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The Chimpanzee's Service Economy: Food for Grooming

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Evidence is presented that the reciprocal exchange of social services among chimpanzees (*Pan troglodytes*) rests on cognitive abilities that allow current behavior to be contingent upon a history of interaction. Food sharing within a captive colony of chimpanzees was studied by means of 200 food trials, conducted on separate days over a 3-year period, in which 6,972 approaches occurred among the nine adults in the colony. The success rate of each adult, A, to obtain food from another adult, B, was compared with grooming interactions between A and B in the 2 hours prior to each food trial. The tendency of B to share with A was higher if A had groomed B than if A had not done so. The exchange was partner-specific, i.e., the effect of previous grooming on the behavior of food possessors was limited to the grooming partner. Grooming did not affect subsequent sharing by the groomer, only by the groomee. The effect of grooming was greatest for pairs of adults who rarely groomed. Nevertheless, the effect was general: 31 dyadic directions showed an increase in sharing following grooming, and only 11 a decrease. Food possessors actively resisted approaches by individuals who had not groomed them. After food trials there was a significant reduction of grooming by previous possessors towards those individuals with whom they had shared. © 1997 Elsevier Science Inc.

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Although chimpanzee (*Pan troglodytes*) society has been characterized as a "marketplace" at which services are traded back and forth among individuals (de Waal 1982), hard evidence for a social economy remains meager. For both chimpanzees and other animals, the theory of recipro-

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cal altruism (Trivers 1971), one pillar of the evolutionary approach to cooperative behavior, is not nearly as well-supported as the theory of kin selection (Hamilton 1964), the other pillar (Wilson 1975).

Reciprocal altruism presupposes that: (a) the exchanged acts are costly to the donor and beneficial to the recipient; (b) the roles of donor and recipient regularly reverse over time; and (c) except for the first act, donation is contingent upon receipt (Rothstein and Pierotti 1988; Taylor and McGuire 1988). Because reciprocal altruism is expected especially when unrelated individuals regularly work together, monkeys and apes have provided a natural focus for research in this area. In a variety of nonhuman primates, positive correlations have been found between the frequency with which individual A benefits B and the frequency with which B benefits A across an entire matrix of group members. Correlational evidence for reciprocity exists for social grooming, food-sharing, and agonistic support (de Waal 1989; de Waal and Luttrell 1988; Packer 1977; Seyfarth 1980).

Unfortunately, correlations between given and received acts of assistance across relationships can come about in multiple ways. Before concluding that giving depends on receiving, potentially confounding variables need to be controlled. 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 due to the symmetrical nature of association. This mechanism, dubbed *symmetry-based reciprocity*, needs to be distinguished from *calculated reciprocity* based on mental record-keeping of given and received favors (de Waal and Luttrell 1988). In most species for which reciprocal altruism has been reported, including nonprimates such as vampire bats (*Desmodus rotundus*; Wilkinson 1984) and impala (*Aepyceros melampus*; Hart and Hart 1992), symmetry-based reciprocity is a likely mechanism. The most convincing evidence that reciprocity persists after association rates have been taken into account concerns chimpanzees. Moreover, only in chimpanzees do reciprocity correlations extend to negative behavior, suggesting retaliation. De Waal (1982, 1992) speaks of "revenge" and "punishment" as part of reciprocal exchange in this species, an idea generalized by Clutton-Brock and Parker (1995).

Apart from the limitations of a correlational approach, some of the behavior patterns selected for the above analyses may not fit the requirement of being costly to the donor. Agonistic intervention on behalf of another individual, for instance, 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, hence relatively risk-free (reviewed by Harcourt and de Waal 1992). Therefore, altruistic and nonaltruistic behavior are being lumped if all types of agonistic interventions are entered into a single reciprocity analysis. This criticism has been expressed most forcefully in relation to alliances among male baboons in which each victorious ally will try to sneak off with the contested resource, an estrus female. Rather than characterize these alliances as cooperative, both Bercovitch (1988) and Noë (1990) have described them as self-serving and opportunistic. According to Smuts (1985), however, alliances among older baboon males may be truly reciprocal.

In view of the problems with analyses at the relationship level, there is a need to turn to the interaction level and analyze sequences of behavior over time. The purpose of the present study is to investigate the hypothesis that reciprocal altruism relies on cognitive abilities that make current behavior contingent upon a history of interaction. Does a beneficial act by individual A towards B increase the probability of a subsequent beneficial act by B towards A? Preliminary evidence for an exchange of affiliative behavior against agonistic support, and vice versa, exists for cercopithecine monkeys. De Waal and Yoshihara (1983) measured postconflict attraction between previous alliance partners, and Seyfarth and Cheney (1984) and Hemelrijk (1994) found that more attention and support was given to previous grooming partners engaged in a fight. Experiments on food-sharing among capuchin monkeys (*Cebus apella*) further support the possibility of one favor being followed by another in the opposite direction (de Waal, in press).

The present study investigates sequences of spontaneous grooming and food-sharing in a captive colony of chimpanzees to determine how services are affected by previous interaction between the same individuals. In doing so, the study addresses the issue of partner-specificity: Does a beneficial act by A towards B affect B's behavior towards A only? The assumption of partner-specificity is at the heart of tit-for-tat, but has thus far not received systematic attention. In captivity, partner presence and food availability can be held constant, and all social interactions within a particular time window can be recorded. Demonstration of sequential reciprocal altruism under these circumstances would strongly suggest similar exchange mechanisms under natural conditions, such as when wild chimpanzees divide meat (Boesch and Boesch 1989; Goodall 1986; Teleki 1973).

Both easy-to-measure behaviors selected for analysis confer benefits to the partner in terms of nutrition (i.e., food) or hygiene and possible calming effects (i.e., grooming). In captivity, with its abundant food supply and leisure time, the cost of these behaviors is rather low, however. For this reason, I prefer to speak of "social exchange," "services," and "favors" rather than of "altruism" with its connotation of sacrifice. How the economy of low-cost services relates to reciprocal altruism is as yet unclear, but it is reasonable to assume that the two are evolutionarily and psychologically related. Tendencies underlying social exchange may have evolved in the high-risk domain of reciprocal altruism after which they generalized to interchanges in which there was less at stake. It seems more logical to assume, however, that the evolution of cooperation started with low-risk exchanges, and that the more costly forms of cooperation grew out of this.

A previous study of the same chimpanzee colony as used here demonstrated that both adult males and females peacefully share branches and leaves with each other (de Waal 1989). As in other studies of chimpanzees (Teleki 1973), and indeed in primates in general (Feistner and McGrew 1989), the vast majority of food transfers was of a *passive* nature, i.e., possessors allowed others to remove food from their hands or mouth, or to collect food from within arm's reach. The sharing was selective, however, in that possessors were not equally tolerant of all individuals: only approximately half of the interactions between a possessor and an interested nonpossessor resulted in an actual transfer of food. It was also found that the ability of a possessor to maintain possession and rebuff approaching individuals was independent of social rank: even the lowest-ranking adult successfully rejected feeding attempts by others. This confirms the remarkable "respect for possession" (Kummer 1991) already noted by Goodall (1971) in her first accounts of food-sharing among wild chimpanzees.

METHODS

Subjects and Housing Conditions

The study was conducted on a well-established group of 20 chimpanzees, including 1 adult male and 8 adult females. Six of the adult females were the same as in the previous study; the other 2 adult females had been juveniles during this study, which took place more than 6 years earlier (de Waal 1989). The adult male was new to the group, introduced a year before the study's onset. Two of the partner combinations among the 9 adults were maternal relatives (both mother-daughter pairs); the other 34 adult-adult combinations were unrelated. All juveniles and infants in the group had been born to the adult females. Group composition did not change during the study except for the birth of 3 infants into the colony, several temporary removals for veterinary reasons, and the permanent removal of 1 adult female by the end of 1993.

The colony lived in an outdoor compound of 750 m^2 at the Field Station of the Yerkes Regional Primate Research Center, near Lawrenceville, Georgia. The compound was equipped with climbing structures and visual barriers. At night and when the weather was cold the group could enter a heated indoor area. Observations took place from a tower with an unobstructed view of the entire compound.

Data Collection

Food trials were conducted approximately twice (maximally thrice) weekly during the springs and summers of a 3-year period, from 1992 through 1994. At variable prescheduled times, extra food was provided by throwing freshly cut branches and leaves into the enclosure. The plant species most often used were sweetgum (*Liquidambar styraciflua*), sassafras (*Sassafras albidum*), American beech (*Fagus grandifolia*), willow (*Salix ssp.*), young blackberry shoots (*Rubus ssp.*), bush clover (*Lespedeza repens*), and black oak (*Quercus velutina*), tied together with honeysuckle vine (*Lonicera ssp.*) into two large monopolizable bundles.

Interactions were recorded as a spoken account into a tape recorder for half an hour following introduction of the food. A food interaction was defined as an approach by a nonpossessor to within arm's reach of a food possessor. A food transfer occurred when the nonpossessor collected food directly from the possessor's hands or mouth, cofed on the bundle or pile held by the possessor, or collected food from within easy arm's reach of the possessor. More detailed descriptions of the behavioral categories can be found in de Waal (1989).

Food trials scheduled at 10:00 a.m. or later were preceded by a 90-min preobservation session. Preobservations ended less than half an hour before onset of the food trial and were conducted in all 3 years. In 1992, 90-min postobservations were taken immediately following the food trial, and in 1993 the same was done with a delay of 2 hours after the food trial. No such postobservations were conducted in 1994. In addition, so-called independent 90-min observations were collected throughout the 3-year period on days without food trials. Overall, 200 food trials, 282 independent observations, 168 preobservations, and 134 postobservations were conducted.

Data collection outside the food trials included 5-minute scan samples of state behaviors (e.g., affiliative contact, play) and point events such as mounting, mating, kissing, embracing, submissive greeting (i.e., pant-grunting), intimidation displays, hooting, and aggression. Most important for the present study, grooming bouts were recorded with an all-occurrences sampling technique: groomer, groomee, and bout duration in seconds.

RESULTS

Reciprocity Correlations

A reciprocity correlation is not simply a comparison between the data points above and below the diagonal of a matrix, because such a correlation is not independent of the order in which individuals have been placed. The only result independent of ordering is a correlation between the entire matrix and its transposition. If this procedure is applied to a symmetric matrix, it results in a correlation coefficient of 1. Our procedure tests how closely the data distribution in a matrix approaches symmetry. Since data points in a matrix are mathematically interdependent (i.e., there are more data points than individuals), the degrees of freedom of a correlation cannot be specified (Schnell et al. 1985). The solution used here is free from distributional assumptions: one-tailed probabilities of reciprocity correlation coefficients were evaluated with a quadratic assignment procedure involving 1,000 random matrix permutations (Dow et al. 1987).

Both social services, grooming and food-sharing, showed reciprocal distributions over the 9 × 9 matrix among adults. The Pearson correlation between given and received grooming bouts per hour of observation was $r = .45$ ($p = .006$), and between given and received food transfers, expressed as a percentage of the possessor's total transfers to other adults, was $r = .26$ ($p = .001$). Reciprocity between these two measures (i.e., grooming and food-sharing) was positive, as expected, but nonsignificant: $r = .24$ ($p = .09$).

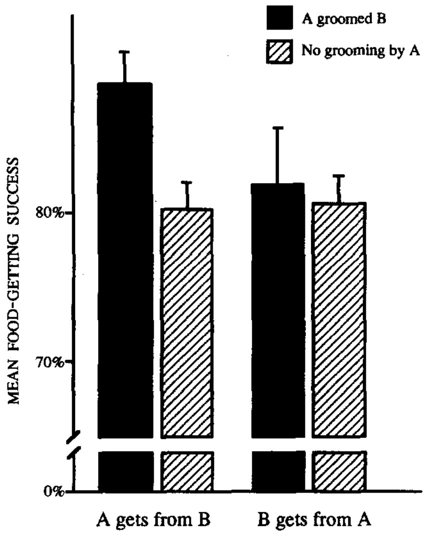
Sharing Following Grooming

Because individuals varied greatly in the number of occasions on which they possessed a sharable quantity of food, the analysis of how grooming affects subsequent sharing could not be based simply on the number of food transfers from individual A to B. A correction was required for the number of occasions on which A actually had food to share, whereas B had none. The measure used here is *food-getting success* (FGS), defined as the proportion of approaches by B to A followed by B's cofeeding with or obtaining food from A (excluding approaches by B to A followed by B's cofeeding with or obtaining food from A (excluding approaches in which B hardly looked at A's food, as when B simply walked by A). Our measure of food receipt thus took into account the inequalities of food possession by comparing food receipt from a particular partner with the interest shown in this partner's food.

Figure 1 shows FGS based on a total of 6,972 approaches among adults during food trials. For each dyadic direction separately, FGS is broken down according to the occurrence of grooming, or not, during preobservations. Thus, in the A to B direction, data for food trials preceded by individual A's grooming of B were pooled to calculate both A's success in obtaining food from B and B's success in obtaining food from A after A had groomed B. The same was done for trials without previous grooming by A to B. As in all analyses, the two conditions were then compared for each dyadic direction separately with a Wilcoxon matched-pairs signed-ranks test (from here on: Wilcoxon). Significant results can therefore not be attributed to covariation of grooming and sharing across dyads (i.e., some dyads both groom and share more); instead, such results indicate behavioral changes in a majority of dyadic combinations (i.e., most dyads sharing more after grooming than without previous grooming).

Only 10.9% of all approaches among adults during food trials followed grooming by the approaching individual, and not all dyadic directions showed approaches under both grooming conditions, i.e., following grooming or no grooming by the approaching individual. Limiting the comparison to those directions in which approaches were observed during both trials with and without previous grooming, it

FIGURE 1. Mean (+ SEM) food-getting success per dyadic direction during food trials. Two conditions are distinguished: either individual A groomed B in the hours prior to the trial, or no previous grooming by A to B occurred. The left-hand side of the graph shows the success of A in obtaining food from B; the right-hand side shows the success of B in obtaining food from A.



was found that A's FGS with B increased after A had groomed B ($z = 3.31$, $p = .0005$, one-tailed), whereas B's FGS with A was unaffected by A's previous grooming of B ($z = .36$, *ns*; Figure 1).

Grooming Effect

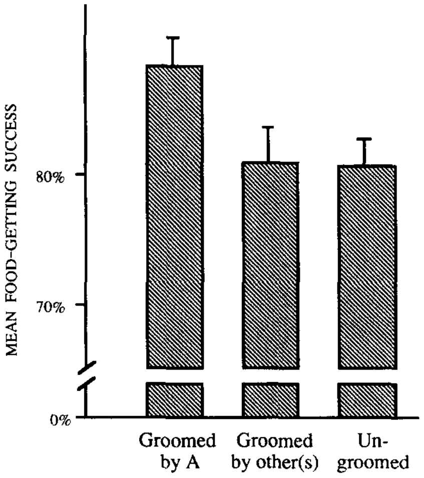
If *grooming effect* is defined as the difference in FGS between food trials preceded by grooming of the possessor by the nonpossessor and trials not preceded by such grooming, dyadic directions involving the adult male showed nearly identical grooming effects (mean ± SEM: 5.3% ± 2.9%) as female-female dyads (5.7% ± 2.0%; Mann Whitney *U* test: $z = .24$, *ns*). Across all dyadic directions, grooming effect correlated negatively with the duration of grooming per hour of independent observation (Spearman Rho = −0.33, $N = 43$, $p = .032$, two-tailed), indicating that increased FGS due to grooming was most pronounced in those dyadic directions in which normally little grooming occurred. Nevertheless, increases in FGS following grooming were general: 31 dyadic directions showed an increase, and only 11 a decrease.

Food trials preceded by grooming were subdivided as to whether A had groomed B for more than 300 s or less. A's FGS did not vary across these two conditions (Wilcoxon: $N = 17$, $T = 69$, *ns*), suggesting that it is the act of grooming rather than its duration that matters.

Partner-Specificity

To investigate if the increase in sharing following grooming applied specifically to the individual which had done the grooming, A's FGS with B was compared across

FIGURE 2. The mean (+ SEM) food-getting success of individual A in relation to food possessor B under three conditions: A groomed B prior to the food trial; adult(s) other than A groomed B; and none of the adults groomed B (ungroomed). A's FGS was significantly elevated only after A had done the grooming.



three conditions: after A had groomed B; after adult(s) other than A had groomed B; and after none of the adults had groomed B. Only the first FGS was significantly elevated: A's FGS was higher after A had groomed B than after another adult had groomed B (Wilcoxon: $z = 2.00$, $p = .023$, one-tailed; Figure 2).

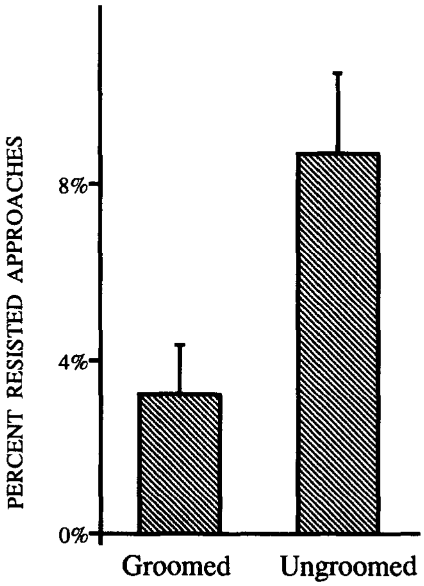
Rejection Behavior

The number of aggressive claims among adults was negligible: only 1.1% of transfers involved use of force. Even the most dominant individuals rarely resorted to aggression and waited patiently, sometimes begging with hand held out, until they could pull a branch out of a bundle or cofeed with the possessor.

The overwhelming majority of food transfers was passive, i.e., the food possessor allowed another individual to take food or collect it from nearby rather than give it to him or her. The possessor could prevent food collection by the other by walking off, turning the back to the other, pulling the food away, and so on. It was speculated that the effect of grooming on subsequent sharing might be due to such so-called *resistance* being shown disproportionally to individuals who had failed to groom the possessor. In support of this hypothesis, the percentage of approaches meeting with resistance was reduced if the approacher had previously groomed the possessor (Wilcoxon: $z = 3.21$, $p = .0007$, one-tailed; Figure 3).

Only a portion of resistance involved agonistic behavior (e.g., threat-barking, screaming, and gesticulating by the possessor). When tested separately, these ago-

FIGURE 3. The mean (+ SEM) percentage of approaches meeting with active resistance from the food possessor after the possessor had been groomed by the approaching individual, or not.



nistic responses, too, occurred less often towards a partner who had previously groomed the possessor (mean ± SEM per dyadic direction: 1.0% ± 0.6%) than if the same partner had not groomed the possessor (3.4% ± 0.9%; Wilcoxon: $z = 2.41$, $p = .008$, one-tailed).

Grooming Following Sharing

After food trials, grooming activity dropped sharply. In 1992, the mean (± SEM) frequency of grooming bouts per hour per adult was 0.63 ± 0.17 during independent observations, but only 0.40 ± 0.14 during postobservations (comparing grooming output per individual adult: Wilcoxon: $N = 9$, $T = 0$, $p < .01$, two-tailed). When food trials of this period were divided as to whether or not sharing had occurred, a nonsignificant trend was found for grooming in return for received food. Food recipients groomed their benefactor in 6.7% ± 1.8% of the postobservations compared to 6.2% ± 0.9% without food receipt from the same partner (Wilcoxon: $z = 1.33$, *ns*). A stronger effect concerned a reduction of grooming in the sharing individuals themselves. They groomed the beneficiaries of their sharing in 5.5% ± 2.0% of the postobservations, which was below the rate of 6.3% ± 1.0% if they had not shared with them (Wilcoxon: $z = 2.58$, $p = 0.1$, two tailed).

A less dramatic decrease in grooming was observed in 1993, when postobservations were delayed. The hourly grooming rate dropped from 0.69 ± 0.15 during independent observations to 0.51 ± 0.18 during postobservations (Wilcoxon: $N = 7$, $T = 1$, $p < .05$, two-tailed). No effects on grooming rate, neither by the sharing individual nor by the recipient, could be demonstrated for the postobservations of this period.

DISCUSSION

The above data make it very likely that the reciprocity correlations previously reported for chimpanzees (de Waal 1989; de Waal and Luttrell 1988) rest on an exchange mechanism in which social services are provided contingent on services previously received from the same partner. Apart from circumventing the problem of symmetry-based reciprocity (see the introduction), this study addressed two further alternative hypotheses.

According to the first hypothesis, both grooming and sharing between A and B reflect a common variable, such as the state of the relationship. If this were true, one would expect the most pronounced link between subsequent services to concern the same direction within the dyad. In other words, grooming by A to B should correlate especially with sharing of A with B. Instead, we found turn-taking, that is, grooming by A to B specifically increased the sharing of B with A. The same hypothesis would predict sharing to be followed by increased grooming in the same direction. The opposite was found, however: previous sharing went together with reduced grooming of the beneficiary of the sharing. Both effects are consistent with an exchange model, not with a state-of-the-relationship model.

The second alternative hypothesis is that the receipt of a service affects an individual's social attitude towards *all* possible partners, not just the partner who provided the original service (Hemelrijk 1994). This could be called the good-mood hypothesis, that is, the receipt of grooming creates a general benevolent attitude. Our data contradict this hypothesis as well: previous grooming affected the FGS of the groomer only, not that of other adults approaching the groomed food possessor.

In sum, we found that: (a) grooming increases the probability that the recipient of the service will share with its donor; and (b) sharing decreases the probability that the donor of the service will groom its recipient. We are not dealing, therefore, with mere variation across time that causes grooming and sharing tendencies to rise and fall in tandem, but with an exchange mechanism in which donations and receipts of services are stored in memory for at least 2 hours and exert distinct, partner-specific effects on the subsequent behavior of donors and recipients. In line with this interpretation, food possessors protested more, sometimes aggressively, if approached by a partner who had not groomed them before the trial.

Whereas it is entirely possible that monkeys, bats, and other animals engage in similar exchanges, only for chimpanzees do we at present have evidence for the entire set of features expected if reciprocity were cognition-based: partner-specificity, selective protest, retaliation, turn-taking, and the effect of one service on another. Before concluding that the mechanisms of tit-for-tat are the same in chimpanzees and other animals, more carefully controlled studies will be necessary on other species. At the very least, reciprocal exchange may be most pronounced in chimpanzees.

At the same time, it should be noted that the observed effect on sharing in our study, although significant, was relatively small. Over the years, our chimpanzees seem to have grown increasingly tolerant during food trials, moving from a FGS among adults of nearly 60% (de Waal 1989) to the 81.9% of the present study. The majority of approaches between adults occurred without previous grooming between them: if preceded by grooming there was an average increase in FGS for the groomer of 5.6%. The most dramatic result was perhaps the number of dyadic directions that jumped to a 100% FGS following grooming. Only 1 of 43 dyadic directions with approaches under both conditions reached an FGS of 100% in the absence of previous grooming by the approaching party. If the approacher had groomed the food possessor, on the other hand, no less than 17 dyadic directions reached this high success level.

How these observations of sequential mutual exchange relate to truly costly exchanges, such as those in which one individual risks his life for another, is as yet unclear. The present data are perhaps best interpreted as support for the existence of a *service economy* among chimpanzees. Reciprocal altruism may be part of this economy and may have been instrumental in its evolution, yet the economy covers a much wider range of phenomena than those traditionally defined as "altruistic" (i.e., fitness reducing for the donor, and fitness enhancing for the recipient). Female sexual proceptivity, for example, most likely is an important currency in the chimpanzee's service economy (Stanford et al. 1994; Yerkes 1941) even though no one would argue that a female's willingness to mate reduces her fitness or constitutes cooperative behavior in the usual sense. The concept of "service" or "favor" does cover such behavior and permits a broader perspective on the psychological mechanisms underlying reciprocal exchange in primates.

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