

How to Repair Relationships – Reconciliation in Wild Chimpanzees (*Pan troglodytes*)

Roman M. Wittig & Christophe Boesch

*Department of Primatology, Max Planck Institute for Evolutionary Anthropology,
Leipzig, Germany*

Abstract

Reconciliation appears to repair the relationships of former opponents after being disturbed by aggressive interactions. Despite a consensus about the benefit of reconciliation, how former opponents achieve this benefit remains unclear. Variation within reconciliation is evident in many species, but understanding what causes the variation has been mostly neglected until now. We collected 178 events of reconciliation of both sexes in a community of wild chimpanzees (*Pan troglodytes*) in the Taï National Park, Côte d'Ivoire. Our data provide evidence for the relationship-repair function of reconciliation, as aggression disturbed tolerance levels among former opponents and reconciliation restored tolerance to normal levels again. Partners with highly beneficial relationships reconciled more often compared with partners of low mutual benefit. Latency and duration of reconciliation varied in combination, such that short reconciliations were initiated soon after the conflict, while long reconciliations were initiated later. Latency increased with the risk of further aggression, while duration decreased when costs were incurred from interruption of beneficial activities. In contrast, the complexity of reconciliation varied according to the intensity of the preceding conflict, such that reconciliation was more complex after more intense conflicts. Our results suggest that relationships between opponents are increasingly disturbed with increasing conflict intensity and reconciliation repairs all relationships independent of their relationship value. We propose that the function of reconciliation is to reduce the disturbance created by aggression, but the more frequent the reconciliation, the more beneficial it is for former opponents.

Correspondence: Roman M. Wittig, Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA. E-mail: rwittig@sas.upenn.edu

Introduction

Aggressive interactions damage the relationship of conflict partners, as they create stress and interrupt tolerance levels between opponents (Maestripiéri et al.

1992; Aureli et al. 2002). Damaging a relationship is costly as it jeopardizes the benefits related to relationships (e.g. food-sharing, grooming, support). Reconciliation, the friendly post-conflict interaction among former opponents, appears to repair relationships by restoring tolerance to normal levels (Cords 1992) and reduces stress induced by aggression (e.g. Aureli & van Schaik 1991b; Castles & Whiten 1998b; Kutsukake & Castles 2001). Therefore, reconciliation provides considerable benefit for high-value partners. Although reconciliation is beneficial, it nonetheless entails costs, as for example the risk of further aggression (Aureli & van Schaik 1991b; Cords 1992). Such potential costs may even prevent former opponents from reconciling conflicts under certain circumstances (Wittig & Boesch 2003a).

Although a consensus exists over the benefits of reconciliation, almost nothing is known about how opponents achieve the benefit that is provided by reconciliation. Call et al. (1999) found two clusters of conciliatory behaviours, one that seemed to serve relationship repair between high-value partners, while the other was used during reconciliation by opponents of unspecific relationships. Moreover, other studies have reported that opponents used intense social behaviours, behaviours with exposition of vulnerable body parts (e.g. groom, mount, genital inspection), more frequently for reconciliation, although the repertoire of reconciliation also contained less intense social behaviours (Petit & Thierry 1994a; Abegg et al. 1996). More intense social behaviours might be needed after confrontation that requires negotiation to achieve reconciliation. Such explicit reconciliation, in contrast to implicit reconciliation, was suggested for more egalitarian species as a reflection of a species dominance structure (de Waal 1989). For an intra-species comparison, however, these findings rather suggest that intense social behaviours are more effective in achieving reconciliation. Thus it could be that some conflict situations need more intense or complex repair than others and former opponents vary the behaviours used to achieve reconciliation accordingly.

Since the first study on reconciliation by de Waal & van Roosmalen (1979), reconciliation has been studied in almost three dozen different mammal species (Appendix). When comparing the pattern of reconciliation within and between species, we found great variation. Intra-specific variation is of special interest and probably varies for several reasons. For example, it may indicate that individuals reconcile differently under different levels of relationship damage. A strongly damaged relationship might require a long and intensive reconciliation in order to restore tolerance levels and reduce stress. Therefore, the investment of opponents in the repair of their relationship should positively correlate with the strength of the damage done by the preceding conflict.

Two factors, conflict intensity and relationship quality, potentially affect the damage to relationships. Rhesus macaques (*Macaca mulatta*) showed a stronger behavioural stress response to heavy aggression when compared with light aggression (de Waal & Yoshihara 1983). Moreover, severe aggression in longtailed macaques (*Macaca fascicularis*) was reconciled more often than milder aggression (Koyama 2001), and the intensity of conflicts affected the tendency to reconcile in Japanese macaques (*Macaca fuscata*: Schino et al. 1998). These

results indicate that damage to a relationship increases with the intensity of the conflict and probably other conflict characteristics.

In contrast, other studies have failed to detect a relationship between conflict intensity and behavioural stress responses (*M. fascicularis*: Aureli 1997; *M. fuscata*: Kutsukake & Castles 2001; *Papio anubis*: Castles & Whiten 1998b). Instead, opponents were more stressed either after conflicts with frequent as opposed to rare associates (Aureli 1997) or after conflicts with kin as opposed to non-kin (Kutsukake & Castles 2001). These results indicate that damage to a relationship increases with relationship quality or other relationship characteristics. As the results are not consistent across studies as to which effects are causing damage to relationships, a multivariate approach is required.

Variation is also found in the timing of reconciliation, probably because of the fact that opponents sometimes have to compromise high benefits of reconciliation with accompanied high costs. For example, opponents should quickly re-establish mutual tolerance as a precondition for beneficial interactions (Cords & Thurnheer 1993), or minimize the time being exposed to the costs of stress (Sapolsky 1998). Therefore, reconciliation should be initiated soon after a conflict. However, as stress and tension decrease with time (Aureli & van Schaik 1991b), aggression can be revived when reconciliation is initiated too quickly after the conflict (Wittig & Boesch 2003a). Thus both extremes of latency of reconciliation contain high costs and benefits such that the timing of initiation of reconciliation is likely to be a compromise. Therefore, we need to consider both costs and benefits for the understanding of the variation within reconciliation.

Conflict partners of most species reconciled preferably with high-value partners (Aureli et al. 2002), and most species also showed evidence for intra-species variation within reconciliation in different features (Appendix). First, for most species, variability was found for the duration between conflict and reconciliation and some authors specifically stated that the latency of reconciliation was not equal (Gust & Gordon 1993 (*Cercocebus torquatus*): range 1–8 min; Arnold & Whiten 2001 (*Pan troglodytes*): range 1–13 min). Secondly, many species showed several typical behaviours for reconciliation (Appendix), ranging from short touches to long bouts of allogrooming, indicating that the duration of reconciliation varies greatly (de Waal & Ren 1988; Aureli et al. 1993). Thirdly, opponents sometimes employed several different behaviours in the same reconciliation, therefore increasing what we refer to here as the complexity of reconciliation. Stumptailed macaques (*Macaca arctoides*), for example, combined allogrooming with contact sitting (Call et al. 1999), sooty mangabeys (*C. torquatus*) joined allogrooming and embracing in the same reconciliation (Gust & Gordon 1993) and female gorillas (*Gorilla gorilla*) reacted with combinations of several behavioural elements to aggression by males (Watts 1995).

Finally, neither victims nor aggressors were exclusively initiating reconciliation in any of the studies conducted (Appendix). Both partners can profit from reconciliation, as both face stress after aggression (Aureli 1997). However, a subordinate opponent might profit more from a good relationship with

a dominant partner than the reverse, as relationships might have asymmetrical benefits for each partner (Cords & Aureli 2000).

Wild chimpanzees are a good model to investigate the function of and the reasons for intra-species variation within reconciliation, as they use reconciliation (Arnold & Whiten 2001; Preuschoft et al. 2002; Wittig & Boesch 2003a) and they optimize conflicts based on cost and benefit strategies (Wittig & Boesch 2003b). The first aim of this study is to test whether the function of reconciliation in wild chimpanzees is about relationship repair. After aggression, the interaction pattern between former opponents should be disturbed without reconciliation and be as before with reconciliation. High-benefit partners should show a higher tendency to reconcile. Secondly, we aim to understand how variation in reconciliation, in terms of latency, duration, complexity and initiator of reconciliation, is influenced by the preceding conflict. We expect that variation in reconciliation is dependent on the extent of the damage to opponents' relationships and the costs and benefits of reconciliation.

Methods

Study Site and Data Collection

Data were collected between October 1996 and April 1999 in the Taï Chimpanzee Project study area, in the Taï National Park, Côte d'Ivoire (West Africa, 5°52 N, 7°22 W; further information: Boesch & Boesch-Achermann 2000). In October 1996, the 'North-community' consisted of four males (three adults, one adolescent), 14 females (11 adults, three adolescents) and 13 juveniles and infants.

We aimed to change the focal animal each day, observing 10 adult females once and four males twice per month. There was, however, some variability in individual observation frequency because of the fission–fusion character of chimpanzee societies, death and the habituation level. The result was 80 all-day follows of males (Macho/Marius: 31 days each, Brutus/Nino: 9 d each) and 123 all-day follows of females (between 10 and 15 d per female).

R.W. collected the following four types of data during all-day follows: (a) all-day focal animal sampling (Altmann 1974) of a focal chimpanzee, recording activities, social interactions and vocalizations; (b) recording of the focal animal's party composition, by scanning the presence of individuals within visibility of the focal animal every 10 minutes; (c) identity and number of females with genital swellings per day; (d) specific information at each feeding site regarding the foods consumed by the focal animal, food monopolizability and number of competitors present. A total of 791 of 1071 collected conflicts had complete information recorded and had juvenile or infant participation excluded.

Operational Definitions

A conflict was defined as an aggressive dyadic interaction commencing with the exchange of an aggressive behaviour and ending with either submission, flight

or non-aggressive behaviour, which were not directly followed by further aggressive interactions. The first affiliative interaction between former opponents after a conflict was defined as reconciliation when no other interaction with participation of the focus individual was observed between conflict and reconciliation. Aggressive interactions consisted of threats (e.g. barks, arm wave), non-contact aggression (e.g. displays) and contact aggression (e.g. bites, hits), while affiliative interactions consisted of friendly behaviours with body contact (e.g. kiss, genital touch, embrace, grooming). We took three measurements to describe variation found within reconciliation: (a) the latency of reconciliation, which was the time elapsing between conflict and reconciliation, (b) the duration of reconciliation, which was the time between the start of the first affiliative interaction to the end of the last affiliative interaction of reconciliation, and (c) the complexity of reconciliation, which was the number of different behavioural elements used during the reconciliation. As both latency and duration of reconciliation showed a strongly skewed distribution (Fig. 1), we defined, for each of them, four ordinal categories that corresponded with their quartiles (Table 1). Skewed distributions of the latency of reconciliation are a normal phenomenon and are already known from the first study on reconciliation in chimpanzees (de Waal & van Roosmalen 1979).

Measuring Reconciliation

We demonstrated the occurrence of reconciliation, using two methods. First, the corrected conciliatory tendency (CCT; Veenema et al. 1994), in order to show that reconciliation did not occur by chance. Thus, we computed a baseline that represents the mean interval among the consecutive affiliative interactions, without conflicts in between, for each dyad. Then we calculated the CCT for each dyad using the following formula: $CCT = (A - D)/no. \text{ conflicts}$, with A, attracted pairs, which is the number of reconciliations with a latency shorter than baseline, and D, dispersed pairs, which is the number of reconciliations with a latency longer than baseline. The relative preponderance of attracted pairs ($CCT > 0$) showed that the dyad had a tendency to reconcile.

Secondly, we applied an altered version of the 'time-rule' (Aureli & van Schaik 1991a; Castles & Whiten 1998a) to determine whether or not the occurrence of reconciliation depended on the preceding conflict. The 'time-rule' implies that reconciliation needs to be initiated faster after a conflict than baseline. To compare the latencies of each dyad with their baseline, we calculated for each dyad the relative latency (latency/baseline). Relative latencies of reconciliation smaller than 1 indicated that the occurrence of reconciliation was dependent on the preceding conflict. The PC-MC method (de Waal & Yoshihara 1983), as applied in other studies (e.g. Arnold & Whiten 2001; Preuschoft et al. 2002), was not applicable in Tai, as mean party duration was only about 25 min (Lehmann & Boesch 2004).

To demonstrate the function of reconciliation we calculated relative latencies per dyad for two other types of interactions: (a) the first affiliative inter-opponent

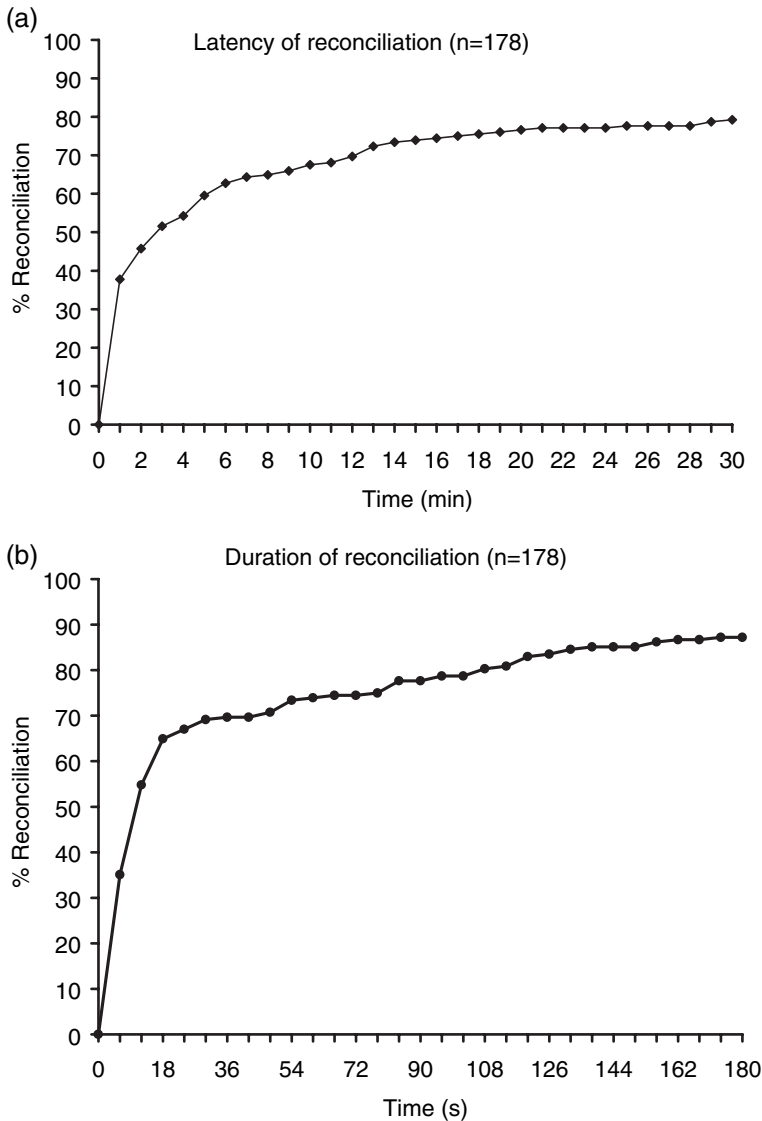


Fig. 1. Cumulative distribution of latency and duration of reconciliation over time in Tai chimpanzees. Graph (a) shows the percentage of reconciliation that was initiated within a certain time, while graph (b) shows the percentage of reconciliation that continued for a certain time

interaction after reconciliation (post-conciliatory interaction, $n = 113$ in 43 dyads), and (b) the first affiliative inter-opponent interaction after unreconciled conflicts (post-non-conciliatory interaction, same 43 dyads), where, for example, consolation or redirected aggression occurred. Relative latencies of post-conciliatory interactions are expected to equal 1, if reconciliation sets tolerance levels to

Table 1: Variables considered in the multivariate statistical process

No.	Name	Type	Variable definitions and categories
Independent variables			
1	Conflict duration	Continuous	Duration from start of first aggressive behaviour to end of the conflict (in seconds)
2	Conflict intensity	Ordinal multinomial	Intensity of the conflict scored by the most intensive single aggressive behaviour: 1 = aggressive vocalization or gesture; 2 = non-contact aggression, no movement; 3 = non-contact aggression, including movement; 4 = physical contact aggression, one action; 5 = physical contact aggression, many actions
3	Rank difference (r.d.)	Ordinal multinomial	Difference of ranks in the linear dominance hierarchy between conflict partners (rank subordinate – rank dominant) see: Wittig & Boesch (2003c); different category ranges, because of different numbers in sex classes; categories of r.d. in M–M dyads (four males): <i>small</i> for rank neighbours, <i>middle</i> for r.d. = 2, <i>large</i> for r.d. = 3; categories of r.d. in F–F dyads (12 females): <i>small</i> for r.d. ≤ 3, <i>middle</i> for 3 < r.d. ≤ 6; <i>large</i> for r.d. > 6; categories of r.d. in M–F dyads (16 individuals) <i>small</i> for r.d. ≤ 5, <i>middle</i> for 5 < r.d. ≤ 10, <i>large</i> for r.d. > 10
4	Association index	Ordinal binomial	Relative scoring of the dyadic association index (Nishida 1968): <i>rare</i> = M–M: ≤50% of observation time, others: ≤25%; <i>frequent</i> = M–M: > 50%, others: > 25%
5	Relationship benefit	Ordinal multinomial	Scoring of the cooperative character of the relationship of dyads: <i>low</i> = no food sharing, no support within dyad; <i>medium</i> = either food sharing or support within the dyad; <i>high</i> = both food sharing and support within the dyad
6	Initiator's sex	Binomial	Sex of the initiator of aggression: <i>m</i> = male aggressor; <i>f</i> = female aggressor
7	Recipient's sex	Binomial	Sex of the recipient of aggression: <i>m</i> = male aggressed; <i>f</i> = female aggressed
8	Initiator's rank	Binomial	Dominance relationship of the conflict partners from the perspective of the initiator: <i>dom</i> = aggressor dominant over aggressed; <i>sub</i> = aggressor subordinate to aggressed

Table 1: Continued

No. Name	Type	Variable definitions and categories
9 Conflict context	Multinomial	Context in which the conflict occurred: <i>sex</i> = conflict about oestrus females; <i>food</i> = conflict about food or possession of tool; <i>social</i> = conflict about hierarchy or social partners and default category
10 Resource monopolization	Ordinal multinomial	Relative scoring of the monopolizability of the resource that is fought over: <i>monopolizable by 1</i> = resource can be monopolized by one competitor; <i>monopolizable by few</i> = resource can be monopolized by some of the competitors; <i>not monopolizable</i> = resource is not monopolizable
11 Competitor proportion	Ordinal multinomial	Proportion (prop.) of competitors present in the party in relation to all potential competitors (in social context: adults in party/all adults; in sex context: males in party/all males; in food context: adults feeding/all adults in party): <i>few</i> for prop. ≤ 0.33 ; <i>some</i> for $0.33 < \text{prop.} \leq 0.66$; <i>many</i> for prop. > 0.66
12 Initiator victory outcome	Multinomial	Outcome of the conflict from the perspective of the initiator: <i>w</i> = initiator wins aggressive interaction; <i>l</i> = initiator loses; <i>n</i> = no winner
Dependent variables		
13 Latency of reconciliation	Ordinal multinomial	Time (t) between the end of the conflict and the start of the reconciliation split into categories which correspond with the four quartiles: <i>very short</i> for $t \leq 20$ s; <i>short</i> for $20 < t \leq 144$ s; <i>long</i> for $144 < t \leq 774$ s; <i>very long</i> for $t > 774$ s
14 Duration of reconciliation	Ordinal multinomial	Time (t) between the start and the end of the reconciliation split into categories which correspond with the four quartiles: <i>very short</i> for $t \leq 4$ s; <i>short</i> for $4 < t \leq 12$ s; <i>long</i> for $12 < t \leq 70$ s; <i>very long</i> for $t > 70$ s
15 Complexity of reconciliation	Ordinal multinomial	Number of different behavioural elements used during reconciliation: <i>simple</i> = one behavioural element; <i>advanced</i> = two behavioural elements; <i>complex</i> = three and more behavioural elements
16 Initiator of reconciliation	Binomial	Individual that initiates reconciliation: <i>aggressor</i> or <i>victim</i> of aggression

Variables are numbered and the type of data, the variable definition and the variable scoring are shown from left to right. The names of categories are printed in italics for clarity.

normal. In contrast, relative latencies of post-non-conciliatory interactions should be > 1 , as disturbed tolerance levels were not repaired.

Variables

Table 1 displays the independent variables (with definitions and scoring of categories) that were considered as predictors for variation within reconciliation. Relationship benefit (no. 5), association index (no. 4) and sex of conflict partners (no. 6 + 7 and the interaction) predicted the occurrence of reconciliation, while conflict intensity (no. 2) and conflict context (no. 9) predicted the initiator of reconciliation in chimpanzees (Wittig & Boesch 2003a). Initiator's rank (no. 9), rank difference (no. 3) and their interaction were predictors of the outcome of the aggressive interaction (Wittig & Boesch 2003b,c). Conflict duration (no. 1) and initiator victory outcome (no. 12) predicted the risk of further aggression (Wittig & Boesch 2003a), while resource monopolization (no. 10), competitor proportion (no. 11) and the interaction of context and competitors were strong indicators for the strength of competition in chimpanzees (Wittig & Boesch 2003c). Therefore variables 1–12 (plus the three interactions of initiator's sex with recipient's sex, rank difference with initiator's rank and conflict context with competitor proportion) were possible predictors for the variation in reconciliation, while variables 13–16 were the dependent variables tested in the multivariate analyses.

The effect sizes of the three categories of relationship benefit for the prediction of the occurrence of reconciliation (Wittig & Boesch 2003a) proved that both low and medium benefit influence the occurrence of reconciliation negatively and with similar strength. Therefore, we merged low and medium benefit to one category (small benefit partners) for simplicity, when using one-way statistics.

Multivariate Dyadic Approach

We employed a multivariate approach to detect the independent variables that affected the variation within reconciliation. All predictors were considered simultaneously as independent variables in each of the multivariate analyses. As many of the independent variables (e.g. rank difference, association index, relationship benefit) were different for the same individual with different partners, we conducted our analyses on a dyadic level. However, as repeated measurements of individuals can inflate the type I (α) error, we controlled for this and ruled out the influence of repeated measurements on variables (see Statistical Process). The strength of our results was therefore similar to an individual-based analysis, but included the advantage that we were able to detect dyadic variability.

Statistical Process

In order to test differences in CCTs, we conducted a permutation test, which is an extension of the network analysis test by Dow & de Waal (1989). We created a matrix of the CCTs of all individuals and calculated the mean difference

between the subgroups we wanted to compare. Afterwards, we sampled the data set without replacements and calculated from this sample the mean difference between subgroups again. The procedure was repeated 5000 times and we checked if the original mean values were found inside or outside the 95% confidence interval of the approximate distribution of differences between mean values. The tests were two-tailed with a significance level of $p < 0.05$ and Bonferroni-corrected when multiple tested.

In order to compare dyadic interactions with a baseline, we conducted a bootstrap test. We calculated the mean relative latencies of interactions per dyad and then sampled the mean values of each PCI with replacements (Manly 1997). We repeated this bootstrap procedure 5000 times to estimate the distribution of the samples. Afterwards, we calculated a bias-corrected 95% confidence interval, which considers a skewed distribution of samples (Efron & Tibshirani 1994). Finally, we checked whether the baseline (1) was found within or outside the 95% confidence interval of the approximate distribution of relative latencies of dyads. This bootstrap test was conducted two-tailed with a significance level of $p < 0.05$.

To detect the variables that affect the variation found within reconciliation, we executed multivariate analyses as follows:

(a) In order to eliminate repeated measurements of the same conflict type per dyad, we summarized conflicts in one data point for cases that had the same initiator and receiver of aggression, had the same initiator of reconciliation, and were identical in all other independent variables (Table 1), apart from conflict duration and conflict intensity, which were scored with mean and median values respectively. For the summarized data points, we calculated the mean of latency and duration of reconciliation and then we assigned each mean to the appropriate category of quartiles (Table 1). In addition, we used the median for the complexity of reconciliation. The resulting balanced data set of 146 out of a total of 178 conflicts with reconciliation was used for the multivariate analyses.

(b) We used a generalization of the logistic regression called generalized linear model (GLZ; McCullagh & Nelder 1989; Agresti 1996) to examine the functional relationship between the occurrence of one dependent variable (Table 1: variables 14–16) and several independent variables (Table 1: variables 1–13). For GLZs, we chose an ordinal multinomial error distribution and a logit link function (McCullagh & Nelder 1989). The best model was selected by the best subset method, which is an iterative method based on maximum likelihood estimation [likelihood statistics (LR)], and Akaike's information criterion (AIC), which takes into account the number of independent variables in the model (Akaike 1973). The significance of the independent variables and their categories was assessed using Wald statistics for the best model (Dobson 1990). The estimate coefficient β is an indicator for the strength of the effect that a category of an independent variable has on the occurrence of the dependent variable. The probability that the tested PCI occurred was e^β more likely with one unit increase of the independent variable, after adjusting for all other variables. The further away β was from 0, the bigger the influence of the category of the independent variable.

(c) As we were analysing at a dyadic level, we controlled for a possible inflation of the type I (α) error because of multiple measurements of the same actor. Therefore, we included both the identity of the initiator of the conflict and of the reconciliation as additional independent variables and tested the best model again (similar procedure as that used by Côté & Festa-Bianchet 2001). When the significant explanatory independent variables remained significant, we were able to assume that the effect was not due to the replicated observations of the same individual (Bland & Altman 1995). For the sake of simplicity, we have presented in the results only the significant variables of the best models, which remained significant ($p < 0.05$) after including the identities of the initiators of the conflict and of the reconciliation.

All multivariate analyses (GLZ) were performed in STATISTICA[®] 99 edition (StatSoft 1999). Non-parametric statistics were carried out in STATXACT[®] 5 (Cytel Software 2001), using exact statistics for samples of $n \leq 15$ (Mundry & Fischer 1998). The bootstrap confidence intervals and the permutation tests were computed in S-Plus (Insightful Corporation 2001). All tests were performed as two-tailed.

Results

Occurrence of Reconciliation

We observed 791 conflicts in 90 of the 105 adult dyads, of which 48 dyads used reconciliation at least once, while the other 42 dyads never implemented reconciliation (Table 2). Almost one of four conflicts (178/791) was followed by reconciliation. The mean conciliatory tendency (CCT) of dyads was 15.85% for Tai chimpanzees. Conciliatory tendencies varied greatly between the sexes. Female–female dyads had a lower CCT than male–female dyads ($CCT_{F-F} = 5.92\%$; $CCT_{M-F} = 26.96\%$; permutation test and Bonferroni: $n_{FF} = 44$, $n_{MF} = 40$, $p < 0.016$). In contrast male–male dyads ($CCT_{M-M} = 14.56\%$) did not differ from male–female dyads (permutation test and Bonferroni: $n_{MM} = 6$, $n_{MF} = 40$, ns) and female–female dyads (permutation test and Bonferroni: $n_{MM} = 6$, $n_{FF} = 44$, ns).

Function of Reconciliation

Reconciliation was demonstrated following the time-rule (Fig. 2), as dyads of all three sex combinations reconciled faster than the baseline (bootstrap tests: M–M, $n = 5$, $p < 0.05$; M–F, $n = 29$, $p < 0.05$; F–F, $n = 9$, $p < 0.05$). In contrast, post-reconciliatory interaction occurred as fast as baseline for dyads with male participation (bootstrap tests: M–M, $n = 5$, ns; M–F, $n = 29$, ns), while for female–female dyads, post-reconciliatory interactions were faster than baseline (bootstrap test: F–F, $n = 9$, $p < 0.05$). Friendly interactions after unreconciled conflicts however occurred slower than baseline within each sex combination (bootstrap tests: M–M, $n = 5$, $p < 0.05$; M–F, $n = 29$, $p < 0.05$; F–F, $n = 9$, $p < 0.05$). Hence, aggression interrupted the usual interaction pattern among

Table 2: Conciliatory tendency (CCT) of adult Tai chimpanzees

CCT (%) a/d/n interactions*	Females														
	Males							Females							
	Brutus	Macho	Marius	Nino	Belle	Castor	Dilly	Fossey	Goma	Loukoum	Mystere	Narcisse	Perla	Ricci	Venus
Brutus	9 (1/0/10)	38 (3/0/5)	13 (2/0/14)	0 (0/0/1)	0 (0/0/1)	20 (2/0/8)	100 (1/0/0)	0 (0/0/1)	33 (1/0/2)	33 (1/0/2)	100 (1/0/0)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	67 (2/0/1)
Macho	12 (46/16/190)	38 (6/0/10)	1 (9/8/87)	38 (6/0/10)	0 (0/0/10)	0 (0/0/10)	0 (0/0/10)	25 (2/0/6)	50 (1/0/1)	44 (4/0/5)	23 (4/1/8)	0 (1/1/0)	0 (0/0/3)	17 (2/1/3)	22 (2/0/7)
Marius		-11 (1/2/6)	15 (2/0/11)	-11 (1/2/6)	0 (0/0/3)	0 (0/0/5)	20 (1/0/4)	33 (2/0/4)	100 (1/0/0)	36 (5/0/9)	14 (1/0/6)	0 (0/0/7)	43 (3/0/4)	60 (3/0/2)	43 (9/0/12)
Nino		0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	25 (2/0/6)	13 (1/0/7)	0 (0/0/2)	50 (2/0/2)	16 (4/1/14)	20 (1/0/4)	25 (1/0/3)	0 (0/0/3)	0 (0/0/1)	20 (2/0/8)
Belle		16 (1/0/9)	10 (1/0/9)	16 (1/0/9)	16 (1/0/9)	16 (1/0/9)	0 (0/0/1)	0 (0/0/2)	0 (0/0/1)	0 (0/0/6)	0 (0/0/1)	20 (1/0/4)	0 (0/0/1)	0 (0/0/1)	0 (0/0/2)
Castor		0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/5)	-33 (0/1/2)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/3)
Dilly		33 (1/0/2)	33 (1/0/2)	33 (1/0/2)	33 (1/0/2)	33 (1/0/2)	33 (1/0/2)	33 (1/0/2)	50 (2/0/2)	0 (1/1/3)	0 (0/1/2)	0 (0/0/1)	-25 (0/1/3)	0 (0/0/1)	33 (3/0/6)
Fossey		0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	50 (1/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/2)
Goma		0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	0 (0/0/3)	0 (0/0/1)	0 (0/0/1)	0 (0/0/2)	0 (0/0/1)	0 (0/0/2)
Loukoum		0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/3)	0 (0/0/1)	0 (0/0/1)	0 (0/0/2)	0 (0/0/1)	0 (0/0/2)
Mystere		0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/5)	0 (0/0/7)	0 (0/0/3)	0 (1/0/2)
Narcisse		0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/6)	0 (0/0/2)	0 (0/0/2)
Perla		0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/1)	0 (0/0/2)
Ricci		0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)
Venus		0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)	0 (0/0/2)

*For each dyad are indicated the CCT (the number of attracted interactions/number of dispersed interactions/number of conflicts without reconciliation).
Blank cells indicate no conflict observed in this dyad.

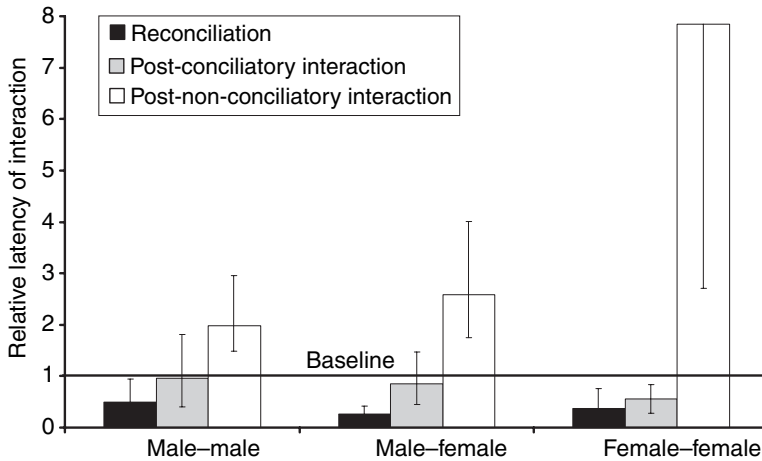


Fig. 2: Comparison between latency of reconciliation, latency of the first post-conciliatory interaction and latency of the first unreconciled interaction with baseline in Taï chimpanzees. Mean delays of relative latencies (relative latency = interval between interaction divided by baseline) of the dyads are presented for each sex class, while relative baseline is 1. Confidence intervals (95%) are shown for a two-sided distribution, calculated with bootstrap method

opponents, as opponents of unreconciled conflicts needed longer than usual to interact again. Reconciliation reinstated normal interaction rates for dyads with males but not in female–female dyads (Fig. 2). Female–female pairs, however, had a second fast friendly interaction (the first being the reconciliation), again faster than when no conflict occurred before.

Finally, we checked whether conciliatory tendencies increased with the relationship benefit of opponents (Fig. 3). We merged low and medium relationship benefit into one category of small benefit (see Methods) and compared it with high-benefit partners. Male opponents of high relationship benefit showed higher CCTs than those of smaller benefit (permutation test: $n_{\text{low}} = 4$, $n_{\text{high}} = 2$; $p < 0.05$) and the same was true for female opponents (permutation test: $n_{\text{low}} = 38$, $n_{\text{high}} = 6$; $p < 0.05$). For mixed sex dyads, however, no difference was observed (Fig. 3; permutation test: $n_{\text{low}} = 32$, $n_{\text{high}} = 8$; ns), although they showed the highest average CCT. High-benefit partners of the same sex had a higher tendency to reconcile conflicts than partners with smaller cooperation benefit.

Variation in Latency and Duration of Reconciliation

More than 50% of the reconciliations were initiated within 3 min (median 144 s) after the conflicts (range 2 s to 251 min; Fig. 1a). Reconciliation was initiated more quickly after conflicts with female victims, after conflicts between conflict partners of a small rank difference and after short conflicts, while conflict partners took longer to initiate reconciliation after conflicts with male victims and long conflicts (Table 3a).

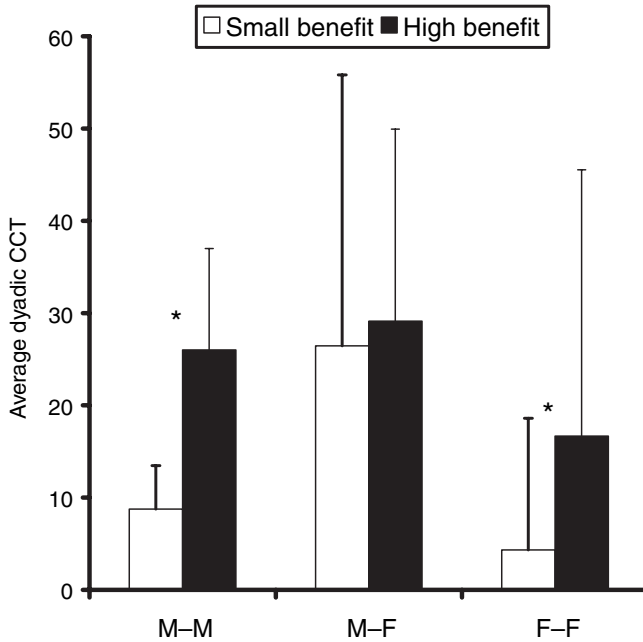


Fig. 3: Comparison of conciliatory tendencies (\pm SD) between high- and small-benefit partners within each sex class of Tai chimpanzees. Small-benefit partners have a low and medium relationship benefit.

*Significant differences between the samples (for p-values see text)

About 50% of reconciliations were shorter than 12 s (range 1–1026 s; Fig. 1b). Reconciliation was shorter after food conflicts, after conflicts between opponents with a small rank difference and after conflicts with female victims, while reconciliation was longer after conflicts over sex (with medium duration), after conflicts between opponents with a large rank difference and after conflicts with male victims (Table 3b).

Consequently, either opponents used short reconciliation soon after the conflict, when they had a small rank difference and female victims, or opponents initiated long reconciliation with some delay, when they had a big rank difference and male victims (Fig. 4). Additionally, long fighting resulted in late reconciliation while food conflicts were reconciled more quickly than those over sex.

Variation in the Complexity of Reconciliation

Most reconciliation (60.3%) was carried out in a simple form using only one behavioural element for the interaction, while 30.1% were advanced (two behavioural elements) and 9.6% were complex reconciliations (three and more behavioural elements). Intensity of the preceding conflict was the only predictor of reconciliation complexity (GLZ: $LR\chi^2_{8,146} = 19.6$, $p = 0.0121$; Table 4). Gentle aggression (conflict intensity level 1) led to simple reconciliation, while hard

Table 3: Independent variables affecting (a) the latency and (b) the duration of reconciliation in Tai chimpanzees

Independent variables	Wald	df	p-value	Category	n	Very short (%)	Short (%)	Long (%)	Very long (%)	β	Wald	p-value
(a) Latency of reconciliation^a												
Receiver's sex	9.96	1	0.0016	Male	63	11.1	25.4	25.4	38.1	-0.59	9.96	0.0016
				Female	83	36.1	24.1	24.1	15.7	0.59		
Rank difference	10.73	2	0.0047	Small	76	30.3	28.9	21.1	19.7	0.70	9.41	0.0022
				Middle	46	19.6	17.4	26.1	36.9	-0.41	3.13	0.0769
				Big	24	20.8	25	33.3	20.9	-0.29	0.97	0.3251
Conflict duration	4.61	1	0.0318	Continuous	146	↓	↔	↑	↑	-0.98	4.61	0.0318
(b) Duration of reconciliation^b												
Receiver's sex	7.68	1	0.0056	Male	63	23.8	19.1	22.2	34.1	-0.61	7.68	0.0056
				Female	83	26.5	32.5	22.9	18.1	0.61		
Rank difference	12.75	2	0.0017	Small	76	23.7	32.9	22.4	21.0	1.08	12.66	0.0004
				Middle	46	28.2	26.1	21.7	24.0	-0.24	0.49	0.4845
				Big	24	25.0	8.3	25.0	41.7	-0.84	4.75	0.0293
Conflict context	12.66	2	0.0018	Social	81	22.2	18.5	23.5	35.8	-0.29	1.29	0.2566
				Sex	29	6.9	55.2	27.6	10.3	-0.68	4.36	0.0368
				Food	36	47.2	22.2	16.7	13.9	0.97	12.61	0.0004

The table shows the significant independent variables and the estimate-coefficient (β) of the categories.

(a) GLZ: $LR\chi^2_{3,146} = 30.0, p < 0.0001$; (b) GLZ: $LR\chi^2_{6,146} = 38.3, p < 0.0001$.

^aLatency of reconciliation = very short (first quartile): $t \leq 20$ s; short (second quartile): $20 s < t \leq 144$ s; long (third quartile): $144 s < t \leq 774$ s; very long (fourth quartile): $t > 774$ s.

^bDuration of reconciliation = very short (first quartile): $t \leq 4$ s; short (second quartile): $4 s < t \leq 12$ s; long (third quartile): $12 s < t \leq 70$ s; very long (fourth quartile): $t > 70$ s.

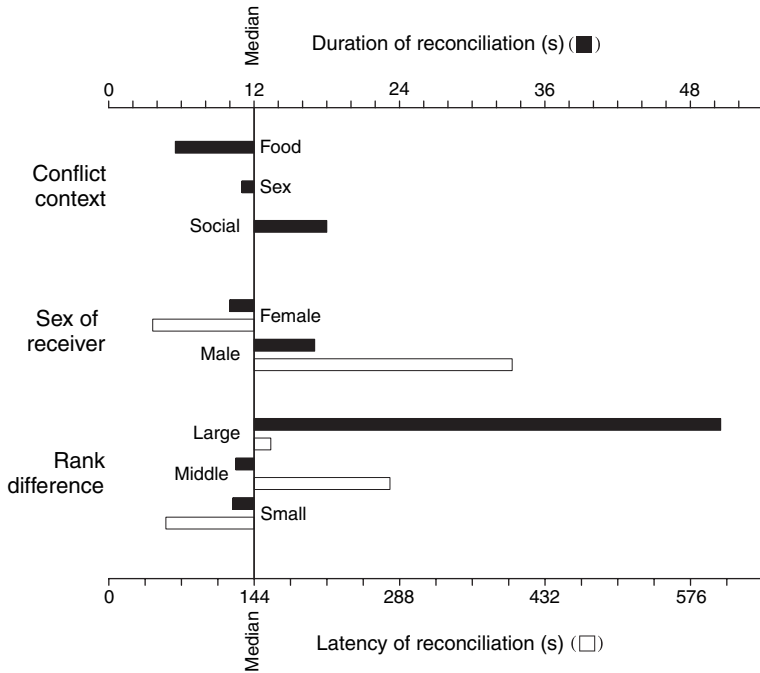


Fig. 4: Median latency (□: bottom scale) and duration (■: top scale) of reconciliation for the influencing variables in Tai chimpanzees. Median latencies and durations of the variable categories are shown as deviations of the overall median values for latency ($\bar{x} = 144$ s) and duration ($\bar{x} = 12$ s) of reconciliation, indicated by the median line. Deviations to the left mark that latency or duration for the category were shorter than median, while deviations to the right show latency or duration were longer than median. Only significant variables are presented

fighting (conflict intensity level 5) was followed by advanced and complex reconciliation (Fig. 5). Conflicts with medium intensity (levels 2–4) did not differ in their variability of reconciliation complexity from the average proportion, as expected for an ordinal variable with a linear influence. Hence, opponents increased the complexity of reconciliation with the intensity of the preceding conflict.

Initiator of Reconciliation

Aggressors initiated less reconciliation than victims of aggression (39.7% vs. 60.3%). We tested which form of reconciliation (latency, duration and complexity) was initiated by aggressors compared to by victims. Aggressors initiated more simple reconciliation, while victim initiators seemed to favour advanced and complex reconciliation (Table 5a). When lumping advanced and complex reconciliation to one category (GLZ: $LR\chi^2_{1,146} = 8.91$, $p = 0.0062$), victims initiated more non-simple reconciliation ($\beta = -0.5$, Wald = 7.5, $p = 0.0062$) while aggressors favoured simple forms of reconciliation ($\beta = 0.5$, Wald = 7.5, $p = 0.0062$).

Table 4: Independent variables affecting the complexity of reconciliation in Tai chimpanzees

Complexity of reconciliation										
Independent variables	Wald	df	p-value	Category	n	Simple (%)	Advanced (%)	Complex (%)	β	p-value
Conflict intensity	14.87	4	0.0049	Level 1	30	76.7	23.3	0.0	0.94	0.0025
				Level 2	31	67.7	19.4	12.9	0.32	0.2494
				Level 3	42	50.0	40.5	9.5	-0.28	0.2442
				Level 4	30	60.0	30.0	10.0	0.06	0.8385
				Level 5	13	38.5	38.5	23.0	-1.04	0.0052

The table shows the significant independent variables and the estimate-coefficient (β) of the categories.

GLZ: $LR_{88,146}^2 = 19.6$, $p = 0.0121$.

Complexity of reconciliation = simple: one behavioural element; advanced: two behavioural elements; complex: three and more behavioural elements.

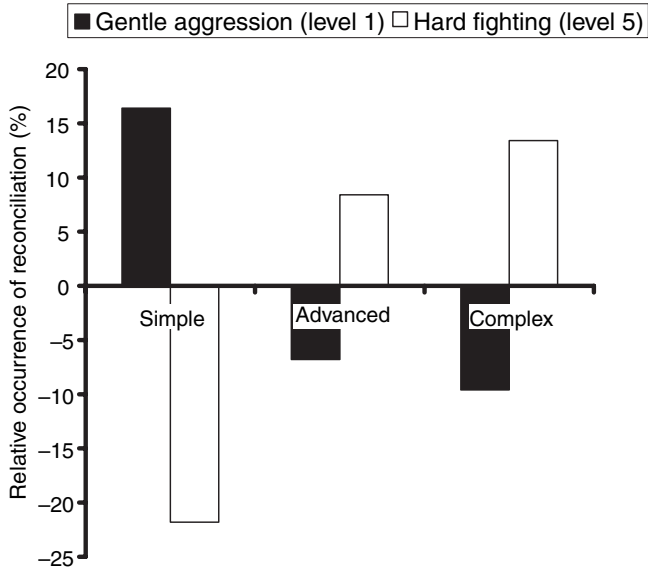


Fig. 5: Complexity of reconciliation depending on the intensity of the preceding conflicts in Tai chimpanzees. The relative occurrence of reconciliation is shown for the two significant categories of gentle aggression (level 1: ■) and hard fighting (level 5: □). Positive values indicate higher frequencies and negative values indicate lower frequencies of reconciliation than for an even distribution of the complexity of reconciliation over conflict intensity

For victim-initiated reconciliation, sex of the victim (male 47.7%; female 52.3%) played a role in the latency and duration of reconciliation (Table 5b). Female victims started reconciliation soon after the conflict while male victims waited longer and used long reconciliation.

Discussion

Aggression in Tai chimpanzees decreased the interaction rate of former opponents and reconciliation restored interaction rates to normal levels. A high relationship benefit increased the tendency to reconcile between same-sex partners, while reconciliation in mixed sex dyads was independent from the cooperative benefits of relationships. Characteristics of reconciliation varied widely in Tai chimpanzees. Both latency and duration of reconciliation were short after conflicts among rank neighbours or when females were attacked. In addition, latency of reconciliation increased with the duration of the preceding conflict, while duration of reconciliation was short after food conflicts. Furthermore, complexity of reconciliation increased with the intensity of the preceding conflict. Finally, our analysis revealed that victims of aggression initiated more complex reconciliation compared with aggressors, and female victims initiated shorter reconciliation and sooner after a conflict compared with male victims.

Table 5: Independent variables affecting initiator of reconciliation in Tai chimpanzees

Independent variables	Wald	df	p-value	Category	n	Aggressor (%)	Victim (%)	β	Wald	p-value
(a) Initiator of reconciliation										
Complexity of reconciliation	7.60	2	0.0223	Simple	88	48.9	51.1	0.73	6.64	0.0099
				Advanced	44	27.3	72.7	-0.21	0.24	0.5219
				Complex	14	21.4	78.6	-0.52	1.33	0.2486
(b) Victim initiates reconciliation										
Latency of reconciliation	11.94	3	0.0076	Very short	19	21.1	78.9	-0.99	4.59	0.0322
				Short	20	45	55	0.13	0.12	0.7342
				Long	21	42.9	57.1	-0.39	0.87	0.3507
				Very long	28	71.4	28.6	1.25	10.34	0.0013
Duration of reconciliation	7.98	3	0.0463	Very short	24	45.8	54.2	-0.01	0.00	0.9999
				Short	22	31.8	68.2	-0.68	2.63	0.1051
				Long	16	37.5	62.5	-0.41	0.80	0.3703
				Very long	26	69.2	30.8	1.10	7.19	0.0073

Part (a) distinguishes between aggressor and victim initiated reconciliation, while part (b) distinguishes male or female victim initiated reconciliation. The table shows the significant independent variables and the estimate-coefficient (β) of the categories. (a) GLZ: $LR\chi^2_{2,146} = 8.13, p = 0.0172$; (b) GLZ: $LR\chi^2_{6,88} = 20.71, p = 0.0021$.

Function of Reconciliation

While aggression among Tai chimpanzees seemed to disturb the tolerance levels between opponents, reconciliation seemed to restore the tolerance levels of conflict partners to normal. These results strongly support the proposition that reconciliation functions to repair relationships following a conflict. Our findings correspond with two experimental studies. Cords (1992) showed that longtailed macaques (*M. fascicularis*) exhibit a higher tolerance of proximity with former opponents after reconciled compared to non-reconciled conflicts and Cheney & Seyfarth (1997) demonstrated that sarannah baboons (*Papio cynocephalus ursinus*) tolerated the approach of former opponents after reconciliation at higher rates than under control conditions. To our knowledge, our study is the first to show that reconciliation restores tolerance to levels like before the conflict.

Reconciliation seems to be adaptive for same-sex partners with highly cooperative relationships, as friendly interactions were remarkably up to eight times less frequent when no reconciliation occurred. Same-sex dyads in Tai reconciled more with partners with which they usually shared food and support. The reconciliation pattern of Tai chimpanzees shares similarities with that of captive longtailed macaques (*M. fascicularis*), where cooperation over food determined reconciliation (Cords & Thurnheer 1993), and with that of mountain gorillas (*G. gorilla*), where alliance partners reconciled more than others (Watts 1995). Compared with wild chimpanzees, captive chimpanzees may have different incentives for reconciliation, as they did not reconcile more with supporters, but rather with preferred grooming partners (Preuschoft et al. 2002). Mixed-sex dyads showed the highest conciliatory tendencies of all dyads, but, contrary to same-sex dyads, they did not reconcile more with high-benefit partners. This indicates that mixed-sex dyads gain different benefits from reconciliation compared with same-sex dyads. Budongo chimpanzees had a higher reconciliation rate between mating partners compared with dyads that never copulated (Arnold & Whiten 2001). A relaxed relationship with a potential mating partner could be beneficial for males, as females may be more willing to mate with them, and for females, as sexual harassment by males may be avoided (Niemeyer & Anderson 1983; Paul 2002).

Variation in Reconciliation

Reconciliations in Tai chimpanzees were highly variable, with latency, duration, complexity and initiation of reconciliation varying according to the costs and benefits accompanied by reconciliation. Opponents, for example, delayed reconciliation after long conflicts. The risk of further aggression is known to increase with conflict duration (Wittig & Boesch 2003a) and tension is known to reduce over time (Aureli & van Schaik 1991b). This suggests that former opponents require some time after long conflicts before they can approach to reconcile without risking further aggression.

Moreover, reconciliation in Tai chimpanzees was shorter after food conflicts compared with sex and social contexts. When competing over limited food resources, delaying reconciliation is costly and conflict partners should resume feeding soon after the conflict before the food is depleted. Thus, the potential loss of time spent in accessing limited resources appears to shorten the duration of reconciliation. In varying reconciliation, chimpanzees take into account not only the risk of further aggression – higher after longer conflicts – but also the cost of interrupting beneficial activities. So that in conflicts over food, which are often monopolizable sources (Wittig & Boesch 2003c), individuals used shorter reconciliation than after conflicts over less-restricted resources.

Tai chimpanzees showed a strong interaction between latency and duration of reconciliation, both being predicted by the same variables. Former opponents performed either a short reconciliation soon after the conflict or a long reconciliation after waiting for some time. The fact that females fight preferably over food while males usually engage in social conflicts (Wittig & Boesch 2003b), could explain why female victims initiated shorter reconciliations sooner after conflicts, compared with male victims. Female victims appeared to accept an increased risk of further aggression when reconciliation carried the potential benefit of rapid access to a limited food resource. This may explain why post-conflictory interactions among females occurred faster than baseline. In contrast, male victims that fight mainly in social contexts waited longer to reconcile with a former opponent. With no apparent benefits to offset the risk of further aggression, males seem to wait longer to initiate reconciliation. Males might only seek long-term benefits of reconciliation such as relaxed relationships (Koyama 2001), while females might also take into account potential immediate benefits of reconciliation.

Close-ranking chimpanzees had shorter reconciliations sooner after conflicts than distantly ranked opponents, and they usually fought harder (with more intensity) than distantly ranked ones (Wittig & Boesch 2003b). One explanation for having shorter reconciliations is that close-ranking opponents are hesitant to engage in protracted reconciliations when this increases the likelihood of further aggression. However, rank difference has been ruled out as a predictor of further aggression in chimpanzees (Wittig & Boesch 2003a). A second explanation is that chimpanzees are more stressed by the presence of close-ranking individuals than by far-ranking ones as with female capuchins, *Cebus capucinus* (Manson & Perry 2000). Thus conflicts between close-ranking opponents compared with distantly ranked opponents appeared to be more disturbing, as rank neighbours might not be able to accept subordination as easily as distantly ranked subordinates. It could be that Tai chimpanzee opponents shortened the latency of reconciliation when relationships seemed strongly disturbed.

Repairing the Damage

Tai chimpanzees reacted with more complex reconciliation after more intense aggression. This reaction suggests that the disturbance to the opponents'

relationship increased with the intensity of fighting. Longtailed macaques (*M. fascicularis*) also required more reconciliation after more intense fighting, since they showed a greater proportion of reconciled conflicts after more severe aggression (Koyama 2001). However, the question remains whether or not the disturbance is stress related. Three studies did not detect an increased frequency of behavioural stress indicators with an increase of intensity of conflicts (*M. fascicularis*: Aureli 1997; *M. fuscata*: Kutsukake & Castles 2001; *P. anubis*: Castles & Whiten 1998b). Instead *M. fascicularis* and *M. fuscata* rather had increased stress indicators after conflicts with opponents of high affiliation rates or high relatedness.

The discrepancy of results could have several explanations. Self-directed behaviours might not be the most reliable indicators of acute stress, because rates of self-directed behaviour can sometimes remain stable or even decrease after aggression (e.g. *C. capuchinus*: Manson & Perry 2000; *P. troglodytes*: Arnold & Whiten 2001). More direct measures of stress are needed to understand the interactions of conflict intensity, relationship quality and stress (e.g. heart rate: Aureli et al. 1999; hormones: Sapolsky 1986; Creel 2001). Furthermore, other studies may have used categories of conflict intensities that were too broad. In our study, two extreme values predicted the complexity of reconciliation. A last possible reason is that individuals in despotic societies, such as both macaque species mentioned above (Thierry 2000; Thierry et al. 2000), perceive the mere presence of a dominant partner as stressful as open aggression (Sapolsky 1993; Castles et al. 1999; Abbott et al. 2003). Thus, *M. fascicularis* and *M. fuscata* would not be more stressed by contact aggression than by non-contact aggression.

The difference in dominance styles between the egalitarian chimpanzees and the despotic macaques also opens another explanation for the discrepancies between studies. In egalitarian societies, subdominant individuals have the chance to win a conflict (de Waal & Luttrell 1989; Wittig & Boesch 2003b). Here aggression can be seen as a way to negotiate the possession of a resource. After a conflict, the former opponents probably need to negotiate the investment in relationship repair. The increase of reconciliation complexity due to increased severity of fighting, thus, might be a type of negotiation about relationship repair. Using de Waal's (1989) terms, Tai chimpanzees engage in explicit reconciliation, requiring complex interactions, while the former opponents in despotic macaque species show implicit reconciliation, when reconciliation does not need negotiation. This leads to the conclusion that the disturbance for the relationships among opponents can vary in Tai chimpanzees, and therefore an increased level of disturbance of relationships requires an increased complexity of reconciliation to repair the relationships of former opponents.

Conclusion

We conclude that conflicts in Tai chimpanzees disturbed the relationship between opponents and that reconciliation repaired the relationship. Reconciliation cleared up the disturbance with a more complex pattern for more intense

conflicts. However, high value relationships were reconciled for all levels of disturbance. Therefore, we suggest that the function of reconciliation is to reduce disturbance in all relationships. Previous authors have suggested reconciliation occurs as a repair mechanism in high-value relationships only, either through stress reduction or cooperation repair (Aureli 1997; de Waal & Aureli 1997). Our data have shown that disturbance resulting from intense fighting is also repaired by reconciliation independent from relationship quality of opponents. Repair of low-value relationships has not previously been predicted, but its occurrence in primates could be beneficial in societies where out-competed partners may react with revenge and contra-intervention (de Waal & Luttrell 1988; Drukker et al. 1991; Aureli et al. 1992; Silk 1992). Because it might be as beneficial to have a friend as it is costly to have an enemy, social living animals should both prevent losing friends and making enemies. Thus reconciliation not only maintains the beneficial relationship of high-value partners, but also seems to prevent low-benefit partners turning into enemies.

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Appendix: Species with conducted studies on reconciliation since 1979. Findings are provided on variation in behaviours and initiators of reconciliation in primates and non-primate mammals. The appendix shows the within species variation and allows for between species comparison

Species	Type of behaviour ^a	Major initiator ^b
Prosimii		
<i>Eulemur fulvus</i> ¹	?	V
<i>Lemur catta</i> ²	gr	A = V
Plathyrrhini		
<i>Callithrix jacchus</i> ³	gr, pl	?
<i>Cebus apella</i> ⁴	co, gr, pl	?
<i>Cebus capucinus</i> ⁵	hb, mo	A
<i>Saimiri sciureus</i> ⁶	?	?
Catarrhini		
<i>Cercocebus torquatus</i> ⁷	co, em, gr	V
<i>Cercopithecus aethiops</i> ⁸	?	?
<i>Colobus guereza</i> ⁹	em, gr	V
<i>Erythrocebus patas</i> ¹⁰	gr	A
<i>Macaca arctoides</i> ^{11,12}	?	V
<i>Macaca fascicularis</i> ^{13,14}	?	V
<i>Macaca fuscata</i> ^{15,16}	gr	A, A = V
<i>Macaca maurus</i> ¹⁷	gr	V
<i>Macaca mulatta</i> ^{12,18,19}	em, gr, ls	A
<i>Macaca nemestrina</i> ^{20,21}	mo	A = V
<i>Macaca nigra</i> ²²	co, gr, mo, pl	A = V
<i>Macaca silenus</i> ²³	co, gc, gr, mo	A = V
<i>Macaca sylvanus</i> ²⁴	?	?
<i>Macaca tokeana</i> ¹⁹	co, gr, mo	A = V
<i>Papio anubis</i> ²⁵	co, mo	A
<i>Papio papio</i> ²⁶	gr	A = V
<i>Papio ursinus</i> ²⁷	gv	A
<i>Rhinopithecus roxellanae</i> ²⁸	co, em, gr, hh	V
<i>Semnopithecus entellus</i> ²⁹	em	V
<i>Theropithecus gelada</i> ³⁰	gr, ls	V
<i>Trachypithecus obscura</i> ³¹	co, em, gr, mo	A, V
Hominidae		
<i>Gorilla gorilla</i> ³²	em, to	?
<i>Pan paniscus</i> ³³	gc	A*
<i>Pan troglodytes</i> ^{34,35,36,37}	co, gc, ki	A = V, V
<i>Homo sapiens</i> ³⁸	ap, em, so	A, A = V

Appendix: Continued

Species	Type of behaviour ^a	Major initiator ^b
Other Mammalia		
<i>Carpa hircus</i> ³⁹	ki	A
<i>Crocota crocota</i> ⁴⁰	gc [†] , to	V
<i>Tursiops truncatus</i> ⁴¹	br, co	?

^aBehaviour typically used in reconciliation, ap: apologies, br: body rubbing, co: contact (e.g. sitting, laying), em: embrace, gc: genital contacts, gr: grooming, gv: grunt vocalization, hb: hold-bottom, hh: hold-hand, ki: kiss or mouth-mouth contact, ls: lip-smack, mo: mounting, pl: play, so: share or offer object, to: touch.

^bThree rough proportion of major initiator of reconciliation, A: mostly by aggressor (A initiates more than 60% of reconciliation), V: mostly by victim (A initiates < 40% of reconciliation), A < V: aggressor and victim about equally (A initiates between 40% and 60% of reconciliation).

*Contact aggression; [†]genital contact is greeting.

¹Kappeler (1993); ²Rolland & Roeder (2000); ³Westlund et al. (2000); ⁴Verbeek & de Waal (1997); ⁵Leca et al. (2002); ⁶Pereira et al. (2000); ⁷Gust & Gordon (1993); ⁸Cheney & Seyfarth (1989); ⁹Björnsdotter et al. (2000); ¹⁰York & Rowell (1988); ¹¹Perez-Ruiz & Mondragon-Ceballos (1994); ¹²de Waal & Ren (1988); ¹³Aureli et al. (1989); ¹⁴Aureli (1992); ¹⁵Aureli et al. (1993); ¹⁶Kutsukake & Castles (2001); ¹⁷Matsumura (1996); ¹⁸de Waal & Yoshihara (1983); ¹⁹Demaria & Thierry (2001); ²⁰Judge (1991); ²¹Castles et al. (1996); ²²Petit & Thierry (1994a); ²³Abegg et al. (1996); ²⁴Aureli et al. (1994); ²⁵Castles & Whiten (1998a); ²⁶Petit & Thierry (1994b); ²⁷Silk et al. (1996); ²⁸Ren et al. (1991); ²⁹Sommer et al. (2002); ³⁰Swedell (1997); ³¹Arnold & Barton (2001); ³²Watts (1995); ³³de Waal (1987); ³⁴de Waal & van Roosmalen (1979); ³⁵Preuschoft et al. (2002); ³⁶Arnold & Whiten (2001); ³⁷Wittig & Boesch (2003a); ³⁸Butovskaya et al. (2000); ³⁹Schino (1998); ⁴⁰Wahaj et al. (2001); ⁴¹Samuels & Flaherty (2000).