

# Cooperation in primates and humans: closing the gap

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### 1.1 Why does cooperation pose a challenge?

In common usage, we speak of cooperation if individuals actively assist or support others: the emphasis is on behavior. For evolutionary biologists, cooperation involves actions or traits that benefit other individuals. They stress the outcomes of these behaviors, in particular the consequences for the fitness of the interacting individuals. Cooperative acts that are beneficial for both actor and recipient are said to be mutualistic. A cooperative act that is costly to the actor is termed altruistic; if the recipient is a relative, the interaction is sometimes called nepotistic<sup>1</sup>. The behavioral definition and the outcome-based definition usually label the same phenomena cooperative.

Cooperation has been described at all levels of biological organization, from molecules, organelles and cells, to individuals or groups of the same species and even individuals of different species (Hammerstein 2003b). The contributions to this volume focus on cooperation in the form of behavioral interactions between individuals, largely within species. This kind of cooperation can be manifested through single behavioral acts, such as giving an alarm call or providing a conspecific with agonistic support, but also through long-term behavioral tactics or roles, such as helping relatives raise their offspring, or even through organismal adaptations, such as renouncing reproductive activity. Frequently encountered examples of cooperative behaviors in nature are coalition formation, the exchange of grooming or other forms of body care, alarm calling, predator inspection, protection against attacks by predators or conspecifics, supporting injured group members, helping in the reproduction of others (cooperative breeding), egg trading among hermaphrodites, nursing of other females' infants, communal defense of food sources or territory boundaries, interactions between neighboring territory owners, sharing of special skills or information, food sharing and cooperative hunting (see Dugatkin 1997, Clutton-Brock 2002).

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<sup>1</sup> Note that we adhere to a broad definition of cooperation, in that both actor and recipient or only the recipient can benefit. The narrow definition requires the presence of altruistic acts, i.e. only the recipient benefits. We prefer the broad definition because it may be extremely difficult in practice to determine whether some action is altruistic; it includes mutualism, and it complies more closely with common usage.

As indicated by these examples, cooperative acts come in a myriad of forms. Nevertheless, they all share a central problem: the vulnerability of the cooperator to being exploited by selfish partners. Opportunities for exploitation come in two main forms, depending on the context of cooperation. First, they may arise due to the time delay inherent in reciprocity. When altruistic acts are exchanged reciprocally between members of a dyad, the partner who benefited from an earlier altruistic act can defect, either by renegeing when his turn arises, or by returning less than he received. The second opportunity for exploitation is free riding, which arises when an individual does not (equally) contribute to the creation or maintenance of a shareable benefit or good (this can happen at the level of the dyad or at that of the group, in which case the benefit is called a public good). An additional threat to evolutionary stability of cooperation is risk-avoidance in mutualism. It arises when a mutualistic benefit can only be produced through some costly collective action by two or more partners, and one individual bows out at the moment of the dangerous collective action, thereby exposing the partner(s) to considerable risk of injury (see van Schaik, this volume). Agonistic coalitions or cooperative hunting of dangerous prey provide exemplary contexts for such risk. These three problems make cooperation less likely in nature. In some cases, such as high-risk altruistic support in agonistic conflicts or high-risk collective action, where opportunities for exploitation go hand in hand with risk avoidance, cooperation may be particularly unlikely or unstable.

However, cooperation is rife in nature, and an explanation for its origin and maintenance is therefore needed. Consequently, it has been the focus of much empirical and theoretical work for over a century. In the first section of this introductory chapter, we provide a brief overview of the history of the study of cooperation, from Darwin to the mid-1990s, for novices to the field. Although much progress has been made, this work has not led to a definitive solution of the cooperation problem. Nonetheless, much contemporary research on cooperation is building on three pillars of earlier efforts, namely nepotism, reciprocity and mutualism. We revisit these three pillars in the next section, which also serves as an overview of the contributions to this volume. However, it should not be forgotten that these explanatory models focus on selected acts of cooperation, and that animals in nature may be involved in multiple forms of cooperation with the same partners simultaneously.

A major rationale for this book is that an explosion of recent work on humans has done much to highlight the contrasts in cooperative behavior between humans and other animals, in particular great apes. In the next section of this introduction, we therefore explore the major differences and preview the chapters that focus on humans. We also address the important question as to why human cooperation became so fundamentally different from that among all other primates and non-eusocial animals. We close this chapter by drawing attention to some unresolved questions, in particular with respect to work on non-human primates.

## 1.2

### Cooperation: a brief history of the main ideas

The struggle for life and the survival of the fittest are concepts that emerged from Darwin's (1859) reasoning that led him to identify natural selection as the agent responsible for adaptations. Accordingly, individuals who out-compete their conspecifics in the struggle for access to resources and mates enjoy greater reproductive success and, hence, pass on more copies of their genes to the next generation. Thus, competition naturally emerged as the main concept in explaining many aspects of organismal adaptation in evolutionary biology. Against this background, it is particularly difficult to explain the existence of behaviors that benefit others at the expense of the ego. Darwin was well aware that such cooperative acts do occur in nature at different levels, in different forms, and with different consequences for the actors involved, and he clearly recognized that altruistic behaviors presented 'a special difficulty', potentially fatal to his whole theory of natural selection. All subsequent work on the evolution of cooperation has focused on identifying the conditions under which altruistic acts can be evolutionarily stable against exploitation (see Dugatkin 1997).

Kropotkin (1902) re-affirmed the importance of cooperation in nature. He dealt with the defection problem, albeit implicitly, by relying on group selection or its even more improbable cousin, species selection, to explain all cooperative behavior in nature. Moreover, many of his examples would nowadays be ascribed to byproduct mutualism (see below).

Group selection continued to be invoked as an explanatory device for cooperation throughout the first half of the 20th century by influential scholars, such as Allee (1938, 1951), and later most explicitly Wynne-Edwards (1962). It was the rejection of group selection, inspired by Wynne-Edwards's book, more than any other development that pushed evolutionary and behavioral biologists who rejected group selection to systematically search for explanations for seemingly altruistic behaviors in nature (Hamilton 1963, 1964, Maynard Smith 1964, Williams 1966). By the early 1970s, these biologists had responded to this challenge by erecting two major explanatory frameworks to explain this kind of vulnerable cooperative behavior: kin selection and reciprocity (Hamilton 1964, Trivers 1971).

For ultimate explanations of altruism, the most fundamental distinction is that between interactions between either related or unrelated individuals. As first pointed out by Hamilton (1964), kin selection theory can provide a potent explanation for nepotistic behavior. Because a disposition to help close relatives will automatically enhance the propagation of genes in other individuals that are identical by descent from a common ancestor, the benefits of altruistic acts (B) towards relatives also accrue to the actor, discounted by the degree of relatedness,  $r$ , between the two, i.e. the probability that they share the same allele through descent from a common ancestor. This makes altruistic acts, with cost C, more likely to evolve between relatives, as expressed in Hamilton's now famous inequality  $Br > C$ .

The explanation of altruistic acts directed at unrelated individuals requires a different approach. Trivers (1971) offered the groundbreaking idea that re-

ciprocal altruism, now generally called reciprocity, in which two individuals alternate between providing and obtaining benefits, can provide a simple, but sufficient evolutionary mechanism for many cases of cooperation between unrelated individuals. He suggested that reciprocity is especially common among long-lived animals, because they have more opportunities to exchange altruistic acts. Moreover, reciprocity should flourish in species that live in stable groups in which individuals recognize each other, as well as in species characterized by social tolerance, because dominants do not prevent others from reciprocating. In his contribution to this volume, Trivers reviews the evidence for reciprocal altruism that has accumulated over the last three decades.

Reciprocity differs from mutualism by the presence of a time delay between incurring the cost of the altruistic act and receiving the benefit when the partner reciprocates. As the duration of the time delay approaches zero, reciprocity grades into mutualism (e.g. Rothstein & Pierotti 1988). Thus, a discrete time delay is usually considered necessary before reciprocity needs to be invoked. However, as it gets longer, discounting of the benefits should make it harder for reciprocity to be stable (Stephens et al. 2002).

Reciprocity “may be the most perplexing and difficult category of cooperation to explain” (Dugatkin 1997). Accordingly, Trivers’s idea has been explored in great detail (Trivers, this volume). Most tests have used the formal similarity of the problem to that modeled by the two-person Prisoner’s Dilemma (PD) game developed in game theory (Axelrod & Hamilton 1981). The ESS (evolutionarily stable strategy; Maynard Smith 1982) solution to the one-shot PD game is to defect, but examination of the situation in which players interact again in the future suggested that cooperation could be robust (Axelrod & Hamilton 1981). In particular, a strategy called ‘Tit-for-tat’, which starts out as a cooperator and then simply repeats the move of the other player in the previous round, provided a robust solution in that it was never exploited by other strategies and produced high payoffs when paired with other cooperative strategies. Dissatisfaction with the lack of biological reality of this approach has spawned the development of the biological markets framework, in which the choice of partners and communication receive special attention (Noë et al. 1991, Noë & Hammerstein 1994, see below).

Kin selection and reciprocity remain the most important explanations for altruistic acts by animals, and for cooperation in general, to this day. However, more recently, a new and improved form of group selection, called trait-group, intrademic or multi-level selection, has been added to our explanatory arsenal (Wilson 1983, Sober & Wilson 1998). A trait group comprises all individuals that affect each other’s fitness. Natural selection operates both within and between such trait groups. If groups with more cooperators out-produce other groups, cooperation can be favored by between-group selection, but only if this effect is greater than the result of within-group selection, which acts against cooperators. This approach did not acquire a great following, however, although it can be argued that selective association of cooperating dyads within a larger group (as in many primate groups) is equivalent to the formation of trait-groups.

A separate strand of thought drew attention to the possibility that we may misinterpret much animal behavior and see altruistic acts where none exist.

Thus, some of what is labeled as reciprocity may in fact represent byproduct mutualism (Dugatkin 1997). In such cases, one animal benefits from what a second animal is doing but would also be doing in the absence of the first animal. One good example is the phenomenon of group augmentation, where animals directly benefit from being in a group, and are therefore expected to coordinate their behavior (Kokko et al. 2001). The behavioral definition of cooperation excludes such byproduct mutualism from cooperation, because we cannot observe any special cooperative acts, even if the animals coordinate or synchronize their activities (cf. Clutton-Brock 2002). Usually, byproduct mutualism is easily distinguished based on this definition, but there are some cases that look deceptively like true cooperation. In several species of fish, piercing the skin, for example due to predator attack, causes the release of a compound ('Schreckstoff') that elicits alarm in other fishes. However, the compound has its own immediate function in protecting the fish against fungal infection, and its production is therefore not altruistic (Magurran et al. 1996).

A variation on this theme is that seemingly altruistic acts, such as grooming another individual or giving an alarm call, are not altruistic at all because they impose no costs on the actor or may even carry an immediate benefit (e.g. Dunbar & Sharman 1984). Thus, such interactions are in effect mutualistic. However, even if they are, this does not mean that there is nothing left to study; even in mutualistic interactions, there may be plenty of opportunities for conflict or asymmetric distribution of benefits. Moreover, the presence of undeniable examples of truly altruistic acts (e.g. risky alarm calls: Sherman 1977; blood donation: Wilkinson 1984; predator mobbing: e.g. van Schaik et al. 1983) suggests that this alternative cannot explain all forms and examples of cooperation.

Finally, individuals may be coerced into cooperative behavior. For instance, breeders may force younger relatives into helping them raise more young (Emlen & Wrege 1992), dominants may force subordinates into providing services (Teblich et al. 1996) or group members may harass owners of food into food sharing (Stephens & Gilby 2004). However, the conditions under which such coercion leads to stable cooperation are probably quite restrictive (Kokko et al. 2001), so that cooperation for these reasons is probably rare.

## 1.3

### The pillars of cooperation

#### 1.3.1

##### Kin selection

Hamilton's (1964) fundamental insight was that altruistic behaviors could be explained evolutionarily if we focus on the gene rather than the individual as the unit of selection. Theoreticians have repeatedly re-evaluated Hamilton's rule by making the genetic assumptions increasingly explicit and realistic. Perhaps surprisingly, this very simple rule was found to hold up fairly well under such close scrutiny (Michod 1982). Empirically, as reviewed by Silk (this volume), many of the cooperative and altruistic acts performed by animals, including non-human

and human primates, are directed towards relatives, and thus potentially best explained by kin selection (see also Griffin & West 2002). Silk also demonstrates for non-human primates that alternative explanations of behavior, or theoretical objections to preferential association by kin, do not obviate the need for kin selection.

Although many phenomena in animal behavior can be adequately explained by nepotism, this does not mean that all interactions between kin are nepotistic (West et al. 2002). Nor does it mean that all cooperation among kin is necessarily nepotism (unilateral altruism); kin also engage in mutualistic cooperation or in reciprocity (Clutton-Brock, this volume). The reason that this simple fact is often overlooked is that mutualism and reciprocity are often studied explicitly among non-kin in order to control for nepotism. Indeed, as stressed by both Silk (this volume) and Chapais (this volume), other forms of cooperation may also be more common among kin, because relatives tend to be available as partners, cooperation with relatives produces additional inclusive fitness benefits, and because kinship may act to stabilize mutualistic and reciprocal actions because it reduces the benefits of defection (cf. Wrangham 1982). Thus, reciprocity and risky mutualism may well have originated among kin and provided the lineage with the basic behavioral and emotional mechanisms, which were then in place to be applied to the same acts with non-kin. However, Chapais (this volume) warns that kin-biased cooperation may be less common than this argument suggests because only non-relatives may be competent partners for particular kinds of cooperation, for example agonistic coalitions.

Kin selection may also contribute to a deeper understanding of altruistic phenomena typically examined from other angles. For example, kin selection may be a critical component of reproductive skew theory, which, using different models, attempts to explain why reproduction is not equally distributed among the members of a social unit (Johnstone 2000). The concession model posits that moderate reproductive skew is the result of dominants granting some reproduction to subordinates. Genetic relatedness is a crucial variable when it comes to predicting which individuals should be granted which share of total reproduction. The most important prediction of the concession model is that high relatedness among the members of a social unit should produce high reproductive skew (Keller & Reeve 1994). Forfeiting individual reproduction in favor of a close relative could be interpreted as altruistic behavior. Such high reproductive skew is indeed found among related males in coalitions of lions or howler monkeys: the top-ranking male monopolizes all or most of the reproduction (Pope 1990, Packer & Pusey 1991, see also Cooney & Bennet 2000). However, viable alternative explanations for reproductive skew exist that do not involve concessions and do not make this prediction (Clutton-Brock 1998a, Johnstone 2000).

Kin may make the best collaborators, but at the same time they are the worst possible mates because incest carries a high risk of leading to deleterious effects (Keller & Waller 2002). Inbreeding avoidance is now known to be widespread and underlies sex differences in dispersal (Clutton-Brock 1989a, Lehmann & Perrin 2003). Sex-linked dispersal, in turn, may strongly affect the degree to which members of the dispersing sex remain spatially associated (e.g. Vigilant et al. 2001, Fredsted et al. 2004), the critical precondition for cooperation in all species

but humans. The fact that mating with kin is to be avoided has imposed clear limitations on the reach of kin selection. Due to the modest fecundity of most individual birds and mammals, the number of relatives that can be clustered in space is rather small, especially if they subsequently mate with non-relatives and relatedness is diluted again. More obviously, inbreeding avoidance and sex-biased dispersal explain the rarity of strong intersexual kin-based cooperation (again with the exception of humans; cf. Rodseth et al. 2003). The exceptions to this rule among animals may be found where the stability provided to cooperative interactions by kinship is extremely important (Clutton-Brock, this volume).

### 1.3.2

#### Reciprocity

The debate on reciprocity over the past quarter century has been dominated by the two-player PD model, in both its one-shot and iterated versions (see above). This model assumes that defection in a one-shot game is the ESS, and efforts focus on overcoming this tendency to defect. Increasingly sophisticated mathematical models have been developed in increasingly fine and arcane detail to explore the conditions and consequences of reciprocity in this model (reviewed by Dugatkin 1997). However, Noë (1990, 1992) and Hammerstein (2003b), among others, have questioned the extent to which the PD adequately describes the situation in mobile organisms from fishes to primates (but see Trivers, this volume). In the words of Hammerstein (2003b), “some theoretical ideas appear to be so compelling that the lack of supporting evidence is indulged by major parts of the scientific community”.

The main reason for this criticism is that animals in nature only rarely seem to engage in repeated PD games. The PD model focuses only on one component, partner control (decisions for future interactions based on outcomes of previous interactions), whereas there are additional important components of cooperative relationships among animals: partner selection and communication about willingness to undertake a cooperative interaction or about payoff distribution. Partner choice, for example in the form of switching to another partner when the current partner defected, allows for selective association of trustworthy players. The notion of partner choice naturally leads to consideration of the role of other potential partners available to the players, and hence to the idea of cooperation markets, where partners select the most profitable partners and the value of commodities or services depends on their relative demand and supply. Biological market theory (Noë et al. 1991, Noë & Hammerstein 1994, see Noë, this volume) therefore contributes to developing a broader alternative in general, and it provides a powerful explanatory tool for the understanding of primate social behavior, in particular (Barrett & Henzi, this volume).

Likewise, communication about the intentions of each player before the interactions and negotiation with them about payoffs is likely to make reciprocity much more stable than under the conditions of PD games. Thus, communication before engaging in risky cooperation is frequently observed in primates (Smuts & Watanabe 1990, Noë 1992). Subtle communication may also take place about the price of a service. For instance, in the grooming market of primates, dis-

cussed in detail by Barrett & Henzi (this volume), females must groom longer to get access to desirable infants of other females when there are fewer infants in the group, and the price is set by the refusal of mothers to provide access to the infants after shorter grooming bouts (R. Noë & T. Weingrill pers. com.).

Cooperation in nature offers a paradox. Lots of (unrelated) animals seem to engage in cooperation, yet only quite rarely do we see them engage in contingency-based reciprocity (Noë 1990, Hammerstein 2003b), even though experiments indicate that they are capable of it (Hemelrijk 1994). There may be two main reasons for this discrepancy. The first reason is still largely speculative. Animals in stable social units can use their previous experience with any of the group members to make decisions about whether to cooperate in the future, and thus engage in generalized reciprocity. This cognitively non-demanding behavioral rule is theoretically most likely in small groups (Pfeiffer et al., in press), and has been demonstrated experimentally (Rutte & Taborsky, in review), but it is not known how important this mechanism is in nature.

The second reason for the absence of contingency in cooperation that involves altruistic acts is well established. Pairs (dyads) of cooperating animals seem to be concerned with costs and benefits on a much longer time scale than that of the interaction; they form social relationships, such as bonds or friendships, within which a broad range of cooperative acts is usually exchanged. Thus, in addition to altruistic acts of the same kind, as envisaged by reciprocity, they also exchange altruistic acts of different kinds, for example grooming for support in agonistic conflicts (see Mitani, this volume) and various kinds of mutualism and perhaps byproduct mutualism. Individuals in a bond do not evaluate the immediate costs and benefits of their behavioral decisions, as demanded by the theory of reciprocal altruism, but rather evaluate the long-term balance of the benefits and costs of all the acts exchanged in the relationship (cf. Pusey & Packer 1997).

The presence of these bonds is well documented in primates (Cheney et al. 1986), and recent work has shown that bonds have a positive impact on fitness, even after controlling for rank effects (Silk et al. 2003). Similar observations are available for friendships in humans. Aureli & Schaffner (this volume) note that these bonds, because of the important benefits they provide to both partners (cf. van Schaik & Aureli 2000), must be protected against the negative impacts of conflicts. It is important to remember that animals in every cooperative relationship also encounter many opportunities for conflict, and thus face the challenge of maintaining their relationship, with the net benefits it brings, in the face of the potentially disruptive effects of these conflicts. This threat to the relationship explains the ubiquity of reconciliation in primates and other social animals (Aureli & Schaffner, this volume).

Because so many altruistic acts and commodities are exchanged in these relationships, it is difficult to imagine that the players can maintain careful score cards on these actions, let alone on the costs and benefits they entail. Animals and even humans usually seem to cooperate without carefully calculating the costs and benefits of each act. This perspective also reduces the concern about the cognitive demands of engaging in reciprocity (Dugatkin 2002a, Hammerstein 2003b, Stevens & Hauser 2004). As detailed by de Waal & Brosnan (this vol-



ume), most cooperating dyads in most species use emotion-based mechanisms involving attitudinal symmetries that are cognitively simple. Chimpanzees are capable of the ‘calculated reciprocity’ required by reciprocity models, as obviously are humans, but this mechanism may be rare among other species, if it occurs at all (see also Brosnan & de Waal 2002, Stevens & Hauser 2004).

The stress on social relationships should not be taken to mean that all reciprocity takes place in the framework of bonds. However, one would expect such cases to be associated with greater emphasis on strict reciprocity (see also Barrett & Henzi, this volume). Indeed, in humans strict reciprocity is seen only among ‘casual acquaintances’ (Silk 2003). Reciprocity in nature among animals that do not necessarily have bonds may likewise be rather strict (e.g. grooming among impala, which have unstable associations: Hart & Hart 1992; egg-trading among simultaneously hermaphrodite fishes: Fischer 1980). These cases may derive their stability from the fact that the altruistic services or commodities are parceled out in small packages, leading to frequent alternation taking place in rapid sequence.

### 1.3.3

#### **Mutualism**

Mutualism as an explanation for cooperative behavior is theoretically simple. Numerous examples exist, from living in groups, which dilutes predation risk, to coalitions, where all participants gain in rank or gain access to limiting resources (Clutton-Brock 2002). However, this simplicity is only apparent. Mutualism is vulnerable to free riding, where partners (in the case of dyadic mutualism) or other group members (if group-level, or public benefits are produced) can harvest benefits without providing corresponding benefits in return. In dyadic mutualism, the costs are often opportunity costs because partner switching might produce greater benefits. In the case of group-level benefits, the costs tend to be real because the acts themselves, while providing a clear net benefit to the actors, are costly. The free riders who do not join-in in producing the benefit, thus harvest a larger net benefit. This problem is known in the social sciences as the collective action problem, and it is also demonstrably present in primate groups (van Schaik 1996, Nunn 2000, Nunn & Deaner 2004). We should only expect to see mutualism where these threats are somehow dealt with.

Mutualism and byproduct mutualism can be seen within and between species, and our focus here is on intra-specific interactions. Byproduct mutualism (e.g. individual escape behavior against predators that serves to alert other group members) does not require the presence of bonds or even stable association. However, dyad-level mutualistic exchanges usually take place within an existing long-term relationship, in which both partners have an interest in keeping the beneficial cooperation going, and incentives to large-scale defection are therefore minimal. Hence, the distinction between reciprocity and mutualism becomes somewhat artificial and may be of no concern to the animals. Similarly, as discussed for the case of reciprocity, kinship may shore up the stability of these relationships.

At least among non-human primates, examples of dyadic cooperative relationships are far more numerous than mutualism that involves more players or even entire groups. And where particular cases of mutualism can involve two or more players, those involving only two tend to be more common. For instance, the agonistic coalitions among primate males described by van Schaik et al. (this volume) almost always contain only two members, especially the risky varieties where coalition members attack a higher-ranking male to take over his top-dominant position. Similarly, the communal nursing among female house mice described by König (this volume) most commonly involves only two females. The relationship perspective may explain why this is so. First, when animals cooperate in pairs, it is easier to exert control over the partner's behavior. In pairs, the costs of partner control, for example by punishment (Clutton-Brock & Parker 1995), can be recouped again when the partner subsequently behaves in a more cooperative manner. In group-level mutualism, this punishment is altruistic (Fehr & Gächter 2002), because all other group members benefit as well without incurring any costs. Second, in dyadic cooperation, it is also easier to exert partner choice. A dissatisfied individual can usually switch to another partner in the group, whereas in group-level mutualism it would require either expulsion of free-riding partners or dispersal to other groups with more cooperative partners, both of which are likely to carry considerable cost. The rarity of smooth collective action among animals other than eusocial species is perhaps the main distinction between humans and other animals in this context.

One of the few well-documented cases of multi-player mutualism in primates is the cooperative hunting described among chimpanzees in the Taï Forest by Boesch et al. (this volume). The very existence of this behavior shows that the individuals somehow deal with free riding, whereas among chimpanzees elsewhere, dominant males, who did not necessarily participate in the hunt itself, tend to end up with the prey and control its distribution. Multiple males also participate in other areas, but it is only in the Taï Forest that individuals take on complementary roles, resulting in the ability to subdue larger prey (Boesch et al., this volume). The authors note that the forest structure in Taï makes such close cooperation critical to achieving success. At other sites, group hunting is more like byproduct mutualism; males merely hunt simultaneously but still end up better off, despite attempts by dominants to monopolize the distribution of meat. The true cooperation in the Taï Forest is made possible by the 'fair' distribution of meat, but why this works there and not elsewhere is not clear. The answer is eminently important for the evolution of the strong tendency to mutualism we see in humans.

Other instances of mutualism near the group-level end of the spectrum also exist. For instance, helpers in cooperative breeders that are not related to the breeders may help because of the advantages of being in the social unit (group augmentation: Kokko et al. 2001, Clutton-Brock, this volume). Residents allow them to join and stay, not only due to benefits gained from the help, but also from reduced risk of predation or attacks by neighboring groups. Helpers gain these same benefits, but are expected to contribute to the semi-public goods through helping, such as providing sentinel service. Experimental evidence on helpers in a cooperatively-breeding cichlid fish suggests that helpers prevented from help-

ing are attacked more and work harder upon return (Balshine-Earn et al. 1998, Bergmüller & Taborsky 2005).

In all successful cases of mutualism, free riding is kept in check. In the behavioral examples discussed above, this is done through behavioral control. Sometimes, however, mutualism works due to restraint by dominants. Thus, in groups, dominants may peripheralize the subordinates to gain greater safety, but the benefit of the selfish herd tends to be a sufficient incentive for the subordinates to stay (Hamilton 1971), if only because dominants refrain from stronger peripheralization because that would entice the subordinate to leave and join other groups.

In cases without obvious behavioral control, the presence of successful mutualism requires that the conditions restrict either the opportunities or the incentives for free-riding. A good example is provided by the distribution of communal nursing described by König (this volume). Here, females are unable to recognize their young; they are therefore unable to favor their young over those of others. Because this ability to recognize young emerges some time before weaning, however, it is probably no coincidence that most of the observed cases of communal nursing involve related females. A more subtle example is provided by the formation of fruiting bodies in normally solitary amoebas that form colonies to reproduce. The cells of *Dictyostelium discoideum* cooperatively form fruiting bodies that produce spores. These sit on top of stalks, which are therefore reproductive dead ends. Yet, all cell lines are represented equally in the production of stalks and fruiting bodies (Foster et al. 2004), probably because defection is prevented biochemically. The gene *DimA* is involved in the production of stalks. Hence, the absence of *DimA* would potentially allow the cell to forgo participation in stalk production. However, absence of the gene also pleiotropically results in exclusion from the stalk, thus keeping such a benefit to defection in check.

Perfectly stable mutualism should be found where defection is impossible, and hence no additional mechanisms of partner control are required. The cooperation among components within entities, such as the organelles within a cell, or by cells within a body, might be stable because the opportunities for defection by partner cells have largely been eliminated. The very long delay between the origin of simple unicellular organisms, and the eukaryotic cell and multicellular organisms, however, suggests that this transition may not be easy, and that active policing remains necessary (e.g. Michod 2003).

## 1.4 Cooperation among humans

Primates differ from many other animal lineages in that they show rather good evidence for cooperation, especially in long-term relationships (beyond simple protection of offspring by mothers), although it remains to be seen to what extent this picture is due to poor documentation for other lineages (Dugatkin 1997). One thing is clear, however; humans are dramatically different even from other primates. “Human cooperation represents a spectacular outlier in the animal

world” (Fehr & Rockenbach 2004). We are a species in which there is far more cooperation than in any other non-eusocial species. In this section, we will try to document exactly how humans differ from other primates, then examine the proximate mechanisms (emotional, cognitive) that underlie these differences, and finally briefly address the possible selective agents that gave rise to these differences.

First, humans tend to engage much more commonly in group-level cooperation, whereas most cooperation in nature is at the level of dyads. Human groups can behave almost as superorganisms (allowing functionalism in sociology to treat social groups, rather than individuals, as the unit of analysis), setting communal goals and engaging in communal tasks. One expression of the strong organization at the group level is individual specialization and division of labor, often by sex.

Undertaking cooperation at the group level rather than that of the dyad poses more serious cheater detection problems. As we noted earlier, it is easier for an individual to control the behavior of a partner in a dyad than it is to control the behavior of a group of individuals; selective association or punishment are likely to be costlier, and the required coordination in the case of group-level action may be cognitively complex as well (see also Boyd & Richerson 1988). Humans must therefore possess cognitive and emotional mechanisms that act to detect even subtle ways of defection and control the behavior of group members. Gächter & Hermann (this volume) review an array of mechanisms that act to stabilize the intrinsically very fragile group-level cooperation.

Second, humans tend to engage in extremely high-risk cooperation, much more than other animals, even than chimpanzee males. Coalitionary killing by male chimpanzees is otherwise unique among primates, but tends to involve serious asymmetries in the collective strength of the opposing parties (Wrangham 1999, Wilson & Wrangham 2003). In the typical case, three or more males from one community attack and kill a single male from a neighboring community. As a result, risk of injury to the attackers is limited. Chimpanzee males also attack large and potentially dangerous prey (adult red colobus monkeys: see Boesch et al., this volume), but the literature contains no references to males getting injured. In both cases, the risk of injury is kept low because of the close coordination of the attacks.

Human war is similar to coalitionary killing of males in many respects, and probably predates the origin of states (Keeley 1996), although it is perhaps not homologous with that among chimpanzees. However, human coalitionary killing, at least among contemporary humans, differs from that among chimps in that it also occurs between parties with much more symmetric collective strengths. The more balanced power of human armies implies higher individual risks to fighters. The appalling loss of life in many historically-documented wars attests to this, yet in numerous cases soldiers are not forced into battle and fighting is largely voluntary.

The third difference is more gradual than the other ones, but still worth noting. Humans tend to cooperate with non-kin more than other primates. In non-human primates, “the most costly forms of cooperation are reserved for close kin” (Silk, this volume). There is some evidence that male baboons and Bar-

bary macaques that form leveling coalitions are non-relatives (see van Schaik et al., this volume). Chimpanzee males represent the strongest exception to Silk's generalization. As we saw, they engage in risky collective combat, yet surprisingly, the collaborators need not be close (maternal) kin (Mitani, this volume). Humans, of course, are arguably even more extreme than chimpanzees in this respect. Human military history is littered with descriptions of acts of amazing bravery aimed at comrades who are not relatives, although descriptions often invoke kin-colored terminology, such as brothers-in-arms. There is no firm explanation for these anomalies as yet, although Chapais' (this volume) competence principle may play a major role; where the competence of the partner becomes an increasingly important factor in deciding the success of cooperative actions, it is increasingly less likely that a close relative is at hand that is sufficiently competent. Yet, there is probably far more to it than that.

Fourth, humans are willing to incur some cost to punish non-cooperators in the group-level kind of cooperation in which individuals contribute to common goals and free riders risk the breakdown of all cooperative effort. Thus, strong reciprocity (Gintis 2000) combines altruistic rewarding of cooperators with altruistic punishment of defectors (called moralistic aggression in Trivers 1971), both of which are costly to the actor.

So far, there is no evidence for altruistic punishment among animals in nature, as suggested by studies of species engaging in collective, high-risk defense of territories against neighboring social groups, in ring-tailed lemurs (Nunn & Deaner 2004), lions (Heinsohn & Packer 1995) or even chimpanzees (D. Watts pers. com.). However, de Waal & Brosnan (this volume) describe experimentally-induced costly refusal to cooperate, thus challenging the categorical uniqueness of altruistic punishment. However, even if confirmed in capuchins and/or chimpanzees, this does not mean that its presence in other primate species can be generalized, because these two genera are among the most socially tolerant and intensely cooperative among all primates. Moreover, it is possible that altruistic punishment in non-human primates is always directed at cheating partners, whereas humans often direct altruistic punishment at individuals they observed cheating in interactions with third parties. The difference critically depends on the presence of societal norms, for which there is no evidence so far in non-humans.

A fifth difference concerns the role of reputation in facilitating reciprocity. Reputation is almost certainly much more important in human than in non-human primates. The three basic preconditions for reputation are individual recognition, variation in personality traits, and curiosity about the outcome of interactions involving third parties. The first two of these are met in most non-human primates, but the third may require awareness of third-party relations, which involves cognitive abilities so far demonstrated in only a few species (Cheney & Seyfarth 2003), although it may be more widespread. There is good evidence that primates use information on their experience with others in the past to predict their behavior in the future (Silk 2002a), and it is almost inevitable that this information is also used to select partners in whom they invest in order to establish social bonds. Yet, there is no evidence that they use reputation based on third-party interactions. Obviously, this does not mean

that none do, but it would take careful observations and experiments to demonstrate it.

Humans, in contrast, commonly engage in indirect reciprocity (Alexander 1979), in which an ego's tendency to cooperate with a partner depends on the latter's reputation, which is established not only based on the ego's direct experience with the individual but also on this individual's behavior toward others, which is either observed directly by ego or reported to ego by third parties. No doubt, this use of reputation is enhanced by language. The displacement quality of language allows one to learn about the behavior of others even if the acts were not observed and the actors are not present, although the reliability of this information is subject to manipulation due to the very same quality of displacement.

Reputation is vital for an individual's success in society, and individuals show great concern over their reputation. Milinski (this volume) shows that reputation is also an unexpectedly powerful mechanism for maintaining group-level mutualism (the creation of public goods), which is especially vulnerable to the free-riding problem. In experiments, players became more cooperative when such public goods games were alternated with indirect reciprocity games. In other words, the concern with maintaining a good reputation, with its obvious benefits in indirect reciprocity, spills over into the public-goods situation. Since humans are normally engaged in multiple cooperative relationships simultaneously, this finding spells hope for improvement of the management of common or public resources.

The final difference is that humans exchange goods and services using token-based ('mercantile') exchange; we trade. At least among members of the same society, this usually works, even if the participants are perfect strangers without too much risk of exploitation or worse, because of guarantees put in place by societies. This trade requires not only the ability to weigh the value of goods or services relative to those of other goods or services of different kinds, but also to manipulate symbolic representations of values, and subsequently to accept in themselves arbitrary tokens as intermediary payment that can later be exchanged for other goods or services (Ofek 2001). These abilities could not have evolved if a system of trust had not been put in place; our subsistence style would be all but impossible without it, since we critically depend on the products and services of others. Obviously, nothing among animals in nature compares to this system, although the generous food sharing and trading of these favors for subsequent services in chimpanzees (see Boesch, this volume; Mitani, this volume) is clearly the foundation upon which our trade is built.

These differences can be summed up as follows: humans are far more likely to cooperate, both at the dyadic and especially at the group level, and we do so with non-relatives and often in situations of extremely high risk, apparently even with strangers (but see Trivers, this volume). This tendency would seem to expose us to unacceptably great risks of defection, but we have evolved special mechanisms, including cheater detection, the use of reputation to gauge the quality of potential partners and, most spectacularly, altruistic punishment to keep the tendencies toward defection by partners in check. According to Fehr & Fischbacher (2003), all of this boils down to our unique capacity to establish

and enforce social norms: rules of social conduct that are internalized and are upheld even if the individual is not directly affected.

Given this uniquely derived level of cooperation, we must expect the presence of derived psychological mechanisms that provide the proximate control mechanisms for these cooperative tendencies (cf. Trivers 1971). It is tempting to look to other uniquely derived human features, such as language, advanced intelligence or cultural transmission of social norms, as functional prerequisites for the evolution of these mechanisms. While they are undoubtedly involved, the evidence suggests a critical role for unique emotions as the main mechanisms. Extreme vigilance toward cheaters, a sense of gratitude upon receiving support, a sense of guilt upon being detected at free riding, willingness to engage in donation of help and a zeal to dole out altruistic punishment at free riders – all these are examples of mechanisms and the underlying emotions that are less developed in even our closest relatives. Moreover, many of the emotions reflect societal equivalence in norms, such as those of fairness and justice. Emotions can be seen as the mechanisms used by evolution to achieve the optimum ('rational') outcomes without explicit reasoning or calculation (cf. van Hooff 2001). This might explain the emotional flavor to virtually all human decision-making (as no doubt in animal decision making).

Some of these mechanisms are also present in animals (see Brosnan & de Waal 2004), but they are certainly much exaggerated in our species (see also McGuire 2003). Uniquely, humans dispense the costliest of tendencies, altruistic punishment, even toward perfect strangers whose free-riding did not affect them (Fehr & Gächter 2002). Evolutionary biologists have a serious challenge explaining these tendencies, and Gächter & Hermann (this volume) briefly review the lively debate that has ensued about altruistic punishment, although no doubt the last word on this has not yet been spoken (see also Fehr & Henrich 2003).

The critical difference as we now see it, is that in humans these emotions have become normative, i.e. we have these emotions also when we are not directly involved, whereas the bulk of the evidence for animals still supports the notion of self-centered emotions, although great apes may turn out to be an exception (Flack & de Waal 2000).

The question obviously arises as to how humans could have become such a spectacular outlier in just a few million years. This question has recently spawned an active research effort. The dramatic differences with even our closest relatives suggest that the regular processes of kin selection or relationship-based cooperation involving reciprocity and mutualism are inadequate. Moreover, because the greatest qualitative difference is in group-level cooperation, one could argue that coordinated group activities, such as cooperative hunting and gathering accompanied by a division of labor and especially warfare, may underlie the amazing willingness to invest in cooperative relationships among humans. This has led to suggestions involving language and culture as the key pacemakers of group-level cooperation.

The most detailed hypothesis is the cultural group selection model offered by Richerson et al. (2003). They argue that conformist transmission (Boyd & Richerson 1985), a regular adaptation, can create groups that differ systematically and persistently from other groups, even in the absence of genetic differentia-

tion and in the presence of migration between groups. Suppose that the Pleistocene saw major, rapid changes in the environment, destroying local adaptations. Further suppose that a successful novel invention gets established in one group, and is subsequently maintained by conformist transmission, and that some of these inventions favored group-level cooperation and strong group coordination (Boyd & Richerson 2002), with its attendant massive fitness benefits in a hostile environment. Successfully cooperating groups could now out-compete and displace other groups that lacked this invention.

A simpler alternative has recently been proposed (Panchanathan & Boyd 2004). Our interdependence at the dyadic level, including extensive indirect reciprocity with people we hardly know, has led to a critical reliance on reputation. Our pursuit of a good reputation in all contexts has, as a byproduct, created prosocial behavior at the group level, including altruistic punishment (which enhances reputation: see Milinski, this volume). We should expect to see major advances in this area in the near future. Trivers (this volume) provides a set of constructive suggestions and criticisms of previous approaches that should help focus future work on human cooperation on realistic assumptions and predictions.

## 1.5

### Summary and outlook

Let us now briefly review the important advances that have been made in research on cooperation among individuals in dyads and groups, as well as flag issues that still remain to be solved by future work. The frontier of cooperation research has recently moved to humans, and many of the theoretical problems surrounding cooperation in animals seem to have been settled. However, that does not mean that there is no need for further empirical work on animal cooperation. Here, as in the rest of this book, we focus largely on primates.

Although altruism directed at kin is theoretically straightforward, some questions nonetheless remain. Thus, it is still unknown whether animals have a cut-off relatedness for all kinds of altruistic acts (i.e. consider those above a particular  $r$  value family, regardless of the kinds of acts they direct at them), or whether they differentiate among relatives depending on the cost of the acts involved (e.g. protecting only closer kin against higher-ranking opponents or predators: see Chapais, this volume; see also chapters in Chapais & Berman 2003). Likewise, debate continues to rage as to whether non-human primates recognize and classify kin entirely on the basis of association history or whether they also use other clues, summarized under the header phenotype matching. These questions are obviously related; differentiation among degrees of kin requires mechanisms of kin recognition that permit finer estimates of relatedness than using a simple cut-off point. The recent development of non-invasive genetic techniques will no doubt help us to find answers to both these questions.

Kin discrimination can strongly improve the power of kin selection and thus the behavioral reach of nepotism. In particular, if kin recognition is extended to



the paternal component of kinship, we should expect richer patterns of nepotism in group-living animals. New studies that estimate the paternal component of relatedness suggest that kin discrimination among non-human primates is based on more than familiarity through association (Widdig et al. 2001, Buchan et al. 2003), but because other studies suggest otherwise (see Paul & Kuester 2003), it is important to identify the causes of these discrepancies.

At a more practical level, the use of non-invasive genetic techniques brought to light some clear mismatches between clustering of kin due to differential dispersal and the importance of kinship in social behavior. Thus, several prosimians (and perhaps orangutans) show evidence for female philopatry (Kappeler et al. 2002, Wimmer et al. 2002), but at least in some (e.g. *Mirza coquereli*), females do not seem to engage in any social behaviors that might benefit from having kin as partners. On the other hand, male chimpanzees are both philopatric and form strong alliances, yet they do not seem to select close kin more than expected (Vigilant et al. 2001). The necessary re-evaluation of the importance of nepotistic cooperation in philopatry (e.g. Wrangham 1980, Waser 1988) suggested by these cases will be facilitated by more descriptions from the field.

Turning now to cooperation among unrelated animals, we saw that animals generally do not play a PD-kind of game. Some of the theoretical work spawned by the PD model has actually begun to address these concerns. Models suggest that the ability to select partners, and subsequent selective association with them, favors the evolution of cooperation (e.g. Peck 1993), as does, obviously, communication, for instance in the form of the ability to punish non-cooperators (Boyd & Richerson 1992).

Our discussion was organized according to the three classic explanatory models of cooperation: nepotism, reciprocity and mutualism. However, cooperation among animals observed in naturalistic conditions often contains a mix of these categories of cooperation. Variables affecting the presence of cooperative behaviors in nature are the number of players and the degree to which the cooperative acts are enacted within a stable local context. Thus, three categories of naturalistic cooperation can readily be recognized: (i) dyadic cooperation, but without social relationships between the partners, (ii) dyadic cooperation in the context of long-term relationships, and (iii) group-level cooperation in stable groups. Table 1.1 groups some of the examples mentioned in the text so far into these three categories, which are characterized by different threats to the stability of cooperation and hence by different behavioral solutions. Not included in the table are the cases where the solutions do not require behavioral action. These include, for dyadic, anonymous cooperation, byproduct mutualisms, such as a selfish herd effect, and for group-level cooperation, cases of mutualism that are stabilized by structural safeguards against free-riding, such as in the amoeba example.

The value of this table should be heuristic, in that it suggests new approaches. Noë (1990), Hammerstein (2003b), Silk (2002b) and others have pointed at the large gap between theory and empirical observations on animals that are mobile and form long-term relationships. Market models provide a promising avenue (Bshary & Noë 2003) to examine partner choice, especially for dyadic cooperation, but active attempts to model real cases might produce new questions for

**Table 1.1.** Cooperation among independent animals, such as non-human primates.

Category	Threat	Solutions	Examples, labels
Dyadic, without relationships	Absence of reciprocity	1. Partner control: parceling altruism in small packets; 2. Leave	1. Strict reciprocity; 2. Anonymous donations in humans
Dyadic, in long-term relationship	Asymmetric investment	1. Partner change; 2. Negotiation about payoffs	1. Unilateral altruism toward kin; 2. Friendships, alliances
Group-level	Free-riding; taking of larger shares than 'fair'	1. Switch groups; 2. Altruistically expel or punish free-riders; 3. Altruistically reward cooperators	1. Helping by paying for staying + group augmentation; 2. Group-level mutualisms (e.g. communal defense, nursing); 3. Generosity: establishment of reputation through alarm calling, mobbing, food sharing, etc.

other aspects of cooperation, for example for partner control through communication (see also Bowles & Hammerstein 2003). For primates, we need more work on the natural history of alarm calls and mobbing; it is quite conceivable that a rich interpretation is needed, in which animals undertake these acts in order to establish and maintain reputation (of the immediate, not the third-party variety), which would favor their being accepted as group members or as partners in dyadic bonds (cf. Maklakov 2002).

Of special interest to biological anthropology would be a more precise mapping of differences between humans and great apes. We noted that great apes seem to be more prone to collaboration with non-kin than other primates; this is not only true for male chimpanzees but also for female bonobos (Hohmann et al. 1999). Great apes also show remarkable tolerance toward curious imitators of their skills (van Schaik 2003). If these copiers are unrelated, and if their acquiring the skills improves their fitness, are those who allow themselves to have their skills copied not altruistic? Generous food sharing, as seen in chimpanzees (Boesch, this volume; Mitani, this volume) can be regarded as investments into a good reputation (as in humans: Bird et al. 2001), but if reputation is the key to understanding group-level cooperation, this might explain why chimpanzees show more of it than other non-human primates. The same holds true for the possibility of norms in chimpanzees. It is therefore conceivable that more detailed work on primates will show that cooperation provides yet another case where the actual gap between human and non-human primates is less wide than generally perceived.

## **Acknowledgments**

We thank Tim Clutton-Brock, Barbara König, Ronald Noë and Claudia Rutte for discussion and comments.