International Journal of Primatology (© 2006)
DOI: 10.1007/s10764-006-9078-4

Reconciliation and Consolation in Captive Western Gorillas

Giada Cordoni,[1,2] Elisabetta Palagi,[1,2,3] and Silvana Borgognini Tarli[2]

Received November 29, 2004; revision March 7, 2005; accepted April 24, 2005

*We studied post-aggression mechanisms in a captive group of western gorillas (Apenheul Primate Park, The Netherlands) and compared them with those of wild mountain gorillas (*Gorilla beringei*). We found the same trend for reconciliation that wild mountain gorillas show: reconciliation occurred only between adult male-female dyads, while it was absent in the other sex-age class combination. There were both solicited and nonsolicited contacts; the latter finding is in contrast with the result obtained in wild mountain gorillas, in which consolation was absent. Immature females were more likely to offer consolation toward both related and unrelated individuals. Consolation did not reduce the likelihood of further attacks among group members. It may be that, as the α-male plays a fundamental role in preventing the spread of conflicts throughout the entire group, triadic contacts become ineffective for the function. The levels of consolation were higher in absence of reconciliation than in its presence, suggesting that consolation may function as an alternative mechanism in stress reduction of the victim.*

KEY WORDS: consolation; reconciliation; solicited contact; western gorilla.

INTRODUCTION

Sociality is a feature of many primate species. Consensus is growing that the major benefits of social life are increasing safety against predators

[1]Centro Interdipartimentale Museo di Storia Naturale e del Territorio, Università di Pisa, 56010 Calci, Pisa, Italy.
[2]Dipartimento di Biologia, Università di Pisa, 56017 Pisa, Italy.
[3]To whom correspondence should be addressed; e-mail: betta.palagi@museo.unipi.it.

(in particular for females and their vulnerable offspring), defense of food resources, and collective rearing of offspring (Aureli, 1997; van Hooff, 2001; Walters and Seyfarth, 1987). Whatever the reasons may have been for animals to live together, competition is part and parcel of social life (Aureli, 1997; Aureli *et al*., 2002; Walters and Seyfarth, 1987). It may lead to aggressive encounters within group members developing cooperation (coalition and alliances) among conspecifics (Cords, 1997; van Hoof, 2001).

It is believed that conflict management reduces the cost of conflicts for social animals and prevents further aggression (Aureli and Smucny, 2000; Aureli *et al*., 2002; Wittig and Boesch, 2003). Opponents may exhibit a variety of interactions (reconciliation, third-party solicited contact, consolation, renewed aggression, redirected aggression, no contact), weighing carefully advantages and disadvantages (Wittig and Boesch, 2003). Interaction of ecological, social, demographic, phylogenetic, and life-history variables may affect the frequency and the form of post-conflict contacts (Palagi *et al*., 2004; Watts *et al*., 2000).

Most studies on conflict management have focused on chimpanzees (Arnold and Whiten, 2001; de Waal and van Roosmalen, 1979; Fuentes *et al*., 2002; Palagi *et al*., 2006; Preuschoft *et al*., 2002; Wittig and Boesch, 2003), bonobos (de Waal, 1987; Palagi *et al*., 2004), and cercopithecines (Aureli, 1992; Call *et al*., 2002; Cheney *et al*., 1995; Koyama, 2001; York and Rowell, 1988). Nevertheless, among great apes there are few data on post-conflict mechanisms in gorillas. Only one published study on reconciliation and consolation in wild mountain gorilla is available (Watts, 1995a,b).

Recently, in light of new molecular data, Parnell (2002) and Stokes *et al*. (2003) proposed 2 different species of gorillas comprising 5 distinct taxa: *Gorilla gorilla* (western species) and *Gorilla beringei* (eastern species). Because the primary social structure in both species seems to be similar with the presence of 1 dominant silverback, several mature females and their immature offspring (Parnell, 2002; Stokes *et al*., 2003; Watts, 1995a; 2003), it would be interesting to verify if post-conflict strategies are comparable as well. Even if studies on the social system of western gorillas have for most part relied on indirect observations, e.g., night-nest counts (Parnell, 2002; Stokes *et al*., 2003), researchers report an organization similar to that of mountain gorillas, yet with some exceptions: e.g., all-male or multimale groups are very rare in populations of western gorillas (Parnell, 2002; Stoinski *et al*., 2003; Stokes *et al*., 2003). All known gorilla populations seem to be characterized by female and male dispersal and a polygynous mating system (Parnell, 2002; Stokes *et al*., 2003; Watts, 1995a; Yamagiwa *et al*., 2003). Male ability to protect females and their offspring from intraspecific aggressions seems to influence female transfer decision

(Stokes *et al*., 2003; Watts, 1996, 2003). The social features might affect the development of relationships among group members. Though most evidence comes from studies on mountain gorillas (Harcourt, 1979; Watts, 1995a,b, 1996, 2003), in western gorillas it is also expected that females have more affinitive interactions and maintain higher proximity levels with males to obtain their protection. Conversely, friendly contacts and agonistic support seem to be uncommon among females, and their social relationships seem to be differentiated along kinship lines when kin reside together (Watts, 1994, 1995a,b, 1996, 2003). However, differentiation of social relationships along genealogical lines is well known in mountain gorillas, whereas we still know too little about western gorillas to be certain whether the same also applies to them.

We investigated post-aggression mechanisms in captive western gorillas and compared them with those of wild mountain gorillas (Watts, 1995a,b) by testing the following predictions:

1. Because the social structure of the 2 species seems to be similar and "post-conflict reunions are not an artifact of captivity or limited space" (Aureli *et al*., 2002, p. 7) we expect to find the same trend for reconciliation both in wild *Gorilla beringei beringei* and captive *Gorilla gorilla gorilla*.
2. Researchers have demonstrated consolation proper both in chimpanzees (de Waal and van Roosmalen, 1979; Palagi *et al*., 2006; Wittig and Boesch, 2003) and bonobos (Palagi *et al*., 2004). Empathy, the cognitive ability to perceive the distress of a conspecific, is a necessary prerequisite for consolation (Preston and de Waal, 2002). Because gorillas have cognitive abilities similar to those of chimpanzees and bonobos (Byrne and Whiten, 1988; O'Connell, 1995; Tomasello and Call, 1997), we expect to find consolation in gorillas. Moreover, in light of the findings by Watts (1995b), males are expected to be the main consolers, directing their consolatory contacts particularly to females.
3. Some authors suggested that consolation may substitute for reconciliation to buffer the tension from a conflict not yet overcome (Palagi *et al*., 2004; Watts *et al*., 2000; Wittig and Boesch, 2003). If that is the case, consolation in the absence of reconciliation is expected at higher rates than in its presence.
4. If triadic contacts function to reduce the spreading of aggression at group level (Watts *et al*., 2000), we expect that their occurrence reduces the probability of further attacks among all group members.

Table I. The colony of *Gorilla gorilla gorilla* at the Apenheul Primate Park (Apeldoorn, The Netherlands)

Subject	Sex	Class	Year of birth	Origin, arrival date
Bongo (BO)	M	Adult	1973, wild	Cameroon, 1974
Lobo (LO)	F	Adult	1973, wild	Cameroon, 1975
Mintha (MI)	F	Adult	1974, wild	Cameroon, 1975
Mandji (MA)	F	Adult	1975, wild	Cameroon, 1975
Dalila (DA)	F	Adult	1972, wild	Copenhage-unk, 1991
Irala (IR)	F	Adult	1985, captivity	Krefeld-3438/1, 1997
Uzuri (UZ)	M	Adolescent	1994, captivity, MA's son	Apenheul primate park
Miliki (MK)	F	Adolescent	1994, captivity, DA's daughter	Apenheul primate park
Bibi (BI)	F	Juvenile	1997, captivity, LO's daughter	Apenheul primate park
Kisiwa (KW)	F	Juvenile	1997, captivity, DA's daughter	Apenheul primate park
M'Bewe (MB)	M	Juvenile	1997, captivity, MI's son	Apenheul primate park
Kidogo (KI)	M	Juvenile	1998, captivity, MA's daughter	Apenheul primate park
M'Kono (MN)	M	Juvenile	1999, captivity, IR's daughter	Apenheul primate park
Zoezi (ZO)	F	Infant	2000, captivity, LO's son	Apenheul primate park
Nemsi (NE)	F	Infant	2001, captivity, MA's daughter	Apenheul primate park
Gyasi (GY)	F	Infant	2002, captivity, DA's son	Apenheul primate park

METHODS

Study Group

We collected behavioral data during 4 mo of observation (May–September 2003) of *Gorilla gorilla gorilla* in the Apenheul Primate Park (Apeldoorn, The Netherlands). The composition of the colony of 16 individuals did not change during the study period (Table I).

The subjects occupied indoor and outdoor (an island surrounded by a boundary ditch) facilities of about 330 m^2 and 10,000 m^2, respectively. Individuals were able to avoid each other in both enclosures; thus the environment was not crowded. The group received abundant food (fruits, vegetables, seeds) 4 times/d in May and September (0830, 1200, 1345, and 1530 h) and 5 times/d in June, July, and August (0830, 1130, 1300, 1430, and 1600 h).

Data Collection

We carried out observations in the indoor and outdoor facilities daily over 1 period of 6 h, which spanned morning and afternoon, including

feeding times after 0900 h. As some sections of the outdoor facility were out of sight, the 4 observers, which included Cordoni and Palagi, stopped the data collection until they could observe the focal individual again. A training period preceded systematic data collection and lasted until observations by different observers matched in 95% of cases.

We collected all agonistic interactions among individuals by sampling all occurrences (313 h of observation) (Altmann, 1974). For each agonistic encounter we recorded: 1) the opponents; 2) context, i.e., circumstance in which the aggression took place, e.g., feeding, prefeeding; 3) type of conflict, unidirectional or bidirectional; 4) aggressive behavioral patterns—threats and chase-fleeing, biting, slapping, pushing, pulling, stamping, brusque rushing; and 5) presence of allies.

We distinguished agonistic patterns according to 2 stages of increasing intensity: stage 1, threats, e.g. chest-beating, rigid quadrupedal stance and chase-fleeing and stage 2, aggressions with physical contacts—biting, slapping, pushing, pulling, stamping, or brusque rushing).

After the last aggressive pattern of any given agonistic event, we followed the victim as the focal individual for a 30-min post-conflict period (PC). Control observations (MC) took place in a next possible day at the same time as the original PC, on the same focal individual, in the absence of agonistic interactions during the 30 min before the beginning of MC and when the opponents were simultaneously present in 1 of the 2 enclosures to ensure that they had the opportunity to interact (de Waal and Yoshihara, 1983; Kappeler and van Schaik, 1992). Both for PC and MC we recorded: 1) starting time (min), 2) type of first affinitive interaction, 3) the minute of first affinitive contact, 4) initiator of the affinitive contact, and 5) partner identity. A third party as an individual other than the victim and the aggressor.

Data Analysis

We collected 127 PC-MC pairs. We carried out reconciliation and triadic contacts analyses at the individual level on adults and juveniles.

In the case of reconciliation for each individual we determined the number of attracted, dispersed, and neutral pairs over all PC-MC pairs. In attracted pairs, affinitive contacts occur earlier in the PC than in the MC (or in the PC, but not in the MC), whereas in dispersed pairs affinitive contacts occur earlier in the MC than in the PC (or they did not occur at all in the PC). In neutral pairs, affinitive contacts occur during the same minute in the PC and the MC, or no contact occurs in either the PC or the MC.

To avoid coding the same incident twice, for each individual we used only PC-MC pairs in which that individual was the focal individual, and entered them under its name. To evaluate individual reconciliation, we used the measure of Corrected Conciliatory Tendency (CCT) of Veenema *et al.* (1994), defined as "attracted minus dispersed pairs divided by the total number of PC-MC pairs." We used individual CCT to determine the group mean CCT.

In the case of consolation, for each focal individual we determined the number of attracted, dispersed, and neutral pairs (as in the case of reconciliation), but considered all PC affinitive contacts with any third party in both PC and MC.

When the victim approached or invited a third party before the PC affinitive contact, we labeled the contact as solicited. Conversely, when a third party approached or invited the victim before the PC affinitive contact, we labeled the contact as not solicited (consolation proper). Following a recent article on post-conflict third-party affiliation by Call *et al.* (2002), we calculated individual Triadic Contact Tendencies (TCT, a calculation similar to CCT) and used them to find out the mean TCT of the group.

We used the Wilcoxon matched-pair, signed-ranks test (corrected for ties; Siegel and Castellan, 1988) to assess differences between the number of attracted and dispersed pairs. When using dyads, we used the Monte Carlo method with 10,000 iterations to avoid errors due to non-independence of the data.

We used the binomial test (Siegel and Castellan, 1988) to check for differences between adult males and adult females in initiating first affinitive contact after a conflict.

We used the G-test (Siegel and Castellan, 1988) to compare the frequencies of further attacks among group members when neither reconciliation nor triadic contacts occurred and when only solicited and not solicited contacts were present. We also used the test to compare the rates of presence and absence of consolation when reconciliation occurred and when it was absent. Because 63 of 127 cases came from only 2 of the individuals, we had to solve the problem with data pooling concerns the independence of dyads used in the G-tests. We included in the G-test a maximum of 10 aggressive encounters for each individual, selecting such agonistic contacts randomly.

All the analyses are 2-tailed, and the level of significance is 0.05. Probabilities between 0.05 and 0.1 are reported as trends. We performed statistical analyses via Microsoft Excel and SPSS 9.05.

RESULTS

Agonistic Interactions

By the all-occurrences sampling method (Altmann, 1974), we recorded 198 agonistic encounters. We collected 115 aggressions among adults, 79 between adults and juveniles, and 4 among juveniles.

Considering all sex-class combinations, we recorded 75 conflicts among females (F-F), 111 between females and males (F-M), and 12 among males (M-M).

The frequency of high-intensity conflicts (stage 2) is significantly higher than that of low-intensity ones (stage 1; analysis at individual level: Wilcoxon's $T^+ = 0$, ties $= 0$, $N = 10$, $p < .01$).

We observed redirection of aggression in only 5 cases.

Post-Conflict Interactions Between Opponents

We collected 128 PC-MC pairs. Considering reconciliation at group level, there is a significant difference between attracted and dispersed pairs (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 6$, ties $= 31$, $N = 45$, $p < .01$). Figure 1 shows the temporal distribution of first affinitive contacts among PC-MC. The mean CCT of all dyads was 14.4% ± 4.5 SEM (Table II).

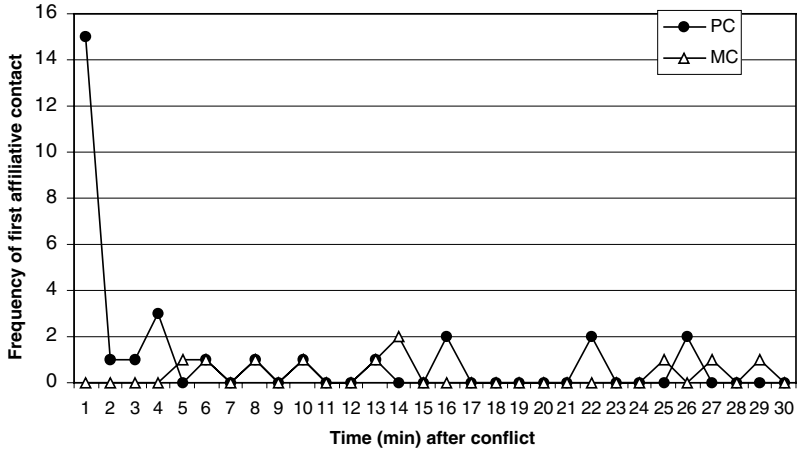

Fig. 1. Temporal distributions of first affinitive contacts in PC (black circles) and MC (white triangles) for reconciliation.

Table II. Reconciliation, solicited and nonsolicited contacts (consolation): Conciliatory tendencies, number of attracted (A), dispersed (D), and neutral (N) pairs for each focal individual

	Contacts between opponents				Contacts between victims and third parties							
Focal	A	D	N	CCT %	A Solicited	A Not solicited	D Solicited	D Not solicited	N Solicited	N Not solicited	TCT % Solicited	TCT% Not solicited
Bibi	1	0	5	16.7	5	8	0	3	0	2	100.0	38.5
Dalila	0	0	1	0	*****	0	*****	0	*****	2	*****	0
Irala	3	1	3	28.6	1	11	0	2	0	0	100.0	69.2
Kidogo	2	2	2	0	4	3	0	2	0	0	100.0	20.0
Kisiwa	0	0	4	0	3	0	0	1	0	0	100.0	−100.0
Lobo	2	0	4	33.3	2	6	1	0	0	1	33.3	85.7
Mandji	2	2	5	0	1	4	0	2	0	0	100.0	33.3
M'bewe	1	2	5	−12.5	3	2	0	0	0	1	100.0	66.7
Mintha	2	0	28	6.7	1	4	0	4	0	4	100.0	0
Miliki	2	0	9	18.2	3	3	0	3	0	1	100.0	0
M'kono	1	0	6	14.3	2	3	2	0	2	1	0	75.0
Uzuri	9	2	21	21.9	3	14	1	2	1	2	40.0	66.7
TOTAL	25	9	93		28	58	4	19	3	14		
Group CCT% ± SEM				10.6 ±4.0							79.4 ±11.0	29.6 ±15.0

As regards reconciliation among adults, there is a significant difference between attracted and dispersed pairs only in F-M dyads (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 0$, ties $= 3$, $N = 12$, $p < .05$, mean $CCT_{F-M} = 31.6\% \pm 8.8$ SEM). There is no significant difference in F-F dyads (Wilcoxon's $T^+ = 0$, ties $= 11$, $N = 12$, n.s.), and it was not possible to compare attracted and dispersed pairs in M-M dyads because of the small sample size ($N = 1$) (Fig. 2).

Taking into account the reconciliation between adults and juveniles, there is statistical significant difference between attracted and dispersed pairs (Wilcoxon's $T^+ = 2.5$, ties $= 16$, $N = 20$, n.s.).

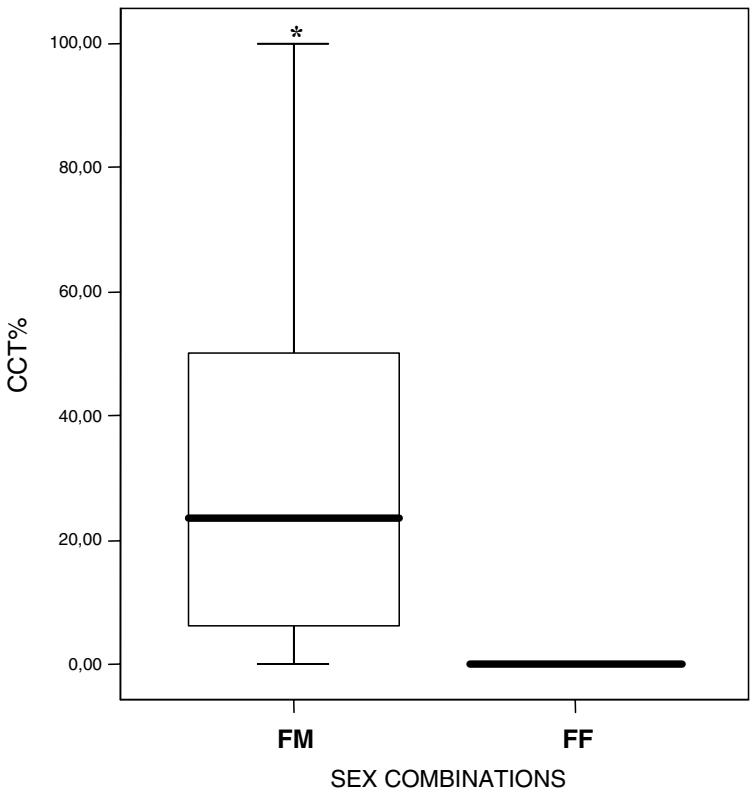

Fig. 2. CCT levels according to the sex-class combination of the adult opponents. Solid horizontal lines indicate medians; length of the gray boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values. $^*p < .05$.

Table III. Group of first affinitive contacts for reconciliation and consolation-frequencies of the various items

Kind of first contact	Reconciliation	Consolation
Contact sitting	1	4
Embrace	1	1
Grooming	0	1
Play	1	10
Touching	21	36
Touching in walk	1	5

It was not possible to verify the occurrence of reconciliation among juveniles owing to the small sample size ($N = 1$).

Considering only adult male-female aggressions, the binomial test revealed no significant difference between males and females in initiating first affinitive contact after a conflict (binomial test: $N_1 = 6$, $N_2 = 7$, n.s.).

Taking into account the intensity level of agonistic encounters (independently of sex-age classes of the opponents), there is a significant difference between attracted and dispersed pairs for conflicts with physical contacts (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 0$; ties = 31; $N = 45$; $p < .001$, mean CCT 16.2% ± 4.3 SEM). As regards low intensity conflicts, there is no significant difference between attracted and dispersed pairs (Wilcoxon's $T^+ = 1$; ties = 8; $N = 9$; n.s.).

Considering first affinitive contacts used to reconcile, there is a significant difference between attracted and dispersed pairs only for touching (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 0$; ties = 0; $N = 10$; $p < .01$) (Table III).

Post-Conflict Interactions Between Victims and Third Parties

We analyzed every possible contact between victims and third parties, distinguishing contacts as either solicited or not solicited (consolation proper) by the victim. Considering the entire group, there is a significant difference between attracted and dispersed pairs both for solicited contacts (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 0$, ties = 2, $N = 11$, $p < .05$) and consolation (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 3.5$, ties = 1, $N = 12$, $p < .05$). The temporal distributions of first affinitive contacts among PC-MC for consolation and solicited contacts are in Fig. 3a and b, respectively.

The mean TCT of all focal individuals for solicited contacts is 76.4% ± 12.6 SEM and for consolation is 41% ± 15 SEM (Table II). Comparing

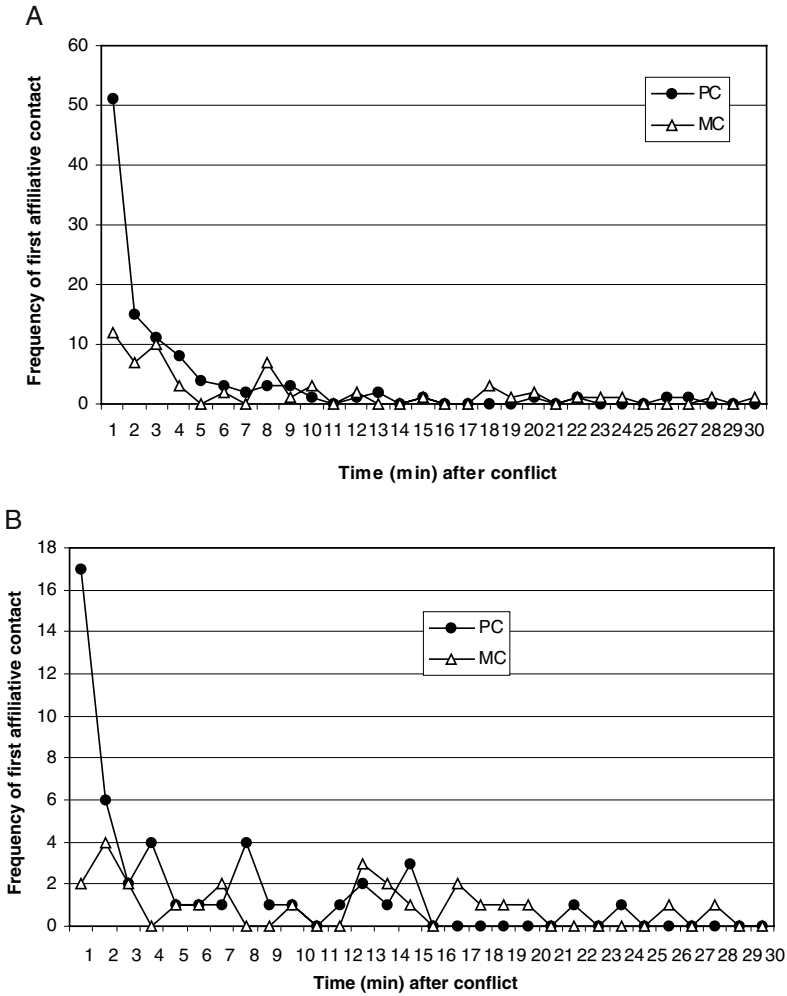

Fig. 3. (**a**) Temporal distribution of first affinitive contacts in PC (black circles) and MC (white triangles) for nonsolicited contacts (consolation). (**b**) Temporal distribution of first affinitive contacts in PC (black circles) and MC (white triangles) for solicited contacts.

individual TCT of solicited contact and consolation, there is no significant difference (Wilcoxon's $T^+ = 44$, ties $= 0$, $N = 11$, n.s.). There is a significant difference between individual CCT and TCT of solicited contacts (TCT solicited contacts > CCT: Wilcoxon's $T^+ = 4$; ties $= 0$; $N = 11$; $p < .05$) and, comparing individual CCT with consolatory TCT, we obtained a

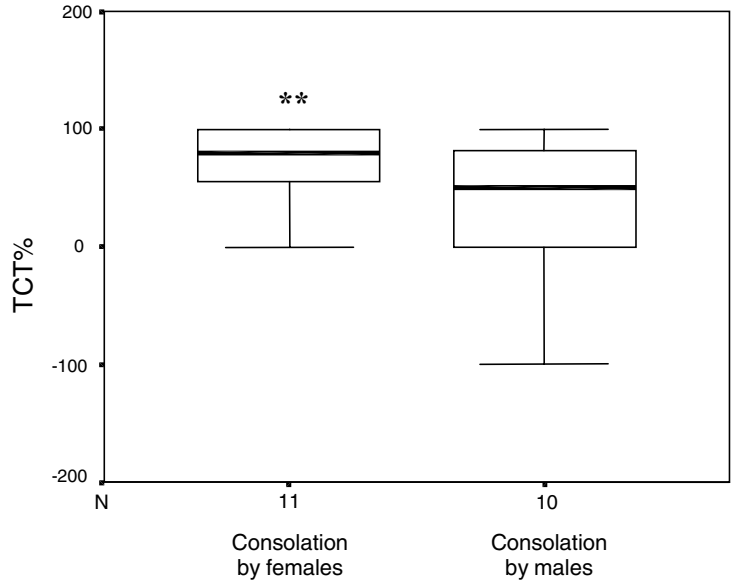

Fig. 4. TCT levels according to the sex of consoler. Solid horizontal lines indicate medians; length of the gray boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values. $^{**}p < .01$.

statistical trend (TCT of not solicited contacts > CCT: Wilcoxon's $T^+ = 11$; ties $= 0$; $N = 11$; trend).

According to the sex-class, in the case of females as consolers there is a significant difference between attracted and dispersed pairs both for solicited (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 0$, ties $= 2$, $N = 9$, $p < .05$; mean TCT $= 70.4\% \pm 15.2$ SEM) and non-solicited contacts (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 0$, ties $= 1$, $N = 11$, $p < .01$; mean TCT $= 69.2\% \pm 10.3$ SEM). In the case of males as consolers there is a statistical trend for solicited contacts (Wilcoxon's $T^+ = 0$, ties $= 1$, $N = 6$, trend) and there is no difference for consolatory contacts (Wilcoxon's $T^+ = 9$, ties $= 1$, $N = 10$, n.s.; Fig. 4).

Considering the age-class, in the case of immature individuals as consolers, there is a significant difference between attracted and dispersed pairs both for solicited (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 2.5$, ties $= 1$, $N = 9$, $p < .05$ mean $TCT_{Imsoll} = 63.9\% \pm 23.2$ SEM) and not solicited contacts (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 4.5$, ties $= 1$, $N = 12$, $p < .05$ mean $TCT_{Imcons} = 40.1\% \pm 14.9$ SEM; 20 contacts toward their mothers, 22 contacts toward their siblings and 32 contacts toward unrelated individuals). In particular, there is a

significant difference between attracted and dispersed pairs both when immature individuals consoled kin (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 0$, ties $= 2$, $N = 9$, $p < .05$; mean TCT $= 49.1\% \pm 11.5$ SEM) and when they consoled nonkin (Wilcoxon's $T^+ = 5$, ties $= 1$, $N = 10$, $p < .05$; mean TCT $= 51.7\% \pm 19.6$ SEM). TCT values for related and unrelated dyads are not different (Wilcoxon's $T^+ = 21$, ties $= 0$, $N = 7$, n.s.).

In the case of adults as consolers, there is a statistical trend for solicited contacts (Wilcoxon's $T^+ = 4$, ties $= 0$, $N = 8$, trend) and no significant difference for consolation (Wilcoxon's $T^+ = 0$, ties $= 1$, $N = 5$, n.s.; 2 contacts toward their offspring and 3 contacts towards unrelated individuals).

As for reconciliation, taking into account first affinitive contacts used to console there is a significant difference between attracted and dispersed pairs only for touching (attracted pairs > dispersed pairs: Wilcoxon's $T^+ = 0$; ties $= 0$; $N = 8$; $p < .05$) (Table III).

After a conflict, comparing the rates of further attacks among group members when neither reconciliation nor triadic contacts occurred ($N_{\text{presence attacks}} = 5$, $N_{\text{absence attacks}} = 10$) and when only triadic contacts were present ($N_{\text{presence attacks}} = 13$, $N_{\text{absence attacks}} = 74$), there is a statistical trend ($G = 2.43$; df $= 1$; ns).

Time Association

To compare the rates of consolation in the presence and absence of reconciliation, we counted how many times consolatory contacts followed or preceded conciliatory contacts in the PC, obtaining the following results: when reconciliation occurred, consolation occurred in 5 cases and was absent in 8 cases. When reconciliation did not occur, consolation occurred in 63 cases and was absent in 3 cases.

Comparing these values, there is no statistical significance ($G = 20.083$; df $= 1$; $p < .001$).

DISCUSSION

In the wild, Watts (1995a) found that reconciliation did not occur among individuals of the same sex-class, but it occurred in adult male-female dyads. We obtained the same results for captive western gorillas (prediction 1 confirmed). The high rates of conciliatory contacts between males and females affected the occurrence of reconciliation at group level. According to Cords (1997, p. 40) "... reconciliation was directed strategically to valuable partners, but also the likelihood of its occurrence could be

adjusted when the value of partners changed …". Moreover, our findings are in agreement with the hypothesis that reconciliation is not an artefact of captivity or limited space (prediction 1 confirmed) (Aureli, 2004; Aureli *et al*., 2002; Colmenares, 2004; Kappeler, 1993).

Many authors described social relationships as investments from which partners should gain benefits (Aureli *et al*., 2002; Cords, 1997; Cords and Aureli, 2000; Paoli, 2004; Preuschoft *et al*., 2002; Watts, 2004). Relationship value seems to influence the occurrence of conciliatory tendencies among fellows (Aureli *et al*., 2002; Cords, 1997; Cords and Aureli, 2000; Preuschoft *et al*., 2002). In gorillas, both in captivity (at least in the Apenheul colony) and in the wild, reconciliation seems to occur only in dyads with valuable social bonds, i.e., adult male-female pairs (Cords and Aureli, 2000; Watts, 1995a; Watts *et al*., 2000). Moreover, considering the initiator of first affinitive contacts after adult male-female conflicts, we did not find any significant difference between the 2 sexes. This result suggests that reconciliation is a male-female strategy: males could induce females to stay close to them and females, the most vulnerable part in conflicts, could reduce the likelihood of renewed aggressions by males (Preuschoft and van Schaik, 2000; Watts, 1995a).

Considering triadic contacts, our findings highlight the presence of consolation and solicited contacts in the Apenheul colony (first part of prediction 2 confirmed). Further, as for the age and sex of consolers, we underscore that immature females are responsible for most triadic contacts (last part of prediction 2 not confirmed). This result can be partly due to the presence of many mother-offspring pairs. The parent-offspring relationship is characterized by an emotional link between individuals that enhances the ability to perceive the other's distress, e.g., screaming of an infant and, consequently, to provide or receive care (Preston and de Waal, 2002; Schino *et al*., 2004). As consolation is present among related individuals our data support the idea. It is plausible that immature gorilla females, feeling threatened by an aggressive situation, seek reassurance from their mothers, instead of offering reassurance.The emotional linkage between parent and offspring might have a profound effect on reproductive success (Preston and de Waal, 2002). Watts *et al*. (2000) suggested that contacts with related targets could have indirect fitness benefit if they decrease the likelihood of further attacks and quickly alleviate stress.

Nevertheless, we found that immature gorillas directed consolatory contacts also toward unrelated individuals at significant levels. Aureli and de Waal (1996) proposed the Social Cognition Hypothesis to explain in part the occurrence of consolation in chimpanzees: empathy—the cognitive ability to perceive the distress of a conspecific—seems to be a necessary prerequisite for the occurrence of consolation (Aureli and Schaffner, 2002; Aureli

and Smucny, 2000; Cords, 1997; de Waal and Aureli, 1996; Preston and de Waal, 2002). Even if empathy may be the prime mover of consolatory contacts, other factors have to concur to the occurrence of consolation. Given that among group living primates, victims of recent aggressions are often the target of renewed attack (Aureli and van Schaik, 1991), it is even possible to hypothesize that group members should avoid interacting with them (Aureli *et al*., 1994; Schino *et al*., 2004). In this perspective, why do the immature gorillas, the most vulnerable part of the group, console unrelated and related victims to the same extent? We can try to suggest some hypotheses on this opened question. Because initiating an affinitive contact with an unrelated victim demands consideration of possible risks (Watts *et al*., 2000; Wittig and Boesch, 2003), it may be that infants and juveniles are less able to evaluate such risks. In addition, immature subjects, protected by their mothers, probably face fewer risks in initiating triadic contacts compared to adults.

In chimpanzees, Palagi *et al*. (2006) found that the occurrence of consolation reduced the likelihood of further attacks among group members. From this perspective, third parties may gain direct benefits from initiating consolatory contacts. In the Apenheul gorillas, we did not obtain the same finding (prediction 4 not confirmed). Because in gorilla society the α-male plays a fundamental role in preventing the spreading of conflicts throughout the entire group, triadic contacts may become ineffective for this function.

Watts *et al.* (2000, p. 293) stated that "consolation may even substitute for reconciliation in stress reduction and protection." Two captive studies on *Pan paniscus* (Palagi *et al.*, 2004) and *Pan troglodytes* (Palagi *et al*., 2006) showed a higher level of consolation in the absence of reconciliation. For the Apenheul gorillas we found the same result (prediction 3 confirmed). When reconciliation fails to occur, consolation seems to function as a post-conflict alternative mechanism for reducing stress in the victim.

Finally, formulating general patterns on consolation is clearly difficult, given the strong dependence of consolatory contacts from a wide range of variables related both to the social context and to the high individual variability typical of the great apes.

ACKNOWLEDGMENTS

The University of Pisa (Italy) supported the research. We thank the Apenheul Primate Park (The Netherlands): the Director Leobert E.M. de Boer, General Curator Frank Rietkerk, and the gorilla keepers for allowing and facilitating this work; Daniela Antonacci and Elena Chiarugi for

collaboration in the data collection; Tommaso Paoli and Leonardo Dapporto for useful discussions.

REFERENCES

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour* 49: 227–265.

Arnold, K., and Whiten, A. (2001). Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Behaviour* 138: 649–690.

Aureli, F. (1992). Post-conflict behaviour among wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.* 31: 329–337.

Aureli, F. (1997). Post-conflict anxiety in nonhuman primates: The mediating role of emotion in conflict resolution. *Aggr. Behav.* 23: 315–328.

Aureli, F. (2004). Is reconciliation an artefact of captivity?. *Folia Primatol.* 75: 75.

Aureli, F., and Schaffner, C. M. (2002). Relationship assessment through emotional mediation. *Behaviour* 139: 393–420.

Aureli, F., and Smucny, D. (2000). New directions in conflict resolution research. *Evol. Anthropol.* 6: 115–119.

Aureli, F., and van Schaik, C. P. (1991). Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): II. Coping with the uncertainty. *Ethology* 89: 101–114.

Aureli, F., Cords, M., and van Schaik, C. P. (2002). Conflict resolution following aggression in gregarious animals: A predictive framework. *Anim. Behav.* 63: 1–19.

Aureli, F., Das, M., Verleur, D., and van Hoof, J. A. R. A. M. (1994). Postconflict social interactions among Barbary macaques (*Macaca sylvanus*). *Int. J. Primatol.* 15: 471–485.

Byrne, R. W., and Whiten, A. (eds) (1988). Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans. Claredon Press/Oxford University Press.

Call, J., Aureli, F., and de Waal, F. B. M. (2002). Postconflict third party affiliation in stumptailed macaques. *Anim. Behav.* 63: 209–216.

Cheney, D. L., Seyfarth, R. M., and Silk, J. B. (1995). The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Anim. Behav.* 50: 249–257.

Colmenares, F. (2004). Post-conflict affiliation in non-human primates: An artefact of captivity?. *Folia Primat.* 75: 80.

Cords, M. (1997). Friendships, alliances, reciprocity and repair. In Whiten, A., and Byrne, R. W. (eds), *Machiavellian Intelligence II*. Cambridge University Press, Cambridge, UK, pp. 24–49.

Cords, M., and Aureli, F. (2000). Reconciliation and relationship qualities. In Aureli, F., and de Waal, F. B. M. (eds.), *Natural Conflict Resolution*. University of California Press, Berkeley, pp 177–198.

de Waal, F. B. M. (1987). Tension regulation and nonreproductive functions of sex in captive bonobos (*Pan paniscus*). *Nat. Geograph. Res.* 3: 318–335.

de Waal, F. B. M., and Aureli, F. (1996). Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. In Russon, A. E., Bard, K. A., and Parker, S. T. (eds.), *Reaching into Thought: The Minds of the Great Apes*. Cambridge University Press, Cambridge, UK, pp. 80–110.

de Waal, F. B. M., and van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behav. Ecol. Sociobiol.* 5: 55–66.

de Waal, F. B. M., and Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus monkeys. *Behaviour* 85: 224–241.

Fuentes, A., Malone, N., Sanz, C., Matheson, M., and Vaughan, L. (2002). Conflict and postconflict behavior in a small group of chimpanzees. *Primates* 43: 223–235.

Harcourt, A. H. (1979). Social relationships among female mountain gorillas. *Anim. Behav.* 27: 251–264.
Kappeler, P. M. (1993). Reconciliation and post-conflcit behaviour in ringtailed lemurs, *Lemur catta* and redfronted lemurs, *Eulemur fulvus rufus*. *Anim. Behav.* 45: 901–915.
Kappeler, P. M., and van Schaik, C. P. (1992). Methodological and evolutionary aspects of reconciliation among primates. *Ethology* 92: 51–69.
Koyama, N. F. (2001). The long-term effects of reconciliation in Japanese macaques (*Macaca fuscata*). *Ethology* 107: 975–987.
O'Connell, S. M. (1995). Empathy in chimpanzees: Evidence for theory of mind? *Primates* 36: 397–410.
Palagi, E., Cordoni, G., and Borgognini Tarli, S. (2006). Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). *Am. J. Phy. Anthropol.* 129: 105–111.
Palagi, E., Paoli, T., and Borgognini Tarli, S. (2004). Reconciliation and consolation in captive bonobos (*Pan paniscus*). *Am. J. Primatol.* 62: 15–30.
Paoli, T. (2004). Aggressività e riconciliazione nei primati non-umani. In Telleschi, T. (ed.), *Per una cultura del conflitto e della convivenza*. PLUS Pisa University Press, Pisa, pp. 161–181.
Parnell, R. J. (2002). Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *Am. J. Primatol.* 56: 193–206.
Preston, S. D., and de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behav. Brain Sci.* 25: 1–72.
Preuschoft, S., and van Schaik, C. P. (2000). Dominance and communication. In Aureli, F., and de Waal, F. B. M. (eds.), *Natural Conflict Resolution*. University of California Press, Berkeley, pp. 77–105.
Preuschoft, S., Wang, X., Aureli, F., and de Waal, F. B. M. (2002). Reconciliation in captive chimpanzees: A reevaluation with controlled methods. *Int. J. Primatol.* 23: 29–50.
Schino, G., Geminiani, S., Rosati, L., and Aureli, F. (2004). Behavioral and emotional response of Japanese macaque (*Macaca fuscata*) mothers after their offspring receive an aggression. *J. Comp. Psychol.* 118: 340–346.
Siegel, S., and Castellan, N. J. (1988). *Nonparametric Statistics for the Behavioral Sciences*, 2nd ed. McGraw-Hill, New York.
Stoinski, T. S., Hoff, M. P., and Maple, T. L. (2003). Proximity patterns of female western lowland gorillas (*Gorilla gorilla gorilla*) during the six months after parturition. *Am. J. Primatol.* 61: 61–72.
Stokes, E. J., Parnell, R. J., and Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behav. Ecol. Sociobiol.* 54: 329–339.
Tomasello, M., and Call, J. (1997). *Primate Cognition*. Oxford University Press, Oxford, UK.
Van Hooff, J. A. R. A. M. (2001). Conflict, reconciliation and negotiation in non-human primates: The value of long-term relationships. In Noe, R., Van Hooff, J. A. R. A. M., and Hammerstein, P. (eds.), *Economics in Nature-Social Dilemmas, Mate Choice and Biological Markets*. Cambridge University Press, Cambridge, UK, pp. 67–89.
Veenema, H. C., Das, M., and Aureli, F. (1994). Methodological improvements for the study of reconciliation. *Behav. Proc.* 31: 29–38.
Walters, J. R., and Seyfarth, R. M. (1987). Conflict and cooperation. In Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R., and Struhsaker, T. (eds.), *Primate Societies*. The University of Chicago Press, London, pp. 306–317.
Watts, D. P. (1994). Agonistic relationships of female mountain gorillas. *Behav. Ecol. Sociobiol.* 34: 347–358.
Watts, D. P. (1995a). Post-conflict social events in wild mountain gorillas (Mammalia, Hominoidea). I. Social interactions between opponents. *Ethology* 100: 139–157.
Watts, D. P. (1995b). Post-conflict social events in wild mountain gorillas. II. Redirection, side direction, and consolation. *Ethology* 100: 158–174.
Watts, D. P. (1996). Comparative socioecology of mountain gorillas. In McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *Great Ape Society*. Cambridge University Press, Cambridge, UK, pp. 16–28.

Watts, D. P. (2003). Gorilla social relationships: A comparative overview. In Taylor, A. B., and Goldsmith, M. L. (eds.), *Gorilla Biology—A Multidisciplinary Perspective*. Cambridge University Press, Cambridge, pp. 302–327.

Watts, D. P. (2004). Conflict management and resolution and 'valuable relationships'. *Folia Primatol.* 75: 72.

Watts, D. P., Colmenares, F., and Arnold, K. (2000). Redirection, consolation, and male policing-how targets of aggression interact with bystanders. In Aureli, F., and de Waal, F. B. M. (eds.), *Natural Conflict Resolution*. University of California Press, Berkeley, pp. 281–301.

Wittig, R., and Boesch, C. (2003). The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour* 140: 1527–1560.

Yamagiwa, J., Kahekwa, J., and Basabose, A. K. (2003). Intra-specific variation in social organization of gorillas: Implications for their social evolution. *Primates* 44: 359–369.

York, A. D., and Rowell, T. E. (1988). Reconciliation following aggression in Patas monkeys (*Erythrocebus patas*). *Anim. Behav.* 36: 502–509.