

15 Cooperation, Coalition, and Alliances

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Abstract

In primates, cooperative acts have been observed such as communal rearing of offspring, cooperative mobbing of predators, supporting others in fights, and grooming others. Grooming builds up a social bond between the partners, helps in repairing relationships, and produces all kinds of benefits for the groomee, such as the reduction of parasites, and of tension. Although the costs for the groomer are low, it has been regarded as an altruistic act and therefore is expected to be preferably directed toward kin or to be repaid by being reciprocated or exchanged for another service (e.g., support in fights, help in rearing offspring in the case of communal breeding systems, or access to some object, such as food, or some individual such as a female, an infant, or members of another group).

The formation of coalitions may result in the maintenance or the increase of the dominance of an individual, in the expulsion of certain individuals from a group, in taking over a group, in the defense of the home range against other groups, in getting access to estrus females, and in the protection of an infant or adult female. The degree of cognition involved in coalitions is unclear.

Which members of a group cooperate differs from species to species; it may be influenced by genetic relations, by the size and the composition of the group (the sex ratio), the degree of competition, and by the distribution of food.

15.1 Introduction

Cooperation in primates varies greatly among members of a group. For instance, individuals groom the fur of others, they help others in fights, collect food together (for communal hunting in chimpanzees, see Volume 2 Chapter 14), share food, and may help in raising the offspring of others. Furthermore, group members cooperate against danger from the outside. They mob predators together and form coalitions to defend their home range against other groups.

For a long time behavioral acts, such as coalition formation, grooming, and food sharing, have been regarded as “altruistic” (costing the actor more than it receives) and therefore, the main explanations have been the theories of kin selection (Hamilton 1964) and reciprocal altruism (Trivers 1971). But in the course of time, it has become increasingly clear that as a rule these supposedly altruistic acts are beneficial for both cooperation partners. For instance, grooming a high ranking individual implies that the groomer does not suffer attacks during grooming. Furthermore, whereas coalitions were originally supposed to require high cognitive abilities, it is increasingly acknowledged that these patterns may arise from simple behavioral rules (as for cognitive mechanisms, see also Volume 2 Chapter 17). Besides, cooperation depends on the social system and the kind of primate involved (such as Old World monkeys versus New World monkeys). We intend to treat these aspects below.

15.2 Social system

Cooperation among individuals of a group depends on the species and its social system. There are many species of primates, and they live in many different kinds of social systems, as solitary individuals, monogamous pairs, single-male groups, multimale groups, or fission–fusion systems (Chapter 12). In group-living species with many females, the males usually migrate and the females remain in their natal group for life (female-philopatry), e.g., baboons, macaques, and vervets. Wrangham (1980) refers to these species as “female-bonded,” because the females are more kin-related than the males. In such groups, female social relationships and cooperation are developed much further than among the males of the group and also further than among females of species that are not female-bonded, the so-called female-transfer species. In chimpanzees, for instance, males stay together and females migrate. Here, relationships among males are more cooperative than among females (male-bonded). Greater cooperation among the resident than the migrating sex has been attributed to the closer relatedness of the resident sex. Evidence for closer relatedness in the resident sex is found among macaques (Ruiter 1998) and chimpanzees (Goldberg and Wrangham 1997). Although it has also been argued that male chimpanzees that cooperate are more often more closely related than those that do not, this is not supported by evidence from DNA-typing methods (Goldberg and Wrangham 1997). Furthermore, social relationships differ between Old World monkeys and New World monkeys: among Old World monkeys they are more developed (Dunbar 1993). The causes of these differences are unknown.

15.2.1 Grooming

Grooming occurs in all primate species (Goosen 1987), and of all affiliative social acts it is the one that is displayed most frequently. It consists in picking through the fur to remove parasites and to clean small injuries. An individual may clean its own fur (autogrooming) or that of another (allogrooming). Because allogrooming is a social act, it has sometimes been questioned whether it has any cleaning function at all. That allogrooming actually aims at cleaning is shown by Zamma (2002): Japanese macaques groom more often those spots of others and of themselves that tend to house more lice and eggs. Furthermore, in his study of 17 spots on the bodies of 19 species of primates, Barton (1985) has shown that individuals groom others particularly at spots that they themselves cannot easily reach. Therefore, spots on the skin that are groomed more often by others are groomed less often by the individual itself and vice versa.

Since in species that live in larger groups, individuals spend more time grooming, grooming clearly also has a social function (Dunbar 1991). Note that this correlation with group size appears more clearly among Old World monkeys than among New World monkeys. This may arise because coalition formation is more important in Old World monkeys and grooming may be helpful in building up alliances. In line with this, it has been found that individuals groom more often those partners they also support more frequently. This has been observed in several species such as female chimpanzees (Hemelrijk and Ek 1991), male chimpanzees (Watts 2002), gorillas (Watts 1997), baboons (Seyfarth 1976; Smuts 1985b), and male bonnet macaques (Silk 1992b).

Grooming relationships are influenced by the composition of the group, namely the sex ratio, for instance, among males of the genus *Macaca* (Hill 1994) and among females of a number of female-bonded species (Hemelrijk and Luteijn 1998). Food provisioning led to a female-biased sex ratio in a number of groups of species of the genus *Macaca* (Hill 1994, 1999). This arose because provisioned food was offered in clumps and thus led to stronger competition, and this drove several males away. Groups that were not provisioned had a more equal sex ratio, because in these groups competition for concentrated food sources was less, which may have allowed males to be friendlier among themselves and groom each other more often. Further, more grooming among males in the case of an even sex ratio may arise because the number of males to be groomed is greater and the number of females to groom with is smaller than in groups with a female-biased sex ratio, and the higher number of potential male partners to affiliate with may result directly in more affiliation among males. Grooming relationships among females seem to be influenced by competition for access to males; in a

large comparative study of female-bonded species of primates, Hemelrijk and Luteijn (1998) discovered that the degree of reciprocation of grooming among females increases with the increase in the relative number of adult males in the group. This was attributed to female competition for access to males; the fewer males present, the stronger the competition among females to affiliate with males, and this competition hindered females from building up good relationships among themselves. This argument is supported by the fact that grooming reciprocation increases more strongly with sex ratio among females in a single-male group (where sex ratio depends on group size) than in a multimale group; even if the number of males increases in multimale groups, this increase is not entirely to the profit of the time the males have available for females. There are two reasons for this: first, because males will intervene in interactions of other males with females and second, because males will interact among themselves, which reduces the time available for positive social interaction with females. In single-male groups, however, interactions and interventions among males are lacking. That the degree of grooming reciprocation may be used as a measure of female-bonding is supported by the fact that grooming reciprocation is higher in species that are female-bonded than those in which females transfer.

The positive effect of grooming on relationships is supposed to be a reduction of tension, increase of trust, and restoration of the relationship after a fight. As regards tension, grooming calms and relaxes the groomee (Terry 1970; Goosen 1975): its heartbeat slows down (Boccia et al. 1989) and the rate at which it shows a displacement behavior, such as scratching, decreases (Schino et al. 1988). Keverne and coauthors (1989) have shown that being groomed is felt to be pleasurable for it increases the concentration of endorphins in the brain. Grooming is supposed to maintain relationships in the light of competition, because hamadryas females with an established relationship are observed to groom each other more often if a dyad is accompanied by others than if the dyad is temporarily separated in cages (Stammach and Kummer 1982).

Grooming is also used to restore a relationship: often after fights, the frequency of grooming and other affiliative behavioral acts increase compared to the situation when no fights take place. This is known as "reconciliation" and has been shown to occur in species of all major radiations of primates (Aureli and de Waal 2000; Aureli et al. 2002). Being attacked implies that there is a high chance that more aggression will follow. Postconflict reunion reduces this aggression and restores the relationship. This function appears from the elegant experiments by Cords (1992). She determined at what distance pairs of long-tailed macaques could drink next to each other without trouble. Then she showed that, after aggression among the members of a pair, its ability to jointly exploit the

resource was seriously reduced. If, however, after such a conflict, a friendly reunion took place, the use of the resource was completely restored to normal.

Relationships are, however, not always damaged by aggression; the damage depends on the context in which the aggression takes place. In the case of competition over food, the relationship keeps its status quo even without reconciliation. Furthermore, the occurrence of reconciliation depends on the value of the relationship. According to the “valuable relationship hypothesis,” reconciliation particularly occurs in relationships of great value (Aureli and de Waal 2000). This theory is supported by the following experiment by Cords and Thurnheer (1993): when macaque partners are obliged to cooperate with each other to obtain food, they reconcile three times more often than when cooperation is not necessary. In line with this, reconciliation has been shown to occur more often in those relationships that are characterized by a high frequency of support (such as in macaques among members of a matriline; and in gorillas reconciliation occurs in the cooperative relationship between the sexes rather than among females [Watts 1995a, b]). Further, in general, more friendly postconflict reunion occurs among those individuals that exchange high levels of friendly behavior. Note that reconciliation by juveniles is already performed in the same way as that by adults, thus cognitive requirements are slight (Aureli et al. 2002).

15.2.1.1 Grooming: kin selection, reciprocation, and exchange

Grooming does not only lead to social bonding but may also be considered an altruistic trait because of the costs to the actor and the advantage for the receiver. Although its cost (expenditure of energy) is low (Wilkinson 1988), grooming may cost time that might be used for: (a) vigilance and (b) foraging. Two studies report a decrease in vigilance, one among captive rhesus monkeys and the other among wild blue monkeys. In rhesus macaques, mothers become less vigilant during grooming and consequently their infants were more often harassed by group members (Maestripieri 1993). Blue monkeys became significantly less watchful of predators when grooming than when foraging or resting (Cords 1995). Grooming does not diminish time for foraging (Dunbar and Sharman 1984): in two species of baboons (olive baboons and gelada baboons), increased foraging time was associated with a decrease in the length of time spent on resting, but time spent on grooming remained the same. This may be an indication of the importance of grooming. Indeed, baboons and macaques devote up to 20% of their time to grooming others (Dunbar 1988).

Within the framework of grooming as an altruistic act, the distribution of grooming partners can be explained either by the theory of kin preference (Hamilton 1964) or by reciprocal altruism (Trivers 1971). In support of kin selection, the most intense grooming bonds are found between mother and offspring, and in general in most primates, individuals aim their grooming primarily at their kin (Gouzoules and Gouzoules 1987; Schino 2001).

When altruistic acts are directed toward unrelated individuals, the expectation is that something should be received in return (Trivers 1971). During a certain part of their grooming bouts—ranging from 5%–7% for *M. radiata* (Manson et al. 2004) to 74% in *Callithrix jacchus* (Lazaro-Perea et al. 2004)—partners groom each other alternately. Recent models suggest that parceling of grooming bouts in small periods, in which the role of actor and receiver alternates, is a method of achieving reciprocation (Connor 1995). In grooming bouts of female chacma baboons, where both partners groom each other in turn, the total grooming duration by both partners is indeed significantly correlated between bouts (Barrett et al. 1999, 2000). Similar findings were made in white-faced capuchin monkeys and bonnet macaques (Manson et al. 2004) but not in Japanese macaques (Schino et al. 2003). Furthermore, it was argued that the time during which an individual grooms another should increase as a sign of the increasing trust among partners (model of “raise-the-stakes,” Roberts and Sherratt 1998). Increasing bout lengths have not, however, been confirmed in empirical studies of either capuchin monkeys or baboons (white-faced capuchins, Manson et al. 2004) (chacma baboons, Barrett et al. 2000). Instead in chacma baboons, bout length even decreased over time.

Grooming may either be reciprocated for its own sake or interchanged for another service, e.g., support, reduction of aggression, or access to something or someone (such as a female, an infant, or another group) or support in rearing offspring (in communal breeding systems). Here, a major problem is how to define reciprocation operationally. Reciprocation and interchange may be considered as a correlation between the number of times each individual gives something to a partner and how often it receives this service from him/her in return. This summed value over a period of time may be studied at the group level, the so-called actor–receiver model (Hemelrijk 1990a, b). Reciprocation in grooming occurs in many species, for instance, among both males and females in chimpanzees in captivity (Hemelrijk and Ek 1991), and among male chimpanzees under natural conditions (Watts 2000a), among female Samango monkeys (Payne et al. 2003), blue monkeys (Rowell et al. 1991), baboons (Seyfarth 1976), marmosets (Lazaro-Perea et al. 2004), female Japanese macaques (Schino et al. 2003), and gorillas (Watts 1994). Such a correlation of reciprocation may, of course, occur as a side effect of other correlations. For instance, when

higher-ranking individuals groom others more often and when everyone grooms others more often according to the rank of the partner, grooming reciprocation follows automatically (Hemelrijk 1990b). To exclude such alternative explanations, partial matrix correlations are useful (Hemelrijk 1990a). Both in chimpanzee males and females (Hemelrijk and Ek 1991; Watts 2002) and in savannah baboons (Seyfarth 1976; Hemelrijk 1991), grooming reciprocation remained manifest even after partialling out the effect of other variables such as dominance and support. In other studies, grooming reciprocation was present while controlling for kinship (hamadryas baboons, Stambach 1978) (vervet monkeys, Fairbanks 1980), (Japanese macaques, Muroyama 1991). Only in a few studies was no reciprocation of grooming observed (bonobos, Franz 1999).

Apart from being reciprocated, grooming may also be exchanged for other services. For instance, Seyfarth (1977) argues that higher-ranking females are more attractive to groom because from them more effective support in fights can be expected in return. Since females will compete to groom the highest-ranking partners, and since higher-ranking females will win this competition, each female will in the end groom most frequently with those partners adjacent in rank and be groomed most often by those ranking just below her. Seyfarth used this model to explain the observation that in several female-bonded primate species, such as baboons (Seyfarth 1976), vervets (Fairbanks 1980), and stump-tail macaques (Estrada et al. 1977), females aimed at grooming up the hierarchy and mainly at those that were next in hierarchy (Seyfarth 1980). Since then, these patterns have statistically been studied in many species. In a number of them, particularly Old World monkeys (such as certain species of macaques, e.g., rhesus monkeys [Kapsalis and Berman 1996], chimpanzees [Hemelrijk and Ek 1991; Watts 2000b], and bonobos [Franz 1999; Vervaecke et al. 2000]), these patterns were, at least partly, confirmed but in others evidence is lacking, for instance, in female langurs (Borries et al. 1994), blue monkeys (Cords 2000, 2002), and in New World monkeys, such as wedge-capped capuchins, *Cebus olivaceus* (O'Brien 1993), and tufted capuchins, *Cebus apella*, in both wild (Di Bitetti 1997) and captive colonies (Parr et al. 1997). There was even a trend against grooming higher-ranking animals because individuals groomed down the hierarchy among capuchins and in callitrichids, (Lazaro-Perea et al. 2004). In callitrichids, this is suggested to have a function in the communal breeding system: the breeding female (i.e., the alpha-female) uses grooming to make lower-ranking individuals stay in her group in order to help her bring up her young.

Furthermore, the relation between grooming and the receipt of support is doubted. Although correlations were found in studies of several species, such as vervets (Seyfarth 1980), baboons (Seyfarth 1976; Hemelrijk 1990a), female chimpanzees (Hemelrijk and Ek 1991), male chimpanzees (Watts 2002), bonobos

(Vervaecke et al. 2000), capuchins (O'Brien 1993), and one group of bonnet macaques (Silk 1992a), they were lacking in an earlier study of the same group of bonnet macaques (Silk 1982), in rhesus macaques (de Waal and Luttrell 1986) and female baboons (Silk et al. 2004). The relation is supported by two experimental studies dealing with vervets and long-tailed macaques. Seyfarth and Cheney (1984) recorded a call of vervets that seems to solicit support from others. They played it back to individuals of a natural colony of vervets that had recently been groomed by the caller and to others that had not. The duration during which individuals looked up at the speaker was considered to be an indication of the tendency to support the caller. Among nonrelatives, individuals looked at the speaker longer when the caller had recently groomed them. In this experiment it remains uncertain, however, whether looking up at the speaker actually indicates a readiness to support him or her. Therefore, in an experiment with long-tailed macaques (Hemelrijk 1994), actual support was measured directly. Trios of females were separated from the group. After two high-ranking individuals had been given the opportunity to groom, a fight was provoked between one of them and a low-ranking female. The frequency with which the third high-ranking female intervened in the fight was counted. The third female appeared to support only the other high-ranking female, and she did so more often after she had been groomed by her than if not. This supports the notion of a relationship between being groomed and supporting. It is not definitive evidence for an exchange, however, because being groomed may increase the tendency to support in general, even on behalf of those by whom the supporter was not groomed at all. Furthermore, individuals appear to support the aggressor but not the victim; therefore, it is as yet unknown whether a similar association with grooming holds also for victim support (which is more risky). Besides, these experiments do not show whether varying amounts of grooming lead to varying amounts of support.

Henzi and Barrett (1999) suggest that the receipt of support is not the major benefit of grooming because grooming occurs also among females that do not support at all, for instance in certain groups of chacma baboons (in the Drakensberg). Instead, they argue that the short-term benefit of grooming is the decrease of risk of aggression and harassment from others during the grooming bout itself (as suggested for bonnet macaques [Silk 1982] and capuchin monkeys [O'Brien 1993]), because support is rare in female-bonded species, although those females groom each other. Further, Henzi and Barrett (1999) argue that the degree to which grooming should be reciprocated or exchanged for something else depends on the competitive regime; when resources are widely distributed and cannot be monopolized, competition is weak, individuals equal each other in power, and grooming should be reciprocated. If resources can be monopolized, however, competition is intense, power differences are great, and grooming should be

exchanged for increased access to resources. In line with this, in a comparison between groups and in a study of the changes in the same group over time, grooming appears to be reciprocated if competition is weak rather than intense (Barrett et al. 1999, 2002). An alternative explanation for this is found in the fact that in both cases, intense competition is associated with a sex ratio that is more skewed toward adult females. Weaker grooming reciprocation in groups with more females has been discovered in several primate species by Hemelrijk and Luteijn (1998) and is attributed to stronger competition among females for access to males. Note that differences in degree of competition for access to males may also explain the pattern of grooming reciprocation in the baboons studied by Barrett and coworkers.

Grooming is also supposed to be exchanged for access to food. The best evidence for this comes from an experiment with long-tailed macaques by Stambach (1988). Stambach trained individual members of a group to become experts in operating a food apparatus. During the period in which it was the expert, this individual appeared to be groomed significantly more often.

Note that “food sharing” in primates almost exclusively means passive tolerance toward others when others take away a bit of food and that active giving is extremely rare (McGrew 1992). In a food exchange experiment among captive chimpanzees, de Waal (1997) found some evidence that females allow others to take away food more easily if they have been groomed by them in the preceding 2 h than if not. Food sharing and its reciprocation seems, however, largely a matter of mutual tolerance rather than intentional reciprocation, as is shown in experiments with brown capuchin monkeys (Waal 2000).

If males groom females, this is further supposed to increase a male’s access to mating partners, for instance in chimpanzees, baboons, and rhesus monkeys. In chimpanzees, this has been regarded as a kind of “bargaining for sex” (Goodall 1986). However, chimpanzee males groomed those females more often with whom they mated more frequently mainly during the period of female tumescence, and this relation neither resulted in a long-term bond (Hemelrijk et al. 1992) nor led to more offspring from the females that were groomed more often by the male (Hemelrijk et al. 1999; Meier et al. 2000). Hence, male grooming of females may simply function to calm down the male’s aggressive tendency or the tendency of the female partner to flee, and therefore, it need not be considered as a kind of exchange or currency. Furthermore, male rhesus monkeys mainly groom females during the mating season, and captive females prefer males who groom them most (Michael et al. 1978); yet, there are no long-term reciprocal bonds between the sexes (Maestripieri 2000). Long-term sociopositive relationships between males and females have been described, however, for savannah baboons (Smuts 1985b; Seyfarth 1978a, b).

In several species, grooming is used to get access to newborn infants, e.g., in chimpanzees, baboons (Rowell 1968), patas monkeys (Muroyama 1994), and moor macaques (Matsumura 1997). Furthermore, if low-ranking female chacma baboons want access to a newborn from a higher-ranking mother, they need to groom the mother longer in proportion to the size of the difference in rank (Henzi and Barrett 2002).

15.3 Coalition formation

A coalition (and alliance) is a coordinated attack by two or more individuals (the coalition partners or allies) on one or more opponents, the so-called targets (Chapais 1995). Coalitions may start in several ways: two individuals may attack a common victim, a coalition partner may spontaneously participate in an ongoing fight, or it may join after being enlisted by one of the combatants. Here, we deal only with those coalitions that are targeted at other group members and not at other groups (for coalitions against other groups see [Section 15.5](#)). Several types of coalitions are distinguished on the basis of their form and their effect (Chapais 1995; van Schaik et al. 2004). As regards form, the distinction is between coalitions of members: (a) that rank above the target (called “all-down”), (b) that rank below the target (called “all-up”), or (c) of which one ranks above the target and another below it (called “bridging” coalitions or alliances). As regards effects, a distinction is made between: (a) alliances that reinforce the existing rank-order, and therefore are “conservative”; (b) coalitions that cause one individual to change rank and thus are “rank-changing”; or (c) coalitions that cause more individuals to change rank, e.g., when two lower-ranking individuals defeat a top male, and thus are “revolutionary.” Coalitions usually involve three individuals (a triad), but more individuals may participate (a polyad).

As regards the cognition involved in the formation of coalitions, opinions differ. Harcourt (1988) suggests that primates form coalitions for strategic reasons and that they must take into account a complex set of information about their own power and that of their allies in comparison to that of their opponent and allies and so on. Along these lines, in a comparative study between a captive group of long-tailed macaques and one of chimpanzees, coalitions of chimpanzees appeared to be more frequent and larger than those of macaques, and this was considered as an indication of their greater cognition (de Waal and Harcourt 1992). Others argue, however, that coalition behavior may develop with little planning and anticipation of the results because individuals may passively learn to recognize the advantage of joining forces (Chapais 1995). Along similar lines, the pattern of coalitions in sooty mangabeys may result from simple behavioral

rules such as “support the higher-ranking individual in a conflict” and “solicit support from potential allies that outrank yourself and the target” (Range and Noe 2005). Even more complex cognition has been suggested to be involved in reciprocation of support. This will be treated below.

During fights, individuals may display so-called enlisting behavior by which they seem to try to attract others into the fight. This may consist of a rapid movement of the head between the opponent and the individual from whom help is requested, called “headflagging” in baboons and “pointing” in long-tailed macaques (de Waal et al. 1976; Noë 1992). In chimpanzees it is part of “side-directed behavior” (de Waal and van Hooff 1981), which consists of several behavioral actions that are shown by fighting animals to a third individual that is not (yet) involved in the fight. One action is the so-called “hold-out-hand” gesture in which an individual stretches out its hand toward a potential helper (de Waal and van Hooff 1981). The effectiveness of such solicitation behavior in chimpanzees is unclear. In contrast to the positive results by de Waal and van Hooff (1981), in another study of the same colony by Hemelrijk et al. (1991) most support was obtained without preceding side-directed behavior and it was clear that side-directed behavior was not a precondition for acquiring help in fights. Besides, side-directed behavior was rarely followed by support, and there was no indication that it increased the chance of receiving help. Note that also if the analysis was confined to cases of hold-out-hand behavior, hold-out-hand appeared not to result in obtaining support. This is in line with the experimental observations of chimpanzees by Hare and coauthors (2004): they discovered that chimpanzees are unable to understand pointing toward an object (Tomasello et al. 1997) but that chimpanzees easily anticipate the stretching arms of those who want to take away something that is of interest to them. Thus, it appears that they are better equipped to compete than to cooperate. Side-directed behavior is mostly displayed by females when they are threatened and is significantly concentrated on higher-ranking individuals; thus, side-directed behavior may be beneficial to the soliciting individuals in the sense that it tends to bring them nearer to a high-ranking individual, which may have a protective effect as a threat to the original opponents (Hemelrijk et al. 1991).

In interventions in fights, it is usually the aggressor and the winner of the fight that is supported. This is less risky than supporting the victim. Notable exceptions are mothers supporting their offspring (see [▶ Section 15.3.1.2](#)) and the “control role” of the alpha-male. For instance, in a captive colony of Japanese macaques (Watanabe 1979), the alpha-male more often than other males supports aggresses, in particular babies and youngsters, against adults. This is called a “control role.” A similar control role in the form of supporting losers is described for the alpha-male in gorilla groups by Watts (1997). Here, males

intervene in fights among females. Because this may promote egalitarianism among females, the male may use it to keep females in his group. Male intervention hinders, however, the formation of alliances among females.

15.3.1 Functions of coalition

As regards their function, Smuts (1987) distinguishes a number of main types of coalitions:

- a. Coalitions to take over a single-male group: This has been reported for males of grey langurs (Hrdy 1977).
- b. Coalitions among males to get access to an oestrous female that is in consort with another male: These coalitions do not affect dominance relationship and are common in savannah baboons (Smuts 1985a). Coalition partners are typically of middle rank (Noe and Sluijter 1995). Packer (1977) found that the male that enlisted help from another was the one to obtain the female, but in a later study Bercovitch (1988) showed that males that solicited were as likely to obtain the female as those that were solicited, and Noë (1992) himself observed that both partners of a coalition may enlist each other's help simultaneously.
- c. Coalitions to repel outside males: This has been reported among females as well as among males. Coalitions among males occur between groups of species living in single-male groups such as gorillas, hamadryas baboons, and gelada baboons. Coalitions among males of a single group have been described in multimale groups of chimpanzees, red colobus monkeys, spider monkeys, white-faced capuchin monkeys, and sometimes also among savannah baboons. In chimpanzees (Wrangham 1999; Wilson and Wrangham 2003) and white-faced capuchin monkeys (Gros-Louis et al. 2003), male coalitions may even result in killing an adult of another group.
- d. Coalitions among females or between a male and a female to protect infants: Although the main protectors of youngsters are their mothers, in all species virtually all group members will defend an infant if it is in danger (for instance, against an attack by an adult male).
- e. Coalitions among females to protect an adult female against an attack by a male: Mobbing a male to protect a female may be useful for females (even unrelated ones) since it warns males that hostility to females is risky.
- f. Coalitions to increase the dominance position of one or both member(s): Here, we will treat results for youngsters and for adults separately.

15.3.1.1 Adults

Coalitions to increase the dominance position among adults have been reported for Japanese macaques, rhesus, Barbary macaques, stump-tailed macaques, mantled howlers, red howlers, chimpanzees, and gray langurs.

When females are observed to attack males together, they are assumed to increase their dominance over males. This is mentioned for Japanese monkeys, rhesus monkeys, and bonobos (Chapais 1981; Thierry 1990; Parish 1994), and indeed in these species certain females are dominant over certain males. Such coalitions are not a precondition for female dominance, however, because a spatial model of individuals that group and compete (via dominance interactions) shows that female dominance can also arise only from competitive interactions in the absence of coalitions (Hemelrijk et al. 2003). According to this model, the stronger female dominance in bonobos compared to common chimpanzees may be due to their greater cohesion in grouping. Furthermore, stronger female dominance among rhesus macaques as compared to Celebes macaques (Thierry 1990) may arise from their higher intensity of aggression. Both factors, cohesion and intensity of aggression, increase hierarchical differentiation, and this reduces the size of the initial difference in dominance between the sexes (Hemelrijk et al. 2003).

When males support females, they usually benefit in terms of dominance. For instance, in Japanese macaques, an alpha-male supported females of lower-ranking matriline against the alpha-female with whom he had an unstable dominance relationship. Similarly, in rhesus monkeys and chimpanzees, females supported the alpha-male against other males, and in vervets support by females influenced dominance relations among males (Chapais 1995).

Among the three top-ranking males in chimpanzees, coalitions may induce changes of dominance in several ways. For instance, among wild chimpanzees, a top-ranking alpha-male (A) had an unstable relationship with the stronger beta (B). When the gamma-male (C) supported the alpha against the beta, (C) rose in rank above (B) (Nishida 1983). One-and-a-half years later, however, support by the beta caused (C) and (A) to reverse dominance again (Uehara et al. 1994). Thus, the gamma-male played out the alpha-male against the beta-male and this happened also in captivity (de Waal 1982).

In captivity, at other times, the beta-male and gamma-male were observed to join against the alpha-male (a revolutionary alliance). Thus, both rose in rank above the alpha-male (de Waal 1982). Such competition among males has sometimes fatal consequences (Watts 2004). Revolutionary alliances have further been described for male langurs and male Barbary macaques (Chapais 1995).

However, in none of these species did males form coalitions to obtain oestrous females.

15.3.1.2 Youngsters

In a number of female-bonded species (Wrangham 1980), there is also a complex support system that provides young females with approximately the dominance rank of the mother. It has been called a “matrilineal dominance system” and a “nepotistic hierarchy,” because the support involves kin. The matrilineal dominance system implies that all daughters rank immediately below their mother and that among sisters the youngest sister has the highest rank (so-called youngest ascendancy). This classical form of a nepotistic dominance hierarchy is found in rhesus macaques, Japanese macaques, and long-tailed macaques. It comes about as follows. First, closely related females (i.e., a grandmother, mother, or elder sister) support juvenile females and cause them progressively to outrank all adult females that rank below their mother. This process has been detected by an analysis of data of observational studies, and it has also been experimentally demonstrated by Chapais and coworkers in admirable studies on colonies of Japanese macaques and long-tailed macaques (Chapais 1995, 1996; Chapais et al. 2001; Chapais and Gauthier 2004). They created subgroups of three or six juvenile Japanese macaques (with one or two peers of the same matriline) and then added an adult. In this situation, a low-ranking juvenile female appeared to be able to outrank peers in the presence of closely related females but not in the presence of more distantly related kin, such as aunts, grandaunts, or cousins, due to lack of support from them. After female dominance over a lower-ranking matriline was “assigned,” it was maintained by mutual support among members of the same matriline against those of a lower matriline: from that time onward, the young females joined opportunistically in ongoing conflicts against lower-ranking females (called “the common targeting principle”). Within matrilines, younger sisters are dominant over older ones (“youngest ascendancy” rule). This is caused by the mother’s support of a younger daughter against her older ones. If the mother is absent, dominant unrelated individuals will also support younger sisters against older ones. Thus, the network of alliances of females extends beyond her kin.

However, in some groups the matrilineal dominance system is incomplete (weakly nepotistic) (Chapais 2004). For instance, youngest ascendancy is lacking in some feral groups of Japanese macaques (Hill and Okayasu 1995), provisioned groups of Barbary macaques (Prud’homme and Chapais 1993), and one captive group of Tonkean macaques (Thierry 2000). Furthermore, in baboons, daughters

may outrank their mother during adulthood (Combes and Altmann 2001). Chapais and Lecomte (1995) give three explanations of weak nepotism: demographic, (phylo)-genetic, and ecological. The demographic explanation comes from a model by Datta and Beauchamp (1991), who simulated the effects of demography on female dominance relations by comparing two populations that differ in their growth rate. One population is growing fast (with 2.8 offspring per female) and the other is declining (with 0.6 offspring per female). Thus, in the declining population, matriline are smaller and potential allies are fewer than in the increasing population. Since a mother needs support from one of her dominant sisters to remain dominant over her daughter(s) and this ally is more likely to be lacking in a declining population than a growing one, mothers will more often become subordinate to their daughters. Similarly, for a youngster to become dominant over her older sister, she needs another sister and her mother as allies. These are more often alive in a growing than in a declining population, and according to Datta (1992) this explains the consistency of the youngest ascendancy rule in provisioned and expanding groups of rhesus macaques and Japanese macaques and the lower occurrence of outranking older sisters in the declining population of baboons.

A genetic explanation is given to explain the absence of the youngest ascendancy rule in provisioned colonies of Barbary macaques and in a feral colony of Japanese macaques, where allies were present. In Barbary macaques Prud'homme and Chapais (1993) suggest this difference may be a genetic one because they discovered that unrelated individuals rarely supported a younger sister against her older sister (although they support her against lower-born females). This differs from what is known of rhesus macaques and Japanese macaques.

An ecological cause is suggested for the absence of the youngest ascendancy rule in feral colonies of Japanese macaques (Hill and Okayasu 1995). Due to the wide spatial dispersion during foraging, the frequency of aggression was rare, and consequently, support was rare too.

Note that apart from species that are weakly nepotistic, there are also those that are clearly non-nepotistic such as Hanuman langurs (Koenig 2000). Furthermore, in nonfemale-bonded species, such as gorillas and chimpanzees, matrilineal dominance does not exist and young females rank according to their age and power.

How can we explain why the matrilineal system evolved in some female-bonded species but not in others? In a comparative study of egalitarian and despotic species of the genus *Macaca*, Thierry (2000) attributes this to differences in degree of despotism. He argues that the matrilineal dominance system is more complete in despotic species due to the higher frequency of support among kin (so that more power differentiation develops between matriline). He believes

that this also implies a lower frequency of acts of support among non-kin and that in egalitarian species support is distributed the opposite way, that is, it is more frequent among non-kin than among kin. Furthermore, he shows that dominance styles are phylogenetically conserved (Thierry et al. 2000). This begs the question of what caused the start of the interspecific differences in degree of nepotism between egalitarian and despotic macaques. According to Chapais (2004), this originates from a difference in the “strength of competition” due to the distribution of food. In the case of clumped food, supporting others will be more advantageous. Thus, a nepotistic system develops in which there is a high frequency of support of both kin and non-kin (in contrast to only kin as suggested by Thierry). When food is dispersed and causes scramble competition, it cannot be monopolized and support becomes less useful (both among kin and among non-kin).

15.4 Support: kin selection, reciprocation, and exchange

Support in fights, or coalition, is often thought to be “altruistic” because of the costs (in the form of risks) to the actor and the benefits to the receiver.

As regards the benefits of receiving support, it increases the likelihood of winning a fight, as larger coalitions beat smaller ones (wedge-capped capuchin monkeys [Robinson 1988], bonnet macaques [Silk 1992a]).

The cost of coalitions is difficult to estimate, but often it is assumed that one partner bears most of the costs while the other reaps the benefits (presenting thus a case of altruism). If so, the theory of kin selection and that of reciprocal altruism are believed to explain these supposedly altruistic acts.

As regards kin selection, in Old World primates, individuals support kin more often than non-kin, e.g., in pigtailed, stumptails, rhesus, Japanese macaques, chacma baboons, yellow baboons, and gorillas. Furthermore, individuals aid kin more often if they are more closely related (pig-tailed macaques, chimpanzees, and rhesus monkeys).

In cases of reciprocal altruism, support is supposed to be reciprocated or exchanged for something else. Reciprocation of support is found in a comparative study of rhesus macaques, stump-tailed macaques, and chimpanzees by de Waal and Luttrell (1988). Since the authors statistically partialled out effects of proximity, kinship, and same-sex combination, they argue that reciprocation indicates that individuals keep mental records of the number of acts received from each individual and that they match the number of acts they give to what they have received from each partner. However, in this study, the effects of dominance ranks

and grooming behavior are ignored and data over five consecutive seasons were lumped together. Therefore, what seems to be proof of keeping mental records may have been simply a side effect.

Reciprocation appears to be a side effect, for instance, in the long-term study of the same colony of chimpanzees analyzed per season by Hemelrijk and Ek (1991). It involves a sex difference since chimpanzee males reciprocated support whereas females did not. Males, however, only reciprocated support if their hierarchy was stable; if it was unstable, males supported those they groomed (Hemelrijk and Ek 1991). Because of this, and since there was insufficient indication that there was any negotiation for support—because individuals did not significantly comply with requests from others (Hemelrijk et al. 1991)—it seemed that males might have joined in one another's fights opportunistically in order to attack common rivals. This may have been the cause of the reciprocation among males. Since males may benefit directly from such joint attacks, supporting behavior is selfish (Bercovitch 1988; Noe 1990) and there is no need for the participants to keep records.

As in chimpanzee males, reciprocation of support has been reported in one study of male baboons (Packer 1977) but not in another (Bercovitch 1988). This difference possibly is related to a difference in the stability of the hierarchy (Hemelrijk and Ek 1991).

The sex difference in reciprocation of support is in line with detailed earlier studies by de Waal (1978, 1984), in which he found that male coalitions were mainly opportunistic and only corresponded with their social bonds during periods in which the position of the alpha-male was clear (de Waal 1984). Female coalitions, however, were more stable and always coincided with their social bonds (Hemelrijk and Ek 1991). Thus, whereas male coalitions seem to serve status competition, female coalitions are directed toward protection of kin and affiliation partners.

Furthermore, de Waal and Luttrell (1988) studied reciprocity of "revenge." By revenge, one means attacking someone while supporting another for the reason that the subject has received similar "contra-support" before. In this study, it was found that revenge is reciprocated only among chimpanzees, not among the two monkey species (i.e., macaques). This is interpreted as if the individuals aim their support against some individual because they have been attacked in a similar way: they have suffered support against themselves. De Waal and Luttrell consider this a sign of a greater cognitive capacity in chimpanzees because chimpanzees keep track not only of acts of support but also of revenge. However, there are two objections against this interpretation. First, they lumped together data of five seasons despite changes in dominance ranks and in the stability of the power of the top-male. In a study in the same colony, but in an

analysis of support data per season, Hemelrijk and Ek (1991) found no reciprocation of revenge. Therefore, the apparent reciprocation of revenge may have resulted from the lumping together of data, and in any case it is unlikely that individuals keep track of acts of revenge over a period longer than one season. Second, reciprocation of revenge has also been observed in monkeys, e.g., bonnet macaques (Silk 1992a), and also among related female gorillas (Watts 1997), which pleads against the hypothesis of the need of high cognition for such reciprocation.

15.4.1 Communal rearing and allomothering

Usually the mother takes care of the infant alone. In callitrichids (tamarins and marmosets), however, everyone (both parents and mature offspring) assists in rearing the newborns by carrying them and provisioning them. Mature offspring postpone their departure from their natal territory and delay independent breeding (Rapaport 2001). In a number of female-bonded species, youngsters are protected and helped in fights so that they rank immediately below their mothers (matrilineal dominance system, see preceding section) and in all species youngsters are protected in fights that are dangerous. Furthermore, in many species, unrelated individuals may nurse and carry youngsters (allomothering); they cuddle the infant, embrace it, groom, and protect it (McKenna 1979). Allomothers are usually young, nulliparous females, ranking below the mother; often they are sisters of the infant. In this way, the allomother learns how to handle an infant, which increases the chance of survival of her own offspring (Lancaster 1971). An advantage to the mother seems to be the shortening of the interbirth interval (Fairbanks 1990) and the increase of her reproductive success (Ross and MacLarnon 2000). On the basis of detailed comparative studies of macaques, Thierry (2004) argues that two assumptions suffice to explain interspecific variation in degree of allomothering in *Macaca*: (a) attraction to infants and (b) constraints of social structure (McKenna 1979). First, all females are strongly attracted to all infants. Second, in certain species mothers protect the infants with greater care than in others and therefore, in these species, allomothering is counteracted. These species are the species that belong to the two despotic grades of macaques, whose aggression is intense and among whom power differences are great. This may cause problems for females when they have to retrieve their infants. In contrast to this, in egalitarian species, power differences are small and aggression is mild. Thus, differences in the degree of allomothering result from a kind of social epigenesis.

15.5 Collective defense of home ranges

Species and groups differ in the way in which they use their home range. Depending on this, fights with other groups may aim at the defense of only one food source (e.g., fruit tree) or of a whole territory (Cheney 1987). A number of species have special intergroup calls that are meant to separate the groups spatially (e.g., in mantled howler, capuchin, mangabey, siamang, yellow-headed titi). Most territorial species, however, have intergroup calls that incite the other group to fight them (e.g., dusky titi, gibbon spp., vervet, colobus).

If actual fights between groups occur, in chimpanzees this may lead to killing an adult of the other group (Wilson and Wrangham 2003; Wilson et al. 2004).

Usually, males are more active than females in fights between groups. In macaques, however, females may also participate. In both sexes, higher-ranking individuals participate more often than lower-ranking ones (Cooper 2004).

15.5.1 Behavior against predators

When primates meet a predator, they flee individually (so do large species) or hide (in particular, smaller species). Furthermore, they may protect themselves and their group members in other ways such as: (a) by mobbing the predator, (b) by scanning the environment for early discovery of predators, and (c) by warning other group members.

Mobbing predators has been described for baboons, rhesus monkeys, and all three ape species. Each of these species was observed to attack tigers or lions (Cheney and Wrangham 1987). Scanning the environment has been described for a number of primate species such as red-bellied tamarins (Caine 1984) and chacma baboons (Hall 1960). In a series of experiments, tamarins appeared to scan most frequently during the most dangerous periods of the day and in the presence of the most dangerous stimuli. Further, tamarins appeared to divide the duty of scanning among group members. In relation to protection against predators, the spatial distribution of the individuals of the different sex age categories in progressions has also been studied in baboons (Altmann 1979; Rhine and Westland 1981).

Most primates use alarm calls to warn against predators. Such calls are altruistic in the sense that they are harmful to the sender, because it attracts the attention of the predator to the caller, but beneficial to others that are close by. It has been debated whether kin-selection is the main evolutionary force behind these calls because it is usually kin that is protected by these calls. However, newly immigrant males also tend to call loudly in spite of the fact that they have no

kin-members in the group (Cheney and Seyfarth 1981). Many species of primates use different alarm calls for different predators. Such a differentiation is described for vervets, red colobus, Goeldi marmosets, pygmy marmosets, cotton-top tamarins, and gibbons (Cheney and Wrangham 1987; Dugatkin 1997). Vervets emit different calls when the predator is a leopard, an eagle, or a snake (Struhsaker 1976). In playback experiments of the different calls, vervets appeared to respond to leopard alarms by climbing into the trees; at eagle alarms they looked up, and at snake alarms they looked down. Because of the fine distinction between these alarm calls (almost resembling human language), it has been asked whether alarm calling can be considered intentional warning. Evidence points against this, because vervets continue to give alarm calls after everyone in the group has heard them (Cheney and Seyfarth 1985) and because the intensity of these alarm calls and other protective actions by mothers remained similar whether or not their daughters were informed about the presence of the predator (Cheney and Seyfarth 1990).

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