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Cooperation in Nonhuman Primates

Function and Cognition

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Abstract

It has long been hypothesized that the demands of establishing and maintaining social relationships in complex societies place strong selective pressures on cognition and intelligence. What has been less clear, until recently, is whether these relationships, and the skills they require, confer any reproductive benefits, and whether such benefits vary across individuals. During the last few years, much progress has been made in resolving some of these questions. There is now evidence from a variety of species that animals are motivated to establish close, long-term bonds with specific partners, and that these bonds enhance longevity and offspring survival. The cognitive and emotional mechanisms underlying cooperation, however, are still not understood. It remains unclear, for example, whether animals keep track of favors given and received, and whether they rely on memory of past cooperative acts when anticipating future ones. Although most investigations with captive primates have indicated that cooperation is seldom contingency-based, several experiments conducted under more natural conditions suggest that animals do take into account recent interactions when supporting others. Moreover, while interactions within dyads are often unbalanced over short periods of time, pairs with strong bonds have strongly reciprocal interactions over extended time periods. These results suggest that the apparent rarity of contingent cooperation in animals may not stem from cognitive constraints. Instead, animals may tolerate short-term inequities in favors given and received because most cooperation occurs among long-term reciprocating partners.

Introduction

It has long been hypothesized that the demands of establishing and maintaining bonds in large social groups has placed strong selective pressures on animal

cognition. Research over the last thirty years has demonstrated that many animals—including, in particular, nonhuman primates—may indeed recognize other individuals' social relationships, intentions, and perhaps even knowledge states (Cheney and Seyfarth 2007; Call and Tomasello 2008). What has been less clear, until recently, is whether these relationships, and the skills they require, confer any reproductive benefits, and whether such benefits vary across individuals. Doubts even persist about whether animals have the cognitive capacity or motivation to maintain long-term relationships. It remains unclear, for example, whether animals keep track of past cooperative acts when anticipating future ones. Some problems are methodological, arising from the difficulties of testing cooperation experimentally under natural conditions. Others stem from the different results obtained from observations of wild animals as opposed to those living in captivity.

Here, I first describe results which suggest that the ability to maintain long-term social relationships confers significant reproductive benefits. Thereafter I discuss some of the many outstanding questions regarding the function of cooperation in animals and the cognitive mechanisms that may underlie them. My discussion is restricted to species that exhibit relatively low reproductive skew including, in particular, Old World monkeys and apes.

Cooperation among Long-Term Partners

Function

If knowledge of other individuals' relationships and mental states is adaptive, it should be possible to identify correlations between social knowledge and reproductive success. Although these have not yet been documented, there is growing evidence that animals are motivated to form social bonds, and that there is individual variation not only in the strength and consistency of social bonds but also that this variation is correlated with reproductive success.

Several studies have demonstrated that primates balance grooming exchanges with long-term partners. Among female baboons (*Papio hamadryas* spp.), for example, grooming within dyads is often unbalanced over short periods of time. However, pairs who groom each other frequently have strongly reciprocal grooming relations over extended time periods (Silk and House 2011). A similar pattern characterizes male chimpanzees (*Pan troglodytes*) (Mitani 2009b).

The close bonds that arise through long-term grooming relationships are also correlated with reproductive success. Female chacma baboons (*P. h. ursinus*) who maintain strong bonds with other adult females experience higher offspring survival and live significantly longer than females with weaker bonds (Silk et al. 2009, 2010). These effects are independent of dominance status, suggesting that close bonds may offset any fitness loss due to low rank.

Importantly, the fact that most females' partner changes are not due to the death of the partner suggests that some females may be more skilled or more motivated than others in maintaining relationships with preferred partners over time. These findings parallel evidence from humans which shows that social integration enhances longevity and health (Holt-Lunstad et al. 2010).

There remains some uncertainty about the direction of the causal links between social bonds and fitness. One causal factor may be related to stress. For example, female mice (*Mus musculus*), who often rear pups communally, reproduce more successfully when they are allowed to choose their nestmates than when nestmates are assigned randomly (Weidt et al. 2008). Rat (*Rattus norgevicus*) sisters with well-balanced affiliative relationships exhibit lower glucocorticoid levels, fewer tumors, and higher survival rates than sisters with less well-balanced relationships (Yee et al. 2008). Similarly, female chacma baboons display marked increases in glucocorticoid levels when a preferred partner dies. In the same population, females experience lower glucocorticoid levels when their grooming interactions are focused on only a small number of partners, and females with more focused grooming patterns show less pronounced responses to various stressors, including the immigration of potentially infanticidal males (Cheney and Seyfarth 2009).

Mechanisms

The psychological mechanisms that underlie animals' social interactions and relationships are not yet understood. Because we have no evidence that animals can plan or anticipate the benefits that might derive from a long-term relationship, a number of investigators have argued that animals' cooperative interactions are motivated only by short-term rewards, such as the opportunity to handle an infant or gain access to food. According to these arguments, social interactions are not founded on long-term patterns of affiliation but are based instead on short-term by-product mutualism or biological markets motivated by the likelihood of immediate reward (Noe and Hammerstein 1994). These arguments certainly have some validity. Much cooperative behavior in primates and some other animals (e.g., spotted hyenas, *Crocuta crocuta*) occurs in the form of low cost services like alliance support against lower-ranking opponents (Smith et al. 2010). Because these alliances confer direct and immediate benefits by reinforcing the status quo, they may represent a form of mutualism. Similarly, when a female baboon grooms another, she may simply be engaging in a short-term negotiation with a trading partner who controls a desirable commodity, like an infant (Henzi and Barrett 2007).

Not all social interactions, however, are based on the value and supply of alternative trading partners; many others reflect long-term patterns of affiliation. Although female baboons, for example, form long-term bonds with only a small number of other females, these bonds can endure for years despite short-term fluctuations in interaction rates. Moreover, grooming often occurs in the

absence of an immediate reward, and it is seldom evenly balanced between partners within single bouts—even among partners who have strongly reciprocal grooming interactions over extended periods of time.

Contingent Cooperation

Over the last decade, there has also been increasing skepticism about the relevance of contingent-based reciprocity in the social interactions of animals. Because most cooperative interactions like grooming occur between long-term partners"(often kin) for whom any single altruistic act may be relatively insignificant, many investigators are now convinced that the sort of reciprocal altruism first proposed by Trivers (1971) may be both rare and fragile in nature (Hammerstein 2003; Clutton-Brock 2009). Although there is limited experimental and correlational evidence that animals sometimes rely on memory of recent interactions when behaving altruistically toward others, interpretation has been complicated by a paucity of convincing examples, the absence of important controls in some early tests, and a number of experimental studies seeming to indicate that animals lack the cognitive or empathetic ability to sustain contingent cooperative exchanges.

Reciprocal altruism (Trivers 1971; see also Schino and Aureli 2009) occurs when the donor of an altruistic act incurs an immediate cost but receives delayed benefits when the recipient reciprocates the altruistic act at some future time. For reciprocal altruism to evolve, individuals must have a high probability of meeting again, and they must be able to detect or avoid cheaters. Reciprocal altruism can be distinguished from mutualism, in which both participants receive immediate benefits that outweigh any associated costs, and from kin selection, in which the donor gains inclusive fitness benefits despite incurring costs. Because the costs and benefits of many altruistic acts are difficult to quantify, I will here use the term *contingent cooperation* rather than *reciprocal altruism* to describe altruistic behavior whose occurrence is contingent upon a specific previous supportive act. This definition is agnostic with respect to the precise costs and benefits of the altruistic behavior; it posits only that *A*'s support of *B* is causally dependent upon a previous supportive act by *B* toward *A*.

Cognitive Constraints

Doubts persist about whether animals possess the cognitive abilities to sustain contingent cooperation. These include the ability to remember specific interactions, to delay reward, to track favors given and returned, to plan and anticipate future outcomes, and to distinguish between cooperators and defectors (Stevens et al. 2005a; Henzi and Barrett 2007; Melis and Semmann 2010). Some of these objections may be unjustified. Playback experiments on baboons have

demonstrated, for example, that females' behavior is strongly influenced by the memory of single interactions with specific individuals (Cheney and Seyfarth 2007). If a baboon hears another female's "reconciliatory" grunt shortly after being threatened by her, she behaves as if the grunt is causally related to the recent fight and directed specifically to her, as a signal of benign intent. As a result, she is more likely to approach her former opponent and to tolerate her opponent's approaches than if she has heard the grunt of another female unrelated to her opponent. By contrast, if she hears the same female's threat-grunts shortly after grooming with that female, she acts as if she assumes that the calls are being directed at another female, because females seldom threaten a recent grooming partner. In both cases, females' responses appear to be guided by memory of the quality of a specific recent interaction. The extent to which this memory is explicit is as yet unknown.

Other purported cognitive limitations can also be questioned. There is now a large literature on animals' numerical discrimination abilities suggesting that quantity assessments are widespread across many taxa (Shettleworth 2010b). Similarly, although many tests with primates have suggested a general failure to delay rewards beyond short time periods, there appears to be considerable interindividual variation in self-imposed delayed gratification. Moreover, the ability of primates and other animals to delay gratification in contexts that do not involve food rewards remains largely untested. Thus, contingent cooperation in animals is not necessarily constrained by the inability to delay reward or to quantify past cooperative acts.

It has also been assumed that animals are not capable of contingent cooperation because it demands the anticipation of future interactions. Leaving aside for the moment the question of whether mental projections of future outcomes are necessary to sustain contingent cooperation, the assumption that animals are unable to anticipate future events may not be valid. There is a long history in experimental psychology of tests demonstrating that many animals accurately and predictably anticipate future rewards and outcomes (Shettleworth 2010b). Furthermore, a growing number of experiments suggest that primates make prospective decisions based on certainty judgments about their past behavior (Hampton, this volume).

It is also doubtful whether nonhuman primates are unable to distinguish cooperators from noncooperators. In tests conducted in captivity that require two individuals to work together to obtain a food reward, both capuchin monkeys and chimpanzees are more likely to cooperate with partners with whom rewards are shared more equitably (de Waal and Davis 2003; Melis et al. 2006b, 2009; Silk and House 2011). Chimpanzees also recognize which partners are most effective (Melis et al. 2006a) and show a limited ability to increase their rate of cooperation with partners who have cooperated with them in the past (Melis et al. 2008). They may also be able to resolve conflicts of interests when working together to achieve a common goal (Melis et al. 2009).

Emotional Constraints

In humans, inequity aversion, tolerance, and the motivation to engage in joint activities are important catalysts for cooperative behavior. Whether primates are motivated by these emotions, however, remains unclear. Some experiments have suggested that primates reject food offered by humans if a rival is receiving a better reward (e.g., Brosnan and de Waal 2003). Other studies have failed to replicate these findings and suggest that the food rejections are due not to perceived inequality but rather to frustration at seeing, but not obtaining, a preferred food item (e.g., Bräuer et al. 2006; Dubreuil et al. 2006). In captivity, chimpanzees seem generally indifferent to inequitable returns to themselves and others. In experiments in which chimpanzees have the opportunity to deliver food to a partner at no cost to themselves, for example, subjects show no sensitivity to the consequences for their partner (Silk et al. 2005; Jensen et al. 2006). They do not behave spitefully or withhold food from their partner, they simply ignore their partner's returns. In other experimental paradigms, however, chimpanzees have been observed to assist one another in collaborative tasks involving food rewards (Greenberg et al. 2010), suggesting that chimpanzee helping behavior may involve some consideration of partners' outcomes.

It has also been argued that a lack of social tolerance may contribute to the low levels of cooperation displayed by chimpanzees in many experiments. Bonobos (*Pan paniscus*) achieve higher levels of success in some cooperative tasks than do chimpanzees, seemingly because their willingness to share rewards with their partners prompts continued cooperation (Hare et al. 2007). It remains unclear, however, whether bonobos also show higher degrees of cooperation and tolerance under natural conditions, where the structure and rewards of the task are not determined by humans. It is not known, for example, whether bonobos show higher levels of cooperation than chimpanzees when hunting, or whether they share their kills more equitably. Similarly, it is not apparent whether bonobos ever engage in any behavior that is as cooperative and potentially costly as chimpanzees' patrolling behavior (Mitani et al. 2010), or if they do, whether they are more likely than chimpanzees to share risks equitably.

Taken together, results suggest that cooperation in animals may be sustained by qualitatively different mechanisms than it is in humans. Indeed, experiments explicitly designed to compare the behavior of children and chimpanzees indicate that humans may be uniquely motivated to engage others' attention, share their intentions, emotions, and knowledge, and impose sanctions on noncooperators (Tomasello et al. 2005; Warneken and Tomasello 2009; Melis and Semmann 2010). It is also possible, however, that inequity aversion may be less universal in humans than is often supposed. Surveys of people living in societies that lack large-scale religions and economic markets tend to reveal a general indifference to unfair outcomes (Henrich et al. 2010), suggesting

that what is often regarded as a species-specific prosociality in humans is not entirely the result of innate psychological mechanisms.

Measuring Contingent Cooperation

For several reasons, it has proved difficult to investigate contingent cooperation under natural conditions. First, in the absence of experiments, it is almost impossible to determine whether a given altruistic act is causally dependent upon a specific prior interaction. Second, many altruistic acts occur in different currencies (e.g., grooming and alliance support) whose relative values are difficult to calibrate. Moreover, even altruistic acts that occur in the same currency may not carry equal value for each participant. In species which form dominance hierarchies, a low-ranking individual may value alliance support from a more dominant partner more highly than vice versa. As a result, the individual may provide substantially more support to the dominant partner than is received in return yet still regard the relationship as reciprocal. Given these tautological assumptions, almost any relationship can be termed reciprocal. Finally, the degree to which interactions are regarded as reciprocal may be a function of the timescale under consideration. As already mentioned, grooming exchanges within single bouts are often unbalanced and asymmetrical. Nonetheless, over longer time periods, partners with close social bonds exhibit a high degree of reciprocity in their grooming interactions.

Observational Evidence

Correlations between grooming and alliance support have been documented in a variety of primates (Silk 2007c). In a meta-analysis involving 14 primate species, Schino et al. (2007) found a weak but highly significant correlation between grooming and alliances among long-term partners over extended periods, but little evidence that alliance support is motivated by a specific recent grooming bout. Indeed, in one study of captive Japanese macaques, kin were never observed to support each other in the half hour after grooming, even when they had the opportunity to do so (Schino et al. 2007). Similarly, although female spotted hyenas form the majority of their alliances with close kin, there is no evidence that this support is reciprocal or based on the memory of a specific recent interaction (Smith et al. 2010).

Among male chimpanzees, individuals who groom most often are also those who form alliances and share meat at the highest rates. Cooperation thus involves the exchange of services in different currencies, with males reciprocating grooming for support, support for meat, and so on. Although exchanges are often asymmetrical within dyads over short time periods, they become more evenly balanced over longer periods of time and are not simply a by-product of association frequency or genetic relatedness (Mitani 2006; Boesch 2011).

The most costly cooperative behavior shown by male chimpanzees occurs during boundary patrols, when the males from one community make incursions into the territories of their neighbors (Mitani et al. 2010; Boesch 2011). These incursions are risky and sometimes fatal, because a small party or lone individual is vulnerable to attack if they encounter a larger party; incursions, therefore, cannot be undertaken alone. Although it remains unclear whether patrols are planned, they appear to involve some degree of shared intentionality and a high degree of mutual support. Little is known about the mechanisms that motivate chimpanzees to initiate and participate in these highly cooperative and potentially costly activities. It is not known, for example, whether chimpanzees take into consideration memory of another individual's behavior during previous patrols when deciding whether or not to join him in a patrol. Whether cooperation in this context is more, or less, contingent upon memory of previous events, remains unclear.

In sum, most observational studies suggest that cooperation under natural conditions is not contingent upon specific recent events. Instead, reciprocal exchanges tend to emerge gradually among regular partners over repeated interactions, despite not being balanced over short time periods.

Experimental Evidence

Although chimpanzees' interactions with preferred partners become reciprocal over extended periods of time, tests on captive subjects suggest that reciprocity is not contingency-based. For example, in one experiment with captive chimpanzees, subjects were given a choice of cooperating with either an individual who had previously helped them or one who had not (Melis et al. 2008). Although there was some evidence that subjects increased their cooperation with the more helpful partner, this effect was relatively weak, and subjects did not consistently avoid noncooperators. In another experiment deliberately designed to test whether cooperation was contingency-based, Brosnan et al. (2009) found no evidence that chimpanzees were more likely to provide food to a partner if that partner had previously provided food to them. Melis et al. (2006b) suggest that chimpanzees may be capable of contingent reciprocity, but that long-term partner preferences which develop over repeated interactions may override the decisions that chimpanzees make on the basis of immediate exchanges and rewards.

The lack of evidence for contingent cooperation in tests with captive animals may also result from the stringent standards set by these experiments, which have typically required proof of equal back-and-forth exchanges in a single currency—food—whose amounts and timing are determined by humans. These requirements may have set the bar unrealistically high, leading investigators to underestimate the extent to which a recent cooperative interaction may motivate animals to cooperate again.

Several investigations conducted under more natural conditions have provided more positive indications of contingent cooperation. Unfortunately, however, interpretation has been complicated by the lack of follow-up experiments to correct for potential confounds. For example, in the well-known study of vampire bats (*Desmodus rotundus*) most reciprocal exchanges of blood occurred among close kin (Wilkinson 1984). Although some individuals regularly exchanged blood with unrelated partners, it was not clear whether any specific act of regurgitation was contingent upon a specific recent donation.

An investigation of mobbing behavior in pied flycatchers (*Ficedula hypoleuca*) provides more convincing evidence for contingent cooperation (Krams et al. 2008). In this experiment, subjects had the opportunity to help one of two neighbors mob an owl. One of these neighbors had recently helped the subjects to mob an owl at their own nest box, while the other had been prevented from doing so by the experimenters. Subjects were significantly more likely to help previous supporters than apparent defectors, suggesting that cooperative behavior was contingent upon memory of the neighbors' behavior. However, the possibility that the birds' behavior might have been influenced by any recent interaction with their neighbors—not just a supportive one—was not addressed.

This confound was also present in Seyfarth and Cheney's (1984) playback experiment on wild vervet monkeys. Although subjects were more attentive to the recruitment call of an unrelated female after grooming with her than after no interaction, it remained unclear whether subjects might have been equally responsive after any interaction with her, including even aggression. Subsequently, Hemelrijk (1994) demonstrated that grooming increased the probability of actual alliance support in an experiment with captive long-tailed macaques.

Recently, we conducted a playback experiment with wild baboons that attempted to control for some of these confounds (Cheney et al. 2010). In the test condition, a subject was played the recruitment call of another female at least 10 minutes after she had groomed with that female and then separated without any further interactions. This playback was designed to mimic a context in which the former grooming partner was threatening another individual and soliciting aid. Each subject's responses were compared to her responses in two control conditions. The first control was also conducted after the subject and the same female had groomed and then separated for at least 10 minutes. In this case, however, no playback was conducted. This control was designed to test whether a recent friendly interaction might simply motivate the subject to approach her partner again, even in the absence of any solicitation for support. In the second control, the same female's threat-grunts were played to the same subject at least 10 minutes after the subject had threatened that female. This control was designed to test whether subjects' responses to a recruitment call were primed by any prior interaction, not just a friendly one.

Results provided some support for delayed contingent cooperation among unrelated individuals. Hearing the recruitment call of a recent grooming partner caused subjects to move in the direction of the loudspeaker and approach their former partner. When the subject and her partner were close kin, no such effect was observed. Importantly, subjects' responses were not influenced by *any* type of recent interaction, because subjects only responded to their former partner's recruitment call after grooming, and not after aggression. Similarly, their responses were not prompted only by the motivation to resume a friendly interaction, because prior grooming alone did not elicit approach. Instead, subjects were most likely to approach their grooming partner when they had also heard her recruitment call. Thus, females' willingness to attend to the recruitment calls of other individuals appeared to be prompted at least in part by memory of a specific friendly interaction.

In sum, several factors may interact to motivate contingent cooperation in animals under natural conditions: the strength of the partners' social relationship, the nature of their recent interactions, and the opportunity to reengage in some form of cooperative behavior. Animals appear to possess many of the cognitive abilities thought to be essential for the emergence of contingent cooperation, if only in rudimentary form. Nonetheless, such cooperation appears to be less common than the noncontingent cooperation that develops among kin and long-term partners.

Detection of Noncooperators

If cooperation depends in part on the memory of previous behavior, why do animals seldom avoid or punish cheaters and free-loaders? In captivity, chimpanzees continue to work with noncooperators despite receiving inequitable returns (Melis et al. 2006b, 2009). While they retaliate against an individual who steals food from them, they do not attempt to punish those who obtain disproportionate rewards, and they are not spiteful (Jensen et al. 2007b; Melis et al. 2009; Silk and House 2011).

Under natural conditions, free-loaders also appear to be tolerated. To provide two examples, individual lionesses (*Panthera leo*) vary predictably in their participation in territorial conflicts. In playback experiments that simulated the approach of an aggressive intruder, some females consistently advanced toward the source of the calls, whereas others consistently lagged behind, avoiding the potential cost of a conflict (Heinsohn and Packer 1995). Advancers appeared to be aware of the laggards' behavior, because they often looked back at them; nonetheless, they did not subsequently avoid or punish them. It is possible that advancers tolerate laggards because they derive inclusive fitness benefits through the laggards' survival and reproduction. Laggards may also cooperate in other currencies, such as hunting. It is also possible, however, that lions do not have the cognitive ability to recognize laggards as free-loaders, with the result that laggards are able to exploit advancers.

Similarly, male chimpanzees do not participate equally in boundary patrols. Some individuals are allowed to reap the benefits of territorial integrity without incurring any costs. Mitani (2006, 2009a) offers several possible explanations for chimpanzees' tolerance of free-loaders. First, the benefits of patrolling may be greater for some individuals than others. Perhaps patrolling is a costly signal that enhances an individual's dominance or access to females. Second, patrolling may yield indirect fitness benefits in the form of enhanced survival and reproduction of close kin. Thus, males with more kin in the community may engage in higher rates of patrolling. Finally, chimpanzees may lack the cognitive capacity to foster or infer deceptive intent. If true, animals may well not be capable of achieving the sort of contingent cooperation manifested by humans, which is sustained in part by inequity aversion and sensitivity to envy, spite, and deception (Jensen et al. 2007b; Melis and Semmann 2010).

This last objection, however, only denies the possibility for human-like contingent cooperation in animals; it does not rule it out entirely. The detection of cheaters does not, in principle, require the ability to impute complex mental states like deception to others. It could arise through relatively simple associative processes, by which animals learn to avoid individuals whose presence is associated with a negative experience.

Indeed, mental state attribution may be irrelevant to contingent cooperation in animals. Schino and Aureli (2009) have argued that the focus on cognitive constraints in discussions of contingent cooperation is misguided and confuses proximate and ultimate explanations for behavior. Altruistic behaviors may be favored by natural selection because of the subsequent benefits they confer, but what motivates animals to behave altruistically are the previous benefits they have received. In this view, the accumulation of multiple, cooperative exchanges over time causes animals to form partner-specific emotional bonds that prompt future altruistic behavior. Thus, reciprocity may be maintained by a kind of partner-specific "emotional book-keeping" (Schino and Aureli 2009) that permits long-term tracking of multiple partners and facilitates cooperation in different behavioral currencies. The resulting bonds that develop between preferred partners may motivate future positive interactions without the need for explicit tabulation of favors given and returned, or calculations of anticipated benefits (Aureli and Schaffner 2002). For unrelated females who interact at low rates, a single grooming bout may temporarily elevate a female's positive emotions toward her partner sufficiently above baseline to influence her immediate interactions with her. In contrast, grooming and support among females with close bonds (who are also usually kin) should be less subject to immediate contingencies and less influenced by single interactions. Many of these proximate mechanisms may also motivate social interactions in humans. It seems unlikely that the formation of close bonds among humans is driven by expectations that such bonds will enhance health and longevity.

Finally, it is important to emphasize that while the absence of punishment in animals may derive partly from cognitive constraints, a strict accounting

of services given and received is likely maladaptive in stable societies where individuals establish close bonds and interact regularly in a variety of contexts. In fact, although the cognitive constraints that supposedly limit contingent cooperation in animals is often contrasted with humans' sensitivity to inequitable exchanges, human friendships are rarely contingency-based. Numerous studies have shown that people seldom keep tabs of costs and benefits in interactions with regular partners (Silk 2003a). Although people become resentful and dissatisfied when exchanges within a friendship are consistently unbalanced, tallying of favors given and received is typically reserved for infrequent associates.

These observations emphasize, again, the importance of separating proximate and ultimate explanations when considering cooperation in animals. Whether animals have the cognitive capacity to engage in contingent cooperation is one issue; whether it is adaptive for them to do is another. It may well be that the relative rarity of contingent cooperation in animals stems less from the inability to keep track of recent interactions (and even, perhaps, to anticipate future ones) than from the willingness to tolerate short-term inequities with long-term partners.

Future Directions

We are only beginning to understand the many functions of cooperative behavior in animals and the cognitive and emotional mechanisms which underlie them. There have been only a handful of direct experimental tests of contingent cooperation under natural conditions, and we do not yet understand how supportive, reciprocal relationships emerge from single interactions that are often asymmetrical. Similarly, as yet there have been few attempts to document the reproductive benefits of cooperation and strong social bonds. Here, I highlight three of many possible foci for future research.

Cognition

I have argued that contingent cooperation may not require complex cognition, such as the ability to detect cheaters or to plan future cooperative acts based on memory of previous ones. Nonetheless, some animals may engage in such mental activities. There is growing evidence that many animals have some access to their knowledge states (Smith et al. 2010). Such metacognition may permit animals to weigh alternative strategies in novel contexts; it may also serve as a precursor to reading others' minds. Playback experiments indicate that baboons remember the nature of specific interactions with specific individuals, although the extent to which this memory is explicit remains to be determined. Similarly, some forms of cooperative behavior in animals (in particular, the boundary patrols of chimpanzees) strongly suggest shared intentionality,

planning, and episodic memory. To date, however, these cognitive abilities have been examined only under captive conditions, in tests whose rules and constraints are determined by humans. A challenge for future research will be to devise the experimental means to examine mental state attribution and metacognition under more natural conditions, in contexts where these abilities may be of survival value.

Personality

Recent evidence from baboons indicates that females vary in the strength and stability of their social relationships, and that this variation contributes significantly to individual variation in reproductive success. The fact that some females fail to maintain the same partners over time also suggests that some individuals may be less skilled or motivated than others at maintaining bonds. Although the proximate mechanisms underlying these individual differences are not yet understood, they may well be related to personality traits associated with attributes like anxiety and confidence. In female primates there tends to be no correlation between stress and dominance rank or number of kin. Instead, glucocorticoid levels are more strongly influenced by the size and stability of a female's social network (Cheney and Seyfarth 2009). These observations suggest that some individuals may be more adept than others at recruiting allies, reconciling with others, or assessing the strength and stability of others' relationships. Whatever the cause, results point to the need for a stronger focus on the relation between behavior and personality.

Personality traits are influenced not only by genetic factors but also by environmental factors that affect gene expression. In both humans and rhesus macaques (Macaca mulatta), for example, a specific polymorphism in the serotonin transporter gene is associated with deficits in neurobiological functioning and poor control of aggression (Suomi 2007). Mothers carrying a certain version of the allele are more likely to be abusive, and both they and their infants exhibit higher cortisol levels. Indeed, maternal effects have been shown to have a profound impact on offspring dominance, hypothalamic-pituitary-adrenal axis, and personality in a variety of species (Jablonka and Raz 2009). These effects may persist across generations. Thus, genetic variation affecting factors such as serotonin and oxytocin reactivity, anxiety, and social reward may influence the strength and stability of an individual's social bonds, which in turn exert epigenetic effects in offspring. Differences in personality traits may well explain some of the individual variation in cooperative behavior.

Integration of Field and Laboratory Studies

There is currently some disconnect between results obtained in experiments with captive animals and observations derived from field observations. For example, chimpanzees in captivity seem relatively indifferent to inequitable

outcomes to others and themselves and fail to reciprocate favors in back-and-forth exchanges. In the wild, however, chimpanzees often exchange grooming, alliances, and meat with specific long-term partners. In captivity, tasks which require cooperation are easily disrupted by disparities in the participants' dominance ranks, the size of the rewards, and the degree to which rewards can be monopolized. Under natural conditions, however, chimpanzees not only share meat (if inequitably) but also regularly participate in risky boundary patrols that are obligately cooperative. These discrepancies point to the need both for more detailed investigations of cooperation in the wild and, in captivity, for experiments that carry greater external validity and relevance for the participants.