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# Reconciliation in Mandrills (*Mandrillus sphinx*)

Pete Otovic  
*University of South Florida*

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Reconciliation in Mandrills (*Mandrillus sphinx*)

by

Pete Otovic

A thesis prepared in partial fulfillment  
of the requirements for the degree of  
Master of Arts  
Department of Psychology  
College of Arts and Sciences  
University of South Florida

Co-Major Professor: Sarah Partan, Ph.D.  
Co-Major Professor: Judith Bryant, Ph.D.  
Jon Rottenberg, Ph.D.  
Ann Weaver, Ph.D.

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## Table of Contents

List of Tables .....	iii
List of Figures .....	iv
Abstract .....	v
Chapter One .....	1
Group Life .....	1
Conflict Management .....	2
Reconciliation .....	4
Effects of Reconciliation .....	6
Third-Party Affiliation .....	6
Why Animals Reconcile .....	7
Predictors of Reconciliation .....	10
Variation in Conciliatory Tendency .....	11
Mandrills .....	13
Do Mandrills Reconcile? .....	14
Hypotheses to be Tested .....	16
Chapter Two .....	18
Subjects .....	18
Data Collection .....	19
Baseline Data Collection .....	19
Conflict Data Collection .....	19
Post-Conflict Observations .....	19
Matched-Control Observations .....	20
Chapter Three .....	22
Reconciliation .....	23
Reconciliation with the PC-MC Method .....	23
Reconciliation with the Time Rule .....	24
Reconciliation with the Rate Method .....	24
Selective Attraction .....	25
Silent Bared-Teeth Face as Conciliatory .....	25
Additional Analyses .....	26
Conciliatory Tendency .....	26
Sex Effects .....	27
Kinship Effects .....	27
Effects of Percentage of Time in Peaceful Proximity .....	28
Effects of Baseline Silent Bared-Teeth Face Exchange Rate .....	29
Effects of Peaceful Signal Exchange After a Conflict .....	30
Displacement Behavior .....	30
Relationship Disturbance .....	31
Chapter Four .....	33

Limitations and Future Directions .....	42
List of References .....	46

## List of Tables

Table 1	Typical Approaches to Analyzing Reconciliation Data, Operationalization of Conflicts and Operationalization of Affiliation	53
Table 2	Demographics of Mandrills in Sample	54
Table 3	Mandrill Ethogram	55
Table 4	Summary of Conflicts	58
Table 5	Baseline Silent Bared-Teeth Face Rate, CCT, and Number of Conflicts by Dyad	60
Table 6	CCTs as a Function of Baseline SBTF Rate with CCTs Calculated For Entire Group	61
Table 7	Rates of Displacement Behavior After Conflicts Followed by Peaceful Signals (a) and After Conflicts not Followed by Peaceful Signals (b) Between Former Opponents	62

## List of Figures

Figure 1	Patterns of post-conflict behavior	63
Figure 2	Peaceful signal exchange over time in post-conflict and matched-control observations	63
Figure 3	Rate of silent bared-teeth face exchange in post-conflict and matched-control observations	64
Figure 4	Percentage of silent bared-teeth face exchange with former opponents in PC and MC	64
Figure 5	Conflict rate as a function of % time in peaceful proximity	65
Figure 6	Conflict rate as a function of baseline SBTF exchange	65
Figure 7	% of 1 <sup>st</sup> peaceful contacts in post-conflict and matched-control	66

## Reconciliation in Mandrills (*Mandrillus sphinx*)

Pete Otovic

### ABSTRACT

This study aimed to examine whether mandrills (*Mandrillus sphinx*) reconcile their conflicts. The data were collected from a captive group of nine mandrills (5 males and 4 females) at the Lowry Park Zoo that ranged in age from 3 to 16 years at the time of study. After a conflict was observed, the behavior of one of the two former opponents was documented for a period of ten minutes using continuous recording methods. On the next possible observation day, at the same time of the previous conflict, the behavior of the same individual was recorded for an additional ten minutes. Former opponents exchanged peaceful or affiliative signals sooner after a conflict than during control periods. These post-conflict signals were selectively directed towards former opponents, and were most likely to be exchanged in the first two minutes after a conflict's termination. The silent bared-teeth face comprised 62.5% of the first peaceful interactions between former opponents. The best predictor of the likelihood of reconciliation was the dyad's baseline rate of silent bared-teeth face exchange. Mandrill dyads with higher rates of silent bared-teeth face exchange at baseline had higher conflict rates and spent less time in non-aggressive proximity than those with lower rates of silent bared-teeth face exchange. These results are consistent with the Insecure Relationship Hypothesis, which posits that individuals with insecure relationships are more likely to reconcile because their relationships are more likely to be damaged by a



conflict than those with secure relationships. The exchange of peaceful post-conflict signals did not appear to have an effect on the behavior of the former opponents.

Chapter One

Introduction

*Group Life*

Living in stable social groups can have many benefits as well as liabilities for wild animals. Gregarious animals may enjoy decreased predation rates due to increased alertness for approaching predators (Caro, 1986; van Schaik, 1983), dilution (Wrona & Dixon, 1991), confusion of the predator (Fels, Rhisiart, & Vollrath, 1995) and cooperative defense against predators (Bertram, 1975). Group-living animals may also acquire foraging benefits, which include obtaining prey that require cooperative efforts (Creel & Creel, 1995) and the facilitation of finding food (Templeton & Giraldeau, 1995). Finally, finding a mate is made easier for social animals (Wiley, 1991). On the other hand, in addition to increased risk of infection from parasites (van Vuren, 1996), gregarious animals are susceptible to having conflicts of interest over limited resources such as food and mates (Krause & Ruxton, 2002), direction and speed of travel (Menzel, 1993), and time spent performing cooperative tasks (van Schaik & van Noordwijk, 1986).

A conflict of interest among group-living animals can have various immediate and long-term outcomes. Immediately following conflict, opponents may show a range of responses, from tolerance and avoidance of open conflict to aggression (de Waal, 2000). Aggressive encounters may yield negative consequences, which include the risk of physical injury from the initial encounter (Setchell, 2005), renewed attack following an initial conflict (Aureli & van Schaik, 1991; York & Rowell, 1988) and damage to the quality of social relationships (Aureli,

Cords, & van Schaik, 2002). Because these consequences can disturb typical interaction patterns, conflict may reduce the benefits of living in a group. For example, Aureli (1992) found that wild long-tailed macaques foraged for shorter periods of time following an aggressive conflict than during baseline. He hypothesized that this is due to reduced tolerance of the recipient of aggression around a preferred resource (e.g., food) or to the fact that the recipient must pay more attention to the other group members to avoid renewed attack, thereby diverting its attention away from foraging. Aggressive conflict also has non-social consequences. Both aggressors (Aureli, 1997; Castles & Whiten, 1998b) and recipients of aggressive behavior (Aureli, van Schaik, & van Hooff, 1989) increase displacement behavior (e.g., self-scratching) after a conflict, which indicates uncertainty and anxiety in non-human primates (Maestriperi, Schino, Aureli, & Troisi, 1992; Schino, Schucchi, Maestriperi, & Turillazzi, 1988). Uncertainty and anxiety are stress responses; persistent activation of stress responses reduces an individual's fitness by impairing immune system functioning, growth and development, reproductive ability and by causing brain damage (Henry, 1982; von Holst, 1985; Kaplan, 1986; Sapolsky, 2005; Uno, Tarara, Else, Suleman & Sapolsky, 1989). Both social and non-social consequences of conflict provide the impetus for individuals to develop means to reduce or mitigate it.

### *Conflict Management*

Due to the adverse consequences of aggression, conflict management strategies are thought to have evolved both to prevent and repair damage following aggression (Preuschoft & van Schaik, 2000). One way to manage conflict is through the use of honest signals that communicate an individual's competitive ability and thus help to prevent conflict from escalating into full-blown aggression. These signals, such as the blue throat color in male tree

lizards, *Urosaurus ornaus* (Thompson & Moore, 1991), white forehead patches in male collared flycatchers, *Ficedula albicollis* (Part & Qvarnastrom, 1997), and the red and violet coloration on the face, rump, and genitalia of male mandrills, *Mandrillus sphinx* (Setchell & Wickings, 2005), are referred to as badges of status (Rohwer, 1982) and are usually triggered by the release of hormones. In animals that live in stable groups, a second way to manage aggressive conflict is through the formation of dominance hierarchies (de Waal, 1986), which serve to regulate access to preferred resources when they are defendable (Silk, 1987). A third way is through ritualized behavioral displays, which are sometimes nested in dominance hierarchies and function to communicate individual emotions or intentions (Hinde, 1985). Such communications can prevent conflict from intensifying into physical aggression. Examples include threat displays (e.g., staring in baboons and chest beating in gorillas; Estes, 1991), formalized indicators of dominance (e.g., mock biting in stump-tail macaques; Demaria & Thierry, 1990), and formalized indicators of subordination (e.g., the silent bared-teeth display in rhesus macaques; de Waal & Luttrell, 1985; the pant-grunt and bob display in male chimpanzees, Nishida & Hiraiwa-Hasegawa, 1987). These displays tend to be unidirectional in species with dominance hierarchies, meaning that a formal dominance (or subordination) indicator is only emitted by the dominant (or subordinate) individual in a dyad.

In order to maintain the group's integrity, conflict management also must include a means to resolve conflicts that do escalate into aggression (de Waal, 1987). Affiliative post-conflict reunions between former opponents may serve to mitigate the effects of aggressive conflicts, which would decrease some of the risks of aggressive encounters.

*Reconciliation*

Aggression has historically been viewed as an anti-social instinct, virtually impossible to control, that serves to disperse conspecifics in order to facilitate more equitable access to resources (Lorenz, 1966). Research that contributed to this viewpoint involved studying aggressive interactions between individuals that did not need one another, did not know each other, and would not be likely to see one another again (Johnson, 1972). Hence, aggression was thought to result only from the expression of internal factors such as hormones and genes and external factors such as past experience; the consequences of aggression for social relationships were ignored. This perspective is sometimes referred to as the Individual Model of Aggression (de Waal, 2000). It predicts that 1) aggression will be rare among closely bonded individuals, 2) contact following aggression will be aggressive (due to motivational continuity), and 3) aggression will result in dispersal of the opponents. However, in a pioneering study, de Waal and van Roosmalen (1979) discovered that following an aggressive interaction in chimpanzees, former opponents sought friendly contact with one another shortly after a conflict. More specifically, this crucial study revealed a higher frequency of affiliative behavior between former opponents following a conflict than during baseline. In addition, there were specific behaviors, such as kissing and embracing, which occurred more frequently in the first post-conflict interaction than in later post-conflict interactions. This affiliative post-conflict contact was labeled “reconciliation”. This research was a major contribution to the gradual paradigm shift from a focus on the strictly negative connotations surrounding aggression to a standpoint that considers aggression as a social means of negotiating relationships arising from a conflict of interest, which is known as the Relational Model of Aggression (de Waal, 1996). In contrast to the Individual Model of Aggression, the Relational

Model predicts that 1) aggression and peaceful post-conflict interactions will be common among closely bonded individuals, 2) post-conflict contact between opponents will be affiliative and will occur at a higher rate than at baseline, and 3) peaceful post-conflict interactions will reduce anxiety of the opponents and restore baseline proximity between them (de Waal, 2000).

Reconciliation may take a number of forms. It includes shorter latencies to friendly contact (de Waal & van Roosmalen, 1979) or friendly vocalizations (Silk et al., 1996) between former opponents after a conflict relative to baseline or to a matched-control time period. Some researchers also label the post-conflict interaction reconciliation if the former opponents are in proximity to one another sooner after the conflict than during a corresponding matched-control or baseline period (Cords, 1993). Former opponents in many gregarious animals besides chimpanzees have demonstrated an increased tendency to affiliate in one way or another shortly after a conflict. These include mountain gorillas (Watts, 1995), bonobos (de Waal, 1987), capuchins (Verbeek & de Waal, 1997), vervet monkeys (Cheney & Seyfarth, 1989), patas monkeys (York & Rowell, 1988), sooty mangabeys (Gust & Gordon, 1993), golden monkeys (Ren et al., 1991), colobus monkeys (Bjornsdotter et al., 2000), spectacled langurs (Arnold & Barton, 1997), baboons (Castles & Whiten, 1998a; Petit & Thierry, 1994a; Silk et al., 1996; Swedell, 1997; Zaragoza & Colmenares, 1997), macaques (Abegg et al., 1996; Aureli et al., 1994; Aureli et al., 1997; Aureli et al., 1989; Demaria & Thierry, 2001; Judge, 1991; Matsumura, 1996; Petit & Thierry, 1994b; de Waal & Ren, 1988; de Waal & Yoshihara, 1983), lemurs (brown lemurs, Kappeler, 1993; ringtailed lemurs, Palagi et al., 2005), dolphins (Weaver, 2003), hyenas (Hofer & East, 2000; Wahaj et al., 2001), and domestic goats (Schino, 1998). Anecdotal evidence has also been reported for mouflons

(Pfeffer, 1967), lions (Schaller, 1972), dwarf mongooses (Rasa, 1977), and feral sheep (Rowell & Rowell, 1993).

*Effects of Reconciliation*

As predicted by the Relational Model of Aggression, peaceful post-conflict interactions between former opponents have many positive effects on the individuals involved. First, after such peaceful reunions, the risk of renewed attack is dramatically reduced relative to unreconciled conflicts (Aureli & van Schaik, 1991b; Castles & Whiten, 1998a; Cords, 1992). Second, baseline tolerance between former opponents is restored following a peaceful reunion (Cords, 1992), which suggests reduced fear in the subordinate and reduced aggression in the dominant individual. Third, following a friendly reunion, rates of self-directed behavior are reduced in both the aggressor and the recipient of aggression relative to both unreconciled conflicts and those conflicts where affiliative post-conflict contact was sought from a third party member (i.e., an individual not involved in the conflict) (Aureli, 1997). Finally, rates of affiliative behavior are restored to baseline levels following a peaceful reunion between former opponents (Koyama, 2001).

*Third-Party Affiliation*

Peaceful post-conflict interactions may also be observed between one of the individuals involved in a conflict and a different group member not involved in the conflict. This is referred to as post-conflict third-party affiliation (Call, Aureli, & de Waal, 2002). There are two basic forms of third-party affiliation after a conflict. Solicitation refers to when one of the animals involved in a conflict initiates affiliative interaction from a bystander, and consolation refers to when the bystander initiates affiliative interaction with one of the animals involved in the conflict (Palagi et al., 2004). Consolation in particular has only been observed thus far in

chimpanzees (de Waal & van Roosmalen, 1979), bonobos (Palagi et al., 2004), and stump-tail macaques (Call, Aureli, & de Waal, 2002). Although it is relatively rare, consolation may replace reconciliation under certain circumstances, such as when the former opponent is not available for interaction (de Waal & Aureli, 1996).

*Why Animals Reconcile*

Thus far, two hypotheses explain the majority of the occurrences of and variation in peaceful post-conflict interactions, the Valuable Relationship hypothesis and the Uncertainty Reduction hypothesis. The Valuable Relationship hypothesis suggests that individuals within dyads reconcile in order to repair the damage to their relationships because these relationships confer fitness benefits to the individuals. According to this hypothesis, reconciliation may be viewed as communication between conspecifics about the value of each relationship (van Schaik & Aureli, 2000). Individuals within more valuable dyadic relationships are predicted to reconcile at a higher rate than individuals within less valuable dyadic relationships (Cords & Aureli, 2000). Researchers disagree about how to measure value in a relationship. Some posit that dyads with strong bonds, which include high rates of affiliative interaction and frequent proximity, are likely to derive value from their relationship (Kummer, 1978). Others have suggested that high rates of affiliation are only indicative of the compatibility of the dyad and should not be confused with a valuable relationship, which should be characterized by an exchange of benefits that increase the fitness of each individual in the dyad (Cords & Aureli, 2000). Behavioral qualities or dispositions that could increase another's fitness (and hence be of value) include tolerance around preferred resources, food sharing, cooperation while hunting, protection against predation and other conspecifics, reproductive receptivity, and support in aggressive encounters (van Schaik & Aureli, 2000). Beneficial behaviors confer



value to a partner, but they are predicated on both the availability of the partner for advantageous relations and individual traits (such as size, dominance status, reproductive condition) that make the relationship more valuable (Cords & Aureli, 2000). Empirical evidence supporting the Valuable Relationship hypothesis has been documented by Aureli (1997), who found that long-tailed macaques displayed a higher self-scratching rate after a conflict with individuals with whom they exchanged a high rate of affiliative behavior than after conflicts with individuals without such bonds. Aureli also found that those individuals with strong dyadic bonds (and who displayed increased self-scratching after a conflict) reconciled more often than individuals with weaker bonds. Perhaps the strongest evidence supporting this hypothesis is the experimental research of Cords and Thurnheer (1993), who discovered that pairs of long tailed macaques increased their reconciliation rate substantially after they were trained to cooperate in order to obtain food.

The Uncertainty Reduction hypothesis suggests that individuals reconcile in order to signal benign intentions and terminate the fighting, thereby attenuating the uncertainty of the former opponents (Aureli & van Schaik, 1991b; Silk, 1996). This hypothesis is based on the assumption that, after a conflict, opponents display increased rates of displacement behavior as a result of the anxiety arising from risk of renewed aggression and possibly the status of the damaged relationship (Aureli, 1997; Aureli, Cords, & van Schaik, 2002). Evidence that supports the reduction of uncertainty includes a decrease in self-directed behavior and increased tolerance between former opponents after reconciling (Aureli & van Schaik, 1991b; Cheney et al., 1995; Cords, 1992).

It is plausible that both hypotheses are correct, the former being an ultimate explanation of why gregarious animals reconcile and the latter being a proximate explanation (Cords &

Aureli, 1996). Although the two hypotheses are not mutually exclusive, Silk (1996) has argued that the empirical evidence seems to support the Uncertainty Reduction hypothesis, whereas the evidence supporting the relationship repair function of the Valuable Relationship hypothesis is ambiguous. As an alternative explanation for a higher occurrence of reconciliation in dyads with valuable relationships, Silk hypothesized that since peaceful post-conflict interactions facilitate future friendly interactions, and individuals within dyads with strong bonds are more highly motivated to interact affiliatively than individuals within dyads without strong bonds, individuals with strong bonds would be more likely to exchange peaceful post-conflict behavior than those without such bonds. Furthermore, Silk conjectured that in order to conclude that reconciliation has a relationship repair function, long-term effects on the relationship should be demonstrated. Although results from her research with baboons did demonstrate an increase in affiliative vocalizations (e.g., grunts) in the ten minutes after a conflict relative to a matched-control period, they did not reveal an increase in affiliative behavior between reconciled opponents in the ten days following the conflict relative to the affiliative behavior between unreconciled opponents (Silk et al., 1996). Based on this evidence, Silk concluded that the function of peaceful post-conflict interactions is not to repair relationships, but merely to signal the end of a conflict with no long-term guarantees.

A long-term increase in affiliative behavior after a reconciled conflict may not be required to demonstrate a relationship repair function. Instead, restoration of affiliative behavior to baseline levels, along with a reduction in aggressive behavior, may be sufficient (see Aureli, Cords & van Schaik, 2002). As evidence to support this idea, Koyama (2001) found that affiliative behavior between Japanese macaques in the ten days following a reconciled conflict returned to baseline levels. She also found a decrease in affiliative and

increase in aggressive behavior among dyads in the ten days following unreconciled conflicts relative to baseline.

### *Predictors of Reconciliation*

The majority of published research on reconciliation in gregarious non-human primates includes evidence supporting its existence, although the tendency to reconcile varies considerably both within and between groups and species. The lowest percentage of peaceful post-conflict behavior has been reported by Cheney and Seyfarth (1989), who found that vervet monkeys reconcile only seven percent of their conflicts. de Waal and Ren (1988) found that stumptail macaques reconcile 56 percent of their conflicts, which is the highest percentage of conflicts followed by affiliative behavior thus far. According to de Waal (2000), the conditions for a particular species to reconcile include an ability to discriminate among individuals in a group, the existence of conflicts of interest between group members, an ability to remember previous conflicts, and advantages to the preservation of cooperative relationships. Aureli, Cords, and van Schaik (2002) suggested that within-group aggression, not simply conflicts of interest, must also be a requisite, since conflict resolution may not be as pervasive in groups where conflict management strategies prevent the aggressive escalation of conflicts. Kappeler (1993) failed to find reconciliation in a semi-captive group of ringtailed lemurs, *Lemur catta*, but also found low rates of aggression between individuals that tolerate and/or support each other. Aureli et al. (2002) made a few further amendments to de Waal's stipulations. One modification is that for reconciliation to occur there must be increased risks for renewed aggression in the period of time immediately following a conflict, since one of the primary effects of peaceful post-conflict reunions is a reduced probability of renewed aggression between former opponents. Reconciliation is also predicted to be a conflict

management strategy in groups where the consequences of aggression lead to a loss or reduction in advantages derived from the relationship between the two individuals involved. Hence, Aureli et al. (2002) predicted that if the advantages associated with an attempt at reconciling outweigh the costs of the risks of renewed aggression, peaceful post-conflict reunions are likely to occur. Schaffner and Caine (2000) did not find reconciliation in red-bellied tamarins, *Saguinus labiatus*, but no loss of benefits seemed to arise from the preceding conflict between valuable relationship partners. After a conflict, baseline behavior patterns appeared to be restored without any obvious attempts at reconciliation (Schaffner et al., 2001).

Assuming that one function of reconciliation is the repair of a damaged relationship (the Valuable Relationship hypothesis), one would predict that individuals within dyads with more valuable relationships would display higher conciliatory rates than those with less valuable relationships within the same group. Watts (1995) found that female gorillas reconcile with male gorillas, but not with each other. Since female gorillas only form valuable relationships or strong bonds with males, damage to a relationship with another female would not necessarily result in a loss of benefits.

### *Variation in Conciliatory Tendency*

Other factors likely to explain apparent within-group variation in conciliatory tendencies include the security of a relationship (Cords & Aureli, 2000) and the compatibility of the two individuals (Cords & Aureli, 2000). The security of a relationship is defined by the consistency of the behavior of each individual in a dyadic relationship towards each other, which can be measured by observing the signs of tension during an approach, the presence of appeasement or friendly gestures during an approach, or the directness with which an approach is made (Cords & Aureli, 2000). Although this hypothesis has not been directly tested, there is

a small amount of evidence that is consistent with the idea. For example, Cords (1988) found that unrelated juvenile long-tailed macaques had a higher conciliatory tendency than related juvenile individuals. She posited that relationship security may be an important factor for conciliatory tendency, since all juveniles played with one another and were considered to have valuable and compatible relationships. Compatibility of a relationship refers to how well the individuals get along and may be measured in many ways, including the Relationship Quality Index (RQI), which is a measure of affiliative behavior relative to agonistic behavior within a dyad (Weaver & de Waal, 2000).

Differences in how behaviors are operationalized are another cause of observed variability in conciliatory tendencies. Researchers often vary in how they operationalize a conflict or affiliative behavior, and this may also lead to the appearance of variation in conciliatory tendency both between and within groups and species (see Table 1). While studying chimpanzee reconciliation, Fuentes et al. (2002) required three or more non-contact agonistic behaviors to constitute a conflict, whereas de Waal and van Roosmalen (1979) and Preuschoft et al. (2002) only required one. de Waal and Ren (1988) defined conflicts among stumptailed macaques as interactions with facial and vocal threats that are accompanied by a chase of at least two meters, whereas others have used all occurrences of aggression to indicate a conflict (e.g., Kappeler, 1993; Koyama, 2001). Preuschoft et al. (2002) did not include any vocalizations in their definitions of affiliative behavior, but Silk et al. (1996) did. In addition, Cords (1993) considered proximity to be affiliation, whereas Palagi et al. (2005) did not.

Finally, the analytical methods used to determine the existence of reconciliation may be responsible for some variability. There are three methods that are typically used to determine whether dyads reconcile their conflicts within a group. The PC-MC method compares the

latencies to the first affiliative behavior between former opponents after a conflict (Post Conflict; PC) to those in a matched-control period (Matched Control; MC) (de Waal & Yoshihara, 1983). The rate method compares the rate of affiliative behavior in the PC observation to rates during either the MC or baseline (Judge, 1991). Finally, the time rule compares the total number of first affiliative behaviors exchanged at each of ten one minute blocks in the PC to the total number of first affiliative contacts at the corresponding MC one minute blocks (Aureli et al., 1989). Researchers have obtained different results applying different methods to the same data. For instance, Kappeler (1993) found evidence for reconciliation in brown lemurs using the time rule but not using the PC-MC method.

### *Mandrills*

Expanding the array of group-living organisms in which reconciliation is studied will further facilitate our ability to predict when reconciliation is likely to occur and help illuminate its function. One species whose conciliatory tendencies have yet to be examined are mandrills (*Mandrillus sphinx*). Mandrills are terrestrial, forest-dwelling primates that reside throughout western Africa, including Gabon, Cameroon, Guinea and Congo (Grubb, 1973). Mandrills are one of the most sexually dimorphic primate species, with adult males being over three times the size of adult females (Wickings & Dixson, 1992). Adult males possess violet, red, and blue coloration on their snout, rump, and genitalia. The intensity of this pigmentation is highly positively correlated with dominance rank (Setchell & Wickings, 2005) and serves as a social badge of status. The species forms female philopatric groups (they remain in their native group) that may number as high as 600 individuals in the wild (Abernathy et al., 2002). The female philopatric groups have been reported to include one or more permanent adult males (Rogers et al., 1996), although male presence may only be seasonal (during breeding season,

Abernathy et al., 2002). Adult males vary in their group association, ranging from being solitary to living in the group's periphery to being intimately associated with the group (Rogers et al., 1996; Setchell & Dixson, 2001). In the wild, males leave their natal groups before they reach adulthood (9-10 years of age) (Abernathy et al., 2002). In captivity, male emigration is replaced by peripheralization (Setchell & Dixson, 2002).

The intensity of male coloration is believed to affect the probability of violent aggression between unfamiliar conspecifics (Preuschoft & van Schaik, 2000). The association between coloration intensity, conflict and reconciliation remains to be explored. Violent aggressive encounters between male mandrills are particularly risky because of the males' large canines, up to 44 mm or 1.73 inches (Setchell & Dixson, 2002). Not surprisingly, mandrills employ formal signals or indicators of submission, which include fleeing/avoidance, screaming and presentation, and of dominance, which include chasing and lunging (Setchell & Wickings, 2005).

### *Do Mandrills Reconcile?*

Mandrills seem to be an ideal candidate in which to investigate reconciliation since they meet some but not necessarily all of the requisites proposed by de Waal (2000) and Aureli et al. (2002). Several lines of evidence suggest that mandrills are not likely to reconcile their conflicts, males in particular, which have been the focus of the majority of the previous research. First, adult males spend little time in each other's company (Setchell & Wickings, 2005). Second, they do not seem to form cooperative alliances or coalitions (Setchell & Wickings, 2005), which is thought of as one of the most important aspects of a valuable relationship (van Schaik & Aureli, 2000). Third, in a despotic species such as mandrills, fear of approaching the dominant individual may reduce the likelihood of reconciliation (de Waal &

Ren, 1988). Preuschoft and van Schaik (2000) predicted that in despotic species, dominant individuals may not rely on cooperation from subordinate individuals, since if dominants needed the support of subordinates, the subordinates would possess some leverage (e.g., withholding cooperation; Vehrencamp, 1983) that they could manipulate to force the dominant individual to become more egalitarian. Finally, mandrills may not display enough aggression to warrant the development of post-conflict reunions; formal indicators of dominance and submission may mitigate open conflicts.

In contrast, other evidence suggests that mandrills would be likely to reconcile. First, juvenile and adolescent males have high rates of play and other affiliative interactions with one another (Charpentier, Peignot, Hossaert-McKey, & Wickings, 2004). Play may be a valuable aspect of mandrill relationships, considering the importance of play in developing social and survival skills. Second, mandrills are terrestrial foragers and primarily herbivorous (Mellen et al., 1981). They may be tolerant of conspecific proximity because resources are scattered, and this tolerance may be sufficient to constitute relationships with enough value to warrant their repair. Third, even though physical conflict is rare in adult male mandrills (Setchell & Wickings, 2005), adolescent males engage in a relatively high rate of aggression (Charpentier et al., 2004). Fourth, females are philopatric and form matrilineal hierarchies among related females so they seem likely to form valuable relationships and reap the accompanying benefits (such as kin based agonistic support). de Waal and Ren (1988) did not find an effect for kinship on reconciliation rates in another female philopatric species (rhesus macaques, *Macaca mulatta*) but that was probably because the effects for bond strength had been factored out. Thus, it is possible that female mandrills only form strong bonds with their kin. Fifth, mandrills are thought to be closely related to baboons (Stammach, 1987) and mangabeys



(Disotell, 1994), and both of those species reconcile (Gust & Gordon, 1993; Silk et al., 1996). Sixth, males and females may form valuable relationships, which could possibly warrant reconciliation between sexes. A male that has a close relationship with a female could benefit from the female's reproductive receptivity. Due to the extreme sexual dimorphism in mandrills, having a close relationship with a male could be very valuable to a female because the male is capable of protecting her from other sexually harassing males or her infants from infanticidal males (Smuts, 1985). A relationship that offers protection of offspring is believed to be one of the most valuable relationships (along with those that offer agonistic support) formed in non-human primates (van Schaik & Aureli, 2000). Seventh, the function of the silent bared-teeth face (SBTF) in mandrills, a signal in which the animal retracts its lips in a horizontal figure eight shape and thereby displays its canines and premolars, has been poorly understood; its interpretation has ranged from aggressive to affiliative in nature (see Laidre & Yorzinski, 2005, for a short review). Laidre and Yorzinski (2005) have recently suggested that the silent bared-teeth face serves a conciliatory role; mandrills were more likely to exchange silent bared-teeth faces after an agonistic interaction than before one. The silent bared-teeth face may signal benign intentions and thus may have evolved for use in peaceful post-conflict reunions. Additional work by Bout and Theiry (2005) demonstrated that the silent bared-teeth face was mostly exchanged in peaceful situations such as friendly contact, play, mating or socio-sexual interactions, and friendly following. But they also reported that mandrills are likely to produce the silent bared-teeth face after an aggressive exchange. Importantly, usage of the signal did not covary with dominance, meaning that it is unlikely to communicate information about social status.

### *Hypotheses*

The purpose of this study was to examine conflict and post-conflict interactions in a group of captive mandrills. This study was designed to test the following hypotheses:

(1)  $H_1$ : Mandrills reconcile.

*Predictions:* (a) The number of attracted pairs is greater than the number of dispersed pairs. (b) Mandrills display shorter latencies to peaceful signal exchange with their former opponents during post-conflict samples than during corresponding matched-control samples.

(c) The frequency of first peaceful signal exchanges between former opponents is greater in at least one one-minute block in the post-conflict observation than the mean rate of peaceful signal exchange during corresponding matched-control observations.

(d) Former opponents display higher rates of peaceful signal exchange in post-conflict samples than during corresponding matched-control samples.

(e) The percentage of peaceful signals exchanged between former opponents is greater in post-conflict samples than during corresponding ten minute matched-control samples.

(2)  $H_1$ : The mandrill silent bared-teeth face (SBTF) serves a conciliatory role.

*Prediction:* (a) The silent bared-teeth face will be more likely to be the first peaceful exchange between former opponents after a conflict than during corresponding matched-control observations.

## Chapter Two

### Method

#### *Subjects*

Behavioral data were collected from a captive group of mandrills (*Mandrillus sphinx*) housed at the Lowry Park Zoo in Tampa, FL. During the majority of the study, the group consisted of nine individuals: two adult females, one adolescent female, one juvenile female, two adult males and three adolescent males (Table 2). The outdoor enclosure measures approximately 40' x 25', and the animals inhabit it from 0900 to 1700. They are indoors during all other times. The animals are fed at 0900 and 1700 and have ad libitum access to water. At the time of study, the group had been intact for approximately six years, the exception being the youngest female, who was born in 2002. Due to a couple of severe aggressive encounters, the beta male (Milo) was permanently isolated from the alpha male and the females a little less than three weeks after data collection began. From that day forward, two groups were rotated on exhibit. On one day, the group consisted of Nestor, Miller, Mukobi, Moesha, Jalisa, Jinx, Jerome, and Jasper (all but Milo). On the following day, the (bachelor) group consisted of Milo, Mukobi, Jasper, and Jerome. This rotation was conducted on a daily basis for the rest of the study. Moreover, one and a half months later Mukobi was found dead at the bottom of the moat that separates the mandrill exhibit from the visitor viewing area. Thus, from that day forward the bachelor group consisted only of Milo, Jasper, and Jerome. In addition to the perpetually changing nature of the mandrill groups, in

June of 2006 the three remaining adolescent males were transferred out of the group to a new facility.

#### *Data Collection*

Three types of behavioral data were collected: baseline data, conflict data, and post-conflict data. Each drew on the behaviors from Table 3. Behavioral data were recorded on a Dell laptop computer with Noldus Observer 5.0 software. Data recording methods followed Preuschoft et al. (2000) and de Waal and Yoshihara (1983) and were entirely observational.

*Baseline data collection.* All occurrences of behavioral states and events in Table 3 were collected using 20-minute focal animal samples (Altmann, 1974). Focal individuals were randomly selected using a random number generator. Once a sample had been collected on all group members, the process of random sampling began again.

*Conflict data collection.* Data collection on conflicts took priority over baseline observational recording. When conflicts occurred during a focal animal sample, the focal sampling was discontinued and data were collected on the conflict. In this study, a conflict was characterized by particular non-physical and physical forms of aggression. Non-physical aggression was operationalized as ground slaps, head jerks and threat grunts (level 1 aggression; see Table 3) that were accompanied by either lunging towards or chasing another animal (level 2 aggression). Physical aggression was defined as biting, hitting, or grabbing (level 3 aggression). When the conflict began, the identity of the aggressor, recipient, and level of aggression were recorded. The conflict was assumed to be ended immediately after the last aggressive exchange (including level 1 aggression) had terminated.

*Post-conflict (PC) data collection.* After the conflict ended, the distance between the opponents was immediately recorded. In addition, all occurrences of the behavior of one of

the opponents were recorded for ten minutes; this was the post-conflict or PC sample. If within two minutes of the PC's inception, further aggression between the individuals involved was observed, the PC observation started over. The majority of research indicates that increased affiliation in the PC period relative to the MC period is limited to the first two or three minutes after the observation's inception (see Kappeler & van Schaik, 1992). However, Rolland and Roeder (2000) had to use 60-minute PC observations in order to demonstrate reconciliation in ring-tailed lemurs. Therefore, a ten-minute PC duration was chosen as an intermediate duration (Aureli & van Schaik, 1991a). Which opponent was observed after a conflict depended upon how many PC-MC pairs the individual had previously been involved in, how many times each individual had been followed as an aggressor or recipient, and visibility of the former opponents. Particular attention was paid to the frequency and timing of affiliative and peaceful behavior, including the exchange of the silent bared-teeth face, lip-smacking, grooming, head-shaking, playing, non-aggressive touching and peaceful proximity (Table 3). Peaceful proximity was defined as any time an animal was within 2 meters of the focal animal without exchanging any agonistic signals or performing any displacement behavior. This was typically characterized as two individuals sitting near one another without exchanging any overt signals, and seemed to be the most common affiliative behavior between male mandrills (personal observation).

*Matched-control (MC) data collection.* For each PC sample collected, a corresponding ten-minute matched-control (MC) sample was collected from the same focal animal on the next day of observation and at approximately the same time as the previous PC observation. The individual must not have been in a conflict in the ten minutes prior to the start of the MC observation. When possible, the researcher began a MC observation when the spatial

distance between the former opponents was approximately equal to the distance between opponents at the inception of the corresponding PC observation. In other words, if the researcher could not match the time of day and proximity of the former opponents from the post-conflict observation within the same week the initial conflict transpired, preference was given to matching the time of day (as an alternative to throwing out the conflict). The aim of this criterion was to eliminate confounds due to initial proximity (Call, 1999).

## Chapter Three

### Results

Data were collected for a total of 51 dyadic conflicts (see Table 4). Conflicts were recorded from 19 of a possible 36 dyads. 35 of the conflicts involved non-contact threats and chasing, whereas the remaining 16 conflicts involved physical aggression.

Reconciliation data were analyzed in four ways, each of which tests a different prediction concerning whether mandrills reconcile. These include the PC-MC method (de Waal & Yoshihara, 1983), the time rule (Aureli et al., 1989), the rate method (Gust & Gordon, 1993), and selective attraction (de Waal & Yoshihara, 1983). The Corrected Conciliatory Tendency or CCT (Veenema, 1994) was used to determine the percentage of conflicts reconciled at group and dyadic levels. The data were analyzed for consolation using the PC-MC method. All analyses were two-tailed, and Wilcoxon matched pairs tests were used whenever possible in order to ensure that any group differences were not due to one or a few individuals. Results with probability levels of .05 or lower were considered significant, while those with probability levels ranging from .06-.08 were considered tendencies or trends. All means are reported  $\pm$  SE. Although there were 36 possible combinations of dyads, most analyses were limited to 32 of those dyads. This is because the beta male (Milo) was only in the group with the adult females for a very short time before the animals were separated into two groups (see Method). Milo did not interact with the females enough to provide any reliable data during the limited time he had access to them.

*Reconciliation*

*Reconciliation with the PC-MC Method.* One method that was used to determine whether the mandrills reconcile compares the latencies for former opponents to affiliate in the PC and MC samples. This is called the PC-MC method (de Waal & Yoshihara, 1983). If two former opponents exchange peaceful or affiliative behavior at an earlier time in the PC observation than in the MC observation, they are labeled as an ‘attracted’ pair. If they exchange peaceful or affiliative behavior earlier in the MC than in the PC, the pair is labeled as ‘dispersed’. Finally, if the former opponents exchange peaceful or affiliative behavior at the same time in each observation period (including if they fail to exchange any affiliative behavior in either sample) they are labeled ‘neutral’ pairs (de Waal & Yoshihara, 1983). Using this method, the animals demonstrate reconciliation if the number of attracted pairs is significantly greater than the number of dispersed pairs according to a Wilcoxon matched-pair signed ranks test. Figure 1 reveals that the number of attracted pairs ( $N = 29$ ) was significantly greater than the number of dispersed pairs ( $N = 6$ ),  $Z = -2.68$ ,  $N = 9$ ,  $p = .008$ . This finding supports prediction 1a.

While PC-MC pairs were labeled as attracted if the latency to affiliate was shorter in the PC than in the MC, the latency differences may not be significantly different statistically from one another. Thus, a second comparison was made between the mean latency to affiliate in the PC and the mean latency to affiliate in the MC using a two-tailed between-subjects t-test. Former opponents exchanged peaceful signals much earlier after a conflict ( $62.94s \pm 16.18s$ ) than during corresponding matched-control sessions ( $270.97s \pm 51.39s$ ),  $t(19.28) = 3.86$ ,  $p = .001$  (rerun). This finding is consistent with prediction 1b.



*Reconciliation with the Time Rule.* The ‘time rule’ was also implemented to determine whether there was evidence of reconciliation (Aureli et al., 1989; Kappeler, 1993; Veenema et al., 1994). This approach involves parsing the 10-minute PC and MC observations into ten one-minute blocks (ten for the PC, ten for the MC) and recording the total number of first affiliative behaviors that occur within each minute block lumped across all PC-MC pairs. Next, the total number of first affiliative behaviors within each PC block is compared to the number within each corresponding MC block (e.g., total number of first affiliative behaviors exchanged in the PC from 0-1 minutes versus the per-minute rate of affiliative behaviors exchanged in the MC) using a Wilcoxon matched pairs test (Aureli & van Schaik, 1991a). If the frequency of affiliative behavior in any of the one-minute PC sample blocks was greater than the per-minute MC rate, reconciliation was considered to have occurred. Figure 2 shows that the frequency of peaceful signals exchanged between former opponents was significantly elevated in the first ( $Z = -2.67, N = 9, p = .008$ ) and second ( $Z = -1.96, N = 9, p = .050$ ) minutes after a conflict relative to those in the matched controls. This finding corroborates prediction 1c.

*Reconciliation with the Rate Method.* In contrast to the PC-MC method, the rate method compares rates of affiliative behavior between former opponents in the PC sample to the rates of affiliative behavior derived from the MC sample. If the rate of affiliative behavior is significantly higher in the PC than in the MC using a Wilcoxon matched-pairs signed ranks test (Gust & Gordon, 1993), this group of mandrills will have provided evidence of reconciliation. This analysis was limited to the rates of silent bared-teeth face exchanges, since two-thirds of the first affiliative exchanges between former opponents after a conflict were silent bared-teeth faces (see below). Figure 3 shows that the per minute rate of silent

bared-teeth face exchanges was significantly greater between former opponents in the PC ( $.29 \pm .11$ ) than in the MC ( $.03 \pm .01$ ) periods ( $Z = -2.67, N = 9, p = .008$ ), which substantiates prediction 1d.

*Selective Attraction.* To determine whether former opponents preferentially contact each other after a conflict and do not simply display overall higher interaction rates (which is an alternative explanation of greater observed attracted than dispersed pairs), the percentage of peaceful behavior exchanged between former opponents in the PC sample was compared to the percentage in the MC sample. The percentage of peaceful signal exchange was calculated by dividing the cumulative frequency of peaceful signal exchanges with the former opponents by the cumulative frequency of peaceful signal exchanges with any group member. A Wilcoxon matched pairs test was used to test the prediction that the percentage of peaceful signals exchanged with the former opponent is greater in the PC than in the MC across all opponent pairs. If the percentage of peaceful signals exchanged with a former opponent was higher in the PC observation than in the corresponding MC observation, the pair was considered to be selectively attracted. This analysis was limited to the exchange of silent bared-teeth faces, since this was by far the most common peaceful signal exchanged after a conflict. Figure 4 indicates that former opponents directed a significantly greater percentage of silent bared-teeth faces towards one another in PC ( $.50 \pm .08$ ) than in MC ( $.16 \pm .08$ ) periods ( $Z = -2.429, N = 9, p = .015$ ). This result is consistent with prediction 1e.

*Silent bared-teeth face as conciliatory.* To test the hypothesis that silent bared-teeth face exchanges serve a conciliatory role, the number of silent bared-teeth face exchanges that were observed as the first exchange between former opponents after a conflict was compared to the number of silent bared-teeth face exchanges exchanged between former opponents in

matched-control observations using a chi-square goodness of fit test (de Waal & Yoshihara, 1983). If the frequency of silent bared-teeth face exchanges that comprise the first exchange between former opponents after a conflict is found to be significantly greater than the latter two frequencies, it would suggest that silent bared-teeth face exchanges are used as a conciliatory gesture. Figure 7 shows that silent bared-teeth face exchanges comprised 64.5% of the first peaceful exchanges between former opponents in the PC, relative to only 12.5% in the MC. A chi-square analysis corroborated that this difference was significant,  $X^2(N = 47, df = 1) = 11.47, p < .05$ . This finding substantiates prediction 2a.

#### *Additional Analyses*

*Conciliatory Tendency.* Since the data are consistent with the idea that mandrills reconcile, additional analyses were conducted in order to more closely inspect the distribution of peaceful post-conflict signals. Thus, a conciliatory tendency was calculated for the entire group, each dyad, kin and non-kin, and intra- and intersexual dyads using a version of the original conciliatory tendency formula that corrects for increased observation duration and for baseline levels of affiliative behavior, both of which may result in an inflation of attracted (and dispersed) pairs relative to neutral pairs (CCT, Veenema et al., 1994). This allowed comparisons of the tendency to reconcile between various subgroups (kin vs. non-kin, males vs. females, etc).

$$\text{Corrected Conciliatory Tendency (CCT)} = 100 \times \frac{(\# \text{ attracted pairs} - \# \text{ dispersed pairs})}{(\text{total number of all pairs})}$$

There was a total of 29 attracted pairs, 6 dispersed pairs, and 16 neutral pairs. Using the above formula, the CCT for the entire group was 45.10%.

*Sex effects.* Previous studies have noted differences in conciliatory tendencies between the sexes (Watts, 1995). These differences have often been linked to differences in relationship value (Aureli et al., 2002). However, a Mann-Whitney U test indicated that there were no differences in CCTs between sexes (male-male= 50%, female-female = 50%). However, when limiting the analysis to dyads that had fought at least twice, intrasexual dyads ( $46.60 \pm 5.60$ ) tended to have higher CCTs than intersexual dyads ( $28.76 \pm 8.02$ ),  $U = 12.5$ ,  $N = 15$ ,  $p = .071$ . In addition, a chi-square analysis revealed that conflicts were more frequent in intrasexual dyads than in intersexual,  $X^2 (N = 51, df = 1) = 8.82$ ,  $p < .010$ . (Note that the chi-square analysis should be interpreted with caution because it appears to violate the independence assumption; each individual can potentially contribute to each cell).

*Kinship effects.* It is often reported that related individuals are more likely to reconcile than unrelated individuals (Aureli et al., 2002). This variance is believed to be the result of kin relationships being more valuable than relationships with non-kin. However, kin are also considered to have more secure relationships than non-kin (Cords & Aureli, 2000). Consequently, if relationship security and not value mediates conciliatory tendencies, one would expect non-kin to reconcile more often than kin.

There were no differences in CCTs between kin ( $31.75 \pm 18.75$ ) and non-kin ( $47.39 \pm 8.73$ ),  $t(13) = .845$ , n.s. However, a chi-square test revealed that non-kin engaged in more conflicts than kin,  $X^2 (N = 51, df = 1) = 12.25$ ,  $p < .05$ . According to a between subjects t-test, there were no differences in the proportion of time spent in proximity between kin ( $.10 \pm .03$ ) and non-kin ( $.06 \pm .02$ ) when all dyads were included in the analysis,  $t(30) = -1.214$ , n.s. However, when the data from dyads containing the alpha male and any of the females were excluded, a between subjects t-test showed that kin tended to spend a greater proportion of

their time in peaceful proximity ( $.10 \pm .03$ ) than did non-kin ( $.03 \pm .01$ ),  $t(26) = -2.082$ ,  $p = .055$ . Finally, when all dyads were included, a two-tailed between subjects t-test failed to find a difference between the rate (per 10 mins) of silent bared-teeth exchange in non-kin ( $.64 \pm .21$ ) and kin ( $.26 \pm .06$ ),  $t(30) = 1.713$ , n.s. However, if the analysis is limited only to dyads that do not include the alpha male, non-kin tended to exchange the silent bared-teeth face at a higher rate ( $.59 \pm .23$ ) than did kin ( $.12 \pm .05$ ),  $t(22) = 2.003$ ,  $p = .064$ .

*Effects of percentage of time in peaceful proximity.* According to the Valuable Relationship hypothesis, animals reconcile in order to repair damage to relationships that provide fitness benefits to the individuals. Although relationship value has been characterized in many ways, some consider rates of affiliative behavior to be indicative of the quality, compatibility, or value of a relationship. Thus, the Valuable Relationship hypothesis would predict that dyads with high rates of affiliative behavior would reconcile more often than those with low rates of affiliative behavior. Hence, an analysis was conducted to determine whether there was a relationship between the percentage of time individuals spend in peaceful proximity with one another and their propensity to reconcile. CCTs did not appear to differ as a function of the percentage of time spent in peaceful proximity,  $U = 35.00$ ,  $N = 18$ ,  $p = .617$ . The dyads were parsed into two groups using a median split of the percent proximity values to demarcate the groups. The group that spent more time in peaceful proximity had a CCT of  $46.85 \pm 23.09$ , whereas dyads that spent less time in peaceful proximity had a CCT of  $43.67 \pm 13.19$ . A between subjects t-test and Figure 5 show that dyads that spent less time in proximity had a higher rate of conflict per 10 minutes ( $.035 \pm .010$ ) than those who spent more time in peaceful proximity ( $.010 \pm .004$ ),  $t(19.82) = 2.38$ ,  $p = .027$ .

*Effects of baseline silent bared-teeth face exchange rate.* It is plausible that relationship security and not value per se is responsible for the pattern of reconciliation in some cases. One way to operationalize the security of a relationship is to examine the rate of appeasement signals or signals of benign intentions between individuals. Dyads with high rates of appeasement or benign signal exchange are considered less secure than those with low exchange rates. This follows from the notion that an encounter between individuals with insecure relationships, such as an approach, produces uncertainty in the animal approached about the intentions of the approacher. Thus, individuals within these insecure dyads would have a greater need to signal their peaceful intentions prior to approaching one another than those with secure relationships. There is considerable evidence from this study and others that is consistent with the idea that the silent bared-teeth face of the mandrill is a signal of benign intent. Mandrill dyads with high baseline rates of silent bared-teeth face exchange are considered insecure, and those with low baseline rates are considered secure. Hence, an analysis was conducted to determine whether there was a relationship between the security of a relationship and the likelihood of reconciliation. Dyads were parsed into two groups (high and low silent bared-teeth face exchange) using the median baseline silent bared-teeth face rate as a cutoff. When the analysis was limited to dyads that engaged in at least two conflicts, a between subjects t-test showed that dyads with higher baseline rates of silent bared-teeth face exchange had a higher CCT ( $76.33 \pm 11.41$ ) than dyads with lower rates of silent bared-teeth face exchange ( $16.6 \pm 10.51$ ),  $t(7.948) = -3.850$ ,  $p = .005$  (see Table 5 for individual data). Due to the fact that each mandrill CCT was based on a limited number of conflicts, CCTs were also calculated using the total number of conflicts in each group (higher and lower baseline SBTF rates). Table 6 shows that the dyads with lower baseline SBTF

rates had a CCT of 16.7, whereas the dyads with higher baseline SBTF rates had a CCT of 55.3. In addition, a between-subjects t-test revealed that the rate of conflict per 10 minutes tended to be higher for dyads who had higher baseline silent bared-teeth face exchange rates ( $.03 \pm .010$ ) than for dyads with lower baseline silent bared-teeth face exchange rates ( $.01 \pm .004$ ),  $t(18.995) = -1.86$ ,  $p = .079$  (Figure 6). This finding was also substantiated by a positive correlation between baseline silent bared-teeth face exchange rate and conflict rate,  $r(32) = .48$ ,  $p = .005$ . A Pearson product moment correlation between the percentage of time spent in peaceful proximity and rate of silent bared-teeth face exchange was not significant,  $r(32) = .017$ , n.s. When the data from the dyads including the alpha male and any of the females were removed, the result was still not significant,  $r(28) = -.241$ , n.s. Finally, a Mann-Whitney U did not reveal a difference in the rate of silent bared-teeth face exchange per 10 minutes for mandrills that spent more time in peaceful proximity ( $.31 \pm .11$ ) relative to those who spent less time in peaceful proximity ( $.59 \pm .20$ ),  $U = 89$ ,  $N = 32$ ,  $p = .14$ . However, when the data from the dyads that included the alpha male and the females were excluded, mandrills that spent less time in peaceful proximity to one another had a higher rate of silent bared-teeth face exchange ( $.65 \pm .22$ ) than those who spent more time in peaceful proximity to one another ( $.16 \pm .05$ ),  $t(26) = 2.12$ ,  $p = .05$ . The groups (higher and lower time spent in peaceful proximity) were created using a median split.

#### *Effects of peaceful signal exchange after a conflict*

*Displacement behavior.* According to the Uncertainty Reduction hypothesis, anxiety is a mediator of reconciliation. In other words, animals with higher levels of post-conflict anxiety should reconcile more than those with lower levels of post-conflict anxiety. Exchanging peaceful post-conflict signals is thought to function to restore anxiety levels to

baseline conditions. One way to measure anxiety in non-human primates is to record rates of displacement behavior, such as scratching, self-grooming, yawning, and body shaking. In order to explore the effects of aggressive conflicts and peaceful post-conflict signals on the mandrills' anxiety levels, their rates of displacement behaviors were recorded and compared over time. More specifically, each individual's rate of displacement behavior was calculated for each of the ten one-minute blocks for post-conflict observations that were followed by peaceful signal exchange and for post-conflict observations that were not followed by peaceful signal exchange. The post-conflict rates of displacement behavior were compared to the mean rate of displacement behavior in each individual's matched-control sessions.

There was no evidence supporting the notion that the displacement behavior of former opponents was elevated after a conflict. A Wilcoxon matched pairs signed ranks test did not show a difference between rates of displacement behavior in post-conflict observations that were not followed by peaceful signals relative to their corresponding matched-control observations (Table 7). However, the Wilcoxon matched pairs test did reveal that individuals who exchanged peaceful signals after a conflict had a lower per minute rate of displacement behavior in the first ( $.36 \pm .12$ ), second ( $.32 \pm .12$ ), and ninth ( $.36 \pm .19$ ) minutes after the signal exchange than they did in their corresponding matched-control sessions (see Table 7).

*Relationship disturbance.* Aureli et al. (2002) posited that, in order for animals to reconcile, they must have aggressive conflicts that disturb the relationship between the two individuals involved. If the aggressive conflicts do not have an effect on the former opponents, there would not be any need to reconcile. Schaffner et al. (2005) found that red bellied tamarins do not reconcile, but also found that former opponents were just as likely to be in proximity to one another after a conflict as during corresponding matched-control



observations. Because peaceful post-conflict behavior among mandrills is more frequent between animals with insecure relationships, it is plausible that what the mandrills are doing is not reconciling per se. Hence, an analysis was conducted to examine the effects of aggressive conflicts and peaceful post-conflict signals on the likelihood of proximity. The proportion of observations in which the former opponents were in proximity to one another after a conflict that was not followed by peaceful signal exchange did not differ from that of the matched-control observations,  $X^2(N = 67, df = 1) = 4.42$ , n.s. In contrast, former opponents were more likely to be in proximity after conflicts followed by peaceful signal exchange than after conflicts with no peaceful exchange,  $X^2(N = 40, df = 1) = 8.21$ ,  $p < .05$ . In addition, former opponents were more likely to be in proximity after a conflict followed by peaceful signal exchange than during matched-control observations,  $X^2(N = 71, df = 1) = 4.41$ ,  $p < .05$ .

## Chapter Four

### Discussion

Mandrills exchanged peaceful signals with one another sooner and more frequently after they engaged in an aggressive conflict than during matched-control observations. In addition, mandrills with higher baseline rates of silent bared-teeth face exchange were more likely to fight than those with lower baseline rates of silent bared-teeth face exchange. The mandrills who had higher rates of conflict also had lower rates of affiliative behavior. Finally, mandrills with higher baseline rates of silent bared-teeth face exchange were more likely to reconcile than those with lower baseline rates of silent bared-teeth face exchange. The silent bared-teeth face constituted two-thirds of the first peaceful exchanges between former opponents.

The data indicated that former opponents reconciled regardless of whether the PC-MC method, time rule, or rate method was used. According to the time rule, reconciliation was limited to the first two minutes after a conflict. In the majority of gregarious animals that reconcile, peaceful signals are exchanged within three minutes of the preceding conflict (Kappeler & van Schaik, 1992).

It is likely that one function of the mandrill silent bared-teeth face is to signal an individual's benign intentions. Signals of benign intent are similar to appeasement signals, which are directed from subordinates to dominants in order to reduce the likelihood of receiving aggression. However, unlike appeasement signals, signals of benign intent can also be used by dominants to reduce the fear of subordinates. Data collected during this and other

studies are consistent with the notion that the silent bared-teeth face has this function. First, the silent bared-teeth face is not a unidirectional signal; it is performed by both the dominant and subordinate members of a dyad (Setchell & Wickings, 2005). Appeasement signals, in contrast, are usually directed from subordinates to dominants. Second, the silent bared-teeth face is more likely to precede peaceful interactions than it is to precede aggressive interactions (Bout & Thierry, 2005; Laidre & Yorzinski, 2005). Finally, the mandrills from this study who had higher rates of conflict also exchanged the silent bared-teeth face at higher rates during baseline. Individuals who have high rates of aggression would have a greater need to signal their peaceful intentions prior to an approach than those who do not frequently engage in aggressive interactions.

The baseline rate of silent bared-teeth face exchange may be a reliable indicator of the security of a relationship. Cords and Aureli (2000) reported that one way to operationalize the security of a relationship between individuals is to compare the likelihood that an approach is preceded by or appears simultaneously with an appeasement signal. Although the silent bared teeth face is not an appeasement signal per se, both appeasement signals and signals of benign intent would be expected to be elevated in insecure dyads. Not only did mandrills with higher rates of silent bared-teeth face exchange have higher rates of conflict, but mandrills with higher rates of conflict also spent less time in non-aggressive proximity than those with lower rates of conflict. A combination of high rates of aggression and little time spent near one another without behaving aggressively seems like an idea description of an insecure relationship.

Furthermore, it is commonly assumed that kin have more secure relationships than non-kin (Cords & Aureli, 2000). Among the mandrills, kin engaged in fewer conflicts and tended

to have lower baseline rates of silent bared-teeth face exchange than non-kin. Moreover, with the exception of the dyads that included the alpha male and any of the females, kin tended to spend more time in peaceful proximity than did non-kin.

Animals with secure relationships might not have as great a need to signal their benign intentions while approaching one another. This is most likely because, within a secure relationship, an approacher's intentions are more predictable. Animals with insecure relationships benefit from signaling their benign intentions while approaching to avoid aggression or supplantation. Subordinates could benefit from signaling peaceful intentions by reducing the probability of attack or increasing the dominant's tolerance of them. Dominants could benefit from directing signals of benign intent to subordinates by promoting group cohesion, preventing group dispersal, reducing the uncertainty of a subordinate, and facilitating peaceful interaction in some cases (Preuschoft & van Schaik, 2000). The function of the silent bared-teeth face, therefore, seems analogous to the function of grunts in baboons, who are a close relative of mandrills (Cheney et al., 1995). Grunts are primarily used to signal a dominant female's peaceful intentions towards an unrelated subordinate female. This is supported by the fact that, during baseline, grunts are most commonly directed from a dominant female to an unrelated subordinate female. Cheney et al. (1995) reported that an approach by a dominant was not as likely to supplant a related subordinate relative to an approach to an unrelated subordinate.

Interestingly, the best predictor of mandrill conciliatory tendency was the baseline silent bared-teeth face rate of the dyad. Mandrills that had higher baseline rates of silent bared-teeth face exchange had higher conciliatory tendencies than those who exchanged the silent bared-teeth face at lower rates during baseline. In light of the present evidence which

suggests that mandrills with high silent bared-teeth face exchange rates have insecure relationships, it seems that the mandrills who were most likely to reconcile were those with insecure relationships.

Research conducted with other human and non-human animals suggests that relationship security plays an important role in the likelihood of reconciliation. For instance, Russian children are more likely to reconcile conflicts with their acquaintances than with their friends (Butovskaya, Verbeek, Ljungberg, & Lunardini, 2000). Acquaintances typically do not know as much about each other and engage in more intense aggressive encounters relative to friends. Therefore, one of the primary differences between acquaintances and friends may very well be relationship security. Furthermore, in human children, friends are often more likely to reconcile than siblings (Dunn, 2004, p. 37). Once again, it is plausible that one of the main differences between friends and siblings is the security of the relationship. In addition, non-kin reconcile more frequently than kin in spotted hyenas (Wahaj et al., 2001). As with primates, hyena kin spend more time with one another, exchange more affiliative behavior, and are much more likely to form alliances than are non-kin. Moreover, as with the mandrills in this study, conflicts between the hyenas were much more frequent between non-kin than between kin. Therefore, it is likely that the hyenas with insecure relationships also have the highest conciliatory tendencies

Since mandrills with insecure relationships were the most likely to reconcile, the pattern of reconciliation in mandrills was in direct contrast to predictions derived from the Valuable Relationship Hypothesis. Because insecure dyads had higher rates of aggression, and dyads with higher rates of aggression had lower rates of affiliative behavior, it is highly unlikely that these are the most valuable relationships formed within the group. Furthermore,

no correlation was found between affiliative behavior and conciliatory tendency. The results from other species also pose challenges to the Valuable Relationship Hypothesis. For instance, hyenas are characterized by female philopatry, and females are more likely to form alliances than males (Wahaj et al., 2001). Hence, the Valuable Relationship Hypothesis would predict that females should have higher conciliatory tendencies than males. However, there was not a difference in conciliatory tendencies between male and female dyads. Finally, in chimpanzee societies, males are thought to have the most valuable relationships because they are philopatric and cooperate more often than do females. The presence of male philopatry and cooperative inclination has been used to explain why male dyads reconcile a greater percentage of their conflicts than do females (Cords & Aureli, 2000). However, Preuschoft et al. (2001) reported that agonistic support, a valuable form of cooperation, was not a reliable predictor of conciliatory tendency among chimpanzees. It is plausible that relationship security, and not value per se, explains the differences in chimpanzee conciliatory tendencies. For instance, both dominance rank and coalition partners can change very rapidly in male chimpanzees, whereas female dominance hierarchies tend to remain relatively stable over time (de Waal, 1982). Furthermore, in contrast to males, female chimpanzees do not show elevated rates of displacement behavior after a conflict with a member of the same sex (Koski, Koops, & Sterck, 2007). Accordingly, males may experience more post-conflict anxiety and have a stronger propensity to reconcile because their relationships are less secure and thus more susceptible to damage from an ensuing conflict.

Alternatively, it is possible that insecure relationships are more likely to be reconciled than valuable relationships if the signals used for reconciling are more common between

rivals than between friends during baseline. Unlike many other primates, mandrills do not use affiliative signals to reconcile. This behavior pattern is somewhat consistent with Silk's Benign Intent Hypothesis (Silk, 2000). This hypothesis posits that peaceful post-conflict behavior does not function to repair the damage inflicted upon valuable relationships, but instead serves to convey that the conflict is over and that the intentions of the signaler are no longer malicious. Silk reported that female baboons selectively direct post-conflict grunts to other females who have infants. This inclination decreases as the infant ages. Silk concluded that such post-conflict signals function to facilitate infant handling and in no way function to repair damage to a relationship. Instead, the signals are indicative of an individual's temporary benign intentions that sometimes help them obtain a desired resource (e.g., handling an infant). Although there is no evidence that mandrills reconciled to promote friendly interactions, their post-conflict interactions do seem to consist of short-term signals of peaceful intentions and do not seem to be oriented towards repairing valuable relationships. This is evidenced by the fact that there were not many affiliative behaviors that followed conciliatory signals and that post-conflict signals were not directed towards good or valuable relationship partners. In addition, one of the primary means by which hyenas reconcile is engaging in greeting displays. Since greeting displays seem to reduce uncertainty in tense situations, it is plausible that they are analogous to the mandrill silent bared-teeth face (Setchell & Wickings, 2005). It would be interesting to determine whether the distribution of hyena greeting displays during baseline would be similar to the distribution of the mandrill silent bared-teeth face. It is important, however, to note that East et al. (1993) reported that the distribution of hyena greeting displays was similar to the distribution of grooming interactions in primates. Finally, it is often noted in the human

conflict resolution literature that there is a qualitative difference between the way that children reconcile with friends and the way they reconcile with others, such as siblings or non-friends. With friends, children are more likely to utilize conciliatory strategies, such as negotiation, that allow them to overcome the preceding conflict and resume their social encounter (Verbeek, Hartup, & Collins, 2000). In contrast, resolution strategies with non-friends or siblings are typically not geared towards continuing a social interaction. This may be analogous to what is seen in non-human primates. Species who selectively reconcile valuable relationships may be more likely to use physical contact as a conciliatory gesture, which could increase the chances of former opponents grooming one another or engaging in a play bout. In contrast, species that are more likely to reconcile insecure relationships might be more likely to use peaceful signals that do not necessarily aim to promote social interaction. For instance, the mandrills hardly ever engaged in friendly interactions after exchanging peaceful post-conflict signals.

It is interesting that mandrills reconcile in light of the fact that aggressive conflicts do not seem to have the same disruptive effects or distribution that is characteristic of the majority of animals that reconcile. There are three pieces of evidence consistent with this view. First, the present study did not find that the rates of displacement behavior were elevated after conflicts that were not followed by any peaceful behavior. Hence, it is possible that aggressive conflicts in mandrills do not produce a significant amount of uncertainty in the former opponents. However, it might not be relevant that the rates of displacement behavior were not elevated after a conflict. For instance, Manson, Perry, and Stahl (2005) reported that wild white-faced capuchins reconcile, but their rates of displacement behavior did not increase after a conflict. Perhaps anxiety does not manifest in



the same ways in all non-human primates, or it may be that anxiety is not always a mediator for reconciliation. It should be noted, however, that there is a fair amount of support for the Uncertainty Reduction Hypothesis, which posits that post-conflict anxiety levels determine the likelihood of reconciliation. Second, Schaffner et al. (2001) reported that red-bellied tamarins do not reconcile because the preceding aggressive conflicts did not seem to alter typical interaction patterns. The present data from mandrills indicate that aggressive conflicts that were not followed by peaceful signals did not reduce the probability that the former opponents were in proximity to one another. Finally, Kappeler (1993) failed to find evidence that ringtailed lemurs reconcile, but noted that conflicts did not occur between animals with high rates of agonistic support or tolerance. Hence, Aureli et al. (2002) have postulated that conflicts must occur between individuals with valuable relationships in order for animals to reconcile. Similar to the ring-tailed lemurs, mandrills who spent lots of time together were much less likely to fight than those who spent little time together.

It is also noteworthy that mandrills exhibit a conciliatory tendency that is higher than those reported for the majority of species that have been studied. This is in contrast to what would be predicted of the mandrills. For instance, Thierry (2000) reported that among macaque species, those in which unidirectional conflicts are common have low conciliatory tendencies. The majority of conflicts witnessed in the present study were unidirectional, comprised of one animal pursuing and occasionally physically attacking another animal, who would flee (personal observation). Additionally, mandrills are fairly despotic animals. Despotic animals typically have much lower conciliatory tendencies relative to those living in egalitarian societies (de Waal & Luttrell, 1989).

Signals of benign intent do seem to have the same uncertainty reduction effects as affiliative signals when exchanged after a conflict. Cheney et al. (1995) found that when dominant female baboons emit a grunt towards unrelated subordinate females after a conflict, the subordinates were less likely to be supplanted in response to an approach by the dominants. Likewise, mandrill former opponents were more likely to be in proximity to one another after the exchange of peaceful post-conflict signals relative to both conflicts not followed by peaceful signals and to matched-control periods. However, it is not quite clear that this indicates greater tolerance after a peaceful exchange. It seems that there was a qualitative difference between proximity during baseline and post-conflict encounters. Whereas proximity during baseline was usually characterized by two individuals sitting near one another, post-conflict proximity mainly involved the former opponents standing next to one another after they had exchanged the silent bared-teeth face. It was almost as if they remained next to one another after exchanging silent bared-teeth faces to confirm that the other's intentions were peaceful. More specifically, when two former opponents were in proximity after a conflict, it often followed a particular pattern. One animal would attack the other and then terminate the attack. The animal that was formerly being attacked would stop, turn and face its pursuer. Many times the two animals would exchange the silent bared-teeth face and take a few steps towards one another, which resulted in the animals being within two meters of each other (and hence in proximity). Often, the aggressive encounter would not lead to a true dispersal that was then followed by an approach. Instead, former opponents were already very close to two meters from one another immediately after the aggressive encounter terminated. Therefore, measuring proximity might have been more meaningful if the animals had already been dispersed due to the initial aggressive encounter and then later

approached one another. On a related note, the present study revealed that the rate of displacement behavior of mandrills was lower for the first two minutes after the post-conflict exchange of a signal of benign intent relative to baseline. Thus, it is plausible that these signals do reduce post-conflict anxiety due to uncertainty.

*Limitations and future directions*

The most notable limitation of this study is the small number of conflicts that were recorded. This was due to the zoo administration's frequent shifting and manipulation of group compositions in order to mitigate the aggressive conflicts that transpired during the study period. Consequently, it was difficult to demonstrate variation in conciliatory tendencies, since not all animals fought and many who did fight only were observed to do so once. Although mandrill dyads with higher baseline rates of silent bared-teeth face exchange tended to reconcile more often than those with lower silent bared-teeth face rates, the number of conflicts was low enough to potentially bias conciliatory tendency values. Since dyads that have low baseline rates of silent bared-teeth face exchange also have low rates of conflict, their conciliatory tendencies in particular are based on a limited number of conflicts. Thus, it is possible that the conciliatory tendency values would change as more data are collected.

In addition, it was difficult to determine the effects of exchanging peaceful post-conflict signals due to the relatively small number of conflicts observed and because there was only one observer collecting the data. It was not feasible to videotape the mandrills. When the camera was zoomed out far enough to capture the mandrill enclosure, it was too difficult to ascertain the identity of the individuals. Conversely, when the camera was zoomed in close enough to determine individual identities, it was very difficult to follow the fast-moving

mandrills with the camera. Moreover, although interobserver agreement could be calculated if there was another person observing the interactions, it was not feasible to recruit and train an independent observer due to the time constraints on the study (since the adolescents were leaving in June). Nevertheless, the pattern of results is noteworthy and different from the vast majority of research concerning reconciliation in non-human animals. Indeed, it is more difficult to demonstrate a trend or significance with a small sample size; the pattern of results from this study is robust enough to overcome the low statistical power of the analyses. Finally, if the CCTs are calculated for each group as a whole (instead of individual dyads within the group), which bases the CCT on more conflicts, dyads with higher baseline silent bared-teeth face exchange rates still had a much greater conciliatory tendency relative to dyads with lower baseline silent bared-teeth face rates. Therefore, although it may be premature to make strong inferences from these data, the results at least warrant further investigation of how and why animals reconcile.

Another drawback of this study is that some of the results are inconsistent. For instance, although mandrills with higher rates of silent bared-teeth face exchange had higher conflict rates than those with lower silent bared-teeth face exchange rates and mandrills with higher conflict rates spent less time in non-aggressive proximity, there was not a direct relationship between silent bared-teeth face exchange rates and time spent in non-aggressive proximity. In addition, kin did not spend more time in non-aggressive proximity to one another, nor did they exchange the silent bared-teeth face at a lower rate, than did non-kin when all dyads in the group were considered. However, this pattern of results is in part due to the fact that the alpha male used the silent bared-teeth face for more than just a signal of his benign intentions. The alpha male also frequently used the silent bared-teeth face to

solicit copulation from the females in the group; he did not simply direct the silent bared-teeth face towards animals with which he had insecure relationships. It has been reported elsewhere that male mandrills use the silent bared-teeth face during sexual encounters (see Dixson, 1998). Since the silent bared-teeth face involves revealing one's large canines, it is possible that the signal and the large canines first evolved because they facilitated female mate assessment. Also consistent with the idea that the large canines of the adult male mandrills evolved via sexual selection is the fact that mandrills do not seem to use these canines for food-related purposes.

Furthermore, the alpha male performed more silent bared-teeth face displays than any other group member. When he directed the display towards other group members, its distribution did not vary with conflict rates or time in non-aggressive proximity. This is probably due to the fact that mandrills are despotic animals, and therefore all of the other group members are wary of the alpha male, who is far and away the largest and most powerful individual in the group. Since it is likely that all of the group members feared the alpha male, he probably directed the silent bared-teeth face to all of them in order to put them at ease. Thus, both the dual function of the silent bared-teeth face (courtship and peace signaling) as well as the more non-selective usage of the gesture from the alpha male make it more difficult to show a direct relationship between relationship security and the silent bared-teeth face exchange rate.

Moreover, the alpha male also spends most of his time in non-aggressive proximity with the adult females, neither of which were his kin. Consequently, the mean percentage of time spent in proximity with non-kin is inflated and misrepresents the behavior of the other

mandrills in the group, which is that kin typically spend more time in non-aggressive proximity than do non-kin.

Future research should examine whether it is possible to predict the distribution of peaceful post-conflict signals based on whether signals of benign intent or affiliative signals are exchanged after a conflict. For instance, mandrills exchange signals of benign intent and not affiliative signals after a conflict, and the mandrills that are more likely to reconcile are those that have insecure relationships. Mandrills that have insecure relationships are characterized by having higher rates of conflict and benign intent signal exchange during baseline, and they are also more likely to be unrelated. Similarly, hyenas are more likely to reconcile with non-kin than kin and are thought to have more valuable and secure relationships with kin than with non-kin. It is likely that the signals they use for reconciliation (greetings) are also signals of benign intent and not necessarily affiliative signals (but see East et al., 1993). Finally, baboons use signals of benign intent signals to reconcile, and it is plausible that they are more likely to direct these signals towards those with whom they have an insecure relationship. Thus, it is possible that animals who exchange signals of benign intent after a conflict will be more likely to reconcile with insecure relationship partners, and that animals who exchange friendly or affiliative signals after a conflict are more likely to reconcile with valuable relationship partners.

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Table 1: Typical Approaches to Analyzing Reconciliation Data, Operationalization of Conflicts and Operationalization of Affiliation

<b>Animal</b>	<b>Method</b>	<b>Conflict</b>	<b>Affiliation</b>	<b>Reconciled?</b>	<b>Author</b>
<i>Lemur catta</i>	PC-MC	staring, spat calls, lunge,	greeting, grooming, huddle-with	<i>L. catta</i> : No	Kappeler (1993)
<i>Eulemur fulvus rufus</i>	Time rule	chase, grab, bite		<i>E. fulvus</i> : PC-MC: No Time rule: Yes	
<i>Lemur catta</i>	PC-MC	staring, spat calls, lunge, chase, grab, bite	body-body and olfactory contact, grooming, greeting	Yes	Palagi et al. (2005)
<i>Macaca arctoides</i>	PC-MC	facial and vocal threats only accompanied by lunges or pursuits > 2m	non-agonistic body contact	Yes	de Waal & Ren (1988)
<i>Macaca fascicularis</i>	PC-MC Time rule	threats and submissive behavior	proximity (50 cm or less), body contact, exchange of affiliative signals	Yes	Cords (1993)
<i>Pan troglodytes</i>	PC-MC	3 or more non-contact agonistic events, agonistic contact	no definition provided	Yes	Fuentes et al. (2002)
<i>Pan troglodytes</i>	PC-MC	tug, brusque rush, trample, bite, grunt-bark, shrill-bark, flight, crouch, shrink/flinch, bared-teeth scream	kiss, embrace, grooming, gentle touch, finger-in-mouth, sexual behavior, social play, contact sitting	Yes	Preuschoft et al. (2002)
<i>Papio cynocephalus ursinus</i>	Rate	head bobs, eye threats, vocal threats, lunges, chases, bites, attacks	approach, grooming, groom present, touching, embracing, grunts	Yes	Silk et al. (1996)

Table 2: Demographics of Mandrills in Sample

Animal	Sex/ age class	Age	Relative	Relationship	Coefficient of relatedness
Nestor (N)	AM	16	Milo	Son	0.5
			Jasper	Son	0.5
			Moesha	Daughter	0.5
			Mukobi	Son	0.5
			Jerome	Son	0.5
			Jinx	Daughter	0.5
Miller (R)	AF	13	Milo	Son	0.5
			Moesha	Daughter	0.5
			Mukobi	Son	0.5
Milo (M)	AM	9	Moesha	Sister	~.5
			Mukobi	Brother	~.5
			Miller	Mother	.5
Moesha (O)	AdF	7	Milo	Brother	~.5
			Mukobi	Brother	~.5
			Miller	Mother	.5
Mukobi (P)	AdM	6	Milo	Brother	~.5
			Moesha	Sister	~.5
			Miller	Mother	.5
Jalisa (A)	AF	13	Jasper	Son	.5
			Jerome	Son	.5
			Jinx	Daughter	.5
Jasper (E)	AdM	8	Jinx	Sister	~.5
			Jalisa	Mother	.5
			Jerome	Brother	~.5
Jerome (J)	AdM	6	Jasper	Brother	~.5
			Jinx	Sister	~.5
			Jalisa	Mother	.5
Jinx (X)	AdF	3	Jasper	Brother	~.5
			Jerome	Brother	~.5
			Jalisa	Mother	.5

Table 3: Mandrill Ethogram (Based on Setchell, 1999)

**Affiliative/peaceful behaviors**

Silent bared-teeth face: mouth retracted horizontally and vertically at the corners so the canines are partly exposed. Mouth remains closed in the center and the incisors are covered by the lips and only partly visible, resulting in a figure-eight shape.

Lip-smacking: lips quickly opened and closed together audibly.

Head-shake: head is rotated from one side to the other, sometimes repeated back to original position. Typically accompanies Silent bared-teeth face .

Non-aggressive touching: making physical contact with another without any signs of threat or agitation (such as yawning, etc)

Playing: engaging in relaxed chasing, biting, wrestling that is almost always accompanied by a relaxed, open-mouthed play face (teeth are usually covered).

Allogrooming: picking through the fur of another individual with either hands or mouth

Peaceful proximity: individuals are within ~ two meters of one another without exchanging any agonistic signals. Further, both individuals must not perform any of the following anxiety indicating behaviors: yawn, scratch, body shake

**Submissive behaviors**

Scream: sharp, occasionally repeated vocalization with open-mouthed bared teeth expression.

Present: directing rear end towards another individual, usually while looking back at the animal

Crouch: making itself smaller and closer to the ground, usually in response to another's approach or threat

Look away: abruptly directing gaze away from another



Table 3: (Continued)

Avoid: leaving another when it approaches or moves out of proximity to another animal by walking at a normal pace

Flee: avoiding another by running away from it

**Level 1 aggression**

Head Jerk: staring at another and emphatically nodding the head down and forward with mouth closed

Threat Grunt: a short bark directed at another group member

Ground Slap: Striking one or both hands on the ground quickly and with force.

**Level 2 aggression**

Lunge: moving towards an animal rapidly for a distance of less than 2m in an aggressive context  
(e.g. not accompanied by a play face and usually preceded or followed by level 1 or level 3 aggression)

Chase: moving rapidly towards another animal for a distance of greater than 2m in an aggressive context

**Level 3 aggression**

Hit: striking another using its extremities

Grab: clasping or attempting to clasp another animal quickly in an aggressive context

Bite: placing its mouth on the body of another and clamping down in an aggressive context

Table 3: (Continued)

**Distance**

Proximity: within 2m of the focal individual. 0-1m = near, 1-2m = far

**Anxiety related behaviors**

Yawning : an animal opens its mouth and exposes all of its canines

Half yawn: a yawn where the teeth remain covered by the lips

Body shake: trembling in a vigorous shaking motion

Scratch: vigorous, repeated raking of the skin/hair with fingers

Auto-grooming: manual or oral manipulation of own fur

Table 4: Conflict information

Dyad	Date	Time	Aggression level	Aggressor	A, D, or N?
Jerome-Miller	1/24/06	2:46p	1 + 2	Miller	NEUTRAL
Jerome-Jasper	1/25/06	11:53a	1 + 2	Jerome	ATTRACTED
Nestor-Milo	2/6/06	4:56p	2	Nestor	NEUTRAL
Moesha-Jinx	2/7/06	4:50p	1 + 2	Moesha	ATTRACTED
Jinx-Moesha	2/8/06	1:55p	1 + 2	Moesha	NEUTRAL
Mukobi-Jasper	2/8/06	2:14p	2 + 3	Mukobi	ATTRACTED
Milo-Nestor	2/10/06	12:02p	2	Nestor	NEUTRAL
Nestor-Milo	2/10/06	1:57p	2	Nestor	NEUTRAL
Jinx-Moesha	2/10/06	2:16p	2	Moesha	ATTRACTED
Mukobi-Jasper	2/14/06	2:23p	2 + 3	Mukobi	NEUTRAL
Jalisa-Moesha	2/22/06	4:30p	2	Moesha	NEUTRAL
Jinx-Mukobi	2/22/06	4:41p	1 + 2	Mukobi	DISPERSED
Jasper-Mukobi	2/23/06	11:08a	3	Mukobi	ATTRACTED
Mukobi-Jasper	2/24/06	10:37a	2	Jasper	DISPERSED
Jasper-Mukobi	2/24/06	11:20a	3	Jasper	ATTRACTED
Jasper-Mukobi	2/24/06	11:15a	3	Jasper	ATTRACTED
Mukobi-Jasper	2/24/06	11:33a	3	Jasper	ATTRACTED
Jasper-Mukobi	2/24/06	10:29a	2 + 3	Jasper	DISPERSED
Jasper-Mukobi	2/27/06	12:48p	3	Mukobi	ATTRACTED
Miller-Jasper	2/27/06	4:02p	2 + 3	Miller	ATTRACTED
Milo-Jasper	3/6/06	2:12p	3	Milo	ATTRACTED
Jasper-Jerome	3/8/06	4:52p	3	Jasper	ATTRACTED
Mukobi-Jasper	3/10/06	4:30p	2 + 3	Jasper	ATTRACTED
Mukobi-Jasper	3/14/06	4:52p	2	Jasper	ATTRACTED
Jasper-Mukobi	3/14/06	3:58p	1 + 2	Jasper	DISPERSED
Moesha-Jalisa	3/21/06	2:00p	2 + 3	Moesha	ATTRACTED
Jasper-Nestor	3/27/06	3:37p	2	Nestor	ATTRACTED
Miller-Jerome	3/29/06	4:57p	1 + 2	Miller	NEUTRAL
Jerome-Milo	4/3/06	2:30p	2	Milo	ATTRACTED
Jasper-Miller	4/10/06	4:46p	2	Miller	ATTRACTED
Jasper-Miller	4/10/06	5:10p	1 + 2	Miller	ATTRACTED
Jerome-Jinx	4/21/06	11:25a	3	Jinx	ATTRACTED
Miller-Jasper	4/21/06	11:44a	1 + 2	Miller	DISPERSED
Jasper-Miller	5/1/06	4:10p	2	Miller	ATTRACTED
Jinx-Moesha	5/3/06	11:27a	1 + 2	Moesha	ATTRACTED
Jerome-Jasper	5/11/06	3:43p	1 + 3	Jerome	ATTRACTED
Jinx-Jasper	5/17/06	11:41a	2	Jasper	ATTRACTED
Jerome-Jalisa	5/19/06	3:00p	2	Jalisa	NEUTRAL
Moesha-Jalisa	5/21/06	4:39p	2	Moesha	ATTRACTED
Jinx-Jalisa	5/21/06	3:50p	3	Jalisa	DISPERSED
Jerome-Nestor	5/23/06	4:32p	2	Nestor	NEUTRAL
Nestor-Miller	5/23/06	2:54p	2	Nestor	NEUTRAL

Table 4: (Continued)

<b>Dyad</b>	<b>Date</b>	<b>Time</b>	<b>Aggression level</b>	<b>Aggressor</b>	<b>A, D, or N?</b>
Miller-Jerome	5/23/06	4:14p	2	Miller	ATTRACTED
Miller-Nestor	5/25/06	1:16p	2	Nestor	NEUTRAL
Nestor-Jasper	5/25/06	2:30p	1 + 2	Nestor	ATTRACTED
Jasper-Moesha	6/8/06	11:10a	1 + 2	Moesha	NEUTRAL
Jerome-Moesha	6/10/06	12:20p	1 + 2	Moesha	ATTRACTED
Moesha-Jalisa	6/16/06	11:08a	2	Moesha	NEUTRAL
Moesha-Jinx	6/24/06	11:22a	2	Moesha	ATTRACTED
Jerome-Jalisa	6/26/06	12:04p	2	Jalisa	NEUTRAL
Jerome-Moesha	6/26/06	12:04p	1 + 2	Moesha	NEUTRAL

Table 5: Baseline Silent Bared-Teeth Face Rate, CCT, and Number of Conflicts by Dyad

<b>Dyad</b>	<b>SBTF rate</b>	<b>CCT</b>	<b>Number of conflicts</b>
Jinx-Jasper	0	1	1
Jinx-Mukobi	0	-1	1
Jinx-Jalisa	0.013396	-1	1
Jerome-Jinx	0.025124	1	1
Jasper-Moesha	0.140008	0	1
Milo-Jasper	0.264601	1	1
Jerome-Nestor	0.362674	0	1
Jerome-Milo	0.363141	1	1
Jerome-Jalisa	0.027319	0	2
Jerome-Moesha	0.123854	0.5	2
Nestor-Jasper	0.770125	1	2
Nestor-Miller	0.306443	0	2
Miller-Jerome	0.393546	0.3	3
Jerome-Jasper	0.45076	1	3
Milo-Nestor	0.369165	0	3
Moesha-Jalisa	0.448638	0.5	4
Jinx-Moesha	0.608408	0.8	5
Jasper-Miller	0.613595	0.6	5
Mukobi-Jasper	2.904901	0.4	12

Table 6: CCTs as a Function of Baseline SBTF Rate with CCTs Calculated for Entire Groups

<b>(LOWER SBTF)</b>	<b>SBTF RATE</b>	<b>CCT</b>	<b>CONFLICTS</b>	<b>A</b>	<b>D</b>	<b>N</b>	<b>CCT</b>
Jinx-Jasper	0	1	1	1			
Jinx-Mukobi	0	-1	1		1		
Jinx-Jalisa	0.013396	-1	1		1		
Jerome-Jinx	0.025124	1	1	1			
Jerome-Jalisa	0.027319	0	2			2	
Jerome-Moesha	0.123854	0.5	2	1		1	
Jasper-Moesha	0.140008	0	1			1	
Milo-Jasper	0.264601	1	1	1			
Nestor-Miller	0.306443	0	2	0	0	2	
<b>TOTAL</b>				<b>4</b>	<b>2</b>	<b>6</b>	<b>0.167</b>
<b>(HIGHER SBTF)</b>	<b>SBTF RATE</b>	<b>CCT</b>	<b>CONFLICTS</b>	<b>A</b>	<b>D</b>	<b>N</b>	<b>CCT</b>
Jerome-Milo	0.363141	1	1	1			
Milo-Nestor	0.369165	0	3			3	
Miller-Jerome	0.393546	0.33	3	1		2	
Moesha-Jalisa	0.448638	0.5	4	2		2	
Jerome-Jasper	0.45076	1	3	3			
Jinx-Moesha	0.608408	0.8	5	4		1	
Jasper-Miller	0.613595	0.6	5	4	1		
Nestor-Jasper	0.770125	1	2	2			
Mukobi-Jasper	2.904901	0.416667	12	8	3	1	
<b>TOTAL</b>				<b>25</b>	<b>4</b>	<b>9</b>	<b>0.553</b>

Table 7: Rates of Displacement Behavior After Conflicts Followed by Peaceful Signals (a) and After Conflicts not Followed by Peaceful Signals (b) Between Former Opponents

<b>(a)</b>				<b>(b)</b>			
<b>Minute</b>	<b>PC</b>	<b>Baseline</b>	<b>Z</b>	<b>Minute</b>	<b>PC</b>	<b>Baseline</b>	<b>Z</b>
<b>1</b>	0.363636	0.557656	-1.969*	<b>1</b>	1.705882	0.628431	1.161
<b>2</b>	0.318182	0.557656	-2.559*	<b>2</b>	1.117647	0.628431	0.876
<b>3</b>	0.681818	0.557656	-.699	<b>3</b>	1.058824	0.628431	0.308
<b>4</b>	0.590909	0.557656	-.732	<b>4</b>	1.411765	0.628431	0.734
<b>5</b>	0.727273	0.557656	-.146	<b>5</b>	1.764706	0.628431	1.113
<b>6</b>	0.5	0.557656	-.765	<b>6</b>	1.764706	0.628431	0.592
<b>7</b>	0.954545	0.557656	-.601	<b>7</b>	1.117647	0.628431	1.492
<b>8</b>	0.5	0.557656	-1.024	<b>8</b>	0.647059	0.628431	0.45
<b>9</b>	0.363636	0.557656	-2.457*	<b>9</b>	0.647059	0.628431	1.018
<b>10</b>	0.545455	0.557656	-1.739	<b>10</b>	0.529412	0.628431	1.208

\* =  $p < .05$









