

The Evolution of Cooperation in Primate Groups

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Primates don't donate to NPR or give blood. But they do perform a variety of behaviors that are thought to be altruistic. That is, they act in ways that reduce their own fitness, but increase the fitness of their partners. For example, male chimpanzees form alliances and patrol the borders of their territories, sometimes launching lethal attacks on members of other communities (Goodall et al. 1979; Nishida et al. 1985; Boesch and Boesch-Achermann 2000; Watts and Mitani in preparation); vervet monkeys give alarm calls when they detect predators (Struhsaker 1967; Seyfarth et al. 1980); captive cebus monkeys and chimpanzees allow others to share their food (de Waal 1997a, 1997b, 2000); macaque females defend juveniles from harassment by other group members (Chapais 1992); langurs and howlers spend considerable amounts of time carrying other females' infants (Paul 1999); and monkeys in a number of species spend 10-20% of their waking hours removing dirt, debris, and ectoparasites from the hair and skin of other group members (Dunbar 1991).

Over the last 25 years, primatologists have collected large quantities of information about the distribution of these charitable activities. Evolutionary theory predicts that altruism will occur when benefits increase the actor's own inclusive fitness (Hamilton 1964) or when benefits are exchanged by reciprocating partners (Trivers 1971; Axelrod and Hamilton 1981). Thus, examinations of kinship and reciprocity, have dominated efforts to account for the distribution of altruistic behavior among primates (Gouzoules and Gouzoules 1987; Dugatkin 1997; Silk 1987, 2001). Data that do not conform to predictions derived from these models have been discounted, denied, or simply ignored because they don't fit into our theoretical paradigms. However, empirical and theoretical work in experimental economics suggests that humans cooperate when

standard evolutionary theory tells us that they shouldn't. Efforts to develop systematic explanations of human behavior that explain these anomalies have generated new models of the motives that give rise to human cooperation, including strong reciprocity (Gintis 2000; this volume).

The goal of this paper is to review what we know about the evolutionary forces that underlie cooperation in primate groups, and to evaluate the possibility that the motives that give rise to strong reciprocity in humans also produce cooperation in primate groups. The literature provides very strong evidence that kin selection play a fundamental role in the lives of nonhuman primates; shaping social organization, dispersal strategies, dominance hierarchies, and patterning of affiliative interactions. There is reasonably good evidence of reciprocity and interchange within dyads, but very little systematic evidence of punishment. Experimental studies indicate that cooperation is contingent on the nature of previous interactions among partners, but the proximate mechanisms that generate these contingencies are unknown.

Analyses of the evolutionary mechanisms underlying cooperation in primates rely on assumptions about the relative magnitude and nature of the effects of these kinds of behaviors on individual fitness. In fact, it is virtually impossible to quantify the effects of a single behavioral act or social interaction on lifetime fitness. This problem is common to almost all studies of the adaptive function of social behavior in animals. We rely on what Grafen (1991) calls the "phenotypic gambit", the assumption that the short-term benefits that individuals derive from social interactions are ultimately translated into long-term differences in fitness. Animals who are regularly supported in agonistic confrontations, protected from harassment, or allowed to share access to desirable

resources are expected to gain short-term benefits that are ultimately translated into fitness gains.

The Evolution of Altruism Via Kin Selection

In general, natural selection favors the evolution of behaviors that increase an individual's relative fitness. Altruistic behaviors, that reduce individual fitness, contradict this logic. The theory of kin selection, developed by the late W.D. Hamilton, relies on the insight that relatives share some of their genetic material because they have a common ancestor (Hamilton 1964). If individuals behave altruistically to their relatives, then they have some chance of conferring benefits upon individuals who carry copies of their own genes. The likelihood of this happening is based upon the genetic relationship between the actor and the recipient. Hamilton demonstrated that altruistic behaviors will be favored by selection when the costs of performing the behavior, c , are less than the benefits, b , discounted by the coefficient of relatedness between actor and recipient, r . The coefficient of relatedness is the average probability that two individuals acquire the same allele through descent from a common ancestor. This principle, which is generally called Hamilton's rule, is stated as: $rb > c$.

Two basic insights can be derived from Hamilton's Rule. First, it is clear that when $r = 0$, this inequality cannot be satisfied. This means that unconditional altruism (via kin selection) will be restricted to kin ($r > 0$). Second, costly altruism will be limited to close kin, as the conditions for Hamilton's rule become progressively more difficult to satisfy as costs rise. During the 1950's, the famous British evolutionary biologist, J.B.S. Haldane, is said to have worked through these simple calculations on the back of an

envelope one evening in a pub, and announced that he would give up his life to save two brothers or eight cousins.

Multi-level selection models (Wilson 1997) provide an alternative mathematical representation of the processes that underly Hamilton's model of kin selection. In the inclusive fitness approach, fitness effects are accounted to the bodies in which the genes causing the effects are expressed, while in the multi-level selection approach, fitness effects are partitioned into within and between group components (Reeve and Keller 1999). The two approaches are mathematically equivalent, but their heuristic value may vary in different circumstances.

Kin Recognition

The coefficient of relatedness, r , is the critical element for determining an adaptive course of action in social interactions that are influenced by kin selection (Hamilton 1987). In order to meet the conditions of Hamilton's rule, animals must make sure that they limit altruistic behavior toward kin ($r > 0$). For species in which kin are clustered in discrete locations, such as in burrows or nests, spatial location may provide sufficient information for kin discrimination (Blaustein et al. 1987). For other animals, however, the problem is more complicated. Hamilton (1987) predicted that the ability to identify kin would be most fully developed in species that live in social groups; when there are opportunities for costly behaviors, such as egg dumping; and when passive, context-dependent mechanisms for distinguishing kin from nonkin are not likely to be effective.

Primates fit all three of these conditions. Most primates live in large and relatively stable social groups (Smuts et al. 1987). Even the most solitary primates, like orangutans and galagos, have regular interactions with familiar conspecifics (Bearder 1989; Galdikas 1988). Primates engage in a variety of fitness-reducing behaviors, including infanticide (van Schaik and Janson 2000); severe intragroup aggression (McGrew and McLuckie 1986); and intense feeding competition (Dittus 1979, 1988). Most primates live for extended periods of time in groups that include both relatives and nonrelatives, so context-driven mechanisms for distinguishing kin are likely to be of limited use. Thus, primates are expected to exhibit finely developed kin recognition abilities.

A number of different perceptual mechanisms underlie kin recognition in animal species. For example, sea squirts are able to recognize other sea squirts who carry the same allele on the hypervariable histocompatibility locus (Pfennig and Sherman 1995). Some animals, including most mammals, are thought to learn who their relatives are during the course of development, drawing cues about kinship from patterns of association and interactions.

Close association early in life is generally thought to be the basis for kin recognition in primate groups (Bernstein 1991; Walters 1987a). The importance of familiarity is supported by evidence from cross-fostering experiments. Foster mothers routinely accept strange infants, even when they are not the same sex or exact ages as their own infants (Bernstein 1991; Deets 1974).

Early association allows for recognition of maternal kin, but not paternal kin. Close associations between males and females are uncommon in most nonmonogamous primate species, limiting infants abilities to learn who their fathers are. Other proxies for

paternity are liable to error. For example, in multi-male species, male rank is often correlated with reproductive success, but the association is far from perfect. In some species that form one-male groups, such as patas and blue monkeys, incursions by nonresident males may occur during the mating season (Cords 1987). Even in pair-bonded species, like gibbons and callicebus monkeys, females sometimes mate with males from outside their groups (Mason 1966; Palombit 1994; Reichard 1995).

For species in which a single male monopolizes mating opportunities, age may be a good cue of paternal kinship (Altmann 1979). Among baboons in Amboseli, Kenya, high ranking males monopolize access to females (Altmann et al. 1996) and agetates are therefore likely to be paternal halfsiblings. Adult females interact at higher rates with agetates than others, generating significant differences in the rate of interactions between paternal halfsiblings and unrelated females (Smith 2000). Similar patterns characterize female rhesus macaques on Cayo Santiago (Widdig and Nürnberg 2001).

There is also tantalizing evidence that monkeys and apes may actually be able to recognize paternal kin based on phenotypic cues alone. In baboons and rhesus macaques females distinguished *among* agetates, showing slight preferences for paternal halfsiblings over nonkin (Smith 2000; Widdig and Nürnberg 2001). In the laboratory, chimpanzee females are able to match digitized photographs of unfamiliar females with their sons, but not their daughters (Paar and de Waal 1999). Since the chimpanzees were unfamiliar with the animals in the photographs and had no physical, auditory, or olfactory contact with them, their ability to identify mother-son pairs suggests that chimpanzees use phenotypic cues to assess paternal kinship.

Social Organization Facilitates Kin Selection

The structure of social groups in many primate species facilitates the evolution of cooperation via kin selection. Virtually all monkeys and apes live in stable social groups. Primate infants are completely dependent on their mothers (and sometimes their fathers) for support at birth, but become gradually more independent as they mature. Bonds between mothers and their offspring commonly continue beyond weaning, which marks the end of nutritional dependence. In some species, such as pair-bonded siamangs and owl monkeys, fathers are active participants in offspring care. In some species, such as marmosets and tamarins, older offspring act as “helpers at the nest” and their support enhances parental reproductive success (Garber 1997). Extended family ties are presumably the product of kin selection.

Dispersal patterns play an important role in the evolution of cooperation via kin selection. In all primate species, members of one or both sexes disperse from their natal groups (Pusey and Packer 1987). While natal dispersal presumably evolved to prevent inbreeding (Pusey and Wolf 1996), the *patterns* of dispersal may reflect selective pressures that favor kin-selected altruism (Wrangham 1980). In many primate species, members of only one sex (usually males) disperse, while members of the other sex remain in their natal group throughout their lives (Pusey and Packer 1987). When only one sex disperses, members of the nondispersing (philopatric) sex live among kin of varying degrees of relatedness. Thus, in baboon, macaque, and vervet groups, females grow up within a complex network of maternal and paternal kin: mother, grandmother, sisters, brothers, aunts, uncles, and cousins.

In these species, maternal kin spend much of their time in close proximity, and virtually all behaviors that are generally classified as altruistic, including grooming, food sharing, benign alloparenting, and alarm calling, show matrilineal kin biases (reviewed by Bernstein 1991; Silk 1987; Gouzoules and Gouzoules 1987; Walters 1987a; Silk 2001). We don't know whether the distribution of these behaviors fits predictions derived from Hamilton's rule because the costs and benefits associated with these behaviors have not been measured. Nonetheless, the matrilineal bias in social behavior seems likely to be the product of kin selection.

More compelling evidence comes from studies of coalition formation, interactions in which one individual intervenes on behalf of another in an ongoing agonistic interaction. Monkeys who intervene in ongoing disputes put themselves at some risk, as monkeys are equipped with sharp teeth that they sometimes use to bite their opponents. Primates can be wounded in these disputes, sometimes seriously. Thus, coalitions provide “the clearest evidence of primates engaging in behavior that benefits another at some risk and/or cost to self” (Bernstein 1991).

Monkeys, particularly females, often intervene in ongoing disputes in support of their relatives. Females are significantly more likely to support kin than nonkin in aggressive disputes (Berman 1983a, 1983b, 1983c; Chapais 1983; Cheney 1983; Datta 1983a, 1983b; Kaplan 1977, 1978; Kurland 1977; Massey 1977; Silk 1982), particularly against higher ranking opponents (Chapais 1983, Chapais et al. 1991; Cheney 1983; Hunte and Horrocks 1987; Kurland 1977; Netto and van Hooff 1986; Pereira 1989; Silk 1982; Walters 1980; Watanabe 1979). Since allies run some risk of being threatened,

chased, attacked, or injured when they intervene against higher ranking monkeys, females are evidently willing to take greater risks on behalf of kin than on behalf of nonkin.

Support has both short-term and long-term consequences. In the short-term, animals who obtain support are more likely to win disputes and less likely to become involved in escalated attacks. In the long-term, support facilitates rank acquisition (see Chapais 1992 for a detailed analysis of this process). During infancy, infants are protected by their mothers and close female kin when they are threatened by other group members, particularly females lower ranking than their own mothers (Berman 1980; Datta 1983a; Cheney 1977; de Waal 1977; de Waal and Luttrell 1985; Horrocks and Hunte 1983; Johnson 1987; Lee 1983a, 1983b; Lee and Oliver 1979; Paul and Kuester 1987; Pereira 1989; Walters 1980). As they grow older, young juveniles obtain support when they challenge peers whose mothers are lower ranking than their own mothers and when they challenge adults who are subordinate to their own mothers. Initially, juveniles can defeat older and larger juveniles only when their own mothers are nearby (Datta 1983a, 1983b; Horrocks and Hunte 1983; Walters 1980). Eventually, immatures are able to defeat all group members who are subordinate to their own mothers, even when their mothers are not in the vicinity. Since juveniles are able to defeat everyone that their own mothers can defeat (but not their mothers themselves), offspring acquire ranks just below their mothers.

The same process, repeated over generations and across families, generates matrilineal dominance hierarchies in which all members of the same matriline occupy contiguous ranks. Moreover, all members of a given matriline rank above or below all the members of other matrilines. Matrilineal dominance hierarchies have now been

documented in at least seven species of macaques, baboons, and vervet monkeys (Chapais 1992). These dominance hierarchies are remarkably linear and stable over time, perhaps because matrilineal units operate as corporate units (Silk 1993). These arrangements have important fitness consequences for females: high ranking females typically mature at earlier ages, give birth to healthier infants, and have shorter interbirth intervals than low ranking females do (reviewed by Silk 1987, 1993; Harcourt 1987).

Primates are discriminating nepotists. Thus, Japanese macaques and rhesus macaques treat distant kin much like nonkin (Kapsalis and Berman 1996a; Chapais et al. 1997). It is not clear whether monkeys do not recognize distant relatives as kin (Kapsalis and Berman 1996a) or support for distant kin fails to meet the criteria for altruism specified by Hamilton's rule. Nepotism is also contingent on the circumstances. Among Japanese macaques, younger sisters commonly rise in rank over their older sisters. This process is sometimes contentious, and younger sisters "target" their older sisters for rank reversals. When females intervene in disputes involving their older sisters and subordinate nonkin, they are as likely to intervene against their sisters as they are to support them. In contrast, when females intervene in conflicts involving kin that are not targeted for rank reversals, females are much more likely to intervene on behalf of their relatives than their opponents (Chapais et al. 1994). Thus, females "apparently solve the conflict of interest between egotism and nepotism by maximizing their own rank among their kin on the one hand, and by maximizing the rank of their kin in relation to non-kin on the other" (Chapais 1995: 129).

When females disperse, and males remain in their natal group, there are parallel opportunities for kin-selected altruism among males. Male philopatry is associated with

strong male bonds among chimpanzees (e.g. Goodall 1986), muriquis (Strier 1992, 2000), spider monkeys (Symington 1990), Costa Rican squirrel monkeys (Boinski 1994), and in some populations of red colobus monkeys (Struhsaker 2000; but see Starin 1994). For those interested in the evolutionary roots of human behavior, male bonding in chimpanzees is of particular interest. Male chimpanzees spend much of their time in the company of other males. They groom one another, hunt together, share meat, and collectively patrol the borders of their territories (Goodall 1986; Mitani et al. 2000; Simpson 1973; Watts 2000; Wrangham and Smuts 1980). In some populations, pairs or trios jointly control access to receptive females and share matings (Watts 1998).

Primatologists have generally assumed that kin selection underlies male cooperation, but this conclusion has been undermined by several recent findings. First, affiliative and cooperative behavior are not linked to matrilineal kinship in two Ugandan chimpanzee communities (Goldberg and Wrangham 1997; Mitani et al. 2000). Second, genetic analyses of paternity in the Tai chimpanzee community revealed that half the infants sampled were fathered by males outside the community (Gagneux et al. 1997, 1999). If chimpanzees were only able to recognize maternal kin, this would clearly limit the extent of maternal relatedness within chimpanzee groups and limit the potential for kin selection to operate. Taken together, these data strongly suggest that “male chimpanzees do not always choose important social partners on the basis of genetic ties” (Mitani et al. 2000).

However, new data from Gombe indicate that all infants from that community are sired within the community (Constable et al. 2001). Moreover, reconsideration of the genetic data from Tai reveals mistakes in the original analysis. All but one of the infants

sampled can be linked to a community male with a very high level of certainty (Constable et al. 2001). Moreover, evidence that chimpanzees can identify kin from phenotypic features alone (Paar and de Waal 1999) suggests that paternal kinship could underlie cooperative activity among chimpanzees. Thus, it is too early to discount the role of kinship in the evolution of cooperative behavior among male chimpanzees.

When both sexes disperse, opportunities for kin selection to operate are more limited, but may still be important. Red howlers provide a particularly compelling example of this. The number of females in red howler groups is confined within narrow limits: groups with too few females are unable to defend their territories, while groups with too many females face competition for food and become more attractive targets for male takeovers which then leads to infanticide (Pope 2000a). So, when groups reach the optimal size, maturing females must disperse. Dispersal is very costly for females, particularly when local habitats are fully saturated. Some females never succeed in establishing new groups, and those that do succeed begin to reproduce later than females who remain in their natal groups. The high costs of dispersal generate intense competition among females over recruitment opportunities for their daughters. Adult females actively harass maturing females in an effort to force them to emigrate. Females actively intervene on behalf of their daughters in these contests (Crockett 1984; Crockett and Pope 1993). In most cases, “only the daughters of a single presumably dominant adult female are successful at remaining to breed” (Pope 2000b).

Kin selection also shapes the life histories of male red howlers. Males gain access to breeding females in a variety of ways. When habitats are not crowded, they may join up with migrant females and help them establish new territories. But as habitats become

more saturated, males can only gain access to breeding females by taking over established groups and evicting male residents. This is a risky strategy because males are often injured in takeover attempts (Crockett and Pope 1988). Moreover, males tend to remain in their natal groups longer, helping their fathers resist takeover attempts. Thus, when habitats are saturated, single males are at a distinct disadvantage in obtaining access to breeding females.

Competition among males generates powerful incentives for cooperation. Thus, males form coalitions and cooperate in efforts to evict residents. After they have established residence, males collectively defend the group against incursions by extragroup males. However, cooperation involves clear fitness costs because only one male fathers infants within the group. Not surprisingly, coalitions that are made up of related males last on average 8.2 years, while coalitions among unrelated males last only 2.3 years (Pope 1990). Coalitions composed of kin are also less likely to experience dominance changes, which often lead to infanticide, than coalitions composed of unrelated males (Pope 1990).

In summary, there seems little doubt that kin selection plays an important role in the evolution of cooperation in primate groups. Our efforts to evaluate the *extent* of kin selection are limited by the difficulty of quantifying the effects of social behavior on fitness and our limited knowledge of paternal kinship.

Reciprocity in Primate Groups

Reciprocal altruism provides another vehicle for cooperation in primate groups (Axelrod and Hamilton 1981; Trivers 1971). Primates easily meet the necessary

conditions for reciprocal altruism: they recognize their partner as individuals and have frequent opportunities to interact with group members. Moreover, they seem to be able to monitor and remember their partners' responses and adjust their subsequent behavior accordingly (references below).

Although primates are prime candidates for reciprocal altruism, there is much less evidence of reciprocity than of kin selection (Seyfarth and Cheney 1988; Noë and Hammerstein 1995). This may be due to the fact that it is difficult to detect reciprocal altruism in nature (Seyfarth and Cheney 1988). We can tabulate the frequency and duration of services performed within dyads, but we can't translate these values directly into fitness units and calculate the balance between benefits given and received. This is particularly complicated when exchanges involve different currencies or reciprocity is delayed in time. Even if we find tight associations between altruism given and received among partners, it is possible that the association is causally linked to a third variable that we haven't taken into account, such as kinship (Hemelrijk and Ek 1991). In naturalistic settings it is often difficult to determine whether the delivery of benefits is contingent on reciprocity.

Much of what primatologists have written about reciprocity involves grooming. Grooming is an obvious candidate for reciprocal exchanges because it is common and involves complementary roles: I'll scratch your back if you scratch mine. Grooming is the most common form of social behavior among nonhuman primates, occupying up 20% of every day (Dunbar 1991). The functions of grooming are not fully understood. Grooming is thought to be beneficial to the recipient because ectoparasites, such as ticks, lice, and botflies, are removed and wounds are cleaned (Saunders 1988;

Henzi and Barrett 1999). This suggests that grooming would be concentrated on regions of the body that animals cannot reach themselves; and this is often the case (Pérez and Veà 2000). However, grooming solicitations do not correspond perfectly to accessibility, and this suggests that other factors may also be in play. Anyone observing monkeys groom would suspect that grooming is intensely pleasurable: animals who are being groomed seem to be utterly relaxed. In fact, grooming lowers heart rates and raises levels of beta-endorphins (Aureli and Smucny 2000). Grooming may also have social functions (Dunbar 1988; 1991), providing a means to reinforce social bonds and cultivate valuable social relationships.

While grooming seems to be beneficial to recipients, those who provide these services incur some costs. At the very least, the groomer expends time and energy in servicing its partner. The groomer may also become more vulnerable to attacks by predators or other group members because vigilance is reduced during grooming (Cords 1995; Maestriperi 1993).

If grooming is the product of reciprocal altruism, then grooming (among nonkin) should be limited to reciprocating partners. Several lines of evidence suggest that this may be the case. First, in large groups, grooming is restricted to a relatively limited subset of potential partners. For example, female baboons in the Okavango Delta of Botswana groomed on average only 8 of the other 18 adult females in their group; and most females concentrated most of their grooming on an even smaller number of females (Silk et al. 1999). In general, the extent of selectivity is related to the number of available partners. In small groups, females distribute their grooming evenly across the group, but as groups grow larger, grooming is less evenly allocated across potential partners (Silk et

al. 1999). This may reflect cognitive constraints on females' ability to keep track of large numbers of relationships (Henzi and Barrett 1999) or ecological constraints that limit the amount of time that females can afford to spend grooming (Dunbar 1991; Henzi et al. 1997).

Is grooming reciprocated? A definite answer to this question is surprisingly elusive. Among male chimpanzees, there are positive correlations between the amount of grooming given and received, but grooming is not evenly balanced within dyads (Watts 2000). There are also cases in which grooming is evenly balanced within the majority of dyads. Thus, adult female baboons in the Okavango Delta tended to groom each of their partners as often as their partners groomed them (Silk et al. 1999). Similarly, in white-faced capuchins, grooming is evenly balanced within the majority of dyads (Manson et al. 1999). In some cases, grooming roles are alternated within bouts (Barrett et al. 1999; Muroyama 1991), but others in which grooming tends to be reciprocated over longer time scales (Navarette et al. in preparation).

There are many groups in which grooming is unbalanced within dyads, and disparities in grooming given and received are sometimes linked to dominance rank. In some groups, high ranking partners receive more grooming than they give each of their partners (Chapais 1983; Fairbanks 1980; Seyfarth 1980; Silk 1982; Sambrook et al. 1995; Stambach 1978; Watts 2000), in other groups high ranking partners give more grooming than they receive in return (Altmann et al. 1998; O'Brien 1993; di Bitetti 1997; Linn et al. 1995; Parr et al. 1997). Most primatologists assume that these imbalances exist because grooming is exchanged for other commodities such as coalitionary support (Seyfarth 1977), food (de Waal 1997a), tolerance (Silk 1982; Fairbanks 1980), or access

to attractive infants (Muroyama 1994, Henzi 2001), or maintaining group cohesion (Altmann et al. 1998).

Seyfarth (1977) was the first to suggest that monkeys might exchange grooming for support in agonistic interactions. His argument was based on the notion that high ranking animals make powerful coalition partners. He reasoned that females might groom higher ranking monkeys who would in return provide support for them when they were harassed by other group members. Grooming and support are positively correlated among unrelated vervets in Amboseli (Seyfarth 1990) and white-faced capuchins in Costa Rica (Perry 1996). However, kinship was not known for the capuchins, and the observed correlation between grooming and support might actually arise because females selectively support and groom close kin (Hemelrijk and Ek 1991). This is apparently the case among rhesus macaques on Cayo Santiago where grooming and support are correlated among related females, but not unrelated females (Kapsalis and Berman 1996b). However, grooming and support are correlated among male bonnet macaques (Silk 1992) and male chimpanzees (Mitani et al. 2000) and these results are not confounded by maternal kinship. Researchers have failed to find consistent associations between grooming and support among in several cases (Fairbanks 1980; Silk 1982; de Waal and Luttrell 1986).

Although the naturalistic data provide only tepid support for Seyfarth's model, two experimental studies demonstrate a direct link between grooming and support in Old World monkeys. Using tape-recorded vocalizations of females' screams, which signal distress and are often used to recruit support, Seyfarth and Cheney (1984) showed that free-ranging vervet females were more attentive to screams of unrelated females if they

had been groomed by the screaming female shortly before they heard the scream than if they had not been groomed by her. Similarly, Hemelrijk (1994) artificially induced fights among unrelated female macaques housed temporarily in groups of three. When fights between two females occurred, aggressors sometimes received support from the third female. Support was more likely to be given to the aggressor if she had previously groomed the potential supporter.

Grooming may also be used to obtain other valuable benefits. Female bonnet macaques are less likely to be harassed while they are grooming higher ranking females than when they are grooming lower ranking females (Silk 1982), and grooming may confer protection. Female monkeys may also use grooming to obtain access to infants. For reasons that are not altogether clear, female monkeys are strongly attracted to newborn infants (Paul 1999; Maestriperi 1994; Silk 1999). Females gather around new mothers, attempting to smell, nuzzle, touch, and inspect the genitals of newborn infants. Macaque and baboon mothers do not seem to welcome this interest in their infants, even though most of the interactions seem relatively benign. In these species, new mothers are often approached and groomed at higher rates than they are at other times (Altmann 1980) and some researchers suggest that females trade grooming for access to newborn infants (Muroyama 1994; Henzi 2001).

Food Sharing

Food sharing plays a fundamental role in the organization of traditional human societies (Foley 1987). While gathered foods are generally redistributed only to family members, meat is typically shared with all members of the group. In primates, which rely

mainly on plant foods, food sharing is generally uncommon and limited to offspring (Foley 1987; McGrew 1992). Chimpanzees represent a major exception to this rule—males hunt regularly and successfully and they share access to their kills (Boesch and Boesch-Achermann 2000; Goodall 1986; Mitani and Watts in preparation). This has generated considerable interest in the dynamics of hunting and food sharing among chimpanzees.

In chimpanzees, hunting is usually a collective activity. At some sites, hunters take different roles in stalking, ambushing, and snatching prey (Boesch 1994; Boesch and Boesch 1989; Boesch and Boesch-Achermann 2000). At other sites, hunting involves no obvious coordination (Stanford 1996; Busse 1978; Goodall 1986; Mitani and Watts 1999; Uehara et al. 1992). Surprisingly, there is little consensus about why male chimpanzees hunt. In some primates, predatory activity increases when plant foods become scarce (Dunbar 1983; Foley 1987). Chimpanzees rely heavily on ripe fruit and they may hunt to compensate for seasonal shortages of their preferred foods (Teleki 1973; Takahata et al 1985; Stanford 1996, 1998). However, hunting seems to have a social component as well. Males are most likely to hunt when they are in large groups, and hunting success generally increases with party size (Stanford 1996). This suggests that males may hunt to obtain meat that they can trade for sexual access to females (Stanford 1996, 1998; Stanford et al 1994) or they may use meat to cultivate social bonds with other males (Nishida et al. 1992; Boesch and Boesch-Achermann 2000; Mitani and Watts in preparation).

Careful analyses of the distribution of fruit, hunting effort, and food sharing at Ngogo, a site in the Kibale Forest of Uganda (Mitani and Watts in preparation) suggest

that hunting may enhance the quality of social bonds among males. In Ngogo, chimpanzees hunt most often when fruit is most abundant, ruling out the possibility that males hunt to compensate for food shortages. Males did not share selectively with sexually receptive females and receptive females did not mate selectively with males who shared food with them, suggesting that males do not trade meat for sex. However, males did share meat selectively with males who shared meat with them and with males who regularly supported them in agonistic interactions. Moreover, males who hunt together also tend to groom one another selectively, support one another, and participate in border patrols together (Mitani et al. 2000). Frequent participation in border patrols is, in turn, linked to male mating success (Watts and Mitani in preparation). It is not clear whether the patterns detected at Ngogo characterize chimpanzees at other sites.

In captivity, food sharing extends to provisioned plant foods. De Waal (1997a) observed chimpanzees for several hours before and after they were fed fresh cuttings of leaves and branches, delicacies that the chimpanzees clearly relished. Those who possessed leaves and branches were more likely to share their booty with animals who had previously groomed them than with animals who had not groomed them in the past few hours. Moreover, if there had been no grooming before provisioning, the possessor was more likely to respond aggressively to efforts to take food from their pile. The possessor's largesse was not simply a result of being groomed—the chimps limited their generosity to the animals that had just groomed them. Furthermore, the possessor's largesse was not simply a reflection of the quality of the relationship between the two animals—the chimps were more likely to share with those that groomed them than those that they had groomed themselves. However, the magnitude of the effect of prior

grooming was influenced by the nature of the relationship between the two individuals—for pairs that rarely groomed, sharing was strongly contingent on recent grooming, while for pairs that groomed at higher rates, recent grooming had a smaller impact on sharing.

De Waal and his colleagues have also studied the mechanisms underlying food sharing in captive capuchin monkeys. In one set of experiments, a pair of familiar monkeys are held in adjacent cages separated by wire mesh (de Waal 1997b). The holes in the mesh are large enough to allow the monkeys to reach into the adjacent cage and take food items. The experimental design is simple. First, one monkey is given food. Later, the other monkey is given food. All transfers of food in both phases of the experiment are monitored by the observers.

In this experimental situation, a considerable amount of food changed hands. Owners virtually never handed food to their partners or pushed it through the holes in the wire mesh, but they often sat very near the mesh partition with their food. When they did so, the monkey in the adjacent cage was able to reach through the wire mesh and take pieces of food, often from within the owner's reach and in plain sight. In general, more food was taken from male owners than from female owners. Females, but not males, tended to exchange food reciprocally. That is the rate of transfer from the owner to her partner in the first phase of the experiment was correlated with the rate of transfer when their roles were reversed in the second phase of the experiment. Transfer rates were also affected by the quality of social relationships among females, as dyads that tended to associate frequently and fight little had higher transfer rates than dyads that associated less often and fought more frequently.

De Waal (1997b) initially used the term “sharing” to refer to these food transfers, but subsequently suggested that “facilitated taking” might be a better label for them (de Waal 2000). He points out that the capuchins rarely gave food to their partners directly (de Waal 1997b), even though they did little to protect their food from theft. Thus, capuchins may be strongly motivated to be near their partners, and food transfers may be an inadvertent side effect of their sociability. This interpretation is consistent with evidence that the quality of social bonds influences food transfer rates (de Waal 1997b). It is also supported by a second set of experiments in which two females housed in adjacent cages were given food at the same time, but the food items differed in their desirability (de Waal 2000). Females spent more time near the mesh partition when a monkey was in the adjacent cage than when it was empty, but they dropped less food near the partition when the it was occupied by another monkey. Moreover, females tended to spend less time near the partition (and within their partner’s reach) when they had more desirable foods than their partners. Thus, females seem to be drawn to favored companions, but are also wary of losing food to them. Observed rates of food transfer are the product of a compromise between these competing motivations (de Waal 2000).

Using a different experimental paradigm, De Waal and Berger (2000) explored capuchins willingness to participate in cooperative tasks. As in the previous experiment, monkeys were held in adjacent cages separated by a wire mesh partition. Here, the monkeys had to pull a counter-weighted bar to bring a tray holding a baited food bowl within reach. De Waal and Berger examined the monkeys’ participation in this task under three different conditions. In the solo condition, only one food bowl was baited and a

single monkey was able to pull the bowl to within reach. In the cooperative condition, only one food bowl was baited, but it required joint action by both monkeys to pull the bowl within reach. In the mutualistic condition, both bowls were baited and it required joint action by both monkeys to pull the bowl within reach. Monkeys were equally successful in the solo and mutualism conditions, pulling the food bowl forward approximately 85% of the time. Monkeys succeeded on the cooperative task only 40% of the time. However, when monkeys did succeed on the cooperative task more food was transferred than in the successful solo trials. Moreover, a larger fraction of food transfers were tolerated (in sight and reach of the owner) than in solo trials.

De Waal and Berger (2000) argue that these experiments show that “capuchins cooperate even if it is obvious that only one of them, and which one, will be rewarded”, and that that capuchins “exchange labor for payment”. But given the small size of the cages, the capuchins marked affinity for their partners, and the messiness of their eating habits, both parties may be relatively certain that they will obtain food if they cooperate in pulling the bowl forward. Moreover, it is not clear that food transfers reflect an exchange of labor for payment. Even in solo trials, some food is transferred and the incremental effects of cooperation on food transfers and tolerance is relatively small. In solo trials 7-9 pieces of food are transferred on average and 58% of those transfers are tolerated by the owner. In cooperative trials, these numbers increase only slightly; 9-11 pieces are taken and 65% of these transfers are tolerated.

Mechanisms Underlying Reciprocity in Primates

Balanced exchanges between partners and interchange across currencies are often interpreted as evidence that monkeys practice reciprocal altruism. De Waal has questioned this interpretation, suggesting that balanced exchanges might simply arise from mutual tolerance or high rates of association between partners, rather than from contingent exchanges that require careful record keeping (de Waal and Luttrell 1988; de Waal 1997b; de Waal 2000; de Waal and Berger 2000) “If members of a species were to direct aid preferentially to close associates, a reciprocal distribution would automatically result due to the symmetrical nature of association” (De Waal 2000). De Waal calls this “symmetry-based reciprocity”, and suggests that proximity should be controlled in analyses of reciprocity (De Waal and Luttrell 1988).

There are both logical and empirical reasons to doubt that symmetry-based reciprocity accounts for the distribution of altruistic behavior in primate groups. Symmetry-based reciprocity implies that proximity can be treated as an independent variable which is not affected by the nature of interactions between individuals. It seems more likely that association patterns reflect the nature of affiliative relationships between individuals. Thus, animals preferentially associate with those that tolerate, groom, and help them, they don't preferentially tolerate, help, and groom those that they just happen to associate with. Second, it seems unlikely that symmetry-based reciprocity would be stable against invasion by cheaters. Those who accepted help from close associates, but did not return it, would be at a distinct advantage. In fact, there is no evidence for symmetry-based reciprocity in primate groups. Significant correlations between benefits given and received are maintained, even when proximity is controlled statistically (de

Waal and Luttrell 1988). Moreover, several experimental studies demonstrate contingencies between benefits given and subsequently received (Seyfarth and Cheney 1984; Hemelrijk 1994; de Waal 1997a, 1997b, 2000).

De Waal's (2000) observations of fluctuations in the rate of food transfer within dyads over the course of successive experiments led him to suggest that reciprocity may be based on a tendency to mirror the social predispositions of partners, responding positively to positive social overtures and negatively to negative social overtures. "If facilitated taking is mediated by such general social predispositions, this would mean that, rather than keeping track of exact amounts of given and received food, the monkeys follow a simple tolerance-breeds-tolerance scheme" (de Waal 2000: 260). Attitudinal reciprocity is assumed to be less cognitively demanding than "calculated reciprocity" which relies on precise quantification of benefits given and received in different currencies.

Attitudinal reciprocity is analogous to strong reciprocity because both processes focus on the proximate motives that generate cooperation and assume that reciprocity could occur without concern for longterm consequences. However, it is not clear how evolution could sustain attitudinal reciprocity (or strong reciprocity) in primate groups. It seems likely that individuals who systematically returned somewhat less than they received would benefit at the expense of their partners. To avoid this, costs and benefits must be translated into affect, a process that may hide the calculus of reciprocal altruism, but does not eliminate it.

Punishment

Strong reciprocity relies on the tendency to punish noncooperators. Among nonhuman primates there is considerable evidence of negative reciprocity. Thus, animals use aggression or other forms of costly sanctions to shape the behavior of group members (Clutton-Brock and Parker 1995a, 1995b) or to exact revenge (de Waal and Luttrell 1988; Silk 1992). But there is very little evidence that monkeys and apes use aggression or negative sanctions to shape the behavior of third parties or to punish deviation from social norms.

Several researchers have reported episodes of aggressive behavior that could be interpreted as punishment. For example, in the Mahale Mts. of Tanzania, a young adult male was brutally attacked by eight members of his own group (Nishida et al. 1995). The authors speculated that this young male may have been victimized because he did not conform to social rules—he did not defer to higher ranking males and launched unprovoked attacks on adult females. Members of a captive group launched aggressive attacks on two young females who did not come into their indoor cages when the group was called in for the night and caused the groups' evening feeding to be delayed (de Waal 1996: CHECK). The problem with these two observations (and other anecdotal observations) is that they are based on single events. In these cases, conspicuous aggressive responses to unusual types of behavior may be more salient than occasions in which unusual behaviors were ignored. Without systematic analyses of the consequences of aberrant behaviors, it is difficult to be certain that violations of social norms are consistently punished.

The only systematic evidence of third party punishment comes from an experimental study on rhesus macaques conducted by Hauser and Marler (1993a, b, Hauser 1997). Rhesus macaques give characteristic calls when they discover food items (Hauser and Marler 1993a). Taking advantage of this situation, Hauser and Marler conducted an experiment in which observers surreptitiously dropped handfuls of coconut or monkey chow and waited for monkeys to find it (Hauser and Marler 1993b). When monkeys found the food, they sometimes called and sometimes remained silent. Calling has little effect on the likelihood of being detected after finding food, but calling significantly reduced the likelihood of being harassed after discovery by other group members. Monkeys who discovered food and subsequently called were less likely to be supplanted, chased, or attacked by higher ranking monkeys than monkeys who remained silent after they found food (Hauser personal communication). Apparently, these rules apparently apply only to females. Males virtually never call when they find food, and are rarely punished (Hauser and Marler 1993b; Hauser 1997).

These data provide intriguing evidence that rhesus macaques punish group members who violate social norms. However, the weight of this conclusion is limited by the fact that these results have not been replicated, and no other observers have reported similar findings in other groups or species.

Prospects for Finding Strong Reciprocity in Primate Groups

For primates, cooperation is bounded by kinship and reciprocity and involves pairs of animals who have long-term social bonds. Most primatologists have assumed that reciprocal altruism is ultimately responsible for reciprocity within dyads, an

assumption that is bolstered by experimental evidence that cooperative behavior is contingent on the nature of previous interactions. However, De Waal (2000) has suggested that reciprocal exchanges in capuchins may be the product of attitudinal reciprocity, a tendency to mirror the predispositions of their partners. If he's right, then we have reason to believe that strong reciprocity is rooted in the behavior of nonhuman primates. However, it is also possible that the monkeys' initial attitude toward its partner reflects the quality of their social relationship, and this is based on a long series of cooperative exchanges over time.

Good evidence of punishment would provide support for the idea that strong reciprocity operates in primate groups. Presently, systematic evidence for punishment rests on a single experiment. These data are quite provocative, but their significance won't be established until these experiments are replicated and extended to other species.

To understand the role of strong reciprocity in primate groups we need to know more about the proximate factors that motivate cooperative behavior. Strong reciprocity in humans seems rooted in a deep sense of fairness and concern for justice which is extended even toward strangers, but we have no systematic evidence that other animals have similar sensibilities. Even those who have argued most forcefully for the emergence of moral sentiments in monkeys and apes have drawn their evidence from the interactions of close associates with long-term social bonds, not interactions among strangers (de Waal 1996; Flack and de Waal 2000).

The idea of strong reciprocity emerged from carefully designed experimental studies that revealed surprisingly high levels of altruism in one-shot interactions with strangers. It is hard to imagine obtaining comparable data on interactions among

strangers among nonhuman primates. Most primates live in stable social groups where they restrict peaceful social interactions mainly to known group members. Close associations with strangers are fraught with tension, generating aggression and avoidance, not cooperation. Aversions to strangers extend to captive settings. It might be possible to adapt De Waal's experimental studies of capuchins to assess cooperative behavior with anonymous partners, but it is not clear whether capuchins or other primates would tolerate this protocol.

In conclusion, the literature suggests that primates reserve cooperation mainly for kin and reciprocating partners, but punishment is apparently uncommon. While we know a lot about what nonhuman primates do, we know very little about what motivates them to do it. The patterning of cooperative interactions among nonrelatives could be the product of reciprocal altruism, but the same patterns could also arise from strong reciprocity. To identify the proximate mechanisms that generate cooperation in primate groups, we need to develop experimental procedures that allow us to assess the tendency to cooperate in one-shot interactions with strangers. We also need to know more about other primates' propensity to punish violations of social norms. Work addressing these issues in nonhuman primates is needed to assess the evolutionary roots of strong reciprocity.

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