



Reconciliation in Captive Chimpanzees: A Reevaluation with Controlled Methods

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Affiliative postconflict reunions—reconciliations—of former opponents were first demonstrated in the chimpanzees at the Arnhem Zoo. Since then methods have been considerably refined, and reconciliation has been demonstrated in a large number of primates and also some gregarious nonprimates. This study, conducted with a different captive group, is the first to use the revised methodology with chimpanzees. We analyzed a total of 297 agonistic conflicts with the PC–MC method: we observed focal individuals for 15 min after a conflict and during matched control observations the next day. The mean conciliatory tendency of the 16 chimpanzees was 41%, with a range in different age-sex classes of 58% (among adult females) to 19% (among adult vs. immature males). After conflicts, former opponents were selectively attracted to one another. Preferential contact with previous opponents persisted when activity level during matched controls was controlled for statistically. Opponents that were frequent grooming partners reconciled more frequently, but the frequency of agonistic support had no such effect. Our findings thus confirm the existence of reconciliation in chimpanzees, which show one of the highest conciliatory tendencies among primate species.

KEY WORDS: reconciliation; *Pan troglodytes*; apes; friendship; support.

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INTRODUCTION

That aggression is often the prelude to affiliative interactions by reducing interindividual distances was initially overlooked by ethologists. It was not before the late 1970s that systematic studies of social behavior amassed to refute the view that aggression is unavoidably deleterious and leads to increased distances between individuals (de Waal, 1986). Today we know that social animals have vast repertoires of peace-keeping mechanisms, including ritualized submission and appeasement to halt aggression, and preventive mechanisms such as reassurance behaviors by which dominants put nervous subordinates at ease (de Waal, 1986; Moynihan, 1998; Preuschoft, 1995; Preuschoft and van Schaik, 2000; Schenkel, 1967). In primates, as in other intensely social animals, agonistic conflicts regularly lead to conspicuous reunions during which former opponents engage in affiliative behavioral rituals, such as embracing, grooming, or kissing (stump-tailed macaques: Blurton Jones and Trollope, 1968; chimpanzees: van Lawick-Goodall, 1968; spotted hyenas: Kruuk, 1972; lions: Schaller, 1972; dwarf mongoose: Rasa, 1977). Today, we label such affiliative postconflict reunions reconciliations (de Waal and van Roosmalen, 1979).

While it is relatively easy to define reconciliation operationally, the term carries the functional implication of being a mechanism to repair a social bond that has been strained in the previous conflict (Cords, 1992; Kappeler and van Schaik, 1992). The term reconciliation for friendly reunions between former opponents implies (a) an increased probability for friendly interaction after aggressive conflicts, (b) that former opponents actively seek out one another for these friendly reunions, and (c) that these contacts function to mend a disturbed relationship (as demonstrated by Aureli and van Schaik, 1991b; Cords, 1992, 1993; de Waal, 1993).

Evidence of reconciliation in nonhuman animals was first produced for a group of 20 chimpanzees (*Pan troglodytes*) at the Arnhem Zoo, in the Netherlands (de Waal and van Roosmalen, 1979). To document friendly reunions participants in a total of 350 aggressive episodes were observed for 45 min after termination of hostilities. Although no control observations were made outside the context of aggressive conflicts, the data showed that after the conflict, former opponents preferred to affiliate with each other rather than with third parties: If former opponents would affiliate randomly with any of their 19 group mates the percentage of interopponent affiliation should not exceed 1/19 (5.3%) of one opponent's affiliative contacts. However, within 5 min after the conflict 30% of an individual's affiliative contacts were with its former opponent, which indicates selective attraction to the former opponent. Postconflict affiliative contacts started as

early as in the first min after the conflict and reached an asymptote after ca. 16 min.

The problem with this study was that no baseline affiliation frequencies were established. As a consequence, it remains unclear if affiliation was more frequent after conflicts than without a previous conflict. Furthermore, the preference of former opponents to contact one another in the postconflict period may simply have reflected a general preference to affiliate with one another, independently of previous conflicts. This is actually a sound possibility as some studies have shown that individuals that frequently fight also affiliate frequently (*Macaca mulatta*: Bernstein and Ehardt, 1985; de Waal and Luttrell, 1988).

Thus, after this first exploratory study, carefully controlled investigations were needed. The study by de Waal and Yoshihara (1983) on rhesus monkeys set standards that were later followed by most other students of reconciliation (Aureli and de Waal, 2000). Here, postconflict observations were matched with control observations so that interopponent contact frequency is not only compared to opponent-other group member contact frequency, as by de Waal and van Roosmalen (1979), but also the comparison is made for interopponent contact frequency after the conflict versus under standard conditions without a previous fight.

According to this standard procedure, postconflict observations are started immediately after the last aggressive interaction. Along with affiliative interactions that represent the re-establishment of contact after the opponents first dispersed, reconciliation thus includes contacts immediately following hostilities, such as appeasement—initiated by recipients of aggression—and reassurance: initiated by aggressors (de Waal, 1992).

THE VALUABLE RELATIONSHIP HYPOTHESIS

If reconciliations function to repair bonds that have been strained during the previous conflict they should be most predictable among individuals that have particularly valuable relationships (Cords and Aureli, 2000). In fact, in many species reconciliation is more frequent among related than unrelated individuals (Aureli *et al.*, 1997; de Waal and Aureli, 1996). It therefore seems that the closeness of an affiliative bond is a good predictor of reconciliation (Cords, 1997; de Waal and Yoshihara, 1983; Kappeler and van Schaik, 1992). This is the friendship hypothesis (Cords, 1997). Conversely, individuals also have stronger tendencies to reconcile with partners that they need for cooperation, or depend on otherwise (Cords, 1997; Cords and Aureli, 1993;

Cords and Thurnheer, 1993; Kappeler and van Schaik, 1992; van Schaik and Aureli, 2000). The valuable-relationship hypothesis goes back to a classic paper by Kummer (1978), who suggested that we regard social relationships as investments. Accordingly, the value of a relationship refers to how social partners benefit from one another.

Evidently, these two hypotheses are not entirely independent of one another. Friendship is usually measured in the frequency of grooming and spatial proximity between two individuals. Relationship value is frequently inferred from agonistic support or expertise related to food acquisition (Cords, 1997; Cords and Aureli, 1993; Cords and Thurnheer, 1993; van Schaik and Aureli, 2000; Watts, 1995). Relationships characterized by strong bonds are often those in which agonistic aiding is regularly observed (Seyfarth and Cheney, 1984; Sterck *et al.*, 1997). However, friendship is not always reflected in support frequency (de Waal, 1984). In addition, individuals engaged in friendships may differ in how they are useful to one another. Even if the relationship is reciprocal, the partner may pay back in a different commodity for the benefits received (de Waal, 1997a; Hand, 1986). As a result, it is possible that reconciliation is predicted by bond strength (the mutual measure), but not by support frequency, which may be very asymmetric in a dyad.

As the notion that reconciliation in nonhuman animal societies occurs at all has gained ground, studies were designed to demonstrate the occurrence of reconciliation in yet other species. Recently, however, the idea that reconciliation depends on the quality of dyadic relationships has received increasing attention. From a functional perspective, it is to be expected that individuals that depend on one another should be particularly interested in mending their relationship once aggression has occurred between them. Conversely, even in a species in which the mechanism of reconciliation has been demonstrated we may not expect each and every dyad to engage in postconflict affiliation, because not all group members are engaged in particularly valuable relationships with one another.

As a result of the vivid research interest in reconciliation (Aureli and de Waal, 2000), there is now a growing body of evidence documenting reconciliation, mostly in species of primates, but also in goats, hyenas and dolphins (Schino, 2000). Moreover, since most of these studies adhered to the same methodology the results are directly comparable yielding insights in the evolutionary and social dynamics governing the occurrence of reconciliation. Ironically, with all the methodological refinement, the species of the first study, *Pan troglodytes*, has never been re-investigated. As a result, chimpanzees are almost the only species for which no controlled data comparable with those for other species existed. We aim to fill the gap.

SUBJECTS AND METHODS

Subjects

Results are based on observations of an enclosure housed group of chimpanzees at the Yerkes Regional Primate Research Center Field Station, Lawrenceville, Georgia, USA.

The group was composed >10 years prior to the study, and inhabits an outdoor compound of 720 m². The single adult male entered the group in 1991. By the time of our study (May–September 1995) the study group comprised 5 unrelated adult females and their offspring (altogether 17 maternal kin dyads), and one female and one male without maternal relatives in the group. The group contained 19 individuals of all demographic classes (Table I).

Data Collection and Definitions

Wang recorded spontaneously occurring conflicts and postconflict interactions from an observation tower overlooking the compound between 8:00 and 18:00 h, excluding feeding time. Data collection focused on the adults, adolescents, and juveniles ($N = 16$). We considered interactions an agonistic conflict if at least one of the following strictly agonistic behavior patterns occurred: tug, brusque rush, trample, bite, grunt-bark, shrill-bark, flight, crouch, shrink/flinch, or bared-teeth scream (de Waal and van Hooff, 1981; van Hooff, 1973). This criterion is the same as that used by de Waal and van Roosmalen (1979).

Recording of Conflicts

We recorded agonistic conflicts ad libitum and categorized agonistic interactions according to intensity, ranging from biting/trampling over other forms of contact aggression, noncontact aggression and threat, to screaming

Table I. Demographic composition of the study group

Age Class	Age (Years)	Females	Males
Adult	≥10	7	1
Adolescent	8–9	3	1
Juvenile	4–7	2	2
Infant	0–3	2	1

and temper tantrum. One agonistic conflict may include not only the two original opponents but also their supporters. It may thus involve >2 individuals. We divided polyadic conflicts into dyadic components, i.e., the number of agonistic dyads that make up the polyadic conflict in question (de Waal and van Hooff, 1981). As a result, analyses are based either on the number of agonistic conflicts, in which case the focal subject and its main opponent form the unit of analysis, or on all agonistic dyads, in which case all opponents of the focal individual are considered, not just the one with which most intense aggression was exchanged.

Postconflict Observations

Immediately following the last agonistic interaction we initiated a post-conflict observation (PC) on one of the participants: the focal individual. This PC focal individual observation extended for 15 min unless agonism flared again ≤ 2 min, in which case we cancelled the observation and started a new after the aggression had subsided. We chose focal individuals so as to maximize the number of different opponent pairs and the level of aggressive escalation, attempting a balance between focal subjects being initiators versus recipients of aggression. We gave priority in recording to conflicts between adults because they were the rarest.

During the 15 min PC observation period we recorded all affiliative interactions in which the focal individual was involved, irrespective of the identity of the interaction partner. For each affiliative interaction we recorded the time since the beginning of the PC observations and the identity of the partner. We considered potentially conciliatory only PC affiliation that involved the focal individual and ≥ 1 of its former opponents. We did not analyze in detail PC affiliative contacts between other conflict participants, not involving the focal subject.

We defined affiliative interactions by behaviors such as kiss, embrace, grooming, gentle touch, finger-in-mouth, sexual behavior, social play, and contact sitting (de Waal and van Roosmalen, 1979), and considered affiliation without bodily contact unsuccessful initiation and ignored it in the analyses.

Matched-Control Observations

We matched PC observations with control observations (MC) of 15 min duration, carried out the next suitable day at the same time on the same focal individual—provided that it had not been involved in an agonistic conflict 5 min prior to the start of the MC observations. Analogous to PC observations,

we cancelled control observations if agonistic behavior occurred ≤ 2 min after the start of the protocol. During MC observations we recorded all affiliative interactions in exactly the same fashion as during PC observations.

Data on Relationship Quality

We extracted background information on the quality of relationships from an independent set of observations recorded routinely by several observers in the course of the same year during which the reconciliation data were collected. This data set includes affiliative interactions—grooming and contact sitting—based on group scans sampled at 10 min intervals, and instances of agonistic conflicts (same categories as above), including agonistic support that were collected ad libitum (de Waal, 1989).

Data Analysis

Conciliatory Tendency

The PC–MC method allows one to compare the timing of first affiliative contacts. If a focal individual engaged in affiliative contact with a previous opponent earlier in the PC than in the MC observation the opponent pair is an attracted pair (de Waal and Yoshihara, 1983). A pair in this sense is not a dyad but one pair of opponents in one particular conflict. If the focal subject affiliated with a previous opponent earlier in the MC than in the PC observations, it is a dispersed pair. Neutral pairs had contact at the same time in PC and MC, or did not affiliate in either PC or MC. In any given PC or MC observation a focal individual could potentially affiliate with >1 former opponent. Per agonistic dyad, we classified a pair of opponents as attracted, dispersed, or neutral. For each focal individual we then calculated the conciliatory tendency from the number of attracted, dispersed, and neutral pairs of which the focal was one partner. We entered agonistic dyads into the final analysis only under the name of the focal individual, not for its opponent(s). In this way we avoided coding the same incident twice. We did not consider the focal subject's role in the previous conflict, i.e., whether it started or received aggression or lost or won the conflict.

The percentage of opponent pairs that affiliate earlier in the PC than in the MC observations—attracted pairs—defines the conciliatory tendency (CT: de Waal and Yoshihara, 1983). Veenema *et al.* (1994) revised this measure to make it independent of the time window chosen for the PC observations. This corrected conciliatory tendency (CCT) is now the standard

in reconciliation research (Abegg *et al.*, 1996; Matsumura, 1996; Petit and Thierry, 1994; Verbeek and de Waal, 1997). We calculated CCT values for each focal individual, according to the formula of Veenema *et al.* (1994):

$$\text{CCT} = 100 * (\text{attracted pairs} - \text{dispersed pairs}) / (\text{all pairs})$$

For reasons of comparability with other studies, in Table III we also provide de Waal and Yoshihara's (1983) original CT value, i.e., 100 * attracted pairs/all pairs.

Selective Attraction

If a focal individual affiliates preferentially with a former opponent instead of another group member it is selectively attracted to the former opponent. We measured selective attraction as the percentage of affiliation with the former opponent out of all affiliative interactions in which the focal subject participated. This is calculated separately for PC and MC intervals. The comparison between PC and MC intervals reveals whether reconciliation is due to selective attraction between former opponents. These analyses refer to the interactions between a focal individual and her or his main opponent, and are, therefore, based on the number of agonistic conflicts.

Controlling Activity Levels in MC

To ensure that the chances for interactions were equal in both post-conflict and matched control periods some observers have additionally controlled for the distance among individuals (Cords and Aureli, 1993; de Waal and Ren, 1988; Kappeler, 1993; Watts, 1995; York and Rowell, 1988). We did not control for proximity because in the relatively small enclosure it was easy for the chimpanzees at any time to establish contact with another. Instead, we controlled for the overall level of activity because, as a by-product of high activity levels in the period following a fight, interopponent affiliation may occur more frequently in PC than in MC observations. However, MC periods are not uniformly characterized by a low level of social activity. In order to control for activity levels in PC and MC observations, we used nonagonistic interactions as a measure of activity. We classified MC observations in which the focal individual had fewer nonagonistic interactions than the mean number of nonagonistic interactions in all PC periods as inactive and MC periods in which the focal had more interactions than the PC mean as active.

To assess the possibility that focal individuals would affiliate with previous opponents more readily in PC observations because their activity levels are high, we calculated conciliatory tendency separately for PC observations

matched with active versus inactive MC observations. For activity level controls, the unit of analysis is the number of agonistic episodes with the focal subject and its main opponent as the PC and MC pair.

Assessing Relationship Quality

We defined relationship quality by friendship and usefulness. Our measure of friendship is the frequency of grooming or contact sitting. The independent data pool yielded 1,038 grooming and contact sitting episodes, distributed over the 120 dyads of juvenile, adolescent, and adult group members. Friendship is close when 2 individuals groomed or sat in contact >5 times, medium for dyads that groomed/contact sat 1–5 times, and absent in dyads that never groomed/contact sat. These cut-off values split the number of close, medium, and absent friendships per individual into roughly even thirds.

Relationship value or usefulness was reflected in the frequency with which a recipient of aggression received agonistic support from another individual: the supporter. Results are based on a total of 355 incidents of aggressor support involving any of the group members except for the 3 infants. Support frequency was regular when a supporter aided another individual more than once, rare when support occurred once, and never when there was no instance of support in a dyad. These cut-off values ensure that most individuals had ≥ 1 high, medium and low frequency supporter.

Note that both friendship and usefulness are characteristics of dyads. As a result of our procedure, focal individuals had differing numbers of friends and supporters in the three categories. For each individual we calculated the conciliatory tendency (CCT) separately for the three categories of friends and supporters, respectively. Thus, we obtained three values per focal individual characterizing its CCT in close, medium, and absent friendships, and analogously three values characterizing the focal subjects CCT in regular, rare, and never support relationships.

We used the same background data also to assess the number of conflicts per dyad independently from recording reconciliation data.

Statistical Analysis

We compared individual's CCTs, selective attraction, and active versus inactive MC periods via Wilcoxon signed ranks tests. We followed the procedures indicated by Siegel and Castellan (1988), using asymptotic test when $N > 15$, and exact tests when $N \leq 15$. We used one-way repeated measures

ANOVAs to test within individuals whether CCT was predicted by the two measures for the quality of the relationship between the focal subject and the opponent.

RESULTS

Conflicts

There were 298 agonistic conflicts comprising 401 agonistic dyads. The majority (52%) of agonistic dyads involved an adult and an immature subject (adolescent or juvenile); 35% of the dyads involved 2 of the 7 immatures, and only 13% of the dyads involved 2 of the 9 adults, despite our attempt to collect as many adult-adult conflicts as possible.

We distinguished agonistic dyads according to the highest level of agonism observed: 10% involved biting or trampling, 60% were physical aggression, 24% involved chasing or brusque rush, in 3% a threat occurred, and in 3% one opponent started screaming without receiving overt aggression. Again, this is despite our attempt to sample high-intensity conflicts. The number of agonistic dyads in which a focal subject was involved varied from 6 for one of the adult females to 70 for the adolescent male, with a mean of 25.1 (± 16.3 SD).

Virtually the same distributions characterize the independent data set. Here, independently of age, the highest frequency of conflicts occurred in male–male dyads. The lowest conflict frequencies characterized dyads that involved ≥ 1 adult female (AF–AF, AF–YF, AF–YM, AF–AM, Table II).

Conciliatory Tendency

For each of the 16 focal individuals we determined the number of attracted, dispersed, and neutral pairs over all agonistic dyads combined (Table III). Tested across all focal individuals, the proportion of attracted pairs ($44.9\% \pm 12.4\%$ SD) significantly exceeds the proportion of dispersed pairs ($3.7\% \pm 4.0\%$ SD; Wilcoxon Signed Ranks Test: $N = 16$, $z = 3.52$, $p < 0.001$, one-tailed). The average CCT of all individual focals is 41.2% ($\pm 12.8\%$ SD), ranging from 20.0 to 69.2% (Table III).

Conciliatory tendencies varied greatly between demographic classes (Table II). CCT values above the group average occurred in dyads involving an adult female and a male, irrespective of the male's age, and among two adult females. Classes involving immature females exhibited low CCT values,

Table II. Conciliatory tendency and number of conflicts per demographic class

Age–sex class	CCT (%) ± SD	Number of dyads	Mean number of conflicts ± SD ^a
AM–AF	45.7 ± 54.4	7	2.00 ± 1.73
AF–AF	57.9 ± 46.0	12	0.01 ± 0.29
AM–YM	18.6 ± 28.8	3	11.00 ± 2.65
YM–YM	42.8 ± 18.1	3	7.00 ± 4.58
AF–YF	37.5 ± 38.9	19	0.79 ± 0.98
YF–YF	31.1 ± 23.3	5	3.60 ± 3.13
AF–YM	46.0 ± 37.8	17	1.00 ± 0.87
YF–YM	22.5 ± 50.2	13	2.31 ± 2.69
AM–YF	36.4 ± 38.8	5	2.80 ± 1.92

Note. AM: adult male; AF: adult female; YF: juvenile or subadult female; YM: juvenile or subadult male. AF–YM or YF does not include mother–child dyads. Values per age–sex class are averages across dyads of individuals. The same dyads contributed to the CCT and the conflict values.

^aConflict frequencies were extracted from an independent data set covering the same year in which we collected data on reconciliation.

but the lowest value was is for the combination of the adult male with the immature males. With the exception of immature males (YM–YM) the age–sex classes that had frequent conflicts also had relatively low CCT values, and those that had conflicts only rarely exhibited higher CCT values. Immature

Table III. Conciliatory tendencies, numbers of attracted, dispersed and neutral pairs for each focal individual

Focal	Age–sex class	Attracted	Dispersed	Neutral	Total	CCT (%)	CT (%)
Jimoh	AM	16	4	11	31	38.7	51.6
Reinette	SF	15	2	21	38	34.2	39.5
Gwennie	AF	9	0	9	18	50.0	50.0
Socko	SM	22	4	44	70	25.7	31.4
Mai	AF	5	0	20	25	20.0	20.0
Natasha	SF	18	2	25	45	35.6	40.0
Borie	AF	5	0	5	10	50.0	50.0
Georgia	AF	8	1	7	16	43.8	50.0
Rita	SF	5	0	4	9	55.6	55.6
Kate	JF	9	1	13	23	34.8	39.1
Atlanta	AF	3	0	3	6	50.0	50.0
Rhett	JM	7	1	6	14	42.9	50.0
Peony	AF	9	0	4	13	69.2	69.2
Anja	AF	15	1	12	28	50.0	53.6
Bjorn	JM	15	3	16	34	35.3	44.1
Dona	JF	5	0	16	21	23.8	23.8
Sum		166	19	216	401		
Mean						41.2	44.8

Note. CCT: corrected conciliatory tendency (Veenema *et al.*, 1994: (attracted–dispersed)/(all pairs)); CT: conciliatory tendency (de Waal and Yoshihara, 1983: attracted/(all pairs)), is provided for comparability. Age–sex class: A: adult, S: adolescent, J: juvenile, F: female, M: male.

males amongst each other had many conflicts but also exhibited high CCT scores.

Selective Attraction

Focal individuals had affiliative contact with former opponents as well as other group members both during PC and MC observations. If affiliative contact between former opponents represents reconciliation focal subjects should preferentially affiliate with former opponents during postconflict, but not matched, control observations. This is indeed the case: In a mean of 40.8% ($\pm 10.2\%$ SD) of all PC affiliations was the partner a former opponent—this despite the fact that the former opponent is only one of 15 possible partners. This compares to a mean of 12.7% ($\pm 9.9\%$ SD) affiliations with the same individuals in MC intervals. This difference is significant: The proportion of the contacts of the focal individuals with former opponents is greater in PC than MC observations (Wilcoxon Signed Ranks Test: $N = 16$, $z = -3.52$, $p < 0.001$, one-tailed)

Controlling for Activity Level

Focal individuals might affiliate with previous opponents more readily in PC observations only because their activity levels were higher in PC than in MC intervals. We therefore compared the conciliatory tendencies for active and inactive MC intervals. In line with the prediction, the mean conciliatory tendency (CCT) was stronger if the comparison was with inactive as compared to active MC periods. However, the difference is not statistically significant, (Wilcoxon Signed Ranks Test: $N = 13$, $T+ = 56$, $p = 0.20$, two-tailed).

Effect of Relationship Quality

To assess if the conciliatory tendencies were greater between friends, we conducted a one-way repeated measures ANOVA with friendship (close, medium, absent) as the within-subjects factor, and conciliatory tendency as the dependent variable (Fig. 1). Since not all focal individuals engaged in conflicts with partners of either relationship quality we discarded 9 focal subjects for which we could calculate the CCT only for one or two of the three categories. This left us with $N = 7$ individuals. Indeed, friendship, predicted conciliatory tendency (Fig. 1; $F_{2,12} = 5.098$, $p = 0.025$, and sphericity is not

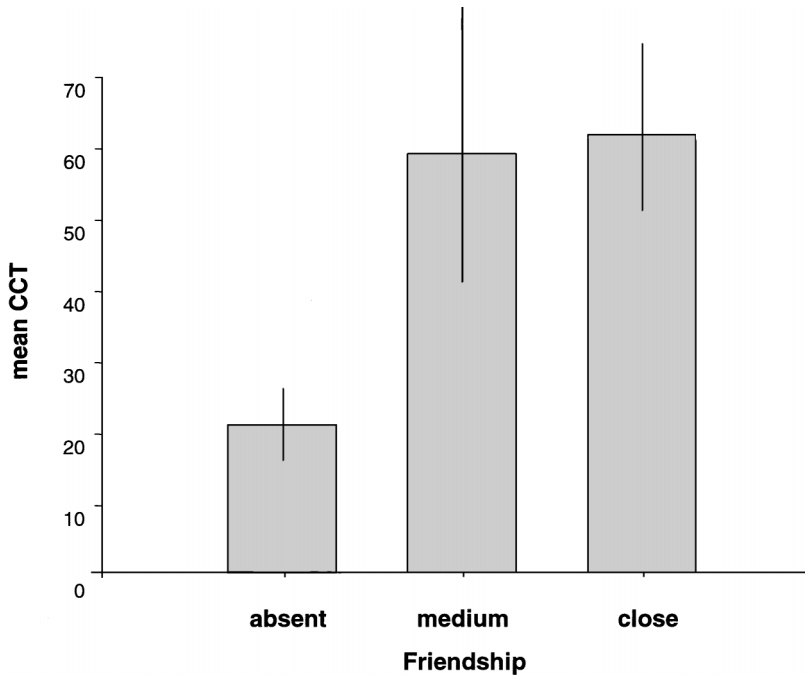


Fig. 1. Mean conciliatory tendencies (CCT) \pm SD of focal individuals ($N = 7$) towards opponents dependent on affiliative relationships, classified as close, medium or no friends. The affiliative relationship was operationalized as frequency of grooming and contact-sitting throughout the year.

significant: Mauchly's $W = 0.825$, $p = 0.617$). Paired comparisons revealed that only the difference between close and absent friendship is significant (Fig. 1; $F_{1,6} = 13.98$, $p = 0.01$), that is to say, focal subjects reconciled more readily with opponents with which they were close friends.

Focal individuals can be expected to reconcile more with opponents that supported them in conflicts on other occasions. We therefore conducted a repeated measures ANOVA with usefulness (support frequency never, rare, regular) as the within-subjects factor, and conciliatory tendency as the dependent variable (Fig. 2). Here, we discarded only 4 focal subjects, which left us with an $N = 12$ focal individuals for which CCT could be calculated for each of the three relationship value categories. Again, sphericity is not significant (Mauchly's $W = 0.688$, $p = 0.152$), but support frequency did not predict the CCT (Fig. 2; $F_{2,22} = 0.198$, $p = 0.822$), that is focal individuals did not reconcile more readily with individuals that supported them when they were aggressed by others.

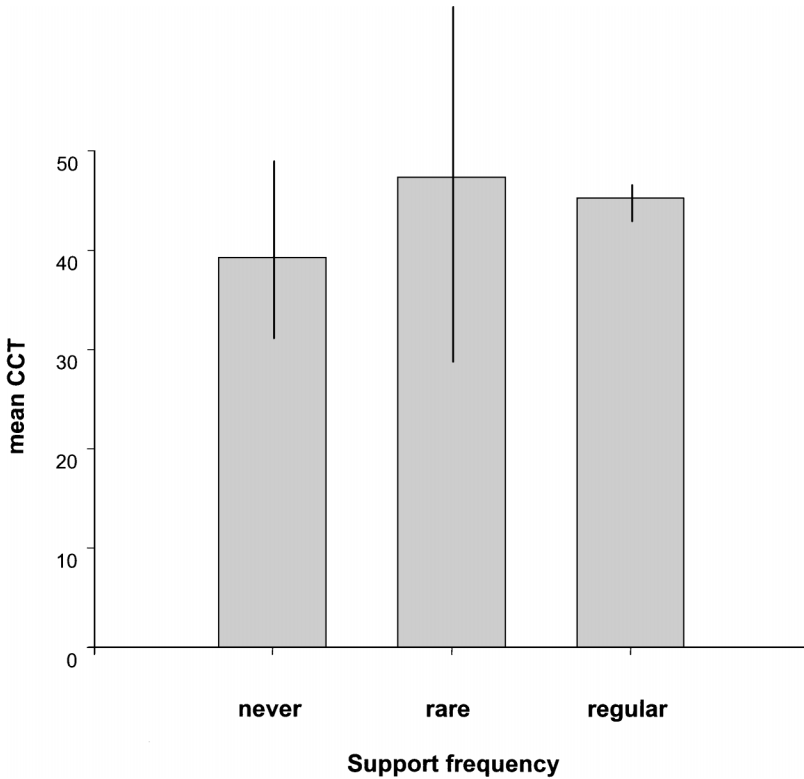


Fig. 2. Mean conciliatory tendencies (CCT) \pm SD of focal individuals ($N = 12$) as a function of relationship value, or usefulness of the opponent. Usefulness was operationalized by the frequency with which the focal individual received aggressor support from the opponent throughout the year.

DISCUSSION

Using an established methodology complemented by rigorous control procedures our study confirms the existence of reconciliation among chimpanzees: Former opponents engaged in affiliative body contact with each other earlier in postconflict than in matched control observations. Individuals preferentially affiliated with a former opponent above all other group members, and this selective attraction was more pronounced in the 15 min after a conflict than in matched control observations. These findings proved robust even after controlling for differences in activity levels between postconflict and matched control observations. Thus, our study complements earlier findings of reconciliation from a colony of chimpanzees at Arnhem

Zoo (de Waal, 1993; de Waal and van Roosmalen, 1979; Griede, 1981). Despite the difference in methods, all the studies evidence the existence of reconciliation in chimpanzees.

We found a conciliatory tendency (CCT) of 41%, averaged over all focal subjects. This is one of the highest values among primates. In fact, the only species with similar percentages of reconciliation are three tolerant macaque species: *Macaca silenus*, (CCT = 44%, 48, 42% in three groups: Abegg *et al.*, 1996), *M. nigra* (CCT = 41%, Petit and Thierry, 1994), and *M. maura* (CCT = 40%, Matsumura, 1996).

Rates and Demography of Reconciliation

Overall group-level CCT values may conceal important variation in the conciliatory tendencies of different subgroups within a social group (Aureli *et al.*, 1997; Aureli and de Waal, 1998; Cords and Aureli, 2000; Thierry, 2000; van Schaik and Aureli, 2000). The CCT value that we used is based on a majority of conflicts in which immatures participated. Yet calculating conciliatory tendencies for different demographic classes separately shows that some individuals, notably the immatures, had CCT values lower than the group average of 41%, while others, notably the adult females, exhibited higher CCT values. We refrained from testing these differences statistically because the number of dyads in the different demographic classes varied greatly. Moreover, the data are not independent, with the same individuals participating in multiple dyads.

In the Arnhem colony, the various demographic classes were also not all equally likely to reconcile: Reconciliation rates among male opponents were higher than the group average, those among females were lower, and male–female opponents ranged in between (de Waal, 1986). In our study, the highest reconciliation rates occurred in female–female dyads and in male–adult female dyads. The lowest CCT value is between the single adult male and the immature males. Amongst one another however, the immature males exhibited above average reconciliation rates.

The differences between the Arnhem results and ours are most likely attributable to differences in group composition and history. Not unlike wild chimpanzee groups, the Arnhem group consisted almost entirely of unrelated individuals, including three adult males, 9 adult females, and 8 immatures of either sex (de Waal and van Roosmalen, 1979). The group was established only 4 years prior to the study. By contrast, the group at Yerkes Primate Center included only one adult male, and the six matriarchs had been housed together for >10 years with most of them having at least one relative living in the group. Judging by the group's history as well as by the reconciliation

and grooming rates, the Yerkes group can be interpreted as female-bonded. The differences between the Arnhem and Yerkes groups also confirm the plasticity of chimpanzee female sociality (Baker and Smuts, 1996; Boesch and Achermann-Boesch, 2000; Pusey *et al.*, 1997; Wrangham, 2000).

Comparison with Reconciliation in Other Ape Species

Reconciliation has also been studied in other species of great apes: captive bonobos at the San Diego Zoo, USA (*Pan paniscus*: de Waal, 1987); and mountain gorillas at the Karisoke Research Center, Rwanda (*Gorilla gorilla beringei*: Watts, 1995). In the bonobo study, as in the Arnhem studies, reconciliation was determined by the percentage of opponent dyads that interacted affiliatively ≤ 10 min after an agonistic conflict. The values of these studies are therefore comparable: Bonobos affiliated with former opponents after 48% of their conflicts (de Waal, 1987). This value is the mean of three groups, and compares to 30.3% for the chimpanzees at Arnhem (averaged over three study periods between 1975 and 1980: de Waal, 1993; de Waal and van Roosmalen, 1979; Griede, 1981). The three bonobo groups differed in composition: two included ≥ 1 adult couple, the third consisted solely of immatures. All groups included 3 or 4 individuals, one of which was unrelated to the others, whereas all other group members were full siblings.

The study on wild gorillas employed controlled methods, using a 30-min interval for PC and MC observations (Watts, 1995). The study combined two observation periods (the summers of 1991 and 1992) and data of two groups with 16–33 individuals. Both groups included 2 adult males and 7–13 females, the remainder being immatures of either sex. Watts (1995) found no reconciliation in dyads of males, or females, or immatures. However, females and males reconciled after conflicts they showed selective attraction to the former opponent, and they contacted each other earlier in PC intervals than in control observations. In fact, male and female mountain gorillas engaged in affiliative contacts within the first minute after 37% of their conflicts.

Thus, even though the different methods used in these studies do not permit quantitative comparisons, it is clear that reconciliation has a firm place in the repertoires of all the great ape species—with the possible exception of orangutans (*Pongo pygmaeus*), for which we know no study on reconciliation.

Reconciliation and Relationship Quality

In the Arnhem studies, even after controlling for contact frequencies, reconciliation was more frequent in demographic classes that also had

frequent agonistic conflicts (de Waal, 1986): adult male–male dyads ranged above male–female dyads, which ranged above female–female dyads. Moreover, in their support decisions adult males did not systematically favor their friends, i.e., they did not provide more support to individuals with which they frequently groomed and sat in contact (de Waal, 1984). By contrast, females supported individuals with which they affiliated frequently, which suggests that males were more opportunistic or were playing a control role or both, quelling squabbles in the group (de Waal, 1984).

In our study the demographic classes that rarely had conflicts tended to reconcile more. High conflict frequencies co-occurred with high CCT values only among the three immature males. This is like the pattern for Arnhem adult males, but it contrasts with the relations among the yerkes single adult male and immature males. The competitive–cooperative relationships among the three natal males after the removal of the old alpha male (1998 – present, pers. obs. SP) suggest that the high reconciliation levels among the immature males in 1995 already indicate the ontogenetic development of a male-bonded system like in the wild (Goodall, 1986).

We were able to predict conciliatory tendencies from the frequency of grooming associations: individuals reconciled more frequently with opponents with which they groomed often. This finding is in line with the friendship hypothesis (Cords, 1997). Conversely, we were unable to show that individuals reconciled more frequently with opponents from which they received frequent support against aggressors. This negative result is puzzling because it contrasts with predictions of the valuable-relationships hypothesis (Cords and Aureli, 1993). Looking at the raw data it is clear that for most individuals, the receipt of support was skewed: over the year, they received support once or twice from several group members, but almost every individual received a disproportionate amount of support (9–20 times) from only one group member. For the adult females, this was chiefly the adult male; for the adolescents and juveniles it was usually the mother.

Grooming networks, were wider, involving larger numbers of individuals with which close bonds were maintained. In sum, there was little overlap between the grooming and support networks of each individual. It is likely that this reflects asymmetry in the flow of benefits within the dyads: Whereas friendship was measured symmetrically, support was of the defend aggressee type, which is usually provided by the more powerful member of a dyad. Therefore, it is probably the result of imbalances in power within dyads that we did not detect a relationship between how useful a partner is as a supporter and how frequently the recipient reconciles with a valuable partner after a conflict.

A Socioecological Perspective on Reconciliation and Valuable Relationships in Apes

In primates, the bonds between group members reflect long-term investments worth maintaining and defending: cooperation partners are resources (Kummer, 1978). This fact adds to the costs of escalation in a conflict, because a relentlessly outcompeted cooperation partner may be able to withhold support and assistance to the aggressor in the future (Aureli and de Waal, 1998; Cords, 1997; de Waal, 1989; Hand, 1986; van Schaik and Aureli, 2000; Vehrencamp, 1983). Therefore, after engaging in an aggressive conflict the former opponents may experience stressful uncertainty about the behavioral inclinations of one another and seek to alleviate this anxiety through a friendly reunion after the conflict (Aureli *et al.*, 1989; Aureli and van Schaik, 1991ab).

Accordingly, the tendency to reconcile should be an indicator of the mutual dependence of two individuals that have to maintain each other's inclination to cooperate against a background of competition and agonistic conflicts. This reasoning accords with our findings. We have reported that general tendencies for reconciliation among great apes differ between demographic classes. In chimpanzees, males are highly dependent on one another for territorial defense against males of neighboring groups (Wrangham, 1999). That dyads of male chimpanzees reconcile higher percentages of their conflicts than dyads of females do is therefore expected vis-à-vis the background of their mutual dependence for cooperation (de Waal, 1986; Goodall, 1986). Yet, when females form close dyadic friendships, as in Tai, Ivory Coast (Boesch and Achermann-Boesch, 2000), we would predict high reconciliation rates for females too, but only within such friendships.

Mountain gorillas form one-male units in which the closest bonds exist between the females and the dominant male. Females amongst themselves do not form strong bonds, and adult males barely tolerate each other's presence. Because of the high risk of infanticide, females are assumed to need male protection (van Schaik, 1996; Watts, 1992). In line with the high value attached to male-female relationships, reconciliation is common between males and females but very rare between members of the same sex (Watts, 1995).

The same pattern holds for Old World monkeys. In species that place high value on cooperation within female kin groups, conciliatory tendencies are higher in kin than in nonkin dyads, and in species where in unrelated partners are highly valued too, conciliatory tendencies are similarly high for both kinds of dyads (Aureli *et al.*, 1997; Aureli and de Waal, 1998; van Schaik, 1989).

On the basis of this regularity it can be predicted that, under natural conditions, bonobos will exhibit high rates of reconciliation between mothers and sons, and between females, because they are the types of dyads that entertain particularly close and supportive relationships (de Waal, 1997b). Similarly, we may even predict reconciliation among orangutans. This ape is usually considered to live solitarily. One might therefore expect that even in captive conditions reconciliation should be absent. However, recent studies suggest that even though orangutans live quite dispersed, they engage in individualized long-term relationships of which the ones between females and flanged resident males are particularly close (van Schaik, 1999). If orangutan society is in fact derived from a chimpanzee-like fission–fusion system the mechanism of reconciliation should surely to be in place and to be expressed if the social conditions allow.

To advance our understanding of how reconciliation is related to the quality of long-term relationships, and the provision of services and commodities among group members, more field studies are needed. Since the causes for interdependence between group members, and thus the value of partners, may differ between wild and captive groups, and because of the effects of group composition some deviation between wild and captive groups is to be expected. Previous studies have also shown that reconciliation is not an artifact of captivity when individuals are forced to get along on very limited space in group compositions over which the animals themselves have no control (Aureli, 1992; Watts, 1995). In view of the close phylogenetic relationships between humans and apes more studies are needed, in particular on the relationship between social structure and the propensities to reconcile in other species of apes. It is only from the combination of controlled, captive studies with more ecologically valid studies conducted in the often harsh natural habitat that we can expect a thorough understanding of peace-keeping against the background of intra- and intergroup competition that was typical for our own ancestors.

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