

# Simple Reactions to Nearby Neighbors and Complex Social Behavior in Primates

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## Abstract

Simple behavioral reactions to nearby neighbors may result in a greater variety of patterns of social interactions, social relationships, and social organization than has been previously assumed. Here, such transitions of micro-rules to macro-patterns are shown for primates in computer models. They concern the emergence of patterns of aggression, including the formation of coalitions and patterns of affiliation, such as reconciliation and grooming reciprocation. It is generally believed that these behavioral patterns require high cognition. While the high cognitive capacities of primates are not denied, these simulations suggest that primates may be less calculative in their daily lives. Simple behavioral reactions and self-organization may suffice to explain their patterns of social behavior.

## Introduction

Compared to many other animal taxa, the social behavior of primates is generally regarded to be more complex in its patterns and underlying cognition. This complexity has often been overestimated, because the same patterns of social behavior are found in taxa that are supposed to be cognitively less sophisticated and recently, for these patterns, cognitively simpler explanations have been given (discussed below).

In earlier empirical studies, coalitions of primates were considered more complex than those of other species, and this was taken as evidence of calculative behavior (Harcourt and de Waal 1992). In later studies, however, coalitions of hyenas proved to be similar (Smith et al. 2010), and coalitions of

primates were found to be explainable by simple behavioral rules (Range and Nöe 2005). The same holds for patterns of affiliative behavior in primates. Whereas early empirical studies suggested that affiliative patterns, such as reconciliation and reciprocation, require sophisticated cognitive deliberations (de Waal 1982), they were later found in species presumed to have less sophisticated cognition, such as goats, hyenas, and dolphins (Aureli and de Waal 2000). The mechanisms thought to underlie reconciliation (a conciliatory tendency, the “deliberation” to reconcile fights with more valuable partners more often, and the ability to distinguish between relationships of different value; Aureli and de Waal 2000) were later considered too complex for these animals (Silk 2007a). Furthermore, record keeping and “moralistic feelings” in primates were initially thought to be the basis of reciprocation and exchange (de Waal 1982); later simple behavioral responses were proposed to explain the observed patterns of behavior (Hemelrijk 1996a). Thus, empirical explanations proceed from assuming complex deliberations to simpler behavioral rules.

This transition from cognitively complex causes to simple ones is also observed in studies of artificial intelligence, for example, in computer models and the building of robots (Pfeifer and Scheier 1999). It appears that the discovery of cognitively simpler explanations is furthered by the use of self-organization models (Camazine et al. 2001; Hemelrijk 2002, 2005).

In this chapter, I discuss to what extent complex patterns of social behavior can be generated without resorting to sophisticated cognition and how they may arise through self-organization from spatial interactions among individuals who follow simple behavioral rules. To avoid the confusion that often surrounds these models, I indicate from the outset what these models can and cannot achieve. The models presented in this chapter are a kind of “null model”: they show that little cognition is needed for primates to generate the observed patterns of social interaction. If simple behavioral reactions can generate certain complex patterns similar to those observed in primates, then this complex behavior can no longer be seen as proof of the sophisticated higher-level cognition that has been presumed to underlie it. Thus, these models illustrate that even if primates have sophisticated cognition (such as, possibly, “knowledge” about social relationships of others), they may not use it in (most of) their daily behavior. This also holds for humans. These models cannot rule out the possibility that complex cognitive processes are used in these social interactions. They show, however, that explanations may be more parsimonious and cognitively simpler explanations should be preferred.

### **Social Organization, Interactions, and Relationships**

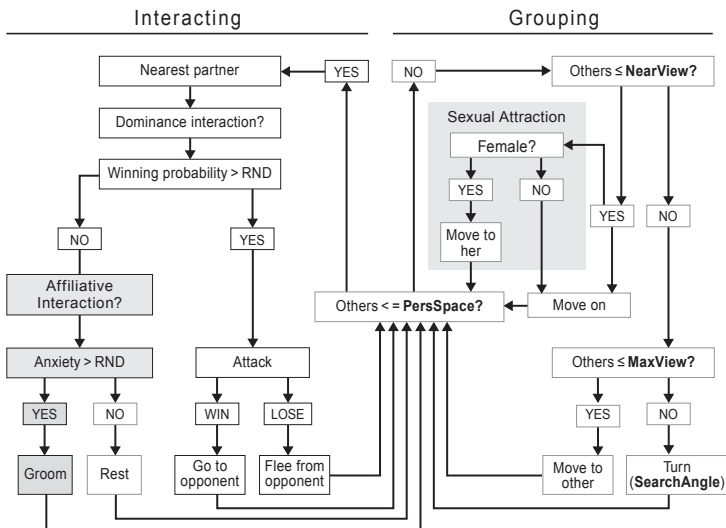
Primates are supposed to use their highest cognition in their aggression, such as their coalitions, and affiliative behavior, such as in exchange and reciprocation of services and in reconciliation of fights (Byrne and Whiten 1997). The

model, DominanceWorld, and its extensions, GroupWorld and GroofiWorld, show, however, that these behavioral patterns may arise from simple social habitual “responses” and the spatial structure in the group. I begin with an outline of the model and then discuss the emergence of aggression patterns in it that resemble those in real primate groups. One pattern, intersexual dominance, is used to make predictions which are subsequently confirmed with empirical data. Finally, I show the emergence of patterns of affiliation (reciprocation and reconciliation).

### DominanceWorld and Its Extensions, GroupWorld and GroofiWorld

DominanceWorld (DomWorld) represents an artificial world consisting of a homogenous space inhabited by artificial individuals that group and compete, but do nothing else (Figure 15.1). In this world, encounters among individuals are not random; they are dependent on the spatial proximity of individuals. Grouping arises from rules of attraction. If individuals are sufficiently close to others (i.e., they have someone in NearView), they continue along their movement direction. Thus, unlike models of schooling (e.g., Hemelrijk and Hildenbrandt 2008), individuals do not align their heading to that of others.

If, however, another individual is too close (i.e., in the personal space of “ego,” PersSpace), a competitive or dominance interaction may take place (it



**Figure 15.1** Outline of behavioral rules in DomWorld and GroofiWorld. The gray-shaded area “sexual attraction” is activated for males in certain runs only. The areas representing “affiliative interaction” were added later in GroofiWorld (gray-shaded). RND: random number drawn between 0 and 1 (see text for explanation).

is not specified what the cause of this competition is, such as food or a sexual partner). After a fight, the winner chases the opponent and the defeated individual flees. Individuals are sensitive to the risk of losing a fight: the greater its chance to be victorious, the more inclined an individual is to undertake an aggressive interaction. An individual's capacity to be victorious is represented through its dominance value. Individuals observe each other's dominance value upon meeting each other. Initially, it is the same for all individuals. Thus, during the first encounter, chance decides who wins. Subsequently, the higher-ranking individual has a greater chance to win. Changes in dominance values reflect the self-reinforcing effect of victories and defeats (Hsu et al. 2006). In the model, this is implemented by an increase of the dominance value of the victorious individual after its victory and a decrease of that of the defeated one by the same amount. Further, the impact of a conflict or the change in dominance values differs depending on the likelihood of an outcome (Hogeweg and Hesper 1985). Thus, when an individual unexpectedly defeats a higher-ranking opponent, this outcome causes a greater change in dominance values of both opponents than when, as would be expected, the same individual conquers a lower-ranking opponent. In this way, rank reversals are made possible.

Intensity of aggression (which ranges in primates from staring to biting) is represented by a fixed scaling factor, called StepDom. This factor is multiplied with the change in dominance value per fight. A high value of StepDom (of 1.0) implies that the impact of a single interaction may be high (e.g., biting); a low value (of 0.1) represents low impact (e.g., threats and staring). As reported later, this will be used to represent differences in fierceness of aggression between species as well as between the sexes.

Parameters are set so that on the computer screen the grouping of individuals resembles that of a macaque group: the number of individuals (8–12) reflects the number of adults in groups of macaques; high and low values of StepDom are set such that there is a great difference between both settings. The behavior of the modeled individuals is analyzed by means of behavioral units and statistical methods similar to those used when studying real primates. For a complete description, see Hemelrijk (1999b, 2000).

One of the shortcomings of the model has been suggested to be the lack of individual recognition among group members, which is clearly present in real animals. However, in DomWorld, individuals recognize the precise rank of others. In reality, this may come about in various ways: by recognizing others individually and remembering the outcome of previous fights with each opponent, by having observed the outcome of fights of that individual with others, or, in the absence of individual recognition, by directly perceiving the health and attitude of the other at the moment of the interaction (e.g., body posture, hair erection), or a combination thereof. In another model, we have studied which aggression patterns result when each individual, a so-called estimator, memorizes its experiences with each opponent and estimates the fighting power of the other on the basis of this memory (Hemelrijk 2000). The results

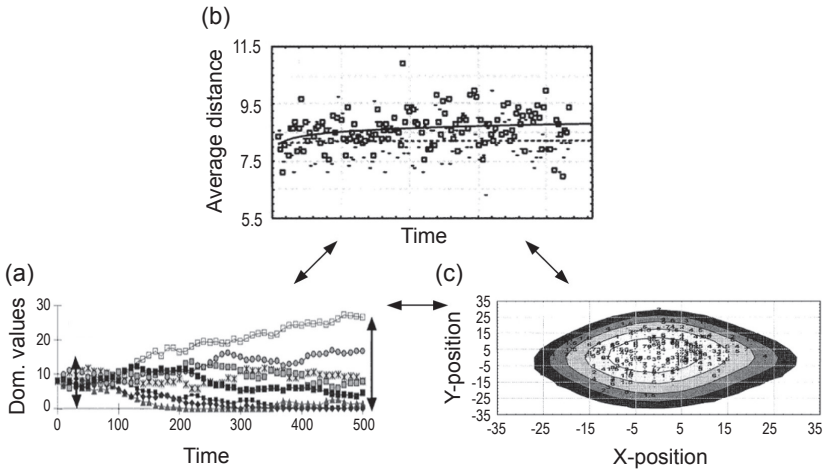
appear to be similar to those of DomWorld without such memory, but they are weaker because everyone has a somewhat different experience with everyone else, and thus a different assessment about the dominance of everyone. Here, I confine myself to the model with clearer patterns in which the precise mechanism of perception of dominance is not specified.

## **Results of DomWorld**

### **Spatial Structure, Dominance Style, Egalitarian and Despotic Societies**

The social system, type of society, or dominance style of many species (e.g., insects, birds, and primates) has been classified as egalitarian or despotic, depending on the way in which benefits are distributed. These benefits include access to mates, food, and safe locations. When benefits are strongly biased toward higher-ranking individuals, the society is called “despotic”; when access to resources is more equally distributed, it is called “egalitarian.” Egalitarian and despotic primate species, such as macaques, differ in many traits. Despotic macaques display aggression that is fiercer (biting rather than staring), less frequent, and more unidirectional. Spatial configuration of individuals in a despotic group is structured with dominants in the center (Itani 1954; Imanishi 1960; Yamada 1966). Usually these differences are explained by optimization of single traits through natural selection. However, Thierry (2004) suggests that in macaques these differences are due to covariation with only two inherited differences: degree of nepotism (i.e., cooperation among kin) and intensity of aggression.

DomWorld delivers an even simpler hypothesis; namely that a mere difference in intensity of aggression produces both types of societies. Analysis of the model specifies in detail how these societies may arise (Hemelrijk 1999b). By increasing only the value of intensity of aggression from mild to fierce, the artificial society switches from a typically egalitarian dominance style to a despotic one. For instance, compared to egalitarian artificial societies, despotic ones are more dispersed, show a lower frequency of attack, their behavior is more rank-related, aggression is more unidirectional, and spatial centrality of dominants is clearer. All of these differences between fierce and mild societies arise via a feedback between the development of the hierarchy and spatial structure that happens only when aggression is fierce (Hemelrijk 1999b, 2000). The steep hierarchy (Figure 15.2a) develops from the fierce aggression, because each outcome has a strong impact. Pronounced rank-development causes low-ranking individuals to be continuously chased away by others and thus the group spreads out (Figure 15.2b). As a result, the frequency of attack diminishes, hierarchy stabilizes, and, because low-ranking individuals flee from everyone they encounter, this automatically brings them at the periphery,



**Figure 15.2** Mutual reinforcement between dominance hierarchy and spatial structure: (a) dominance values (winning tendencies) of each group member (of a single sex) over time; (b) average distance among group members for fierce aggression (open blocks) and mild aggression (short strokes) (Hemelrijk 1999b); (c) dominants are in the center. Darker shades indicate lower dominance rank of group members.

leaving dominant individuals in the center. Thus, a spatial-social structure develops (Figure 15.2c).

In short, the model shows that behavioral traits are interdependent and that a single change of the parameter representing the intensity of aggression causes a switch from a society resembling egalitarian macaques to despotic ones (Hemelrijk 1999b). In real macaques, these differences may be interconnected as they are in the model. In addition to fierce aggression, frequent aggression can cause this switch (Hemelrijk 1999a) because it also leads to a steeper hierarchy. A higher frequency of aggression may, for instance, arise from spatial confinement (e.g., in captivity). Thus, we can expect that captive groups of one and the same species are often more despotic than free-ranging groups.

Dominance style (egalitarian or despotic) is usually considered to be *species specific*, but Preuschoft et al. (1998) suggest that it may also be *sex specific*. In their study of the competitive regime of both sexes of Barbary macaques, Preuschoft et al. found that females behave more despotically than males. This was unexpected because females have a smaller body size and milder aggression. However, the despotic behavior of females should not be regarded as a separate adaptation, because it also occurs in DomWorld. In DomWorld, the sexes are distinguished only by the smaller fighting capacity of the females (i.e., a lower initial dominance and lower aggression intensity). Greater despotism among females was unexpected because of their weaker aggression intensity (Hemelrijk and Gygax 2004), but in DomWorld it is due to the lower initial dominance of females compared to males (which represents,

among other things, sexual dimorphism in body size). Consequently, single events of victory and defeat have more impact on the overall power of females and cause the greater hierarchical differentiation among females than among males: the smaller the initial dominance of females (compared to males), the more despotic the dominance style of females (compared to that of males). The conclusion is that the degree of sexual dimorphism may influence the competitive regime of each sex, both in the model and in real primates.

### **The Socio-Ecological Theory**

According to the socio-ecological theory (van Schaik 1989), dominance style is supposed to be a consequence of the degree of clumping of food sources and of different degrees of competition within and between groups. This theory suggests that despotic societies evolve when food is clumped and competition is high within groups, and egalitarian societies result when competition is high between groups, but low within groups. In line with this, when explicit foraging behavior and food distributions of different degrees of clumping are incorporated in DomWorld (Hemelrijk and Wantia 2005), high clumping of food leads to a despotic society (Hemelrijk et al. 2003). In contrast to the socio-ecological theory, in GroupWorld (an extension of DomWorld to several groups), competition between groups appears to favor despotic rather than egalitarian societies (Wantia 2007). In DomWorld as in real primates, high-ranking individuals usually participate in encounters between groups (Cooper 2004). In GroupWorld, competition between groups with different dominance styles appears to be won, under most conditions, by the group which has a more despotic style. This is due to the greater power of individuals of the highest rank as a consequence of the stronger differentiation of the hierarchy in despotic groups. The outcome of fights between groups depends on the details of the fights and the composition of the groups. When participants of intergroup conflicts fight in dyads or in coalitions of equal size, the despotic group outcompetes the egalitarian one. If, however, individuals of despotic groups fight in smaller coalitions or if their coalitions include fewer males than those of the egalitarian groups, the despotic group runs the risk of losing. Thus, the main conclusion is that group composition and details of what happens in fights between groups should be studied to increase our understanding of the formation of dominance style. This complexity confirms empirical findings on inter-group competition (e.g., see Majolo et al. 2005; Robbins and Sawyer 2007).

### **Model-Based Predictions Concerning the Relative Dominance of Both Sexes**

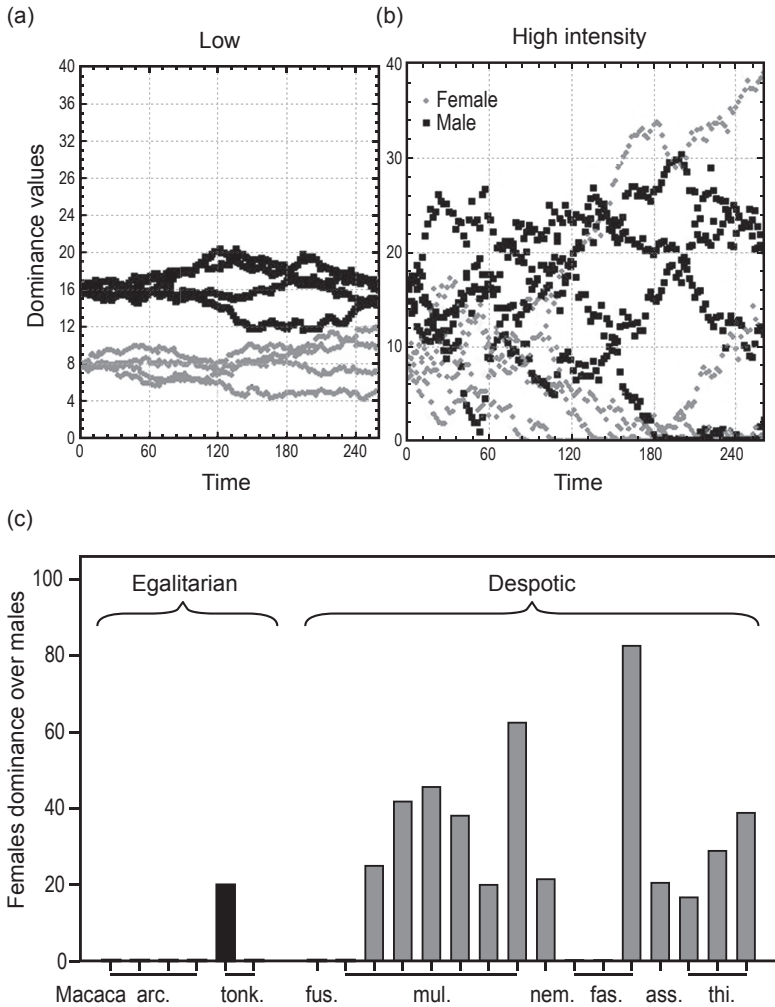
The value of a model becomes clear when the model produces predictions that are subsequently confirmed by empirical tests. DomWorld, for instance, predicts greater female dominance over males, both when the hierarchy is

steeper and when the percentage of males in the group is larger. In a meta-analysis of the relative dominance of males and females in groups of 22 species throughout the primate order, both hypotheses have been confirmed (Hemelrijk et al. 2008).

Although in primate species (apart from Lemuriformes), females are smaller than males and milder in their aggression (due to their relatively smaller canines and weaker muscular structure), they still may be dominant over some males. In *DomWorld* (and in our accompanying empirical studies, Figures 15.3c, 15.4b, and 15.5), we measured the relative dominance position of females compared to males by the ratio of the summed number of males ranking below each female, divided by its maximum (Hemelrijk 1999a). Although females in *DomWorld* differ from males only in their inferior fighting capacity, the model shows that, unexpectedly, females become more dominant over males when species-specific aggression is fiercer (Hemelrijk 1999a; Hemelrijk et al. 2003). This results from the stronger hierarchical differentiation, which causes some males to rank very low and over these males females become dominant (Figure 15.3b). This prediction has been subsequently confirmed in macaques: female dominance over males is greater in despotic macaques than in egalitarian ones, even though the degree of sexual dimorphism in both types of species is the same (Hemelrijk et al. 2008) (Figure 15.3c). Earlier incidental observations of greater dominance of despotic female macaques over males, as opposed to egalitarian females over males, have been attributed to their stronger cooperation to suppress males (as a consequence of their supposedly stronger genetic relatedness) (Thierry 2004). *DomWorld* shows that greater female dominance may also simply arise as a side-effect of more pronounced hierarchical differentiation. In turn, their higher rank may facilitate the cooperation among females in attacks against males.

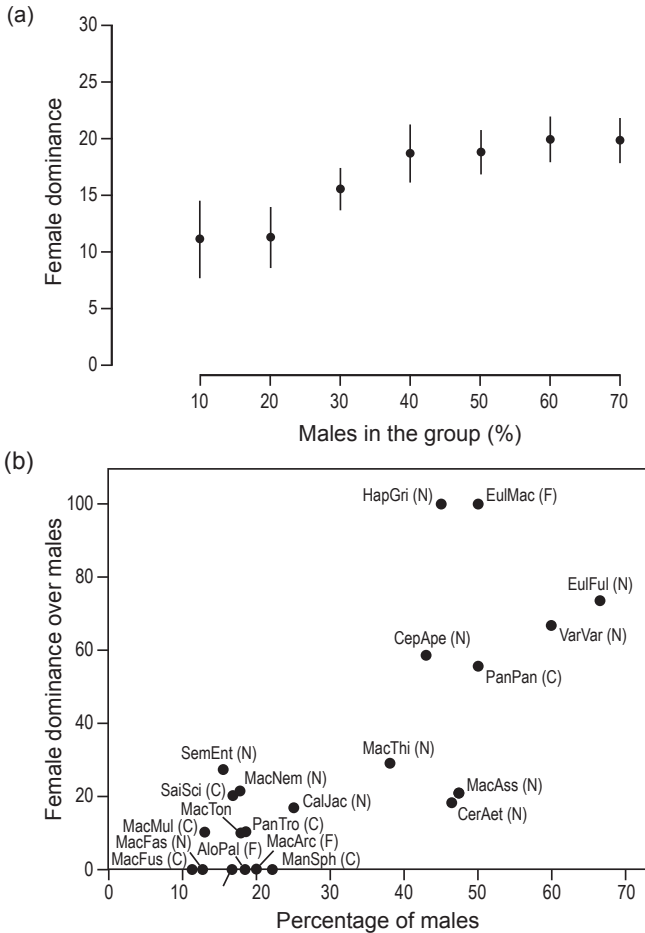
In *DomWorld*, frequent aggression also causes hierarchical differentiation to be pronounced and, as a result, female dominance to be greater. This may explain the difference in female dominance between pygmy chimpanzees and common chimpanzees. Despite their similar sexual dimorphism, female dominance in pygmy chimpanzees is higher than among common chimpanzees. This is usually attributed—just as for despotic macaques—to a higher frequency of the formation of coalitions among pygmy females against males (Parish 1996). However, in line with *DomWorld*, it may also be a side-effect of the difference in density (proximity to neighbors) and thus frequency of aggression between both species (Hemelrijk et al. 2003; Hemelrijk and Wantia 2005). Both are higher in groups of pygmy chimpanzees than in common ones (Stanford 1998). This hypothesis should be tested by comparing different groups of pygmy chimpanzees and by studying the relationship between female dominance and frequency of aggression.

Furthermore, *DomWorld* predicts that when species-specific aggression is fierce, female dominance is higher when there are more males in the group (Figure 15.4a) (Hemelrijk et al. 2008). This arises because a higher proportion



**Figure 15.3** Intersexual dominance relations: female dominance in DomWorld is shown over time for (a) mild and (b) fierce aggression (Hemelrijk 1999b). (c) Empirical data of female dominance in groups of egalitarian macaques (left side) and in groups of despotic macaques (right) (Hemelrijk et al. 2008).

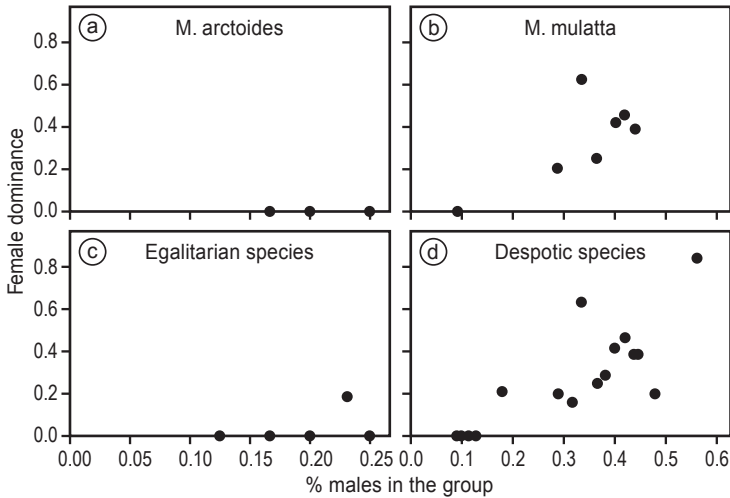
of males causes both sexes to interact more often with males. As a result of being the victim of attacks by males more often, some males become very low in rank and females may become dominant over these males (Figure 15.3b). This is not the case when aggression is mild, because here the hierarchy hardly develops (Figure 15.3a). This has been confirmed in real primates at several levels (Figure 15.4b and Figure 15.5b, d) for all species combined (also if we partial out effects of sexual dimorphism in body size), for several groups of a single species (rhesus macaques), and for several species of despotic macaques.



**Figure 15.4** Percentage of males in a group and female dominance over males (Hemelrijk et al. 2008) in (a) model (average and SE) and (b) real data from primates. Six-letter codes indicate species. Data analysis was based on the independent contrasts method. Environmental conditions: N = natural, F = free-ranging, C = captive condition.

In egalitarian species, both in a single egalitarian species (stump-tailed macaques) and in several ones (Figure 15.5a, c), female dominance (like in the model) was independent of the percentage of males in the group.

In summary, relative dominance between the sexes is not a fixed trait that results merely from sexual dimorphism. Instead, it can be caused by the self-reinforcing effects of dominance interactions; through the frequency and strength of the self-reinforcing effects, female dominance may become dependent on group density and composition.

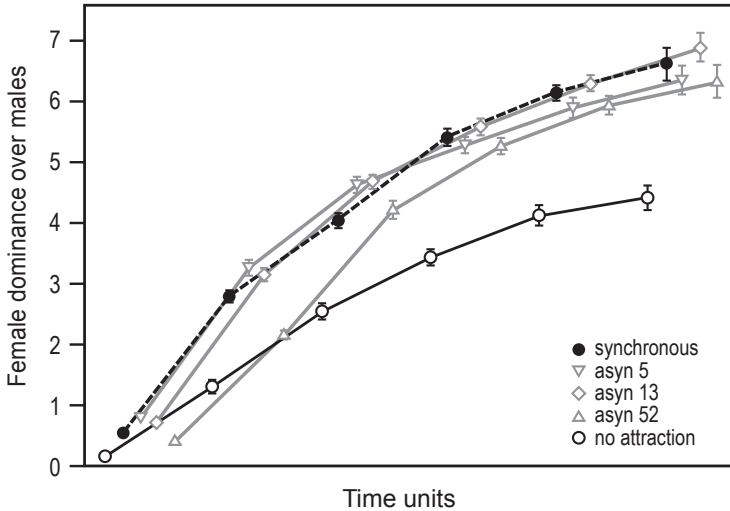


**Figure 15.5** Female dominance relative to males in macaques and percentage of males in the group. (a) Groups of *Macaca arctoides* (Kendall rank correlation,  $N = 4$ ,  $\text{Tau} = 0.33$ , not significant). (b) Groups of *M. mulatta* ( $N = 7$ ,  $\text{Tau} = 0.62$ ,  $P < 0.05$  two-tailed). (c) Groups of several egalitarian species ( $N = 6$ ,  $\text{Tau} = 0.36$ , not significant). (d) Groups of several despotic species of macaques ( $N = 16$ ,  $\text{Tau} = 0.62$ ,  $P < 0.01$  two-tailed, partial for sexual dimorphism,  $P < 0.001$  two-tailed).

### Sexual “Exchange”

Sexual attraction in real animals is usually thought to be accompanied by strategies of exchange. For instance, chimpanzee males are described as exchanging sex for food with certain females (e.g., see Goodall 1986; Gomes and Boesch 2009). Yet, despite detailed statistical studies in which statistical dependency of recurring individuals were taken into account, no evidence has been found to support the idea that males copulate more (or have increased offspring) with precisely those females with whom food has been shared (Hemelrijk et al. 1992; Hemelrijk et al. 1999). Recently, Gomes and Boesch (2009) claim to have found such patterns, but they did not take statistical dependency into account. In general, males have been found to share food with females more often and to be more tolerant toward females during estrus despite the absence of noticeable benefits for males. Thus, another explanation is needed, and DomWorld provides it.

DomWorld represents sexual attraction of males to females by giving the males a greater inclination to approach females than males (by one step), whereas females ignore sexual identity (Figure 15.1). This sexual attraction appears to increase relative female dominance over males, due to the higher frequency of intersexual interactions. Thus, males are more tolerant of females, not as a kind of exchange, but as a kind of “timidity.” Increase in female dominance occurs both when females cycle synchronously and asynchronously and



**Figure 15.6** Female dominance over males over time without sexual attraction (control: no attraction) as well as when attracted to females that cycle synchronously (synchronous) and asynchronously (asyn); 5, 13, 52 are arbitrary intervals between subsequent periods of estrus (Hemelrijk et al. 2003; Hemelrijk and Wantia 2005).

for different cycle lengths (Figure 15.6) (for details of the underlying mechanisms, see Hemelrijk et al. 2003). These results are in line with the observation that female dominance in chimpanzees increases when males are sexually attracted to the females (Yerkes 1940). Studies are needed to determine whether female dominance over males increases during sexual attraction in other species as well.

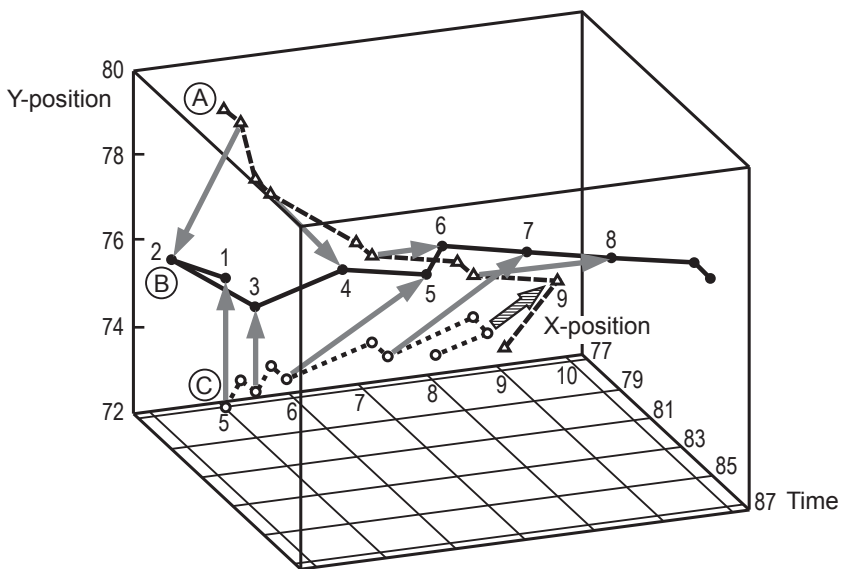
### Coalitions: Reciprocation of Support

Coalitions occur when a third individual aggressively intervenes in a dominance interaction between two opponents. Coalition formation is considered a sign of intelligence because it requires simultaneous negotiations with two or more individuals (Harcourt and de Waal 1992). When reciprocation of support at a group level was found in chimpanzees and macaques, this was thought to have resulted from a desire to pay back in return for services received by keeping records of acts given to and received from each group member (de Waal and Luttrell 1988). In a coalition, an intervener is not only supposed to “support” one of the opponents, she is also supposed to intentionally “oppose” the one she attacks (de Waal and Luttrell 1988). When chimpanzees (but not macaques) appeared to reciprocate “opposition,” de Waal and Luttrell interpreted this as evidence for the higher intelligence of apes compared to macaques.

However, in a subsequent study of the same group of chimpanzees, reciprocation of opposition was absent not only among males, but also among females

as well as all adults (Hemelrijk and Ek 1991). This difference may have resulted from two important shortcomings in the methods of analysis used by de Waal and Luttrell (1988): First, in contrast to Hemelrijk and Ek, de Waal and Luttrell included data collected *ad libitum* and merged data collected over five consecutive summers, although several changes in group stability had occurred, and males had switched ranks and changed coalition partners. Second, their statistical method did not take into account individual variation, whereas the Kr test used by Hemelrijk and Ek does (Hemelrijk 1990).

Furthermore, studies of DomWorld have shown that reciprocation of support in fights may also emerge in the absence of any intention to help others or to reciprocate, or to keep records of acts given and received (Hemelrijk 1996b, 1997). In DomWorld, where individuals merely group and perform self-reinforcing dominance interactions, support is recorded if, by accident, a third individual attacks one of two individuals that were opponents in a preceding activation. Reciprocation at a group level occurs in the model, just as in empirical data, when individuals appear to support more often those partners from whom they have received support more frequently (tested by means of the TauKr correlation between a matrix of support given and received) (Hemelrijk 1990). This occurs in about 50% of the runs. Reciprocation appeared to arise from a kind of social facilitation due to tit-for-tat-like interactions. There were strings of immediate reciprocation of support when two collaborators (A and B in Figure 15.7) together chased away a third individual (C): By fleeing from



**Figure 15.7** Series of events during immediate reciprocation of support. Arrows indicate acts of attack. The accompanying numbers indicate subsequent events. At the ninth time step (thick arrow) one of the supporters attacks the other (Hemelrijk 1997).

one opponent, the victim ended up in the attack range of the other. Such a series ended, for example, when C fled outside the attack range of both collaborators, or when the collaborators entered each other's attack range (and thus, attacked each other), or when uninvolved individuals happened to come too close and thus sparked an interaction with one of the three. In dense groups, uninvolved individuals are often in close proximity to others. Consequently, such series were interrupted sooner and thus, reciprocation happened less often than in sparser groups (Hemelrijk 1996b). Series of immediate reciprocation arise, therefore, from the intertwined effects of aggression and social cohesion, but without the supposed underlying cognition.

### **Reconciliation of Fights, Reciprocation, and the Exchange of Grooming**

Grooming the fur of others has been considered an altruistic trait (i.e., one that is more beneficial to the receiver than the actor). According to the theory of reciprocal altruism, grooming should be either reciprocated or exchanged for other services. Regarding exchange, it has been suggested that individuals groom others of higher rank more often, because more effective support can be expected in return (Seyfarth 1977). Therefore, primates are expected to groom up the hierarchy, particularly in despotic societies. This pattern was not expected for egalitarian societies, because the differences in power, and thus in efficiency of support, are small (Barrett et al. 1999). In addition, individuals were supposed to keep track of the number of grooming acts given and received (de Waal and Luttrell 1988).

Primates have been observed to groom a former opponent more often immediately after a fight than at other times (Aureli and de Waal 2000)—a behavior known as “reconciliation.” To reconcile, individuals are supposed to remember a former fight, be selectively attracted to the opponent, and have a conciliatory disposition. Individuals appeared to reconcile more often with those partners that were more “valuable” (i.e., with whom they groomed more often outside the context of a fight). To explain these findings, primates were supposed to cognitively evaluate and trace the value of an affiliative relationship (Aureli and de Waal 2000). Remarkably, the conciliatory tendency appeared to be higher in egalitarian than in despotic species. This was explained by arguing that in egalitarian societies more reconciliation is needed because individuals are less certain about their relationships due to the similarity of their dominance ranks (Thierry 1990).

All of these patterns (including the differences between egalitarian and despotic societies) emerge, however, in *DomWorld* when a single, cognitively simple, rule is added to groom others (Figure 15.1) (Puga-Gonzalez et al. 2009): when individuals encounter others in their personal space, they consider grooming only when they estimate that they will lose a fight; when they are more anxious, their inclination to groom is greater (Keverne et al. 1989; Schino and Troisi 1992). This rule is based on the well-known calming

and rewarding effect of grooming (see also Shutt et al. 2007). In the model, increased stress is caused by fighting as well as by the time elapsed without grooming (Keverne et al. 1989). To determine how patterns emerge in the model, now called GroofiWorld (Puga-Gonzalez et al. 2009), experiments were conducted in which some of the assumptions, such as that grooming depends on spatial proximity, were omitted. This led to the following explanations.

Reciprocation of grooming emerges without record keeping in the model. It emerges because individuals have a greater chance to groom certain individuals than others, because they are more often closer to them than others. This spatial heterogeneity, in turn, results from aggressive interactions.

In our model, as in baboons (Barrett et al. 1999), individuals groom up the hierarchy when it is steep (thus when aggression is fierce), but not when it is weak. In contrast to what was suggested for primates (Seyfarth 1977; Barrett et al. 1999), this happens *without* the intention of individuals to obtain support in return. In the model, individuals groom others more often the higher the rank of the partners when rank differences are so great that lower-ranking individuals are inhibited to attack out of fear of being defeated. Consequently, they often groom higher-ranking ones instead.

To our astonishment, individuals in GroofiWorld also “reconcile” their fights (as measured by the PC-MC method; Veenema et al. 1994). This happens even though individuals have neither a conciliatory tendency nor insight into the value of affiliative relationships. This seemingly conciliatory behavior arises because former opponents are in closer proximity after a fight than otherwise. Close proximity after a fight may be responsible for patterns that resemble reconciliation in real primates as well: the conciliatory tendency appears to be decreased when distance between opponents after a fight is made more similar to that during the matched control (Matsumura 1996; Call 1999; Arnold and Whiten 2001). Further empirical work is clearly needed.

In both the model and in reality, “reconciliation” is more frequent in societies with mild aggression and a weak hierarchy (resembling egalitarian societies) than in those with fierce aggression. In real primates, Thierry (1990) states that this higher frequency of reconciliation in egalitarian societies is necessary because individuals are less certain about relationships, due to a weak hierarchy. In GroofiWorld, however, higher frequency of reconciliation emerges even though there is no greater uncertainty about relationships. It emerges because a lower percentage of interaction time is spent on grooming when aggression is fierce than mild. This, in turn, results from spatial centrality: dominants have more opportunities to interact with others. Since they experience fewer risks, dominants are more often aggressive and groom others less frequently than lower-ranking individuals. Therefore, grooming becomes rarer when aggression is fierce than mild. Consequently, grooming after a fight is also rarer. In data of real animals, this might well be misinterpreted as if fewer fights are “reconciled.”

In the model, individuals “reconcile” fights more often with their so-called “valuable” partners, although they have neither knowledge nor understanding of their affiliative relationships. This is a side-effect of dominance: individuals groom higher-ranking ones more often and “reconcile” with them more frequently. As a result, they “reconcile” more often with individuals with whom they groom more frequently (i.e., their “more valuable partners”). (This, however, only occurs when the hierarchy is steep.)

### **Evaluation and Future Work**

These kinds of models have been used to study social organization of moving groups of locusts (Buhl et al. 2006), fish (Couzin et al. 2002; Hemelrijk et al. 2010), birds (Hildenbrandt et al. 2010) and primates (de Boekhorst and Hemelrijk 2000). They explain the complexity of social behavior by showing that, although usually attributed to cognition or genetic architecture, complexity may be determined by spatially induced (nonrandom) reactions among individuals as well as by interactions between individuals and their environment. Consequently, these models generate innovative explanations. In the studies related to primates mentioned above, such models show that many complex patterns of social interaction may result from the spatial organization of group members, the self-reinforcing effects of victory and defeat, risk sensitivity of attack, and the tension-reducing effect of grooming.

Further empirical studies are needed to test the above-mentioned parsimonious, model-based hypotheses. In particular, the interconnections between spatial structures, dominance style, intersexual dominance, and patterns of affiliation (e.g., reconciliation, reciprocation, and exchange of grooming) should be pursued.

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