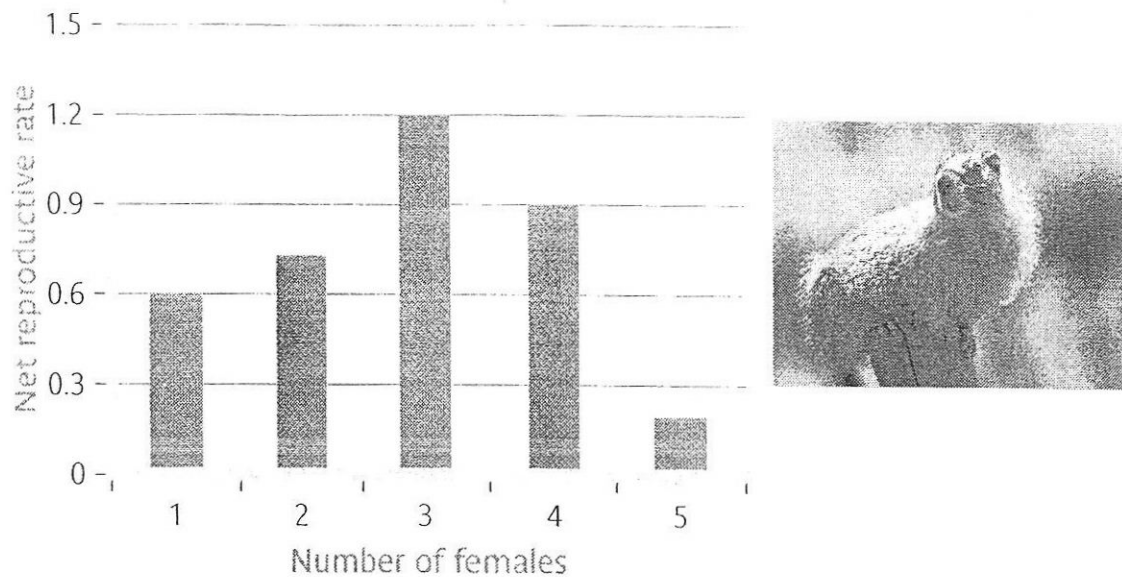


this despite the fact that in larger groups individuals spent less time on vigilance (Figure 8.4b). However, as groups got larger, the animals had to move further per hour in order to forage (Figure 8.4c). There will come a point where this increased travel is energetically uneconomic and at this point the costs of being in such a large group outweigh the benefits.

8.1.3 Optimal group size

As group size increases, the benefits of extra members may begin to level off, whilst the costs in terms of feeding competition may begin to become prohibitive. Thus, there will be an intermediate level of group size that reflects the optimal compromise. There is good evidence of selection for intermediate-sized groups and against extremes. For example, Armitage & Schwartz

Figure 8.5 Net reproductive rate (number of surviving offspring per year) for yellow-bellied marmots (*Marmota flaviventris*) living in groups containing different numbers of adult females. Data from Armitage & Schwarz (2000). Photo © Frank Leung/istock.com.



(2000) studied female reproduction in yellow-bellied marmots, *Marmota flaviventris*, in Colorado, USA. These ground-living squirrels form groups of related females ranging from one to five adults. Female reproductive success was highest in groups of three and significantly lower in lone females and in larger groups (Figure 8.5).

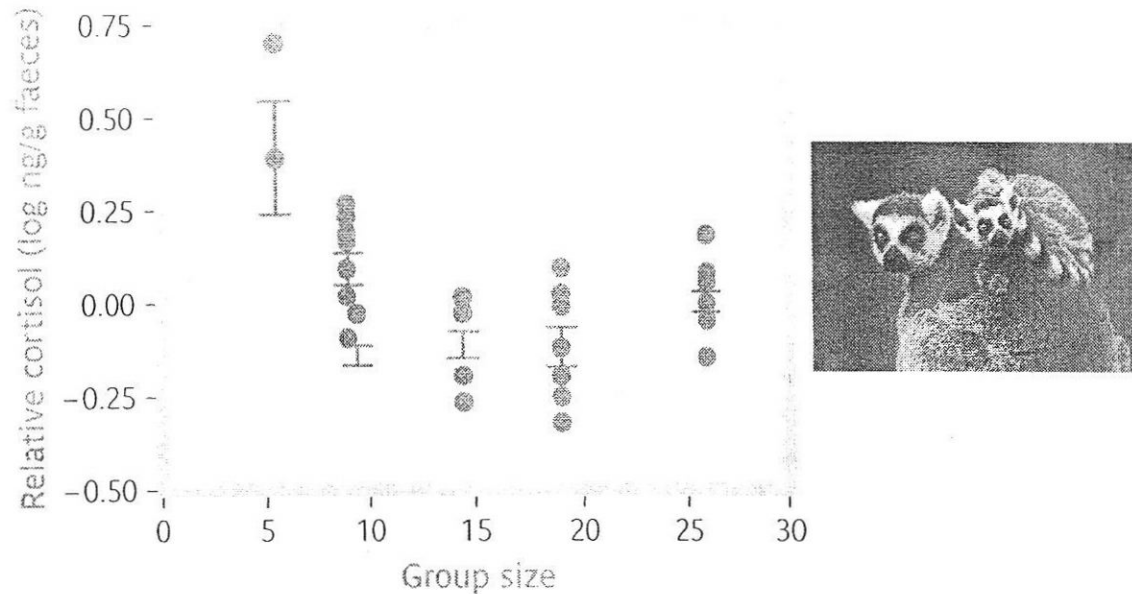
This raises the question of why not all the marmots lived in groups of three. Population dynamics constantly affect group size. When a female dies in a group of three, it becomes a group of two. When a female disperses, she cannot instantly recruit two group-mates and she may have to disperse if local resources are insufficient to feed three mouths. As for groups being larger than optimal, this is a common finding. The reason is that, although reproductive success is lower in a four than a three, an extra female still does better joining an existing group of three than she would by living alone. The residents may try to exclude her, but this will be costly for them. Thus, groups slightly larger than optimal will be common. Only where the group is so big that all parties would gain from its subdivision will the group definitely fission.

These considerations suggest that social animals should have evolved to be sensitive to the size and dynamics of their current group and be able to alter their social behaviour as strategically appropriate. A number of studies show that this is the case. Mantled howler monkeys, *Alouatta palliata*, have a social system similar to that of the yellow-bellied marmots, with similar optimal group size considerations. Half of all females born into groups with two adult females remain in their natal group, whereas only 10% of females born into groups of three, and none of the females born into groups of four, remain (Pope 1998). This shows that females are able to assess local group conditions in their decisions about dispersal.

Ring-tailed lemurs, *Lemur catta*, live in groups of up to 25 females. Pride (2005) showed that levels of cortisol (a stress hormone) in these animals are lowest when they are in intermediate-sized groups and significantly elevated if the group is very small or abnormally large (Figure 8.6). Again, this suggests that the lemurs' cognitive and emotional mechanisms are attuned to the current state of the social group.

Figure 8.10 Cortisol levels of female ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar, are lower in intermediate-sized groups (10–20) than in smaller or larger ones. Error bars represent the mean plus or minus one standard error.

From Pride (2005). Photo © Toos van den Dikkenberg/istock.com.



8.2 Types of group

Animal groups vary not just in size but also in their composition: how many of each sex, with what relationship to one another. In this section, we review some of the main types of social organization that can be found. The social system of a species is often related to its mating system, so before turning to social systems in section 8.2.2, we investigate the different types of mating systems that occur.

8.2.1 Mating systems

Among sexual species there are a number of ways that matings can be distributed between the two sexes. These are as follows:

1. monogamy: both males and females have one mate.
2. polygyny: a male mates with several females, but each female only has one mate
3. polyandry: a female mates with several males, but each male only has one mate
4. promiscuity: any female may mate with any male.

Monogamy, polygyny, and polyandry can be further divided into cases where the mating bonds last for just one breeding event and where there is longer-term association between males and females (e.g. lifetime monogamy versus monogamy for one breeding season). Promiscuity is associated with a lack of long-term bonds between mates, although males and females may have more transient consortships.

Where only one (or neither) sex makes any post reproductive investment in caring for the offspring, the mating system is basically determined by ecology. For example, in mammals where there is little paternal care, females distribute themselves so as to optimize their access to resources and males distribute themselves to optimize their access to females. Thus, if females are dispersed singly around the environment, monogamy may arise simply because a male can only monopolize one female. This happens, for example, in some monogamous deer. If females forage in groups, a male may be able to exclude other males from mating a whole group of females, giving a polygynous harem system, as seen in gorillas or elephant seals. Polygynous harem systems are associated with strong sexual dimorphism in size (see section 6.4.2). If females are aggregated or mobile, but it is uneconomic for any one male to exclude others from access to a female, the system becomes promiscuous. Females in promiscuous systems may benefit from mating multiple males in order to confuse paternity and thus reduce the likelihood of infanticide (section 7.3.3). Males in promiscuous systems, such as that of the chimpanzee, tend to have large testicles, since female mating with multiple males generates competition between the sperm of different males, leading to selection for larger ejaculates.

Polygyny is very common across the animal kingdom, due to Bateman's principle (see section 6.4.1) making it more often beneficial for males to expend energy recruiting multiple mates than it is for females to do so. Polyandry is rarer and often associated with sex-role reversal, as in the case of pipefish (section 6.4.4). Monogamy is much more common in cases where both sexes provide parental care than where just one does. Many more birds than mammals are monogamous, for example, and this is associated with males playing a role in the incubation of eggs and provisioning of chicks (however, see section 6.5.1 on extra-pair copulation).

8.2.2 Social systems

Just as we categorized mating systems in the previous section, we can roughly categorize the social systems most commonly found in animals as: solitary; one male, one female; one male, multiple females; and multiple males, multiple females.

Solitary systems

Solitary systems are characterized by a lack of mating pair bonds and a similar lack of same-sex relationships in adulthood. Note that one sex can be solitary whilst the other is not. In the cheetah, *Acinonyx jubatus*, for example, females are solitary, whereas males form coalitions with their brothers, apparently in order to be able to defend territories from other males. Solitary species may also aggregate temporarily, for example to choose mates.

One male, one female

This type of social organization is strongly associated with mating monogamy (but monogamy can also be found in other types of group, see below). Often, the young will delay dispersal and so the reproducing male and female will form the nucleus of a small family group consisting of themselves, their current infants, and not-yet-dispersed juveniles who may act as helpers at the nest. This is the social system of a large lemur called the indri, for example (Figure 8.7).

One male, multiple females

A polygynous harem mating system often gives rise to a one male, multiple female social system. In gorillas, for example (Figure 8.7), there is only a single mature male, the silverback,

Figure 8.7 Indris (*Indri indri*, left) live in monogamous families where males carry the offspring. Gorillas (*Gorilla gorilla*, centre) live in polygynous groups with a dominant male. Chimpanzees (*Pan troglodytes*, right) live in multi-male, multi-female groups with promiscuous mating and no paternal care of offspring. Left to right: © Wolfgang Kaehler/Alamy; Photodisc; Corel.



in a troop. Other males are tolerated until they reach sexual maturity, at which point they disperse and found or take over groups for themselves. One male, multiple female social systems, because of the sex-ratio imbalance within the groups, generate a cadre of lone or wandering males who have not successfully recruited or captured a group.

The females in such groups may be closely related, either as sisters or mothers and daughters. This comes about by females remaining in their natal group. This is called female philopatry. Where there is female philopatry, there tends to be male dispersal. Female philopatry enhances the benefits of group living, since kin selection gives every female a positive genetic interest in all the young, and collective care and even nursing of offspring may result.

A variant of the one male, multiple female social system is seen in lions, where each pride is associated with a coalition of males rather than just one. The coalition often consists of two males, but can be up to four, and they tend to be brothers. Coalitions are probably favoured for their ability to exclude rivals, whilst larger coalitions, especially of non-relatives, are disfavoured because of the loss in reproductive success with every additional male in the pride.

Multiple males, multiple females

Many animal groups contain multiple adult males and multiple adult females. In the primate literature, these are often described as 'multi-male' groups, to contrast them with harem-based single-male groups. Multiple male, multiple female groups are often based on promiscuous mating, as in the chimpanzee (Figure 8.7). However, this is not a necessary connection. Many colonial birds, for example, maintain monogamous pairs within a wider multiple male, multiple female roost, whilst hamadryas baboons (*Papio hamadryas*) maintain small harems within a larger multiple male, multiple female society.

Unless the social group is vast, one sex or the other of maturing young will tend to disperse. Baboons have female philopatry and male dispersal, and as a consequence matrilineal kin relationships bind many female group members. Chimpanzees, by contrast, have male philopatry and female dispersal, and so patrilineal, father, and brother kin relationships become an important part of group structure.

Consequences of group living

Having briefly surveyed some of the reasons social groups may form, and the types of group that are found, we now turn to the consequences of living in a group. In particular, we focus on two issues: the emergence of dominance hierarchies and the cognitive demands of social life.

8.3.1 Dominance hierarchies

Although the individuals within a group may all share an interest in the group continuing to exist, there will also be conflicts between them over food and access to mates. Members of the same group encounter each other sufficiently often that the outcomes of such contests can be established without a lengthy confrontation each time. Thus, in many mammalian social groups, dominance hierarchies tend to emerge, with some individuals consistently able to displace others from a resource. Ranks in the hierarchy will depend on such factors as size, strength, age, and coalitional support within the group. As these factors change, rank orders are challenged by fighting, and may be reversed. Ranks can be relatively dynamic, as in male chimpanzees, or remarkably stable, as in baboons, where daughters take a place adjacent to their mothers in the hierarchy, which is stable for many years.

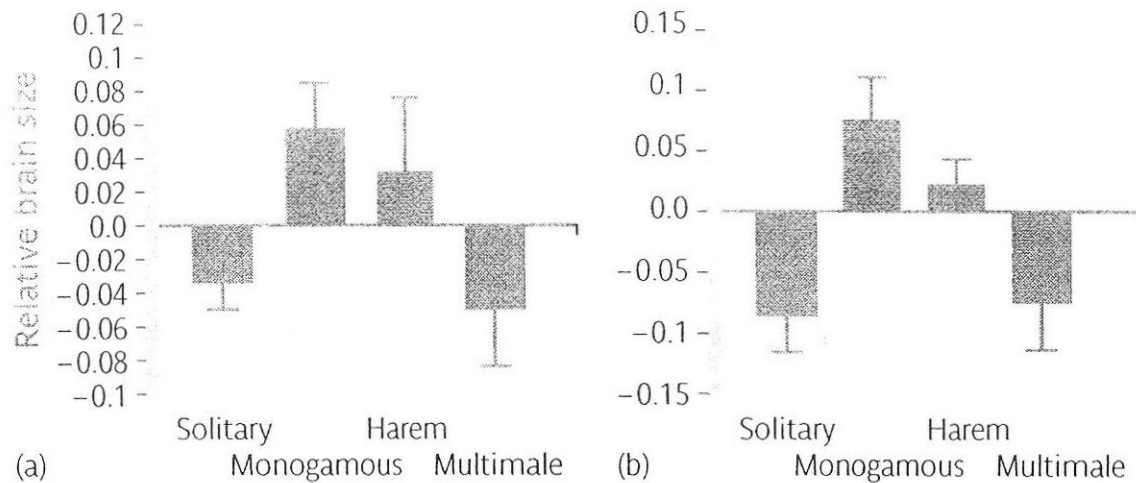
It is important to stress that just because subordinate individuals accept low-ranking positions does not mean that being of low rank is adaptive. Reproductive success tends to be higher for high- than low-ranking individuals, and thus other things being equal it is always in an individual's interest to be of high rank rather than low. However, for low-ranking individuals, the expected cost of contesting their rank may be higher than the expected return (or success may be impossible), meaning that by accepting a low rank such individuals make the best they can of a bad situation. Where dominance hierarchies are steep and stable, low-ranking individuals often show physiological evidence of increased stress and have worse health in the long run as a consequence. However, when the hierarchies are unstable, or need to be constantly maintained through fighting, it is the high-ranking individuals who suffer the most stress (Sapolsky 2005).

8.3.2 The cognitive demands of social life

Social relationships can be psychologically demanding. For example, maintaining a pair bond with a mate means recognizing that individual, keeping track of where they are and what they are doing, and coordinating one's behaviour with theirs. Maintaining a coalition of female relatives is even more demanding, since there might be several individuals to keep track of. These observations lie at the heart of what is known as the social brain hypothesis. In its broadest sense, this is the idea that maintaining social relationships requires devoted brain mechanisms. One of the predictions of the social brain hypothesis is that social species will tend to have relatively larger brains than non-social ones.

Some of the most compelling evidence for the social brain hypothesis is the finding that, separately in carnivores, ungulates, birds, and bats, species that form long-term pair bonds, particularly monogamous ones, have relatively larger brains than those with either social or solitary promiscuous mating systems (Shultz & Dunbar 2007; Figure 8.8). Shultz and Dunbar interpret this as the consequence of selection for greater cognitive capacities to manage the dynamics of a close and long-lasting social relationship.

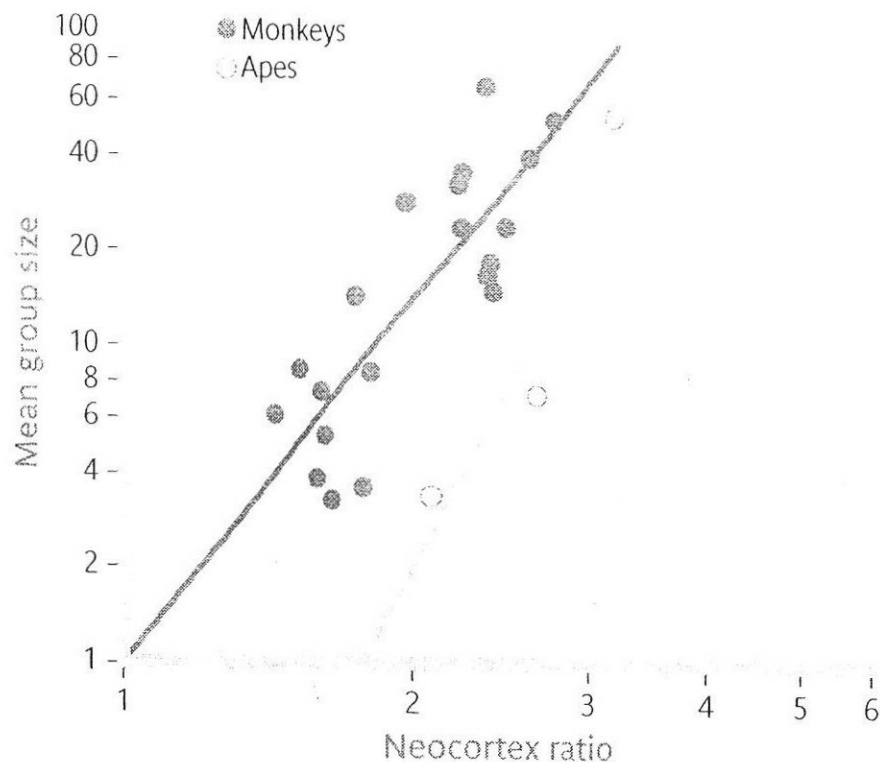
Figure 8.8 Relative brain size (corrected for body size) is larger in species with monogamous or polygynous mating bonds than either solitary promiscuity or promiscuity in multiple male, multiple female groups (a) in 86 species of carnivore and (b) in 69 species of ungulate. Similar results can be shown for birds and bats. Error bars represent one standard error. *From Dunbar & Shultz (2007b).*



Primates provide a slightly different picture. Solitary and monogamous primates have the smallest relative brain size, whilst primates in multiple male, multiple female groups have the largest relative brain size. In fact, across the monkeys and apes, there is a linear positive correlation between relative brain size and social group size (Figure 8.9). Shultz & Dunbar (2007) suggest that what has happened in primates is that the kind of closely coordinated social relationship which in other taxa is reserved for bonded mates is generalized in primates to all other group members. There is good evidence that primate social relationships are particularly intense; individuals maintain long-term reciprocal grooming relationships with several others, form coalitions, and track the kinship, mating, and coalitional status of all the others in their group. This suggests that the cognitive demands of group living will rise directly with total group size, consistent with what the brain data show.

However, correlation (of brain size and group size) does not prove causation and it is important to stress that there are a number of pathways by which the two could come to covary. Grouping reduces predation, for example, and this would allow a slower life history (see Chapter 7). Slow life history favours large brains, since growing brain tissue represents a costly allocation of resources to the soma, which only pays off over the length of the lifespan. Selection for fast life history, such as where predation is high, favours the diversion of these resources to become reproductively active earlier instead. Similarly, the rich resources that allow large groups to form might also fund the energy costs of growing large brains. Testing between these alternative pathways is still going on (Dunbar & Shultz 2007b), but the comparative evidence for a special relationship between social relationships and brain evolution seems relatively strong.

Figure 8.9 Relationship between neocortex ratio (a measure of the relative size of the 'higher' parts of the brain) and group size for monkeys and apes. There is a positive linear relationship overall and a suggestion that apes have relatively larger brains for their group size compared with monkeys. *From Dunbar & Shultz (2007a).*



8.4 Human groups in comparative perspective

Now that we have examined the main forms and consequences of sociality in our relatives, it is time to look briefly at human groups from a comparative, evolutionary perspective. The first point to make is that humans are intensely social. Although human forms of life are very variable from one society to the next, they are always social. It is very rare to find humans living alone. Lack of social connections is something that most people find deeply unpleasant, and is a risk factor for stress-related health problems such as depression.

Second, human groups are typically large by primate standards, and always of the multiple male, multiple female type. From the smallest bands of hunter-gatherers to the largest nation-states, it is normal for several adult males and several adult females to live in close proximity and have intense ongoing social relationships. However, embedded within these broader social networks there are enduring mating/marriage bonds, as we shall see below. Beyond these obvious points, what can we say more specifically about human groups?

8.4.1 The social brain hypothesis

An interesting approach to human group size is to extend the regression line of Figure 8.9 to the neocortex ratio of humans (which is higher than that of any other primate). Reading off the predicted group size on the vertical axis gives a figure of about 150 (Dunbar 1993). Thus, given that neocortex ratio is generally correlated with group size in primates, and given the neocortex ratio that humans have, we should expect humans to live in groups of around 150 individuals.

At first sight this prediction for human group size is immediately contradicted by experience. People can live in any social unit from an Inuit wintering band of a few families, to a mega-city of several million people. However, the latter does not exactly contradict the hypothesis. The social brain idea is that brain capacities constrain the number of other individuals with whom it is possible to have intense, ongoing personal relationships. In a city of millions, not all the inhabitants know each other. Instead, their interactions, to the extent they interact at all, are governed by formal systems of law and policing, monetary exchange, and so on. If a person had to name all those others with whom he or she habitually interacted and could describe the current ebb or flow of their social relationship, the number might be closer to the 150.

A fairer test of the social brain hypothesis for humans is the idea that human groups that are based on purely informal social mechanisms (i.e. do not have any police force or defined hierarchical structure) cannot generally exceed 150 individuals. Dunbar (1993) reviewed a number of documented hunter-gatherer societies and showed that the mean size of their bands was indeed around 150. At any one time, these bands might be subdivided into smaller camps, for ecological reasons, but several camps would be united by mutual friendships and interchanges. Another example comes from the Hutterites, a branch of the Christian Anabaptist movement, who live in Canada and the USA and are committed to living an egalitarian and peaceful life in isolated rural communities. Hutterite communities have a maximum size of 150. When a village approaches this size, land is sought elsewhere for a daughter colony and the group divided into two, often by lots, with one half leaving immediately for the new settlement. The reason the Hutterites do this is that they feel it would be impossible to maintain cohesion and community mindedness within the colony by informal peer pressure alone and so rather than create a police force they prefer to split.

Thus, there is some evidence for the idea that around 150 represents an upper limit on the size of social group whose cohesion can be maintained by informal social communication alone. This means that larger social groups tend to have two important properties. First, they tend to have formal mechanisms of power and social control, like kings, law courts, policing, and so on, that are not so obviously required in very small groups. Second, they tend to have what social scientists call a segmentary organization, which means the whole subdivides into many duplicate parts. An army division, for example, may consist of 20,000 troops, but they will be subdivided into several brigades, who are in turn subdivided into several battalions, who are subdivided into several companies each consisting of several platoons. Each company within a battalion has the same structure and function. The point of the subdivision is to create entities of a manageable size for cohesive and coordinated behaviour. Interestingly, the company, which is the smallest independent unit of an army and the largest within which all the soldiers might all know each other personally, tends to consist of around 150 individuals (Dunbar 1993).

8.4.2 Dominance hierarchies

To what extent are human societies characterized by dominance hierarchies, like social groups of many other species? Sometimes clear hierarchies can be generated, as with military ranks,

chiefs, or other grade systems. However, these seem to be most salient in large social structures where not everyone knows everyone else, such as armies, empires, or universities. Within small social groupings, like hunter-gatherer bands, Hutterite villages, and individual university departments, there tends to be a strong preference at least in principle for egalitarianism and collective consensus.

There is quite a lot of evidence that being at the bottom of a social hierarchy has negative effects on health and well-being in humans. For example, a famous series of studies of the British civil service showed large differences in self-perceived well-being according to the occupational grade reached (Marmot et al. 1991). Moreover, these perceived differences panned out into large differences in the incidence of heart disease, stroke, and other problems, and in life expectancy. Part of the gradient may be explicable in terms of material resources, but this is not a population living in poverty and even the lowest grades have stable and adequate incomes. Lifestyle factors such as smoking and exercise also account for part of the difference. However, at least part of the effect appears to be due to the adverse psychological and stress effects of being at the bottom of a stable social hierarchy.

6.4.3 Mating system

We have noted that within the multiple male, multiple female groups which humans form are nested long-term mating bonds. What, then, is the mating system characteristic of humans? There is clearly a great deal of flexibility, since monogamy, polygyny, and polyandry are all found in human societies. However, they are not found with anything like equal frequency. An influential cross-cultural survey (Murdock 1967) estimated that 82% of human societies were polygynous, about 17% monogamous, and only about 1% polyandrous. However, there are a number of caveats to note. First, in monogamous societies, marriage bonds may be dissolved and if men are more likely than women to marry again, then the system is effectively polygynous via serial monogamy. Second, although most societies are polygynous, most *marriages* are monogamous, since in many societies that allow polygyny, only a few men actually have more than one wife. Thus, we can conclude that human societies are mostly mildly polygynous, which is what the degree of sexual dimorphism in size among humans would predict (see section 6.4.2), but with the flexibility to alter the system according to ecological contingencies.

The degree of polygyny in human societies is conditioned by two main factors (Marlowe 2000). First, the more contribution that males make to their offspring (direct paternal care and resources into the family), the more monogamous the system becomes, other things being equal. This is because the greater the post-reproductive involvement of males, the more beneficial it becomes to have the undivided attention of one. By contrast, where males make a lesser post-reproductive contribution, there is less reason to need one for oneself, as it were, and women might do better choosing a male of higher genetic quality even if he is already married. Going with this, marriages are more stable (divorce is harder and rarer), and women's extramarital affairs are less tolerated, in societies where men make a larger contribution to subsistence.

Second, the greater the gap between the richest and the poorest males, then, other things being equal, the greater the degree of polygyny. For example, some African farming and cattle-herding societies feature very large disparities between the farm or the herd sizes of the richest and poorest men, with rich men having several wives and poor men having none. It is easy to understand why this might be, from an evolutionary perspective. A woman choosing between being a first wife of a poor man and a second wife of a rich man might maximize her reproductive success by choosing the latter if the disparity between them was sufficiently great

(however, on the lack of direct evidence for the benefits of polygynous marriages to women, see Gibson & Mace 2007).

Philopatry

We saw that baboons have female philopatry and male dispersal, whilst chimpanzees have male philopatry and female dispersal. What about humans? In most traditional human societies, neither sex disperses until marriage and then there is variation in whether the wife moves to the husband's group or vice versa. Wives moving to be near their husbands' families is called *virilocality*, whilst husbands moving to be near their wives' families is called *uxorilocality*. Among hunter-gatherer societies, there is no consistent bias towards either virilocality or uxorilocality (Marlowe 2000). Among subsistence farmers and herders, however, virilocality is the most common pattern. This shift seems to arise because of the bias, already discussed in section 7.4, towards passing accumulated resources to sons. This is easier, especially if the resource is land, if the son is nearby. Thus, preferential patrilineal inheritance creates a demand for sons to be near their fathers. Hunter-gatherers have little by way of transmissible wealth and so there is no particular pressure towards virilocality.

Contemporary developed societies have been described as *neolocal*, in that couples often establish households in new locations that are away from both sets of parents. With greater mobility and the transfer of wealth holdings from land towards portable assets such as money, there is not such a strong pressure to remain geographically close to kin.

8.4.5 Joint ventures

It is worth making one more observation about human groups. Through all their great diversity, one feature shines through, namely the high effort devoted to joint ventures. Humans often defend their groups collectively, hunt, forage, or farm collectively, build shelter or irrigation collectively, and form all kinds of associations such as age sets, armies, companies, and sects to undertake joint activities. This key aspect of the human way of life raises issues of cooperation, a subject to which we now turn.

8.5 Cooperation

A key issue for evolutionary theory is how cooperation is maintained within social groups. By cooperation, we mean behaviours that provide benefits to individuals other than the actor and have been selected because they do so. For example, alarm calling by prairie dogs when a predator is spotted (section 4.4.2) is a cooperative behaviour.

Although cooperation is discussed in many different ways (and using many different terminologies) in the literature, there are really only two classes of situation that we need to consider. Where the behaviour positively affects the recipient's lifetime reproductive success but negatively affects the actor's lifetime reproductive success, then the behaviour is true **altruism**. True biological altruism can only evolve through kin selection (section 4.4) or some **similar mechanism** that directs the benefits to individuals disproportionately likely to be also **carrying the alleles** that code for the behaviour. Parental care, for example, is true altruism of **this kind** and is, of course, maintained by kin selection.

The second class of situation is where the behaviour positively affects the lifetime reproductive success of the recipient and also positively affects the lifetime reproductive success of the actor. Such behaviours are often misdescribed as altruism, but are better designated mutual-benefit behaviours. There are interesting issues surrounding the evolution of mutual-benefit behaviours because they often raise issues of cheating and enforcement. For example, let us say that every individual does better in terms of calories gained relative to those expended by going on a group hunt rather than hunting alone. Group hunting is therefore straightforwardly advantageous and should be expected to evolve at the expense of individual hunting. However, an individual who goes along on the group hunt but does not do any actual killing, instead waiting for others to do the kill and then joining the feed, is going to do even better than a normal group hunter. This cheater gets all the benefits of the cooperative venture without paying the costs and cheaters will therefore have high reproductive success and become more numerous, until the point where there are only cheaters in the population. Mutual-benefit behaviours can only be maintained if cheating strategies can be prevented from prospering.

A number of mechanisms have been discussed by which mutual-benefit behaviours can be maintained, which we now review.

8.5.1 By-product benefits

We must first remind ourselves that not all behaviours that provide benefits to others are cooperation nor are prone to the cheating problem. For example, consider deer that live in a group to dilute the risk of predation. Each deer, by being in the group, provides a benefit to all the others (by diluting the predation risk by a certain amount). However, each deer is also doing the best thing for itself (its own risk of predation is lower in the group than outside it). Thus, the mutual benefit arises simply from every individual following its own immediate self-interest. This situation is sometimes described as a by-product benefit because the benefits to others arise simply as a side-effect of the benefits to the actor. Note that there is no cheating problem in situations like this; you cannot take the benefit of being in the group without bearing the cost of being in the group.

8.5.2 Direct reciprocity

A possible mechanism for the evolution of mutual-benefit behaviour was discussed by Robert Trivers (1971). He called the mechanism reciprocal altruism, which is unfortunate since altruism is not involved. It is better named direct reciprocity. The idea is very simple. Individual A helps individual B in some way, and individual B returns the favour to individual A at some later point. Both can end up better off.

Theoretical work shows that direct reciprocity can evolve only if certain conditions are met. The benefit of the behaviour to the recipient must be greater than its cost to the actor. For example, direct reciprocity in food sharing could only evolve if there were times where a calorie of food was more valuable to individual B than to individual A, and times where the reverse was true. (This is quite reasonable; food becomes more valuable the closer to starvation one moves.) Interacting individuals must re-encounter each other multiple times and always have a substantial probability of repeat interaction. Finally, there must be some mechanism for allocating cooperation differentially to individuals who have been cooperative in the past. This is to prevent cheaters—who receive cooperative benefits but never return them—from proliferating. The most obvious mechanism is being able to recognize and remember the individual concerned.

Figure 8.10 In the ring-tailed coati (*Nasua nasua*), individuals intervene in support of those who have supported them in the past. Photo © Fabio Liverani/Nature Picture Library.



These conditions can be summed up in a stability condition for direct reciprocity, which is that $c < wb$, where c is the cost of the behaviour to the actor, b is the benefit of the behaviour to the recipient, and w is the probability of the recipient reciprocating in the future.

There are some interesting cases of mutual benefit through direct reciprocity in nature. The ring-tailed coati, *Nasua nasua*, is a social carnivore from the Americas (Figure 8.10). When there is a fight between two coatis, a third individual may intervene on the side of one or the other. Romero & Aureli (2008) studied a group in a zoo and showed that the more individual A intervened in support of individual B in disputes, the more individual B would intervene in support of individual A when it was A who was in a fight. In addition, the more individual A groomed the fur of individual B, the more likely individual B was to intervene on behalf of individual A. The researchers did not know all the kin relations obtained within the group and so were not able to decisively rule out kin selection as the mechanism maintaining the behaviour, but it looks very much as if there is reciprocity of support in these animals.

Direct reciprocity is also important in humans. In the famous 'live and let live' system in the trenches of the 1914–18 European war, soldiers on one side would allow the other side to go out to repair their defences and collect their casualties, with the other side returning the

Figure 8.11 The Christmas truce of 1914 in France and Belgium, during which soldiers of opposing armies moved about safely, repaired trenches, played football, and even roasted some pigs together, is reputed to have begun with German troops raising signs saying, 'You no shoot, we no shoot', a clear grasp of the principle of direct reciprocity. Photo © 2000 Credit: Topham Picturepoint/TopFoto.co.uk.



favour (Figure 8.11). The conditions for direct reciprocity were favourable, since the same units would face each other across the line for many months and thus have the opportunity for repeat interaction, the costs of not shooting at the enemy outside of a direct assault were low, the benefits were potentially high, and cheating could be immediately detected. Direct reciprocity would be much more difficult to establish in mobile warfare or where the same units did not interact for a prolonged period.

8.5.3 Indirect reciprocity

Direct reciprocity is the idea that we help individuals who have helped us in the past. By contrast, indirect reciprocity is the idea that it might be advantageous to help individuals who we have seen helping others in the past, even if that help was not specifically directed to us. In indirect reciprocity, then, the payback for being helpful to individual A is not that individual A will necessarily return the favour, but rather that by helping A, I will gain a good reputation, in virtue of which others might bestow benefits on me. The disincentive against cheating in an indirect reciprocity system is that cheaters get bad reputations and thereby are denied participation in future joint ventures.

Indirect reciprocity can be an evolutionarily stable strategy as long as, once again, the cost of the cooperative behaviour to the actor is smaller than its benefit to the recipient and, crucially, where the availability of accurate information about every individual's reputation is high. Formally, indirect reciprocity is advantageous where $c < qb$, where q is the probability of having correct information about the partner's prior behaviour. For q to be high, all behaviour of all social group members needs to be visible to everyone else or else there needs to be an accurate system for sharing information about the prior behaviour of others. Human language provides such a mechanism (see below).

Indirect reciprocity has been empirically demonstrated in humans in laboratory settings. Wedekind & Milinski (2000) had participants interact repeatedly in a group where, in turn, they could choose to transfer money to another player. Every Swiss franc given was doubled or quadrupled by the experimenters so that the benefit to the recipient was always greater than the cost to the actor. The participants were made anonymous from each other (they interacted via electronic key pads). However, at the point of making a decision about whether to give to someone, the actor could view how often that person had given to other group members in the past.

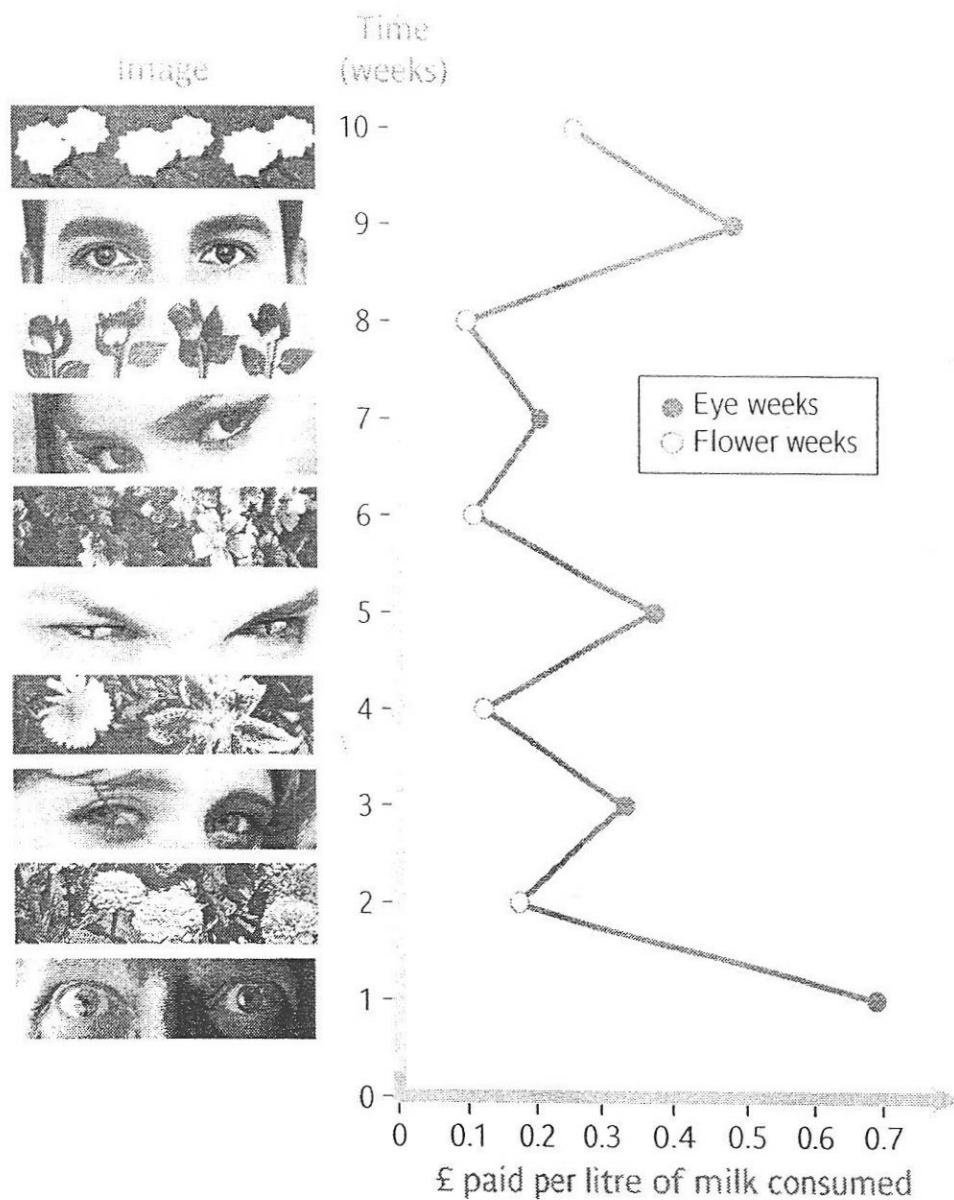
The prediction of the indirect reciprocity model is that those who give to others should themselves be given to and this is exactly what happened. Participants more generous in bestowing benefits also received more benefit, and not especially from those to whom they had given (this was veiled in the experiment by the use of keypads), but from everyone.

Indirect reciprocity is especially significant because humans are often generous towards causes where there is no expectation or even possibility of direct reciprocation, such as giving to charity or doing good works. One explanation of such behaviour is that it is beneficial through its reputational effects. For example, Milinski *et al.* (2006) showed in a laboratory task that people contributed more money to a climate-change fund when other group members would see their decision than when their decision was private. Moreover, people who had been seen to contribute to the fund were more likely to be chosen by others for a different, mutually beneficial cooperation game played later on.

Thus, it seems we humans are concerned about maintaining our reputations and this prompts us to behave cooperatively, even where direct reciprocation is impossible, wherever our actions are visible to others. In fact, it may not be necessary for our actions to actually be visible to others as long as we feel that they are visible. Bateson *et al.* (2006) studied contributions to an honesty box, which pays for supplies in a staff coffee room at Newcastle University. On alternate weeks, above the instructions for payment, they placed either a picture of human eyes or of flowers. Contributions were significantly higher in the weeks when the eyes were displayed (Figure 8.12). Since the eyes were only a picture, there were no actual reputational consequences of their being there, but they were obviously sufficient to make people feel that their behaviour was being seen and therefore known to others.

Indirect reciprocity may be a particularly potent mechanism in humans because human language is an effective means for sharing information about people's past behaviour. It is not necessary for humans to actually see how individual A behaves in joint ventures. Instead, if A is a cheater, someone will talk about him and everyone will come to know. Gossip—who did what with whom and why—is a central conversational activity in all cultures and always of great interest. Sommerfeld *et al.* (2007) studied a similar game to that of Wedekind & Milinski (2000), but this time participants could also write a piece of 'gossip' about the individuals they had interacted with, which would be shared with other participants. The researchers found that gossip information was more positive the more cooperative the person was, and was used by other players in subsequent cooperation decisions.

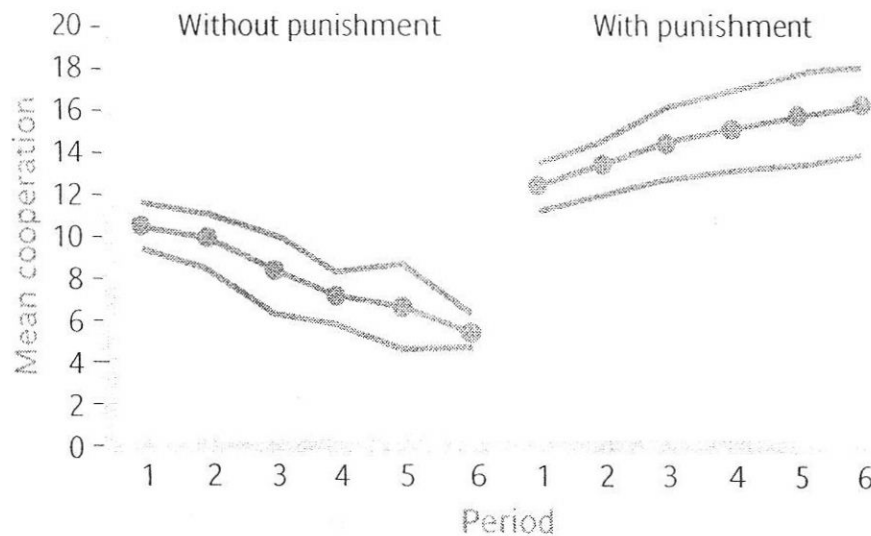
Figure 8.13 Contributions to an honesty box in a coffee room are higher in weeks where there is a picture of eyes on the wall than in weeks where there is a picture of flowers. From Bateson et al. (2006).



8.5.4 Punishment

Another mechanism that can make cooperation stable even in the absence of direct reciprocity is punishment. If cheating individuals are punished, cheating becomes an economic strategy. In laboratory experiments on humans, individuals will punish non-cooperators, even at cost to themselves and even if the cheating was not directed at them. The presence of punishment for non-cooperation sustains cooperation at much higher levels than where there is no possibility of punishment (Fehr & Gächter 2002; Figure 8.13).

Figure 8.5.5 Results from a laboratory experiment where group members (who were kept anonymous from each other) could repeatedly choose to contribute money to a joint venture, but benefited from it regardless of whether they contributed or not. Left: The normal result in such a game is that cooperation gradually declines over time to the point where no one is contributing. Right: When people are given the opportunity to punish others who don't contribute, even at cost to themselves, cooperation is high and remains so over time. Upper and lower lines represent the 95% confidence interval for the mean. From Fehr & Gächter (2002).



This is a very interesting finding, but it does raise further issues, principally, why should people punish? Given that punishment might be dangerous and costly, at first glance it seems like I would always be better off leaving others to do the punishment in my social group. Thus, providing punishment is itself a form of cooperation and is equally subject to problems of cheating. The most promising solutions to this issue focus on the idea that punishing non-cooperators brings reputational benefits (Barclay 2006) and thus links punishment to indirect reciprocity.

8.5.5 Issues surrounding human cooperation

There is a vigorous ongoing literature on human cooperation. This is because the level of cooperation between non-relatives that is found in humans seems to be much higher than that found in other animals. Cooperation in joint ventures must be part of the human success in conquering so much of the planet.

We will not review the entire literature on human cooperation here, but merely make a few observations for the reader who wishes to explore it for him- or herself. The first is that terminology is used rather variably in this literature. Humans are often described as altruistic because they are often prepared to make a short-term sacrifice of resources or time for others. However, it is not clear that such behaviours, like contributing to charities or joint ventures, are really altruistic in the long run. The reputational and social benefits I might derive from doing so could easily outweigh the costs over my lifetime. Theories of 'altruism' discussed in the human literature are usually not theories of altruism at all, but theories of benefits for cooperation.

A second point to make is that what makes humans so special is not that they have directly reciprocal one-on-one social relationships (like friendships, marriages, and so on). As we have seen, these kinds of relationship exist in some form in coaties and other animals. Rather, what makes humans unique is large-scale collective actions, such as a group of dozens or hundreds of men all going to war together. In these behaviours, the difference to the outcome made by one extra man is very small, but the costs to that man of taking part are potentially very large. Thus, there are strong individual disincentives for participation. These collective actions seem to be sustained by some combination of reputational benefits of participation, the danger of ostracism for not taking part, and punishment, which is in turn sustained by reputational benefits to the punishers (Milinski *et al.* 2002; Panchanathan & Boyd 2004; Barclay 2006). The human capacity for language facilitates all this by allowing reputational information to be shared.

However, the issues are not all solved. Contribution to joint ventures is evolutionarily stable in populations where non-contributors are shunned, but where does the shunning of non-contributors to joint ventures come from? Wearing a blue hat is evolutionarily stable in a population where individuals who do not wear blue hats are shunned, but this does not mean that groups of blue hat wearers will necessarily evolve. Thus, there must be some reason why humans evolved a psychology inclined to reward people for contribution to joint ventures and shun those who do not contribute, rather than a psychology inclined to reward people for some other arbitrary characteristic like wearing a blue hat. Boyd (2006) suggests competition between groups as a key factor here. With a norm of taking part in joint ventures stable in one social group, and a norm of wearing blue hats stable in another one, it is likely that the group performing joint ventures would proliferate at the expense of the other group.



Summary

1. Animals live in groups when the benefits of so doing outweigh the costs. Benefits of group living include reduction in predation risk, joint foraging, territory defence, care of young, and information transfer. A key cost is increased feeding competition.
2. Mating systems can be polygamous, polyandrous, monogamous, or promiscuous.
3. Social groups can be based around a single monogamous pair, one male and multiple females, or multiple males and multiple females.
4. According to the social brain hypothesis, close social bonds are cognitively demanding and require specialized brain mechanisms.
5. Human social groups are based on multiple males and multiple females, with a flexible mating system that is most commonly mildly polygynous. They often feature segmentary organization.
6. Cooperation within social groups can be sustained by some combination of kin selection, direct reciprocity, indirect reciprocity, and punishment.
7. Humans are notable for the extent of their cooperation, particularly joint ventures undertaken by large groups.

? Questions to consider

1. Why do you think herbivores often live in vast social groups, whilst carnivores seldom do so?
2. In multiple male, multiple female social systems in primates, why does either one sex or the other disperse, rather than neither or both?
3. Why are the seas and public lakes over-fished, whilst private fishing lakes are well stocked?
4. You may have noticed that there is an uncanny similarity between Hamilton's rule (kin altruism can evolve where $c < rb$), the condition for direct reciprocity to be evolutionarily stable ($c < wb$), and the condition for indirect reciprocity to be evolutionarily stable ($c < qb$). Why do you think these three expressions are so similar to each other?

→ Taking it further

A good account of the benefits of social relationships is Silk (2007). On mating systems and the social brain, see Shultz & Dunbar (2007). For a review of social rank and its relation to stress in humans and other primates, see Sapolsky (2005). The literature on cooperation, especially in humans, grows all the time. For a good overall review, see West *et al.* (2007). For a few of the many different approaches, see Roberts (2005), Milinski *et al.* (2006), Choi & Bowles (2007), and Barclay & Willer (2007).