Smuts, B.B. et al (1987) Primate Societies. U. CHICAGO Press

Dynamics of Social Relationships

Frans B. M. de Waal

The basic tendencies governing interactions among primates are competition, social attraction, and cooperation. The objective of this chapter is to describe and discuss the way in which these different and often conflicting tendencies are integrated into a cohesive system of social relationships. The emphasis lies on proximate explanations, that is, explanations based on immediate causes and goals, and on the social histories, experience, and intelligence of the individuals involved. This approach asks how social mechanisms work rather than, as in evolutionary biology, why they came into existence.

One major problem in studies at the proximate level is an underdeveloped vocabulary to describe and think about subtle characteristics of social relationships. This problem is partly due to the combination of great variability in primate personalities and relationships and a reluctance to borrow from the richest source of social concepts: human language. In primatology we are used to investigating social components, such as the submissiveness, the affinity, or the supportiveness of one individual to another. We run out of words, however, if these different components form a single complex, that is, if they are closely interlinked and simultaneously expressed. A person who is treated with a similar combination of sympathy, submission and corroboration is said to have respectful and loyal colleagues, but these terms are considered inappropriate when applied to animals. It may be difficult, though, to avoid such so-called anthropomorphisms completely if we wish to move from analyses of aspects of social relationships to more encompassing levels.

The dilemma of a primatologist may be compared to that of a pianist listening to a record of a classical piano concert. He is unable to distance himself from the process by which the music is produced. Instead of "pure" enjoyment of a series of patterned sound waves, he automatically imagines a grand piano and feels the chords and melodies, so to speak, in his own fingertips. Similarly, scientists cannot completely distance themselves from primate behavior. Almost everything they see reminds them, consciously or not, of their own experiences and feelings.

Rather than regarding this as a disadvantage, or, worse, denying it, we should exploit the situation (Menzel 1979). Piano players undoubtedly listen more care-

fully and analytically to a piano concert than the average listener. In the same way, our background as social beings provides us with a depth of intuitive insight into social relationships that is bound to guide our thinking and theorizing when studying primates. Allowing for this influence is not the same as uncritically giving in to it. The tradition of rigorous quantification is now so well established in the field of primate behavior that there is hardly any danger of a descent to the level of pet lover's talk. In the history of ethology, references to human behavior have been of great heuristic value, and large parts of our present vocabulary (e.g., threat, appeasement, bonding) started out as anthropomorphisms (Asquith 1984).

New, easily recognizable terms for patterns of interaction or particular types of relationships are not to be confused with an understanding of the mechanisms involved. Such understanding usually comes later, after much research, and may as a matter of fact lead to the rejection of the initial terms. What new metaphors may do, though-and this is essential in science-is to reorganize our views and provide new frameworks for observations and experiments.

A complicating factor in the study of dynamics of primate groups is that the integration and balancing of competitive and cooperative tendencies cannot be understood at a dyadic level, that is, without considering the influence of third individuals or the group as a whole. Some studies indicate, for example, that the expression of interindividual preferences, as measured in dyadic tests, may be inhibited in the group context (Kummer 1975; Vaitl 1977a; Stammbach 1978). Without experimental procedures it is difficult to specify such influences, but Seyfarth (1977) has developed a detailed model that can be tested in the field.

Triadic influences also play a role in dominance relationships, that is, A's dominance over B may depend on C (e.g., Kawai 1958; Kawamura 1958; Hall and DeVore 1965; Varley and Symmes 1966). Recently, a number of observational studies have focused on the role of supportive relationships in structuring and changing the rank order; primates recruit allies to maintain or improve their social position. In this paper I will review some of my own observations of such dominance processes in macaques and chimpanzees. The same themes are recognizable in the work of Dunbar and Dunbar (1975), Chance, Emory, and Payne (1977), Cheney (1977a), Walker Leonard (1979), Walters (1980), and Datta (1983a).

DOMINANCE AND SOCIAL INTEGRATION

The highly structured group life of most primate species did not evolve through disappearance of competitive and aggressive tendencies, but through the development of powerful mechanisms of conflict resolution. The conflict management of group-living species requires reconciliation and tolerance, which allows losers to live together with winners without provoking further violence. Among other things, losers must have a way to indicate their willingness, at least for the moment, to refrain from behaviors that pose a threat to the life, territory, or social position of winners.

The solution to this problem, widely found in the animal kingdom, is to provide losers with a sort of white flag and winners with an understanding of its meaning. The resulting harmonization, and the increased predictability of the direction of possible further conflicts, is often referred to as a dominance relationship.

It does not matter what form the white flag takes. Teeth baring and high-pitched screaming in many monkey species, low panting grunts in chimpanzees, licking of the other's mouth corners in canids, posture freezing in rats, and in general, any behavior that makes one look small and vulnerable can serve to signal submission. Fear may be an important motivational component of these behaviors, but it rarely seems the only motivation involved. In group-living species the subordinate's fear is often mixed with social attraction. Thus, submissive signals, often appearing to take the form of a greeting or the paying of respects, may be given while actually approaching the dominant. This notion of submissive behavior is expressed most succinctly by Schenkel (1967, 319) regarding wolves and dogs: "Submission is the effort of the inferior to attain friendly or harmonic social integration."

We know relatively little about socially positive aspects of dominance relationships. Traditionally most attention has gone to inequalities resulting from the relationship: the dominant's priority of access to limited resources (chap. 26). Although it is logical, from an evolutionary standpoint, to analyze the phenomenon in terms of competition and reproductive benefits, evolutionary analyses may be limited because they tend to isolate dominance from its social context. In baboons and macaques this problem is not immediately apparent because of a fairly close link between social expressions of dominance and priority of access to resources (chap. 25). Dominants go as far as forcefully removing food from a subordinate's cheek pouches. But even in these species, individuals known to be capable of claiming a resource may fail to do so either for lack of motivation or because of a special relationship with the subordinate involved.

If such special relationships become the rule, the problem with priority-of-access criteria of dominance becomes serious. In the large chimpanzee colony of Arnhem Zoo (Netherlands), some females are more successful than adult males in claiming objects or places to sit. It is quite common for these females simply to take the leaves on which a male was feeding out of his hands. At the same time, the adult males in this colony clearly win most of their fights against the same females, and all females show submission toward adult males (Noë, de Waal, and van Hooff 1980). How can we explain this? Are the females dominant or are the males tolerant?

Social integration and peaceful coexistence are important aspects of relationships between dominant and subordinate animals—often as important as the outcome of resource competition. By regarding dominance relationships as a compromise between inevitable antagonistic tendencies and a need for life in cohesive groups, one gets a feeling for the precarious equilibrium that exists between the two. A greater emphasis on the social side of dominance relationships does not necessarily (and should not) conflict with an evolutionary viewpoint. Vehrencamp's (1983) balanced evolutionary model of dominance, resulting from her assumptions concerning the benefits of group living, is an improvement upon the strictly competitive picture emerging from previous models (e.g., Popp and DeVore 1979).

STATUS MECHANISMS

The hierarchical organization of primates depends on the following social mechanisms: formalization, conditional reassurance, and status striving.

Formalization

In many macaque species, facial expressions with baring of the teeth (fig. 34-1) are exclusively shown by the lower ranking of two partners in a relationship. The occurrence of simultaneous teeth baring by two monkeys to each other is extremely rare, and the most dominant individual never bares his teeth in agonistic situations, or, if he does so, it is a sure sign he is on the verge of losing his position (Angst 1975; de Waal 1977).

In chimpanzees, in contrast, mutual teeth baring between individuals is not uncommon during agonistic encounters, and a leader with a stable position may also show this behavior. Exposure of the teeth among chimpanzees appears to signal fear, nervousness, and hesitation, but not submission. At the same time, the chimpanzee has another set of signals, very different in form, to express status differences. The subordinate approaches with bowing movements while uttering a series of soft panting grunts, whereas the dominant makes himself bigger by standing up with his hair erect (fig. 34-2). The dominant may also perform a "bluff-over," which is a passing charge in which one arm is raised and moved over the crouching subordinate; sometimes this display

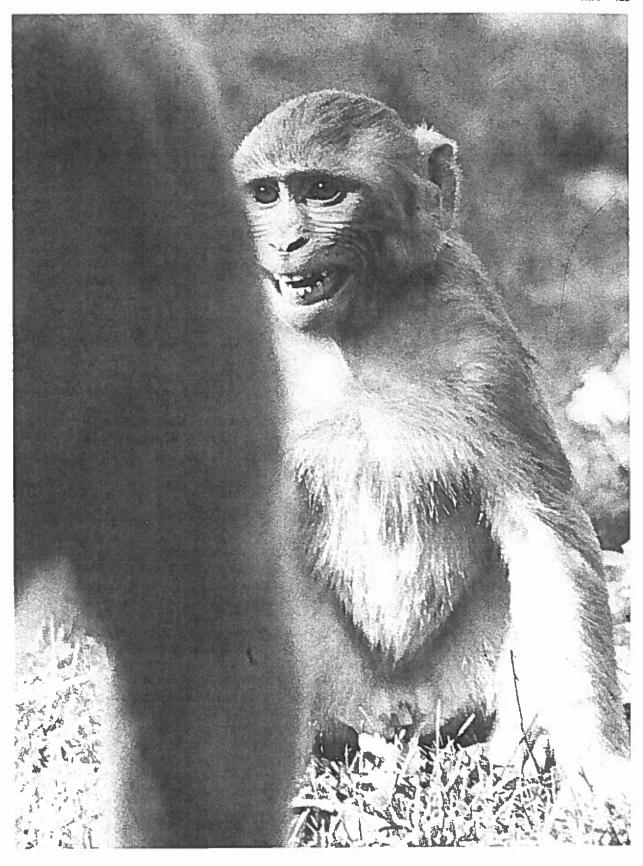


FIGURE 34-1. A juvenile rhesus macaque responds with submissive teeth baring to the approach of an adult male. (Photo: Frans de Waal)



FIGURE 34-2. Chimpanzees communicate their dominance relationships in ritualized encounters. The alpha male (*left*) has his hair on end and draws himself up while approaching another adult male. The subordinate bends down and utters a series of submissive pant-grunts. (Photo: Frans de Waal)

even takes the form of a spectacular jump over the subordinate (Bygott 1974; Noë, de Waal, and van Hooff 1980; de Waal 1982).

These almost ritual encounters confirm the assymmetrical state of the relationship. Dominance relationships that have reached this stage of communication are called formalized here. This term allows for a contrast with nonformal dominance. We all realize that in our own society there often is a difference between a person's formal position and his or her de facto power (for example, the influence of some elder statesmen). This discrepancy is also discernible in nonhuman primates. Coalition networks and other mutual dependencies seem to allow skilled and experienced individuals to exert greater influence than one would expect on the basis of their formal ranks (see "Power versus Rank").

By their extreme consistency of direction, status signals, such as the macaque's teeth baring or the chimpanzee's pant-grunting, contrast sharply with other measures of dominance. Priority of access to resources, aggression, flight, and avoidance may occasionally be in favor of the subordinate party. Since exceptional outcomes can generally be ascribed to variations in social context (for example, the presence/absence of supporters), the absence of similar reversals in the direction of formal status communication suggests that it is "context free." These signals seem to communicate the overall state of the relationship rather than transient outcomes of encounters. They might, in that sense, be interpreted as *meta*communication (Altmann 1962).

Conditional Reassurance

Our studies have produced evidence for reconciliation behavior in both chimpanzees and rhesus monkeys (de Waal and van Roosmalen 1979; de Waal and Yoshihara 1983). The phenomenon is likely to exist in other species as well (e.g., McKenna 1978; Seyfarth 1976). The evidence for reconciliation can be summarized as follows: (1) During a limited period after an aggressive incident there is an increased probability of contact between former opponents. (2) The contact increase is selective, that is, adversaries seek contact with one another rather than with bystanders. (3) The behaviors during these post-conflict contacts differ from those during normal con-

tacts; rhesus monkeys show a higher frequency of embracing and lip smacking, whereas for chimpanzees the mouth-mouth kiss is the most characteristic contact pattern.

There is likely to be some relation between wellestablished dominance relationships and the tendency to reconcile after conflicts. The hypothetical link is that of "conditional reassurance." According to this hypothesis, dominant individuals are prepared to reconcile only with subordinates who clearly and regularly demonstrate that they recognize their position. For example, Kummer (1975) found that fights between male gelada baboons stopped after reaching a decisive outcome. The winner approached the loser with appeasing gestures such as presenting and lip smacking. The animals then proceeded to mounting and grooming, and finally relaxed. Also, Maxim (1976), in experiments on rhesus monkeys, found a link between the establishment of dominance and the development of a more friendly relationship. Conversely, observations by Bernstein (1969) on pigtailed males in a captive troop indicate that violence may persist, even to a fatal point, if the loser of a dominance struggle fails to submit. This is not to say that fights always stop short after submission by the loser; these mechanisms may only work between individuals with good reasons to maintain a relationship.

If peaceful coexistence depends on formalization of dominance relationships, this is presumably due to the dominant reading the signs of submission as indications that his or her position is safe. At this point conditional reassurance comes into play. During the final weeks of dominance struggles among male chimpanzees, for example, if it is becoming evident that male A generally has the upper hand in his confrontations with B, reconciliations will become increasingly rare. This is due to A's systematic rejections of overtures by B. Each time B seeks contact after one of their aggressive encounters, A calmly walks away, avoiding the contact. This may happen many times a day. Only when B starts to utter the first submissive panting grunts, not heard for months between the two males, will A accept Bis attempts to reconcile. It seems as if A blackmails B'by withholding friendly interactions: kissing and grooming contact can only be obtained through a formal ackowledgment of the outcome of the dominance struggle (de Waal 1982, in press).

Status Striving

It is difficult to explain why such an old and valuable concept as Masłow's (1937) dominance drive has been taboo for such a long time. An important factor undoubtedly was that behaviorism, until recently a very influential school of thought, dictated that since we cannot know whether animals have intentions, it is better to describe their behavior as having specific consequences

rather than as aiming at this or that goal. Thus, scientists might speak of an animal's rise in rank, but would avoid speaking of aspirations or striving for status.

That there is little or no purposefulness (in the cognitive sense) in animal behavior is only an assumption. We seem to be reaching a point at which this assumption is starting to hamper further research. Unless we open our eyes to the possibility of intentionality in animals, it seems almost impossible, especially in the case of primates, to make sense of the complex group processes accompanying and producing rank reversals. The number of studies concerning dominance strategies is on the increase, and the result is a cautious change in outlook and language over recent years.

Let me summarize two relatively simple quantitative results relating to aggression in the Arnhem chimpanzee colony. These results can easily be explained if we assume active status striving, whereas they would demand separate and more difficult explanations if status reversals were to be more or less unintended, passive processes of change.

Aggressive actions by females and immatures usually occur in response to particular events in the group (e.g., in order to protect an infant), whereas a much higher proportion of aggressive actions by adult males occur without any obvious reason (de Waal and Hoekstra 1980). It can also be demonstrated that both the intensity and frequency of male aggression decreases after the establishment of formal dominance relationships (de Waal, in press). The most dramatic illustration occurred when a young adult male, Nikkie, started provoking fights with all eight females in the colony. After months of daily confrontation the females, one by one, began to defer to Nikkie by approaching him while uttering pant-grunts of submission. Over the same period, Nikkie's tendency to direct provocative bluff displays at females diminished significantly.

All dominance reversals observed over the years involved adult males. The greater "spontaneity" of their aggression, and the inhibitory effect of their targets' subordination, may be explained by the use of aggressive behavior for the pursuit of a goal that is not immediately visible to us. This hypothetical goal is to maintain or achieve the subordination of as many other individuals as possible.

Retaining the Dominance Concept

More attention to the ways in which ranks are achieved and maintained may solve some of the much discussed problems with the dominance model (see Bernstein 1981 for an overview of the debate). A central problem has been the correlation, or rather the lack of correlation, between different measures of dominance. Is dominance a unitary concept? Can it be used as an intervening variable? The idea behind these questions was that the ex-

planatory value of the model depended on whether a rank order based on one variable, say aggression, provides any information about rank orders based on other variables, say priority in competitive situations. Note, however, the narrowness of this interpretation of explanatory value, being limited to correlations between simultaneously existing distributions of behavior.

Actually, lack of agreement between different measures of dominance is something to be expected, if dominance is a dynamic phenomenon, because rank relationships are likely to change gradually, stage by stage. Thus in long-tailed macaques an almost perfect correlation exists between four agonistic rank criteria as applied to adult group members, but a very poor correlation if juveniles and infants are considered (de Waal 1977). Data suggested that, whereas adults had well-established ranks, youngsters were still in the middle of a long-lasting process of rank acquisition. At a certain point in its ontogeny a particular juvenile might already be dominant over another individual according to one or two criteria, but still be subordinate to the same individual according to other criteria (fig. 34-3; see also chap. 25).

In spite of all criticism, there is no way to discard the dominance model. Dominance relationships, and their transitive arrangement into a hierarchical structure, are too obvious to be ignored. One step necessary to revitalize the concept is its integration with other aspects of group life. The explanatory value of such an extended

model is evident from long-term research on Old World monkeys. These studies demonstrate that accurate predictions of the direction and outcome of dominance processes involving young females can be based on knowledge of their mothers' positions in the hierarchy: daughters usually reach ranks close to their mothers' (chap. 11).

Thus, the dominance model may be more useful in combination with other factors, such as kinship, than in isolation. Previous sections of this chapter suggest the following additional ways to improve the model: (a) distinction between formal dominance relationships, as expressed in ritualized communication, and success in competitive contexts; (b) attention to socially positive aspects of relationships between dominants and subordinates, for example, reconciliation and tolerance; (c) reconsideration of assumptions inherited from behaviorism; and (d) incorporation of the factor time in our analyses.

Finally, it should be noted that the dominance model's usefulness may strongly depend on the species and sex under study. Whereas male chimpanzees seem much more dominance oriented than females (Bygott 1974; Nishida 1979; de Waal 1982), this sex difference does not seem to hold for many Old World monkeys where females are just as involved in dominance strategies as males (e.g., Chance, Emory, and Payne 1977; de Waal 1977; Walters 1980; Hrdy 1981b; chap. 25).

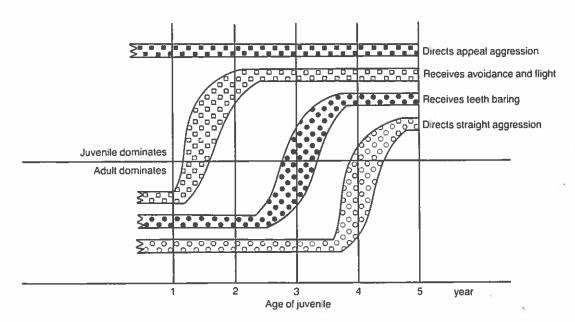


FIGURE 34-3. Young macaques usually achieve dominance over all adults ranking under their mother. This process takes several years. In the beginning the adult still dominates by directing straight aggression to, and receiving flight behavior and submissive teeth baring from, the juvenile. The juvenile dominates in terms of appeal aggression only. In subsequent years the adult starts to respond with avoidance and flight. Eventually, the direction of teeth baring also reverses. After this formal acknowledgement of the new relationship, the juvenile's aggressive behavior may change toward straight aggression. This model of rank acquisition is based on comparisons between age classes (de Waal 1977).

COOPERATION **Side-Directed Communication**

If we regard interactions between adversaries as the main feature of behavior during agonistic interactions, patterns aimed at third individuals can be taken together as side-directed behavior. This is one of the most variable categories of communication in primates. Through sidedirected behavior, individuals make their aggressive encounters "public," that is, open to all kinds of influence by the group. Chimpanzees may do so by begging outsiders, with an outstretched hand, for protection (de Waal and van Hooff 1981), hamadryas females by presenting their hindquarters to a male while threatening another female (Kummer's 1957, 1967, "protected threat"), and rhesus monkeys by different scream types (Gouzoules, Gouzoules; and Marler 1984). For other descriptions see Hall and DeVore, (1965) and Wolfheim and Rowell (1972).

In addition to screaming in defense, macaques use a special form of threat behavior for the recruitment of support. The ears are laid against the head, the eyebrows pulled up, the chin usually pointing upward, and a series of loud grunts is uttered to the opponent while repeatedly looking around at potential supporters with jerky turns of the head. Since this pattern demonstrably increases the probability of receiving support, it was labeled "appeal-aggression" (de Waal, van Hooff, and Netto 1976). It is typically shown by young monkeys when challenging dominant group members. If they succeed in reversing ranks, a process that may take years, young monkeys will start using a different form of threat behavior. "Straight-aggression" refers to the self-confident, silent threat with wide open mouth and staring eyes used by well-established dominants. Thus aggressive macaques seem to use different sets of signals depending on whether they are trying to increase their dominance rank or whether they are reaffirming existing rank positions (de Waal 1977; see also fig. 34-1).

Types of Intervention

Interventions by third individuals can be peaceful, disruptive, or aggressive. For example, in the chimpanzee colony of Arnhem Zoo it is not uncommon for females to "confiscate" a displaying male's weapons (sticks or stones) by removing them from his hands or to placate him by grooming. In macaques, dominant males often give branch-shaking (or cage-shaking) demonstrations during aggressive incidents between others. Such displays may serve as a warning to the combatants that intervention is at hand. But the most common and perhaps the most effective form is the aggressive intervention. This form has received the most attention and is known under various names such as fight interference, agonistic aiding, alliance or coalition formation, and support; see, for example, Kaplan (1977), Cheney (1977a), de Waal

(1977, 1978b), and Walters (1980). Recently I developed a classification of aggressive interventions based on an analysis of several thousand instances observed in the Arnhem chimpanzee colony (de Waal 1984b):

Bond-dependent Interventions. The side an individual takes in aggressive encounters depends on the social bonds with the two combatants. The closer the bond, in terms of friendly contact and grooming, the more likely this individual will be given support against attackers. The main function of these interventions seems to be the protection of friends and relatives.

Scapegoating. Irritations and tensions among highranking group members may lead to redirection by jointly threatening or attacking a bottom-ranking individual. For example, we found evidence that crowding stimulates the occurrence of such aggressive alliances. Their function seems to be the maintenance of peace at the top of the hierarchy.

Exploitative Coalitions. In the Arnhem chimpanzee colony, adult male coalitions are, to a certain degree, independent of previously existing social bonds. This is in contrast to the largely bond-dependent interventions of adult females. Qualitative observations strongly indicate that male coalitions serve status competition and are opportunistic in the sense that they are not based on stable preferences for particular individuals, but on the usefulness and willingness of partners, at a given place and time, to contribute to beneficial conflict outcomes (de Waal 1982). This leads to a testable hypothesis: if the independence between male coalitions and social bonds is related to status competition, it is expected to be greatest during periods of hierarchical instability. Our data confirmed this prediction.

Breaking Up Fights. Since the performance of this type of intervention is usually restricted to a single, highranking member of the group, it is often considered part of a role pattern: the so-called control role. It involves protective and impartial interventions. The goal seems to be to stop aggression rather than to help particular individuals. This behavior definitely benefits weaker group members, but it may also serve the performer himself. Among the Arnhem chimpanzees, there are indications that subordinates who are regularly protected by a performer may mount massive support to prevent his overthrow if his position is challenged (de Waal 1978a). Breaking up fights might, therefore, be part of a strategy aimed at status stabilization.

The extent to which this classification of intervention types is useful for other primate species remains to be tested. However, indications for each type can be found in the literature on macaques and baboons: influence of

(kinship) bonds on interventions (e.g. Massey 1977; Kaplan 1978), scapegoating (e.g., Kawai 1960; de Waal 1977), exploitative coalitions (e.g., Packer 1977; Smuts 1985), and breaking up fights (e.g., Bernstein and Sharpe 1966).

Ambivalence

The principal aim of a coalition is to gain advantage over other competitors in a situation in which all parties compete. This means that there is also a potential for disagreement among the cooperating parties themselves. To illustrate the extremely tense relationships resulting from such intracoalitional competition, let me summarize the situation among three adult males in the Arnhem chimpanzee colony (de Waal 1982).

The oldest male had lost his alpha position to a coalition of two other males. The younger of these two males, however, started to compete with his former coalition partner, the new alpha, over access to the fallen leader. Both tried to sit and groom with him and to prevent the other from doing so. After about 1 year the old male began to develop a preference for the young male. Thus, the youngest and least experienced of the three males

was made alpha male and depended completely on the "old fox." Their coalition lasted several years, but was not free of tense incidents.

In figure 34-4 the young alpha male, in the center, grins and pants while holding out a hand to his coalition partner. This scene illustrates his dependence on the old male. A few minutes before, the two coalition partners had been chasing each other, loudly screaming in a conflict over access to an estrous female. Such conflicts within the ruling coalition created a very unstable situation because there was no one to keep the impressive third male from giving his charging displays and terrorizing the group. This rival male, visible on the left of the picture, is watching how the alpha male hurries to make up with his ally. Only after the reconciliation could alpha reconfirm his position by bluffing over the third male.

Our steadily growing knowledge of dominance processes among chimpanzees in their natural habitat indicates a similar important role for male coalitions as observed in the Arnhem colony (chap. 15). Male baboons also may show exploitative coalition formation (Hall and DeVore 1965; Packer 1977), but for adult male macaques there is much less evidence. It almost seems as if the am-

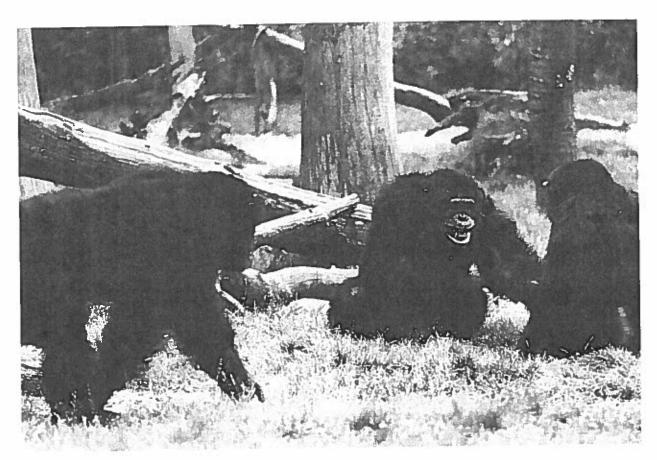


FIGURE 34-4. Under pressure from his displaying rival (*left*), the alpha male (*center*) tries to mend the breach in his coalition by begging his partner (*right*) for reconciliation. (Photo: Frans de Waal)

bivalence discussed above, that is, tension and competition within the coalition, cannot be overcome by male macaques. Part of the reason may be that many macaque species have a mating season, thus concentrating sexual competition in a few months of the year. Under such circumstances, coalition maintenance may demand more efficient mechanisms of tension reduction than those present in macaques (Tilford 1982).

Power versus Rank

One of the most intriguing problems in recent research on dominance is that of restraints on the dominant's control and discrepancies between power and rank. The close interaction between cooperation and competition seems to create plenty of opportunities for individuals to exert greater influence, at least occasionally, than their formal and agonistic ranks would suggest.

Strum (1982) found that during competition over females or meat resident male baboons were more successful than newly immigrated males, in spite of the obvious dominance of new males during aggressive confrontations. She suggests that intimate knowledge of the troop and a well-established set of social connections favor resident males. Other studies of sexual competition among baboons have indicated that males known to be capable of challenging another male do not always do so, even if they have the opportunity (chap. 31). Dependence on supportive relationships may explain this apparent restraint, as it is shown especially toward frequent coalition partners (Rasmussen 1980; Smuts 1985).

Similarly, in small isosexual groups of rhesus monkeys, I found in both male and female groups that the first-ranking monkey was not more successful than the second-ranking one in obtaining and keeping an apple piece that was thrown into their pen (de Waal 1984a). Second-ranking monkeys were able to keep the piece because, although they might be threatened, they were not attacked by alphas. Against lower-ranking monkeys this inhibition was lacking. Since in all groups the two top monkeys formed a coalition against the rest, the selective tolerance may have reflected the need for alpha monkeys to maintain a good relationship with their supporter (see also chaps. 25, 26, 31).

The relationship between the sexes is complex in a large group of captive chimpanzees. Males may depend on females for agonistic support, for reassurance, or for mediation in reconciliations with adversaries. The fact that some females can take priority over adult males may

well be related to the importance of these female behaviors for males (Noë, de Waal, and van Hooff 1980; de Waal 1982). Another example of subordinate control concerns the tactic of low-ranking males to regularly change sides in disputes between dominant males over access to estrus females. Since each dominant needs the subordinate's support in order to have any chance at sexual contact, the subordinate has created a very powerful key position for himself. Apparently, this playing off of one male against the other brings sexual advantages to the subordinate. Nishida (1983b) observed the tactic in the wild and labeled it "allegiance fickleness," while I observed it in captivity and described it as the manipulation of sexual jealousy between others (de Waal 1982). In both cases priority of access was decided by the power balance rather than by the formal rank order.

The concept of power in primate societies is still poorly developed, and all this may sound vague and paradoxical. Why do primates strive for formal dominance if there are other ways to gain certain advantages? What sometimes prevents the most powerful and influential individuals from also attaining formal dominance? We do not have the answers yet, but we should keep in mind that primates, just like humans, may live in double-layered societies with considerable room for influence behind the scenes.

SUMMARY

The dominance concept remains central to the explanation of primate social organization, but three major modifications of the classical concept seem underway: (1) dominance relationships are anything but static; we need to study the proximate mechanisms through which they are established, maintained, and changed; (2) dominance is not a unitary concept; we need to distinguish between, for example, status communication, enforcement of positions, and benefits associated with dominance; and (3) the evolutionary approach has put too much emphasis on competitive aspects; we also need to study dominance in the context of reconciliation, social tolerance, and group cohesiveness. These new approaches are illustrated with selected examples from the literature and from the author's observations on captive macaques and chimpanzees. Special attention is paid to the role of cooperation in agonistic situations and its attenuating effect on power differences between dominants and subordinates.