

Cooperation between non-kin in animal societies

Tim Clutton-Brock¹

Explanations of cooperation between non-kin in animal societies often suggest that individuals exchange resources or services and that cooperation is maintained by reciprocity. But do cooperative interactions between unrelated individuals in non-human animals really resemble exchanges or are they a consequence of simpler mechanisms? Firm evidence of reciprocity in animal societies is rare and many examples of cooperation between non-kin probably represent cases of intra-specific mutualism or manipulation.

As Darwin appreciated, cooperative behaviour—actions adapted to assist others that involve costs to the fitness of participants—poses a fundamental problem to the traditional theory of natural selection, which rests on the assumption that individuals compete to survive and breed¹. Early explanations of cooperative behaviour in animal societies (see Figs 1–4) often argued that it was maintained by benefits to groups or populations^{2,3}, but most recent theoretical treatments are rooted in Hamilton's models of the evolution of cooperation based on the concept of inclusive fitness⁴ and it is now widely accepted that selection operating through benefits to non-descendant kin is commonly involved in maintaining cooperative behaviour (see Box 1).

Alternative paths to cooperation between non-kin

Although kin selection theory provides a satisfactory explanation of cooperation between kin, cooperation between unrelated individuals remains a problem and the evolutionary mechanisms that maintain it are still debated. The most frequent suggestion is that individuals exchange resources or services, suffering temporary net costs as a result of providing assistance, which are exceeded by subsequent benefits when they subsequently receive assistance from individuals that they have previously helped^{5,6}. Explanations of this kind are derived from Trivers' concept of reciprocal altruism⁷, although they are now usually referred to as examples of 'direct' or 'cost-counting' reciprocity to avoid the implication that they involve altruism.

In his original description of reciprocal altruism, Trivers⁷ interpreted cooperative interactions between members of different species (as well as between members of the same species) as reciprocal exchanges of assistance, and pointed out their similarity to the Prisoner's Dilemma games of economists⁸. In these games, two individuals that are constrained to interacting with each other initially agree to cooperate and gain higher pay-offs if they do so than if they refuse, although the highest pay-off is gained by individuals that defect when their partners cooperate. In iterated versions, cooperation can persist if individuals assist each other in turn and avoid partners that are unlikely to reciprocate^{5,6}. The most successful strategies are slightly 'generous' ones where individuals copy the previous behaviour of their partners, cooperating when they do and responding to defection by ceasing to provide assistance, but forgiving occasional lapses⁶. An additional tactic that can reduce the chance that individuals will assist non-cooperators is to monitor interactions between third parties, and models of 'indirect reciprocity' have explored the effects of mechanisms of this

kind^{9–11}. In addition, recent models of 'generalized reciprocity' show that, if cooperative individuals tend to associate with each other, cooperation can be stable if individuals respond cooperatively after they have been assisted by another group member^{12,13}, irrespective of their identity.

Although reciprocity is often suggested as an explanation of cooperation between non-kin, several other evolutionary mechanisms are also capable of maintaining cooperation between unrelated individuals. In some cases, cooperation generates immediate synergistic benefits shared by cooperators that exceed the costs of providing assistance^{14,15} as in the 'public goods' games of economists¹⁶. Mechanisms of this kind probably maintain many mutualistic interactions between species, like the hunting associations found between raptors and carnivores¹⁷ or between different predatory fish¹⁸, as well as many examples of cooperative foraging between unrelated conspecifics, like the cooperative manoeuvres of foraging pelicans¹⁹. I refer to them as cases of mutualism, though some prefer to use the term only to refer to cooperation between members of different species²⁰.

Alternatively, cooperative interactions may be a consequence of manipulative strategies—cases in which the behaviour of one (or both) partners is adapted solely to maximising its own immediate fitness. For example, dominant individuals commonly use coercive tactics (including harassment and punishment) to force others to provide assistance at some cost to their fitness^{21,22}. Manipulation can also involve actions that increase the fitness of their partners. In some cases, manipulators may adjust their behaviour to increase the probability that their partners perform purely selfish actions which increase their own fitness but have coincidental, 'by-product' benefits to the manipulator—a form of manipulation known as 'pseudo-reciprocity' that is probably common in animal strategies^{23,24}. In others, they may use inducements to exploit the fixed tendencies of others, such as their tendency to habituate to regular neighbours (see later). Finally, it has been suggested that cooperative behaviour may represent a costly display that signals an individual's prowess as a rival or its potential quality as a mate²⁵, though as yet there is little evidence that this is the case²⁶.

There is a contrast in the assumptions of models of reciprocity and models of mutualism and manipulation. Whereas models of reciprocity assume that providing assistance has net costs at the time that it is provided, which are offset by subsequent benefits, models of mutualism and manipulation usually assume that the benefits of assistance exceed the costs involved at the time that it is provided. A consequence

¹Department of Zoology, University of Cambridge, Downing Street, Cambridge CB3 9EJ, UK.

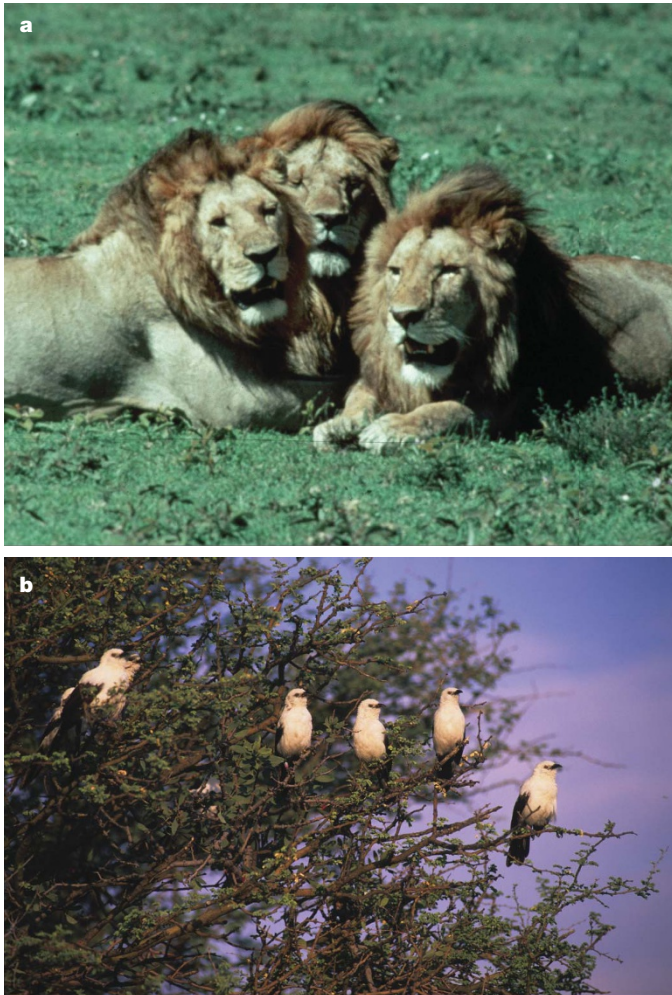


Figure 1 | Territorial choruses in birds and mammals. **a**, Territorial choruses by male lions discourage intruders and are likely to benefit all contributors. (The photograph was taken by C. R. Packer.) **b**, The territorial choruses of pied babblers and many other group-living birds also serve to demarcate territories and to deter intruders. (The photograph was taken by T.H.C.-B.)

of this difference is that, in reciprocity models, cheating strategies that exploit the time-lag between cost and benefit are often favoured, whereas the assumptions of explanations based on mutualism and manipulation usually exclude this possibility. Which of the two approaches to accounting the fitness benefits of providing assistance is appropriate depends less on the actual timing of effects (given that most actions only affect breeding success or survival hours, days or months after they are performed) than on the inevitability of net benefits to cooperators. Where the benefits of providing assistance are not inevitable, so that selection can favour cheating strategies that



Figure 2 | Cooperative mobbing of potential predators by meerkats drives away potential predators. (The photograph was taken by T.H.C.-B.)

exploit the behaviour of cooperators, it is realistic to treat fitness benefits as deferred. However, where providing assistance generates unavoidable benefits that cannot be exploited by cheating strategies, the method of accounting used in models of mutualism and manipulation may be more appropriate. Box 2 provides examples of both scenarios. In the first case, the benefits of cooperation are guaranteed by the synchrony of costs and benefits but, in other cases, they may be maintained by asymmetries in cost or benefit between partners or by contrasts in the constraints operating on different individuals (see below).

Over the last thirty years, theoretical studies of cooperation have focused principally on developing models of reciprocity between non-kin⁶ while empirical studies have explored the role of kinship and, to a lesser extent, of mutualistic interactions and manipulative strategies^{27–29}. The need for an integrated explanation of cooperative behaviour has recently led to systematic attempts to define key concepts and to classify models and mechanisms capable of maintaining cooperative behaviour between non-kin^{20,30–32}. For example, recent reviews³¹ suggest successive distinctions (1) between cases where actions benefit others but involve no costs to initiators and actions involving costs to initiators, (2) between cases where benefits are extracted or voluntary, and (3) between cases where the responses of recipients are costly or cost-free. However, cooperative interactions often involve more than one evolutionary mechanism so that examples of discrete categories of cooperation are rare, and there is the danger that detailed classifications provoke semantic arguments and focus disproportionate attention on unusual mechanisms³³.

The most immediate need is now to assess the relative importance of broader categories of explanations for the maintenance of cooperation in animal societies. How common *is* cooperation between non-kin? Does it commonly involve temporary fitness costs? Do cooperative interactions between non-kin really approximate to exchanges of resources or services as models of the Prisoner's Dilemma suggest, or

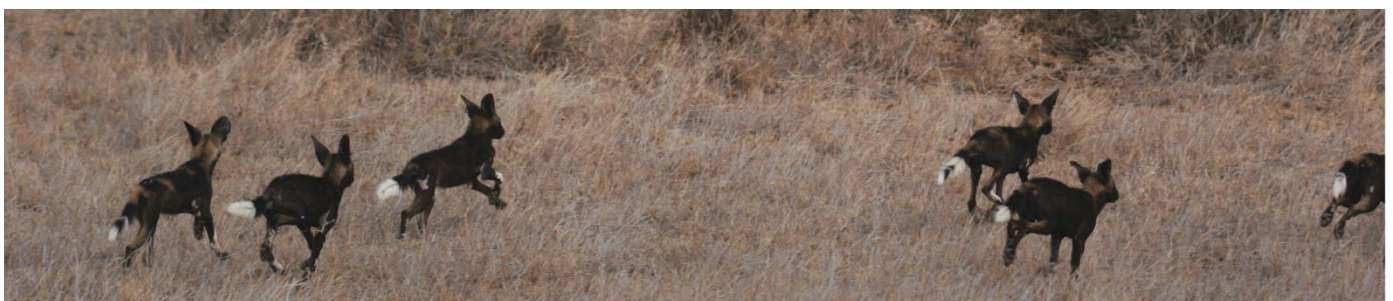


Figure 3 | Cooperative hunting in African wild dogs. The hunting and breeding success of pack members increases with group size. (The photograph was taken by R. Woodroffe.)



Figure 4 | Alternating bouts of allo-grooming in social primates are one of the best documented examples of reciprocity. (The photograph was taken by T.H.C.-B.)

is cooperation more commonly maintained by immediate shared benefits? Do unrelated animals often assist each other as a consequence of manipulative tactics involving coercion or inducement? Answers to these three questions are still unresolved and are of central importance to the direction of future research as well as to the interpretation of results of existing studies. The next three sections evaluate

Box 1 | Cooperating with kin

Where animals form stable breeding groups the members of which assist each other, individuals of one (or, in some cases, both) sexes are usually related to each other. To explain the evolution of cooperation between relatives, Hamilton⁴ 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^{27,71,87,88}. Most recent theoretical treatments are rooted in Hamilton's models of the evolution of cooperation based on the concept of inclusive fitness⁴: this can be reduced to the proposition that cooperation should evolve wherever $Br - C > 0$ where r is the coefficient of relatedness between two individuals, B is the benefit of cooperation to the recipient and C is the cost to the co-operator (Hamilton's Rule).

Over the last forty years, empirical studies of cooperation have provided extensive evidence of the importance of indirect or 'kin-selected' benefits in maintaining cooperative behaviour in animals^{68,89–92}. Among both invertebrates and vertebrates, cooperative behaviour between unrelated individuals that are not potential breeding partners is seldom highly developed even if they live in stable groups or colonies. Most of the more costly forms of cooperative behaviour, such as the provisioning of young born to other individuals, are restricted to species living in groups consisting primarily of relatives^{59,68}. For example, cooperative or eusocial breeding appears to be restricted to lineages with monandrous mating systems, which generate relatively high levels of relatedness^{93,94}. Where the sexes differ in their tendency to associate with relatives, cooperation is typically more frequent and more highly developed in whichever sex associates with relatives⁵⁹. In species where individuals have to choose between assisting close relatives, distant relatives or unrelated individuals, they typically show a strong preference for joining and assisting close relatives^{71,95,96}, unless some form of coercion is involved. And where group members compete, competition between non-kin is usually more intense than between kin⁹⁷.

Box 2 | The Soldier's Dilemma

The contrast between explanations of cooperation based on immediate shared benefits and those based on reciprocity can be illustrated by analogy with the pay-offs of different strategies to ambushed soldiers. Suppose that a four-man patrol of soldiers is ambushed by an unseen number of opponents, that soldiers who fire back attract incoming fire and increase the absolute chance that they will be killed from zero to 10%, and that the probability that the patrol will be overrun (and all members killed) is 100% if no individuals fire back but declines by 25% for each individual that does fire back. In this case, even if all three other members of a patrol fire back, the fourth member can still increase his chances of survival by 15% by doing so too. Under these conditions there is no dilemma: the best strategy for surviving a tour of duty is to fire back when attacked. Cooperative interactions of this kind are common in animal societies and often involve non-kin as well as kin⁵⁹. For example, the synchronized roaring of male lions faced by intruders^{98,99} (Fig. 1a) may resemble the first situation: roaring is likely to be relatively cheap while the potential costs of a successful and determined intrusion by bachelor males to all group members may be very large. Territorial choruses in birds (Fig. 1b) and synchronized mobbing of predators (Fig. 2) may also be maintained by similar net benefits.

Alternatively, suppose that only two members of the ambushed patrol closest to the enemy are in imminent danger and that their chances of surviving depend on the two furthest from the ambush providing covering fire. Assuming that the same individuals support each other in successive patrols, cooperation (firing back) can be maintained through some form of reciprocity^{5,6}. However, in contrast to the first scenario, the temporal separation of the costs of providing assistance and the benefits when the favour is eventually returned provides an opportunity for cheats to exploit the delay, unless indirect reciprocity or the threat of punishment causes the costs of cheating to exceed the costs of cooperation. Cooperative interactions in which individuals do not gain automatic benefits from providing assistance do occur in animal societies but they more usually involve kin or potential breeding partners. For example, social mongooses will attempt to rescue group members caught by dangerous predators in coordinated attacks on the predator¹⁰⁰. Similar interactions involving unrelated individuals are common in human societies in which cheats are usually punished, censured or excluded^{83,101}.

the importance of reciprocity, mutualism and manipulation in maintaining cooperative behaviour between non-kin in animal societies.

Reciprocity

Following the publication of Trivers' paper in 1971 (ref. 7), empirical studies provided a wide range of potential examples of direct reciprocity, including reciprocal assistance in mating competition in olive baboons *Papio anubis*³⁴, the exchange of blood meals in vampire bats *Desmodus rotundus*³⁵ and sequential predator inspection by fish³⁶. Their results stimulated thinking about how variation in the costs and benefits of cooperation might affect the behaviour of individuals, and led to the development of 'market models' predicting how variation in the supply of services or in the benefits they confer may affect how much individuals are ready to 'pay' for them³⁷. The language of human exchanges—negotiate, trade, barter, swap, payment, debt, commodity, currency, settlement, market—came to be widely used to describe cooperative interactions between animals³⁸. In addition, studies suggested that animals often 'interchange' one type of resource or service for another³⁹ and pay for access to resources or services. For example, a recent study of macaques which showed that males were more likely to mate with females they have previously groomed was immediately interpreted as evidence of prostitution in animals^{40,41}. More recently, dissatisfaction with models of the Prisoner's Dilemma as a conceptual framework for interpreting cooperative behaviour in animal societies has increased and several reviews have pointed out contrasts between the assumptions of these models and the conditions under which animals interact^{20,42}. Asymmetries in power and status between cooperating

individuals are often pronounced, generating large differences in the value of assistance which affect the form of interactions and relationships³⁷. Partners often communicate their intentions and modify their behaviour in the course of repeated interactions^{43,44}. Unlike prisoners, social animals are seldom constrained to cooperate with particular partners and can develop profitable relationships and terminate unproductive ones⁴⁵. Partners that are short-changed may punish defectors or join rival coalitions, so that cheating may have substantial costs^{21,22}. While there are certainly analogies between cooperative behaviour in animals and the interactions of partners in Prisoner's Dilemma games or human exchanges, these are not as close as is frequently implied.

Dissatisfaction with empirical evidence of direct reciprocity, especially in natural populations, has also grown^{28,31,32,42}. To provide convincing evidence that cooperative interactions are maintained by direct reciprocity, empirical studies need to demonstrate that the same individuals assist each other repeatedly; that the frequency with which they give assistance is contingent on the frequency with which they receive it; that cooperative behaviour has temporary net costs to the cooperator's fitness and is adapted to provide benefits to their partners; and that partners are not close relatives or prospective mates. Although experimented studies with captive birds and mammals have shown that the probability that individuals will assist each other can be affected by the previous behaviour of partners or other group members^{46–48}, very few attempts have been made to measure the net fitness benefits of cooperation between non-kin in natural populations and it is seldom clear whether cooperative actions entail temporary net costs or immediate net benefits. As a result, few of the studies commonly cited as examples of direct reciprocity in natural populations provide evidence that can definitely exclude the possibility that cooperative behaviour is maintained by immediate shared benefits, manipulative tactics or kin selection (Table 1). For example, although the same male baboons cooperate with each other to steal mating partners from rival males³⁴, there is no evidence that each male benefits in turn, and a simpler alternative is that males gain immediate benefits by synchronising their attacks on rivals⁴⁹. Similarly, while blood sharing in vampire bats is widely cited as an example of reciprocity⁵⁰, field studies do not provide unequivocal evidence that individuals are more likely to give blood to bats that previously have provided them with a meal⁵¹. Several other explanations are feasible: begging may prevent well-fed bats from resting, so that it may pay individuals to donate some of their resources to begging neighbours (see ref. 52) or, alternatively, a proportion of group members are relatives⁵¹ and blood sharing may normally involve kin.

The cooperative interactions between non-kin that most closely resemble the exchanges envisaged by models of direct reciprocity are

those in which two or more individuals repeatedly assist each other within narrow time frames. For example, in many social mammals, allo-grooming sessions in which partners groom each other in turn often involve unrelated individuals as well as relatives⁵³. Across grooming sessions, the duration of bouts given by each partner is usually similar and grooming is usually interpreted as an example of reciprocity^{54,55}. However, in many interactions of this kind, selection may favour individuals that prolong sessions until they have received a fixed amount of assistance (in this case, grooming) to avoid the costs or risks associated with attempting to find an alternative partner, and both partners may parcel their assistance in bouts to minimize the risk of defection. So, although these interactions share some of the properties of the Prisoner's Dilemma models, opportunities for repeated cheating are limited and an alternative interpretation is that they represent examples of pseudo-reciprocity⁵⁶.

Mutualism

Long before the publication of Hamilton's papers⁴, philosophers and scientists (including Darwin) stressed the potential importance of shared, mutualistic benefits in maintaining cooperative behaviour in animal societies^{1,2}. More recent studies provide convincing empirical evidence of effects of this kind and show that cooperation can generate immediate shared benefits. For example, cooperation between hunting partners can increase their per capita success in catching or defending food⁵⁷ (Fig. 3). Similarly, where groups defend communal territories and inter-group competition is frequent, larger groups commonly displace smaller ones, gradually eroding the size of their territories and depriving their members of access to resources^{28,58}. And, in species where group members rear young communally, the (per-capita) costs of raising young to breeders and helpers often decline with rising group size and their success increases^{28,59}. Mutualistic benefits may also help to maintain the long-term affiliative relationships between individuals that are found in many social animals^{60,61}. In some social primates, individuals form long-lasting relationships with non-kin involving association and mutual grooming^{62,63} and are more likely to support other animals in competitive interactions if they have recently been groomed by them^{64,65}. Analysis of long-term data show that differences in the extent and quality of affiliative relationships can affect breeding success⁶⁶. Although both partners must gain from these relationships for it to be worth maintaining them, these relationships may be more realistically interpreted as mutualistic coalitions or alliances than as examples of direct reciprocity.

A common objection to explanations of cooperative behaviour based on shared benefits is that situations of this kind generate opportunities for selection to favour individuals that free-ride on

Table 1 | A personal evaluation of examples of direct reciprocity

Proposed reciprocity	Presence of convincing empirical evidence from natural populations that:				
	The same individuals repeatedly assist each other	Cooperative behaviour is adapted to provide benefits to their partners	The frequency of contributions by individuals is adjusted to the frequency of their partners' contributions	Recipients of assistance do not include relatives or potential mates	Assistance has net fitness costs at the time it is provided in natural populations
Interspecific cleaning in fish	Yes	No	Yes	Yes	No
Egg trading in hermaphroditic fish	Yes	Yes	Yes	No	No
Predator inspection in fish	Yes	No	Yes	Yes	No
Tolerance of floaters in birds	Yes	No	No	Yes	No
Food calling in birds	No	Yes	Yes	Yes	No
Alarm calls in birds	No	Yes	No	No	No
Grooming in ungulates	Yes	Yes	Yes	Yes	No
Alarm signals in deer	Yes	Yes	No	No	No
Allo-parental care in carnivores	No	Yes	No	No	No
Midwifery in bats	No	Yes	No	No	No
Blood sharing in vampire bats	Yes	Yes	No	No	No
Allo-grooming in primates	Yes	Yes	Yes	Yes	No
Grooming interchanges in primates	Yes	Yes	Yes	Yes	No
Supportive coalitions in male baboons	Yes	No	No	Yes	No
Mutual support between female primates	Yes	Yes	No	Yes	No
Food-sharing in chimpanzees	No	No	No	Yes	No

Potential examples of direct reciprocity are taken from ref. 68.

the activities of cooperators, preventing the maintenance of cooperation^{67,68}. This need not necessarily be the case if group size is relatively small and cooperation generates inevitable benefits to the cooperator's breeding success or survival, so that cheats cannot exploit the delay between giving and receiving assistance and there is little opportunity for free-riding strategies to evolve¹⁴ (see Box 2). Many examples of cooperation between non-kin in animal societies, including cooperative foraging or hunting, cooperative defence of territories and mates and cooperative construction of nests and burrows, are likely to generate immediate net benefits which cannot easily be exploited by cheats. Moreover, although shared benefits are capable of maintaining cooperation between non-relatives, in practice, interactions commonly occur in stable, kin-based groups where the indirect benefits of cooperation are likely to reduce the relative benefits of cheating strategies¹⁴.

Where cooperative behaviour is maintained by shared direct benefits, variation in fitness can, in theory, be partitioned into variation between groups and variation between group members⁶⁹. For example, in the first situation described in Box 2, it would be possible to partition fitness into within-group effects generated by the costs of retaliation to individuals and between-group effects generated by differences in the proportion of individuals that retaliate. On these grounds, some theorists prefer to regard cooperative behaviour as a product of group selection⁶⁹ but it is often more practical to compare the relative pay-offs of different strategies to individuals in the population as a whole, treating cooperation maintained by shared benefits as a product of selection operating through variation in the inclusive fitness of individuals^{32,70,71}.

Manipulation

Manipulative interactions differ from the exchanges of resources or services envisaged by models of direct reciprocity in several ways: the behaviour of both individuals need not be adapted to providing assistance to their partner; the costs and benefits of interactions often differ substantially between partners so that there is no alternation of assistance given and received; and cooperative actions or inducements are likely to generate immediate net benefits rather than net costs. In many animal societies, individuals use coercive tactics to manipulate others to perform actions likely to increase their fitness or to avoid activities that jeopardise their interests^{21,22}. In some cases, individuals harass other group members until they assist them: for example, chimpanzees will harass individuals that have killed monkeys until they are given a share of the kill⁵². Alternatively, dominant individuals may punish subordinates that fail to assist them: for example, dominant rhesus monkeys punish subordinates that fail to give contact calls when they discover good feeding sites⁷². In both cases, coercion is likely to force individuals to adopt strategies that would not be optimal if their behaviour was unconstrained.

Manipulation need not involve coercion and can have benefits to other group members as well as costs. For example, in many social animals, the purely selfish activities of individuals can generate coincidental, unselected benefits to other group members known as 'by-product mutualisms'^{27,68}. Where these have substantial effects on fitness, selection may favour individuals that adjust their behaviour to maximise the by-product benefits that they receive, generating examples of 'pseudo-reciprocity'^{24,73}. For example, some eusocial insects protect or provision symbionts whose numbers contribute to their breeding success or survival⁷⁴. In other cases, manipulators modify their behaviour to take advantage of the fixed 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^{39,75,76} (Fig. 4). Similarly, in many primate societies, non-breeding females are strongly attracted by infants and may gain benefits (ranging from experience of parenting to the facilitation of future alliances) by interacting with them⁷⁷. Mothers are initially protective of their infants, but non-breeding females modify their behaviour to induce mothers to allow them

access to their infant, sitting close to them, signalling their friendly intentions and grooming them, so that mothers gradually habituate to their presence and become less restrictive, and persistent 'suitors' are able to hold or play with their infants⁷⁷.

Manipulative tactics also have a role in the establishment and maintenance of long-term mutualistic relationships. In many social mammals that live in stable groups, individuals compete to establish relationships with potential protectors, allies or mates, using a wide range of different forms of affiliative behaviour, including close association, grooming, support in competitive interactions, reassurance and consolation^{60,61,78}. Where alliances are disrupted by conflicts, they may attempt to minimize the consequences of conflicts by reconciling with competitors, supporting winners or consoling losers^{79–81}, and where their status is threatened by rival alliances, they may attempt to disrupt relationships between their rivals by strategic cooperation with their allies⁶⁰.

In many social animals, attempts to establish and maintain useful relationships with other individuals represent one component of a more general strategy of modifying their social environment so as to maximise their fitness. In some species, this involves the use of coercive or cooperative tactics to facilitate the development of long-lasting affiliative relationships with dominant animals, potential allies or prospective mates^{60–62}. In others, similar behaviour is used to adjust the size, age structure or kin composition of the group they live in⁵⁹. In such cases, attempts to assess the costs and benefits of cooperative actions within narrow time frames or to treat interactions as isolated games are likely to be misleading.

Discussion

Research over the last thirty years shows that cooperation in animal societies most frequently involves kin and is seldom highly developed in groups consisting of unrelated individuals (see Box 1). In many cases where non-kin do cooperate with each other in natural populations, one or both partners seem likely to gain immediate benefits from their behaviour and evidence that cooperation has temporary fitness costs is rare. As a result future studies need to be cautious in interpreting cooperative interactions between non-kin as examples of reciprocity.

Theoretical research now needs to explore the evolution of mutualistic interactions and manipulative tactics with as much energy as it has previously devoted to investigating the role of reciprocity. Many interactions between non-kin are likely to be maintained by a combination of mutualism, coercion and inducement and we need to know more about how the different processes that can maintain cooperation interact with each other. In addition, while it is convenient to consider the evolution of mutualistic and manipulative behaviour in non-kin, these strategies are most highly developed in stable groups which typically consist predominantly of relatives, so that both direct and indirect fitness benefits are likely to be involved. Kinship might be expected to affect the readiness of individuals to share benefits and to manipulate each other's activities but, as yet, we know little about these interactions.

The results of research on cooperation in animal societies emphasize both the contrasts and the similarities with human behaviour. Like other primates, humans often assist relatives, share benefits and use coercion and inducement to manipulate each other. As in other social animals, the size of groups may often have an important influence on the fitness of individuals^{82,83}. However, in contrast to other species, reciprocal exchanges of costly services or valuable resources between non-kin are widespread and often involve considerable time delays between assistance given and received and extensive opportunities for cheating^{16,84}. A likely reason for this contrast between humans and other primates is that reliable exchanges of valuable resources require some form of language (and associated psychological capacities) to establish the intentions and expectations of both parties regarding the nature and timing of exchanges^{84,85} as well as the social norms that discourage cheating^{83,86}. Lacking the ability to make specific agreements about

future events, other animals may commonly be restricted to cooperative strategies that generate immediate benefits to their inclusive fitness.

1. Darwin, C. *The Origin of Species* Ch. VIII (The Modern Library, 1859/1958). Although Darwin did not confront the problem of altruistic behaviour directly, he was aware of the challenge posed by the development of sterile castes in some social insects and, in Chapter VIII of *The Origin of Species*, he describes how he thought, at first, that this was fatal to the whole theory of natural selection.
2. Kropotkin, P. *Mutual Aid* (William Heineman, 1908).
3. Wynne-Edwards, V. C. *Animal Dispersion in Relation to Social Behaviour* (Oliver and Boyd, 1962).
4. Hamilton, W. D. The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–52 (1964).
Although they are usually cited as an explanation of the role of kin selection in maintaining cooperative behaviour, Hamilton's papers and Hamilton's Rule (see Box 1) also provide the basis for explaining cooperation between non-kin.
5. Axelrod, R. *The Evolution of Cooperation* (Basic Books, 1984).
6. Nowak, M. A. Five rules for the evolution of cooperation. *Science* **314**, 1560–1565 (2006).
7. Trivers, R. L. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57 (1971). The theoretical interest generated by Trivers' theory caused explanations of cooperation between non-kin based on reciprocity to eclipse all other explanations for more than thirty years.
8. von Neumann, J. & Morgenstern, O. *Theory of Games and Economic Behaviour* (Princeton Univ. Press, 1953).
9. Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity. *Nature* **437**, 1295–1297 (2005).
10. Suzuki, S. & Akiyama, E. Evolution of indirect reciprocity in groups of various sizes and comparison with direct reciprocity. *J. Theor. Biol.* **245**, 539–552 (2007).
11. Roberts, G. Evolution of direct and indirect reciprocity. *Proc. R. Soc. Lond. B* **275**, 173–179 (2008).
12. Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Benheffer, S. Evolution of cooperation by generalized reciprocity. *Proc. R. Soc. B* **272**, 1115–1120 (2005).
13. Rankin, D. J. & Taborsky, M. Assortment and the evolution of generalized reciprocity. *Evolution* **63**, 1913–1922 (2009).
14. Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* **268**, 187–196 (2001). Kokko's model shows that shared fitness benefits can maintain costly cooperation between non-kin in small groups—but that their capacity to do so is greatly enhanced if r exceeds 0.
15. Brown, J. S. & Vincent, T. L. Evolution of cooperation with shared costs and benefits. *Proc. R. Soc. Lond. B* **275**, 1985–1994 (2008).
16. Bowles, S. & Gintis, H. in *Genetic and Cultural Evolution of Cooperation* (ed. Hammerstein, P.) 429–444 (Dahlem Univ. Press, 2003).
17. Paxton, M. Foraging associations between pale chanting goshawks, honey badgers and slender mongooses. *Gabar* **3**, 82–93 (1988).
As Trivers pointed out, cooperative interactions between members of different species cannot be attributed to kin selection—but this does not necessarily suggest that they represent examples of reciprocity.
18. Bshary, R., Hohner, A., Ait-el-Djoudi, K. & Fricke, H. Interspecific communicative and coordinated hunting between groupers and giant Moray eels in the Red Sea. *PLoS Biol.* **4**, 2393–2398 (2006).
19. McMahon, B. F. & Evans, R. M. Foraging strategies of American white pelicans. *Behaviour* **120**, 69–89 (1992).
20. West, S. A., Griffin, A. S. & Gardiner, A. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**, 415–432 (2007).
West *et al.* prefer to use mutualism to refer only to interactions between species, whereas I use it here to refer to all $+/+$ interactions, where the behaviour of individuals is adapted to generating benefits to their partners, whether they involve heterospecifics or conspecifics.
21. Clutton-Brock, T. H. & Parker, G. A. Punishment in animal societies. *Nature* **373**, 209–216 (1995).
22. Cant, M. A. & Johnstone, R. A. Self-serving punishment and the evolution of cooperation. *Evol. Biol.* **19**, 1383–1385 (2006).
23. Connor, R. C. Pseudoreciprocity: investing in mutualism. *Anim. Behav.* **34**, 1652–1654 (1986).
24. Leimar, O. & Connor, R. C. in *Genetic and Cultural Evolution of Cooperation* (ed. Hammerstein, P.) 202–222 (MIT Press, 2003).
The models of pseudo-reciprocity produced by Connor and Leimar have attracted less attention than models of reciprocity but the processes they capture may help to explain many examples of cooperation between non-kin in animals.
25. Zahavi, A. & Zahavi, A. *The Handicap Principle: a Missing Piece of Darwin's Puzzle* (Oxford Univ. Press, 1997).
26. Wright, J. Berg, E. de Kort, S. R., Khazin, V. & Maklakov, A. A. Cooperative sentinel behaviour in the Arabian babbler. *Animal Behav.* **61**, doi:10.1006/anbe.2001.1838 (2001).
27. Brown, J. L. *Helping and Communal Breeding in Birds* (Princeton Univ. Press, 1987).
28. Clutton-Brock, T. H. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72 (2002).
29. Russell, A. F. in *Ecology and Evolution of Cooperative Breeding in Birds* (eds Koenig, W. & Dickinson, J.) 210–227 (Cambridge Univ. Press, 2004).
30. Lehmann, L. & Keller, L. The evolution of cooperation and altruism: a general framework and classification of models. *J. Evol. Biol.* **19**, 1365–1378 (2006).
31. Bergmüller, R., Russell, A. F., Johnstone, R. A. & Bshary, R. Integrating cooperative breeding into theoretical concepts of cooperation. *Behav. Process.* **76**, 61–72 (2007).
Bergmüller's review provides a comprehensive classification of types of reciprocity.
32. West, S. A., Griffin, A. S. & Gardner, A. Evolutionary explanations for cooperation. *Curr. Biol.* **17**, R661–R672 (2007).
33. Taborsky, M. Cooperation built the Tower of Babel. *Behav. Process.* **76**, 95–99 (2007).
34. Packer, C. Reciprocal altruism in olive baboons (*Papio anubis*). *Nature* **265**, 441–443 (1977).
35. Wilkinson, G. S. Reciprocal food sharing in the vampire bats. *Nature* **308**, 181–184 (1984).
36. Milinski, M. No alternative to Tit for Tat in sticklebacks. *Anim. Behav.* **39**, 989–991 (1990).
37. Noë, R. & Hammerstein, P. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**, 1–11 (1994).
Market theory provides important predictions concerning the magnitude of costs and benefits that apply as much to explanations of cooperation based on mutualistic interactions or manipulative tactics as to those based on reciprocity, so evidence that its predictions are confirmed does not necessarily support the interpretation of cooperative interactions as exchanges.
38. de Waal, F. B. M. & Berger, M. L. Payment for labour in monkeys. *Nature* **404**, 563 (2000).
39. Watts, D. P. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* **139**, 343–370 (2002).
40. Gummert, M. D. Payment for sex in a macaque mating market. *Anim. Behav.* **74**, 1655–1667 (2007).
41. Barras, C. A biological market for monkey prostitution. *New Sci.* **197**, 6 (2008).
This article represents an extreme example of the tendency to emphasise similarities between cooperative interactions between non-kin in animals and exchanges in human societies—but there are many others.
42. Hammerstein, P. in *Genetic and Cultural Evolution of Cooperation* (ed. Hammerstein, P.) 83–93 (Berlin Univ. Press, 2003).
43. Smuts, B. B. & Watanabe, J. M. Social relationships and ritualized greetings in adult male baboons *Papio cynocephalus*. *Int. J. Primatol.* **11**, 147–172 (1990).
44. McNamara, J. M., Gasson, I. E. & Houston, A. I. Incorporating rules for responding to evolutionary games. *Nature* **401**, 368–371 (1999).
45. Enquist, M. & Leimar, O. Evolution of cooperation in mobile organisms. *Anim. Behav.* **45**, 747–757 (1993).
46. Clements, K. C. & Stephens, D. W. Testing models of non-kin cooperation: mutualism and the prisoner's dilemma. *Anim. Behav.* **50**, 527–535 (1995).
47. Hauser, M. D., Chen, M. K. & Chen, F. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proc. R. Soc. Lond. B* **270**, 2363–2370 (2003).
48. Rutte, C. & Taborsky, M. The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): direct versus generalised reciprocity. *Behav. Ecol. Sociobiol.* **62**, 499–505 (2008).
Rutte and Taborsky provide convincing evidence that prior experience of cooperative interactions in rats affects their tendency to respond cooperatively to other individuals.
49. Bercovitch, F. B. in *Reproductive Ecology and Human Evolution* (ed. Ellis, P. T.) 369–396 (Aldine de Gruyter, 2001).
50. Dawkins, R. *The God Delusion* (Bantam, 2006).
51. Wilkinson, G. S. Reciprocal altruism in bats and other mammals. *Ethol. Sociobiol.* **9**, 85–100 (1988).
Wilkinson's study of blood sharing in vampire bats is commonly cited as the classic example of reciprocity but his results do not exclude the possibility that cooperation is maintained by kin selection, mutualism or manipulation.
52. Gilby, I. C. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim. Behav.* **71**, 953–963 (2006).
53. Hart, B. L. & Hart, L. Reciprocal allogrooming in impala. *Anim. Behav.* **44**, 1073–1083 (1992).
54. Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. Market forces predict grooming reciprocity in female baboons. *Proc. R. Soc. Lond. B* **266**, 665–670 (1999).
Barrett and Henzi's studies of grooming in wild baboons provide some of the most sophisticated evidence that grooming affects the extent of tolerance and the frequency of aggression in natural populations, but can be interpreted as examples of pseudo-reciprocity (or manipulation) as well as of evidence of reciprocity.
55. Barrett, L. & Henzi, S. P. in *Cooperation in Primates and Humans* (eds Kappeler, P. M. & Schaik, C. P. v.) 209–232 (Springer, 2006).
56. Connor, R. C. Impala allogrooming and the parceling model of reciprocity. *Anim. Behav.* **49**, 528–530 (1995).
57. Creel, S. & Creel, N. M. *The African Wild Dog: behavior, ecology and conservation* (Princeton Univ. Press, 2001).

58. Wrangham, R. W. An ecological model of female-bonded primate groups. *Behaviour* **75**, 262–300 (1980).
59. Clutton-Brock, T. H. in *Cooperation in Primates and Humans* (eds Kappeler, P. M. & van Schaik, C. P.) 173–190 (Springer, 2006).
60. de Waal, F. B. M. *Chimpanzee Politics* (Allen and Unwin, 1982).
61. Smuts, B. B. *Sex and Friendship in Baboons* (Aldine, 1985).
62. Mitani, J. C. Male chimpanzees form enduring and equitable social bonds. *Anim. Behav.* **77**, 633–640 (2009).
63. Gomes, C. M., Mundry, R. & Boesch, C. Long-term reciprocation of grooming in wild West African chimpanzees. *Proc. R. Soc. Lond. B* **276**, 699–706 (2009).
64. Seyfarth, R. M. & Cheney, D. L. Grooming alliances and reciprocal altruism in vervet monkeys. *Nature* **308**, 541–543 (1984).
65. Hemelrijk, C. K. Support for being groomed in long-tailed macaques *Macaca fascicularis*. *Anim. Behav.* **48**, 479–481 (1994).
66. Silk, J. B., Alberts, S. C. & Altmann, J. Social bonds of female baboons enhance infant survival. *Science* **302**, 1331–1334 (2003).
67. Boyd, R., & Richerson, P. J. The evolution of reciprocity in sizeable groups. *J. Theor. Biol.* **132**, 337–356 (1988).
68. Dugatkin, L. A. *Cooperation Among Animals: An Evolutionary Perspective* (Oxford Univ. Press, 1997).
- Dugatkin's comprehensive review of cooperative behaviour in animals provides an important synthesis of theory and evidence.**
69. Wilson, D. S. & Wilson, E. O. Rethinking the theoretical foundation of sociobiology. *Q. Rev. Biol.* **82**, 327–348 (2007).
70. West, S. A., Griffin, A. S. & Gardiner, A. Social semantics: how useful has group selection been? *J. Evol. Biol.* **21**, 374–385 (2007b).
71. Gardiner, A. & Grafen, A. Capturing the superorganism: a formal theory of group adaptation. *J. Evol. Biol.* **22**, 659–671 (2009).
72. Hauser, M. D. Costs of deception: cheaters are punished in rhesus monkeys *Macaque mulatta*. *Proc. Natl Acad. Sci. USA* **89**, 12137–12139 (1992).
73. Connor, R. C. Altruism among non-relatives: alternatives to the 'prisoner's dilemma'. *Trends Ecol. Evol.* **10**, 84–86 (1995).
74. Bourke, A. F. G. in *Behavioural Ecology: an Evolutionary Approach* (eds Krebs, J. R. & Davies, N. B.) 203–227 (Blackwell, 1997).
75. Barrett, L., Gaynor, D. & Henzi, S. P. A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Anim. Behav.* **63**, 1047–1053 (2002).
76. Cheney, D. L. & Seyfarth, R. M. *Baboon Metaphysics: the Evolution of a Social Mind* (Univ. Chicago Press, 2007).
77. Henzi, S. P. & Barrett, L. Infants as a commodity in a baboon market. *Anim. Behav.* **63**, 915–921 (2002).
78. de Waal, F. B. M. The integration of dominance and social bonding in primates. *Q. Rev. Biol.* **61**, 459–479 (1986).
79. Aureli, F., van Schaik, C. P. & van Hoof, J. Functional aspects of reconciliation among captive long-tailed macaques. *Am. J. Primatol.* **19**, 39–51 (1989).
80. Aureli, F. Post-conflict behaviour among wild long-tailed macaques *Macaca fascicularis*. *Behav. Ecol. Sociobiol.* **31**, 329–337 (1992).
81. Seed, A. M., Clayton, N. S. & Emery, N. J. Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Curr. Biol.* **17**, 1–7 (2007).
82. Turchin, P. *War and Peace and War: the Rise and Fall of Empires* (Pi Press, 2005).
83. Richerson, P. J. & Boyd, R. *Not By Genes Alone: How Culture Transformed Human Evolution* (Univ. Chicago Press, 2005).
84. Smith, E. A. in *Genetic and Cultural Evolution of Cooperation* (ed. Hammerstein, P.) 401–428 (Dahlem Univ. Press, 2003).
85. Stevens, J. R. & Hauser, M. D. Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn. Sci.* **8**, 60–65 (2004).
86. Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. The evolution of altruistic punishment. *Proc. Natl Acad. Sci. USA* **100**, 3531–3535 (2003).
87. Grafen, A. How not to measure inclusive fitness. *Nature* **298**, 425–426 (1982).
88. Grafen, A. in *Behavioural Ecology: an Evolutionary Approach* (eds Krebs, J. R. & Davies, N. B.) 62–84 (Blackwell, 1984).
89. Trivers, R. L. & Hare, H. Haplo-diploidy and the evolution of the social insects. *Science* **191**, 249–263 (1976).
90. Bourke, A. F. G. & Franks, N. R. *Social Evolution in Ants* (Princeton Univ. Press, 1995).
91. Solomon, N. G. & French, J. A. *Cooperative Breeding in Mammals* (Cambridge Univ. Press, 1997).
92. Koenig, W. & Dickinson, J. (eds) *Ecology and Evolution of Cooperative Breeding in Birds* (Cambridge Univ. Press, 2004).
93. Boomsma, J. J. Kin selection versus sexual selection: why the ends do not meet. *Curr. Biol.* **17**, R673–R683 (2007).
94. Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320**, 1213–1216 (2008).
95. Emlen, S. T. & Wrege, P. H. The role of kinship in helping decisions among white-fronted bee-eaters. *Behav. Ecol. Sociobiol.* **23**, 305–315 (1988).
96. Hatchwell, B. J., Ross, D. J., Fowlie, M. K. & McGowan, A. Kin discrimination in cooperatively breeding long-tailed tits. *Proc. R. Soc. Lond. B* **268**, 885–890 (2001b).
97. Boncoraglio, G. & Saino, N. Barn swallow chicks beg more loudly when brood mates are unrelated. *J. Evol. Biol.* **21**, 256–262 (2007).
98. Packer, C. *et al.* in *Reproductive Success* (ed. Clutton-Brock, T. H.) 363–383 (Univ. Chicago Press, 1988).
99. Heinsohn, R. G. & Packer, C. Complex cooperative strategies in group-territorial African lions. *Science* **269**, 1260–1262 (1995).
100. Rood, J. P. Banded mongoose rescues back member from eagle. *Anim. Behav.* **31**, 1261–1262 (1983).
101. Young, P. in *Genetic and Cultural Evolution of Cooperation* (ed. Hammerstein, P.) (Dahlem Univ. Press, 2003).

Acknowledgements I thank M. Bell, S. Bowles, R. Boyd, M. Cant, A. Cockburn, N. Davies, A. Gardner, S. Hodge, R. Johnstone, A. Russell, S. Sharp, J. Silk, J. Stevens, M. Taborsky and S. West for discussions or for comments on this manuscript. I also thank C. R. Packer and R. Woodroffe for the use of their photographs.

Author Information Reprints and permissions information is available at www.nature.com/reprints. Correspondence should be addressed to the author (thcb@cam.ac.uk).