
The Strategic Dynamics of Cooperation in Primate Groups

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I. INTRODUCTION

The evolution of cooperation has played an important role in evolutionary biology over the last 40 years. There is a broad consensus that Hamilton's theory of kin selection (Hamilton, 1964) provides a basis for understanding the deployment of altruism among relatives in a wide range of animal taxa (Crozier and Pamilo, 1996; Dugatkin, 1997; Emlen, 1997; Sachs *et al.*, 2004). In contrast, there is considerably less agreement about the evolutionary processes that regulate the distribution of benefits to nonrelatives. Although Trivers (1971) introduced the theory of reciprocal altruism nearly 35 years ago, researchers have produced relatively few examples of reciprocal altruism in nature (Dugatkin, 2002; Hammerstein, 2003; Noë, 2005, 2006). Even the most carefully documented examples, such as predator inspection in schooling fish (Milinski, 1987) and egg-trading in simultaneous hermaphrodites (Fisher, 1988), have been disputed (Connor, 1992, 1995; Dugatkin, 1997; Hammerstein, 2003; Sachs *et al.*, 2004). This has led some researchers to focus on other processes, such as by-product mutualism, group augmentation, and market forces, to explain the evolution of cooperation among nonrelatives (Clutton-Brock, 2002, 2005; Connor, 1986, 1992, 1995; Kokko *et al.*, 2001; Noë, 2005, 2006).

Here I consider the nature of cooperation among nonkin in nonhuman primate groups, concentrating on evidence for turn-taking, collaboration, and coordination. Nonhuman primates are an appropriate group of animals to focus on for several reasons. First, nonhuman primates (primates, hereafter) perform a variety of services on behalf of other group members. They groom one another; provide support in agonistic encounters; collectively defend

access to mates, food resources, and territories; actively donate food or tolerate scrounging; provide alloparental care; and warn group members when they detect predators. Second, primates fulfill a number of the basic requirements for contingent reciprocity: they live in stable social groups, recognize group members as individuals, and have large brains and good memories. Third, there is a rich body of naturalistic and experimental data about the deployment of cooperative behavior in a number of primate species. While there is abundant evidence of kin biases in cooperative behavior (Chapais and Berman, 2004; Silk, 2002a, 2005), the role of contingent reciprocity in primates remains controversial (Barrett and Henzi, 2002, 2005; Noë, 2005, 2006; Stevens and Hauser, 2004; Stevens *et al.*, 2005a).

Controversy about the forces that shape cooperation among nonrelatives in primate groups persists for at least two different reasons. First, there is considerable disagreement about what the term “cooperation” means. Here I argue that game theory provides a way to avoid unproductive disputes about terminology and to focus our attention on the processes that favor the distribution of benefits to unrelated individuals.

Second, controversy persists because it is difficult to measure critical parameters under naturalistic conditions. Thus, much of the evidence that I describe here comes from experimental studies conducted in the field and laboratory. I begin with the first experiments on cooperation which were conducted in the 1930s, and carry on to the present. This body of experimental work provides an important complement to naturalistic observations of cooperation. Well-designed experiments constrain the range of possible explanations for cooperation; they provide a measure of control over theoretically relevant parameters, including the effort required to solve a task, the benefits acquired when a task is completed successfully, and the temporal sequence of events; and crucially, they make it possible to test whether cooperation is contingent of the previous cooperative behaviors of others. In addition, when experiments using the same protocol are conducted on different groups or species, they provide a standardized baseline for comparative analyses. This literature includes an array of valuable methods and innovative designs for apparatuses that could be adopted or adapted in new experiments.

II. (AVOIDING) DEFINITIONS OF COOPERATION

Take care of the sense and the sounds will take care of themselves

The Duchess to Alice in *Alice in Wonderland*

Cooperation means different things to different people. Boyd and Richerson (2006) define cooperation as “costly behavior performed by one individual that increases the payoff of others.” In contrast, Noë (2006) suggests that we use the word cooperation “for all interactions or series of interactions that, as a rule (or ‘on average’), result in net gain for all participants. The term includes all other terms that have been used for mutually rewarding interactions and relationships: reciprocity, reciprocal altruism, mutualism, symbiosis, collective action and so forth.” Sachs *et al.*’s definition focuses on the behaviors that benefit others, regardless of the effect on the actor (Sachs *et al.*, 2004). Bronstein (2003) differentiates between mutually beneficial interactions with members of the same species and members of other species. She applies the term cooperation to the former and mutualism to the latter. Brosnan and de Waal (2002) define cooperation as “the voluntary acting together of two or more individuals that brings about, or could potentially bring about, an end situation that benefits one, both, or all of them in a way that could not have been brought about individually.” Stevens and Hauser (2004) adopt Clements and Stephens’s (1995) definition of cooperation as “joint action for mutual benefit.” There is one common element of all these definitions of cooperation: benefits are provided to other conspecifics, but not consensus about the impact on the actor.

There is no easy way to resolve this semantic muddle, but there is a way around it. Following the Duchess’ advice to Alice, we can make progress by focusing on the dynamics of interactions that confer benefits on other individuals, rather than worrying about what terms we should use to describe them. Game theory provides a useful way to discipline our thinking about the strategic dynamics of these kinds of interactions. There are several different games that represent situations that correspond to various definitions of “cooperation.” These games allow us to explore the conditions under which natural selection will favor individuals who provide benefits to unrelated partners.

It should be noted that these games were mainly developed by economists and were meant to apply to real-life situations. The names that these games were given reflect everyday scenarios which were used as exemplars of the processes involved. For example, the Prisoner’s Dilemma gets its name from a situation in which two prisoners are interviewed separately and are given the choice between informing on their partners in exchange for a lighter sentence or remaining silent. This situation is used to explore the dynamics of altruism (remaining silent) when there is a temptation to defect (informing on the partner). The games have a generality that extends beyond their names. (For more about the logic underlying game theory, see Maynard Smith, 1982; McElreath and Boyd, in press.)

III. GAME THEORY MODELS OF FORMS OF “COOPERATION”

A. ITERATED PRISONER’S DILEMMA

The Iterated Prisoner’s Dilemma is the best known of these games. In the one-shot version of the Prisoner’s Dilemma, players benefit if they both cooperate, but each is better off if the other cooperates and they act selfishly themselves. For example, two monkeys are threatened by a predator, like a leopard. If either one mounts a counterattack, they are likely to drive the predator away. But this is a costly thing to do, as there is some danger associated with confronting the leopard. However, if one holds back while the other chases the leopard, the one that holds back will be protected without incurring the costs of confronting the predator. The same will hold for the other monkey. So, the monkeys face a real dilemma. Not knowing what the other will do, both monkeys have a strong incentive not to confront the leopard themselves. Defectors, who hold back, will always be favored. The payoff matrix for this game is laid out in Table I.

The dynamics of the Prisoner’s Dilemma are fundamentally altered when two individuals face the same situation repeatedly. Then, contingent strategies may be favored. That is, one monkey may protect her partner from the predator, as long as her partner protected her before. These kinds of contingent strategies can be sustained as long as $b > c(1 - 1/t)$, where b is the benefit derived from the other’s helpful act, c is the cost of the helpful act, and t is the likelihood that they will interact again in the future. This repeated process is the foundation of the theory of reciprocal altruism (Axelrod and Hamilton, 1981; Trivers, 1971). Subsequent theoretical work has shown that a variety of contingent strategies, not just strict tit for tat, can be evolutionarily stable under the appropriate conditions.

TABLE I
 THE PRISONER’S DILEMMA

| Player 1 | Player 2 | |
|------------------------|----------------|---------|
| | Cooperate | Defect |
| Cooperate ^a | $b - c, b - c$ | $-c, b$ |
| Defect | $b, -c$ | $0, 0$ |

^aEach individual has the opportunity to cooperate by helping the other individual. Helping increases the payoff of the receiver by two units and reduces the payoff of the actor by one unit.

TABLE II
 THE STAG HUNT

| Player 1 | Player 2 | |
|-------------------|----------|--------|
| | Stag | Hare |
| Stag ^a | s, s | $0, h$ |
| Hare | $h, 0$ | h, h |

^aHunters can either hunt stag or hare. Hunting hares together does not affect success; they always get a small payoff, h . If they hunt stag together, they are likely to succeed, and achieve a high payoff, s . A stag hunter who hunts alone fails and receives a payoff of 0.

B. STAG HUNT

The Stag Hunt describes a situation in which two individuals can profit from working together. Hunting alone, each individual is only able to catch small game, like hare. But if they hunt together, they are able to take much larger game, such as stags. One stag weighs considerably more than two hares, so it is profitable for two individuals to hunt together and share the kill. Both players earn higher payoffs if they both hunt stags than if only one hunts stag or if they both hunt hares (Table II). Of course, it will not be profitable for individuals to cooperate unless they are likely to obtain a reasonable share of the stag. It is not necessary that both partners get the same payoff, only that each partner gets a bigger payoff from participating in the Stag Hunt together than they would get from hunting hare alone.

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C. BATTLE OF THE SEXES

The Battle of the Sexes game describes another kind of strategic interaction that can lead individuals to provide benefits to others. Imagine that two people would like to be together, but they have different preferences about what to do. One wants to go to the climbing gym, the other wants to watch monkeys at the zoo. If the benefits of being together outweigh the benefits of pursuing their own preferences, then they will make some kind of compromise about where to go (Table III). The compromise may be reached by taking turns, bargaining, or relying on some kind of conventional asymmetry (e.g., age, dominance rank, sex). The Battle of the Sexes reveals the importance of coordination. In this situation, the highest payoff is obtained when both individuals do the same thing, and neither has an incentive to provide misleading information about their intentions. It would make no sense to promise to meet at the climbing gym, and then head for the zoo.

TABLE III
 THE BATTLE OF THE SEXES

| Player 1 | Player 2 | |
|---------------------------|--------------|------|
| | Climbing gym | Zoo |
| Climbing gym ^a | b, a | 0, 0 |
| Zoo | 0, 0 | a, b |

^aIndividuals have to rendezvous at either the climbing gym or the zoo. Both players receive higher payoffs when they end up in the same place. However, player 1 prefers to meet at the climbing gym, while player 2 prefers the zoo.

TABLE IV
 CHICKEN GAME (ALSO KNOWN AS THE SNOWDRIFT GAME OR HAWK-DOVE GAME)

| Player 1 | Player 2 | |
|-------------------|----------------|-------------|
| | Wash | Do not Wash |
| Wash ^a | $b - c, b - c$ | $b - c, b$ |
| Do not Wash | $b, b - C$ | 0, 0 |

^aThe dishes need washing. If they are washed both players get a benefit, b . If the two players share the burden of washing, they each pay a cost, c . If only one washes, he pays a bigger cost C . However, $b - C > 0$, so individuals prefer washing alone to waking up to dirty dishes.

D. GAMES OF CHICKEN

Finally, there is one more way that these kinds of problems may be played out. In games with a Chicken or Hawk-Dove payoff structure, both players benefit from a given outcome, but neither wants to incur the costs associated with securing it. To see how this works, imagine the following domestic dilemma: a couple confronts a sink full of dirty dishes. There are four possible outcomes in this situation: one partner does the dishes, the other partner does the dishes, they do them together, or they leave them in the sink. Suppose that both partners would prefer to do the dishes, even if they have to do them alone, over leaving them in the sink overnight. But both would rather prefer that the other does the washing up by themselves than wash the dishes together. In this situation, cooperation is individually beneficial, but each partner is better if they can persuade the other to wash the dishes by themselves (Table IV).

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This game differs from the Prisoner's Dilemma in one critical way. Here, each player obtains a higher payoff from cooperating even when its partner defects than if both defect, the opposite of the ordering in the Prisoner's

Dilemma. But even though each partner is prepared to cooperate, they can still benefit if they can induce the other to perform the altruistic act. This conflict of interest may be resolved by flipping a coin, taking turns, or relying on a conventional asymmetry, such as the person who cooks does not have to do the dishes.

IV. WHICH KINDS OF GAMES DO PRIMATES PLAY?

Social life may provide animals with opportunities to play all of the games described above. However, researchers interested in the evolution of “cooperation” have focused mainly on situations that correspond to the Iterated Prisoner’s Dilemma and the Stag Hunt. Below, I review the substantial body of naturalistic and experimental work on reciprocity that has been conducted in the field and laboratory. Next, I describe a body of research which focuses on situations in which animals must work together to achieve joint goals, and loosely approximates the dynamics of the Stag Hunt. Researchers interested in cooperation have given considerably less consideration to coordination problems, although such situations must arise regularly in the everyday lives of group-living animals. I describe a small body of work which focuses on the dynamics of coordination in primate groups. Finally, I sketch how Games of Chicken may be played in primate groups.

V. THE ITERATED PRISONER’S DILEMMA IN PRIMATE GROUPS

A. CONTINGENT RECIPROCITY IN THE NONEXPERIMENTAL SETTINGS

In the Iterated Prisoner’s Dilemma, each player cooperates as long as its partner cooperates, although there is considerable latitude in the characteristics of the strategies that may be employed. (Recall the payoff matrix in Table I). In this game, the behavior of each player is influenced by the behavior of the other player partner in previous moves, and cooperation is therefore contingent on previous cooperation.

The first efforts to study contingent reciprocity in primates were based on correlational analyses of dyadic interactions. For example, in one of the first empirical applications of the theory of reciprocal altruism, Packer (1977) showed that male savannah baboons (*Papio cynocephalus*) are most likely to recruit support from the males that recruited support from them. Subsequently, it has been reported that chimpanzees (*Pan troglodytes*) share food most often with those that share most often with them (de Waal, 1989;

Mitani, 2005), and female savannah baboons, macaques (*Macaca* spp.), and capuchins (*Cebus* spp.) spend the most time grooming females who spend the most time grooming them (Manson *et al.*, 2004; Silk *et al.*, 1999). Grooming may be balanced within bouts (Barrett *et al.*, 1999; Cords, 2002) or across bouts (Manson *et al.*, 2004; Schino *et al.*, 2003). Not all exchanges involve a single currency. Seyfarth (1977) was the first to suggest that support might be exchanged for grooming, and subsequently showed that female vervets (*Chlorocebus aethiops*) selectively support unrelated females that groom them most often (Seyfarth, 1980). However, the empirical regularity of exchanges between grooming and coalitionary support remains in dispute (Barrett and Henzi, 2002, 2005; Schino, 2001; Stevens *et al.*, 2005).

Correlational studies like these suffer from a number of shortcomings. One problem is that the observed associations could be the product of a third factor that has not been measured or taken into account, such as kinship or dominance rank (Hemelrijk and Ek, 1991). Moreover, even if relevant confounding variables can be excluded or controlled statistically, correlational analyses do not address the problem of contingency. That is, would one animal stop grooming its partner if its partner did not respond to solicitations for support or failed to groom in return? If we cannot specify what currencies are being exchanged or assess the value of the commodities being traded, we cannot tell whether the pattern of interactions satisfies the conditions for the Iterated Prisoner's Dilemma. Even the absence of statistically significant correlations may not rule out reciprocity if one of the exchange commodities, such as coalitionary support, is rare but valuable (Schino, 2001).

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B. EXPERIMENTAL STUDIES OF CONTINGENT RECIPROCITY

The difficulties of studying the processes underlying exchanges in nature lead us to experimental studies in which animals are able to take turns providing benefits to one another. Claims about whether primates practice contingent reciprocal strategies depend on the statistical relationship between the behavior of the two players, so it is important to scrutinize the analyses and results with some care.

1. *Naturalistic Experiments on Contingent Reciprocity*

Seyfarth and Cheney (1984) designed the first explicit experimental test of the theory of reciprocal altruism in primates. They showed that wild vervet monkeys were more attentive to the tape-recorded screams of unrelated group members if they had been groomed recently by the caller than if

they had not been groomed recently by the same monkey. Interestingly, contingent effects were restricted to unrelated dyads. For close kin, the likelihood of providing support was not influenced by recent grooming. Seyfarth and Cheney were able to control for variation in the quality of social bonds by using a within-subject design in their analysis. However, because the conflicts were simulated by the experimenters, there was no opportunity for the listeners to come to the caller's aid in a real dispute, leaving some doubt about the likelihood that they would do so.

This problem was addressed in a study of captive long-tailed macaques (*Macaca fascicularis*; Hemelrijk, 1994). In this experiment, unrelated monkeys from a large social group were temporarily housed in groups of three. Grooming was artificially induced by dropping a sticky treat onto the back of one of the two higher-ranking animals. Then, aggression was induced by giving a treat to the lowest-ranking member of the trio. Hemelrijk found that in all seven of the trios that she tested, monkeys were more likely to provide support for the lower-ranking female if that female had previously groomed them. The magnitude of this effect ranged from a threefold increase in the likelihood of providing support to a one-third increase in the likelihood of providing support. Hemelrijk also considered the possibility that grooming *per se*, regardless of its direction, increased the likelihood of subsequent support. She found that in five of the seven dyads, females were more likely to provide support to females who had previously groomed them than to females that they had groomed themselves.

Chimpanzees seem to exchange grooming for access to food (de Waal, 1989), in much the same way that monkeys exchange grooming for agonistic support. To assess the contingency between grooming and food sharing more systematically, de Waal (1997a) observed captive chimpanzees for several hours before and after they were provided with a desirable food item, leafy branches. Chimpanzees that gained possession of the branches sometimes allowed others to take leaves from them. They were especially likely to allow those who had groomed them in the previous hours to share their food. Possessors were also less likely to respond aggressively when chimpanzees that had groomed them recently attempted to obtain food than when others attempted to obtain food. de Waal also examined the possibility that chimpanzees who had been groomed were uniformly more tolerant than chimpanzees who had not been groomed, but this was not the case. Chimpanzees selectively tolerated those that had groomed them. However, the relationship between grooming and tolerance only held for those who did not groom often. For pairs that groomed at higher rates, tolerance did not depend on grooming in the period before provisioning. One interpretation of these data is that some dyads keep track of exchanges over

short timescales, while others monitor exchanges across longer periods. Similar variation in the timescale of reciprocity has been reported for wild white-faced capuchins (*Cebus capucinus*; Manson *et al.*, 2004).

These studies suggest that vervets, long-tailed macaques, and chimpanzees are more likely to provide benefits to individual group members if that individual has recently groomed them. One of the main strengths of these three studies is that they assess the contingencies between grooming and other forms of altruism in fairly naturalistic settings. However, these studies were not designed to follow the sequence of interactions within dyads. If contingent reciprocity is operating in these situations, then we would expect support or tolerance by the former recipient of grooming to be associated with subsequent grooming, while the failure to provide support or tolerate sharing would lead to subsequent reductions in grooming. While these studies suggest that monkeys and apes reward cooperators, it is not clear that they subsequently withhold cooperation from noncooperators.

2. *Laboratory Experiments on Contingent Reciprocity*

The first explicit study of turn-taking in primates that I have found was conducted in the 1930s on monkeys and children (Wofle and Wofle, 1939). In this experiment, two monkeys were placed in adjacent cages. Each monkey could reach a rope that was attached to a lever. When the rope was pulled, the lever pivoted and delivered a grape to the monkey in the adjacent cage. Unfortunately, Wofle and Wofle tested a rather odd set of monkeys and did not always form pairs consisting of animals of the same species. All of the monkeys pulled the levers regularly and delivered rewards to their partners, but there is no information about whether their pulling was contingent on the behavior of their partners. Wofle and Wofle compared the monkeys' performance when the levers were baited with grapes and when they were not baited, and they also evaluated the monkeys' performance when there was another monkey in the adjacent cage and when they were alone. Half the monkeys pulled more when the lever was baited than when it was not baited. Of these four monkeys, none differentiated between the presence and absence of another monkey in the adjacent cage. (In parallel experiments on four pairs of children, children who were older than 3 years generally provided rewards for their partners, pulled more when the levers were baited than unbaited, and did not pull the levers when their partner was not present. Two children under the age of 3 years did not make these distinctions.)

de Waal and his colleagues have conducted a series of studies of food exchanges in captive brown capuchins, *Cebus apella*. Their first set of experiments was modeled on Nissen and Crawford's (1932) experiments with chimpanzees. Nissen and Crawford placed two chimpanzees in

adjacent enclosures and provided food or tokens that could be fed into a food dispenser to one of the two individuals. In this situation, possessors sometimes responded positively to begging, but did not often donate food spontaneously. Nissen and Crawford emphasized that dyads that had close social bonds were most likely to exchange food in the experimental setting.

Capuchins are good subjects for these kinds of experiments because they are extremely gregarious and are very tolerant of others' efforts to take bits of their food. de Waal (1997b) placed two capuchins in adjacent enclosures separated by wire mesh. In one series of tests, food bowls were placed at the far ends of the two enclosures, so that only one of the monkeys could reach each bowl (Fig. 1). In the first phase, one bowl was baited with cucumbers. After 20 minutes, the food bowl on the other side was baited with apples. In a second set of tests, foods were presented in the opposite order so that the first monkey got apples and the second monkey got cucumbers (nearly all capuchins prefer apples over cucumbers).

When the possessor carried food close to the wire mesh, the monkey on the other side was sometimes able to obtain pieces of the possessor's food. More than half of the time, the monkey without food waited "... for discarded pieces, collecting or trying to collect them from within the possessor's reach" (de Waal, 1997b). In an additional 40% of cases, the monkey without food obtained food when the possessor was out of reach of the food item or its back was turned. The possessor rarely made deliberate efforts to deliver food to the other monkey, and the possessor did not often overtly resist the other monkey's attempts to take food. Because the other

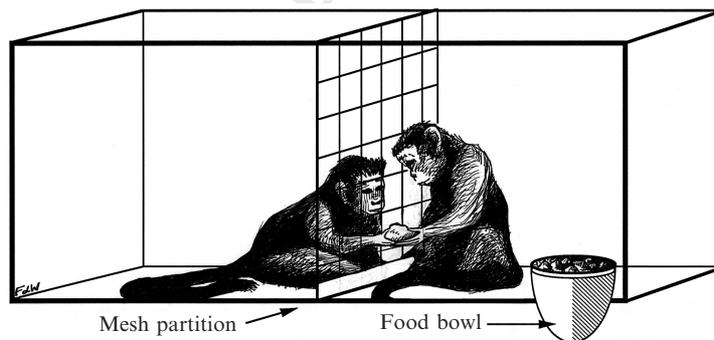


FIG. 1. Cage configuration used in de Waal (1997b) and de Waal (2000). The monkeys are placed in adjoining enclosures divided by a wire mesh partition. The monkeys can reach through the mesh partition but cannot reach the food bowl on the far side of the adjacent cage. The dimensions of the test chamber are $144 \times 60 \times 60 \text{ cm}^3$. (Drawing by Frans de Waal after an actual video still.)

monkey is only able to get food when the possessor carried it to the mesh barrier, but the possessor is otherwise fairly passive, de Waal (2000) subsequently characterized capuchin food transfers as “facilitated taking,” rather than food sharing.

To determine whether monkeys obtain food selectively from those who obtain food from them, de Waal assessed the pattern of transfers within dyads. When he included all types of transfers in the analysis, the correlation was not significant. But when he excluded the transfers that occurred when the possessor was out of reach of the food item or its back was turned, a significant positive correlation emerged. Thus, monkeys generally obtained most of the food from the monkeys who obtained most of the food from them. The magnitude and direction of the correlations varied considerably across individuals (range ≈ 0.7 to -0.4), with females generally showing stronger and more positive correlations than males. This experiment shares some of the same liabilities as naturalistic correlational studies. High levels of food transfers within dyads might reflect strong mutual social tolerance, not a contingent behavioral strategy (de Waal, 1997b).

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To address this problem, de Waal (2000) conducted another set of experiments in which he tracked food transfers within dyads across time. In some trials, pairs of monkeys were provided with the same food at the same time, in some they were given access to the same foods in turn, and in some they were given access to different foods at different times. A number of results emerge from this set of experiments. First, although the monkeys are attracted to their partners and generally tolerated their partners' efforts to take food from them, there are limits to their largesse. Monkeys spent more time near the partition when there was another monkey in the adjoining cage than when they were alone, but they were much less likely to drop whole pieces of food near the partition when there was another monkey in the adjoining cage. Moreover, when one monkey was given more attractive food than the other monkey, the owner of the more attractive food item spent less time near the partition. These data suggest that monkeys weigh the benefits and costs of proximity; when they are likely to lose more than they gain by being near the partition, they spend less time there. However, in the absence of evidence that the possessor would have eaten the food that its neighbor takes, it is not clear whether the loss of food represents a real cost to the possessor.

de Waal's main objective in these experiments was to determine whether food transfers were contingent. By testing the same dyad on multiple occasions, de Waal was able to examine the effects of behavior in one round on behavior in subsequent rounds, a key requirement for examining contingency. He categorized each dyad based on the behavior of the first player in the first trial. If the number of tolerant transfers in the first trial

was higher than the mean number of tolerant transfers in subsequent trials for the same dyad, the dyad was classified as having a high initial tolerant transfer rate. If the number of tolerant transfers in this trial was lower than the mean number of tolerant transfers in subsequent trials for the same dyad, the dyad was classified as having a low initial tolerant transfer rate. Then, de Waal computed the mean number of tolerant transfers in subsequent trials for both types of dyads. He found that dyads with high initial tolerant transfer rates had significantly higher transfer rates in subsequent trials than dyads with low initial tolerant transfer rates.

de Waal used this procedure to categorize dyads so that he would be able to correct for differences in the overall levels of tolerant transfers across dyads, and he would be able to exclude the possibility that some dyads have high rates of tolerant transfers simply because they spend a lot of time together and were very tolerant of scrounging. However, this procedure for categorizing dyads is problematic. By definition, the dyads that were classified as having a high initial tolerant transfer rate were more tolerant in earlier trials than later ones, while those that were classified as having low initial tolerant transfer rate were more tolerant in later trials than in initial ones. de Waal's finding that there was an absolute difference in the number of tolerant transfers among dyads with high and low initial transfer rates does not demonstrate that the amount of tolerance in one trial was positively associated with the amount of tolerance in the next trial, a crucial element required for demonstrating contingency.

de Waal and Berger (2000) used a bar pull apparatus to evaluate whether capuchins trade effort for access to food. This apparatus was inspired by Crawford's (1937) experiments on chimpanzees. de Waal's version of the apparatus consists of a long tray with one pull bar at each end. The tray can be counterweighted so that it is too heavy for one monkey to pull forward on its own. When the bar is pulled forward, both monkeys can reach rewards placed in food cups on the tray. By manipulating the location and baiting of the food cups, a number of different questions have been addressed. In de Waal and Berger's experiment, three different treatments were compared. In one treatment, the bar was counterweighted so that it was too heavy for one monkey to pull in alone, but only one bowl was baited. In another treatment, the bar was too heavy for one monkey to pull alone, and both bowls were baited. In a third treatment, one monkey was able to pull the bar in alone and only its own bowl was baited.

de Waal and Berger found that the monkeys were considerably less successful in pulling in the bar when only one bowl was baited, but it took two monkeys to pull in the bar (food obtained in 39% trials), than they were when both bowls were baited (89%) or when one monkey was able to obtain food on its own (85%). However, more food was obtained by the

monkey who did not have access to a food bowl when both monkeys worked together to pull in the bar than when one monkey was able to pull in the bar without help. In addition, monkeys were more tolerant of others' effort to obtain food when help had been provided. Although helping is associated with increased access to food, the magnitude of the effect is relatively small and the direction of causality is unclear. Monkeys who pulled in the food bar by themselves tolerated about 59% of all attempts to take food, while monkeys who had help pulling in the bar tolerated 65% of all attempts. This could mean that monkeys selectively rewarded helpers with tolerance and would justify the paper's title, *Payment for Labour*. Alternatively, monkeys may have been more likely to help those that were generally tolerant of them; and tolerance may not have been contingent on prior help.

Hattori *et al.* (2005) trained brown capuchins to complete a two-step sequence to obtain food rewards. First, the monkeys had to pull a tab in one box, and then they had to push a block in a different box. After the sequence was completed, one reward was released in each of the boxes. Initially, each individual was taught to perform both of the necessary tasks in the appropriate order. Then, the monkeys were tested in pairs. Each individual was confined to a single box, and the two boxes were separated by a transparent window. To obtain rewards, each individual had to perform the appropriate task. Hattori and his colleagues tested three unrelated pairs; all succeeded in the task. In one treatment, Hattori and his colleagues altered the payoff structure, so that only one individual obtained a reward in each trial. The roles of the players alternated between trials. The three pairs succeeded in the majority of trials (70–90%), even though only one individual obtained a reward in each trial. Hattori and his colleagues conclude that these data provide evidence for a “primitive form of reciprocal altruism.”

Although the monkeys frequently succeeded in the task, the data do not provide clear evidence of contingency. While successful trials were much more likely to be followed by successful trials ($n = 44$) than unsuccessful trials ($n = 2$), the relatively small number of unsuccessful trials ($n = 8$) were equally likely to be followed by successful trials as unsuccessful trials. (These values do not include trials during one session which the experimenters were forced to rerun, but the pattern does not change substantially when this session is included.) This suggests that these monkeys may have been unilateral cooperators, not contingent reciprocators.

Hauser *et al.* (2003) developed an ambitious experimental protocol to examine contingent behavioral strategies in cotton-top tamarins, *Saguinus oedipus*. In these experiments, two tamarins were placed in adjacent enclosures, divided by a partition. One monkey could pull on an L-shaped bar in

front of the cages to bring food items within reach. During the training phase, the monkeys learned to pull in the bar whenever food was placed on their own side, but never to pull the bar when food was placed on the other side.

In one experiment, five tamarins were each paired with two unrelated female “stooges.” (Pairs were composed of members of different groups.) One of these tamarin stooges was trained to always pull the bar, the other stooge was trained to never pull the bar. The pull bar was available to nonstooge subjects and stooges on alternate trials within sessions. In every trial, the bar was baited so that the monkey that pulled the bar provided food to the other monkey, but obtained no food itself. In half the sessions, the stooge made the first move, and in half the sessions the nonstooge subject made the first move. Overall, tamarins pulled more often for the stooge that provided food to them (38%) than for the stooge that did not provide food for them (7%). These differences were apparent from the beginning of each session, suggesting that the tamarins remembered something about the behavior of their partners during previous sessions.

Hauser *et al.* found that the rate of pulling for altruistic stooges declined across trials within each session, but there was no significant decline in the frequency of pulling across sessions. They attribute the decline within sessions to end game effects, which are sometimes observed when humans play repeated games. End game effects probably occur because players anticipate the end of a game and know that they will be able to defect without suffering retribution from their partner. However, when they are observed, end game effects are typically seen only in the very last rounds of games, creating a more precipitous decline in altruism than the tamarins displayed. Moreover, in order to be sensitive to end game effects, players need to know how exactly long the game will last, something that the tamarins are not likely to have known. Thus, this does not provide a completely satisfactory explanation for the decline in the rate of pulling across trials within sessions.

Hauser *et al.* conducted three additional experiments that were intended to determine whether the tamarins were sensitive to the altruistic motivations of their partners. None of these experiments involved the stooges. In one of these experiments, subjects were paired in a game that consisted of 5 sessions of 24 trials. In the first three sessions, the bar was baited so that the subject provided food to its partner, but received no food itself. In the fourth session, the bar was baited so that the subject provided food to itself and its partner. In the fifth session, the bar was baited as in the first three sessions. Hauser *et al.* reasoned that if monkeys simply pulled when their partners had pulled, the rate of pulling would be higher in session 5 than in the first three sessions. But if the monkeys distinguished between altruistic

behavior and self-interested behavior, the rate of pulling would not increase. In the first session, tamarins pulled about 38% of the time, and this rate declined to about 25% in the second and third sessions. In the fourth session, when both animals obtained benefits, subjects pulled in all trials. Pulling rates in session 5 were not significantly elevated over the pulling rates in the first three sessions. They conclude that “? to impact upon the level of altruistic food giving, it appears that prior actions must also be altruistic.” However, it is also possible that the tamarins may have perceived that the payoff matrix in session 4 was different than the payoff matrix in the other sessions and behaved differently.

In the third experiment, the distribution of rewards was changed between trials. In the first trial, the monkey that pulled (Player 1) obtained one food item and the other monkey (Player 2) received three food items. In the next trial, Player 2 was given access to the pull bar. If it pulled, it would obtain no rewards, but Player 1 would obtain two food items. If both monkeys pulled in each round, both would receive three food rewards. The monkeys who took the role of Player 1 pulled in nearly all trials (97%), while the monkeys who took the role of Player 2 rarely pulled (3%). This value is considerably lower than the rate of pulling when paired with unconditional altruists (38%) and lower than the rate of pulling when paired with unconditional defectors (7%) in the first experiment. Hauser *et al.* interpret this difference to mean subjects are “sensitive to the costs borne by their partners when deciding whether to pull.” Alternatively, monkeys may be ignoring the benefits that their partner obtains, and pull only when they benefit directly.

Finally, Hauser *et al.* evaluated the tamarins’ responses to a partner who did not actively participate in the distribution of rewards. In this case, tamarins were paired with passive partners who never had access to the pull bar. After the test subject pulled, a human experimenter flipped the bar pull around and delivered a reward to the test subject. Thus, the test subject was unconditionally rewarded in every trial, but the rewards were not provided by the partner. In these sessions, the test subjects pulled 10% of time, only slightly more often than they pulled for the stooge that never pulled.

Based on these data, Hauser *et al.* concluded that “tamarins altruistically give food to genetically unrelated conspecifics, discriminate between altruistic and selfish actions, and give more food to those who give food back. Tamarins therefore have the psychological capacity for reciprocally mediated altruism.” This conclusion was modified in a subsequent paper (Stevens and Hauser, 2004) which emphasized the fact that the tamarins pulled less than half the time even when paired with unconditional altruists and that the likelihood of pulling declined across trials within sessions. For these reasons, Stevens and Hauser concluded that tamarins do not

demonstrate “robust reciprocity.” However, Chen and Hauser (2005) reanalyzed results from the pairings among nonstooge subjects. They borrowed techniques used in economics to detect the strategies underlying the tamarins behavior. According to their analysis, the tamarins’ behavior most closely approximates a strategy called “two tits for a tat,” which means that it takes two acts of cooperation by one player to induce the other player to begin cooperating again.

C. IS THERE SOLID EVIDENCE OF CONTINGENCY?

It is very difficult to detect the existence of contingent reciprocity in naturalistic settings, forcing investigators to rely on statistical evidence of associations between various forms of help given and received within dyads. These kinds of data are problematic because observed associations could be the product of variables that have not been measured. One solution to this problem has been to statistically control for the effects of third variables, such as rates of association. However, this does not solve the problem because it does not identify the causal factors creating the relationship between variables, no matter how many there are.

Although there are many reasons to be dissatisfied with correlational evidence, it is important to remember that these correlations *could* be the product of contingent reciprocal strategies. This is a case in which the absence of evidence should not be mistaken for evidence of absence.

Given the continuing controversy over the empirical status of contingent reciprocity in nature and the relevance of primates for understanding the evolutionary roots of cooperation in humans, it is surprising that there have been so few experimental studies of contingent reciprocity in primates. These studies are largely consistent with the prediction that altruism by one member of a dyad individual will increase the likelihood that the other member of the dyad will behave altruistically. However, none of the experiments provide entirely convincing evidence that primates reward cooperators and punish defectors in a consistent way.

Being groomed apparently makes long-tailed macaques and vervets more likely to provide support to their former grooming partners and makes chimpanzees more tolerant of efforts to take food from them. However, these studies do not tell us whether monkeys and chimpanzees also punish defectors by refusing to provide benefits to them in the future. The capuchins that Hattori *et al.* tested cooperated frequently, even when only one individual obtained a reward, but they did not seem to punish defectors consistently. de Waal and Berger’s conclusion that capuchins trade labor for food rewards may be correct, but their analysis does not establish the contingency between labor and payment.

While Hauser's experiments were explicitly designed to examine contingencies, even Hauser *et al.* have found the results somewhat difficult to interpret (references above). None of these studies have convinced skeptics that primates regularly practice contingent reciprocity.

D. DO COGNITIVE LIMITATIONS PRECLUDE CONTINGENT RECIPROCITY?

Some researchers have argued that cognitive constraints and psychological biases may preclude the deployment of contingent reciprocal strategies, even in highly encephalized animals like primates (Barrett and Henzi, 2002, 2005; de Waal, 2000; Dugatkin, 2002; Stevens and Hauser, 2004; Stevens *et al.*, 2005a; Visalberghi, 1997). For example, primates may lack the ability to assess and keep track of benefits given and received across time and currencies (Barrett and Henzi, 2002, 2005; de Waal, 2000) or wait for delayed rewards (Stevens and Hauser, 2004).

Recently, researchers have begun to develop experimental procedures to investigate these capacities in primates. Primates are adept at evaluating the value of resources involved in exchanges (Brosnan and de Waal, 2003; Brosnan *et al.*, 2005; Drapier *et al.*, 2005; Dubreuil *et al.*, 2006; Hyatt and Hopkins, 1998; Padoa-Schioppa *et al.*, 2006; Sousa and Matsuzawa, 2001). There is a considerable variation in primates' willingness to wait for delayed rewards (Beran, 2002; Beran *et al.*, 1999; Stevens *et al.*, 2005b), and some species are considerably more patient than others. If such capacities have been subject to natural selection, then it is not obvious that cognitive constraints preclude the capacity for contingent reciprocity.

VI. STAG HUNTS IN PRIMATE GROUPS

A. STAG HUNTS IN THE WILD

In the Stag Hunt, both players derive greater benefits from working together than either could achieve alone (Table II). There are at least four kinds of interactions that can be interpreted as natural analogues of the Stag Hunt: coalition formation, group hunting, joint mate guarding, and revolutionary coalitions.

In East African baboon groups, males form consortships with (or mate guard) receptive females. On the days when females are most likely to conceive, high-ranking males monopolize access to them. In some cases, two lower-ranking males jointly challenge the higher-ranking male and attempt to gain control of the female. These interactions can escalate to energetically costly chases and physical confrontations. The challengers often succeed in driving the higher-ranking male away, and one of them

begins to consort with the female. Packer (1977) found that males most often solicited support from the males that most often solicited support from them, and hypothesized that these interactions were the product of reciprocal altruism. However, he did not examine the temporal sequence of solicitations and subsequent support, and did not demonstrate that support was contingent on prior aid. Subsequent studies of coalition formation among male baboons indicated that it is often difficult (based on dominance, age, or prior events) to predict in advance which of the two coalition partners will end up with the female (Bercovitch, 1988). This suggests that these coalitions may not conform to a strict tit-for-tat model.

The Stag Hunt provides a useful way to think about the dynamics of these coalitions. Males who are most likely to form coalitions and challenge consorting males hold middle-ranking positions and have limited access to receptive females (Bercovitch, 1988; Noë, 1990, 1992). If either of the challengers attempted to disrupt a high-ranking males' consortship on their own, they would almost surely fail. However, when two mid-ranking males team up, they become a formidable force. As long as each male has some probability of ending up with the female, it may be profitable for both to participate in the coalition. This may explain why males who form coalitions are typically very close in rank. These coalitions may involve short-term reciprocal altruism, so that shirking is not possible. If this is the case, then the overall decision about whether to challenge the consorting male has a Stag Hunt payoff structure.

Chimpanzees are active and skilled hunters, mainly taking arboreal red colobus monkeys. In the Taï forest, chimpanzees seem to have developed a well-organized, collaborative strategy for hunting colobus. Hunters take different roles in stalking, ambushing, and capturing prey (Boesch, 1994; Boesch and Boesch, 1989; Boesch and Boesch-Achermann, 2000). Meat is commonly shared, although hunters receive a larger share than those who do not participate in the hunt. Males typically hunt in groups, and they are considerably more successful in capturing prey when they hunt in groups than when they hunt alone (Boesch, 1994). Chimpanzees in Taï obtain the highest *per capita* returns when they hunt in groups of four or groups of more than six (Boesch, 1994). Thus, hunting at Taï may conform to the payoff matrix of the Stag Hunt (Boesch *et al.*, 2005). Males who hunt together achieve higher payoffs than males hunting alone and achieve higher payoffs than those who do not contribute to the hunt. At other sites, male chimpanzees do not hunt cooperatively, and hunting in groups does not seem to bring higher *per capita* returns than hunting alone (Gilby *et al.*, 2006; Mitani *et al.*, 2002; Muller and Mitani, 2005). Capuchins, which hunt squirrels, coatis, and other small animals, do not seem to coordinate their hunting tactics or adopt different roles in hunts (Rose, 1997).

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Like male baboons, chimpanzees often mate-guard receptive females (Goodall, 1986; Hasegawa and Hiraiwa-Hasegawa, 1990; Muller and Mitani, 2005; Nishida, 1979, 1983; Tutin, 1979). In the Kibale Forest, some pairs of high-ranking males jointly defend access to females (Duffy, 2006; Watts, 1998) and rebuff other males' attempts to mate. Cooperation allows males to fend off other males' approaches and keep close tabs on female at the same time. Coalition partners share matings with the female that they are guarding (Duffy, 2006; Watts, 1998). At Ngogo, participation in these coalitions depends on the level of competition that males face. For males acting alone, the likelihood of successfully controlling access to females declines as the number of males present increases. Males switch from mate guarding alone to joint mate guarding when they are in large parties. Males that switched from solo mate guarding to coalitionary mate guarding earned a "greater share of copulations than they could have expected from solo mate guarding in those parties (which would have been unsuccessful). Also, males tended to switch from solo mate guarding to two-male coalitions, and from two-male to three-male coalitions, when their expected share of copulations from attempts at solo mate guarding dropped below 50% and 33.3%, respectively" (Watts, 1998, p. 52).

Some of the coalitions that females form may also conform to the payoff matrix of the Stag Hunt. In species that form matrilineal dominance hierarchies, challenges against higher-ranking females are extremely rare and dominance hierarchies remain stable over years and even decades (reviewed in Silk, 2002a). This suggests that it may be prohibitively costly for females to confront higher-ranking females on their own. However, hierarchies are disrupted occasionally when lower-ranking females mount successful challenges against members of higher-ranking matriline. These revolutionary events are often precipitated by collective challenges from lower-ranking females (Engh *et al.*, 2006; Samuels *et al.*, 1987). While coalitionary aggression by females is normally biased in favor of close kin (Kapsalis, 2004; Silk, 2002a), these revolutionary coalitions often involve short-term alliances among females from several different matriline. It seems likely that females who mount collective challenges are more likely to defeat higher-ranking females than females who act alone.

B. SOLVING COLLABORATION PROBLEMS IN THE LABORATORY

A number of experiments that have been designed to probe primates' propensity for cooperation take the form of the Stag Hunt. Although the protocols of these experiments vary considerably, they are built on the same basic logic: two animals must work together to obtain rewards. If either one does not participate, neither will profit. Because none of these experiments

were designed with the Stag Hunt explicitly in mind, some of them do not conform precisely to the payoff matrix of the game. In some cases, the reward is too small to share, and in other cases not all individuals have a realistic chance of obtaining rewards. Nonetheless, these experiments provide interesting insights about the factors that influence performance in interactions that take this basic form.

The first example of this type of experiment was conducted by Meredith Crawford in the 1930s. Crawford (1937) presented five chimpanzees (combined into seven different pairs) with a heavy box that contained food rewards. Two ropes were attached to the box. The box was too far away for the chimpanzees to reach the food placed on it, and too heavy for a single individual to pull forward by themselves. After considerable training, including explicit instruction to pull at the same time, three of the pairs learned to pull the ropes simultaneously without prompting and succeeded in obtaining food regularly. One pair never succeeded in pulling the box forward. (Film footage of these experiments can be viewed at http://www.emory.edu/LIVING_LINKS/crawfordvideo.html.) Two of the four chimpanzees who were members of these four dyads learned to recruit their partners to pull on the ropes and were attuned to their partner's position and behavior. Unfortunately, data for the three remaining pairs are not presented. Crawford also attached a balance scale to the ropes and measured the duration and force of each partner's efforts; in most pairs, one partner pulled considerably harder than the other. Crawford also presented the same chimpanzees with two other tasks that required similar types of collaborative effort. None of the chimpanzees were able to solve the new tasks. A few years later, Warden and Galt (1943) posed the box pull task to three pairs of monkeys of different species; none succeeded in working together to obtain rewards.

Povinelli and O'Neill (2000) used the box pull paradigm to examine whether experienced chimpanzees would actively recruit, instruct, or shape the behavior of naive partners. They trained two animals to work together successfully and then paired these experts with untrained partners. Only one of the five naive subjects mastered the task, and her success did not seem to be related to the behavior of her expert partners.

In an early series of field experiments, monkeys were required to shift a heavy stone to obtain food rewards buried below (Guinea baboons, *Papio papio*; Fady, 1972; Japanese macaques, *Macaca fuscata*; Burton, 1977; rhesus and tonkeana macaques, *Macaca tonkeana*; Petit *et al.*, 1992). In the early stages of the experiments, the stones were light enough for a single individual to move alone. This enabled the monkeys to learn that food was hidden under stones, and allowed the experimenters to calibrate the weight that individual animals could lift. As the experiment proceeded,

heavier and heavier stones were used, until the monkeys were unable to shift them on their own. At this point, they could only obtain food if they worked together. The Japanese macaques, rhesus macaques, and baboons virtually never succeeded in working together to displace the heaviest stones, while the tonkeana macaques succeeded only occasionally. Petit *et al.* attribute the (limited) success of tonkeana macaques to their tolerance of conspecifics which made it possible for them to work on the same stone at the same time. Although the baboons did not work together, the females and juveniles neatly solved the problem by digging tunnels under the stones, and the adult male simply took food away from them (Fady, 1972).

Chalmeau and his colleagues have conducted a series of experiments in which two individuals must simultaneously pull two handles to release a food reward (chimpanzees: Chalmeau, 1994; Chalmeau and Gallo, 1996; orangutans, *Pongo pygmaeus*: Chalmeau *et al.*, 1997a; brown capuchins: Chalmeau *et al.*, 1997b). Initially, the handles were placed close together and one individual was able to manipulate the apparatus alone. Then the handles were moved apart so one animal was unable to pull both at the same time. In this phase, joint action by two individuals was required to solve the task. In these experiments, only 1 small food reward was released from the apparatus at a time, but up to 11 rewards were available in a single session.

Chalmeau (1994) first tested a group of six chimpanzees. One dyad, which was composed of the dominant adult male and a 2-year-old female, produced the great majority of successful responses in the group. Although

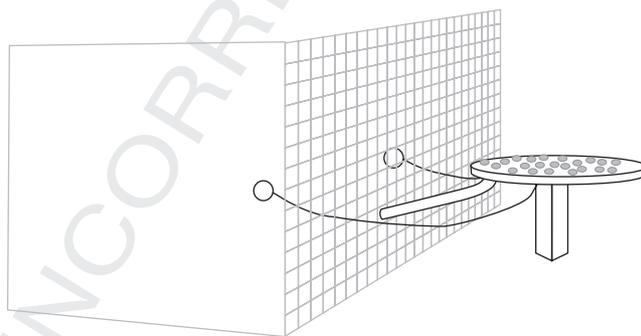


FIG. 2. Device used in Chalmeau *et al.*'s experiments. Two handles are linked to a mechanical device that distributes small food rewards (e.g., sugar lumps or grapes). The handles are too far apart for one individual to pull both at the same time. When both handles are displaced by more than 3 cm at the same time, a food reward drops into an opaque tube and rolls to the edge of the cage. (Redrawn from Fig. 1 in Chalmeau, 1994.)

others occasionally used the apparatus, the alpha male generally monopolized access to it and commandeered rewards that others managed to obtain. The alpha male and infant did not profit equally from their joint efforts. The dominant male ate 99.5% of the rewards that the infant helped him obtain. Chalmeau *et al.* (1997a) used the same apparatus with a pair of subadult orangutans. They became adept at manipulating the apparatus and succeeded in obtaining 86% of the available rewards. Again, rewards were not shared evenly within the pair; one of the orangutans obtained 92% of the rewards. Chalmeau *et al.* (1997b) also used the apparatus to test two small groups of capuchins. Seven of the 11 animals in these 2 groups eventually learned to operate the apparatus. Rewards were not distributed in proportion to effort. Some individuals obtained considerably more rewards than expected (if rewards were distributed evenly among cooperating partners), while others received fewer rewards than expected. In both groups, the oldest and highest-ranking male obtained the greatest absolute number of rewards and the most rewards per unit effort.

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Some of the same capuchins were later retested using a different apparatus (Visalberghi *et al.*, 2000). In this experiment, two handles were attached to a long transparent tray. When both handles were pulled at the same time, the tray tilted and released two rewards, one at each end of the tray. Visalberghi and her colleagues individually tested four closely related dyads that were tolerant enough of each other to drink peacefully in proximity. These four pairs all succeeded in obtaining rewards, although there was considerable variation in the rate of pulling within and between pairs and variation in the proportion of pulls that involved joint action by two individuals. In most pairs, one partner pulled considerably more than the other. There was no overt aggression over access to food, but one monkey sometimes took both rewards.

Some of the experiments that de Waal and his colleagues have conducted on brown capuchins take the form of the Stag Hunt. In one of the bar pull experiments described earlier, the monkeys were as successful in obtaining rewards when they had to work together as when one monkey was able to obtain food on its own (de Waal and Berger, 2000). de Waal and Davies (2003) used the same device to assess the effects of competition and kinship on performance in tasks that required joint effort. They placed food cups at the distal ends of the tray (dispersed treatment) and they also placed food cups side by side (clumped treatment) in the middle of the tray. To take food from the cups when they were dispersed or clumped, the monkeys had to pull the bar in far enough that it locked into position. In this experiment, the monkeys were tested in pairs, but they were not separated from one another. de Waal and Davies tested six unrelated pairs and five mother–daughter pairs, all from the same social group. The monkeys were more likely to

succeed in obtaining food when the distal food cups were baited than when the adjacent food cups were baited. The mother–daughter dyads were more successful than the unrelated dyads, particularly in the clumped trials, and the mother–daughter dyads were also more likely to obtain equal portions of the rewards in both dispersed and clumped trials. Among unrelated dyads, dominants monopolized food in clumped trials and were considerably more likely to pull in these trials than subordinates were.

Brosnan *et al.* (in press) used the weighted bar pull to examine how the quality of rewards influenced brown capuchins' success in tasks that required joint effort. They compared three different distributions of rewards: both get two slices of apple, both get one grape, and one gets two slices of apple and the other gets one grape. (All of the subjects preferred one grape over two slices of apple.) Unrelated pairs of monkeys pulled more when they each got a grape or when one got a grape and the other got two slices of apple than when both got apples. Pairs that tended to divide access to valued rewards equitably were considerably more successful in pulling (65%) than pairs that did not divide rewards equitably (26%), and this difference was not an artifact of kinship.

Melis *et al.* (2006a,b) have conducted a series of experiments on chimpanzees that were intended to evaluate the effects of social conditions on collaboration in chimpanzees. All of their experiments made use of an apparatus originally designed by Hirata (2003; cited in Melis *et al.*, 2006a) which consisted of a flat platform that slid back and forth on metal rails. A rope was threaded through two holes in the platform so that the platform could be pulled forward when both ends of the rope were pulled at the same time. If only one end of the rope is pulled, the rope comes unthreaded, and the platform cannot be moved (Fig. 3). One individual can pull the platform forward when the ropes are placed close together, but two individuals must work together when the ropes are placed far apart. Food bowls are attached to the platform, and food can only be retrieved when the platform is pulled forward.

In their first set of experiments, Melis and her colleagues attempted to replicate Hare and Tomasello's (2004) finding that competition enhances the effectiveness of cooperation among chimpanzees. They manipulated the distribution of food rewards (clumped or dispersed) and the presence of a competitor (present or absent). When a competitor was present, she was able to pull the platform in the opposite direction, and out of reach of the test pair. In this experiment, 12 individuals were tested in 6 unique dyads. All of the chimpanzees knew how to manipulate the platform when the ropes were placed close together and were strongly motivated to obtain food rewards when they were tested alone. Melis *et al.* found that three dyads cooperated consistently in all conditions, while three dyads failed

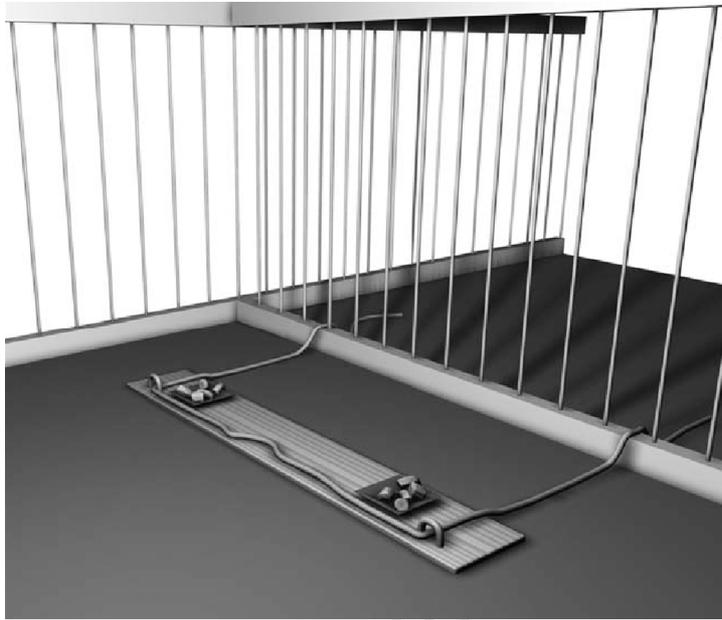


FIG. 3. Device used by Melis *et al.* (2006a,b). Two food trays are mounted on a wooden platform. A rope is threaded through holes on the distal ends of the platform. If two chimpanzees pull on the rope at the same time, the platform is brought within reach. If only one chimpanzee pulls on the rope, the rope comes unthreaded, and the platform cannot be moved. This device is based on a design by Hirata (2003). (Figure reprinted from Melis *et al.* (2006a) with permission from Elsevier.)

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consistently in all conditions. The presence of a potential competitor and the clumped distribution of food had no impact on chimpanzees' performance. Moreover, success or failure did not seem to be linked to the age or sex of individuals.

The inconsistency of the chimpanzees' performance suggested that the relationship between the individuals who had been paired together might be the key to their success. To test this, Melis and her colleagues initiated a second study with a larger number of chimpanzees housed at chimpanzee sanctuary in Uganda. First, Melis *et al.* evaluated the extent of tolerance while feeding for each dyad, and then she and her colleagues evaluated how successful the same pairs were in retrieving rewards using the same apparatus that they used in the previous experiment. The results indicate that dyads that were most tolerant of one another were also most successful in working together. Moreover, when chimpanzees that had succeeded in the first set of trials were paired with less tolerant partners, their success rate

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declined. At the same time, when chimpanzees that had failed in the first set of trials were paired with more tolerant partners, they worked together more successfully. All but 1 of the 16 chimpanzees they tested was able to succeed at the task with at least 1 partner. When pairs did fail, it was often because the lower ranking of the two chimpanzees was reluctant to enter the testing room or pull on the rope when the dominant was present. Thus, chimpanzees' success in this task seems to depend on the quality of their relationship with their partner.

In a second set of experiments, Melis and her colleagues examined how the need for collaboration and the skill of potential collaborators influenced the chimpanzees' behavior. In these experiments, the test subject was able to admit another chimpanzee from an adjoining enclosure by removing a wooden peg from a hole in the door, which allowed the door to slide open. The experimenters manipulated the need for help by shifting the position of the ropes. In the solo treatment, the ropes were close together so that one chimpanzee could grasp and pull both ropes at the same time. In the collaborative treatment, the ropes were too far apart for one chimpanzee to pull both ropes at the same time. The chimpanzees were significantly more likely to admit the other chimpanzee in the collaborative condition than in the solo condition, suggesting that they could recognize the need for assistance. In the next phase of the project, the experimenters gave the chimpanzees a choice between two potential assistants who varied in their effectiveness in the task at hand. The two assistants were placed in rooms that adjoined the testing room, and the test subject could admit either of them by placing the peg in the appropriate door. In the first testing session, the chimpanzees did not distinguish between the two assistants, but in the second testing session, they showed strong preferences for the more effective assistant. The patterning of the chimpanzees choices across trials suggests that the chimpanzees were likely to switch from one assistant to the other after unsuccessful trials, but were likely to recruit the same assistant again after successful trials.

The most of the work on collaboration has involved capuchins or apes, but Cronin *et al.* (2005) examined collaboration in four mated pairs of cotton-top tamarins. To obtain rewards, each of the monkeys had to pull on a counterweighted handle and line up two holes. When the holes were aligned on both sides, food rewards dropped down onto the floor of the enclosure. All four pairs of tamarins succeeded in coordinating their pulls and obtained rewards on nearly every trial.

In all of the experiments described so far, both partners perform the same task to earn rewards. Several other protocols have been developed which require each partner to perform complementary tasks in sequence or

simultaneously to obtain food rewards. Werdenich and Huber (2002) trained common marmosets (*Callithrix jacchus*) to pull a rope that was attached to a lever that contained a food bowl at one end. When the rope was pulled, the food bowl swung to within reach. Initially, the marmosets were trained to use the apparatus by themselves. Then, the apparatus was modified so that one had to pull the rope, and the other had to grasp the food bowl and remove the lid. Although the food bowl always contained 10 pieces of food, it was possible for one individual to monopolize the contents of the bowl. Werdenich and Huber created 16 dyads (with 8 different individuals). In most of these dyads, one partner consistently pulled the rope and the other partner consistently grasped the food bowl. Eight of the 16 dyads succeeded in the task when they had to work together. The successful dyads were the ones in which the dominant partner did not monopolize the food rewards, even when it had secured the food rewards alone.

As described above, Hattori *et al.* (2005) evaluated brown capuchin's capacity to solve a task that required them to perform complementary actions. The monkeys were first trained to perform both parts of the task, then they were paired with a partner and confined to one part of the apparatus. The three pairs that Hattori and his colleagues tested learned to solve the task, each individual performing the appropriate action in their own box. They succeeded in obtaining rewards on virtually every trial.

In another series of experiments, individuals must exchange information to obtain rewards. One individual (the Informant) knows where food is located but cannot obtain access to the food itself. The other individual (the Operator) does not know where the food is located but can gain access to the food if it knows where it is located. Both individuals must work together to obtain rewards, and neither has an incentive to lie or defect. This protocol was first used by Mason and Hollis (1962), who designed an apparatus with two trays connected by an expanding accordion-like device. When the Operator pulled a handle connected to one of the devices, the closest tray moved to within reach of the Operator and the other tray moved to within reach of the Informant. Four parallel sets of trays were available. During the test phases of this experiment, all of the trays were covered so that only the other individual (the Informant) could see which trays contained food rewards. In order to obtain food, the Informant had to provide some kind of information to the Operator about which device was baited. Mason and Hollis found that young rhesus macaques were able to succeed in informing their partners about where food was located and achieved high levels of proficiency in this task. Povinelli *et al.* (1992a,b) and his colleagues subsequently demonstrated that both rhesus macaques and chimpanzees succeeded at a very similar task when paired with human partners.

In some cases, primates can learn to exchange services for food. A young hamadryas baboon (*Papio hamadryas*) male learned to use an L-shaped tool to pull a food tray within reach (Beck, 1973). In the experiment, the tool user was confined to one part of the enclosure and could not reach the tool. Other group members had access to the tool, but did not know how to use it. One group member, who was both the tool user's mate and full sister, developed the habit of bringing the tool to the male and placing it within his reach. This greatly reduced the average amount of time it took for the male to gain access to the food. The rewards were not evenly distributed, but the cooperating pair obtained more food than others. The male ate about three-quarters of the food, the female ate about 15%, and other group members shared the remainder.

Two language-trained chimpanzees were trained to exchange food for tools (Savage-Rumbaugh *et al.*, 1978). One chimpanzee, named Sherman, was trained to name and use several different kinds of tools to obtain food rewards. Sherman used a computer keyboard to request his partner, Austin, to pass him the appropriate tool from an adjacent enclosure. Although the chimpanzees initially had to be coached to make and respond to requests, they became highly proficient at this task, eventually requesting the correct tool and providing the tool that was requested in virtually every trial. In an unspecified fraction of trials, Sherman shared the rewards that he obtained with his helper, Austin.

C. WHAT ARE THE NECESSARY CONDITIONS FOR SUCCESS IN THE STAG HUNT

A number of the experiments that were designed to examine joint efforts do not conform precisely to the Stag Hunt payoff matrix. These "design flaws" give us some insight about the necessary conditions for joint action. The data suggest that the likelihood of obtaining rewards provides an important incentive to participate in joint tasks. This depends on both how the task is structured and the monkeys' relationships with their partners.

Chalmeau's experiments on chimpanzees and capuchins were conducted in a group setting, and only one food reward was available on each trial. In the pairs that did work together, rewards were not evenly divided. If high-ranking animals monopolize the apparatus or control access to rewards, then other group members may have little opportunity to learn how the apparatus worked and little incentive to participate in joint action (Cronin *et al.*, 2005; Melis *et al.*, 2006a; Mendres and de Waal, 2000). Even when Visalberghi *et al.* (2000) retested some of the same animals in pairs and two rewards were released on each trial, it was possible for one individual to monopolize both rewards. de Waal and Davies (2003) showed that monkeys

were more likely to pull together when rewards were dispersed than when they were clumped together and easily monopolized by one individual. Subordinate partners were particularly reluctant to pull when rewards were clumped. Perhaps it is not a coincidence that monkeys worked together more effectively when they were able to see each other, but their rewards could not be appropriated by their partners (Cronin *et al.*, 2005; Hattori *et al.*, 2005).

Social tolerance may also facilitate success in joint tasks. Tonkeana macaques, which are well-known for their pacific temperaments, were able to work on the same stone at the same time, permitting them to occasionally dislodge the heaviest stones (Petit *et al.*, 1992). Similarly, marmoset and chimpanzee pairs that shared food most equitably when they were able to obtain food without working together were the ones that succeeded most effectively when joint action was required (Melis *et al.*, 2006a; Werdenich and Huber, 2002). Similarly, pairs of capuchins that distribute valuable rewards equitably are more likely to succeed in joint tasks than pairs in which one partner monopolizes access to the most valuable rewards (Brosnan *et al.*, in press). Both Brosnan and her colleagues and de Waal and Davies (2003) found that close kin cooperated more effectively than unrelated pairs and were more likely to divide resources equitably than nonkin. Differences between related and unrelated pairs were most pronounced in situations in which one partner could potentially monopolize access to rewards.

Many of these types of experiments were designed to examine the cognitive capacities that underlie cooperation, and some of the variation in performance on these tasks has been linked to variation in cognitive abilities. For example, in Chalmeau's early experiments on capuchins, the monkeys succeeded in obtaining rewards some of the time, even though they seemed to have little grasp of the requirements of the task. That is, individuals pulled on the handles without regard to the location or behavior of other group members (Chalmeau *et al.*, 1997). In their follow-up experiment, Visalberghi *et al.* (2000) demonstrated that the capuchins were more likely to pull when their partner was on the platform and in reach of the handle than when they were on the platform, but not in reach of the handle. However, they did not time their pulls to coincide with their partners' pulls. Thus, the capuchins learned to make an association between the task and the location of their partner, but they did not seem to focus on pulling as a critical element of the task. Even so, this was enough to allow the monkeys to pull simultaneously 6–52% of the time. The tamarins that Cronin *et al.* (2005) tested were more likely to manipulate the levers when their partner was present than when their partner was absent, but required considerable training to master the task. Taken together, these data suggest that

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monkeys may learn to adjust their own efforts in association with the presence or location of their partners. This association is sometimes sufficient to produce successful results in collaborative tasks. In contrast, the chimpanzees that Melis and her colleagues (2006a,b) tested required very little training to master the double rope apparatus.

Variation in success across tasks is sometimes attributed to the nature of the task itself. For example, Mendres and de Waal (2000) suggest that capuchins did not learn to work together in Chalmeau *et al.*'s (1997) experiments because the "task may not have been intuitively understandable." Brosnan and de Waal (2002) provide a similar explanation of an unpublished experiment in which capuchins did not succeed in a collaborative task. Similarly, Visalberghi *et al.* (2000) suggested that the monkeys might not have succeeded because the apparatus that Chalmeau designed was opaque and "did not allow the capuchins to see how it functioned." Both Mendres and de Waal (2000) and Visalberghi *et al.* (2000) did obtain better results in their experiments with what were judged to be more "intuitive" apparatuses. However, in both cases, it was not just the apparatus that was changed. A number of other changes in the experimental protocols were also made. In the original experiment, the monkeys were tested in a group setting and offered a single reward on each trial. Visalberghi and her colleagues individually tested pairs known to get along well together and provided two rewards, rather than just one. Mendres and de Waal (2000) also tested animals in pairs and prevented one from monopolizing the other's reward. In addition, they altered the structure of the experiment by requiring both animals to work together, but allowing only one to earn a reward. Thus, their experiment conformed more closely to the payoff matrix of an Iterated Prisoner's Dilemma than a Stag Hunt.

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Great apes may have a more complete grasp of their partner's role in these tasks than monkeys do. Although it took many trials before the successful pairs succeeded at Crawford's box pull task, two of the four chimpanzees that mastered the task began to gesture to their partners to approach the apparatus and sometimes waited until they were near the ropes before they began pulling themselves. In the chimpanzee group that Chalmeau tested, the adult male sometimes tried to collect the infant and bring her to the apparatus (Chalmeau, 1994), and learned to look at the infant before pulling on his own handle (Chalmeau and Gallo, 1996). Chimpanzees reliably distinguish between tasks that require a partner and tasks that they can perform alone (Melis *et al.*, 2006b), suggesting that they have some understanding of the role of their partners.

Apes may make use of the ability to take the perspective of others in performing joint tasks. Three of the four chimpanzees that Povinelli *et al.* (1997a) tested in the Operator/Informant task, immediately succeeded

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when they switched roles, but monkeys do not seem to be able to do this as readily (Hattori *et al.*, 2005; Mason and Hollis, 1962; Povinelli, 1997b).

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Apes may be quicker to learn how to solve tasks that require joint effort, but it is not entirely clear what exactly they learn about them. The chimpanzees in Crawford's experiments did not immediately succeed in two other tasks that required joint action (simultaneously pulling on a single rope, simultaneously pulling two handles), suggesting that they had mastered the specific skills necessary to solve the box pull task, but could not generalize their knowledge to other tasks.

VII. THE BATTLE OF THE SEXES IN PRIMATE GROUPS

Coordination problems must arise regularly in animal groups. It is likely that the dynamics of the Battle of the Sexes game are in play whenever decisions about group movements or group activities have to be made. Individuals of different age, sex, and reproductive status have quite different metabolic needs and reproductive priorities. This means that they will derive different benefits from feeding on particular foods or participating in alternative activities like resting, grooming, and feeding. The benefits of staying together, which may include the ability to defend resources or reduce vulnerability to predators (Sterck *et al.*, 1997; Wrangham, 1980), apparently override individual preferences about where to go and what to do. For example, female baboons normally give birth overnight and are visibly tired the next day. However, the birth of an infant has no detectable influence on group movements (Altmann, 1980). Unfortunately, we have made little progress in understanding the strategic dynamics of decision making about group movements and activity patterns in the wild (Boinski and Garber, 2000), perhaps because this is a problem that cannot be easily studied in the laboratory or addressed experimentally in the field.

The benefits of coordination among group members may be relevant to understanding the evolution of some forms of low-cost signals in animal groups. Ethological analyses of communication emphasize the importance of signals in coordinating activity in social groups (Markl, 1985), and many of the signals used in these contexts are not costly to produce (Silk, 2002b; Silk *et al.*, 2000). Mountain gorillas (*Gorilla berengei berengei*) and baboons give soft grunts (Rendall *et al.*, 1999; Stewart and Harcourt, 1994) when they are ready to move from one place to another. Hamadryas baboons use an elaborate series of signals to coordinate group movement and midday reunions (Kummer, 1995; Sigg and Stolba, 1981). In situations like these, there may be conflicts of interest about movement or activities, but a strong

incentive for members of the group to stay together. When animals obtain no benefit from deceiving others about their intentions, there is no need for the integrity of signals to be preserved by their high cost.

There is also evidence that monkeys use low-cost vocalizations to provide information to other group members about their disposition and motivation. Female baboons and macaques often give quiet calls as they approach others (Cheney *et al.*, 1995; Silk *et al.*, 2000). In baboons, these calls carry acoustic information about individual identity (Owren *et al.*, 1997) and rudimentary referential information (Rendall *et al.*, 1999). Grunts directed to lower-ranking females are effective in facilitating affiliation and inhibiting supplants (Cheney *et al.*, 1995; Silk *et al.*, 2000). Female baboons also grunt to former opponents in the minutes after conflicts have ended. When females grunt after conflicts, they are less likely to resume fighting and more likely to interact affiliatively (Silk *et al.*, 1996). Playback experiments demonstrate that the calls of former aggressors reduce the former opponent's concern about becoming the target of redirected aggression by the aggressor (Cheney and Seyfarth, 1997; Cheney *et al.*, 1995). In both baboons and macaques, females nearly always give quiet calls before they attempt to handle other females' infants (Bauers, 1993; Silk *et al.*, 2000, 2003). In rhesus macaques, females who call as they approach are less likely to handle infants roughly than females who do not call (Silk *et al.*, 2000).

My colleagues and I have argued that these kinds of situations present coordination problems for individuals (Silk *et al.*, 2000). When a high-ranking monkey approaches a lower-ranking monkey, there is some ambiguity about what will happen next. The high-ranking monkey might solicit grooming from the low-ranking monkey, attempt to handle her infant, or attack her. Given the high costs of being attacked, subordinate monkeys are likely to flee whenever high-ranking monkeys approach. This presents a problem for high-ranking monkeys who want to be groomed or handle infants, and for low-ranking females who may be forced to give up desirable resting spots or interrupt feeding bouts. Reliable, predictive signals can solve the females' dilemmas. If high-ranking females signal that their intentions are benign, low-ranking females will have no need to flee. Theoretical work demonstrates that honest, low-cost predictive signals can evolve under a range of conditions (Maynard Smith and Harper, 2003).

VIII. GAMES OF CHICKEN IN PRIMATE GROUPS

Games that have a Chicken payoff may also be played in primate groups, but there is little empirical evidence that bears directly on this issue. Various kinds of competitive encounters might approximate the dynamics

of the Chicken game. To see how this might work, consider the following scenario. A pair of monkeys, George and Tony, is feeding in a fruiting tree. Another monkey approaches and threatens them. George and Tony are more likely to defeat the interloper if they both fight, but both would prefer to continue feeding while the other fights. If George is prepared to fight, even if Tony does not, then this is a Chicken payoff. George's decision about whether to feed or fight may be influenced by the benefits he gains from feeding in the fruit tree; if he gets most of the fruit, he might be more willing to defend it. If neither is willing to fight alone, then a collective action problem arises.

The experiments on collaboration reviewed above suggest that animals may sometimes provide benefits to others because it is more beneficial to perform acts that benefit themselves and others than to refrain from acting altogether. For example, Crawford (1937) found that in successful pairs, one chimpanzee often pulled harder than its partner. If the harder working partner obtained more benefits from pulling hard than from matching the lackluster efforts of its partner, then it may be playing a game of chicken.

IX. CONCLUSIONS

Over the last 75 years, researchers have employed a diverse set of methods and a large variety of apparatuses in their efforts to work out how, when, and why primates cooperate. Although we can find fault with some of the protocols, choice of subjects, and analytic procedures used in many of the early experiments, these experiments provided valuable methods and ideas that have been incorporated into contemporary work. For example, Meredith Crawford's experiments with the weighted box were the inspiration for the bar pull device developed in Frans de Waal's laboratory. The bar pull has proven to be an extremely useful experimental tool that has been adapted for a broad range of species, ranging from chimpanzees, capuchins, and tamarins, to spotted hyenas (*Crocuta crocuta*; Drea and Frank, 2003).

These pioneering studies also contain some useful ideas that have not been widely adopted. For example, Crawford attached a balance scale to the ropes the chimpanzees pulled on and was able to measure each individual's effort. None of the subsequent experiments based on Crawford's design have included this valuable bit of information. No one has followed up on the idea of presenting animals in social groups with naturalistic tasks that require joint effort to solve, like moving heavy rocks to obtain buried food items.

Naturalistic and experimental data are largely consistent with predictions derived from the theory of reciprocal altruism and the Iterated Prisoners' Dilemma framework, but none of the experimental or naturalistic studies provide conclusive evidence that primates deploy contingent behavioral strategies.

Researchers have presented collaborative problems to tamarins, marmosets, macaques, capuchins, orangutans, and chimpanzees using a variety of different devices. The evidence suggests that their motivation to collaborate is influenced by the likelihood of profiting from their actions, which may in turn be a function of the degree of tolerance among partners. However, not all species have succeeded in all tasks, suggesting that a failure to grasp the role of the partner or the requirements of the task may limit the deployment of collaborative strategies. However, it is not clear that such constraints necessarily preclude the evolution of collaboration in nature. Many primates have specialized vocalizations and gestures that they use to recruit support in coalitionary aggression, to solicit grooming, and to invite others to play. Moreover, they are adept at directing these overtures to those who are most likely to respond positively (Perry *et al.*, 2004; Schino *et al.*, 2006; Silk, 1999). In these social contexts, both monkeys and apes act *as if* they understand that their goals (such as being groomed or thwarting an attack) depend on the behavior of their partners.

Although it is useful to conduct experimental studies of cooperation in the laboratory, the ultimate goal is to understand the evolutionary forces that shape cooperation in nature. So, it is important to consider what the evidence from the laboratory tells us about the nature of cooperation in the wild. The lack of robust empirical evidence for contingent reciprocity could mean that reciprocal altruism is not the principal mechanism underlying cooperation among unrelated individuals in primate groups, and suggests that alternate mechanisms such as by-product mutualism, group augmentation, and market forces may be at work (Clutton-Brock, 2001; Connor, 1986, 1992, 1995; Kokko *et al.*, 2001; Noë, 2006). At the same time, there is little evidence showing that primates consistently fail in naturalistic tasks that require them to take turns giving and receiving rewards. In fact, the naturalistic experiments on interchange in vervets, macaques, and chimpanzees provide the most compelling empirical evidence for contingent reciprocity in nature. Success in collaborative tasks is, as expected, strongly influenced by the prospects for obtaining rewards. This suggests that the expectations about the distribution of rewards may strongly influence the prospects for joint activity under natural conditions.

Additional experimental work on these questions is badly needed. These data can provide an important complement to naturalistic observations of behavior. The conceptual framework outlined here may provide the basis

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for fruitful discussions of the evolutionary forces shaping cooperative behavior. Examination of strengths and limitations in existing empirical work may help researchers find ways to design new experiments and conduct observations that yield more conclusive findings.

X. SUMMARY

The processes that influence the distribution of benefits to other group members have been one of the central themes of evolutionary biology over the last 30 years. There is a broad consensus that kin selection underlies altruistic behavior among genetic relatives and that nepotistic altruism is common in nature. In contrast, there is much less agreement about the processes that underlie beneficent behavior toward nonrelatives or the importance of such processes in nature. Early enthusiasm for reciprocal altruism has given way to caution, as few robust examples of contingent reciprocity, turn-taking, and exchange have been found in nonhuman animal species. This has generated interest in a broader range of processes, such as coordination and collaboration, that may favor helpful behavior toward nonkin. Here, I review observational and experimental evidence about turn-taking, collaboration, and coordination in primate groups. I describe four game-theoretic models in which individuals can benefit from providing help to others (Iterated Prisoner's Dilemma, Stag Hunt, Battle of the Sexes, and Games of Chicken) and argue that the formal payoff structures derived from these models provide a clear and cogent framework for understanding the processes underlying various types of cooperative interactions. I use this framework to review observational and experimental evidence of cooperation among primates. Research conducted by behavioral ecologists has focused mainly on turn-taking, and studied situations that correspond loosely to the Iterated Prisoner's Dilemma model. Naturalistic research documents the pattern of associations between help given and received and explores the temporal span of reciprocity and the currencies exchanged. Experimental work on the Iterated Prisoner's Dilemma has been designed to illuminate the contingencies between giving and receiving benefits. Evidence for contingent reciprocity in nature and the laboratory is inconclusive for primates, leading some to suggest that cognitive constraints on memory and psychological biases that favor immediate rewards over delayed rewards preclude contingent reciprocity. Research conducted by comparative psychologists has mainly focused on the cognitive and psychological capacities that enable animals to cooperate effectively. This work focuses on situations in which animals must work together to achieve a joint reward, a situation that corresponds loosely to the payoff structure of the

Stag Hunt model. Primates seem to succeed in some collaborative tasks in the laboratory, but not in others. Success seems to be facilitated by tolerance of partners, expectation of obtaining rewards, and having some understanding of the requirements of the task. Coordination problems, which correspond loosely to the payoff matrix of the Battle of the Sexes game, have been given considerably less attention, although animals must solve many coordination problems in the course of their everyday lives. A limited body of evidence suggests that some primates have evolved vocalizations which serve as honest signals of intent, and facilitate coordination of group movements and social interactions.

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