

POST-CONFLICT BEHAVIOR IN CAPTIVE WESTERN LOWLAND GORILLAS
(*GORILLA GORILLA GORILLA*)

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POST-CONFLICT BEHAVIOR IN CAPTIVE WESTERN LOWLAND GORILLAS
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SUMMARY

Post-conflict behaviors, including reconciliation, redirected aggression, and consolation, have been observed in several primate and non-primate species. These behaviors are thought to help re-establish rates of affiliation and tolerance to baseline levels, by terminating the victim's stress response, and reducing the social tension created by conflict. Post-conflict behavior was examined in two groups (N = 13) of captive western lowland gorillas, a species for which no previous conflict resolution data exist. The post-conflict/matched-control method was used to observe the groups at Zoo Atlanta. Analyses of 223 conflicts (using chi-square, Wilcoxon signed ranks, and Kolmogorov-Smirnov tests) showed significantly more affiliation between former opponents after a conflict when compared to control periods, indicating reconciliation. Results also showed significantly more affiliation between the victim and a third-party after a conflict, indicating consolation. Both solicited and unsolicited consolation were observed. Instances of redirected aggression were very few, and thus not included in the analyses. The majority of the affiliative interactions were social proximity, which suggests that unlike most nonhuman primates, proximity, rather than physical contact, may be the main mechanism for resolving conflicts in western lowland gorillas. Post-conflict behavior was not uniform throughout the groups, but rather varied according to dyad type (for instance, adult-adult, juvenile-juvenile, adult-juvenile, etc.). Effects of kinship and the intensity of aggression during a conflict on post-conflict behavioral patterns were analyzed.

CHAPTER 1

INTRODUCTION

Social relationships are very valuable to primates that exist in social groups. Group living is adaptive, and confers several advantages to an individual, including cooperation in locating the best resources, rearing offspring, detecting predators, and protection from predators. These benefits ultimately contribute to the species' reproductive survival. But living in a group has certain disadvantages, which can undermine the benefits of sociality. Group living entails the simultaneous exploitation of resources, which invariably leads to competition and conflicts of interest. In order to strike a stable balance between these costs and benefits, primates have evolved mechanisms for controlling aggression, regulating conflict, and restoring relationships. The mechanisms that function in re-establishing rates of affiliation and tolerance to baseline levels within a social group have been termed as post-conflict behaviors, and they include reconciliation, redirected aggression, and consolation.

Post-Conflict Behaviors—Terminology and Function

Reconciliation can be defined as friendly interactions between former opponents shortly after an aggressive conflict (Aureli & de Waal, 2000a). Redirection occurs when the target of aggression behaves in an agonistic manner towards a third-party shortly after a conflict (Kappeler & van Schaik, 1992). Consolation occurs when there is an increase

in friendly interactions between a third-party and the target of aggression a short time after the termination of a conflict (de Waal & van Roosmalen, 1979). If the interaction is initiated by the victim, it is called solicited consolation (Verbeek & de Waal, 1997). If the interaction is initiated by a third-party, it is referred to as unsolicited consolation.

Reconciliatory behaviors are thought to have a variety of functions. First, reconciliation has been hypothesized to repair, restore, and preserve social relationships that have been strained by conflict (de Waal, 1989). Second, it may help reassure former opponents of restored tolerance. This hypothesis was tested by Cords (1992) during a study of the reconciliatory function of affiliative post-conflict interactions in a group of long-tailed macaques (*Macaca fascicularis*). It was found that dyads that reconciled after a conflict were quicker to tolerate one another at a co-drinking site, as compared to dyads that were prevented from reconciling after conflict.

Reconciliation may also help terminate the victim's stress response, social tension, and anxiety, all of which may be indicated by increased autogrooming, body shaking, and scratching following an aggressive encounter (Aureli & van Schaik, 1991b; Aureli, van Schaik, & van Hooff, 1989). The occurrence of reconciliatory behaviors also seems to decrease the probability of a second attack by either the former opponent, or other group members (Aureli & van Schaik, 1991b). Finally, it has been hypothesized that reconciliatory behaviors provide a signal indicating the termination of conflict, so that normal relations and interactions can be resumed (Silk, 1997).

Redirected aggression may function to divert attention away from the victim and onto a third-party, thereby decreasing the risk of a second attack (Scucchi, Cordischi, Aureli, & Cozzolino, 1988). Consolation serves to calm the victim, reduce the tension created by

conflict, and assure the victim of a restored social situation (Cords, 1993; de Waal & van Roosmalen, 1979).

History of Post-Conflict Behavior Research

The phenomena of reconciliation and consolation in primates were first identified in a group of chimpanzees (*Pan troglodytes*) at the Arnhem Zoo, in the Netherlands (de Waal & van Roosmalen, 1979). It was found that soon after an aggressive encounter, participants in the conflict preferred making contact with each other (rather than with other group members), and during the contact, exhibited some specific patterns of behavior like “kiss,” “embrace,” “hold-out-hand,” “submissive vocalization,” and “touch.” These behaviors were classified as reconciliation. It was also observed that the victims of aggression often made contact with a third-party, exhibiting similar behavioral patterns; these interactions were classified as consolation.

Research on conflict regulation conducted in the last two decades, after these initial observations of post-conflict behaviors in chimpanzees, has found the occurrence of post-conflict behaviors to be a cross-species phenomenon. A thorough literature review reveals that conflict regulation mechanisms have evolved in almost all primate species studied to date (see list in Appendix A). In addition, researchers have found quantitative evidence for the existence of these mechanisms in non-primate species such as domestic goats (Schino, 1998), spotted hyenas (Hofer & East, 1998), feral sheep (Rowell & Rowell, 1993) and bottlenose dolphins (Samuels & Gifford, 1997). Apart from quantitative evidence, several anecdotal descriptions of reconciliatory behaviors exist

(mouflon: Pfeffer, 1967; spotted hyena: Kruuk, 1972; lion: Schaller, 1972; dwarf mongoose: Rasa, 1977).

One important finding in the history of post-conflict research has been that conflict regulation mechanisms vary across different species, different groups within a species, and between different dyads within a group. Some of the factors that have been hypothesized to be responsible for the variation in these mechanisms include the degree of social tolerance or despotism in a society (dominance style), relationship quality, kinship, age, intensity of aggression, sex, social structure, conciliatory tendencies, and predation pressure. A few studies that highlight the importance of some of these factors are discussed below.

Degree of Social Tolerance or Despotism

Species termed as socially despotic have been found to reconcile less than those described as tolerant. For example, in a comparative study of reconciliation in stumptail macaques (*Macaca arctoides*) and rhesus macaques (*Macaca mulatta*), de Waal and Ren (1988) found that stumptails exhibited a higher conciliatory tendency than rhesus monkeys, demonstrated a larger repertoire of reassurance behaviors, and showed reconciliation among all relationship classes and group members, as compared to rhesus monkeys. These differences were hypothesized to be because of the more relaxed dominance style and social tolerance in stumptails, which permitted greater flexibility in reconciliation patterns. Lower reconciliation rates in rhesus monkeys (a despotic species) were hypothesized to be because subordinates might fear approaching dominant animals.

Aureli, Das, and Veenema (1997) have found that the dominance style of a species affects the relationship between kinship and reconciliation frequency. For instance, *Macaca fascicularis* and *Macaca fuscata* (two despotic species) show a stronger kin bias in reconciliation frequency when compared to *Macaca arctoides* and *Macaca sylvanus* (socially tolerant species).

Kappeler (1993) found that redfronted lemurs (*Eulemur fulvus rufus*) exhibit reconciliatory behaviors, but ringtailed lemurs (*Lemur catta*) do not. Ringtailed lemurs have a pronounced dominance hierarchy, whereas redfronted lemurs lack formalized dominance hierarchies and are more socially tolerant. Reconciliatory behaviors have also been observed in patas monkeys (*Erythrocebus patas*), which have inconsistent dominance relationships and are more socially tolerant (York & Rowell, 1988).

Relationship Quality

Relationship quality has been found to be an important factor affecting conflict regulation mechanisms. Current hypotheses, relating to relationship quality, as to why variations in post-conflict behavioral patterns exist between dyads within a group include (Cords & Aureli, 1993):

- 1) The “valuable social partner” hypothesis, which states that there should be a higher rate of occurrence of reconciliatory behaviors between individuals who are valuable social or ecological partners.
- 2) The “compatibility of social partners” hypothesis, which implies that there should be a higher rate of occurrence of reconciliatory behaviors between individuals who frequently engage in affiliative interactions.

- 3) The “security of a relationship between social partners” hypothesis, which maintains that the variation in rates of reconciliation between two equally valuable partners depends on the security of the relationship between the participants in the conflict.

The “valuable social partner hypothesis” has been the only one that has been tested experimentally, and found to be valid (Cords & Thurnheer, 1993). This study examined reconciliation in long-tailed macaques (*Macaca fascicularis*), and the results indicated that there was a significant effect of a social partner’s value (as a social or ecological resource) on rates of reconciliation after a conflict. The value of a relationship was increased, by training each pair of macaques to perform a cooperative task in which each monkey gained access to food only if the other was feeding nearby at the same time. Rates of reconciliation after training were significantly higher than at baseline.

An observational study of the effect of relationship quality on conciliatory tendency and frequency of reconciliation was conducted by Castles, Aureli, and de Waal (1996). The study compared two groups of pigtail macaques (*Macaca nemestrina*); one was a newly established group, and the other was a well-established group with concentrated social networks. The results indicated that in both groups, there was a higher frequency of reconciliation between dyads with strong prior affiliative bonds. When comparing the two groups, it was found that there was a higher frequency of reconciliation after conflict in the well-established group. These results confirm that frequency of reconciliation after conflict is affected by relationship quality, both among dyads with a group, and among two groups of the same species.

De Waal and Yoshihara (1983) found that in rhesus monkeys (*Macaca mulatta*), conciliatory tendency increased with bond strength between individuals. Schino, Rosati, and Aureli (1998) examined intragroup variation in conciliatory tendencies in captive Japanese macaques (*Macaca fuscata*), and found a higher frequency of reconciliation among individuals with a good relationship (when compared to those with a poor relationship). Periera, Schill, and Charles (2000) found a similar pattern while studying post-conflict behavior in captive Guyanese squirrel monkeys (*Saimiri sciureus*). Female squirrel monkeys that had strong affiliative bonds to begin with, engaged in friendly interactions following more conflicts than did individuals with weak bonds.

Kinship

Several studies have found kin related effects on post-conflict behavior. York and Rowell (1988) examined reconciliation patterns in patas monkeys (*Erythrocebus patas*), and found a higher degree of reconciliation among maternally related individuals when compared to unrelated individuals. Additionally, individuals were selectively attracted to their opponent's matrilineal relatives, when compared to other unrelated animals. In a study of reconciliation in rhesus monkeys, de Waal and Yoshihara (1983) found a higher conciliatory tendency among kin than non-kin. Other studies that have found a higher frequency of reconciliation among kin than non-kin include Schino et al. (1998) in captive Japanese macaques (*Macaca fuscata*), Castles et al. (1996) in pigtail macaques (*Macaca nemestrina*), and Aureli et al. (1989) in long-tailed macaques (*Macaca fascicularis*).

Cheney and Seyfarth (1989) studied reconciliation and redirected aggression among vervet monkeys (*Cercopithecus aethiops*). They found that vervet monkeys showed a higher rate of reconciliation among non-kin, when compared to kin. They hypothesized that this pattern might be because of the unstable and less predictable relationships among unrelated individuals (post-conflict behaviors will thus help repair relationships), whereas similar reconciliation patterns might not be required for related individuals since they have higher rates of friendly interactions anyway.

Age

Reconciliation among juveniles has been observed in rhesus and long-tailed macaques (Cords & Aureli, 1993; de Waal, 1984). Studies of cercopithecine monkeys have shown that juveniles are often targets of aggression (Pereira, 1988; Silk, Samuels, & Rodman, 1981). Thus, Cords and Aureli (1993) argue that it would be in a juvenile's best interests to have mechanisms to achieve conflict resolution to counter the aggression received, encourage tolerance, lower individual tension levels, and receive agonistic support from peers. They found that juvenile long-tailed macaques (*Macaca fascicularis*) exhibited the same frequency and form of reconciliatory behaviors, as did the adults of the species.

Watts (1995a) found no evidence of reconciliatory behaviors between juvenile mountain gorillas (*Gorilla beringei beringei*). He hypothesized that the lack of reconciliation was because long-term alliances between juvenile gorillas may not be maintained, relationships between juveniles may be very resilient, and alliances between juveniles do not have much effect on foraging efficiency. However, it was found that

juveniles frequently sought and received consolation from their mothers, and juveniles frequently redirected aggression towards immature non-opponents (Watts, 1995b).

Other studies involving post-conflict behavior in juveniles include de Waal and Aureli (1997), who maintain that consolation may develop through mother-infant relationships. They found that consolation is present in juvenile rhesus macaques, but disappears with age. This finding is supported by the social constraints hypothesis, which states that third-parties will initiate affiliative interactions only when there is a very low risk of them becoming targets of aggression, or when potential gains are very high (de Waal & Aureli, 1996; Watts, Colmenares, & Arnold, 2000). Thus, adults in a group might exhibit lower levels of consolation amongst themselves, in order to lower the risk of becoming a target of aggression. Schino et al (1998) found that conflicts between immature Japanese macaques were more often reconciled than those between dyads of other age combinations, and immatures had a higher conciliatory tendency.

Intensity of Aggression

There are mixed results from studies looking at the effects of the intensity of aggression in a conflict on post-conflict behavior. Schino et al. (1998) found that the intensity of aggression (recording threat, chase, and physical assault, with a threat being the least intense) affected the likelihood of reconciliation in a captive group of Japanese macaques. Conciliatory tendency was found to be least after a chase, and highest after a physical assault. But, the difference in conciliatory tendencies was found to be significant only when comparing post-threat and post-chase situations.

Cords and Aureli (1993) found that the intensity of aggression was not closely related to the likelihood of reconciliation during a study of juvenile long-tailed macaques. They classified aggressive acts into contact (hits, bites, and holds) versus non-contact (threats and chases) aggression. They found that there was a greater frequency of reconciliatory behaviors following a conflict involving contact aggression, when compared to non-contact aggression, but this difference was not statistically significant.

In a study involving redfronted lemurs, Kappeler (1993) recorded the intensity of aggression on a scale of 1 to 5 (level 1: only aggressive or submissive signals were exchanged; level 2: conflict also involved aggressive acts that did not result in physical contact; level 3: aggressive acts resulting in physical contact; level 4: aggressive acts including chases completed within 10 minutes; level 5: aggressive acts including a chase exceeding 10 minutes). He found that the reconciliation rates after conflicts increased from level 1 to level 2, but decreased thereafter.

As is evident from the literature review, much of the research on post-conflict behavior in primates has been conducted on species in which either females or males reside permanently in natal groups, or there are clearly defined dominance hierarchies (Watts, 1995a). To gain a deeper insight into conflict resolution, research must be conducted on species with different social systems (Kappeler & van Schaik, 1992). Gorillas represent an excellent opportunity to conduct such studies, as both males and females disperse from natal groups, and studies of mountain gorillas suggest that there is no established dominance hierarchy among females (Harcourt, 1978; Stewart & Harcourt, 1987; Watts 1994). Since post-conflict behaviors are dependent on social dynamics, which in turn are affected by ecological variables like habitat, resource availability, diet,

and foraging strategies (Doran & McNeillage, 2001), I will now briefly describe mountain gorilla ecology and social structure, and discuss how this affects post-conflict behavior.

Mountain Gorillas: Ecology, Social Structure, and Post-Conflict Behavior

The habitat of the mountain gorilla (*Gorilla beringei beringei*) consists of high-altitude montane forests in the Albertine Rift of east/central Africa. Mountain gorillas feed mainly on terrestrial herbaceous vegetation-- leaves, shoots, and stems of terrestrial herbs. This is an abundant and widely distributed resource, and so there is very little within-group feeding competition (Fossey & Harcourt, 1977; Watts, 1996).

Mountain gorillas live in single or multi-male groups. Males and females generally transfer out of their natal groups once they reach sexual maturity to avoid inbreeding. Females transfer directly into another group, whereas males become solitary, or join all-male “bachelor” groups (Watts, 1996). Male-female relationships are thought to form the core of mountain gorilla sociality for a number of reasons (Watts, 1992, 1996):

1. Both sexes engage in natal transfer, resulting in adults that are generally unrelated and unfamiliar. This tends to discourage male-male and female-female affiliative bonds.
2. Males mediate in female-female conflicts, and provide protection against infanticide. Thus, males are valuable social partners for females.
3. Males compete for access to females and thus tend to coexist through tolerance or avoidance, rather than male-male affiliative bonds.
4. Abundant and non-monopolizable food resources produce few opportunities for contest competition between females. Thus, there is no selection for feeding

aggression (since this will not lead to greater resource acquisition), no alliance formation, and unclear female dominance hierarchies (Doran & McNeillage, 2001; Wrangham, 1980).

5. Most unrelated females do not groom each other, or help each other in conflict.

Therefore, a failure to reconcile after an agonistic interaction does not imply a loss of a “valuable” partner (Watts, 1995a, 1995b).

Given the mountain gorilla social structure, it is not at all surprising that Watts (1995a, 1995b) found evidence for post-conflict behaviors only between males and females, but not between same-sex dyads. Reconciliation was absent even in females who were maternally related, and females who had frequent affiliative interactions. It was also found that immatures (juveniles and 2- and 3-yr-old infants) did not reconcile with other immatures after a conflict. The lack of reconciliation between immatures was hypothesized to be because of the following reasons (Watts, 1995a): (1) As both males and females disperse from natal groups, long-term alliances may not be maintained. (2) Relationships between juveniles may be very resilient.

Watts (1995a) hypothesized that females frequently reconciled with males because of any one or more of the following reasons (these results support the valuable-relationships hypothesis):

1. In order to have continued social access, females may need to appease males. This reduces the chances of further aggression, and helps calm the females.
2. Females may need to show their allegiance to males through some form of reconciliation.

3. Males are mediators during conflicts between females. If a female exhibits affiliative behaviors towards a male after such interventions, it makes it more likely for the male to support that particular female during the next conflict.

Watts (1995b) found that female mountain gorillas exhibited lower levels of redirected aggression than immatures and subordinate males, females frequently sought and received consolation from adult males, and juveniles sought consolation from their mothers. The affiliative interactions exhibited by females towards males might be because females need males to protect them, and they need to show allegiance in order to maintain a good relationship. Males may be offering consolation as a mate-retention strategy, given that females can transfer out of the group. Usually, female dyads have inconsistent agonistic relationships (Watts, 1995a), and so females may exhibit low levels of redirection because targets can retaliate. Targets can also retaliate because gorilla matrilineal groups are small (because of female dispersal), and thus there is limited support from maternal relatives. Furthermore, females do not receive much support from unrelated females.

No such data on post-conflict behavior in western lowland gorillas exist. The present study will thus fill this gap in the literature by looking at a previously unstudied species. Furthermore, the focus of post-conflict research in the past has been on comparisons between different species, and hypothesizing about reasons for variations in post-conflict behavior between different groups of primates. Following the same tradition, previous data on post-conflict behavior and social structure in mountain gorillas were used to make and test predictions about the pattern of conflict resolution that may be seen in western lowland gorillas.

First, since western lowland gorillas live in social groups, and since most primates that live in social groups exhibit conflict regulation mechanisms, it was hypothesized that post-conflict behaviors will be exhibited by captive western lowland gorillas. Second, since there are differences in the social dynamics of western lowland and mountain gorilla groups, we expected to find different post-conflict behavioral patterns in these species. The differences in social organization, group composition, and behavior in the two species have been hypothesized to be a function of ecological variables like habitat, resource availability, diet, and foraging strategies (Doran & McNeilage, 2001; Parnell, 2002; Watts, 2003).

Western Lowland Gorillas: Ecology, Social Structure, and Predicted Post-Conflict Behavioral Patterns

Western lowland gorillas (*Gorilla gorilla gorilla*) live in lowland tropical (and sometimes swampy) forests. The abundance and distribution of food resources differ from that of mountain gorilla habitat. First, terrestrial herbaceous vegetation is less abundant and more sparsely distributed (Watts, 1984). Second, in some lowland habitats, abundant aquatic herbs or Marantaceae forests occur. Most importantly, fruit is abundant, and comprises a large portion of the diet of the western lowland gorilla (Tutin, 1996).

Based on these ecological variables, some inferences can be made about the reasons for the variation in social dynamics in the two species, although there is very limited data available on social structure in western lowland gorillas. Doran & McNeilage (2001) found that although the overall social structure and group size for western lowland gorillas did not differ from that of mountain gorillas, multi-male groups occur less often.

In addition, consumption of a patchy resource like fruit and the presence of swamps result in greater group spread during foraging, greater average day ranges and home range sizes, reduced group cohesion, and more frequent inter-group encounters in western lowland gorillas. Thus, it can be seen that western lowland gorillas have flexible grouping patterns in response to changing resource availability. Furthermore, it can be predicted that consumption of a patchy resource might lead to increased within-group competition, higher frequencies of feeding aggression, and thus, more differentiated female relationships in lowland gorillas.

Further evidence for the variation in social dynamics between the two species can be seen in captive studies of western lowland gorillas. As mentioned earlier, male-female bonds form the core of mountain gorilla society (Watts, 1995a). But, studies of captive western lowland gorillas show a different pattern, with females spending significantly more time with other females than with silverbacks (Stoinski, Hoff, & Maple, 2003). The results from this study showed juveniles and other females to be the primary social partners for a new mother. The authors suggest that these variations could be due to either one of the following reasons:

1. Differences in the captive environment, which lead to the absence of infanticide.

Thus, new mothers do not feel the need for proximity to and protection from the silverback. The captive environment also leads to decreased vegetation. This allows for the silverback to be more visible, thus reducing the female's need to maintain close proximity. Finally, the captive environment does not allow female mate choice, and this may decrease their preference for the silverback.

2. Genuine species differences between mountain gorillas and western lowland gorillas.

Another study by Stoinski, Allard, and Maple (2003) found that in an all-female captive western lowland gorilla group, proximity between females was greater, and contact aggression and affiliative behaviors were more frequent, as opposed to a heterosexual group. This implies that female-female relationships vary with group composition, and females form cohesive groups in the absence of a silverback.

Present Study

The present study examined post-conflict behaviors in two groups of captive western lowland gorillas (*Gorilla gorilla gorilla*) at Zoo Atlanta. More specifically, it examined whether western lowland gorillas exhibited post-conflict behaviors; what were the patterns and frequencies of reconciliation, redirected aggression, and consolation; and finally, how these patterns varied as a function of age, kinship, and the intensity of aggression (contact versus non-contact aggression).

Hypotheses for Present Study

Whether variation in social dynamics between captive western lowland and mountain gorillas actually reflects species differences or is an artifact of the captive environment remains to be determined. However, given that the variation exists, there is an opportunity to see if it results in differences in post-conflict behavior patterns. Thus, we expected to see differences in post-conflict behavioral patterns such as the occurrence of reconciliation between females, and higher levels of redirected aggression and

consolation between females, when compared to mountain gorilla females. Based on the literature review, I hypothesized the following:

1. Captive western lowland gorillas will exhibit post-conflict behaviors.
2. Females will exhibit significant levels of reconciliation, redirected aggression, and consolation.
3. Post-conflict behaviors will vary as a function of kinship, with a higher frequency of reconciliation and consolation after conflicts between kin, when compared to those between non-kin.
4. Post-conflict behaviors will vary as a function of intensity of aggression, with increased post-conflict behavior observed after contact aggression, when compared to non-contact aggression.
5. Post-conflict behaviors will vary as a function of age in the following manner:
 - a) No reconciliation will occur between juvenile-juvenile dyads.
 - b) Reconciliation will occur between juvenile-adult dyads.
 - c) Juveniles will seek and/or receive a higher frequency of consolation than adults.

Thus, the results of the present study are significant for two reasons. First, they are the first description of post-conflict behavior in western lowland gorillas, which will add to the field of primate behavior in general, and to the record of species-specific patterns of conflict regulation in particular. Second, the results of the present study may help further our understanding of the causes for variation in post-conflict behavior as a function of age, kinship, and intensity of aggression.

CHAPTER 2

METHODS

Study Group

The subjects were 13 gorillas ($N = 38$ dyads) living in two groups in outdoor exhibits at Zoo Atlanta. Information about the two study groups is provided in Table 1. There were 2 male-female dyads, 7 female-female dyads, 7 juvenile-juvenile dyads (age range of juveniles was 4 to 7 years), and 22 juvenile-adult dyads (all adults were over 8 years of age). Kinship was defined only in terms of direct mother-offspring and father-offspring relationships, leading to 10 kin dyads and 28 non-kin dyads in the study groups.

Study Site

At the time of the study, the gorillas at Zoo Atlanta were housed in naturalistic outdoor exhibits, separated by dry double moats. Each exhibit consisted of a grass substrate, rock outcroppings, shade trees, saplings, bushes, snags, and an artificial “tree,” which the gorillas had to manipulate for food items. The groups were housed in these outdoor enclosures from around 1000 to 1700 hours. For the rest of the day and night, the gorillas were moved into indoor holding areas (see Lukas, Hamor, Bloomsmith, Horton, & Maple, 1999 for a description of the husbandry routine; and Ogden, Finlay, & Maple, 1990 for a description of housing conditions).

Table 1. List of Subjects.

Name	Sex	Date of Birth	Parentage
Group 1			
Choomba (w)	Female	January 1963	--
Machi (c)	Female	March 1, 1976	Mother: Choomba
Kuchi (c)	Female	October 10, 1984	--
Mia (c)	Female	March 18, 1989	Mother: Machi
Olympia (c)	Female	June 22, 1996	Mother: Mia
Kidogo (c)	Male	April 8, 1998	Mother: Machi
Sukari (c)	Female	May 12, 1998	Mother: Choomba
Lulu (c)	Female	August 22, 1999	Mother: Kuchi
Group 2			
Ozzie (w)	Male	January, 1961	--
Paki (w)	Female	March, 1963	--
Katie (w)	Female	July, 1963	--
Banga (w)	Female	October, 1965	--
Charlie (c)	Male	June 7, 1996	Father: Ozzie Mother: Banga
Jasiri (c)	Male	June 22, 1998	Father: Ozzie Surrogate mother: Paki

Note. (w) denotes wild born individuals and (c) denotes captive born animals.

Sampling Methods

To answer the questions of interest in this study, post-conflict data were collected on 223 aggressive interactions in the 13 animals under study over a period of one year. Since post-conflict behaviors like reconciliation and consolation are hypothetical constructs, certain terms were operationally defined at the beginning of the study. “Conflicts” were defined as interactions in which an initiator behaved aggressively towards a target. The target could ignore the aggression, or could respond with submission, aggression towards the initiator, or redirection towards a third-party (Watts, 1995a). Aggressive acts included lunging, slapping, kicking, pushing, chest-beating, displacements, chases, and fights in which individuals grappled and tried to inflict wounds (Harcourt, 1979; Watts, 1995a, 1995b). Affiliative behaviors that occurred during reconciliation and consolation included grooming, playing, embracing, resting in contact (Watts, 1995a), and spatial proximity of less than 1 meter (Cords, 1993). The ethogram in Appendix B gives a more detailed description of all the aggressive and affiliative behaviors that were recorded.

Post-conflict data were collected using the PC-MC method (de Waal & Yoshihara, 1983), which is the established method used in conflict regulation studies. With this method, the group was observed *ad lib* till a conflict occurred. The identities of the initiator (aggressor in the conflict) and the recipient (victim in the aggressive encounter) were recorded. The level of aggression (contact or non-contact) was also recorded. Then post-conflict (PC) observations were made, which consisted of a focal sample (Altmann, 1974) of both the opponents starting immediately after the termination of the conflict (it should be noted that the term “focal sample” is not used here in the strict traditional sense

of following a single individual; instead a “focal dyad” was followed and all occurrences of certain behaviors were recorded). A focal period of 30 minutes was used, during which any of the behaviors from the ethogram were recorded. If the animals did not engage in any additional aggression, then the observation ended at 30 minutes after the termination of conflict. If the animals engaged in a second aggressive encounter before the 30-minute period elapses, then the individuals were observed for an additional 30 minutes.

On the next day (or at least, within three days), a matched control (MC) observation of the same individuals, at the same time as the corresponding PC (but in the absence of a conflict), was made. This served as a control. If an agonistic encounter (involving either one or both of the individuals under study) occurred within 30 minutes of the start of the MC, MC observations were postponed by 30 minutes.

Data Analyses

The timing of the first friendly interaction between former opponents during one PC and the corresponding MC were compared. If the first affiliative interaction occurred only in the PC, or earlier in the PC than in the MC, the dyadic pair was noted to be “attracted.” If the interaction occurred only in the MC, or earlier in the MC than in the PC, the pair was classified as “dispersed.” Finally, if the interaction occurred at the same time in both the PC and the MC, or there was no interaction in either, the pair was considered to be “neutral.”

Similar observations were made for the victims of the conflict and non-opponents for analyses of consolation and redirected aggression. If the first aggressive behavior was directed by the victim of a conflict towards a third animal only in the PC, or earlier in the

PC than in the MC, the pair was scored as “redirected.” If the aggression occurred only in the MC, or earlier in the MC than in the PC, the pair was classified as “non-redirected.” Similarly, if an affiliative behavior occurred between the victim of a conflict and a third animal only in the PC, or earlier in the PC than in the MC, the pair was scored as “consoled.” If the affiliative behavior occurred only in the MC, or earlier in the MC than in the PC, the pair was classified as “non-consoled.”

To analyze reconciliation, the numbers of attracted and dispersed pairs, obtained by the PC-MC method, were compared using a chi-square test, tested against 1:1 expectation (Aureli et al., 1989). To analyze redirected aggression, a chi-square test was used to compare the number of redirected and non-redirected pairs. Similarly, to analyze consolation, a chi-square test was used to compare the number of consoled and non-consoled pairs. The chi-square test was used for overall analyses, as well as for sub-analyses of the different dyads involved in conflicts (for instance, adult-adult dyads, juvenile-juvenile dyads, etc).

The reconciliation data collected were also analyzed by quantifying the conciliatory tendency (CT), to indicate the “strength of a reconciliation” (deWaal & Yoshihara, 1983). A greater frequency of reconciliatory behaviors has been observed in species with higher conciliatory tendencies; the higher the conciliatory tendency, the stronger is the tendency to reconcile. A corrected conciliatory tendency (CCT) measure described by Veenema, Das, and Aureli (1994) was used, which is defined as follows:

$$CCT = (\text{number of attracted pairs} - \text{number of dispersed pairs}) / \text{total number of pairs}.$$

The CCT is independent of the duration of observation and the baseline level of affiliation. Therefore, it can be used to compare the conciliatory tendency of different

types of dyads. The consolation data were analyzed in a similar manner by quantifying a triadic conciliatory tendency—TCT (Call, Aureli, & de Waal, 2002).

Apart from analyzing the data with chi-square tests, the “time rule” method (Aureli et al., 1989) was also used. The time rule is better for studying functional aspects of post-conflict behaviors (Aureli & van Schaik, 1991a; Veenema et al., 1994). The frequencies of the first post-conflict friendly interaction between former opponents as a function of time were plotted for the PCs and the MCs, and then compared. If the PC frequencies are higher, then this suggests that reconciliation exists. To determine if redirected aggression exists, the PC and the MC frequencies of the first post-conflict agonistic interaction initiated by one of the opponents towards a third-party were compared. To determine if consolation occurs, the PC and MC frequencies of the first post-conflict affiliative encounter between the victim and a third-party were compared. Distributions of the PC and MC affiliative interactions, obtained by the time-rule method, were compared using Kolmogorov-Smirnov two-sample test (Veenema, 2000).

The time-rule method also allows for determining a time frame after a conflict, in which affiliative and/or agonistic interactions can be defined operationally as post-conflict behaviors. For instance, if reconciliation exists, the time at which the PC and MC graphs merge is a suitable time-window to operationally define reconciliation. Only if a post-conflict affiliative interaction occurs within this time frame, can it be considered as reconciliation. The same concept applies to redirected aggression and consolation.

Finally, the Wilcoxon Signed Ranks test was used to look for evidence of post-conflict behaviors at the individual level to avoid results being confounded by the possibility of a few individuals contributing excessively to the data set (Call et al., 2002). The chi-square

test does not take care of this bias. However, the Wilcoxon Signed Ranks test could not be used during the sub-analyses of some of the dyad types because the sample size was too low for the analysis to be of any significance.

CHAPTER 3

RESULTS

Redirected Aggression

The instances of redirected aggression were too few to be analyzed.

Reconciliation

Overall

Out of the 223 conflicts recorded, 127 PC-MC pairs were analyzed; the remaining 96 were considered neutral and not included in the analyses. There were 96 attracted opponent pairs and 31 dispersed pairs, and these differed significantly from expectation (Chi-square test: $\chi^2 = 33.268$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total N = 13; ties = 2; $z = -2.943$; $p = 0.003$). The overall distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.326$; $p < 0.001$), and the greatest difference in the cumulative observations occurred within $t = 2$ minutes; see figure 1 ($z = 1.400$, $p = 0.04$). Reconciliation was observed after 43% of the conflicts. The overall conciliatory tendency (CCT) was 29%. The percentage of conflicts that were reconciled by the former opponents coming into proximity was 76% (mere proximity: 71%; social examine: 5%). The percentage of conflicts that were reconciled by the former opponents coming into physical contact was 24% (contact: 10%; brief contact: 12%; social play with contact: 2%). Overall, the percentage of

reconciliations initiated by the aggressor was 65% and the percentage initiated by the victim was 35%. The conflicts were analyzed according to dyad type (adult-adult, juvenile-juvenile, adult-juvenile, kin-kin, nonkin-nonkin conflicts), and according to conflicts involving contact and non-contact aggression conflicts.

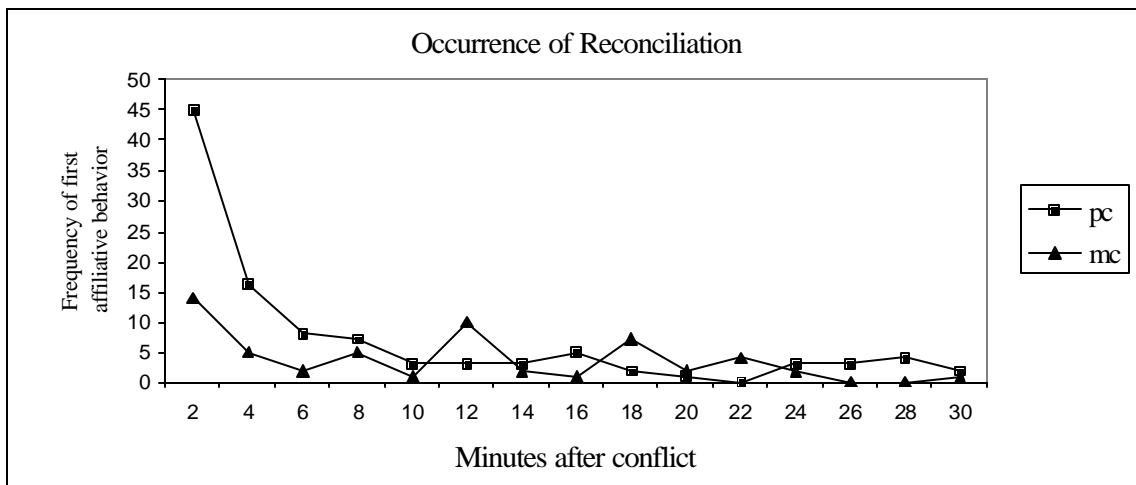


Figure 1. The frequency of the first affiliative interaction between the former opponents in the 30-minute period following a conflict, and the control period.

Adult-Adult Conflicts

Of the 72 adult-adult conflicts, 26 PC-MC pairs were analyzed; the remaining 46 were considered neutral and not included in the analyses. There were 18 attracted opponent pairs and 8 dispersed pairs, and these differed significantly from expectation; 25% of the conflicts between adults were reconciled (Chi-square test: $\chi^2 = 3.846$; $df = 1$; $p = 0.05$; Wilcoxon signed ranks test: Total $N = 7$; ties = 4, and this was too low for the analysis to reach significance). The distribution of first friendly interactions in the PC and MC

sessions differed significantly (Kolmogorov-Smirnov test: $z = 1.664$; $p = 0.008$). The time within which the greatest difference in the cumulative observations occurred could not be determined because there was never a time period within which there was a significant difference in the cumulative observations due to a small sample size within each time period. But the overall distribution differed significantly because the KS test is cumulative over all the time periods. The percentage of reconciliations initiated by the aggressor was around 56% and the percentage initiated by the victim was around 44%. The CCT for adult-adult conflicts was 14%.

Female-Female Conflicts

Since the majority of the adult-adult conflicts were between the adult females, analyses were run without the data from the adult male. This gave us 68 female-female conflicts, out of which 25 PC-MC pairs were analyzed; the remaining 43 were considered neutral and not included in the analyses. There were 17 attracted opponent pairs and 8 dispersed pairs, and these did not differ significantly from expectation; 25% of the conflicts between adult females were reconciled (Chi-square test: $\chi^2 = 3.240$; $df = 1$; ns; Wilcoxon signed ranks test: Total $N = 7$; ties = 4, and this was too low for the analysis to reach significance). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 1.556$; $p = 0.016$). The time within which the greatest difference in the cumulative observations occurred could not be determined. The percentage of reconciliations initiated by the aggressor was around 59% and the percentage initiated by the victim was around 41%. The CCT for female-female conflicts was 13%.

Juvenile-Juvenile Conflicts

Of the 32 juvenile-juvenile conflicts, 23 PC-MC pairs were analyzed; the remaining 9 were considered neutral and not included in the analyses. There were 16 attracted opponent pairs and 7 dispersed pairs, and these did not differ significantly from expectation; 50% of the conflicts between juveniles were reconciled (Chi-square test: $\chi^2 = 3.522$; $df = 1$; ns; Wilcoxon signed ranks test: Total $N = 6$; ties = 1, and this was too low for the analysis to reach significance). The distribution of first friendly interactions in the PC and MC sessions did not differ significantly (Kolmogorov-Smirnov test: $z = 1.327$; ns). The percentage of reconciliations initiated by the aggressor was around 63% and the percentage initiated by the victim was around 37%. The CCT for juvenile-juvenile conflicts was 28%.

Adult-Juvenile Conflicts

Out of the 119 adult-juvenile conflicts, 78 PC-MC pairs were analyzed; the remaining 41 were considered neutral and not included in the analyses. There were 62 attracted opponent pairs and 16 dispersed pairs, and these differed significantly from expectation; around 52% of the conflicts between adults and juveniles were reconciled (Chi-square test: $\chi^2 = 27.128$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 1; $z = -3.084$; $p = 0.002$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 2.962$; $p < 0.001$), and the greatest difference in the cumulative observations occurred within $t = 30$ seconds; see figure 2 ($z = 1.483$, $p = 0.025$). The percentage of reconciliations initiated by the

aggressor was around 68% and the percentage initiated by the victim was around 32%.

The CCT for adult-juvenile conflicts was 39%.

Out of 119 adult-juvenile conflicts, 50 were initiated by an adult, and 69 by a juvenile.

The percentage of reconciliations initiated by juveniles was around 85% and the percentage initiated by adults was around 15%.

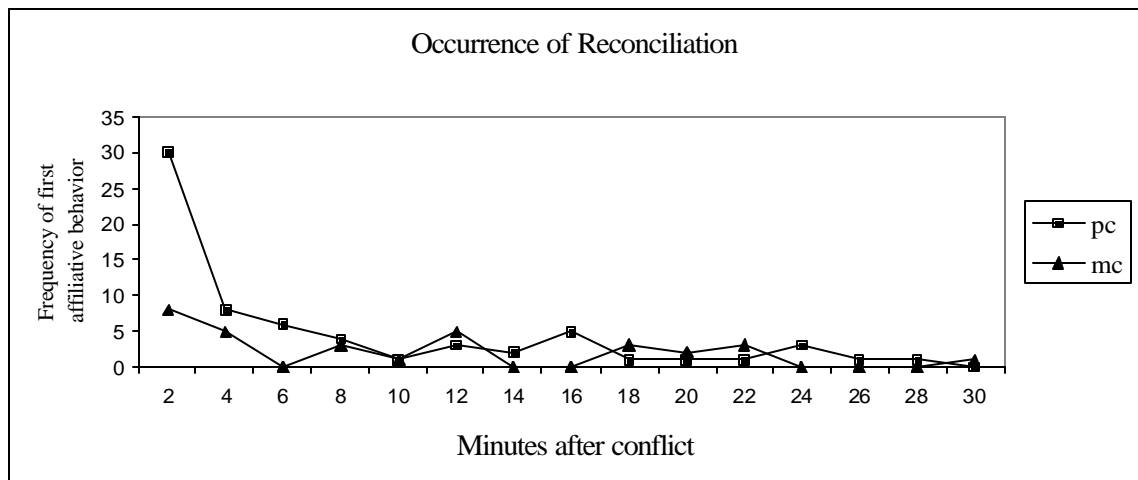


Figure 2. The frequency of the first affiliative interaction between the former opponents in the 30-minute period following an adult-juvenile conflict, and the control period.

Mother-Offspring Conflicts

Adult-juvenile conflicts were divided into mother-offspring and female-unrelated juvenile conflicts. Of the 24 mother-offspring conflicts, 18 PC-MC pairs were analyzed; the remaining 6 were considered neutral and not included in the analyses. There were 13 attracted opponent pairs and 5 dispersed pairs, and reconciliation in this dyad approached significance; around 54% of the conflicts between mothers and their juvenile offspring

were reconciled (Chi-square test: $\chi^2 = 3.556$; $df = 1$; $p = 0.059$; Wilcoxon signed ranks test: Total $N = 12$; ties = 7, and this was too low for the analysis to reach significance). The distribution of first friendly interactions in the PC and MC sessions did not differ significantly (Kolmogorov-Smirnov test: $z = 1.167$; ns). The percentage of reconciliations initiated by the aggressor was around 77% and the percentage initiated by the victim was around 23%. The CCT for mother-offspring conflicts was 33%.

Adult Female-Unrelated Juvenile Conflicts

Of the 87 female-unrelated juvenile conflicts, 52 PC-MC pairs were analyzed; the remaining 35 were considered neutral and not included in the analyses. There were 43 attracted opponent pairs and 9 dispersed pairs and these differed significantly from expectation; around 49% of the conflicts between adult females and unrelated juveniles were reconciled (Chi-square test: $\chi^2 = 22.231$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 12$; ties = 2; $z = -2.820$; $p = 0.005$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 2.55$; $p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined. The percentage of reconciliations initiated by the aggressor was around 72% and the percentage initiated by the victim was around 28%. The CCT for adult female-unrelated juvenile conflicts was 39%.

Kin versus Non-Kin

Conflicts between Kin

Kinship was defined only in terms of direct mother-offspring and father-offspring relationships, leading to 10 kin dyads and 28 non-kin dyads in the study groups. Of the 45 conflicts between kin, 30 PC-MC pairs were analyzed; the remaining 15 were considered neutral and not included in the analyses. There were 22 attracted opponent pairs and 8 dispersed pairs and these differed significantly from expectation; around 49% of the conflicts between related individuals were reconciled (Chi-square test: $\chi^2 = 6.533$; $df = 1$; $p = 0.011$; Wilcoxon signed ranks test: Total $N = 13$; ties = 6; $z = -1.403$; ns). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 1.678$; $p = 0.007$). The time within which the greatest difference in the cumulative observations occurred could not be determined. The CCT for conflicts between kin was 31%.

Conflicts between Non-Kin

Of the 178 conflicts between non-kin, 97 PC-MC pairs were analyzed; the remaining 81 were considered neutral and not included in the analyses. There were 74 attracted opponent pairs and 23 dispersed pairs and these differed significantly from expectation; around 42% of the conflicts between unrelated individuals were reconciled (Chi-square test: $\chi^2 = 26.814$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 2; $z = -2.949$; $p = 0.003$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.087$; $p < 0.001$). The

time within which the greatest difference in the cumulative observations occurred could not be determined. The CCT for conflicts between non-kin was 29%.

Kin did not reconcile conflicts significantly more than non-kin did (Chi-square test: $\chi^2 = 0.463$; $df = 1$; ns; Wilcoxon signed ranks test: Total N = 13; ties = 1; $z = -1.926$; ns).

Contact versus Non-Contact Aggression

Contact Aggression

Of the 127 conflicts involving contact aggression, 81 PC-MC pairs were analyzed; the remaining 46 were considered neutral and not included in the analyses. There were 57 attracted opponent pairs and 24 dispersed pairs and these differed significantly from expectation; around 45% of the conflicts involving contact aggression were reconciled (Chi-square test: $\chi^2 = 13.444$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total N = 13; ties = 3; $z = -2.669$; $p = 0.008$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 2.357$; $p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined. The CCT for conflicts involving contact aggression was 26%.

Non-Contact Aggression

Of the 96 conflicts involving non-contact aggression, 46 PC-MC pairs were analyzed; the remaining 50 were considered neutral and not included in the analyses. There were 39 attracted opponent pairs and 7 dispersed pairs and these differed significantly from expectation; around 41% of the conflicts involving non-contact aggression were

reconciled (Chi-square test: $\chi^2 = 22.261$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 2; $z = -2.956$; $p = 0.003$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 2.711$; $p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined. The CCT for conflicts involving non-contact aggression was 33%.

Reconciliation after contact aggression was not significantly higher than after non-contact aggression (Chi-square test: $\chi^2 = 0.186$; $df = 1$; ns; Wilcoxon signed ranks test: Total $N = 13$; ties = 4; $z = -1.664$; ns).

Initiation of Reconciliation

Overall, the percentage of reconciliations initiated by the aggressor was around 65% and the percentage initiated by the victim was around 35%. The difference between the number of reconciliations initiated by aggressors and victims was statistically significant (Chi-square test: $\chi^2 = 8.167$; $df = 1$; $p = 0.004$). This pattern of the aggressor initiating most of the reconciliation was seen even when conflicts were analyzed according to dyad type. To eliminate any bias resulting from an outlier individual, a Wilcoxon signed ranks test was conducted, which showed that the difference between the number of reconciliations initiated by aggressors and victims was not significant (Total $N = 13$; ties = 2; $z = -0.990$; ns). After the outlier individual was identified and removed, the percentage of reconciliations initiated by the aggressor was around 57% and the percentage initiated by the victim was around 43%. Another chi-square analysis was

conducted, which showed that the difference between the number of reconciliations initiated by aggressors and victims was now insignificant ($\chi^2 = 1.246$; $df = 1$; ns).

Table 2. Summary of Reconciliation Statistics.

Dyad Type	Chi-Square			Wilcoxon	Time-Rule
	Sig.	% reconciled conflicts	CCT	Sig.	Sig.
Overall Reconciliation	$p < 0.001$	43%	29%	$p = 0.003$	$p < 0.001$
Adult-Adult	$p = 0.05$	25%	14%	Low sample size	$p = 0.008$
Female-Female	ns	25%	13%	Low sample size	$p = 0.016$
Juvenile-Juvenile	ns	50%	28%	Low sample size	ns
Adult-Juvenile	$p < 0.001$	52%	39%	$p = 0.002$	$p < 0.001$
Mother-Offspring	$p = 0.059$	54%	33%	Low sample size	ns
Adult Female-Unrelated Juvenile	$p < 0.001$	49%	39%	$p = 0.005$	$p < 0.001$
Kin-Kin	$p = 0.011$	49%	31%	ns	$p = 0.007$
Non Kin-Non Kin	$p < 0.001$	42%	29%	$p = 0.003$	$p < 0.001$
Contact Aggression	$p < 0.001$	45%	26%	$p = 0.008$	$p < 0.001$
Non-Contact Aggression	$p < 0.001$	41%	33%	$p = 0.003$	$p < 0.001$

Consolation

Overall

Of the 223 conflicts recorded, 161 PC-MC pairs were analyzed; the remaining 62 were considered neutral and not included in the analyses. There were 132 attracted opponent pairs and 29 dispersed pairs, and these differed significantly from expectation (Chi-square test: $\chi^2 = 65.894$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 1; $z = -3.063$; $p = 0.002$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 5.003$; $p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined because there was never a time when the difference between PC and MC observations was not significant. But figure 3 clearly indicates that the PC and MC distributions merge at the 5th minute. So the reason why the difference was always significant was because the majority of the data points fell within the 2-minute time-frame, and since the KS test is cumulative, the effect was large enough to be carried over to every other minute. Consolation was observed after 59% of the conflicts. The overall triadic conciliatory tendency (TCT) was 46%. The percentage of conflicts that were followed by the victim coming into proximity with a third-party (or vice versa) was 74% (mere proximity: 65%; social play without contact: 5%; social examine: 4%). The percentage of conflicts that were followed by the victim coming into physical contact with a third-party (or vice versa) was 26% (contact: 18%; brief contact: 8%). We analyzed conflicts according to dyad type (adult-adult, juvenile-juvenile, adult-juvenile, kin-kin, nonkin-nonkin conflicts), and according to conflicts involving contact and non-contact aggression.

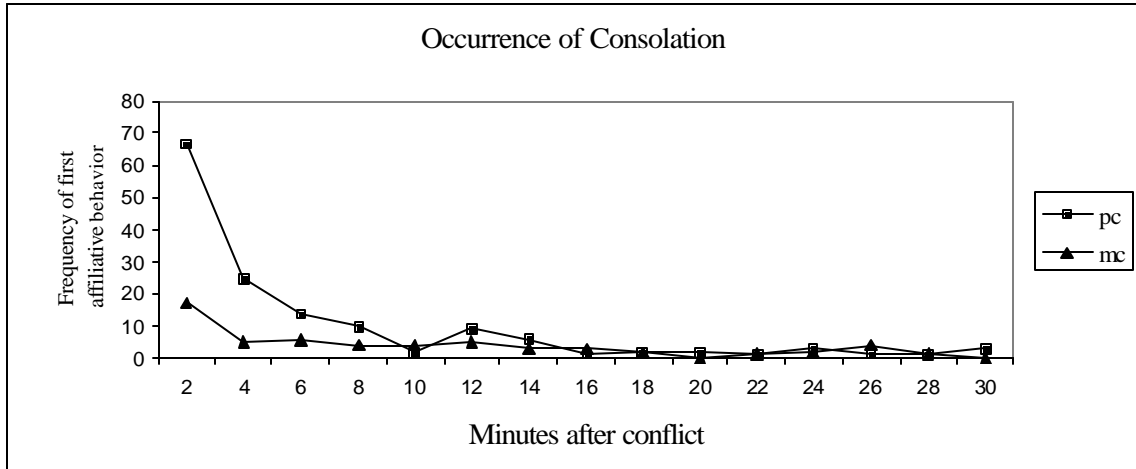


Figure 3. The frequency of the first affiliative interaction between the victim and a third party in the 30-minute period following a conflict, and the control period.

Adult-Adult Conflicts

Of the 72 adult-adult conflicts, 55 PC-MC pairs were analyzed; the remaining 17 were considered neutral and not included in the analyses. There were 44 attracted opponent pairs and 11 dispersed pairs, and these differed significantly from expectation; around 61% of the conflicts between adults were followed by consolation of the victim (Chi-square test: $\chi^2 = 3.846$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 7$; ties = 1; $z = -2.207$; $p = 0.027$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.146$; $p < 0.001$) and the greatest difference in the cumulative observations occurred within $t = 3$ minutes ($z = 1.424$; $p = 0.035$). The TCT for adult-adult conflicts was 49%.

Female-Female Conflicts

Since the majority of the adult-adult conflicts were between the adult females, we ran analyses without the data from the adult male. This gave us 68 female-female conflicts, out of which 51 PC-MC pairs were analyzed; the remaining 17 were considered neutral and not included in the analyses. There were 40 attracted opponent pairs and 11 dispersed pairs, and these differed significantly from expectation; around 59% of the conflicts between adult females were followed by consolation to the victim (Chi-square test: $\chi^2 = 16.490$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; and this was too low for the analysis to reach significance). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 2.970$; $p < 0.001$) and the greatest difference in the cumulative observations occurred within $t = 3$ minutes; see figure 4 ($z = 1.414$, $p = 0.037$). The TCT for female-female conflicts was 43%.

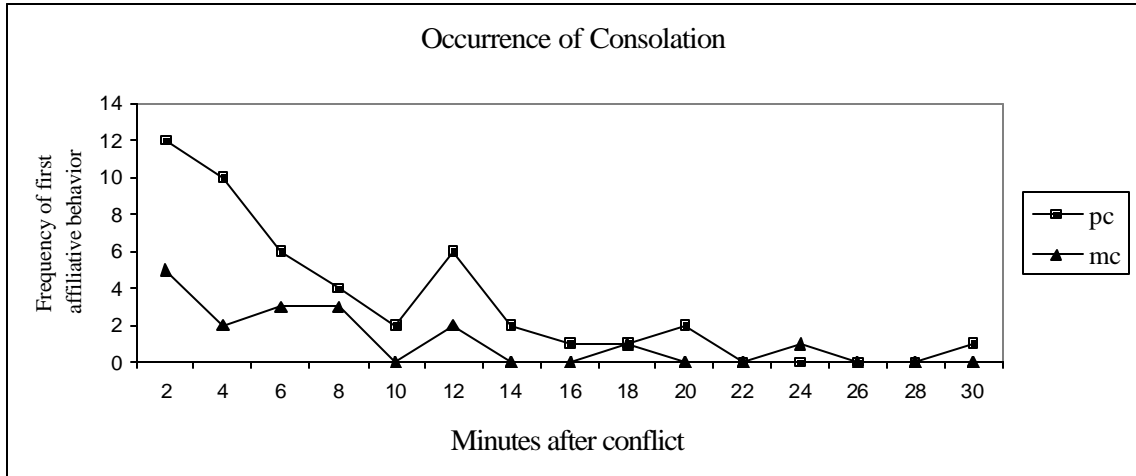


Figure 4. The frequency of the first affiliative interaction between the victim and a third-party in the 30-minute period following a female-female conflict, and the control period.

Juvenile-Juvenile Conflicts

Out of the 32 juvenile-juvenile conflicts, 24 PC-MC pairs were analyzed; the remaining 8 were considered neutral and not included in the analyses. There were 21 attracted opponent pairs and 3 dispersed pairs, and these differed significantly from expectation; around 66% of the conflicts between juveniles were followed by the victim being consoled (Chi-square test: $\chi^2 = 13.5$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; and this was too low for the analysis to reach significance). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 2.309$; $p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined. The TCT for juvenile-juvenile conflicts was 56%.

Adult-Juvenile Conflicts

Of the 119 adult-juvenile conflicts, 82 PC-MC pairs were analyzed; the remaining 37 were considered neutral and not included in the analyses. There were 67 attracted opponent pairs and 15 dispersed pairs, and these differed significantly from expectation; around 56% of the conflicts between adults and juveniles were followed by consolation of the victim (Chi-square test: $\chi^2 = 32.976$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 1; $z = -2.916$; $p = 0.004$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.748$; $p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined because there was never a time when the difference between PC and MC observations was not significant. But figure 5 clearly indicates that the PC and MC distributions merge around the 6th minute. The TCT for adult-juvenile conflicts was 44%.

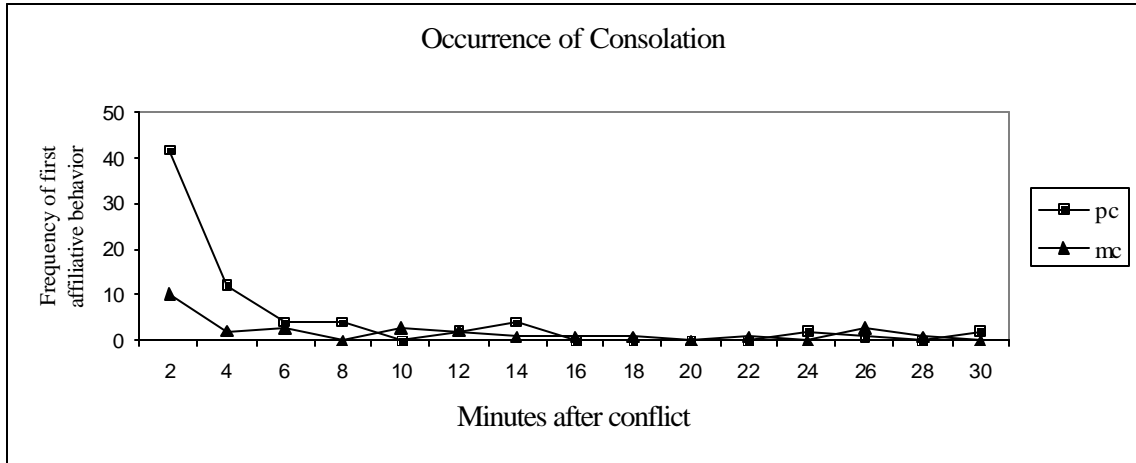


Figure 5. The frequency of the first affiliative interaction between the victim and a third-party in the 30-minute period following an adult-juvenile conflict, and the control period.

Mother-Offspring Conflicts

Adult-juvenile conflicts were divided into mother-offspring and female-unrelated juvenile conflicts. Of the 24 mother-offspring conflicts, there were 6 analyzable PC-MC; the remaining 18 were considered neutral. There were 4 attracted opponent pairs and 2 dispersed pairs. Since the sample size was so low, no statistical analyses were conducted. The large proportion of neutral pairs indicates a lack of consolation.

Adult Female-Unrelated Juvenile Conflicts

Of the 87 female-unrelated juvenile conflicts, 71 PC-MC pairs were analyzed; the remaining 16 were considered neutral and not included in the analyses. There were 59 attracted opponent pairs and 12 dispersed pairs and these differed significantly from

expectation; around 68% of the conflicts between adult females and unrelated juveniles were followed by the victim being consoled (Chi-square test: $\chi^2 = 31.113$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 12$; ties = 2; $z = -2.809$; $p = 0.005$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.525$; $p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined because there was never a time when the difference between PC and MC observations was not significant. But figure 6 clearly indicates that the PC and MC distributions merge at the 6th minute. The TCT for adult female-unrelated juvenile conflicts was 54%.

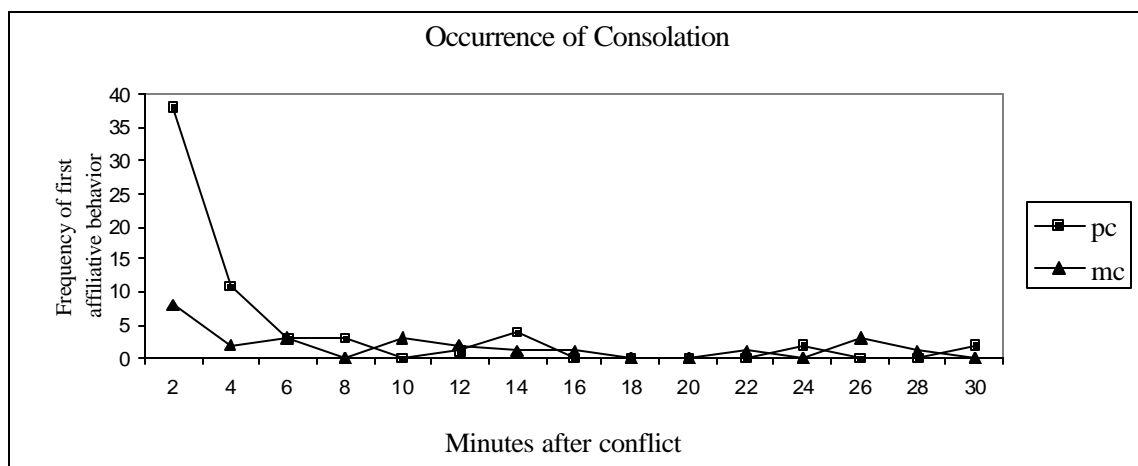


Figure 6. The frequency of the first affiliative interaction between the victim and a third-party in the 30-minute period following an adult female-unrelated juvenile conflict, and the control period.

Kin versus Non-Kin

Conflicts between Kin

Kinship was defined only in terms of direct mother-offspring and father-offspring relationships, leading to 10 kin dyads and 28 non-kin dyads in the study groups. Of the 45 conflicts between kin, 23 PC-MC pairs were analyzed; the remaining 22 were considered neutral and not included in the analyses. There were 17 attracted opponent pairs and 6 dispersed pairs and these differed significantly from expectation; around 38% of the conflicts between kin were followed by consolation of the victim (Chi-square test: $\chi^2 = 5.261$; $df = 1$; $p = 0.022$; Wilcoxon signed ranks test: Total $N = 13$; ties = 6; $z = -2.414$; $p = 0.016$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 1.769$; $p = 0.004$). The time within which the greatest difference in the cumulative observations occurred could not be determined. The TCT for conflicts between kin was 24%.

Conflicts between Non-Kin

Of the 178 conflicts between non-kin, 138 PC-MC pairs were analyzed; the remaining 40 were considered neutral and not included in the analyses. There were 115 attracted opponent pairs and 23 dispersed pairs and these differed significantly from expectation; around 65% of the conflicts between non-kin were followed by the victim being consoled (Chi-square test: $\chi^2 = 61.333$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 1; $z = -3.072$; $p = 0.002$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 4.755$;

$p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined because there was never a time when the difference between PC and MC observations was not significant. But figure 7 clearly indicates that the PC and MC distributions merge at the 10th minute. The TCT for conflicts between non-kin was 52%.

A significantly higher amount of consolation occurred after conflicts between non-kin when compared to conflicts between kin (Chi square test: $\chi^2 = 7.078$; $df = 1$; $p = 0.008$; Wilcoxon signed ranks test: Total $N = 13$; ties = 2; $z = -2.848$; $p = 0.004$).

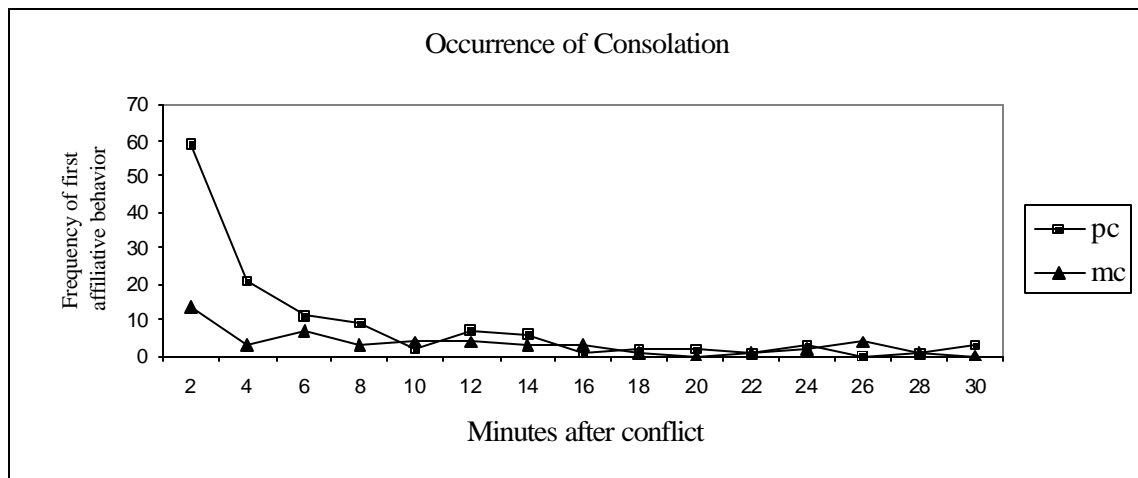


Figure 7. The frequency of the first affiliative interaction between the victim and a third-party in the 30-minute period following a conflict (between non-kin), and the control period.

Contact versus Non-Contact Aggression

Contact Aggression

Of the 127 conflicts involving contact aggression, 96 PC-MC pairs were analyzed; the remaining 31 were considered neutral and not included in the analyses. There were 79 attracted opponent pairs and 17 dispersed pairs and these differed significantly from expectation; around 62% of the conflicts involving contact aggression were followed by consolation of the victim (Chi-square test: $\chi^2 = 40.042$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 1; $z = -3.077$; $p = 0.002$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.681$; $p < 0.001$). The time within which the greatest difference in the cumulative observations occurred could not be determined because there was never a time when the difference between PC and MC observations was not significant. But figure 8 clearly indicates that the PC and MC distributions merge at the 12th minute. The TCT for conflicts involving contact aggression was 49%.

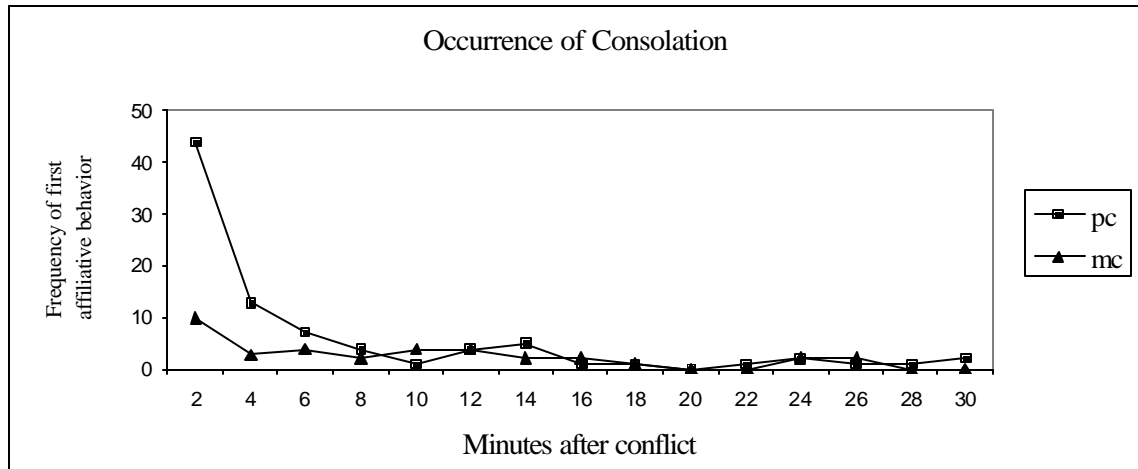


Figure 8. The frequency of the first affiliative interaction between the victim and a third-party in the 30-minute period following a conflict (involving contact aggression), and the control period.

Non-Contact Aggression

Of the 96 conflicts involving non-contact aggression, 65 PC-MC pairs were analyzed; the remaining 31 were considered neutral and not included in the analyses. There were 53 attracted opponent pairs and 12 dispersed pairs and these differed significantly from expectation; around 55% of the conflicts involving non-contact aggression were followed by the victim being consoled (Chi-square test: $\chi^2 = 25.862$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 1; $z = -3.005$; $p = 0.003$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.596$; $p < 0.001$), and the greatest difference in the cumulative observations occurred within $t = 1$ minute; see figure 9 ($z = 1.777$, $p = 0.004$). The TCT for conflicts involving non-contact aggression was 43%.

A significantly higher amount of consolation was not observed after contact aggression when compared to non-contact aggression (Chi-square test: $\chi^2 = 0.419$; $df = 1$; ns; Wilcoxon signed ranks test: Total $N = 13$; ties = 3; $z = -1.686$; ns).

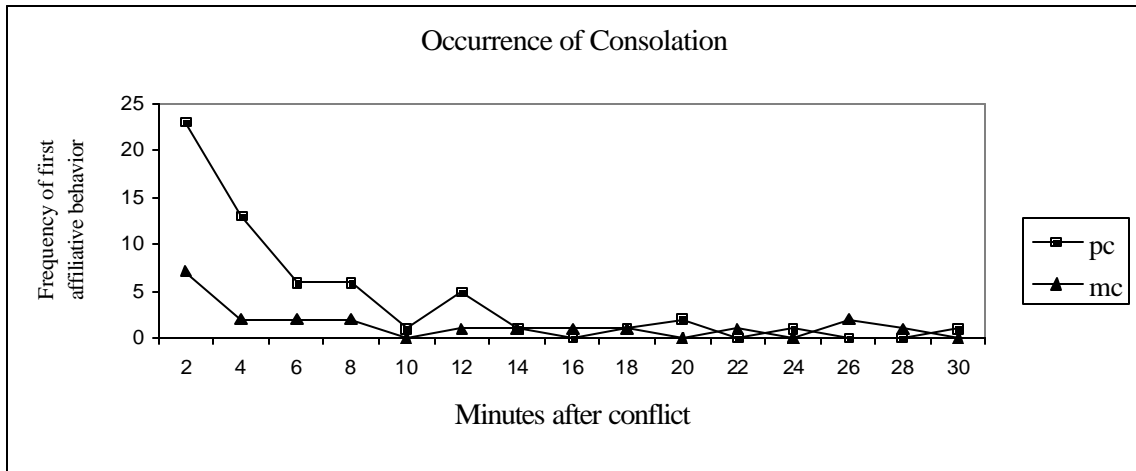


Figure 9. The frequency of the first affiliative interaction between the victim and a third party in the 30-minute period following a conflict (involving non-contact aggression), and the control period.

Table 3. Summary of Consolation Statistics.

Dyad Type	Chi-Square			Wilcoxon	Time-Rule
	Sig.	%	TCT	Sig.	Sig.
Overall Consolation	$p < 0.001$	59%	46%	$p = 0.002$	$p < 0.001$
Adult-Adult	$p < 0.001$	61%	49%	$p = 0.027$	$p < 0.001$
Female-Female	$p < 0.001$	59%	43%	Low sample size	$p < 0.001$
Juvenile-Juvenile	$p < 0.001$	66%	56%	Low sample size	$p < 0.001$
Adult-Juvenile	$p < 0.001$	56%	44%	$p = 0.004$	$p < 0.001$
Mother-Offspring	Low sample size	--	--	Low sample size	Low sample size
Adult Female-Unrelated Juvenile	$p < 0.001$	68%	54%	$p = 0.005$	$p < 0.001$
Kin-Kin	$p = 0.022$	38%	24%	$p = 0.016$	$p = 0.004$
Non Kin-Non Kin	$p < 0.001$	65%	52%	$p = 0.002$	$p < 0.001$
Contact Aggression	$p < 0.001$	62%	49%	$p = 0.002$	$p < 0.001$
Non-Contact Aggression	$p < 0.001$	55%	43%	$p = 0.003$	$p < 0.001$

Solicited and Unsolicited Consolation

Solicited Consolation

40% of the consolations involved the victim of aggression approaching a third-party. Of the 132 instances of consolation, 65 PC-MC pairs were analyzed for solicited consolation; the remaining 62 were considered neutral and not included in the analyses.

There were 53 attracted pairs, and 12 dispersed pairs, and these differed significantly from expectation (Chi-square test: $\chi^2 = 25.862$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 1; $z = -2.932$; $p = 0.003$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.508$; $p < 0.001$).

Unsolicited Consolation

Sixty percent of the consolations involved a third-party approaching the victim of aggression. Of the 132 instances of consolation, 96 PC-MC pairs were analyzed for unsolicited consolation; the remaining 62 were considered neutral and not included in the analyses. There were 79 attracted pairs, and 17 dispersed pairs, and these differed significantly from expectation (Chi-square test: $\chi^2 = 40.042$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 13$; ties = 2; $z = -2.938$; $p = 0.003$). The distribution of first friendly interactions in the PC and MC sessions differed significantly (Kolmogorov-Smirnov test: $z = 3.897$; $p < 0.001$). See Table 4.

A chi-square test found a significant difference between solicited and unsolicited consolation (Chi-square test: $\chi^2 = 5.121$; $df = 1$; $p = 0.024$). To eliminate any bias resulting from an outlier individual, a Wilcoxon signed ranks test was conducted, which showed that the difference was not significant (Total $N = 13$; ties = 3; $z = -1.277$; ns).

Table 4. Solicited versus Unsolicited Consolation.

Type of Consolation	Chi-Square		Wilcoxon	Time-Rule
	Significance.	% conflicts followed by consolation	Significance	Significance
Solicited	$p < 0.001$	40%	$p = 0.003$	$p < 0.001$
Unsolicited	$p < 0.001$	60%	$p = 0.003$	$p < 0.001$

Type of Victim

Adult Female Victim

A significant portion (64%) of the 78 instances of consolation of an adult female victim involved consolation by offspring (Chi-square test: $\chi^2 = 21.73$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; $z = -2.032$; $p = 0.042$). A significant portion (36%) involved consolation by any individual other than offspring (Chi-square test: $\chi^2 = 16.03$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; and this was too low for the analysis to reach significance). A chi-square test found a significant difference between consolation provided by offspring versus non-offspring (Chi-square test: $\chi^2 = 6.205$; $df = 1$; $p = 0.013$). To eliminate any bias resulting from an outlier individual, a Wilcoxon signed ranks test was conducted, which showed that the difference was not significant (Total $N = 6$; ties = 0; $z = -1.160$; ns).

A significant portion (84%) of the instances where an adult female was consoled by her offspring involved unsolicited consolation (Chi-square test: $\chi^2 = 18.132$; $df = 1$;

$p < 0.001$; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; and this was too low for the analysis to reach significance), whereas 16% involved solicited consolation (Chi-square: $\chi^2 = 3.600$; $df = 1$; $p = 0.058$; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; and this was too low for the analysis to reach significance). There was a significant difference between the unsolicited and the solicited consolation (Chi-square test: $\chi^2 = 23.120$; $df = 2$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 6$; ties = 0; $z = -2.201$; $p = 0.028$).

A significant portion (68%) of the instances where an adult female was consoled by an individual other than her offspring involved unsolicited consolation (Chi-square test: $\chi^2 = 11.636$; $df = 1$; $p = 0.001$; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; and this was too low for the analysis to reach significance), while 32% involved solicited consolation (Chi-square test: $\chi^2 = 4.455$; $df = 1$; $p = 0.035$; Wilcoxon signed ranks test: Total $N = 6$; ties = 4; N was too low for the analysis to reach significance). There was no significant difference between solicited and unsolicited consolation (Chi-square test: $\chi^2 = 3.571$; $df = 1$; $p = 0.059$; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; and this was too low for the analysis to reach significance). See Table 5.

Table 5. Consolation Partner for Adult Female Victim.

Adult Female Victim		Chi-Square	Wilcoxon
Consolation Partner	Significance	% conflicts followed by consolation	Significance
Offspring	$p < 0.001$	64%	Low sample size
Unsol. Consolation	$p < 0.001$	84%	Low sample size
Sol. Consolation	$p = 0.058$	16%	Low sample size
Non-Offspring	$p < 0.001$	36%	Low sample size
Unsol. Consolation	$p = 0.001$	68%	Low sample size
Sol. Consolation	$p = 0.035$	32%	Low sample size

Juvenile Victim

A significant portion (44%) of the 50 instances of consolation of a juvenile victim involved consolation by the mother (Chi-square test: $\chi^2 = 6.533$; $df = 1$; $p = 0.01$; Wilcoxon signed ranks test: Total $N = 6$; ties = 2; N was too low for the analysis to reach significance). A significant portion (56%) involved consolation by any individual other than the mother (Chi-square test: $\chi^2 = 25.138$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total $N = 6$; ties = 0; $z = -2.214$; $p = 0.027$). There was no significant difference between consolation provided by the mother versus any other individual (Chi-square test: $\chi^2 = 0.720$; $df = 1$; ns; Wilcoxon signed ranks test: Total $N = 6$; ties = 1; and this was too low for the analysis to reach significance).

Of the 22 instances where the juvenile victim was consoled by his/her mother, 23% involved unsolicited consolation, and this was not significant (Chi-square test: $\chi^2 = 1.286$; $df = 1$; ns; Wilcoxon signed ranks test: Total N = 6; ties = 2; and this was too low for the analysis to reach significance). A significant portion (77%) involved solicited consolation (Chi-square: $\chi^2 = 5.261$; $df = 1$; $p = 0.022$; Wilcoxon signed ranks test: Total N = 6; ties = 1; and this was too low for the analysis to reach significance). There was a significant difference between the unsolicited and solicited consolation (Chi-square test: $\chi^2 = 6.545$; $df = 1$; $p = 0.011$; Wilcoxon signed ranks test: Total N = 6; ties = 2; N was too low for the analysis to reach significance).

A significant portion (39%) of the instances where a juvenile was consoled by an individual other than his/her mother involved unsolicited consolation (Chi-square test: χ^2 could not be determined; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total N = 6; ties = 0; $z = -2.232$; $p = 0.026$). A significant portion (61%) involved solicited consolation (Chi-square test: $\chi^2 = 14.222$; $df = 1$; $p < 0.001$; Wilcoxon signed ranks test: Total N = 6; ties = 0; $z = -2.214$; $p = 0.027$). There was no significant difference between solicited and unsolicited consolation (Chi-square test: $\chi^2 = 1.286$; $df = 1$; ns; Wilcoxon signed ranks test: Total N = 6; ties = 0; $z = -1.186$; ns). See Table 6.

Table 6. Consolation Partner for Juvenile Victim.

Juvenile Victim	Chi-Square		Wilcoxon
Consolation Partner	Significance	% conflicts followed by consolation	Significance
Mother	p = 0.01	44%	Low sample size
Unsol. Consolation	ns	23%	Low sample size
Sol. Consolation	p = 0.022	77%	Low sample size
Non-Mother	p < 0.001	56%	p = 0.027
Unsol. Consolation	p < 0.001	39%	p = 0.026
Sol. Consolation	p < 0.001	61%	p = 0.027

CHAPTER 4

DISCUSSION

Redirected Aggression

The instances of redirected aggression were too few to be analyzed. Redirected aggression has been previously observed in some primate species such as long-tailed macaques (Aureli & van Schaik, 1991a), Japanese macaques (Aureli, Cordischi, Cozzolino, & Scucchi, 1992), vervet monkeys (Cheney & Seyfarth, 1989), pigtailed macaques (Judge, 1982), and olive baboons (Smuts, 1985; but see Castles & Whiten, 1998). Watts (1995b) found that juvenile mountain gorilla victims redirected significant amounts of aggression, as did subordinate males in multi-male groups, who redirected aggression at adult females after conflicts with dominant males.

Species in which redirection has not been observed include stumptailed macaques (Call et al., 2002), olive baboons (Castles & Whiten, 1998; but see Smuts, 1985), spectacled leaf monkeys (Arnold & Barton, 2001b), and bonobos (Palagi, Paoli, & Tarli, 2004). Watts (1995b) found that female mountain gorillas sometimes redirected aggression at third-parties, especially at female opponent's kin, but this was not statistically significant; instead they sought consolation from adult males. They also did not redirect aggression after conflicts with males; instead they reconciled, and thus perhaps did not need an alternate coping mechanism.

It has been hypothesized that redirection might not be necessary when: a) a victim can retaliate against a former aggressor without the risk of renewed attack, as in situations in which the latter is not higher-ranking (Kappeler & van Schaik, 1992; Scucchi et al., 1988); and b) a victim can retaliate against a former aggressor without the risk of the latter receiving agonistic support either from kin (Aureli et al., 1992, 1993), or unrelated individuals (de Waal, 1987; de Waal & Luttrell, 1989). Watts (1995b) suggested that since most mountain gorilla female dyads have undecided agonistic relationships, victims can retaliate against aggressors, instead of redirecting aggression. Furthermore, since most gorilla matrilineal groups are small because of female dispersal, and since it is unusual for mountain gorilla females to give agonistic support to unrelated individuals (Harcourt & Stewart, 1989), retaliation is possible without the risk of agonistic support either from the opponent's kin, or from unrelated individuals.

Although research is yet to reveal whether or not western lowland gorilla females give agonistic support to unrelated and related individuals, undecided dominance relationships (which might allow for bidirectional conflicts) might explain the absence of redirection in the present study. A future extension of this study could reveal whether or not there is a significant amount of retaliation occurring during conflicts between females.

In contrast to Watts' finding of redirected aggression by juvenile mountain gorilla victims, the present study did not find any evidence of redirection by juvenile western lowlands. One of the reasons for this could be that, since a significant proportion of conflicts with juvenile victims was followed by consolation of the juvenile (see section on consolation for more details), they probably did not need an alternate coping mechanism. But juvenile mountain gorilla victims sought and received consolation too;

yet they also exhibited redirection. Thus, another reason for the lack of redirected aggression in the present study could be that a significant proportion of conflicts with juvenile victims in the present study were reconciled (see section on reconciliation for more details). In fact, Aureli and van Schaik (1991a) found that in long-tailed macaques, redirection was less likely to be exhibited if reconciliation had already occurred, indicating that reconciling was far more important for the victim. This also supports the finding that reconciliation is the most effective post-conflict behavior for the reduction of social uncertainty (Aureli & van Schaik, 1991b).

Reconciliation

Overall

The results indicate that western lowland gorillas exhibit reconciliation (overall, around 43% of the conflicts were reconciled). Around 20% of the conflicts were considered reconciled when we defined reconciliation using the time rule of affiliative behavior within two minutes of an aggressive incident. The overall corrected conciliatory tendency (CCT) was 29%. When considering conflicts that were reconciled by actual physical contact, the CCT for the study group was around 6%. The overall percentage of reconciled conflicts (considering the entire 30 minute focal period) that used “contact” as a reconciliatory behavior was 24%. The table in Appendix A shows the range of percent reconciled conflicts (reconciliation being achieved by actual physical contact) for the other primate species studied in the past (Aureli & deWaal, 2000b). It must be mentioned, though, that all these percentages were calculated differently in different

studies, and so cannot be directly compared. But this at least shows us where western lowland gorillas lie within the spectrum.

The other important point to note is that in most of these studies, mere proximity was not considered as one of the affiliative behaviors indicating reconciliation. Very few studies have considered mere proximity as an affiliative behavior indicating reconciliation. For example, the percentage of reconciled conflicts that was due to mere proximity for patas monkeys was 22% (York & Rowell, 1988); for long-tailed macaques, it was 15% (Cords, 1993). Other studies that have used proximity include ones on brown capuchins (Verbeek & de Waal, 1997); black-and-white colobus monkeys (Bjornsdotter, Larsson, & Ljungberg, 2000); and sooty mangabeys (Gust & Gordon, 1993). Cords (1993) suggested that proximity could be considered to be a reconciliatory behavior because opponents show interest in each other by approaching but not continuing or renewing aggression. A change in spatial position can indicate a change in social relationships in the same way as overt friendly signals. Furthermore, she found that “mere proximity” reunions were as effective as reunions with overt displays in functionally reconciling opponents.

The present study showed that the percentage of reconciled conflicts that was due to mere proximity for the western lowland gorillas under study was 76%. It is interesting to note that the majority of post-conflict affiliative interactions were social proximity, which leads us to believe that unlike most primate species studied, proximity, rather than actual physical contact, may be the main mechanism for resolving conflicts in western lowland gorillas. This is not surprising, given that captive western lowland gorillas engage in low levels of affiliative physical contact to begin with. Other species in which post-conflict

reunions are subtle include patas monkeys, which rely more on spatial positioning than on displays for communication (York & Rowell, 1988), and chacma baboons, which rely on soft vocalizations, like grunts, for reconciliation (Cheney, Seyfarth, & Silk, 1995).

Western lowland gorillas can thus be said to have “implicit” reconciliation (their behavior is inconspicuous, and does not unequivocally refer to the conflict), as opposed to “explicit” reconciliation, which has been defined as unusual and conspicuous behavioral patterns which are not usually seen outside the context of reconciliation (de Waal & Ren, 1988). The type of reconciliation exhibited by different species (either explicit or implicit) might depend on personality and temperament differences. Gold and Maple (1994) conducted a personality assessment test with captive western lowland gorillas, and found that the four main personality types to emerge were extroverted, dominant, fearful, and understanding. Future studies of personality might shed more light on species differences in reconciliation patterns.

Female-Female Conflicts

Since the majority of the adult-adult conflicts involved adult females (there was only one adult male in only one of the groups), this part of the discussion will deal with female-female conflicts. When we ran the analyses without the data from the single adult male, the chi-square test did not indicate significant evidence for reconciliation, but the time-rule analysis found significant evidence. This might imply that with a larger sample size, significant evidence for reconciliation could be found with both tests, because, unlike the mountain gorilla social structure, where male-female relationships are thought to be most important (Watts, 1992, 1996), captive western lowland gorilla females have

been found to spend significantly more time with other females than with silverbacks (Stoinski, Hoff, & Maple, 2003). This difference in sociality could lead to the presence of reconciliation in captive western lowland females. Furthermore, most of the conflicts between adult females occurred in the all-female group, and it is not surprising that there was significant evidence for reconciliation (using the time-rule analysis), considering the results from a previous study which found that proximity between females was greater, and contact aggression and affiliative behaviors were more frequent in an all-female group (the same group that was used in the present study), as opposed to a heterosexual group (Stoinski, Allard, & Maple, 2003). A larger sample size, both in terms of the number of subjects, and the number of conflicts in this dyad type, will also be required in order to see whether the difference in the results for the two statistical tests still exists.

Juvenile-Juvenile Conflicts

As predicted, analyses of conflicts between juveniles showed no significant evidence for reconciliation. This is similar to what was found for mountain gorillas-- immatures (juveniles and 2- and 3-yr-old infants) did not reconcile with other immatures after a conflict. Reconciliation among juveniles has been observed in rhesus, long-tailed, and Japanese macaques (Cords, 1988; Cords & Aureli, 1993; Schino et al., 1998; de Waal, 1984; de Waal & Johanson, 1993.). Cords and Aureli (1993) argue that it would be in a juvenile's best interests to have mechanisms to achieve conflict resolution to counter the aggression received, encourage tolerance, lower individual tension levels, and receive agonistic support from peers. Schino et al. (1998) argue that the presence of reconciliatory behaviors in juveniles indicates that an ability to reconcile does not require

high cognitive abilities. However, none of these studies address the issue of why reconciliation exists in juvenile-juvenile dyads per se. For instance, Cords & Aureli (1993) only try to explain why among juveniles, non-kin reconciled more than kin, and males reconciled more than females.

On the other hand, the lack of reconciliation between immature mountain gorillas was hypothesized to be due to the following reasons (Watts, 1995a): (1) As both males and females disperse from natal groups, long-term alliances may not be maintained; (2) Relationships between juveniles may be very resilient because they are play and socio-sexual partners (Watts, 1990, Watts & Pusey, 1993). Do these factors apply to the captive situation? The juveniles in the study groups exhibited a lot of play behavior, which might have strengthened relationships. It might be hypothesized that to a certain extent, resources are abundant and non-monopolizable in the captive situation, and so alliances between juveniles might not have much effect on foraging efficiency. Finally, after conflicts with their peers, juveniles might be reducing stress by seeking consolation from their mothers or other individuals (and, in fact, the juvenile victims in this study did seek and receive consolation from their mothers and other individuals after conflicts with peers; see the section on consolation for more details). Just as in the case for female-female conflicts discussed above, relationship quality data can be used to gain a deeper understanding of this process.

Adult-Juvenile Conflicts

As predicted, adult-juvenile dyads showed significant evidence of reconciliation. Conflicts for this dyad type were not studied in mountain gorillas. We divided adult-

juvenile conflicts into mother-offspring (offspring being defined as limited to juveniles younger than 7 years of age) and adult female-unrelated juvenile conflicts. Analyses of conflicts between mothers and offspring (offspring were juveniles younger than 7 years) revealed a trend towards reconciliation. It was surprising that there was no evidence of significant reconciliation, but this might be because of already pre-existing strong bonds between mother and offspring. A larger sample size (we only had 18 analyzable conflicts) might reveal something more specific. Most probably, the significant result for adult-juvenile conflicts was mostly due to the adult female-unrelated juvenile dyads, which showed significant evidence of reconciliation. Watts (1995a) hypothesized that adults and unrelated juveniles may have less resilient relationships than juvenile peers, and so might need to reconcile more. The present study confirms this hypothesis. A more recent study by Weaver and de Waal (2003) found that adult-unrelated juvenile dyads of brown capuchins showed significant evidence of reconciliation, indicating that reconciliation emerges early in their behavioral repertoire as a natural peace-making strategy and to reduce tension created by conflict. They hypothesized that reconciliatory behaviors emerged from coping mechanisms that re-established homeostasis (a juvenile's most familiar autonomic state). Reconciliatory behaviors are thus adjustments to fluctuating levels of arousal during social interactions (conflicts). Reconciliation is thus an arousal-control mechanism that simultaneously developed with independent mobility (which allows juveniles to interact socially with unrelated individuals). More studies that address adult-unrelated juvenile conflicts specifically need to be conducted in order to gain a deeper understanding of the process.

Kin versus Non-Kin

Kinship was defined in terms of direct mother-offspring (offspring were not necessarily younger than 7 years of age; for instance, Machi-Mia and Choomba-Machi) and father-offspring relationships. A significant portion of conflicts between kin and between non-kin was reconciled (around 49% for kin; around 41% for non kin). Contrary to what was predicted, kin did not reconcile conflicts significantly more than non-kin did. However, it is interesting to note that there were a fewer number of conflicts between kin than between non-kin, and yet the percentage of reconciled conflicts was similar for both.

Studies that have found a higher frequency of reconciliation among kin than non-kin include York and Rowell (1988) in patas monkeys, Castles and Whiten (1998) in olive baboons, de Waal and Ren (1988) in stump-tail macaques, and Kappeler (1993) in red-fronted lemurs, and kinship effects can be explained in terms of kin selection theory (Hamilton, 1964). On the other hand, studies that have found evidence of reconciliation between individuals with a good relationship, rather than with kinship ties, include Cords and Thurnheer (1993) in long-tailed macaques, Periera et al. (2000) in squirrel monkeys, and Arnold and Barton (2001a) in spectacled leaf monkeys.

Cords (1988) found that juvenile male long-tailed macaques showed a higher rate of reconciliation among non-kin, as compared to kin. Cheney and Seyfarth (1989) found a similar pattern with vervet monkeys. Like Cords, they hypothesized that this pattern might be because of the unstable and less predictable relationships among unrelated individuals (post-conflict behaviors will thus help repair relationships), whereas similar

reconciliation patterns might not be required for related individuals since they have higher rates of friendly interactions anyway. Cords (1988) further argued that relationships among kin are secure (as they are based on unchangeable genetic relationships), and so kin do not need to explicitly resolve conflicts.

Since the results of the present study indicate that both kin and non-kin reconcile, it could be suggested that the western lowland gorilla groups under study might have experienced both kinship and relationship quality effects, and the above arguments for both these effects would then hold for western lowland gorillas. Studies that have found both kinship and relationship quality effects on reconciliation include Castles et al. (1996) in pigtail macaques, Aureli et al. (1989) in long-tailed macaques, and de Waal and Yoshihara (1983) in rhesus monkeys. Their explanations for this pattern were similar to those given by Schino et al. (1998), who found that Japanese macaques with good relationships reconciled more often; but among individuals with good relationships, kin reconciled more than non-kin. Thus, they hypothesized that good relationships are more valuable, but among good relationships, kin are more valuable than non-kin.

A future extension of the present study can incorporate relationship quality data to see how exactly this factor influences the likelihood of reconciliation, and its possible interaction with kinship. Furthermore, since most of the previous studies looked at adult-adult kin, whereas, the present study mainly had adult-juvenile kin, the results of the present study must be interpreted with caution. Perhaps adult-juvenile kin exhibit different patterns of reconciliation, and a future extension of this study should look at the effect of kinship ties between adults on reconciliation. Furthermore,

although kin exhibited significant amounts of reconciliation, most of the dyads that made up these kin dyads were mother-offspring (which were found not to reconcile when analyzed separately). This leads to a very small sample size of non-mother-offspring kin dyads, and so the results must be interpreted with caution. A larger sample size would shed more light.

Contact versus Non-Contact Aggression

A significant portion of conflicts involving contact aggression (around 45%) and those involving non-contact aggression (around 41%) was reconciled. Contrary to what was predicted, a significantly higher amount of reconciliation was not observed after contact aggression when compared to non-contact aggression. There are mixed results from studies looking at the effects of the intensity of aggression in a conflict on post-conflict behavior. Schino et al. (1998) found that in a captive group of Japanese macaques, conciliatory tendency was least after a chase, and highest after a physical assault, but this difference was not statistically significant. Similarly, Cords and Aureli (1993) found that in a group of juvenile long-tailed macaques, there was a greater frequency of reconciliatory behaviors following a conflict involving contact aggression, when compared to non-contact aggression, but this difference was not statistically significant.

In a study involving redfronted lemurs, Kappeler (1993) found that significantly larger proportions of low-intensity (non-contact aggression), conflicts were reconciled, when compared to high-intensity conflicts, whereas, Pereira et al. (2000) found that in squirrel monkeys, high-intensity conflicts were more likely to be reconciled.

Castles and Whiten (1998) found that low intensity conflicts in a group of olive baboons were as often reconciled as those of a higher intensity. A more recent study of spectaclled leaf monkeys (Arnold & Barton, 2001a) found that the intensity of aggression had no effect on the likelihood of reconciliation. Although heavy aggression might lead to higher rates of reconciliation because it induces more distress in the victim, when compared to lighter aggression (de Waal & Aureli, 1996), they argue that the victim's need to reconcile was masked by a reduction in the likelihood of reconciliation, caused by a risk of further attack. Similarly, the intensity of aggression had no effect on reconciliation in the group of western lowland gorillas under study; perhaps it was important to reconcile any type of conflict in order to get back to baseline levels of affiliation and tolerance.

Initiation of Reconciliation

Overall, the percentage of reconciliations initiated by the aggressor was around 65% and the percentage initiated by the victim was around 35%. After the outlier individual (Charlie) was removed, the percentage of reconciliations initiated by the aggressor and victim was around 57% and 43%, respectively, and these did not differ significantly, indicating that in the study group, both aggressors and victims were equally responsible for initiating post-conflict affiliative interactions with opponents. Previous studies have found that in some species, the aggressor is responsible for initiating reconciliation; for instance in moor macaques (Matsumura, 1996), patas monkeys (York & Rowell, 1988), rhesus monkeys (de Waal & Ren, 1987), and sooty mangabeys (Gust & Gordon, 1993). Other studies have found that the victim is responsible for initiating reconciliation; for

instance, in chimpanzees (de Waal, 1987), stumptailed macaques (de Waal & Ren, 1988), and black-and white colobus monkeys (Bjornsdotter et al., 2000).

It has been hypothesized that this variation is because of the difference in dominance styles in different species (Matsumura, 1996; de Waal & Luttrell, 1989). Victims will be less likely to initiate reconciliation in a species with a despotic dominance style, because of a higher risk of renewed attack. Victims will be more likely to initiate reconciliation in a species with an egalitarian dominance style. The finding of the present study that both aggressors and victims were equally responsible for initiating reconciliation is consistent with the view that there are undecided dominance relationships among female gorillas (as mentioned before, most of the conflicts between adults involved females; furthermore, when Charlie was excluded, most of the adult-juvenile conflicts were between adult females and unrelated juvenile females).

Consolation

Overall

The results indicate that western lowland gorillas exhibit consolation (overall, around 59% of the conflicts were followed by consolation of the victim). The percentage of conflicts that were followed by consolation when we used the time rule could not be calculated because the time within which the greatest difference in the cumulative observations occurred could not be determined since there was never a time when the difference between PC and MC observations was not significant. So the reason why the difference was always significant was because the majority of the data points fell within the 2-minute time-frame, and since the KS test is cumulative, the effect was large enough

to be carried over to every other minute. The overall percentage of “consoled” conflicts that used “contact” as the consolatory behavior was around 26%. The overall triadic conciliatory tendency (TCT) was around 46%. This value is much higher than what Palagi et al. (2004) found for bonobos (TCT value is around 21%) and what Call et al. (2002) found for stump-tailed macaques (TCT value is around 12%). It must be mentioned, though, that this latter value is something I had to estimate from a graph, since the authors did not specifically state the TCT value. The other important point to note is that in these studies, mere proximity was not considered as one of the affiliative behaviors indicating consolation. When considering conflicts that were followed by contact as the consolatory behavior, the TCT value for the study group was around 13%, which is more comparable to previous research.

To my knowledge, only one study on brown capuchins (Verbeek & de Waal, 1997) has considered mere proximity as an affiliative behavior indicating consolation. The present study showed that the percentage of consoled conflicts that was due to mere proximity for the western lowland gorillas under study was around 74%. Similar to reconciliation, proximity, rather than actual physical contact, may be the main mechanism by which consolation is exhibited in western lowland gorillas. This is not surprising, given that captive western lowland gorillas engage in low levels of affiliative physical contact to begin with.

Dyad Type

When the results were analyzed according to dyad type, a significant portion of adult-adult (including female-female), juvenile-juvenile, adult-juvenile, kin-kin, and

nonkin-nonkin conflicts was followed by consolation of the victim. It must be mentioned, though, that when the adult-juvenile dyad was divided into mother-offspring and adult female-unrelated juvenile conflicts, the former were not followed by consolation of the victim, and so most probably, the significant result for adult-juvenile conflicts was due to the adult female-unrelated juvenile conflicts, which were followed by consolation of the victim.

Conflicts between Kin and between Non-Kin

A significantly higher amount of consolation occurred after conflicts between non-kin when compared to conflicts between kin. When attempting to explain why long-tailed macaques exhibited a higher rate of reconciliation after conflicts between non-kin (when compared to conflicts between kin), Cords (1988) hypothesized that this pattern might be because of the unstable and less predictable relationships among unrelated individuals (post-conflict behaviors will thus help repair relationships), whereas similar reconciliation patterns might not be required for related individuals since they have higher rates of friendly interactions anyway. Cords (1988) further argued that relationships among kin are secure (as they are based on unchangeable genetic relationships), whereas relationships between non-kin are less secure. Similar reasoning can be applied to the fact that in the present study, there was a significantly higher amount of consolation after conflicts between non-kin. A higher amount of distress alleviation might be required after conflicts between individuals with unstable, less predictable, and insecure relationships. A future extension of the present study can incorporate relationship quality data to see how

exactly this factor influences the likelihood of consolation.

Conflicts involving Contact and Non-Contact Aggression

A significant portion of conflicts involving both contact and non-contact aggression was followed by the victim being consoled; and, contrary to what was predicted, a significantly higher amount of consolation was not observed after contact aggression when compared to non-contact aggression. This is also contrary to what de Waal and Aureli (1996) found in chimpanzees: a significantly higher amount of consolation after highly aggressive incidents, when compared to semi-aggressive conflicts. The reason for the absence of any effect of the intensity of aggression on the occurrence of consolation in the group of western lowland gorillas under study was perhaps because both contact and non-contact aggression created enough distress in the victims for consolation to be required. However, this claim cannot be substantiated until we are able collect data on distress levels in victims.

Type of Victim

Adult Female Victim

When the victims were adult females, 64% of the consolations involved their offspring (a significant portion of these were unsolicited, whereas the occurrence of solicited consolation was not significant). Thirty-six percent of the consolations involved individuals other than offspring (both unsolicited and solicited consolation were significant). Overall, the chi-square test found that the primary consolation partner for an adult female victim was her offspring. But, there did not seem to be any specific primary

consolation partner for an adult female victim at the individual level (according to the Wilcoxon) unlike for mountain gorillas, where females frequently seek and receive consolation from adult males (Watts, 1995b). Watts hypothesized that the affiliative interactions exhibited by females towards males might be because females need males to protect them, and so they need to show allegiance in order to maintain a good relationship. Males may be offering unsolicited consolation as a mate-retention strategy, given that females can transfer out of the group.

These situations might not have arisen in the present study because:

- a) there was no male in one of the study groups;
- b) the fact that the male in the heterosexual group was not the primary consolation partner for the females might have been an artifact of captivity. Stoinski, Hoff, and Maple (2003) hypothesized that new mothers do not feel the need for proximity to and protection from the silverback because of differences in the captive environment, which lead to the absence of infanticide. They also hypothesized that the captive environment provides more visibility between group members, thus reducing the female's need to maintain close proximity to the male. Finally, the captive environment does not allow female mate choice, and this may decrease their preference for the silverback; and
- c) genuine species differences might exist between mountain gorillas and western lowland gorillas.

Juvenile Victim

When the victims were juveniles, 44% of the consolations involved their mothers (a significant portion of these consolations was solicited). 56% of the consolations involved individuals other than the mother (both unsolicited and solicited consolation were significant). There did not seem to be any specific primary consolation partner for a juvenile victim unlike for mountain gorillas, where juveniles frequently sought and received consolation from their mothers (Watts, 1995b). Juvenile ring-tailed lemurs also contact their mothers when they are victims of a conflict (Pereira, 1993). Thus, the finding of the present study is surprising. A larger sample size might shed more light on this issue.

Solicited and Unsolicited Consolation

Both solicited and unsolicited consolation were observed; around 40% of the consolations involved the victim of aggression approaching a third-party; and around 60% of the consolations involved a third-party approaching the victim of aggression. There was a significant difference between the amount of solicited and unsolicited consolation, although the Wilcoxon test suggests that one or two individuals might be biasing this result. Species that have been found to exhibit solicited consolation include brown capuchins (Verbeek & de Waal, 1997), bonobos (Palagi et al., 2004), hamadryas baboons (Zaragoza & Colmenares, unpublished data), mountain gorilla juveniles and females (Watts, 1995b), chimpanzees (Arnold & Whiten, 2001; de Waal & Aureli, 1996; de Waal & van Roosmalen, 1979), spectacled leaf monkeys (Arnold & Barton, 2001b), and stump-tailed macaques (Call et al., 2002).

Very few species have been found to exhibit unsolicited consolation—bonobos (Palagi et al., 2004), stumptailed macaques (Call et al., 2002), and chimpanzees (Arnold & Whiten, 2001; de Waal & Aureli, 1996; de Waal & van Roosmalen, 1979).

Hypotheses to explain Consolation

The Social Cognition Hypothesis

This is one of the hypotheses that had previously been put forward to explain the occurrence of unsolicited consolation in chimpanzees but not in macaques. It stated that the “cognitive ability” of chimpanzees was above a certain threshold, and this enabled them to “perceive distress and empathize” with the victim of a conflict, whereas macaque “cognitive ability” fell below this threshold, and so macaques were not capable of consolatory behaviors (de Waal & Aureli, 1996). However, a recent study by Call et al. (2002) found evidence for unsolicited consolation in a monkey species (stumptailed macaques). But, the authors did not infer “empathy” in stumptailed macaques because all third-party contacts consisted of sociosexual behaviors, and this kind of affiliation may serve to prevent redirected aggression by the victim towards the third-party, instead of serving to console the victim (the “redirection hypothesis”).

In another recent study, Palagi et al. (2004) found evidence for both unsolicited and solicited consolation in bonobos. They stated that their results did not fit the “redirection hypothesis” since there were no instances of redirected aggression, and they inferred that their results showed evidence for “empathy” in bonobos. The findings of the present study also do not fit the “redirection hypothesis,” because there was no evidence for redirection after a conflict. However, from a behaviorist perspective, it is not necessary to

use concepts such as “empathy” to explain certain behaviors. These behaviors can be explained in the context of another hypothesis, which is now discussed.

The Social Constraints Hypothesis

This was another hypothesis that had been put forward to explain the occurrence of unsolicited consolation in chimpanzees but not in macaques. It stated that consolation would be more common in egalitarian than in despotic societies. This is because, in a more tolerant species with a less strictly hierarchical organization and the ability of low-ranking individuals to form alliances against higher-ranking individuals (such as in chimpanzees), third-parties have a lower risk of being attacked by the former aggressor (de Waal & Aureli, 1996). This hypothesis assumed that macaques are reluctant to take risks, although de Waal and Aureli (1996) pointed out that this did not mean that macaques completely avoid taking risks; and Call et al. (2002) did find evidence for unsolicited consolation in stump-tailed macaques. The findings of the present study (that unsolicited consolation is exhibited) are consistent with the view that there are undecided dominance relationships among female gorillas (as mentioned before, most of the conflicts between adults involved females; furthermore, when Charlie was excluded, most of the adult-juvenile conflicts were between adult females and unrelated juvenile females), and thus support the social constraints hypothesis.

In a study of post-conflict behavior in spectaclled leaf monkeys, Arnold and Barton (2001b) found no evidence for unsolicited consolation, but significant evidence for solicited consolation. They state that their finding of solicited consolation supports the social constraints hypothesis. Since spectaclled leaf monkeys have an egalitarian society

(Arnold, 1997), contact with third-parties will not increase the risk of aggression. Initiation of affiliation by the victim is tolerated without intervention from former aggressors, as in the case of capuchins (Verbeek & de Waal, 1997), mountain gorillas (Watts, 1995b), and now, western lowland gorillas.

Arnold and Barton (2001b) also found that when consolation occurred either before or in the absence of reconciliation, the time at which it occurred was within the time period during which reconciliation normally occurs; and the affiliation levels during consolation were twice that of baseline levels. Furthermore, the mean latency to contacting a third-party was only slightly longer than to contact a former opponent, and victims sometimes contacted third-parties preferentially over former opponents. These findings indicate that consolation may serve as a substitute for reconciliation. (the “substitution hypothesis”-- de Waal & Aureli, 1996). The finding of the present study is that female-female and juvenile-juvenile conflicts are not reconciled; instead individuals in these dyads sought and received consolation after conflicts. This lends support to the substitution hypothesis. Female and juvenile mountain gorilla victims also sought consolation from males and mothers respectively, when they did not reconcile with their opponents (Watts, 1995b). Bonobos and hamadryas baboons also seem to use consolation as a substitute for reconciliation (Palagi et al., 2004; Zaragoza & Colmenares, unpublished data).

In their study of post-conflict behavior in chimpanzees, de Waal and Aureli (1996) scored approaches as consolation, whether or not they were preceded by a signal that chimpanzees appear to use to solicit support; i.e., the “hold-out-hand” begging gesture previously described by de Waal and van Hooff (1981). Arnold and Barton (2001b)

found that spectacled leaf monkey victims also used a vocalizing signal when approaching a third-party. When these signals were used, the third-party also approached and vocalized. They thus argue that it is not necessary to explain chimpanzee consolatory behavior in terms of concepts like “higher cognitive abilities” and “empathy.” Perhaps chimpanzees just possess a wider range of gestures than do macaques. Appropriate responses to such gestures could thus be learned by trial-and-error, or some form of social learning process. In the present study, however, there was no evidence of any overt signals being used within the context of consolation.

CHAPTER 5

CRITIQUE OF METHODOLOGY

This chapter describes the history of the various methodologies used in conflict regulation research, discusses some of the advantages and disadvantages of the most widely used method (the PC-MC method), and proposes a new way of analyzing post-conflict data. Since the majority of the previous literature is about reconciliation using the PC-MC method, this chapter will only refer to reconciliation, although the discussion applies to other post-conflict behaviors like consolation and redirected aggression as well. In the initial study of reconciliation in chimpanzees, behavioral observations were made only in post-conflict periods (de Waal & van Roosmalen, 1979). The weakness of this method was that post-conflict affiliative behaviors could not be compared with baseline affiliative behaviors. Later studies used the post conflict-matched control (PC-MC) method established by de Waal and Yoshihara (1983), in which observations are made during a post-conflict period, as well as a matched control period. With this method, the group is observed *ad lib* till a conflict occurs. Then post-conflict (PC) observations are made, which consist of a focal sample (Altmann, 1974) of both the opponents starting immediately after the termination of the conflict. On the next day (or at least, within three days), a matched control observation of the same individuals, at the same time as the corresponding PC (but in the absence of a conflict), is made. This serves as a control.

But with the PC-MC method, what is an appropriate duration for the PC/MC observations? This question was addressed by the “time-rule” method introduced by Aureli et al. (1989). This method compares the frequency of the first affiliative interaction between former opponents as a function of time during the PCs with the equivalent distribution during the MCs. The time at which both distributions merge provides an upper limit to the appropriate observation period.

The PC-MC method also allows too many errors of classification, since a particular PC reunion is compared to only a single control observation, and not to a sample of control observations. Thus, the “rate method” was developed, which compares the rate of affiliative interactions between former opponents in the PCs with that during the MCs (Judge, 1991), or with that during baseline observations (de Waal, 1987).

The reconciliation data can also be analyzed by quantifying the conciliatory tendency (CT), to indicate the “strength of a reconciliation” (deWaal & Yoshihara, 1983). The CT measure was originally defined as the ratio of the number of attracted PC-MC pairs to the total number of PC-MC pairs. The disadvantages of this measure are: 1. It is dependent on the duration of observation; and 2. It is affected by baseline levels of affiliative interactions. To ensure a more accurate measure, Veenema et al. (1994) came up with a corrected conciliatory tendency (CCT) measure, which is defined as follows:

$$\text{CCT} = (\text{number of attracted pairs} - \text{number of dispersed pairs}) / \text{total number of pairs}.$$

The CCT is independent of the duration of observation and the baseline level of affiliation. Therefore, it can be used to compare the conciliatory tendency of different types of dyads.

To analyze reconciliation using the PC-MC method, the timing of the first friendly interaction between former opponents during one PC and the corresponding MC are compared. If the first affiliative interaction occurs only in the PC, or earlier in the PC than in the MC, the dyadic pair is noted to be “attracted.” If the interaction occurs only in the MC, or earlier in the MC than in the PC, the pair is classified as “dispersed.” Finally, if the interaction occurs at the same time in both the PC and the MC, or there is no interaction in either, the pair is considered to be “neutral.” The numbers of attracted and dispersed pairs, obtained by the PC-MC method, are compared using a chi-square test, tested against 1:1 expectation (Aureli et al., 1989).

One of the disadvantages of the PC-MC method is that it assumes that each MC is a true control, and does not consider the temporal variation in the probability of the first affiliative contact (Kappeler & van Schaik, 1992). Thus, it will produce false negatives (the proportion of these will be equal to the probability that affiliative interactions occurred earlier in the MC than in the PC). It will also produce false positives (the proportion of these will be equal to the probability that affiliative interactions occurred earlier in the PC than in the MC, but after PC rates have returned to baseline values).

To overcome these problems, some studies have used the “conservative reconciliation method,” which considers conflicts to be reconciled if they are followed by affiliative interactions only in the PC; not in the MC. This method will also produce false negatives because reconciliation might be occurring in the PC but is not recorded, because affiliative interactions also occurred in the MC (Kappeler & van Schaik, 1992). But at least, there will be no false positives, and when trying to find evidence for the presence of

reconciliation, it is better to be as conservative as possible, even if it means that there will be some false negatives.

Another problem arises because the PC-MC method of analyzing the data (and, to my knowledge, the conservative reconciliation method), ignores the neutral pairs, which might make up a large portion of the data set. For instance, consider the situation in which there are 200 conflicts, out of which 150 are considered neutral, 40 are attracted, and 10 are dispersed. A chi-square analysis might find a significant difference between the numbers of attracted and dispersed pairs, but one needs to take into consideration the vast number of neutral pairs, which might actually indicate an absence of reconciliation. I suggest a more stringent method, where we use definite indicators of the presence or absence of reconciliation, especially because whether or not a PC affinitive interaction is classified as an attracted pair depends on the timing of occurrence of an affinitive interaction in the corresponding MC; the latter being due to chance (Veenema et al., 1994). Thus, PC interactions that result in attracted pairs cannot be directly considered to be potential instances of reconciliation. Therefore, I suggest that a pair should be considered as “attracted” if it occurs only in PC, “dispersed,” if it occurs only in MC, and “neutral,” if it occurs in neither the PC nor the MC. A significantly higher number of dispersed plus neutral pairs (compared to the number of attracted pairs using chi-square analyses) will indicate a lack of reconciliation.

Some other disadvantages of the PC-MC method are outlined by Kappeler and van Schaik (1992): the precision of the matched control is affected by group activity, spatial position of former opponents, other agonistic events that produce tension in the group, and temperature. Future studies should take these factors into consideration. Finally,

more experimental research (in which conflicts are induced) needs to be conducted on conflict-regulation mechanisms, in order to gain better control over various factors, and to determine the functional significance of post-conflict behaviors.

CHAPTER 6

CONCLUSIONS AND FUTURE DIRECTIONS

Western lowland gorillas at Zoo Atlanta exhibited post-conflict behavior. In particular, former opponents were more likely to exhibit affiliative behaviors towards one another shortly after a conflict, as opposed to a control period when no aggression had occurred (i.e., former opponents reconciled their conflicts). Victims were more likely to exhibit affiliative behaviors towards third-parties (and vice versa) shortly after a conflict, as opposed to a control period (i.e., victims sought and received consolation after conflicts). Redirected aggression was not observed in this group of western lowland gorillas. Both solicited and unsolicited consolation were observed; this is the first report of unsolicited consolation in a species other than chimpanzees, bonobos, and stumptailed macaques. The majority of post-conflict affiliative interactions were social proximity, which suggests that unlike most primate species studied, proximity, rather than actual physical contact, may be the main mechanism for resolving conflicts in western lowland gorillas.

Although most studies of post-conflict behavior have been carried out in captive settings, there is evidence which suggests that these behaviors are not simply an artifact of captivity or limited space (Aureli et al., 2002). First, some of the studies were conducted on groups that were housed in large enclosures (for instance, Aureli et al., 1994; Kappeler, 1993; de Waal & van Roosmalen, 1979). Similar to the animals in the

present study, the individuals in the previous studies had enough space so that certain group members could be avoided if necessary. Second, some studies have found evidence showing that the frequency of post-conflict behaviors in a group did not change when that group was housed in smaller enclosures (Aureli et al., 1995; Judge & de Waal, 1993; de Waal & van Roosmalen, 1979). Third, 12 out of 13 studies in the wild have found evidence for post-conflict behaviors (Aureli et al., 2002; but see Sommer, Denham, & Little, 2002). Finally, long-tailed macaques showed similar post-conflict behaviors when studied both in the wild and in captivity by the same researcher (Aureli, 1992).

Future research on post-conflict behavior in western lowland gorillas could start with an extension of the present study to look at all four gorilla groups at Zoo Atlanta to obtain a larger sample size, and to look at possible differences due to varying group composition. Relationship quality data must be taken into consideration. Kinship effects can be thoroughly analyzed by looking at adult kin, apart from mother-offspring relationships. It would also be useful to look at differences in post-conflict behavior with respect to age, sex, and dominance relations. Since social proximity was the main behavior exhibited, further study of whether it is as effective a functional post-conflict behavior as overt displays (like contact and grooming) is required. Experimental work (where conflicts are induced) must be conducted to gain better control over various confounding factors. Finally, the shortcomings of the current methodology must be taken into consideration during analyses of post-conflict data; perhaps a more stringent methodology can complement the existing one.

To conclude, although the present study was important in showing evidence for the presence of post-conflict behaviors in a previously unstudied species, it has barely

scratched the surface of the vast area of research that can still be conducted within the realm of conflict resolution. This study can thus be used as a springboard for future research attempting to understand conflict regulation mechanisms not only in western lowland gorillas, but also in other primate and non-primate species through a comparative perspective; and to gain a deeper understanding of social systems in gregarious animals in general.

APPENDIX A

SPECIES IN WHICH RECONCILIATORY BEHAVIOR HAS BEEN OBSERVED

Species	Author(s)	Percent reconciled conflicts
Prosimians		
Ringtailed lemur <i>Lemur catta</i>	Rolland & Roeder (2000)	--
Redfronted lemur <i>Eulemur fulvus rufus</i>	Kappeler (1993)	14-21
New world monkeys		
Brown capuchin <i>Cebus apella</i>	Verbeek & de Waal (1997)	21
White-faced capuchin <i>Cebus capucinus</i>	Leca et al. (2002)	--
Squirrel monkey <i>Saimiri sciureus</i>	Pereira et al. (2000)	--
Common marmoset <i>Callithrix jacchus</i>	Westlund et al. (2000)	--
Old world monkeys		
Sooty mangabey <i>Cercocebus torquatus atys</i>	Gust & Gordan (1993)	55
Vervet monkey <i>Cercopithecus aethiops</i>	Cheney & Seyfarth (1989)	14
Patas monkey <i>Erythrocebus patas</i>	York & Rowell (1988)	31
Golden monkey <i>Rhinopithecus roxellanae</i>	Ren et al. (1991)	43-54

Species	Author(s)	Percent reconciled conflicts
Old world monkeys		
Spectacled langur <i>Trachypithecus obscura</i>	Arnold & Barton (1997)	41-51
Black-and-white colobus <i>Colobus guerza</i>	Bjornsdotter et al. (2000)	--
Gelada baboon <i>Theropithecus gelada</i>	Swedell (1997)	30-45
Olive baboon <i>Papio anubis</i>	Castles & Whiten (1998)	16
Hamadryas baboon <i>Papio hamadryas</i>	Zaragoza & Colmenares (1997)	24
Guinea baboon <i>Papio papio</i>	Petit & Thierry (1994a)	27
Chacma baboon <i>Papio ursinus</i>	Silk et al. (1996)	10-35
Stumptailed macaque <i>Macaca arctoides</i>	de Waal & Ren (1988); Perez-Ruiz & Mondragon-Ceballos (1994)	26-53
Longtailed macaque <i>Macaca fascicularis</i>	Aureli et al. (1989); Aureli et al. (1997); Aureli (1992)	13-40
Japanese macaque <i>Macaca fuscata</i>	Aureli et al. (1993); Aureli et al. (1997); Petit et al. (1997)	12-37
Moor macaque <i>Macaca maurus</i>	Matsumura (1996)	40
Rhesus macaque <i>Macaca mulatta</i>	de Waal & Yoshihara (1983); Call et al. (1996)	7-23

Species	Author(s)	Percent reconciled conflicts
Old world monkeys		
Pigtailed macaque <i>Macaca nemestrina</i>	Judge (1991); Castles et al. (1996)	30-42
Black macaque <i>Macaca nigra</i>	Petit & Thierry (1994b)	40
Lion-tailed macaque <i>Macaca silenus</i>	Abegg et al. (1996)	42-48
Barbary macaque <i>Macaca sylvanus</i>	Aureli et al. (1994); Aureli et al. (1997)	28-33
Tonkean macaque <i>Macaca tonkeana</i>	Demaria & Thierry (1992); Thierry et al. (1994)	46
Great apes		
Mountain gorilla <i>Gorilla beringei beringei</i>	Watts (1995a)	--
Bonobo <i>Pan paniscus</i>	de Waal (1987)	48
Chimpanzee <i>Pan troglodytes</i>	de Waal & van Roosmalen (1979); de Waal (1986)	18-47

Note. Adapted from *Natural Conflict Resolution* (p. 383), by F. Aureli and F. de Waal, 2000b, Berkeley: University of California Press. Copyright 2000 by The Regents of the University of California.

APPENDIX B

ETHOGRAM

Social Agonistic Behavior

Non-Contact Aggression

Stare face: Head tipped slightly downward, eyes hard and fixed. Lips pursed or curled back. A fixed unwavering stare at another, with brow furrowed and facial muscles tense.

Lunge: Rapid, short quadrupedal jump towards another.

Hit surface: Strikes substrate/structure with hand or object.

Stiff stance: Stiff quadrupedal stance, arms bent outward at elbow, legs held rigidly, tight-lip face.

Tight-lip face: A facial expression in which the lips are tightly compressed and the head diverges from side to side.

Strut-walk: While in the stiff stance, the animal walks with stiff, short steps.

Directed chest-beat: An animal chest-beats while orienting towards another animal

Directed object-slap: An animal orients towards another and slaps ground, rock, wall, door, or any other inanimate object in the exhibit.

Bluff charge: An animal runs on the diagonal past another, but does not make contact.

Rush charge: An animal rushes up to, and stops just short of another.

Charge with chest-beat: While charging, an animal beats its chest.

Charge with object-display: While charging, an animal waves or throws an object or slaps ground with an object.

Open-mouth threat: A tense, open-mouth expression with lips raised and pulled back so that canines are exposed; muscles on the forehead are taut and drawn back.

Aggressive chase: Directed aggressive pursuit behind another animal; both animals running.

Displace: Supplant position; an animal approaches another, which then moves away; one individual “causes” another to move away from the location he/she has been occupying; the first may or may not replace the second in space; whole body movement of one individual, which was one or more feet away from the other, when the other is in movement and has approached to within six feet.

Kick at: Rapidly extending hindlimb out and back in direction of another, without making contact.

Arm swing: Sweeps arm out towards another, without making contact.

Object grab: One animal snatches an object/food item from another.

Contact Aggression

Strike/Hit/Slap: Use of forelimb in brief, sharp contact with another.

Kick: Rapidly extending hindlimb out and back in direction of another, and making contact.

Bite: Seizes other with teeth in an aggressive manner; injury may or may not occur.

Push: Animal uses arms or legs to forcefully move another away.

Lunge with hit: Animal rushing at another in short, fast run, with hit.

Hit with object: An animal uses an object to strike out and makes contact with another.

Social Affiliative Behavior

Groom-solicit: One animal requests another to pick through or examine its hair or skin by sitting or standing in front of another.

Social groom: Directed touching/brushing with hands, fingers, lips, and/or teeth, or intense visual inspection of another's skin or hair.

Social approach: One animal moves from beyond contact distance to within contact distance of another.

Proximity: One individual moves to within 3 feet and remains without any interaction for at least 5 seconds.

Contact/touch: One animal reaches with any limb and makes contact with another on any part of the body except the genital region. Includes lying, sitting in contact. Must occur for at least 5 continuous seconds to be recorded.

Brief contact: Any friendly contact that occurs for less than 5 seconds.

Attempted touch: If an animal reaches out as if to touch another, but does not make contact.

Social staring: One animal inspects another within proximity for at least 5 continuous seconds.

Affiliative follow: One animal walks less than two body lengths of another outside the context of social play or aggression.

Offer food: An animal holds food in the hand and then extends that hand towards another.

Play face: Mouth open and corners rounded. Exposed teeth and gums, and laughing motions without vocalizations may be seen.

Social play: One animal initiates play with another. A play sequence may include many behaviors like chasing, sparring, rolling, wrestling, bipedal jostling, and running past and gently cuffing each other in a disjointed, non-aggressive, purposeless fashion. Must occur for at least 5 continuous seconds to be recorded.

Solicit play: One animal engages in a series of postures, movements, or gestures (run away, swagger, chest-beat) that has a high probability of eliciting play from another.

Present: May take two forms. One form is similar to a sexual present, but is much briefer. It may be accompanied by a series of brief glances directed towards the presentee.

Note: Ethogram adapted from Gorilla Behavior Advisory Group (1991, January).
Compilation of gorilla ethograms.

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