

A PROXIMATE PERSPECTIVE ON RECIPROCAL ALTRUISM

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The study of reciprocal altruism, or the exchange of goods and services between individuals, requires attention to both evolutionary explanations and proximate mechanisms. Evolutionary explanations have been debated at length, but far less is known about the proximate mechanisms of reciprocity. Our own research has focused on the immediate causes and contingencies underlying services such as food sharing, grooming, and cooperation in brown capuchin monkeys and chimpanzees. Employing both observational and experimental techniques, we have come to distinguish three types of reciprocity. Symmetry-based reciprocity is cognitively the least complex form, based on symmetries inherent in dyadic relationships (e.g., mutual association, kinship). Attitudinal reciprocity, which is more cognitively complex, is based on the mirroring of social attitudes between partners and is exhibited by both capuchin monkeys and chimpanzees. Finally, calculated reciprocity, the most cognitively advanced form, is based on mental scorekeeping and is found only in humans and possibly chimpanzees.

KEY WORDS: Capuchin monkeys; Chimpanzees; Cooperation; Food sharing; Primate grooming; Proximate mechanisms; Reciprocal altruism

Cooperation can be defined by either its intention or its outcome. In the first case, we focus on the efforts and goals of the involved parties. In the

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second case, we focus on results, and ignore actions that fail to bring about those results.

Most of the literature on the evolution of cooperation implicitly or explicitly employs the second definition, usually phrased in terms of fitness consequences for the actors. Thus, Hamilton (1964) has defined cooperation as either having fitness benefits for both the actor and the recipients or benefitting only the recipient at a cost to the actor. Emphasis on outcomes goes back much further as exemplified by Hayes (1925:340), who declared that "The only thing designated by the word co-operation is the relation between activities that contribute to a common result." Such definitions are not grounded in actual behavior, however. As pointed out by Boesch and Boesch (1989), cooperation should not be defined so narrowly that it leaves out cooperative effort. Definitions that rely on outcome alone become problematic if the conclusion of a behavioral sequence is unknown or if efforts fail even when the actors were working together, such as the common situation in which predators jointly stalk a prey that subsequently escapes. Dugatkin (1997:14) has tried to remedy this situation by defining a cooperative act and a cooperative effort differently:

Cooperation is an outcome that—despite *potential* relative costs to the individual—is "good" in some appropriate sense for the members of a group, and whose achievement requires collection action. But the phrase "to cooperate" can be confusing, as it has two common usages. To cooperate can mean either: (1) to achieve cooperation—something the group does, or (2) to behave cooperatively, that is, to behave in such a manner that renders the cooperation possible (something the individual does), even though the cooperation may not actually be realized unless other group members also behave cooperatively.

Several other aspects of cooperation are often only implicitly considered in previous definitions. First, actors need not be intentionally cooperating, and second, they may attempt to exploit one another. For this article, we 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*. Thus defined, cooperation does not require the actors to be aware that they must cooperate in order to succeed, nor does it exclude failures to achieve a cooperative goal. This definition suits our focus on process rather than outcome and reflects our interest in proximate mechanisms.

Key to understanding cooperation is distinguishing between, while at the same time trying to combine, theories of ultimate causation with a careful study of proximate mechanisms. Ultimate causation theories, or theories of the evolution of cooperation, attempt to ascertain the reasons for a behavior's existence in a species' repertoire. Proximate mechanisms

are the actual cognitive capacities and response patterns that evolved in the animal to fulfil these evolutionary requirements.

Paradoxically, although it is necessary to differentiate between proximate and ultimate explanations in order to understand what exactly is being studied and which questions to ask, it is also necessary to seek an understanding of both. Although research often focuses exclusively on one or the other, no phenomenon can be fully understood by looking at only the evolutionary explanation or the proximate mechanisms. What animals reveal in their actual behavior are the proximate mechanisms. They pursue immediate goals which, in the end, often beyond the cognitive horizon of the actors themselves, translate into benefits that form the material for natural selection. A study of proximate mechanisms helps to determine if evolutionary hypotheses are predicting behavior within the animal's range of abilities, as no matter how elegant or compelling an evolutionary scenario, it is useless if the organism lacks the capability of behaving as the theory predicts (Stamps 1991). While much debate has focused on the evolutionary mechanisms underlying cooperation, much less is known of the proximate mechanisms.

Our interest is in this proximate side of cooperation or, more specifically, reciprocal altruism. Our research on the proximate mechanisms underlying food sharing and cooperation in capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*) has given us a better understanding of the phenomenon. Here we discuss examples of previous reciprocity studies, then our own research on proximate mechanisms of reciprocity in primates and what we have learned from it.

PROXIMATE MECHANISMS OF RECIPROCAL ALTRUISM

Reciprocal altruism is the exchange of goods or services (costly acts) between individuals such that one individual benefits from an act of the other, and then the other individual benefits in return. This differs from mutualism, another common form of cooperation, in which receipt of the benefit is simultaneous by all parties involved rather than temporally separated. High-cost reciprocity is quite rare, one purported example being blood sharing in vampire bats (*Desmodus rotundus*; Wilkinson 1984). Low-cost reciprocity, on the other hand, encompasses services such as mating privileges, grooming (Seyfarth and Cheney 1988; de Waal 1997a), the failure to act (Seyfarth and Cheney 1988), or any service that carries an opportunity cost. This may involve the exchange of a much wider range of phenomena than those traditionally termed *altruistic*. For example, agonistic intervention on behalf of another individual is sometimes risky for the intervener and advantageous for the beneficiary (e.g., when a female

defends her offspring against an attack by a dominant male), but more often intervention is directed against subordinates and hence is relatively risk-free (reviewed by Harcourt and de Waal 1992). One must be careful in an analysis of reciprocal interactions not to lump both high-cost and low-cost, opportunistic interactions in the same analysis (e.g., male baboon alliances: Bercovitch 1988; Noë 1990). For this reason, we use the term *reciprocity* to encompass both high-cost (altruistic) and low-cost (service) exchanges.

Examples of reciprocity are scarce among nonhuman animals because demonstrating it is difficult. The majority of such research comes from social species in which large amounts of observational data have been collected, as these studies are more likely to yield possible avenues for exploring reciprocal interactions. Many examples of reciprocity have been posited in the literature, but often it is found that either the animals are related, and hence kin selection provides an alternative explanation for the observed altruistic exchange (Wilkinson 1988), or else previously unnoticed benefits to the presumed altruist are found, indicating that the observed behavior is better described as mutualism (e.g., both animals receive a benefit simultaneously; Clements and Stephens 1995; Koenig 1988) or pseudo-reciprocity (Connor 1986). Furthermore, it is difficult to assess reciprocity in situations in which the exchanged currencies are not the same. This has been termed a *service economy* (de Waal 1982, 1997a) or *biological market* (Noë and Hammerstein 1991, 1994), in which different goods and services are exchanged within a network of individuals. Moreover, in some instances the same currency will have a different relative value to different individuals, based on such factors as the animal's rank, size, or age (Seyfarth and Cheney 1988; Boyd 1992).

Proposed examples of reciprocity have been found in a number of different species. Here, we briefly review how some of these studies have raised important issues in the study of reciprocity, after which we will look at our own attempts to document and explain reciprocity in capuchin monkeys and chimpanzees.

Coercion versus Free Exchange

If cooperation is the *voluntary* working together of two individuals to achieve some end, then an interaction may appear cooperative without so being. Individuals can be coerced into performing actions which at first appear cooperative, but lack the voluntary nature of cooperation. Dyads and groups of related keas (*Nestor notabilis*) were given access to a lever-like apparatus that released food pellets from one end if a bird stood on the other end (Tebbich et al. 1996). The bird standing on the lever did not have access to the food pellets. The mechanism the keas used to solve this prob-

lem was coercion: the dominant bird would force a subordinate to stand on the lever while the dominant ate.

In dyads, this led to a noncooperative system in which one animal did all the work and reaped no rewards. However, the dominance hierarchy was nonlinear, so every bird was dominant to some other bird. Hence in the group situation, every animal was able to obtain some reward, which superficially resembled a system of reciprocal exchange. However, the exchange of favors was not reciprocal at the dyadic level; in other words, there did not seem to be a contingency between A's help to B and B's help to A. Such a system would not yield the same results in a linear dominance hierarchy, as one individual would receive favors from all involved while another would receive favors from no one. This is seen in the following situation in chimpanzees.

A socially housed group of related chimpanzees was exposed to an apparatus in which they had to pull two handles simultaneously to receive fruit (Chalmeau 1994; Chalmeau and Gallo 1996). One individual could claim all of the reward, and in fact, the alpha male monopolized the rewards and failed to share with his partners. Possibly for this reason, only the youngest infant of the group (a two-year-old female) would use the apparatus with the alpha male, who actively recruited her. Once again, labor was recruited from down the dominance hierarchy, but unlike the keas, the chimpanzee subordinate was not forced to participate; all help was recruited and appeared voluntary. Further unlike the keas, the dominance order was linear so the alpha male received all of the rewards. However, the reward was not likely a factor for the infant female, who was not yet dependent on solid foods and was probably rewarded with play (Chalmeau 1994; Chalmeau and Gallo 1996).

Piscine Predator Inspection

Predator inspection among fish, particularly sticklebacks (*Gasterosteus aculeatus*) and guppies (*Poecilia reticulata*), is a behavior that has received a large amount of attention as a possible example of the tit-for-tat (TFT) solution to the prisoner's dilemma (Milinski 1987; Milinski et al. 1990; Huntingford et al. 1994; Dugatkin 1991, 1998; but see Dugatkin 1997 for the fiery debate on predator inspection and TFT). In this behavior, two or more fish break away from a school to swim closer to an approaching predator. Most likely they gain information on the state of the predator (e.g., its state of activity and alertness), and the rest of the school may learn from their reactions (Magurran and Higham 1988), but they also incur greater risks by getting closer to a predator than the rest of the school. If predator inspection enhances the survival of the individual members, how do they know with whom to cooperate to maximize their fitness?

Experimental work using a “partner” simulated by a mirror has been done on fish of both species (Milinski 1987; Dugatkin 1991, 1997). The mirrors could be adjusted to simulate a defecting companion or a cooperating one, and in both cases the fish followed a “conditional approach” strategy (Dugatkin 1988)—that is, they monitored their partner visually and only continued to advance if their partner continued to do so as well. Furthermore, guppies apparently recognize cooperative tendencies in partners, preferring to associate with better inspectors.

In an experiment in which three guppies were placed in lanes next to each other and allowed to perform a predator inspection, guppies preferred to associate, both immediately after the inspection and 4 hours later, with the individual that maintained the closest average position to the inspector (Dugatkin and Alfieri 1991). However, when a similar preference test was repeated on groups of six free-swimming guppies, there was no evidence for assortative interactions (Dugatkin and Wilson 2000). Apparently guppies can alter their interactions based on their partner’s level of cooperation, although the extent to which this is possible is unknown.

Impala Mutual Grooming

Impala (*Aepyceros melampus*) take turns grooming their partner’s head and neck to remove ticks and other parasites (Hart and Hart 1992). Each episode consists of multiple alternating grooming bouts, in which the initiator is typically the first to groom. Allogrooming is a low-cost form of reciprocity involving low energy expenditure and risk, because if a bout is not reciprocated, the initiator has lost little. Connor (1995) suggests that this is an example of the parceling model of reciprocity. In this model, goods are exchanged in small packets, rather than single, long bouts, making the cost of a defecting partner lower and reciprocity more viable than in situations in which high-cost goods or services are exchanged. Furthermore, in impala allogrooming the benefits are not separated very much in time, making the mechanism for such a cooperative behavior similar to mutualism.

Bat Reciprocal Blood Sharing

Blood sharing by vampire bats involves a much higher cost than impala allogrooming, and the time delays between given and received acts are far longer. Female bats are long-lived animals that roost for life in the same small group in which relatedness is slightly less than that of cousins. To survive, they cannot go longer than three days without a blood meal, and adults miss a meal about once every 10 days. These females exchange blood meals with conspecifics who have failed to feed for one or more nights in a row (Wilkinson 1984). This behavior is very costly, and it is possible that bats remember favors given and received for an extended period

of time, as time delay between giving and receiving is a minimum of one day.

Wilkinson (1984) reported that the vast majority of blood sharing is between mother and offspring, with the remainder among closely related individuals or frequent roost-mates. Since there was no evidence that giving was contingent on previous receipt from the same individual, it is possible that the observed reciprocity results from the symmetrical components of the relationship (i.e., kinship and mutual friendship) rather than any score-keeping and expectation of return (see "symmetry-based reciprocity," below).

Primate Reciprocity

Correlational evidence for reciprocity in nonhuman primates exists for social grooming, food sharing, and agonistic support (e.g., Seyfarth 1980; de Waal and Luttrell 1988; de Waal 1989). However, correlations between given and received acts of assistance across dyadic relationships can come about in multiple ways. Before concluding that giving depends on receiving, potentially confounding variables need to be controlled for. The most obvious variable to control is time spent in association: if members of a species preferentially direct favors to close associates, the distribution of favors will automatically be reciprocal owing to the symmetrical nature of association. This mechanism, dubbed *symmetry-based reciprocity*, needs to be distinguished from *calculated reciprocity*, which is based on mental scorekeeping of given and received favors (de Waal and Luttrell 1988). In most species for which reciprocal altruism has been reported, symmetry-based reciprocity is the most likely mechanism (e.g., blood sharing in vampire bats, Wilkinson 1984; allogrooming in impala, Hart and Hart 1992).

In view of the problems with correlational analyses at the matrix level, assessments need to return to the interaction level, with sequences of behavior analyzed over time. Does a beneficial act by individual A toward B increase the probability of a subsequent beneficial act by B toward A? Preliminary evidence for an exchange between affiliative behavior and agonistic support, and vice versa, exists for cercopithecine monkeys. De Waal and Yoshihara (1983) found increased post-conflict attraction and grooming between previous alliance partners in rhesus monkeys (*Macaca mulatta*). Seyfarth and Cheney (1984) used playbacks of calls that vervet monkeys (*Cercopithecus aethiops*) use to both threaten an aggressor and solicit support to gauge the reaction of individuals that had recently been groomed by the caller. They reported more attention to previous grooming partners. Finally, Hemelrijk (1994) examined agonistic support after experimentally manipulating grooming among long-tailed macaques (*M. fascicularis*) and found indications that support was related to previous

grooming—in other words, individual A supported individual B more if B had groomed A, but not if A had groomed B.

The last study comes closest to demonstrating a temporal connection between one service and another, but what is still missing is evidence for partner-specificity, in other words, that the return service is specifically targeted at the individual who offered the first service. Our research on food sharing and cooperation attempted to address this issue of partner-specificity in reciprocity.

Food Sharing in Primates

Food sharing may be a component of reciprocal exchange. Although food sharing outside the mother-offspring or immediate family context is rare in the majority of primate species (reviewed by Feistner and McGrew 1989), it is common in both capuchin monkeys and chimpanzees. Food sharing lends itself uniquely to experimental research because the quantity and type of food available, the initial possessor of the food, and even the amount of food shared can be manipulated by the experimenter. Second, food sharing provides a quantifiable currency. An observer can see exactly how many times the non-possessor obtains food and can estimate quantities shared. Finally, the observer can tell whether the sharing was active or passive.

Active food-sharing, a rare behavior, consists of one individual handing or giving food to another individual; passive food-sharing, by far the more common kind, consists of one individual obtaining food from another without the possessor's active help. Passive food-sharing covers a broad spectrum, ranging from a lack of protest against others' taking of food to a category called "facilitated taking" in which the food possessor could easily prevent the other from taking food, by staying out of reach, yet nevertheless comes close enough for food transfers to occur.

Three hypotheses have commonly been proposed to explain food sharing in primates: *sharing-under-pressure*, *sharing-to-enhance-status*, and *reciprocity* (reviewed by de Waal 1989). The sharing-under-pressure hypothesis, related to the tolerated theft hypothesis (Blurton Jones 1987), predicts that individuals will share in order to be left alone by potentially aggressive conspecifics. The sharing-to-enhance-status hypothesis predicts that sharing will increase the altruist's standing in the community. Finally, the reciprocity hypothesis predicts that food is exchanged reciprocally for other favors (e.g., is a part of the service economy). Our research attempts to verify whether food sharing is reciprocally distributed as well as to separate these three hypotheses.

Food sharing in capuchins. Capuchin monkeys spontaneously share food (de Waal et al. 1993), so we investigated whether or not these interactions were reciprocal. There are two ways to examine reciprocity. The first is to

look for significant reciprocity correlations between dyads; the second, more detailed method examines changes within each relationship across time. Our initial studies approached food sharing in the first way, looking for reciprocal sharing across dyads. This matrix approach has been used successfully in the study of grooming, alliances, and food sharing (cf. de Waal and Luttrell 1988; de Waal 1989; Hemelrijk 1990a, 1990b).

This initial study (de Waal 1997b) looked for reciprocity correlations across dyads using the delayed exchange test, or DET. For each DET, a pair of monkeys was placed in a test chamber and separated from each other by a mesh partition which allowed for food sharing. Monkey A was given a bowl of cucumber pieces, which were placed well out of reach of monkey B. After 20 minutes, the cucumber was removed, and a bowl of apples was given to monkey B (second test phase). The same pair was given another DET later, with the order in which the monkeys were given food being reversed (Figure 1). As a control, each monkey was given the same test for 20 minutes, but without a partner.

The capuchins displayed an astonishing amount of social tolerance, sharing food on a reciprocal basis. Males tended to share more than females in this experiment, regardless of the sex of the partner. A matrix analysis found that, for the 14 female-female dyads in which the possessor was dominant, more sharing occurred between partners with fewer agonistic interactions, shorter rank distances (i.e., animals who were close together in the dominance hierarchy), and higher levels of proximity.

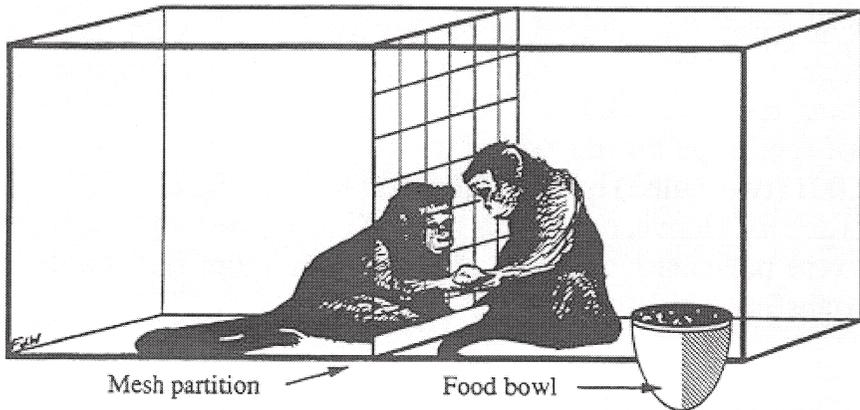


Figure 1. This sketch, made from an actual video still, demonstrates active food sharing in a pair of capuchin monkeys. The monkeys are separated by a mesh partition, and the monkey on the right has access to a food bowl containing apples. Active food sharing, depicted here, is quite rare, but facilitated taking, in which the food possessor drops pieces by the mesh and allows the other monkey to take them, is very common (from de Waal 1997b).

Furthermore, the number of tolerant food transfers in the first test phase was significantly correlated with the number of tolerant food transfers in the second phase. Although cognitive mechanisms such as scorekeeping were not contradicted by these findings, the most parsimonious mechanism given the result is symmetry-based reciprocity—that is, reciprocity based on the symmetrical nature of the relationship. The capuchins were already familiar with each other, and food sharing might have resulted from a combination of affiliation and tolerance toward conspecifics. Our next concern was whether or not reciprocity could be attributed to anything besides the symmetry inherent in the relationship.

In an attempt to exclude symmetry-based reciprocity as an explanation for the observed reciprocity in food sharing, changes within each relationship over time were examined rather than just correlations across dyads. This test was similar to the previous one but incorporated six DETs for each pair. For each DET, individual A was given apple pieces for 20 minutes, and then these were removed and individual B was given carrot pieces for 20 minutes. The roles between individuals remained the same over the six tests. The results were compared across tests to see how sharing in the second test phase was affected by sharing in the first test phase between the same individuals. This approach allowed us to correlate events over time, rather than across relationships, tightening a possible argument for causality between the behavior in both directions within each dyad. Sharing rates were found to co-vary significantly over time within each pair of individuals, indicating that something more than symmetry-based reciprocity was occurring (de Waal 2000).

The second food possessor shared significantly more than average if the first monkey had shared more than average as well (Figure 2). To measure this, we ascertained the mean amount of food each individual shared with their partner, then ranked each test as “high” or “low” food sharing, as compared with the mean amount of food shared with that partner. There was no correlation between rate of food transfer and test order in either test phase, indicating that the measured correlation could not be attributed to test-ordering effects (i.e., a general rising or falling of food transfers over consecutive tests).

Symmetry-based reciprocity cannot account for such temporal covariation within the same dyad. However, calculated reciprocity, or mental scorekeeping, may still be too cognitively complex a mechanism for the capuchins to utilize. To explain these results, de Waal (2000) proposed the mechanism of *attitudinal reciprocity*, that is, each individual’s behavior mirrors the partner’s attitude in close temporal succession (Figure 3). This explanation is simpler than calculated reciprocity, which assumes a literal accounting of given and received services. Instead of the monkeys keeping careful track of how much they give and receive, they may merely re-

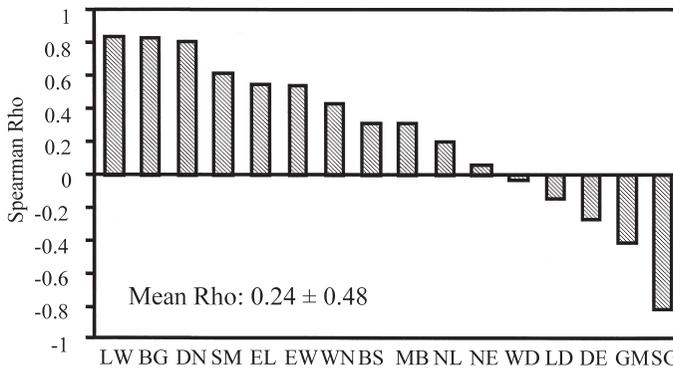


Figure 2. The rate of food transfer toward the partner during the second phase of the Delayed Exchange Test is compared with the rate of transfer received from the same partner during the first DET phase. Data for 16 different female dyads, each tested six times, indicate significant covariation of sharing in both directions within each dyad (from de Waal 1997b).

spond positively (e.g., with proximity and tolerance) to a positive attitude in their partner. Inasmuch as the amount of food transferred between partners rests on proximity and tolerance, such mirroring of social predispositions could explain the reciprocal distribution of food sharing across time without the requirement of careful scorekeeping of services.

Food for grooming in chimpanzees. Similarly to capuchins, chimpanzees share food in a reciprocal manner. De Waal (1989) previously found that food sharing and other social interactions (e.g., grooming) were reciprocally distributed across individuals, with half of the recorded food interactions (50.3%) resulting in food being transferred. However, food sharing in this test correlates positively with association, or the amount of time individuals spend in proximity in non-food situations, so, as with the capuchins, the effects of association must be removed before any explanation other than symmetry-based reciprocity may be invoked. In order to look at reciprocity without the confounding effects of mutual association, the matrix analysis was redone while statistically controlling for its effects. The reciprocity correlation continued to be significant. However, statistical elimination of a variable is not nearly as powerful as eliminating the variable experimentally.

To that end, a new experiment was designed that looked for temporal patterning within each dyad, thereby holding the effect of association constant. For this test, partner specificity was addressed: Does a beneficial act by A toward B affect B's behavior only toward A or toward everyone (de

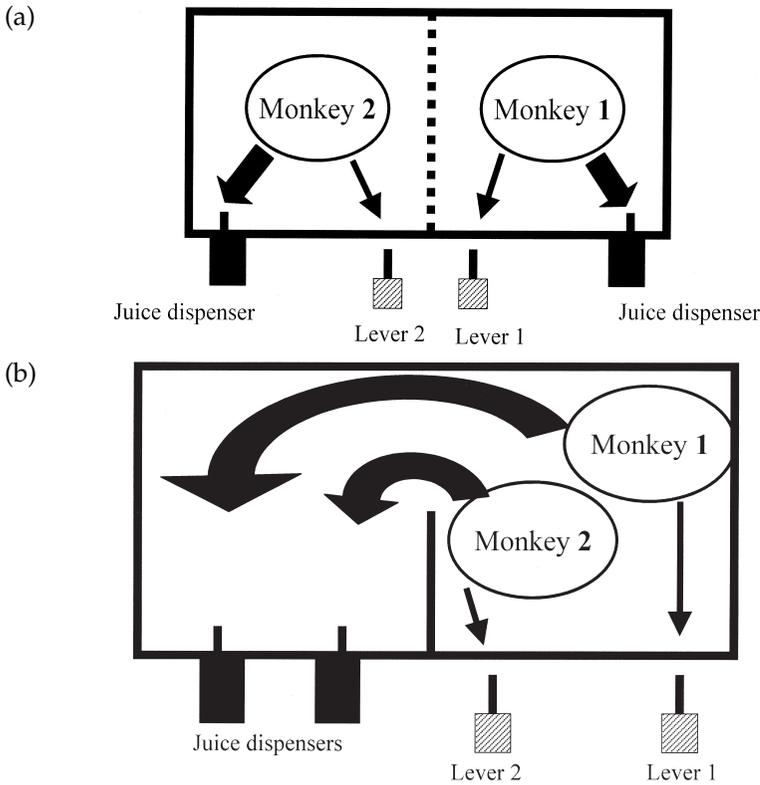


Figure 3. The layout for the cooperative-lever-pressing paradigm in capuchin monkeys. The monkeys had to press the two levers simultaneously to receive a grape juice reward: (a) the initial design, in which the monkeys were separated and each monkey had its own lever and juice dispenser, and (b) the follow-up design, in which the monkeys were together for both the lever-pressing and the reward. Under the first condition, the monkeys did not attend to each other's behavior and only succeeded by chance. When the monkeys were forced into contact with each other and moved together from levers to juice dispensers, they appeared to attend to each other and their success increased (see Figure 4).

Waal 1997a)? To do this, one must ascertain whether B's receipt of a favor by A makes B more likely to share food with A only, or with any individual, and A's and B's behavior must be measured sequentially.

The difficulty in measuring food sharing across time is that after a group-wide food-sharing session, as used in these experiments, the motivation to share is changed (the animals are more satiated). Hence, food sharing cannot

be the only variable measured. A second service that is unaffected by food consumption needs to be included, and for this, grooming between individuals prior to food-sharing bouts was used. The frequency and duration of spontaneous grooming among the chimpanzees was measured during a 90-minute period. Within half an hour after the end of these observations, the apes were given two tightly bound bundles of leaves and branches, and all interactions over food were recorded.

Adults were found to be more likely to share food with individuals who had groomed them earlier in the day. In other words, if A groomed B in the morning, B was more likely than usual to share food with A later in the same day. This result, however, could be explained in two ways. The first is the "good-mood hypothesis," in which individuals who have received grooming are in a benevolent mood and respond by sharing with all individuals. The second explanation is the exchange hypothesis, in which the individual who has been groomed responds by sharing food only with the groomer. The data indicated that the sharing was specific to the previous groomer. In other words, each chimpanzee appeared to remember another who had just performed a service (grooming) and responded to that individual accordingly (shares food). This is compelling evidence for exchange.

Moreover, grooming between individuals who rarely did so was found to have a greater effect on sharing than grooming between partners who commonly groomed. Among partnerships in which little grooming was usually exchanged, there was a more pronounced effect of previous grooming on subsequent food sharing. There are several possible interpretations. Grooming from a partner who doesn't usually groom might be more noticeable, leading the food possessor to share more. Second, perhaps individuals who groom frequently are close associates and thus keep less careful track of favors. Finally, it could be evidence of calculated reciprocity; not only do the chimpanzees regulate their food sharing based on previous grooming, but they recognize unusual effort and reward accordingly.

This study strongly suggests memory-based, partner-specific exchanges in chimpanzees. It goes beyond symmetry-based reciprocity because the same dyads are compared at different times; hence the symmetrical aspect stays constant and cannot explain the observed contingencies. It is also more complex than attitudinal reciprocity because the reciprocation is more than an immediate response to the positive predisposition of the partner. In this chimpanzee study, more so than in the previously discussed capuchin experiment, the time delay between favors given and received was significant and hence the favor was acted upon well after the previous positive interaction. So far, this exchange of grooming and food in chimpanzees is the example that most closely resembles calculated reciprocity among any reported for nonhuman species.

Cooperation in Capuchins

In primates, food sharing among unrelated adults functions to reward (e.g., rewards for fellow hunters: Boesch 1994) or as an exchange for service or support (e.g., coalitions and alliances: de Waal 1997a). Much of the food sharing in chimpanzees involves sharing the carcass after a cooperative hunt (Boesch 1994). Since food sharing may have evolved in the context of cooperative ventures, we began to explore whether food sharing was more common or more pronounced after individuals had cooperated, using paradigms that incorporate both food sharing and cooperation.

Despite a study indicating that capuchins fail to understand cooperation (Chalmeau, Visalberghi, and Gallo 1997), we focused on this species because preliminary work in our own laboratory had indicated a high level of cooperation. After observing several different cooperative tasks, we found that capuchins do in fact understand cooperation if the approach used is intuitive to them.

A hard-to-understand paradigm. In Chalmeau, Visalberghi, and Gallo's (1997) study, capuchins were initially trained to pull a handle toward themselves to receive a reward. After this, the monkeys were trained to pull their handles at the same moment as the others to receive the same reward. The capuchins did succeed at this task; however, Chalmeau, Visalberghi, and Gallo (1997) concluded that they failed to understand cooperation because the number of successes across trials did not increase significantly and because the mean rate of pulling by each individual did not depend on whether its partner was present at the handles.

Why were capuchins unable to learn the contingencies of cooperation? One problem is in the analysis (Chalmeau, Visalberghi, and Gallo 1997). To calculate the rate of pulling when a partner was near versus away from the handles, the investigators used absolute pulling frequencies instead of the rates of pulling corrected for time. The absolute pulling frequency does not tell us how the monkeys are actually using their time at the handles. For example, pulling 100 times in 50 minutes with the partner present and 100 times in 200 minutes with the partner absent means that different pulling rates are used even if the total frequencies are the same. Capuchins are extremely dexterous and prone to manipulate objects (Fragaszy and Adams-Curtis 1991); hence some degree of manipulation of any object is to be expected regardless of the situation.

This flaw in the analysis doesn't necessarily mean that Chalmeau, Visalberghi, and Gallo's (1997) conclusions were wrong. We recently conducted an experiment that was quite similar, which helped us understand why this is a difficult task for capuchin monkeys. In our unpublished experiment, conducted by Matthew Campbell and the two present authors, the capuchins had to press levers simultaneously to receive a grape-juice reward from a nearby dispenser (Figure 3a). Although almost all of the

capuchins initially learned to press a lever to receive juice, only one pair of monkeys received juice in the cooperative task. It was clear, however, that they were not coordinating but had simply learned to press the levers rapidly and frequently until they received the reward by chance.

Following this, the design was changed so that the levers were positioned on one side of the test chamber and the juice dispensers on the other (Figure 3b), forcing the monkeys to move together between the two sides. We hoped this forced contact would lead to communication and coordination between the monkeys, and a realization of the other's necessity for success. However, once again we had only one successful pair. Moreover, only one of that pair learned that she required the other for success. This individual's success rate, but not the other's, increased over the course of the 10 trials (Figure 4). Her pressing rate increased when her partner was close to the other lever (within arm's reach) as opposed to when her partner was distant from the levers, implying her cognizance that her partner's presence was necessary for success. We attempted to test our successful cooperator with other capuchins to see how her understanding would affect their success, but since she was low ranking her behavior was inhibited in the presence of high-ranking companions.

This one monkey's coordination of her own behavior with another individual's random efforts is similar to the deliberate coordination by only

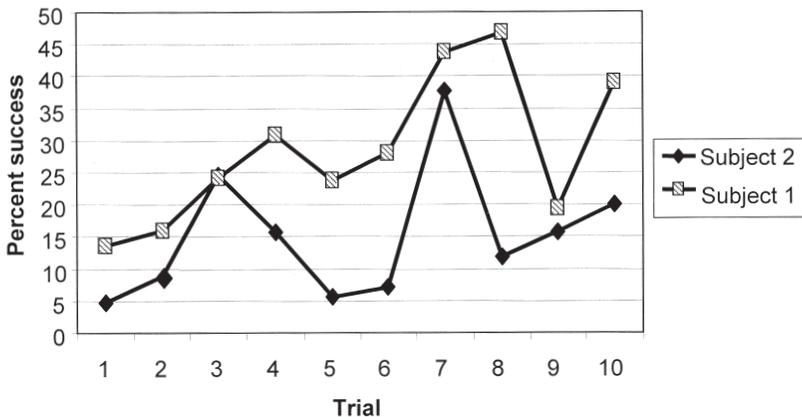


Figure 4. The success rates for two female capuchins in the second design, in which they were forced into contact (Figure 3b). Each point represents the average success rate (number of successful presses per overall number of presses) for a test. One subject had a much higher success rate than the other monkey, meaning that more of her presses obtained rewards. She appears to be the only one to have learned the contingency between her partner's pressing and her own success.

one partner in other cooperative studies on chimpanzees (Chalmeau 1994; Chalmeau and Gallo 1996) and orangutans (*Pongo pygmaeus*: Chalmeau, Lardeux et al. 1997). In chimpanzees, success was achieved when one individual (the alpha male) understood the task and then recruited and coordinated with his partner (an infant female), who acted at random. In a similar experiment on a pair of male orangutans, one male actively recruited his partner, monitored his movements, and anticipated the reward, apparently understanding the task better than his partner. Although we saw no evidence of recruitment, one monkey's understanding of the task was apparently better than the other's, allowing the two to complete the task successfully.

Why did most of the monkeys fail this task when they seemed to master the contingencies of another cooperative task, to be described below, so easily? We think it is because the task was not intuitive to them. First, the apparatus did not change as their efforts became more accurate, so the monkeys could not monitor the results of their unsuccessful attempts. Since lever-pressing did not change as the capuchins got closer to receiving juice, there was no way for the monkeys to sense when they were getting closer to a solution. Furthermore, the monkeys received no kinesthetic feedback from their partner. Failure of the partner to perform the right actions was not felt or easily noticed except in the lack of reward. After examining this, we began a bar-pulling trial that seemed intuitive in the areas in which lever-pressing was not.

The advantage of an intuitive task. The basic paradigm was similar to one developed by Crawford (1937) for juvenile chimpanzees. In our case, two capuchin monkeys had to work together to pull in a counterweighted tray, at which point one or both of them would be rewarded. They were placed in the test chamber and separated from each other by a mesh partition, giving them the option to share food, or not. Each monkey had its own bar to pull in the tray, although these bars could be removed for control tests. Food was placed in transparent bowls so each monkey could see which one would receive the food (Figure 5).

Initially, monkeys were taught to pull in the tray individually, which they quickly learned. At this point (and throughout the experimental period, which lasted three years) each monkey was given regular strength tests to determine how much weight he or she could pull in individually. For trials in which only one monkey pulled, the tray was weighted just under what the individual could pull. For trials in which both monkeys pulled, the tray was weighted more heavily than the strongest individual could pull alone, but somewhat lighter than their combined strengths. Tests were done on seven same-sex pairs of adult capuchins housed in the same social group. Each test consisted of four 10-minute trials. The five test conditions were:

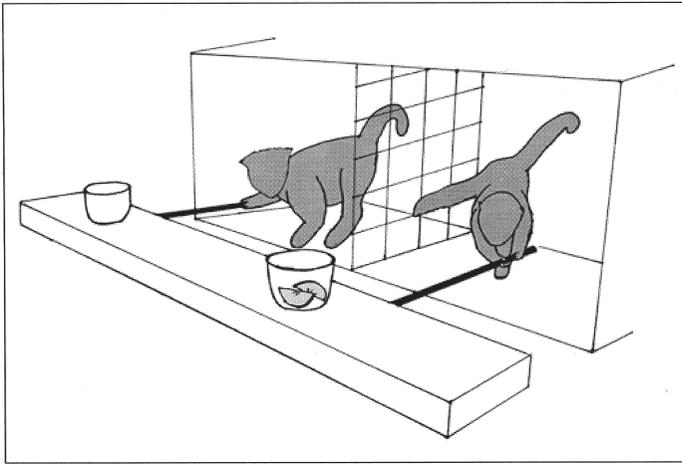


Figure 5. The test chamber used for the cooperative pulling task in capuchin monkeys. Two monkeys are situated in adjacent sections of the test chamber, separated by a mesh partition. The apparatus consists of a counter-weighted tray with two removable pull bars. In the solo effort test, only one monkey had a pull bar and only this individual's food cup was baited. In the mutualism test, both monkeys were required to pull their respective pull bars, and both food cups were baited. In the cooperation test, both monkeys were required to pull, but only one individual's food cup was baited (drawing by S. Brosnan).

1. Solo effort test (SOL), in which only one monkey had a pull-bar and only this individual received food, although *both* monkeys were present in the test chamber. This required no cooperation.
2. Mutualism, or double test (DBL), in which both monkeys were required to pull together and both cups were baited.
3. Cooperation test (COP), in which both monkeys were required to pull together but only one food cup was baited. This represented altruism on the part of the helper.
4. Obstructed view test (OBS), which was the same as the COP test except that the mesh partition was replaced by an opaque one. This eliminated visual communication between the monkeys, but they still could see both cups on the tray, and they could see that only one was baited.
5. Unrestricted cooperation test (UCP), which was the same as the COP test except that the partner was free to move in and out of the test chamber, which had an open connection to part of the group cage. This meant that the helper, needed for successful pulls, was not always at hand.

As expected, the success rate of cooperative trials was significantly lower than that of mutualistic tests or solo efforts. In the unrestricted cooperation tests, bar-pulling attempts by the food possessor significantly decreased when the partner left the test chamber, indicating that the monkeys had learned to associate their partner's presence with successful pulling. They might even have made the more complex association that they could only succeed if their partner helped and that their partner could not help if absent.

Bar-pulling success also decreased significantly in the obstructed view tests as opposed to the cooperation tests (Mendres and de Waal 2000; Figure 6). In the obstructed view test, vocal communication was still possible and the monkeys continued to make pulling efforts at the same rate as in the cooperation tests. Since both monkeys could see the food cups, their success rates should not have decreased if the impetus to pull simply stemmed from seeing food. What changed was their ability to see each other's behavior, indicating that success was at least partially dependent on visual coordination with the partner. The failure to succeed when visual access was cut off indicates that the monkeys were paying attention to each other's actions and potentially coordinating their efforts. This result contradicts previous claims that capuchins don't understand the need for a partner in cooperative tasks.

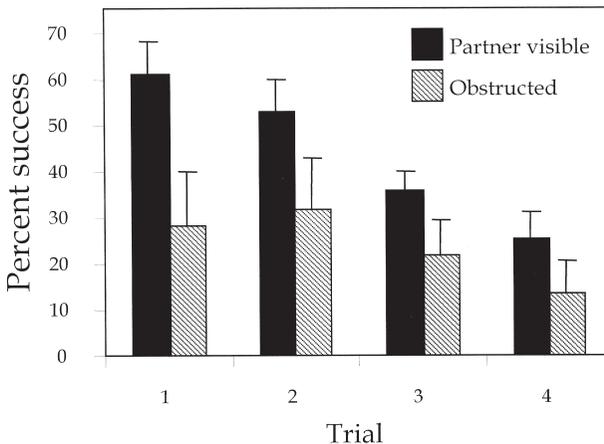


Figure 6. Mean (+SEM) success rate for the cooperation test applied to capuchin monkeys; in one test (COP) both partners had visual contact and in the other (OBS) the view was obstructed by a panel between the partners. Data are presented separately for the four trials in each test, showing that success drops dramatically when visual coordination is prevented (from Mendres and de Waal 2000).

Cooperation and food sharing. One central question underlying this project was whether food sharing would increase in the context of a cooperative enterprise. In a service economy, food can be exchanged for assistance in cooperation, or the converse. Our analyses of the amount of food sharing indicated that capuchins share significantly more in successful cooperative trials than in solo effort trials, in which the partner is present, but does not, and actually cannot, assist (de Waal and Berger 2000).

Furthermore, the partner pulled more frequently after successful trials. Since 90% of successful trials included food transfers to the helper, capuchins are assisting in pulling more frequently after having received food in the previous trial. The simplest interpretation of this result is that motivational persistence results in continued pulling after successful trials. But a causal connection is, of course, also possible—in other words, that pulling after successful trials is a response to the obtained reward and the expectation of more.

The most cognitively demanding interpretation of these results is that the food possessor understands that its partner has helped and that the partner must be rewarded for cooperation to continue. This would represent calculated reciprocity, in which the exchange of favors on a one-on-one basis drives reciprocal altruism. Each individual understands the other's costs (assistance in pulling or loss of food) and returns the favor. This could even represent a form of "gratitude" (a concept to which Trivers alluded in 1971, in relation to reciprocal altruism), in which individuals pay each other back for a previous service or favor.

However, a more likely explanation of the cooperation and food sharing in these trials is a variation on attitudinal reciprocity, in which the possessor and partner feel closer after a coordinated effort. The attention and coordination that the cooperative trial entails may induce a positive attitude in the partner, which is expressed in social tolerance and mutual attraction, which in turn ultimately translates into food sharing. After a food-sharing episode, similar mechanisms lead to increased pulling by the partner and hence further cooperation. This would indicate that a mechanism similar to that suggested for reciprocal food sharing is at work (de Waal 2000).

Although one of our tasks failed to demonstrate an understanding of cooperation in capuchin monkeys, we found that, with a relevant, intuitive task, capuchins are quite good at performing, and apparently understanding, cooperative tasks. The mechanism most likely to underlie cooperation and sharing in capuchins is attitudinal reciprocity. In this case, partners in cooperation are mirroring the attitude shown by their partner. This is separate from symmetry-based reciprocity because these attitudes are not symmetrical characteristics of the relationship but vary across time and circumstances.

CONCLUSION

Although theories about the evolution of cooperation are well established, proximate mechanisms have been much less studied. We are interested in proximate mechanisms of reciprocity, that is, the immediate behavioral goals that animals pursue and what they understand about them, which ultimately contribute to the animal's fitness.

The cognitively least demanding proximate explanation is *symmetry-based reciprocity* in which individuals interact based on symmetrical features of their relationship: these features make both parties react similarly to each other (de Waal and Luttrell 1988). This mechanism requires no scorekeeping because reciprocation is based on preexisting features of the relationship, such as kinship, mutual association, or age similarity. The second mechanism of reciprocity is *attitudinal reciprocity*, in which an individual's willingness to cooperate co-fluctuates with the attitude that the partner shows or has recently shown toward them (de Waal 2000). This divorces cooperative interactions from the symmetrical state of the relationship, making them contingent on the immediately preceding behavior of their partner. The involvement of memory and scorekeeping may be rather minimal in this kind of exchange, however, because the critical variable is general social predisposition rather than precise costs and benefits of exchanged behavior. The third mechanism is *calculated reciprocity*, in which individuals appear to reciprocate on a behavioral one-on-one basis (de Waal and Luttrell 1988). This requires memory of previous events, some degree of scorekeeping, partner-specific contingency between given and received favors, and perhaps even punishment of cheaters. Our research has indicated examples of both symmetry-based and attitudinal reciprocity in brown capuchin monkeys and possible calculated reciprocity in chimpanzees. It is logical to expect that calculated reciprocity, with its higher cognitive requirements, will be found only in a few species whereas cognitively less demanding forms of reciprocity will be more widespread. Thus, we tend to assume, unless evidence to the contrary is reported, that any reciprocal altruism reported in the literature is symmetry-based.

One factor that has made scholars skeptical about the existence of reciprocity among unrelated individuals has been a concern about how such behavior could possibly have evolved in the face of its high initial costs. It has recently been suggested, however, that cooperation could evolve if, following a minimum initial investment, cooperators increased their investment contingent on increasing confidence in the relationship (Roberts and Sherratt 1998). All of the forms of reciprocity described above have been found in relatively low-cost exchanges and may have been a starting point for the evolution of more risky and costly forms of reciprocity. Thus,

strictly speaking, exchanges of grooming for abundant food may not qualify as reciprocal altruism, in that the costs are low, but this sort of service exchange may have formed the evolutionary starting point for more costly forms of exchange.

Both cooperation and reciprocity are far more complex than they initially appear. Most research thus far has focused on ultimate causation, but cooperation cannot be fully understood without equal attention being given to the proximate mechanisms. When new knowledge of proximate mechanisms is combined with the evolutionary viewpoint, a more complete picture emerges, allowing us to understand how behaviors such as reciprocal altruism have evolved and persisted.

Our review greatly benefitted from a stimulating conference on animal cooperation organized by Dr. C. Boesch at the Max Planck Institute for Evolutionary Anthropology, in Leipzig, Germany, in 1999.

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REFERENCES

- Bercovitch, F. B.
1988 Coalitions, Cooperation and Reproductive Tactics among Adult Male Baboons. *Animal Behavior* 36:1198–1209.
- Blurton Jones, N. G.
1987 Tolerated Theft: Suggestions about the Ecology and Evolution of Sharing, Hoarding and Scrounging. *Social Science Information* 26:31–54.
- Boesch, C.
1994 Cooperative Hunting in Wild Chimpanzees. *Animal Behavior* 48:653–667.
- Boesch, C., and H. Boesch
1989 Hunting Behavior of Wild Chimpanzees in the Tai National Park. *American Journal of Physical Anthropology* 75:547–573.
- Boyd, R.
1992 The Evolution of Reciprocity When Conditions Vary. In *Coalitions and Alliances in Humans and Other Animals*, A. H. Harcourt and F. B. M. de Waal, eds. Pp. 493–510. Oxford: Oxford University Press.
- Chalmeau, R.
1994 Do Chimpanzees Cooperate in a Learning Task? *Primates* 35:385–392.

Chalmeau, R., and A. Gallo

1996 What Chimpanzees (*Pan troglodytes*) Learn in Cooperative Task. *Primates* 37:39–47.

Chalmeau, R., E. Visalberghi, and A. Gallo

1997 Capuchin Monkeys (*Cebus apella*) Fail to Understand a Cooperative Task. *Animal Behavior* 54:1215–1225.

Chalmeau, R., K. Lardeux, P. Brandibas, and A. Gallo

1997 Cooperative Problem Solving by Orangutans (*Pongo pygmaeus*). *International Journal of Primatology* 18:23–32.

Clements, K. C., and D. W. Stephens

1995 Testing Models of Non-kin Cooperation: Mutualism and the Prisoner's Dilemma. *Animal Behavior* 50:527–535.

Connor, R. C.

1986 Pseudo-reciprocity: Investing in Mutualism. *Animal Behavior* 34:1562–1584.

1995 Impala Allogrooming and the Parceling Model of Reciprocity. *Animal Behavior* 49:528–530.

Crawford, M.

1937 The Cooperative Solving of Problems by Young Chimpanzees. *Comparative Psychology Monographs* 14:1–88.

de Waal, F. B. M.

1982 *Chimpanzee Politics: Power and Sex among Apes*. Baltimore: Johns Hopkins University Press.

1989 Food Sharing and Reciprocal Obligations among Chimpanzees. *Journal of Human Evolution* 18:433–459.

1997a The Chimpanzee's Service Economy: Food for Grooming. *Evolution and Human Behavior* 18:375–386.

1997b Food Transfers Through Mesh in Brown Capuchins. *Journal of Comparative Psychology* 111:370–378.

2000 Attitudinal Reciprocity in Food Sharing among Brown Capuchin Monkeys. *Animal Behavior* 60:253–361.

de Waal, F. B. M., and M. L. Berger

2000 Payment for Labour in Monkeys. *Nature* 404:563.

de Waal, F. B. M., and L. M. Luttrell

1988 Mechanisms of Social Reciprocity in Three Primate Species: Symmetrical Relationship Characteristics or Cognition? *Ethology and Sociobiology* 9:101–118.

de Waal, F. B. M., and D. Yoshihara

1983 Reconciliation and Redirected Affection in Rhesus Monkeys. *Behaviour* 85:224–241.

de Waal, F. B. M., L. M. Luttrell, and M. E. Canfield

1993 Preliminary Data on Voluntary Food Sharing in Brown Capuchin Monkeys. *American Journal of Primatology* 29:73–78.

Dugatkin, L. A.

1988 Do Guppies Play Tit for Tat during Predator Inspection Visits? *Behavioral Ecology and Sociobiology* 23:395–399.

1991 Dynamics of the Tit-for-Tat Strategy during Predator Inspection in the Guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology* 29:127–132.

- 1997 *Cooperation among Animals: An Evolutionary Perspective*. New York: Oxford University Press.
- 1998 Game Theory and Cooperation. In *Game Theory and Animal Behavior*, L. A. Dugatkin and H. K. Reeve, eds. Pp. 38–63. New York: Oxford University Press.
- Dugatkin, L. A., and M. Alfieri
 1991 Guppies and the Tit-for-Tat Strategy: Preference Based on Past Interaction. *Behavioral Ecology and Sociobiology* 28:243–246.
- Dugatkin, L. A., and D. S. Wilson
 2000 Assortative Interactions and the Evolution of Cooperation during Predator Inspection in Guppies (*Poecilia reticulata*). *Evolutionary Ecology Research* 2:761–767.
- Feistner, A. T. C., and W. C. McGrew
 1989 Food-sharing in Primates: A Critical Review. In *Perspectives in Primate Biology*, vol. 3, P. K. Seth and S. Seth, eds. Pp. 21–36. New Delhi: Today and Tomorrow's Printers.
- Fragaszy, D. M., and L. E. Adams-Curtis
 1991 Generative Aspects of Manipulation in Tufted Capuchin Monkeys (*Cebus apella*). *Journal of Comparative Psychology* 105:387–397.
- Hamilton, W. D.
 1964 The Genetical Evolution of Social Behavior, I and II. *Journal of Theoretical Biology* 7:1–52.
- Harcourt, A. H., and F. B. M. de Waal
 1992 Cooperation in Conflict: From Ants to Anthropoids. In *Coalitions and Alliances in Humans and Other Animals*, A. H. Harcourt and F. B. M. de Waal, eds. Pp. 493–510. Oxford: Oxford University Press.
- Hart, B. L., and L. A. Hart
 1992 Reciprocal Allogrooming in Impala, *Aepyceros melampus*. *Animal Behavior* 44:1073–1083.
- Hayes, E. C.
 1925 Some Social Relations Restated. *American Journal of Sociology* 31:333–346.
- Hemelrijk, C. K.
 1990a A Matrix Partial Correlation Test Used in Investigations of Reciprocity and Other Social Interaction Patterns at Group Level. *Journal of Theoretical Biology* 143:405–420.
 1990b Models of, and Tests for, Reciprocity, Unidirectionality and Other Social Interactions Patterns at a Group Level. *Animal Behavior* 39:1013–1029.
- 1994 Support for Being Groomed in Long-tailed Macaques, *Macaca fascicularis*. *Animal Behavior* 48:479–481.
- Huntingford, F. A., J. Lazarus, B. D. Barrie, and S. Webb
 1994 A Dynamic Analysis of Cooperative Predator Inspection in Sticklebacks. *Animal Behavior* 47:413–423.
- Koenig, W. D.
 1988 Reciprocal Altruism in Birds: A Critical Review. *Ethology and Sociobiology* 9:73–84.
- Magurran, A. E., and A. Higham
 1988 Information Transfer across Fish Shoals under Predator Threat. *Ethology* 78:153–158.

- Mendres, K. A., and F. B. M. de Waal
 2000 Capuchins Do Cooperate: The Advantage of an Intuitive Task. *Animal Behavior* 60:523–529.
- Milinski, M.
 1987 Tit-for-tat in Sticklebacks and the Evolution of Cooperation. *Nature* 325: 433–435.
- Milinski, M., D. Pflüger, D. Kulling, and R. Kettler
 1990 Do Sticklebacks Cooperate Repeatedly in Reciprocal Pairs? *Behavioral Ecology and Sociobiology* 27:17–21.
- Noë, R.
 1990 A Veto Game Played by Baboons: A Challenge to the Use of the Prisoner's Dilemma as a Paradigm for Reciprocity and Cooperation. *Animal Behavior* 39: 78–90.
- Noë, R., and Peter Hammerstein
 1991 Biological Markets. *Trends in Ecology and Evolution* 10:336–339.
 1994 Biological Markets: Supply and Demand Determine the Effect of Partner Choice in Cooperation, Mutualism and Mating. *Behavioral Ecology and Sociobiology* 35:1–11.
- Roberts, G., and T. N. Sherratt
 1998 Development of Cooperative Relationships Through Increasing Investment. *Nature* 394:175–179.
- Seyfarth, R. M.
 1980 The Distribution of Grooming and Related Behaviours among Adult Female Vervet Monkeys. *Animal Behavior* 28:798–813.
- Seyfarth, R. M., and D. L. Cheney
 1984 Grooming, Alliances, and Reciprocal Altruism in Vervet Monkeys. *Nature* 308:541–543.
 1988 Empirical Tests of Reciprocity Theory: Problems in Assessment. *Ethology and Sociobiology* 9:181–187.
- Stamps, J. A.
 1991 Why Evolutionary Issues Are Reviving an Interest in Proximate Behavioral Mechanisms. *American Zoologist* 31:338–348.
- Tebbich, S., M. Taborsky, and H. Winkler
 1996 Social Manipulation Causes Cooperation in Keas. *Animal Behavior* 52: 1–10.
- Trivers, R. L.
 1971 The Evolution of Reciprocal Altruism. *Quarterly Review of Biology* 46: 35–57.
- Wilkinson, G. S.
 1984 Reciprocal Food Sharing in the Vampire Bat. *Nature* 308:181–184.
 1988 Reciprocal Altruism in Bats and Other Mammals. *Ethology and Sociobiology* 9:85–100.