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Review

How is human cooperation different?

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Although cooperation is a widespread phenomenon in nature, human cooperation exceeds that of all other species with regard to the scale and range of cooperative activities. Here we review and discuss differences between humans and non-humans in the strategies employed to maintain cooperation and control free-riders. We distinguish forms of cooperative behaviour based on their influence on the immediate payoffs of actor and recipient. If the actor has immediate costs and only the recipient obtains immediate benefits, we term this investment. If the behaviour has immediate positive effects for both actor and recipient, we call this a self-serving mutually beneficial behaviour or mutual cooperation. We argue that humans, in contrast to all other species, employ a wider range of enforcement mechanisms, which allow higher levels of cooperation to evolve and stabilize among unrelated individuals and in large groups. We also discuss proximate mechanisms underlying cooperative behaviour and focus on our experimental work with humans and our closest primate relatives. Differences in the proximate mechanisms also seem to contribute to explaining humans' greater ability to cooperate and enforce cooperation.

Keywords: cooperation; investing behaviour; mutual cooperation; social information

1. INTRODUCTION

Cooperative behaviour is not unique to the human species. It is a widespread phenomenon between individuals of the same, and even different, species. Here we refer to cooperation in its broadest sense: behaviours which provide a benefit to another individual (recipient) or are beneficial to both the actor and the recipient. Even very simple organisms such as viruses, bacteria and social amoebas cooperate with each other. Solitary amoebas for example form a multicellular differentiated 'slug' when they are starving, which is able to pass through soil barriers that solitary amoeba cannot cross (Brown 2001; Kuzdzal-Fick *et al.* 2007; Brockhurst *et al.* 2008). Very high levels of cooperation are a trademark of several species, including humans and insect societies; in the latter, the great degree of cooperation may be explained by indirect fitness benefits due to high relatedness between colony members (Hamilton 1964). Probably the most striking feature of human societies is their large size in combination with extensive cooperative behaviour between unrelated individuals. Cooperative behaviour is even found between complete strangers who are not likely to meet again in the future. Modern human societies strongly depend on high levels of cooperation between individuals, something

we experience every day. For example, humans engage in mutually beneficial cooperative interactions to reach goals as simple as moving obstacles or as complicated as building bridges or houses or playing symphonies. In addition, humans help others, incurring costs in many different situations on a daily basis. They may help a friend to carry boxes, hold the door open for a colleague, help a blind person to cross the street or donate blood, to name just a few examples.

From inclusive fitness theory, we know that all these behaviours must lead on average to an increase in the direct and/or indirect fitness of the actor (please note that there has lately been a strong debate on the mathematical equivalence of inclusive fitness and multilevel/group selection; see Wilson & Wilson 2007). The importance of indirect benefits in maintaining cooperation has been extensively demonstrated in animals and humans (e.g. Dugatkin 1997; Solomon & French 1997), whereas evidence for intraspecies cooperation between unrelated individuals outside humans is less common (Clutton-Brock 2009). Cooperation between unrelated individuals can evolve if both actor and receiver obtain immediate direct benefits from the interaction, or if individuals, who invest to help others, obtain a future benefit greater than the initial investment, for example via reciprocation (Trivers 1971). In humans many different control mechanisms, such as reward, punishment, ostracism, reputation building, etc., work to maintain and stabilize cooperation, ensuring that partners behave cooperatively and cheaters are kept under

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control. Although some of these mechanisms are shared with other animal species, for others there is little or no evidence in non-human animals. It appears that humans have evolved strategies and psychological mechanisms that allow them to cooperate and control free-riders with great flexibility, leading to high levels of cooperation between unrelated individuals, and even complete strangers, in a wide range of situations.

A great variety of concepts exists that may explain cooperation in nature (see Connor 2010; Leimar & Hammerstein 2010). In the following, we review different forms of cooperative behaviour with the explicit aim to discuss differences between humans and non-humans with regard to the strategies employed to maintain cooperation and control free-riders. Our focus is on strategies and mechanisms that lead to an increase in the actors' direct fitness benefits, since this allows cooperative behaviour to evolve and stabilize between unrelated individuals. We also discuss some of the proximate mechanisms underlying cooperative behaviour and compare them to those of our closest primate relatives, since differences in this regard also seem to explain humans' greatest skills to cooperate and enforce cooperation.

The problem of free-riding differs between situations in which there is a delay between help given and received and situations in which there is the potential for immediate mutual benefits (e.g. individuals must work together to obtain a common goal which otherwise would be inaccessible or harder to obtain), the former being more vulnerable to defection than the latter. We distinguish forms of cooperative behaviour based on their influence on the immediate payoffs of actor and recipient. If the actor has immediate costs and only the recipient obtains immediate benefits, we term this investment. If the behaviour has immediate positive effects for both actor and recipient, we call this a self-serving mutually beneficial behaviour or mutual cooperation (Bshary & Bergmueller 2008). We discuss social dilemmas or collective action problems (CAPs) as a special case of mutual cooperation. However, it should be noted that social dilemmas apply to both types of cooperative behaviour: (i) investment behaviour that creates public benefits and (ii) self-serving mutually beneficial behaviour in groups.

2. INVESTING BEHAVIOUR

Investing behaviour is characterized by a decrease in the actor's immediate payoffs and an increase in the recipient's payoffs. However, actors' lifetime direct fitness must increase in order for that particular behaviour to be under positive selection. Over the past decades, several mechanisms which make investing behaviour between unrelated individuals evolutionarily advantageous have been identified (for a review, see Bshary & Bergmüller 2008), but common to all of them is that in the long term, actors obtain return benefits that offset the initial investment.

(a) *Interdependence and pseudo-reciprocity*
The return benefits can be the consequence of self-serving behaviour by the recipient (pseudo-reciprocity; Connor 1996) or a by-product of the well-being of the

recipient when individuals are interdependent, or have a 'stake' in the welfare of others (Kokko *et al.* 2001; Roberts 2005). A typical example for pseudo-reciprocity are the interspecies ant–butterfly mutualisms, in which larvae of different butterfly species invest in producing nutritious liquids (nectar), which ants can feed from, in exchange for ant protection from predators. Defence by the ants is a by-product since it is in the ants' own selfish interest to defend their food source (Leimar & Connor 2003).

Roberts (2005) proposed the concept of interdependence, which is an extension or generalization of pseudo-reciprocity. Interdependent individuals have a stake in the welfare of others since these others' survival or well-being has secondary consequences for them, as for example due to group augmentation. There is good evidence for this, for example, in cooperative breeding meerkats (*Suricata suricatta*). In meerkats the growth, survival and breeding success of all group members increase with group size (Clutton-Brock *et al.* 2001*b*; see also Jaeggi *et al.* 2010 for a discussion of another cooperative breeder, the marmoset). It has been found that contributions to rearing do not correlate with relatedness, but instead helping is biased towards the philopatric sex (Brotherton *et al.* 2001). This suggests that helpers must gain direct fitness benefits from incrementing group size, and that, as long as the costs of helping are not too high, cheating may not be favoured (Brotherton *et al.* 2001; Clutton-Brock *et al.* 2001*a*). The issue of free-riding in these cases is not that the recipient does not pay back later in time, since the return benefit is the by-product result of his welfare. Instead, the problem of free-riding is a CAP in which other potential actors can free-ride by not contributing and still profiting from the shared benefits (as with territorial defence or alarm calling). In dyadic situations, the risk of defection is low but, as with other CAPs, defection becomes a more serious threat with increasing group size. The problem of free-riding might disappear within certain cost/benefit parameters in which cooperators always do better, regardless of the behaviour of others (Roberts 2005; see §3*a*). As suggested by Roberts (2005), it is possible that interdependence plays an important role explaining investing behaviour in nature, since it is relatively stable against exploitation. It could also provide an explanation for many investing interactions among humans (e.g. food sharing in hunter-gatherers or friendships in human and non-human primates). The difference then between human and non-human interdependence could rely on the proximate mechanisms underlying the investing behaviour *per se*, for example cognitive skills that allow individuals to understand the future consequences of their investments, empathy-mediated behaviour, etc. (see Brosnan *et al.* 2010 for a discussion of cooperation and cognition and de Waal & Suchak 2010, for a discussion of empathy), but not on special control mechanisms.

(b) *Reciprocal behaviour*
Another way by which unrelated individuals may obtain return benefits after an initial investment is

via reciprocation (Trivers 1971; Axelrod & Hamilton 1981). Reciprocal investment (termed 'reciprocal altruism' by Trivers) assumes that investments can be evolutionarily stable when individuals alternate their roles as actor and recipient. In theory, reciprocity can evolve in a population when the actor and the receiver engage in repeated interactions. Reciprocal altruism assumes a contingent relationship between favours given and received: if an individual stops receiving from a cooperative partner, it should in turn stop giving to this partner. Due to the time lag between favours given and received, free-riding becomes a crucial problem. Therefore, without cheater detection mechanisms, reciprocity cannot be evolutionarily stable, because cheaters would always exploit unconditional helpers without any consequences. Control mechanisms such as punishment, parcelling, partner switching, ostracism, etc. create solutions to stabilize investment behaviour.

Since Trivers (1971) proposed his theory of reciprocity, a lot of effort has been dedicated to finding examples of this form of cooperative behaviour in species other than humans which would fit the predictions of the theory and related formalized strategies (e.g. tit-for-tat, Pavlov; Axelrod & Hamilton 1981). Nevertheless, although theoretically very compelling, the empirical evidence remains scarce (Hammerstein 2003; Silk 2007; Clutton-Brock 2009; although see Schino & Aureli 2010). Most studies that suggest reciprocal interactions are based on correlational analyses, which do not rule out intervening third variables (such as association levels) and cannot give information about the cause–effect relationship. In order to test the contingency of behavioural exchanges, studies that look at the temporal sequence of exchanges and experiments that show that cooperative individuals stop cooperating, punish or switch partners after defection are necessary, since only then would it be demonstrated that there is a mechanism to control free-riding. Probably, the best evidence for reciprocity in a tit-for-tat manner comes from interactions in which animals exchange services within very short time frames: allo-grooming in impalas and some primate species (Hart & Hart 1992; Barrett *et al.* 1999) and egg-trading in simultaneous hermaphrodites (Connor 1992). This has been called parcelling, since individuals 'parcel' their investments to reduce the risk of defection. By parcelling the resources or services, individuals force their partners to stay and reciprocate in expectation of obtaining the next parcel. Parcelling reduces the temptation to defect, since there are higher costs associated with leaving and initiating a new interaction. In addition, the time lag between favours given and received is minimal, so that individuals obtain immediate feedback about the cooperativeness of their partner (Connor 1992).

But why is evidence for reciprocal investments in non-human animals so scarce? There are probably different reasons for this. First, the necessary life history and demographic conditions that were initially proposed as being important for reciprocity, highly social species with long life-spans, low dispersal rates, high rates of interaction in stable social groups (Trivers 1971), make by their very nature quantitative tests of reciprocity theory extremely difficult (Seyfarth & Cheney 1988). For example, individuals might reciprocate over longer time scales without keeping an exact record of recent exchanges (Kappeler & van Schaik 2006; Melis *et al.* 2008; Gomes *et al.* 2009; Schino & Aureli 2009), or exchange helping acts in different currencies (interchange; e.g. grooming, coalitionary support, sharing food). In addition, quantifying an exchange of acts becomes a difficult task when there are cost/benefit asymmetries across individuals, since for different individuals the exchanged commodities might have different values. For example, it could be that a low-ranking individual grooms a dominant partner on 10 different occasions, and then at a later point the dominant individual supports her in a fight (Seyfarth & Cheney 1988). Furthermore, an iterated Prisoner's Dilemma framework might not be adequate to represent the socio-ecological conditions under which most highly social species interact, since individuals can switch partners. Models that incorporate partner choice might be more useful to investigate how individuals terminate cooperative relationships with non-cooperators (Noë & Hammerstein 1994; Roberts 1998; Bshary & Noë 2003; Melis *et al.* 2006b; Schino & Aureli 2009).

Second, as several authors have suggested, the cognitive capacities required for reciprocal investment may have been underestimated (Stevens & Hauser 2004; Barrett & Henzi 2005; Hauser *et al.* 2009; see also Brosnan *et al.* 2010). Hauser *et al.* argue that only our own species evolved a particular set of psychological mechanisms and the capacity to integrate these different processes to carry out reciprocal interactions. In their opinion, constraints on memory, skills of quantification, delay of gratification, punishment of non-cooperative individuals, computation of current and future costs and benefits explain the lack of empirical evidence for reciprocity even in species which are phylogenetically closely related to us (Hauser *et al.* 2009). Although these skills and mechanisms are necessary to engage in reciprocal interactions in a prospective way, as humans often do, in which individuals compute the long-term benefits of reciprocal investments and are motivated by the expectation of a future benefit, it is possible that a more basic set of skills and emotion-based mechanisms is sufficient to keep cheaters under control and to allow for the emergence of contingency-based reciprocity (Brosnan & de Waal 2006; Kappeler & van Schaik 2006; Schino & Aureli 2009). Individuals of highly social and long-lived species need to keep track of past positive and negative interactions with different partners over long periods of time, so at the very least they should possess partner-specific memory and minimal quantification skills in order to be able to engage in contingency-based reciprocity.

Chimpanzees, our closest living primate relatives, are one of the best candidate species to exhibit contingency-based reciprocity. Genetic and behavioural analyses have shown that male cooperation takes

place between kin and non-kin (Langergraber *et al.* 2007). Long-term field studies suggest that they reciprocally exchange services (grooming, coalitionary support and meat sharing), and interchange them (grooming for support, grooming for meat and meat for support), with these correlations persisting after variables such as kinship, dominance rank and association frequencies have been controlled for (Watts 2002; Mitani 2006; Gomes *et al.* 2009). Furthermore, in experimental psychological studies, chimpanzees have shown many of the capacities required for reciprocity, such as inhibitory control, low temporal discounting rates (Rosati *et al.* 2007), capacity for numerical quantification (Hanus & Call 2007; Beran 2008), vengeance (Jensen 2007), helping behaviour (Warneken & Tomasello 2006; Warneken *et al.* 2007; Yamamoto *et al.* 2009; Melis *et al.* submitted) discrimination of intentional and accidental actions (Call *et al.* 2004), and discrimination and choice of successful over non-successful cooperative partners (Melis *et al.* 2006*b*).

Despite all these psychological mechanisms and observational data suggesting reciprocity, proving the contingency between acts given and received has proven to be difficult. Studies that have looked at the temporal sequence of cooperative exchanges in captive chimpanzees via observation (de Waal 1997; Koyama *et al.* 2006) or after experimental manipulation of the previous favours received from different partners (Melis *et al.* 2008) have found weak effects or limited evidence for reciprocal interactions. In the study by Melis *et al.* (2008), subjects increased their levels of helping towards a certain partner if this partner had previously helped them, but overall subjects did not help previous 'helpers' more than 'non-helpers'; that is, established preferences towards members in their group were probably not overridden with the experimental manipulation. Although there are different possible explanations for the weak effect found in this study, as discussed above, one possible interpretation is that in species with long-term relationships, accounts of given and received favours take place over longer time scales than were possible in the laboratory setting (see also Gomes *et al.* 2009). However, what seems to be a limitation even in our closest primate living relatives is the capacity to engage in reciprocal interactions in a prospective calculated way. In several experimental studies, pairs of chimpanzees were unable to maximize (or learn to maximize) their own benefits by providing food to each other in a turn-taking manner (Brosnan *et al.* 2009; see also Melis *et al.* 2009; Yamamoto & Tanaka 2009).

(c) *Reciprocity in humans*

In contrast to these findings, humans do have the capacity to engage prospectively in reciprocal interactions. Commonly, reciprocal interactions are divided into direct and indirect reciprocity. In direct reciprocity, a receiver of help returns the favour directly towards the donor at a later point in time (Axelrod 1984). Human direct reciprocity is most often empirically tested with the game theoretical paradigm of the iterated Prisoner's Dilemma. In

experimental studies, humans do directly reciprocate their partners' helpful behaviour and establish successful cooperative relationships (Dawes 1980; Milinski *et al.* 2002*a*; Semmann *et al.* 2004; Rand *et al.* 2009). In indirect reciprocal interactions, a donor helps another individual (the recipient) and obtains the return benefit from a third party. Cooperation can evolve and is sustained via reputation: individuals who help others obtain a good reputation and are more likely to be helped by third-parties in the future (Alexander 1987). Theoretically, reputations can be built through image scoring (Nowak & Sigmund 1998) or standing (Leimar & Hammerstein 2001). Image scoring is the simpler mechanism where every cooperative act increases one's image by one unit and every defective act decreases one's image by one unit, whereas standing also takes justified defection into account (i.e. defection leads to bad standing except when the receiver had bad standing himself). Although the mechanism controlling how reputation is built is still strongly debated (Leimar & Hammerstein 2001; Milinski *et al.* 2001), experimental studies indicate that humans use image scoring (or something very similar) to determine the reputation of others and maintain indirect reciprocal interactions (Nowak & Sigmund 1998; Leimar & Hammerstein 2001; Milinski *et al.* 2001; Panchanathan & Boyd 2003).

Direct and indirect reciprocal interactions in humans can be maintained with punishment and shunning (Clutton-Brock & Parker 1995; Ferriere *et al.* 2002; Bowles *et al.* 2003; Lau *et al.* 2009). Shunning can take place through partner-switching. Partner-switching is a self-serving and at the same time effective enforcement mechanism because the individual cheated switches partners and stops interacting with the cheater, who then incurs a cost by being left out without potential interaction partners. This is theoretically a potentially widespread control mechanism in animals and humans. There is good evidence for this among the interspecies mutualism between client reef fishes and cleaner wrasses (Bshary & Schäffer 2002); client fishes switch to other cleaning stations after defection by a cleaner, which forces the cleaners to change their behaviour. An experimental study with our closest primate relatives, the chimpanzees, has also shown that individuals keep track of past cooperative interactions with others, and preferentially choose the most effective collaborators, suggesting that they could be using the same shunning mechanism to control cheaters in their naturally occurring cooperative interactions (Melis *et al.* 2006*b*). In contrast, although punishing behaviour is frequently executed in animals under many circumstances in order to change the behaviour of others (e.g. trespassing territories, to protect sexual partners, discipline offspring), data on punishment to motivate intra-species cooperation are nearly absent in animals (Hauser 1992; Hauser & Marler 1993; see also Jensen 2010). However, punishment is a key control mechanism in humans. Interestingly, probably the best example of punishing behaviour stabilizing cooperation in animals comes also from the interspecies mutualism between cleaner fishes and their reef clients. Bshary & Grutter (2002,

2006) describe and experimentally show that resident clients chase cleaners which defect (by feeding on mucus instead of ectoparasites) and that this functions as punishment, since in follow-up interactions, cleaners are more cooperative than average after being chased. In a more recent paper (Raihani *et al.* 2010), it is also shown that male cleaners receive delayed benefits from punishing their female partners for cheating.

In contrast, in humans, costly punishment is a very effective and widespread mechanism to promote cooperative behaviour (Boyd & Richerson 1992; Fehr & Gächter 2000; Gintis 2000; Boyd *et al.* 2003; see also Gächter *et al.* 2010). Under laboratory conditions, even third-party and 'altruistic' punishment, where the punisher bears the cost but never benefits from the potential increase in cooperation, has been found in humans. In third-party punishment, observers pay a cost to sanction individuals that violate social (cooperative) norms by behaving uncooperatively, even though their own payoff has not been affected by the violation of the social norm (Fehr & Fischbacher 2004). Since the punishing individual might encounter the defector in the future, in the long term punishers might also benefit from the behavioural changes of the punished individual. The situation is a different one in altruistic punishment since individuals punish defectors although they know they will not meet them again in the future. This has been shown in experimental games, in which the individual who punishes has participated in the cooperative group game and punishes defectors despite knowing that they will not meet the same partners in future games. Thus the punisher punishes even though he knows that he will not benefit from the behavioural changes of the punished individual (Fehr & Gächter 2002; Fowler 2005*a*). Although human subjects who behave in this way are cognitively able to understand the experimental rules and the consequences of their behaviour, it is important to emphasize that the experimental conditions under which altruistic punishment is observed are very artificial and that it is difficult to imagine how such behaviour could have evolved under natural conditions. Thus, both types of punishment have been shown to lead to an increase in cooperation in human social interactions, with the limitation that this type of behaviour is unlikely to be evolutionarily stable.

Humans prefer situations where they have the option to punish, since the threat of punishment increases cooperation. However, humans often refrain from executing the punishing behaviour in cooperative situations in order to avoid the costs and thus maximize their payoffs (Dreber *et al.* 2008). While punishment is a very effective mechanism for promoting cooperation in human groups, it nevertheless poses a second-order social dilemma (Fowler 2005*b*). As with cooperators in a public goods situation, punishers have to bear a cost to punish others and thereby actually reduce their personal payoff. Because of this, punishers are outcompeted by non-punishers in the same way as cooperators are outcompeted by defectors within the same group (Fehr & Gächter 2000; Dreber *et al.* 2008). In summary, punishing behaviour is still

very puzzling in many aspects. It is not clear how costly punishment in humans can be evolutionarily stable, since the second-order dilemma has not yet been solved. Some additional benefit has to be achieved by punishing others (e.g. reputation gain) in order to finally resolve the second-order dilemma (see Earley 2010). In the end, the fact remains that in human cooperative behaviour, punishment or the threat of punishment increases cooperation. One way of avoiding the second-order social dilemma is the instalment of institutions that punish socially unwelcome behaviour. Once institutions are established, they punish antisocial behaviour and enforce the social rules or norms the group has agreed upon, and the costs of the institutions are shared equally by all group members in advance (Gurek *et al.* 2006).

Up to now, we have discussed separately the effects of reputation building in indirect reciprocity situations and costly punishment on human social behaviour. Under natural conditions, it is not possible to separate these effects clearly. Very often, an individual will risk punishment and a loss of reputation with the same uncooperative act. The experimental study by Rockenbach & Milinski (2006) showed that the interplay of punishment and reputation building increases cooperation more than either can achieve on their own. Therefore, is the combination of these two mechanisms one of the most efficient ways to promote cooperative behaviour in humans?

3. MUTUAL COOPERATION

Mutually beneficial cooperative behaviour provides immediate gains for all participants. At a dyadic level, the risk of potential defection is generally low since by acting together, individuals obtain higher benefits than they would obtain by acting alone. Although individuals act in their own immediate interest, and sometimes cooperation is a by-product of their independent but simultaneous actions, often they need to adapt to a greater or lesser degree to their partner's behaviour, synchronizing and coordinating with each other (Leimar & Connor 2003). Examples of dyadic mutually beneficial behaviour in animals include coordinated displays to defend shared resources (e.g. magpie-larks: Magrath *et al.* 2007; siamangs: Geissmann 2000), coalitions and alliances, territorial defence in breeding pairs of different species (e.g. carrion crows; Bossema & Benus 1985), cooperative hunting such as among pairs of jackals, and even interspecies mutualisms such as between groupers and moray eels (Lamprecht 1978; Bshary *et al.* 2006). The problem of free-riding becomes more acute with increasing group size and whenever the cooperative act generates public and non-excludable benefits. Nevertheless, at a group level, predator mobbing, territorial defence and cooperative hunting are widespread phenomena among animals (Bednarz 1988; Boesch & Boesch 1989; Stander 1992; Creel & Creel 1995; Gazda *et al.* 2005). We will first focus on the strategies and conditions that might allow group-level mutual cooperation to be evolutionarily stable despite the higher temptation to free-ride and then

on the proximate mechanisms underlying collaborative coordinated actions between individuals.

(a) *Social dilemmas*

As alluded to above, even in cases of immediate mutual benefits, the problem of free-riders arises with increasing group size, especially if the collective action produces non-excludable public benefits. This is known in the economics literature as the CAP, or the 'tragedy of the commons' or public goods situations (Hardin 1968). In these situations, free-riders in the group can profit from the services of others and gain resources without incurring any personal costs. There is evidence that some animal species which face social dilemma situations, e.g. bacteria, slime moulds and phages, are surprisingly often able to overcome the dilemma and actually sustain a common resource (Crespi & Springer 2003; Velicer & Yu 2003; Sachs & Bull 2005; West *et al.* 2007; Queller & Strassmann 2009). CAPs may also arise in mammals' and birds' cooperative interactions, as for example in territorial defence (Heinsohn & Packer 1995; van Schaik and Kappeler 1996; Nunn 2000). The question then becomes: what mechanisms do animals have to deal with CAPs, and could limitations in animals' enforcement mechanisms account for the difference between human and nonhuman group-level cooperation?

Nunn (2000) and Nunn & Lewis (2001) review different ways in which animals might overcome CAPs. They suggest that dominance hierarchies and asymmetrical benefits might provide a solution to the problem, since privileged groups of individuals invest to the extent that they can profit more from the obtained benefits, so that (some) free-riding from the subordinates would not threaten the collective action. This is probably a relevant explanation in animal species, where strong dominance hierarchies are frequent.

Furthermore, it is possible that free-riding is not a threat in situations in which the benefit to cost ratio is very high. Although individuals do better the more partners cooperate, they might still do better cooperating independent of what others do, since not cooperating is the worst individuals can do (resembling more a chicken or snowdrift game than a Prisoners Dilemma scenario in game-theory terms; Nunn 2000; Kuemmerli *et al.* 2007). It has been shown theoretically and empirically that small group sizes and high group benefits can remove a social dilemma from a public goods situation and make the cooperator strategy, when averaged over many small groups, more successful than the defector strategy (Hauert *et al.* 2002; Semmann *et al.* 2003). In other words, a cooperative strategy will be selected because the direct fitness of a cooperative individual increases irrespective of whether he is in a group with other cooperators or defectors. This is because the increase in fitness is relative to others in the breeding population, and not restricted to others with which the individual interacts (West *et al.* 2006).

Although, in humans, another possible solution to CAPs is coercion and private incentives (punishment and rewards), there is little empirical evidence for this outside humans. As mentioned above, evidence for punishment to motivate intra-species cooperation is nearly absent in animals (with the exception of Hauser & Marler 1993; see Jensen 2010). Evidence for rewards or benefits distributed only among contributors to the collective action has only been reported among chimpanzees after hunting episodes (although note that meat is rather an excludable good). Boesch & Boesch (1989) reported that chimpanzees in the Taï forest distribute the meat fairly between hunters and non-hunters: hunters obtain more meat than bystanders and latecomers, and good hunters receive the most meat. One possible interpretation of this observation is that individuals have the capacity to keep track of others' contributions to the collaborative act, rewarding individuals' contributions to the collaborative act and punishing (in a non-costly way) non-hunters behaviour. Alternatively, a more parsimonious explanation could be that hunters are just good (or skilled) in securing the largest share for themselves. This is an observation that deserves further investigation both in the wild and with controlled experiments in captive settings, since it will shed light on the proximate mechanisms with which chimpanzees (and other species) solve this and similar CAPs.

In contrast to other animal species, humans do have the cognitive capacity to keep track of others' contributions to the collaborative activity and regularly employ control mechanisms such as punishment, reputation and ostracism that allows them to maintain cooperative behaviour in groups. Experimental studies have shown that without these enforcement mechanisms, human groups often fail to sustain a public resource, which every group member is free to overuse (Hardin 1968; Dawes 1980; Berkes *et al.* 1989; Ledyard 1995; Ostrom *et al.* 1999). In the classical experimental setup of the public goods game, four players have to decide simultaneously whether they want to contribute to a public pool. The content of the pool is then doubled and divided equally to the members of the group irrespective of their contribution to the public pool. The situation is a social dilemma because defectors within the same group are always better off than cooperators; the rational choice should always be to refrain from contributing in the first place since any unit invested into the public pool is doubled and divided by four, so that only half of the individual's investment is returned. In these experiments, humans usually start with high levels of cooperation, but are not able to sustain it over time when the game is played repeatedly (Milinski *et al.* 2002*b*). But the control mechanisms mentioned earlier, reputation, punishment and ostracism, can change the outcome of CAPs towards high cooperation (Fehr & Gächter 2002; Milinski *et al.* 2002*b*; see also Gächter *et al.* 2010). Examples of cooperative CAPs in most human societies are garbage disposal and group hunting. Most humans do not litter (e.g. throw their garbage into public places) in their own community, since they may lose reputation or be punished for doing so. In group hunting, humans usually contribute to the hunt since they

face the threat of being ostracized the next time the group goes hunting if they fail to do so. However, there are also examples where humans face CAPs and are not able to sustain the public resources. This is the case for example with the global climate, overfishing of the oceans and, on a more individual level, hygiene in public toilets. Humans fail here since the cooperation enhancing mechanisms (e.g. punishment, reputation and ostracism) cannot be applied in these situations.

(b) *Proximate mechanisms underlying mutual cooperation*

Psychological research suggests that human mutual cooperation is special with regard to the underlying proximate mechanisms. These mechanisms seem to allow humans to employ cooperative strategies more flexibly, more efficiently and in a wider range of situations than can other species (Tomasello *et al*. 2005).

Research on our closest relatives, the chimpanzees and bonobos, suggests that differences in the proximate mechanisms include both non-cognitive (emotional and/or temperamental) and cognitive factors. Regarding the former, low interindividual tolerance levels, resulting from competitive relationships over resources such as food, constrain cooperation between chimpanzees, but not between the more egalitarian bonobos (Chalmeau 1994; Melis *et al*. 2006*a*; Hare *et al*. 2007). Interindividual tolerance levels among chimpanzees predict spontaneous success or failure in cooperative food-retrieval tasks in which both individuals in the dyad could have potentially shared the obtained rewards (Melis *et al*. 2006*a*; see Petit *et al*. 1992; de Waal & Davis 2003; Melis *et al*. 2006*a*; Seed *et al*. 2008 for similar results with macaques, capuchin monkeys and rooks, respectively). If individuals cannot share the spoils obtained in the cooperative enterprise, cooperation will not only break down in the long term, but will not even emerge in the first place. These results have lead to the hypothesis that an important step in human evolution might have been a change in temperament: more tolerant relationships between individuals might have created an adaptive space within which our more complex cooperative and cognitive skills could have evolved (Hare & Tomasello 2005; Tomasello *et al*. 2005; Melis *et al*. 2006*a*; see also Hrdy 2009;[1] Burkart *et al*. 2009).

From a cognitive point of view, the question of interest in coordinated collaborative interactions is whether animals understand the role and intentions of the collaborative partner. This allows individuals to actively coordinate their actions with those of their partner, employing different social and communicative means to facilitate success in the joint action. This stands in contrast to simple co-production, where individuals independently but simultaneously direct similar actions to the common goal. Comparative psychologists interested in the cognitive underpinnings of animal cooperation have generally focused on primates (Crawford 1937; Chalmeau 1994; Mendres & de Waal 2000; Visalberghi *et al*. 2000; Cronin *et al*. 2005; Hattori *et al*. 2005; Hirata & Fuwa 2007;

but see Seed *et al*. 2008; Drea & Carter 2009 for work with rooks and hyenas).

In most studies, pairs of individuals are confronted with a cooperative food retrieval task, in which individuals need to coordinate their actions by pulling simultaneously on a rope/handle in order to retrieve the otherwise out-of-reach rewards. Since in most of these retrieval tasks, subjects can succeed as a by-product of individuals' independent but simultaneous actions, active coordination between partners is often operationalized with measures such as pulling rates in the presence and absence of the partner, and monitoring behaviour between partners (under the assumption that monitoring behaviour takes place to coordinate behaviour between collaborative partners; see also de Waal & Suchak 2010). In a study with capuchin monkeys, Visalberghi *et al*. (2000) found that subjects pulled equally often when the partner was pulling than when it was not. This leads them to conclude that although capuchins can succeed in a joint action due to their simultaneous actions, they do not acquire an appreciation of the role of the partner. However, Mendres & de Waal (2000) and Cronin *et al*. (2005; see also Hattori *et al*. 2005) have argued that capuchins and cottontop tamarins understand the role of the partner in a cooperative task since individuals pull more often in the presence of a partner (Cronin *et al*. 2005), perform better if they can see the partner and monitor their partners more when cooperation is necessary than when it is not (Mendres & de Waal 2000). It is important to note that methodological differences between the different studies (e.g. the apparatus, training phases prior to the test and number of trials during the test phase) make between-studies comparisons difficult. However, even if subjects developed some sensitivity to the role of the partner, subjects often participated in an extensive number of trials before showing efficiency in the task (e.g. hundreds of trials in both Cronin *et al*. (2005) and Hattori *et al*. (2005)). Nevertheless, it seems that with experience, different primate species can learn (with more or less difficulty/ease) the contingencies of a cooperative task.

A later study with chimpanzees (Melis *et al*. 2006*b*; see also Hirata & Fuwa 2007) has provided stronger evidence for what may constitute knowledge of the role of the collaborative partner. In this study, individuals learned within a few sessions to wait for each other, delaying the pulling of the rope until the partner was in position to pull. The task, originally developed by Hirata & Fuwa (2007), required true synchronization since otherwise the rope slipped out of the apparatus. However, more importantly, in a transfer test individuals recruited a partner (by allowing her to enter the testing room) significantly more often when the task required cooperation than when it did not. Furthermore, when given the choice between two different collaborative partners, they preferentially recruited the more skilful partner. The chimpanzees' knowledge about the role of the collaborative partner was evidenced not only by their waiting behaviour, but also by the fact that subjects actively recruited the (most skilful) partner to initiate the joint activity. It is (would be) important to conduct similar studies

with other primate and non-primate species to learn whether this is a derived ability only shared by chimpanzees and humans, or whether this ability has deeper phylogenetic roots (see Seed *et al.* 2008 for negative results with rooks).

Human children, from around their second year of life, are able to coordinate their behaviour with that of an adult partner or peer in cooperative problem-solving activities and social games. They not only coordinate their behaviour with that of their partner, showing knowledge about how the different roles are interrelated with each other, but also employ different communicative strategies to re-engage or direct their partner, if she stops performing her role (Brownell & Carriger 1990; Warneken *et al.* 2006). This ability to influence the partner via communication has been interpreted as evidence for a capacity to form *shared* goals with others. Tomasello *et al.* (2005) argue that the capacity to form shared goals with others, creating joint intentions and a joint commitment to pursue those goals, is what allows humans to engage in a wide range of collaborative activities (from taking a walk together with someone to building skyscrapers), and much more complex forms of collaboration. Forming shared goals and joint intentions goes beyond coordinating the actions with those of a partner. When individuals form shared goals they also want the partner to be aimed at the goal and be successful in his role; that is why it has been argued that some form of communication, in which partners influence not only each other's behaviour but also each others' intentions, is critical to distinguish collaborative activities based on shared intentionality from collaborative activities in which individuals view their partners as mere social tools to reach their own individual goals (Tomasello *et al.* 2005; Warneken *et al.* 2006).

Since intentional communication during cooperative interactions seems to be primarily absent in other species (even in our closest living relatives the chimpanzees), until now there is no evidence for shared intentionality in non-human animals. Even though chimpanzees have shown great flexibility in solving different collaborative problems (e.g. Melis *et al.* 2006*b*, 2009), their behaviour can still be interpreted as the result of viewing their partner as a social tool to reach their own individual goals (Warneken & Tomasello 2006; Melis *et al.* in press).

4. SOCIAL INFORMATION
A major difference between human and non-human animals is the way information about social behaviour is gathered and transmitted. Social information is essential in many situations to maintain cooperative behaviour, since only then can reciprocity and punishment work. An individual cannot be punished for misbehaviour or rewarded for positive social behaviour if others have no information about the individuals' past behaviour. Removing social information in experiments with humans, by making decisions anonymous, leads in almost all conditions to a stark decrease in cooperation (Semmann *et al.* 2004). Although almost all social animals can gather information through experience interacting with a social partner directly,

it is less clear what kind of information they can gather through direct observation. Evidence for animals other than humans using image scoring strategies in cooperative situations has only been found in the interspecies mutualism of cleaner fishes (*Labroides dimidiatus*) and client reef fish species. Cleaner fish feed more against their preference when viewed by eavesdropping clients who use image scoring to find cleaners that cooperate, by removing the clients ectoparasites, rather than defect, by feeding on the client's mucus (Bshary 2002; Bshary & Grutter 2006; see also Earley 2010). With the exception of this interspecies mutualism, there is no good evidence that animals other than humans, not even our closest primate relatives, use information gathered through observation to regulate their cooperative interactions with others (see Russell *et al.* 2008 for some positive evidence with chimpanzees but not with other apes).

Unlike other animals, humans excel at being able to gather social information in more ways than through direct experience. Many of the means for gathering indirect information include language use. Social information is transferred through language in humans, which enables them to build reputations which then can be used, as, for instance, in indirect reciprocity situations. This type of information transfer is usually called gossip (Nakamaru & Kawata 2004; Nowak & Sigmund 2005; Sommerfeld *et al.* 2007). Empirical studies with human subjects have shown that information about social behaviour can be truthfully transmitted through gossip, but that it also has a strong manipulative potential. A possible way to greatly reduce the risk of false information about the social behaviour of a potential partner is to collect the information from more than one source. For example, one usually does not visit a new doctor in the neighbourhood because of one positive, but possibly false, review. One rather collects reviews (gossip) from several different social partners and switches only if the majority have reported this new doctor to be better than the old one. Through multiple gossip sources reliability of the information can be greatly increased (Sommerfeld *et al.* 2008). Exchanging social information about others (i.e. through language) is undoubtedly a very important capacity which contributes to the very high levels of cooperation in human societies.

5. CONCLUSIONS
We have discussed ways in which humans and animals engage in and maintain cooperative interactions. In animals, cooperation in which individuals invest in others without obtaining immediate benefits can mostly be explained via (kin-selected) indirect benefits and direct fitness benefits, which are the by-product of the well-being of the individual being helped (i.e. pseudo-reciprocity or interdependence). Partner-switching probably functions as an important enforcement mechanism in animals, but more empirical evidence is needed. In addition, cooperation in animals can often be explained as the result of individuals obtaining immediate direct benefits. Common to all these mechanisms is that cooperation is maintained in a rather passive way (e.g. returned benefits

are the by-product of the well-being of the individual helped, or the result of the self-serving strategy of switching to a more-profitable partner).

However, in addition, humans have evolved active enforcement mechanisms, such as reward, punishment and reputation building, for which there is little evidence in animals, especially to maintain intra-species cooperation. Humans have evolved unique cognitive mechanisms which allow them to keep track of past interactions with others for long periods of time, keep track of individuals' contributions in collaborative activities and transfer all this relevant information to others. This allows humans to engage in direct and indirect reciprocity and maintain cooperative interactions at a dyadic level between unrelated individuals. At the same time, these enforcement mechanisms are key in maintaining mutual cooperation in large groups and solving CAPs. Although mutual cooperation is a widespread phenomenon in animal societies, the underlying proximate mechanisms differ in humans, which allow them to employ cooperative strategies in a more flexible way and with help of the above-mentioned mechanisms keep cheaters under control in a wider range of situations.

Fundamental differences between human and animal cooperation lie in the complexity of the social network and the information transfer about social behaviour. The possibility of using language to exchange social information is probably the most important difference. Through language, human societies and groups are able to define complex rules, morals, laws and traditions that can be transmitted without direct experience. Furthermore, the social rules do not have to be taught by others, and they can even be learned in written form. Exceptionally in the animal kingdom, humans enforce these social rules by relying on more than just direct punishment and rewards as incentives to behave cooperatively. Humans also appoint representatives and establish institutions that control and punish antisocial behaviour (Yamagishi 1988; McCusker & Carnevale 1995). Without these possibilities to promote cooperative behaviour, it would be unthinkable that the high levels of cooperative behaviour between unrelated individuals could be evolutionarily stable.

ENDNOTE

[1]Hrdy argues that a newly evolved shared childrearing system in our Pleistocene ancestors created the first push in humans to become hyper-social. Her hypothesis is that cooperative breeding leads to newly evolved emotional and temperament adaptations that allowed humans to care also for non-relatives, and to cognitive adaptations that allowed humans to better predict the behaviour of others.

REFERENCES

Alexander, R. D. 1987 *The biology of moral systems*. New York, NY: Walter de Gruyter.

Axelrod, R. 1984 *The evolution of cooperation*. New York, NY: Basic Books.

Axelrod, R. & Hamilton, W. D. 1981 The evolution of cooperation. *Science* **211**, 1390–1396. (doi:10.1126/science.7466396)

Barrett, L. & Henzi, S. P. 2005 The social nature of primate cognition. *Proc. R. Soc. B* **272**, 1865–1875. (doi:10.1098/rspb.2005.3200)

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999 Market forces predict grooming reciprocity in female baboons. *Proc. R. Soc. Lond. B* **266**, 665–670. (doi:10.1098/rspb.1999.0687)

Bednarz, J. C. 1988 Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). *Science* **239**, 1525–1527. (doi:10.1126/science.239.4847.1525)

Beran, M. J. 2008 Capuchin monkeys (*Cebus apella*) succeed in a test of quantity conservation. *Anim. Cogn.* **11**, 109–116. (doi:10.1007/s10071-007-0094-3)

Berkes, F., Feeny, D., Mccay, B. J. & Acheson, J. M. 1989 The benefits of the commons. *Nature* **340**, 91–93. (doi:10.1038/340091a0)

Boesch, C. & Boesch, H. 1989 Hunting behavior of wild chimpanzees in the Taï National Park Ivory Coast. *Am. J. Phys. Anthropol.* **78**, 547–573. (doi:10.1002/ajpa.1330780410)

Bossema, I. & Benus, R. F. 1985 Territorial defence and intra-pair cooperation in the carrion crow (*Corvus corone*). *Behav. Ecol. Sociobiol.* **16**, 99–104. (doi:10.1007/BF00295141)

Bowles, S., Choi, J. K. & Hopfensitz, A. 2003 The co-evolution of individual behaviors and social institutions. *J. Theoret. Biol.* **223**, 135–147.

Boyd, R. & Richerson, P. J. 1992 Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.* **13**, 171–195. (doi:10.1016/0162-3095(92)90032-Y)

Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. 2003 The evolution of altruistic punishment. *Proc. Natl Acad. Sci. USA* **100**, 3531–3535. (doi:10.1073/pnas.0630443100)

Brockhurst, M. A., Buckling, A., Racey, D. & Gardner, A. 2008 Resource supply and the evolution of public-goods cooperation in bacteria. *BMC Biol.* **6**, 20. (doi:10.1186/1741-7007-6-20)

Brosnan, S. F. & de Waal, F. B. M. 2006 Partial support from a nonreplication: comment on Roma, Silberberg, Ruggiero, and Suomi (2006). *J. Comp. Psychol.* **120**, 74–75. (doi:10.1037/0735-7036.120.1.74)

Brosnan, S., Silk, J., Henrich, J., Mareno, M., Lambeth, S. & Schapiro, S. 2009 Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Anim. Cogn.* **12**, 587–597. (doi:10.1007/s10071-009-0218-z)

Brosnan, S. F., Salwiczek, L. & Bshary, R. 2010 The interplay of cognition and cooperation. *Phil. Trans. R. Soc. B* **365**, 2699–2710. (doi:10.1098/rstb.2010.0154)

Brotherton, P. N. M., Clutton-Brock, T. H., O'Riain, M. J., Gaynor, D., Sharpe, L., Kansky, R. & McIlrath, G. M. 2001 Offspring food allocation by parents and helpers in a cooperative mammal. *Behav. Ecol.* **12**, 590–599. (doi:10.1093/beheco/12.5.590)

Brown, S. P. 2001 Collective action in an RNA virus. *J. Evol. Biol.* **14**, 821–828. (doi:10.1046/j.1420-9101.2001.00317.x)

Brownell, C. A. & Carriger, M. S. 1990 Changes in cooperation and self-other differentiation during the second year. *Child Dev.* **61**, 1164–1174. (doi:10.2307/1130884)

Bshary, R. 2002 Biting cleaner fish use altruism to deceive image-scoring client reef fish. *Proc. R. Soc. Lond. B* **269**, 2087–2093. (doi:10.1098/rspb.2002.2084)

Bshary, R. & Bergmüller, R. 2008 Distinguishing four fundamental approaches to the evolution of helping. *J. Evol. Biol.* **21**, 405–420. (doi:10.1111/j.1420-9101.2007.01482.x)

Bshary, R. & Grutter, A. S. 2002 Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.* **63**, 547–555. (doi:10.1006/anbe.2001.1937)

Bshary, R. & Grutter, A. S. 2006 Image scoring and cooperation in a cleaner fish mutualism. *Nature* **441**, 975–978. (doi:10.1038/nature04755)

Bshary, R. & Noë, R. 2003 Biological markets: the ubiquitous influence of partner choice on the dynamics of cleaner fish–client reef fish interactions. In *Genetic and cultural evolution of cooperation* (ed. P. Hammerstein). Cambridge, MA: MIT Press.

Bshary, R. & Schäffer, D. 2002 Choosy reef fish select cleaner fish that provide high-quality service. *Anim. Behav.* **63**, 557–564. (doi:10.1006/anbe.2001.1923)

Bshary, R., Hohner, A., Ait-El-Djoudi, K. & Fricke, H. 2006 Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. *PLoS Biol.* **4**, 2393–2398.

Burkart, J. M., Hrdy, S. B. & van Schaik, C. P. 2009 Cooperative breeding and human cognitive evolution. *Evol. Anthropol.* **18**, 175–186. (doi:10.1002/evan.20222)

Call, J., Hare, B., Carpenter, M. & Tomasello, M. 2004 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Dev. Sci.* **7**, 488–498. (doi:10.1111/j.1467-7687.2004.00368.x)

Chalmeau, R. 1994 Do chimpanzees cooperate in a learning task? *Primates* **35**, 385–392. (doi:10.1007/BF02382735)

Clutton-Brock, T. 2009 Cooperation between non-kin in animal societies. *Nature* **462**, 51–57. (doi:10.1038/nature08366)

Clutton-Brock, T. H. & Parker, G. A. 1995 Punishment in animal societies. *Nature* **373**, 209–216. (doi:10.1038/373209a0)

Clutton-Brock, T. H. *et al.* 2001a Cooperation, control, and concession in meerkat groups. *Science* **291**, 478–481. (doi:10.1126/science.291.5503.478)

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., McIlrath, G. M., White, S. & Cameron, E. Z. 2001b Effects of helpers on juvenile development and survival in meerkats. *Science* **293**, 2446–2449. (doi:10.1126/science.1061274)

Connor, R. C. 1992 Egg-trading in simultaneous hermaphrodites: an alternative to tit-for-tat. *J. Evol. Biol.* **5**, 523–528. (doi:10.1046/j.1420-9101.1992.5030523.x)

Connor, R. C. 1996 Partner preferences in by-product mutualisms and the case of predator inspection in fish. *Anim. Behav.* **51**, 451–454. (doi:10.1006/anbe.1996.0042)

Connor, R. C. 2010 Cooperation beyond the dyad: on simple models and a complex society. *Phil. Trans. R. Soc. B* **365**, 2687–2697. (doi:10.1098/rstb.2010.0150)

Crawford, M. P. 1937 The cooperative solving of problems by young chimpanzees. *Comp. Psychol. Monogr.* **14**, 1–88.

Creel, S. & Creel, N. M. 1995 Communal hunting and pack size in African wild dogs, *Lycaon pictus. Anim. Behav.* **50**, 1325–1339. (doi:10.1016/0003-3472(95)80048-4)

Crespi, B. & Springer, S. 2003 Social slime molds meet their match. *Science* **299**, 56–57. (doi:10.1126/science.1080776)

Cronin, K. A., Kurian, A. V. & Snowdon, C. T. 2005 Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). *Anim. Behav.* **69**, 133–142. (doi:10.1016/j.anbehav.2004.02.024)

Dawes, R. M. 1980 Social dilemmas. *Annu. Rev. Psychol.* **31**, 169–193. (doi:10.1146/annurev.ps.31.020180.001125)

de Waal, F. B. M. 1997 The chimpanzee's service economy: food for grooming. *Evol. Hum. Behav.* **18**, 375–386.

de Waal, F. B. M. & Davis, J. M. 2003 Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia* **41**, 221–228.

de Waal, F. B. M. & Suchak, M. 2010 Prosocial primates: selfish and unselfish motivations. *Phil. Trans. R. Soc. B* **365**, 2711–2722. (doi:10.1098/rstb.2010.0119)

Drea, C. M. & Carter, A. N. 2009 Cooperative problem solving in a social carnivore. *Anim. Behav.* **78**, 967–977. (doi:10.1016/j.anbehav.2009.06.030)

Dreber, A., Rand, D. G., Fudenberg, D. & Nowak, M. A. 2008 Winners don't punish. *Nature* **452**, 348–351. (doi:10.1038/nature06723)

Dugatkin, L. A. 1997 *Cooperation among animals: an evolutionary perspective.* Oxford, UK: Oxford University Press.

Earley, R. L. 2010 Social eavesdropping and the evolution of conditional cooperation and cheating strategies. *Phil. Trans. R. Soc. B* **365**, 2675–2686. (doi:10.1098/rstb.2010.0147)

Fehr, E. & Fischbacher, U. 2004 Third-party punishment and social norms. *Evol. Hum. Behav.* **25**, 63–87. (doi:10.1016/S1090-5138(04)00005-4)

Fehr, E. & Gächter, S. 2000 Cooperation and punishment in public goods experiments. *Am. Econ. Rev.* **90**, 980–994.

Fehr, E. & Gächter, S. 2002 Altruistic punishment in humans. *Nature* **415**, 137–140. (doi:10.1038/415137a)

Ferriere, R., Bronstein, J. L., Rinaldi, S., Law, R. & Gauduchon, M. 2002 Cheating and the evolutionary stability of mutualisms. *Proc. R. Soc. Lond. B* **269**, 773–780. (doi:10.1098/rspb.2001.1900)

Fowler, J. H. 2005a Altruistic punishment and the origin of cooperation. *Proc. Natl Acad. Sci. USA* **102**, 7047–7049. (doi:10.1073/pnas.0500938102)

Fowler, J. H. 2005b Human cooperation—second-order free-riding problem solved? *Nature* **437**, E8. (doi:10.1038/nature04201)

Gächter, S., Herrmann, B. & Thöni, C. 2010 Culture and cooperation. *Phil. Trans. R. Soc. B* **365**, 2651–2661. (doi:10.1098/rstb.2010.0135)

Gazda, S. K., Connor, R. C., Edgar, R. K. & Cox, F. 2005 A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proc. R. Soc. B* **272**, 135–140. (doi:10.1098/rspb.2004.2937)

Geissmann, T. 2000 Duet songs of the Siamang, *Hylobates syndactylus*: I. Structure and organisation. *Primate Rep.* **56**, 33–60.

Gintis, H. 2000 Strong reciprocity and human sociality. *J. Theor. Biol.* **206**, 169–179. (doi:10.1006/jtbi.2000.2111)

Gomes, C. M., Mundry, R. & Boesch, C. 2009 Long-term reciprocation of grooming in wild West African chimpanzees. *Proc. R. Soc. B* **276**, 699–706. (doi:10.1098/rspb.2008.1324)

Gurek, O., Irlenbusch, B. & Rockenbach, B. 2006 The competitive advantage of sanctioning institutions. *Science* **312**, 108–111. (doi:10.1126/science.1123633)

Hamilton, W. D. 1964 Genetical evolution of social behaviour 2. *J. Theor. Biol.* **7**, 17–52. (doi:10.1016/0022-5193(64)90039-6)

Hammerstein, P. 2003 Why is reciprocity so rare in social animals? A protestant appeal. In *Genetic and cultural evolution of cooperation* (ed. P. Hammerstein), Cambridge, MA: MIT Press.

Hanus, D. & Call, J. 2007 Discrete quantity judgments in the great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus*): the effect of presenting whole sets versus item-by-item. *J. Comp. Psychol.* **121**, 227–240.

Hardin, G. 1968 The tragedy of the commons. *Science* **162**, 1243–1248. (doi:10.1126/science.162.3859.1243)

Hare, B. & Tomasello, M. 2005 The emotional reactivity hypothesis and cognitive evolution. *Trends Cogn. Sci.* **9**, 464–465. (doi:10.1016/j.tics.2005.08.010)

Hare, B. A., Melis, A. P., Woods, V., Hastings, S. & Wrangham, R. W. 2007 Tolerance allows bonobos to

outperform chimpanzees on a cooperative task. *Curr. Biol.* **17**, 619–623. (doi:10.1016/j.cub.2007.02.040)

Hart, B. L. & Hart, L. A. 1992 Reciprocal allogrooming in impala, *Aepyceros melampus*. *Anim. Behav.* **44**, 1073–1083. (doi:10.1016/S0003-3472(05)80319-7)

Hattori, Y., Kuroshima, H. & Fujita, K. 2005 Cooperative problem solving by tufted capuchin monkeys (*Cebus apella*): spontaneous division of labor, communication, and reciprocal altruism. *J. Comp. Psychol.* **119**, 335–342. (doi:10.1037/0735-7036.119.3.335)

Hauert, C., De Monte, S., Hofbauer, J. & Sigmund, K. 2002 Replicator dynamics for optional public good games. *J. Theor. Biol.* **218**, 187–194. (doi:10.1006/jtbi.2002.3067)

Hauser, M. D. 1992 Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proc. Natl Acad. Sci. USA* **89**, 12137–12139. (doi:10.1073/pnas.89.24.12137)

Hauser, M. D. & Marler, P. 1993 Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behav. Ecol.* **4**, 194–205. (doi:10.1093/beheco/4.3.194)

Hauser, M., McAuliffe, K. & Blake, P. R. 2009 Evolving the ingredients for reciprocity and spite. *Phil. Trans. R. Soc. B* **364**, 3255–3266. (doi:10.1098/rstb.2009.0116)

Heinsohn, R. & Packer, C. 1995 Complex cooperative strategies in group-territorial African lions. *Science* **269**, 1260–1262. (doi:10.1126/science.7652573)

Hirata, S. & Fuwa, K. 2007 Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates* **48**, 13–21. (doi:10.1007/s10329-006-0022-1)

Hrdy, S. B. 2009 Meet the alloparents. *Nat. Hist.* **118**, 24–29.

Jensen, K. 2007 Other-regarding preferences in chimpanzees. Dr. rer. nat. dissertation, Humboldt-Universität, Berlin, Germany.

Jensen, K. 2010 Punishment and spite, the dark side of cooperation. *Phil. Trans. R. Soc. B* **365**, 2635–2650. (doi:10.1098/rstb.2010.0146)

Kappeler, P. M. & van Schaik, C. P. 2006 *Cooperation in primates and humans: mechanisms and evolution.* Berlin, Germany: Springer-Verlag.

Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* **268**, 187–196. (doi:10.1098/rspb.2000.1349)

Koyama, N. F., Caws, C. & Aureli, F. 2006 Interchange of grooming and agonistic support in chimpanzees. *Int. J. Primatol.* **27**, 1293–1309. (doi:10.1007/s10764-006-9074-8)

Kuemmerli, R., Colliard, C., Fiechter, N., Petitpierre, B., Russier, F. & Keller, L. 2007 Human cooperation in social dilemmas: comparing the Snowdrift game with the Prisoner's Dilemma. *Proc. R. Soc. B* **274**, 2965–2970. (doi:10.1098/rspb.2007.0793)

Kuzdzal-Fick, J. J., Foster, K. R., Queller, D. C. & Strassmann, J. E. 2007 Exploiting new terrain: an advantage to sociality in the slime mold *Dictyostelium discoideum*. *Behav. Ecol.* **18**, 433–437. (doi:10.1093/beheco/arl102)

Lamprecht, J. 1978 Diet, foraging behavior and interspecific food competition of jackals in Serengeti-National-Park, East-Africa. *Z. Saugetierkd.* **43**, 210–223.

Langergraber, K. E., Mitani, J. C. C. & Vigilant, L. 2007 The limited impact of kinship on cooperation in wild chimpanzees. *Proc. Natl Acad. Sci. USA* **104**, 7786–7790. (doi:10.1073/pnas.0611449104)

Lau, G., Moulds, M. L. & Richardson, R. 2009 Ostracism: how much it hurts depends on how you remember it. *Emotion* **9**, 430–434. (doi:10.1037/a0015350)

Ledyard, J. O. 1995 Public goods: a survey of experimental research. In *Handbook of Experimental Economics* (eds J. H. Kagel & A. E. Roth). Princeton, NJ: Princeton University Press.

Leimar, O. & Connor, R. C. 2003 By-product benefits, reciprocity, and pseudoreciprocity in mutualism. In *Genetic and cultural evolution of cooperation* (ed. P. Hammerstein), pp. 203–222. Cambridge, MA: MIT Press.

Leimar, O. & Hammerstein, P. 2001 Evolution of cooperation through indirect reciprocity. *Proc. R. Soc. Lond. B* **268**, 745–753. (doi:10.1098/rspb.2000.1573)

Leimar, O. & Hammerstein, P. 2010 Cooperation for direct fitness benefits. *Phil. Trans. R. Soc. B* **365**, 2619–2626. (doi:10.1098/rstb.2010.0116)

Magrath, R. D., Pitcher, B. J. & Dalziell, A. H. 2007 How to be fed but not eaten: nestling responses to parental food calls and the sound of a predator's footsteps. *Anim. Behav.* **74**, 1117–1129. (doi:10.1016/j.anbehav.2007.01.025)

McCusker, C. & Carnevale, P. J. 1995 Framing in resource dilemmas—loss aversion and the moderating effects of sanctions. *Organ. Behav. Hum. Decis. Process.* **61**, 190–201. (doi:10.1006/obhd.1995.1015)

Melis, A. P., Hare, B. & Tomasello, M. 2006a Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Anim. Behav.* **72**, 275–286. (doi:10.1016/j.anbehav.2005.09.018)

Melis, A. P., Hare, B. & Tomasello, M. 2006b Chimpanzees recruit the best collaborators. *Science* **311**, 1297–1300. (doi:10.1126/science.1123007)

Melis, A. P., Hare, B. & Tomasello, M. 2008 Do chimpanzees reciprocate received favours? *Anim. Behav.* **76**, 951–962. (doi:10.1016/j.anbehav.2008.05.014)

Melis, A. P., Hare, B. & Tomasello, M. 2009 Chimpanzees coordinate in a negotiation game. *Evol. Hum. Behav.* **30**, 381–392. (doi:10.1016/j.evolhumbehav.2009.05.003)

Melis, A. P., Warneken, F. & Hare, B. In press. *Collaboration and helping in chimpanzees. The mind of the chimpanzee: ecological and experimental perspectives.* Chicago, IL: University of Chicago Press.

Melis, A. P., Warneken, F., Jensen, K., Schneider, A., Call, J. & Thomasello, M. Submitted. Chimpanzees help conspecifics to obtain food and non-food items.

Mendres, K. A. & de Waal, F. B. M. 2000 Capuchins do cooperate: the advantage of an intuitive task. *Anim. Behav.* **60**, 523–529. (doi:10.1006/anbe.2000.1512)

Milinski, M. 1990 No alternative to tit-for-tat cooperation in sticklebacks. *Anim. Behav.* **39**, 989–991. (doi:10.1016/S0003-3472(05)80966-2)

Milinski, M., Semmann, D., Bakker, T. C. M. & Krambeck, H. J. 2001 Cooperation through indirect reciprocity: image scoring or standing strategy? *Proc. R. Soc. Lond. B* **268**, 2495–2501. (doi:10.1098/rspb.2001.1809)

Milinski, M., Semmann, D. & Krambeck, H. J. 2002a Donors to charity gain in both indirect reciprocity and political reputation. *Proc. R. Soc. Lond. B* **269**, 881–883. (doi:10.1098/rspb.2002.1964)

Milinski, M., Semmann, D. & Krambeck, H. J. 2002b Reputation helps solve the 'tragedy of the commons'. *Nature* **415**, 424–426. (doi:10.1038/415424a)

Mitani, J. C. C. 2006 Demographic influences on the behavior of chimpanzees. *Primates* **47**, 6–13. (doi:10.1007/s10329-005-0139-7)

Nakamaru, M. & Kawata, M. 2004 Evolution of rumours that discriminate lying defectors. *Evol. Ecol. Res.* **6**, 261–283.

Noë, R. & Hammerstein, P. 1994 Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**, 1–11. (doi:10.1007/BF00167053)

Nowak, M. A. & Sigmund, K. 1998 Evolution of indirect reciprocity by image scoring. *Nature* **393**, 573–577. (doi:10.1038/31225)

Nowak, M. A. & Sigmund, K. 2005 Evolution of indirect reciprocity. *Nature* **437**, 1291–1298. (doi:10.1038/nature04131)

Nunn, C. L. 2000 Collective benefits, free-riders, and male extra-group conflict. In *Primate males: causes and consequences of variation in group composition* (ed. P. M. Kappeler), pp. 192–204. Cambridge, UK: Cambridge University Press.

Nunn, C. L. & Lewis, R. J. (eds) 2001 *Cooperation and collective action in animal behavior*. Cambridge, UK: Cambridge University Press.

Ostrom, E., Burger, J., Field, C. B., Norgaard, R. B. & Policansky, D. 1999 Sustainability—revisiting the commons: local lessons, global challenges. *Science* **284**, 278–282.

Panchanathan, K. & Boyd, R. 2003 A tale of two defectors: the importance of standing for evolution of indirect reciprocity. *J. Theor. Biol.* **224**, 115–126. (doi:10.1016/S0022-5193(03)00154-1)

Petit, O., Desportes, C. & Thierry, B. 1992 Differential probability of 'coproduction' in two species of macaque (*Macaca tonkeana*, *M. mulatta*). *Ethology* **90**, 107–120. (doi:10.1111/j.1439-0310.1992.tb00825.x)

Queller, D. C. & Strassmann, J. E. 2009 Beyond society: the evolution of organismality. *Phil. Trans. R. Soc. B* **364**, 3143–3155. (doi:10.1098/rstb.2009.0095)

Raihani, N. J., Grutter, A. S. & Bshary, R. 2010 Punishers benefit from third-party punishment in fish. *Science* **327**, 171. (doi:10.1126/science.1183068)

Rand, D. G., Ohtsuki, H. & Nowak, M. A. 2009 Direct reciprocity with costly punishment: generous tit-for-tat prevails. *J. Theor. Biol.* **256**, 45–57. (doi:10.1016/j.jtbi.2008.09.015)

Roberts, G. 1998 Competitive altruism: from reciprocity to the handicap principle. *Proc. R. Soc. Lond. B* **265**, 427–431. (doi:10.1098/rspb.1998.0312)

Roberts, G. 2005 Cooperation through interdependence. *Anim. Behav.* **70**, 901–908. (doi:10.1016/j.anbehav.2005.02.006)

Rockenbach, B. & Milinski, M. 2006 The efficient interaction of indirect reciprocity and costly punishment. *Nature* **444**, 718–723. (doi:10.1038/nature05229)

Rosati, A. G., Stevens, J. R., Hare, B. & Hauser, M. D. 2007 The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr. Biol.* **17**, 1663–1668. (doi:10.1016/j.cub.2007.08.033)

Russell, Y. I., Call, J. & Dunbar, R. I. M. 2008 Image scoring in great apes. *Behav. Process.* **78**, 108–111.

Sachs, J. L. & Bull, J. J. 2005 Experimental evolution of conflict mediation between genomes. *Proc. Natl Acad. Sci. USA* **102**, 390–395. (doi:10.1073/pnas.0405738102)

Schino, G. & Aureli, F. 2009 Reciprocal altruism in primates: partner choice, cognition, and emotions. In *Advances in the study of behavior*, vol. 39 (eds H. J. Brockmann, C. T. Snowdon, T. J. Roper, M. Naguib & K. E. Wynne-Edwards). New York, NY: Academic Press.

Schino, G. & Aureli, F. 2010 The relative roles of kinship and reciprocity in explaining primate altruism. *Ecol. Lett.* **13**, 45–50. (doi:10.1111/j.1461-0248.2009.01396.x)

Seed, A. M., Clayton, N. S. & Emery, N. J. 2008 Cooperative problem solving in rooks (*Corvus frugilegus*). *Proc. R. Soc. B* **275**, 1421–1429. (doi:10.1098/rspb.2008.0111)

Semmann, D., Krambeck, H. J. & Milinski, M. 2003 Volunteering leads to rock-paper-scissors dynamics in a public goods game. *Nature* **425**, 390–393. (doi:10.1038/nature01986)

Semmann, D., Krambeck, H. J. & Milinski, M. 2004 Strategic investment in reputation. *Behav. Ecol. Sociobiol.* **56**, 248–252.

Seyfarth, R. M. & Cheney, D. L. 1988 Empirical tests of reciprocity theory: problems in assessment. *Ethol. Sociobiol.* **9**, 181–187. (doi:10.1016/0162-3095(88)90020-9)

Silk, J. B. 2007 Chimps don't just get mad, they get even. *Proc. Natl Acad. Sci. USA* **104**, 13537–13538. (doi:10.1073/pnas.0706166104)

Solomon, N. & French, J. 1997 *Cooperative breeding in mammals*. Cambridge, UK: Cambridge University Press.

Sommerfeld, R. D., Krambeck, H. J., Semmann, D. & Milinski, M. 2007 Gossip as an alternative for direct observation in games of indirect reciprocity. *Proc. Natl Acad. Sci. USA* **104**, 17 435–17 440. (doi:10.1073/pnas.0704598104)

Sommerfeld, R. D., Krambeck, H. J. & Milinski, M. 2008 Multiple gossip statements and their effect on reputation and trustworthiness. *Proc. R. Soc. B* **275**, 2529–2536. (doi:10.1098/rspb.2008.0762)

Stander, P. E. 1992 Cooperative hunting in lions: the role of the individual. *Behav. Ecol. Sociobiol.* **29**, 445–454.

Stevens, J. R. & Hauser, M. D. 2004 Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn. Sci.* **8**, 60–65. (doi:10.1016/j.tics.2003.12.003)

Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005 Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* **28**, 675–735.

Trivers, R. L. 1971 The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57.

van Schaik, C. P. & Kappeler, P. M. 1996 The social systems of gregarious lemurs: lack of convergence due to evolutionary disequilibrium? *Ethology* **102**, 915–941.

Velicer, G. J. & Yu, Y. T. N. 2003 Evolution of novel cooperative swarming in the bacterium *Myxococcus xanthus*. *Nature* **425**, 75–78. (doi:10.1038/nature01908)

Visalberghi, E., Quarantotti, B. P. & Tranchida, F. 2000 Solving a cooperation task without taking into account the partner's behavior: the case of capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* **114**, 297–301. (doi:10.1037/0735-7036.114.3.297)

Warneken, F. & Tomasello, M. 2006 Altruistic helping in human infants and young chimpanzees. *Science* **311**, 1301–1303. (doi:10.1126/science.1121448)

Warneken, F., Chen, F. & Tomasello, M. 2006 Cooperative activities in young children and chimpanzees. *Child Dev.* **77**, 640–663. (doi:10.1111/j.1467-8624.2006.00895.x)

Warneken, F., Hare, B., Melis, A. P., Hanus, D. & Tomasello, M. 2007 Spontaneous altruism by chimpanzees and young children. *PLoS Biol.* **5**, e184. (doi:10.1371/journal.pbio.0050184)

Watts, D. P. 2002 Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* **139**, 343–370. (doi:10.1163/156853902760102708)

West, S. A., Gardner, A. & Griffin, A. S. 2006 Altruism. *Curr. Biol.* **16**, R482–R483. (doi:10.1016/j.cub.2006.06.014)

West, S. A., Griffin, A. S. & Gardner, A. 2007 Evolutionary explanations for cooperation. *Curr. Biol.* **17**, R661–R672. (doi:10.1016/j.cub.2007.06.004)

Wilson, D. S. & Wilson, E. O. 2007 Rethinking the theoretical foundation of sociobiology. *Q. Rev. Biol.* **82**, 327–348.

Yamagishi, T. 1988 Seriousness of social dilemmas and the provision of a sanctioning system. *Soc. Psychol. Q.* **51**, 32–42. (doi:10.2307/2786982)

Yamamoto, S. & Tanaka, M. 2009 Do chimpanzees (*Pan troglodytes*) spontaneously take turns in a reciprocal cooperation task? *J. Comp. Psychol.* **123**, 242–249. (doi:10.1037/a0015838)

Yamamoto, S., Humle, T. & Tanaka, M. 2009 Chimpanzees help each other upon request. *PLoS ONE* **4**, e7416. (doi:10.1371/journal.pone.0007416)