THE CHOICE OF POST-CONFLICT INTERACTIONS IN WILD CHIMPANZEES (PAN TROGLODYTES)

by

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(Acc. 12-IX-2003)

Summary

Some costs of conflicts remain after an aggressive interaction has been terminated. Post-conflict management in social living animals can reduce those costs by means of a variety of interactions implemented after aggression (*e.g.* reconciliation, consolation, redirected aggression). Each post-conflict interaction (PCI) provides different advantages and disadvantages, although the functions may sometimes overlap. Individuals can therefore choose a PCI to achieve the most favourable outcome within a given conflict situation. We examined 876 dyadic aggressive interactions among 18 wild chimpanzees (*Pan troglodytes verus*) of both sexes in the Taï National Park, Côte d'Ivoire. We investigated which conflict-condition led to which type of PCI and related the choice of PCI to its advantages and disadvantages. Taï chimpanzees used reconciliation to resolve conflicts among high value partners and when approaching the former opponent was unlikely to entail further aggression. Consolation seemed to substitute for reconciliation, when were opponents low value partners or approaching the former opponent was too risky, such as when further aggression was likely. Taï chimpanzees renewed aggression after undecided conflicts and when losers were unexpected. They used

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[2] We thank the 'Ministère de la Recherche Scientifique', the 'Ministère de l'Agriculture et des Ressource Animales' of Côte d'Ivoire, the director of the Taï National Park and the 'Projet Autonome pour la Conservation du Parc National de Taï' for permission to conduct this study. We also thank the 'Centre Suisse de la Recherche Scientifique' in Abidjan, the staff of the 'Station du Centre de Recherche en Ecologie' and of the 'Projet Chimpanzé Taï', especially Kpazahi Honora Néné and Nohon Gregoire Kohon, for support in Côte d'Ivoire. We are grateful to Daniel Stahl and Gunter Weiss for their statistical advice, to Elainie Madsen, Martha Robbins and Linda Vigilant for constructive comments. Special thanks are due to Cathy Crockford for constant stimulating discussions and encouragement. This research was funded by the Swiss National Foundation and the Max Planck Society.

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redirected aggression after long conflicts, possibly because friendly PCIs were likely to fail. However, Taï chimpanzees continued with business as usual when conflicts were very short, and they avoided further interactions when the accessibility of the resource was unlimited. Taï chimpanzees appeared to follow a clear-cut evaluation process as they seemed to weigh advantages against disadvantages for the appropriate choice of PCI.

Introduction

Aggression disturbs the relationship of conflict partners and induces social tension within social groups (Cords, 1992; Aureli *et al.*, 1999; Matsumura & Okamoto, 2000). Such costs of conflicts remain present even after the aggression has ended. Post-conflict management is believed to reduce the costs of conflicts for social living animals. Post-conflict interactions (PCI), which in brief is the first interaction of a conflict partner subsequent to aggression, can either reduce those costs (*e.g.* stress reduction: Cords & Aureli, 2000; limit damage to a disturbed relationship: Aureli & Smucny, 2000) or can prevent further aggression (Aureli *et al.*, 2002). Yet, while PCIs represent an advantageous mechanism for social living animals, serious disadvantages may also be accrued (Watts *et al.*, 2000; Aureli *et al.*, 2002). Conflict partners may become trapped in further aggression when, for example, approaching former opponents for reconciliation (Aureli & van Schaik, 1991b; Cords, 1992). Conflict partners can choose from a pool of PCIs that consist of several affiliative or aggressive PCIs, carried out with former opponents or third parties (Aureli & de Waal, 2000). Therefore selecting an optimal PCI requires an evaluation of both the advantages and disadvantages. Individuals choosing a PCI are viewed as going through a decision-making process. The terms decision and choice do not necessarily imply a conscious reasoning process, rather individuals can switch between different behavioural possibilities.

Within group aggression erupts when individuals compete over food, mating partners, social partners or privileges of access to resources (Huntingford & Turner, 1987; Mason & Mendoza, 1993). Subsequently to aggressive interactions, which we will refer to as conflicts, PCIs can be implemented. Conflict partners can choose from a pool of PCI including reconciliation, solicited consolation, renewed aggression and redirected aggression, while in addition conflict bystanders can offer consolation or attack conflict partners (Aureli & de Waal, 2000). Alternatively conflict participants may avoid any further interaction ('no PCI'). Each of the seven options (six PCIs + 'no

PCI') has a potential pay-off, since they carry certain advantages and disadvantages.

Reconciliation, the affiliative PCI between former opponents, repairs the relationship of former opponents by restoring inter-opponent tolerance levels to baseline (Cords & Aureli, 1996). Partners of highly valuable relationships should restore tolerance levels to normal, since otherwise beneficial cooperation might be withheld (Cords & Thurnheer, 1993; de Waal, 1996). Reconciliation also reduces stress indicators (Aureli, 1997; Aureli *et al.*, 1999) and prevents further aggression (Aureli & van Schaik, 1991b; Watts, 1995a; Silk *et al.*, 1996). Moreover approaching former opponents might offer another chance at accessing the resource, which precipitated the fight. Relaxed partners could, for example, share food after reconciliation has reduced stress levels. Although reconciliation appears to reduce most costs of conflicts, it certainly is not implemented after each conflict (Aureli & de Waal, 2000). This may be due to the fact that reconciliation requires former opponents to approach one another thereby giving the opportunity of further aggression (Aureli & van Schaik, 1991b; Cords, 1992). Subordinate partners may thus profit disproportionately from relationship repair, as dominant partners are likely to share better quality food and better support than subordinates (Cords & Aureli, 2000). On the other hand subordinate cooperation partners may tip the scales in certain situations of social leverage (Lewis, 2002), that the need for relationship repair could be similar for both partners. Nonetheless subordinate partners incur comparatively higher risks by approaching former opponents, and might thus be less likely to initiate reconciliation when dominant partners are highly motivated to fight again.

In addition to reconciliation, consolation, the affiliative PCI with third parties, is also proposed as a mechanism to alleviate stress and reduce the risk of further aggression (Das, 2000; Watts *et al.*, 2000). Consolation is unlikely to repair the relationship of conflict partners, since former opponents do not interact directly, however it avoids an opportunity of further aggression. Consolation thus may substitute for reconciliation after conflicts with a high likelihood of further aggression or among low benefit partners, as both serve similar functions of reducing stress and preventing further aggression (Watts *et al.*, 2000). Consolation may even restore tolerance levels of former opponents to baseline levels when carried out with kin of former opponents (Cheney & Seyfarth, 1989; Judge, 1991). Conflict partners profit from consolation by means of stress reduction, while third parties may profit from

TABLE 1. *The pool of post-conflict interactions (PCIs): Overview of advantages and disadvantages of PCIs and the conditions under which each is expected*

Type of PCI	Advantages (A) and Disadvantages (D) for either conflict participants (CP) or third parties (TP)		Conditions under which PCI is expected: PCI implemented more often when
Reconciliation	A* (CP)	stress reduction	–
(a)	A* (CP)	prevent further aggression	–
	A (CP)	relationship repair	relationship benefit is high between CP
	A (CP)	access resource (non-aggressive attempt)	loser only: resource is limited
	D (CP)	possible renewed aggression	renewed aggression is unlikely between CP
Consolation	A* (CP)	stress reduction	–
(b) offered +	A* (CP)	prevent further aggression	–
(c) solicited	A (CP)	no approach of former opponent	renewed aggression is likely between CP
	A (TP)	calm tension	third party only: TP possible target of redirected aggression
	D (CP)	no relationship repair	relationship benefit is low between CP
Renewed Aggression (d)	A (CP)	access resource (second aggressive attempt)	conflict is a draw, resource is limited or highly valuable
			loser only: outcome of conflict is unexpected
	A (CP)	defeat frequent opponent	winner only: CP is rank neighbour
	D* (CP)	costs of aggression	–

TABLE 1. *(Continued)*

Type of PCI	Advantages (A) and Disadvantages (D) for either conflict participants (CP) or third parties (TP)		Conditions under which PCI is expected: PCI implemented more often when
Redirected	A* (CP)	stress reduction	–
Aggression	A (CP)	defuse frustration	loser only: conflict is strong (long and intense)
(e)	A (CP)	deflect aggression	non-aggressive PCI unlikely to stop aggression for CP
	D* (CP+TP)	costs of aggression	–
Third Party	A (TP)	defeat weakened frequent opponent	conflict is strong (long and intense)
Aggression	A (TP)	access resource (first aggressive attempt)	resource is limited or highly valuable
(f)	D* (CP+TP)	cost of aggression	–
No PCI	A (CP)	avoid risks of disadvantages of PCIs	no advantages of PCIs are needed by CP (*e.g.* no stress)
(g)			
	D (CP)	no possibility to access resource	resource is not limited

Conditions relating to the advantages or disadvantages are shown in the same row. Overlapping advantages and disadvantages (*) have no expected conditions (–), since they do not distinguish between the different types of PCI.

offering consolation when they are potential recipients of redirected aggression (Das *et al.*, 1997, 1998). Since there might be a functional difference, we have distinguished between offered consolation (Table 1), initiated by third parties, and solicited consolation, initiated by conflict participants (de Waal, 1993; de Waal & Aureli, 1996; Watts *et al.*, 2000).

In contrast to affiliative PCIs, all aggressive PCIs include the complete spectrum of disadvantages that are associated with aggression such as risk of injury, energy use, disturbed relationships and potential loss of access to the resource (de Waal, 1996; Wittig & Boesch, 2003a; Table 1). Redirected aggression, in which a conflict partner initiates an aggressive PCI with third parties, nonetheless carries advantages. It may reduce aggression-induced stress and frustration (Aureli & van Schaik, 1991a), as losers of conflicts with a high rate of redirected aggression showed lower levels of physiological (Levine *et al.*, 1989; Sapolsky, 2000) and behavioural stress indicators (Aureli & van Schaik, 1991b; Maestripieri *et al.*, 1992). Since winners of conflicts are also stressed by the conflict (Aureli, 1997), they might use redirected aggression to calm their own stress response. Furthermore, individuals may use redirected aggression to deflect the aggressive attention of an opponent to a third party (de Waal & van Hooff, 1981). Sometimes, when conflicts are long or intense, this might be one of the best possibilities for a victim to leave the focus of aggressive attention. In contrast to redirected aggression, third party aggression, in which a third party initiates an aggressive PCI, is neglected in most studies. Advantages for a third party to attack a conflict participant may be either to seize possession of an especially profitable resource (Preuschoft & van Schaik, 2000; Wittig & Boesch, 2003a) or to defeat a frequent opponent caught in a weak position (*e.g.* contra-intervention: de Waal, 1978).

In addition to these most often discussed PCIs, two additional types of post-conflict behaviour, renewed aggression and avoidance of further interactions, are of interest as well (Table 1). While renewed aggression, the aggressive PCI between former opponents, entails costs of conflict, it provides the loser of a conflict with a second opportunity to gain access to the disputed resource. Therefore it can be seen as a re-escalation of the same conflict. Nonetheless renewed aggression is only advantageous for losers with a sufficient likelihood of winning (Wittig & Boesch, 2003a). On the other hand renewed aggression may help winners of conflicts in strengthening

their dominant position against an already weakened opponent (Johnstone & Dugatkin, 2000).

Finally, conflict partners may avoid any interactions (no PCI) in order to prevent any further confrontation. However, avoiding the disadvantages of PCIs means that the advantages are also inaccessible, like stress reduction or a second attempt at accessing a resource. Since stress also reduces over time (Aureli & van Schaik, 1991b), conflict partners, that are only mildly stressed, might not need stress reducing PCIs. Nonetheless, avoiding interactions with party members makes monopolisable resources, that are possessed by them, inaccessible — a clear disadvantage of 'no PCI' for the loser.

Following a conflict social living animals can select an option from the pool of PCIs (six PCIs and 'no PCI'). Since some advantages can be gained from several different options, *e.g.* conflict partners can reduce stress by means of at least three different PCIs (reconciliation, consolation and redirected aggression), advantages and disadvantages that are unique to a PCI should play a decisive role in the evaluation process for the best choice of PCI. Table 1 summarises the advantages and disadvantages of all PCIs and the conditions under which each PCI is expected. Chimpanzees represent an excellent model to investigate the decision-making process behind the choice of PCI. They are highly sociable (Goodall, 1986; Nishida, 1990; Boesch & Boesch-Achermann, 2000) and most of the described options in the pool of PCIs are known to exist in chimpanzees (de Waal & van Roosmalen, 1979; de Waal & van Hooff, 1981; de Waal, 1984; de Waal & Aureli, 1996; Arnold & Whiten, 2001; Preuschoft *et al.*, 2002). However this study is the first to check on most of them for wild populations and in any case to consider all options of the pool of PCIs simultaneously. We investigate the selection process of PCIs in wild chimpanzees, in terms of the factors that influence the choice of PCI and who initiates the PCI. Our underlying hypothesis is that after a conflict chimpanzees use the PCI that provides the most advantages while carrying the fewest disadvantages. Our main questions are:

(1) Do wild chimpanzees apply all seven options from the pool of PCIs (six PCIs and 'no PCI') for post-conflict management?
(2) Under which conditions do wild chimpanzees use each type of PCI and does this choice of PCI follow the proposed evaluation process that takes both advantages and disadvantages into account?
(3) Which are the general rules that reflect the choice of PCI?

Methods

Study site and data collection

Data was 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. During the observation period five chimpanzees disappeared or died (one adult male, two adolescent females, two juveniles) and six infants were born.

R.W. collected the following four types of data during all-day follows of the four males and 10 adult females: (a) all-day focal animal sampling (Altmann, 1974) of a target chimpanzee, recording activities, social interactions and vocalisations; (b) recording of the target's party composition, scanning the presence of individuals in visibility of the target 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 target, food monopolisability and number of competitors present.

We aimed to change the target chimpanzee each day, observing females once and males twice per month. There was however, some variability in individual observation frequency due to 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 days each) and 123 all-day follows of females (between 10 and 15 days per female). 1071 conflicts with complete information were collected. Of these, 876 conflicts were analysed, as we excluded conflicts involving juveniles and infants.

Operational definitions

A conflict was defined as an aggressive dyadic interaction starting with the exchange of the first aggressive behaviour and ending immediately after the last aggressive behaviour within the dyad. We did not incorporate a time-rule, since among other things we investigated which conditions led to more aggression. The winner of the conflict was defined as the one able to access the resource. In food contexts the winner was the one possessing the food after the conflict. In sex contexts the winner was able to assert his or her choice (*e.g.* a female refused copulation, a male disturbed a copulation). In social contexts the winner was the one who neither showed submission, screams nor flight, or, in cases of competition over the access to a social partners, the one who affiliated with the particular social partner afterwards. We defined conflicts as a draw when neither conflict partner won.

A post-conflict interaction (PCI) was defined as the first interaction of the focal conflict partner with another individual subsequent to an aggressive interaction. Six possible PCIs were recorded: (a) *reconciliation*, affiliative PCI between former opponents ($N = 188$); (b) *offered consolation*, affiliative PCI initiated by a third party ($N = 164$); (c) *solicited consolation*, affiliative PCI with a third party initiated by a conflict partner ($N = 176$); (d) *renewed aggression*, aggressive PCI between former opponents ($N = 174$); (e) *redirected aggression*, aggressive PCI with a third party initiated by a conflict partner ($N = 88$); and (f) *third party aggression*, aggressive PCI initiated by a third party ($N = 28$). Avoidance of any further interaction was recorded as (g) *no PCI*, when the focal conflict partner did not interact with any other chimpanzee for the rest of the day ($N = 58$). Affiliative PCIs consisted

of friendly behaviours with body contact (*e.g.* kiss, genital touch, hand holding, embrace, grooming), while aggressive PCIs consisted of threats (*e.g.* barks, arm wave), non-contact aggression (*e.g.* displays) and contact aggression (*e.g.* bits, hits). In the results we distinguish between post-conflict reactions, which are all possible actions after a conflict (from a to g), and post-conflict interactions, which are only the PCIs related to post-conflict management.

Multivariate dyadic approach

We investigated which factors could explain the choice of PCI and whether winner or loser initiated the PCI. We were able to do the winner-loser comparison for inter-opponent PCIs, while this was not possible for PCIs with third parties, since they were either third party initiated or sample size was too small. We employed a multivariate approach to detect the factors that affected the use of each type of PCI. Table 2 displays the independent variables (with definitions and scoring of parameters) that were considered as factors. Each of these variables has been shown to be important in the decision process of wild chimpanzees as to whether or not to initiate aggression (further information: Wittig & Boesch, 2003a, b). All variables of Table 2, plus the interactions of *Initiator's Sex* with *Recipient's Sex*, *Rank Difference* with *Initiator's Rank* and *Conflict Context* with *Competitor Proportion*, were considered simultaneously as independent variables in each of the multivariate analyses. Since many 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, since repeated measurements of individuals can inflate the Type I (α) error, we controlled for a possible inflation of the Type I (α) error and ruled out the influence of repeated measurements on variables (see statistical process). The strength of our results was therefore similar to individual based analysis, but including the advantage that we were able to detect dyadic variability. Additionally, conflict duration was analysed separately on an individual level due to limitations of our binomial testing procedure on continuous predictors. A distinct mid-length conflict duration for a PCI would not be detected, since we tested one PCI against all the others (which would have longer and shorter conflict duarations).

Statistical process

We applied an altered version of the 'time-rule' (Aureli & van Schaik, 1991a; Castles & Whiten, 1998a), to determine whether or not the occurrence of PCIs depended upon the preceding conflict. The 'time rule' implies that a PCI needs to be initiated faster after a conflict than a control interaction. Therefore, we computed four different baselines that represent the normal interaction-intervals in our study group. Baselines for inter-opponent PCIs consisted of a value for each dyad, while baselines for PCIs with third parties had a value for each individual: (a) baseline for reconciliation is the mean interaction-interval of consecutive affiliative interactions for each dyad; (b) baseline of renewed aggression is the mean interaction-interval of any consecutive interaction for each dyad; (c) baseline of consolation is the mean interaction-interval of consecutive affiliative interactions of each individual with any other member of the community; (d) baseline of aggression with third parties is the mean interaction-interval of any consecutive interactions of each individual with any other member of the community. To compare the latencies of PCIs with their particular baselines, we calculated for each PCI event the relative latency (=*latency*/*baseline*), with a relative latency <1

TABLE 2. *Independent variables considered in the multivariate statistical process*

No	Name	Type	Variable definitions and parameter scoring
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 vocalisation 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 (based on subordinate greetings; Wittig & Boesch, 2003b) between conflict partners (rank subordinate – rank dominant); different category ranges, because of different numbers in sex classes; categories of r.d. in m-m dyads (4 males): *small* for rank neighbours, *middle* for r.d. = 2, *large* for r.d. = 3; categories of r.d. in f-f dyads (12 females): *small* for r.d. $\leqslant$ 3, *middle* for 3 < r.d. $\leqslant$ 6; *large* for r.d. > 6; categories of r.d. in m-f dyads (16 individuals) *small* for r.d. $\leqslant$ 5, *middle* for 5 < r.d. $\leqslant$ 10, *large* for r.d. > 10
4	Association Index	ordinal binomial	relative scoring of the dyadic association index (Nishida, 1968): *rare* = m-m: $\leqslant$50% of observation time, others: $\leqslant$25%; *frequent* = m-m: >50%, others: >25%
5	Relationship Benefit	ordinal multinomial	scoring of the cooperative character of the relationship of dyads: *low* = no food sharing, no support within dyad; *medium* = either food sharing or support within the dyad; *high* = both food sharing and support within the dyad
6	Initiator's Sex	binomial	sex of the initiator of aggression: *m* = male aggressor; *f* = female aggressor
7	Recipient's Sex	binomial	sex of the recipient of aggression: *m* = male aggressed; *f* = female aggressed
8	Initiator's Rank	binomial	dominance relationship of the conflict partners from the perspective of the initiator: *dom* = aggressor dominant over aggressed; *sub* = aggressor subordinate to aggressed
9	Conflict Context	multinomial	context in which the conflict occurred: *sex* = conflict about oestrus females; *food* = conflict about food or possession of tool; *social* = conflict about hierarchy or social partners and default category

TABLE 2. *(Continued)*

No	Name	Type	Variable definitions and parameter scoring
10	Resource Monopolisation	ordinal multinomial	relative scoring of the monopolisability of the resource that is fought over: *monopolisable by one* = resource can be monopolised by one competitor; *monopolisable by few* = resource can be monopolised by some of the competitors; *not monopolisable* = resource is not monopolisable
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): *few* for prop. $\leqslant 0.33$; *some* for $0.33 <$ prop. $\leqslant 0.66$; *many* for prop. > 0.66
12	Initiator Victory Outcome	multinomial	outcome of the conflict from the perspective of the initiator: w = initiator wins aggressive interaction; l = initiator loses; n = no winner
13	Winner's Rank	multinomial	dominance relationship of the conflict partners from the perspective of the winner: d = winner is dominant over loser; s = winner is subordinate to loser; n = no winner

Variables are numbered and the type of data, the variable definition and the variable scoring are shown from left to right. *Names of parameters* are in italics for better contrast.

representing PCI events occurring faster than baseline. For each PCI we calculated the mean relative latencies for each dyad (inter-opponent PCIs) or the mean relative latencies for each individual that participated in the conflict and the PCI (PCIs with third parties). Afterwards we sampled the means of each PCI with replacements and repeated this bootstrap procedure 5000 times to estimate the distribution of the samples (Manly, 1997). 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 of the 95% confidence interval of the approximate distribution of relative latencies of each PCI. This bootstrap test was conducted two-tailed with a significance level of $p < 0.05$.

To detect the variables that affects the choice of PCI, we executed multivariate analyses as follows:

(a) In order to eliminate repeated measurements of the same conflict type per dyad, we summarised conflicts in one data point for cases that had the same initiator and receiver of aggression, were followed by the same type of PCI, initiated by the same individual, and were identical in all other independent variables (see Table 2), apart from *Conflict Duration* and *Conflict Intensity*, which were scored with mean and median values respectively. The resulting balanced data set of 595 out of a total of 876 conflicts was used for the non-parametric and multivariate analyses.

(b) We used a generalisation of the Logistic Regression called Generalised Linear Model (GLZ: McCullagh & Nelder, 1989; Agresti, 1996) to examine the functional relationship between the occurrence of one dependent variable (type of PCI) and several independent variables (Table 2). We modelled the likelihood that a particular PCI occurs against the non-occurrence of this PCI ($\hat{=}$ all other PCIs). For the GLZ we chose a binomial 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 (LR: likelihood statistics), and the Akaike's Information Criterion (AIC), which penalises for the number of independent variables in the model (Akaike, 1973). The significance of the independent variables and their parameters 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 an independent variable-parameter 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 independent variable-parameter.

(c) Since we are analysing on a dyadic level, we controlled for a possible inflation of the Type I (α) error due to multiple measurements of the same actor. Therefore we included the identity of the conflict initiator as an additional independent variable and tested the best model again (similar procedure as 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 presented only the remaining significant variables of the best models in the results. For this test the significance level was $p < 0.05$.

All multivariate analyses (named 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 $N \leqslant 15$ (Mundry & Fischer, 1998). When testing related samples with missing values, we used a Friedman-ANOVA with 10000 permutations (Mundry, 1999). The bootstrap confidence intervals were computed in S-Plus (Insightful Corporation, 2001). Tests were performed two-tailed, unless stated otherwise.

Results

Are PCIs dependent on the conflict?

Chimpanzees had the choice of six types of PCI and the option of 'no PCI'. In order to determine if the PCIs were implemented as a consequence of the preceding conflict, we tested the 'time-rule' of whether or not baseline was included in the confidence interval (95% two-tailed) of the latencies of each PCI. Results revealed that all PCIs except solicited consolation were initiated more quickly than baseline (Fig. 1). The occurrence of offered consolation, redirected aggression, third party aggression, reconciliation and renewed aggression was triggered by the preceding conflict (all bootstrap tests: $p < 0.05$), while solicited consolation was not different from the baseline

(bootstrap test: NS). Thus, solicited consolations were independent of the preceding conflicts. As they were indistinguishable from normal interactions, solicited consolations are no longer referred to as a PCI in this paper. The remaining five PCIs can however be considered as post-conflict management.

The effect of conflict duration

The duration of the preceding conflict, calculated on individual levels, varied among the seven different post-conflict reactions (five PCIs, no PCI and normal interaction; Friedman-ANOVA with missing values: $k = 7$, $N = 90$, permutation = 10000, $p < 0.01$). Therefore we ordered the seven possible reactions to a conflict with increasing mean conflict duration (Fig. 2). We found a distinct relation between conflict duration and type of post-conflict reaction. This was not due to individual effects, as each individual that was involved in each type of interaction (5 PCIs and normal interaction) revealed the same effect between conflict duration and type of interaction (Page exact: $L = 651$, $k = 6$, $N = 8$, $p < 0.01$). This suggests that conflict duration influenced the choice of PCI. Comparison between aggressive and affiliative PCIs revealed that shorter conflicts were followed by affiliative PCIs while longer conflicts resulted in aggressive PCIs (Wilcoxon exact: $T = 14$, $N = 15$, $p < 0.01$). Multivariate analysis confirmed this result on a dyadic level and revealed conflict duration to be the only predictor (of list in Table 2) that influenced whether aggressive or affiliative PCIs followed the conflict (GLZ: $LR\chi_4^2 = 15.1$, $N = 545$, $p < 0.01$; Table 3A). Thus, the risk of further aggression increased with conflict duration and Taï chimpanzees preferred affiliative PCIs to manage shorter conflicts while aggressive PCIs were used to manage longer conflicts.

Avoidance of interactions (no PCI)

First, we investigated which conditions resulted in 'no PCI'. Conflict partners were more likely to avoid interactions, when resources were not monopolisable by a single competitor, when conflict partners were rare associates or opponents had a small rank difference (GLZ: $LR\chi_5^2 = 15.9$, $N = 595$, $p < 0.01$; Table 3B). Chimpanzees were thus more likely to implement interactions after conflicts over limited resources and after fighting familiar partners, while fighting over a resource, that was available somewhere else in the party, did not require following social interactions with community

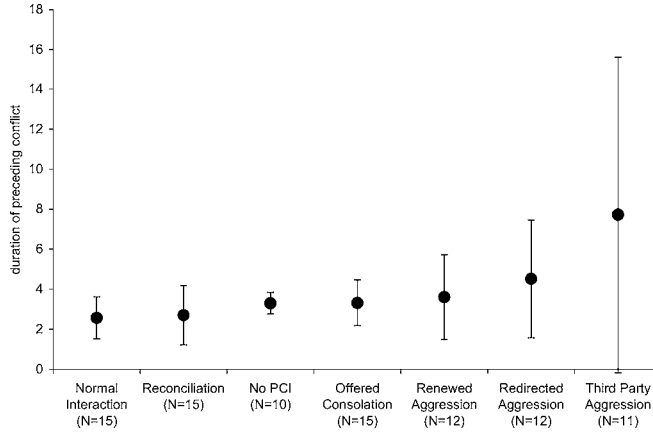

Fig. 2. Average individual conflict duration (second ± standard deviation) preceding the different types of post-conflict reactions in Taï chimpanzees. The post-conflict reactions are ordered from the shortest (left) to the longest (right) average duration of preceding conflicts (differences of conflict duration: (a) among all post-conflict reactions**, (b) same increasing effect for each individual from left to right**, (c) affiliative *vs* aggressive**, $p < 0.01^{**}$).

members. Subsequently we analysed under which conditions the different interactions were implemented.

Normal interactions — business as usual

Since the 'time-rule' analysis showed that solicited consolations were indistinguishable from normal interactions, we tested under which conflict conditions conflict partners continued with business as usual. Multivariate analysis proved that conflict partners continued with normal interactions after very short conflicts or after conflicts among same sex partners (GLZ: $LR\chi^2_5 = 27.18$, $N = 545$, $p < 0.0001$; Table 3C). Thus Taï chimpanzees were able to have business as usual after very short conflicts, while longer conflicts needed conflict management related PCIs. Subsequently we investigated the choice amongst the five PCIs that were dependent on the preceding conflict.

Choice of PCIs

Reconciliation

Conflict partners were most likely to reconcile with opponents of opposite sex, with high benefit partners or with frequent associates (GLZ: $LR\chi^2_4 =$

TABLE 3. *Factors affecting the occurrence of aggressive versus affiliative post-conflict interactions, avoidance of interactions and normal interactions in Taï chimpanzees*

Independent variables	A. Aggressive PCIs *vs* Affiliative PCIs								
	Wald	df	*p*	parameter	*N*	Effect	β	Wald	*p*
Conflict duration	6.02	1	*	continuous	545	$\uparrow^1$	0.83	6.02	*
Independent variables	**B. Avoidance of Interactions (no PCI)**								
	Wald	df	*p*	parameter	*N*	f_p%	β	Wald	*p*
Resource monopolisation	6.79	2	*	by one	283	5.7	−0.54	6.08	*
				by few	159	9.4	0.14	0.38	NS
				by non	153	12.4	0.40	3.56	(*)
Association index	4.34	1	*	rare	384	9.9	0.38	4.34	*
				frequent	211	5.7	−0.38		
Rank difference	6.03	2	*	small	211	10.1	0.55	5.78	*
				middle	247	8.5	0.06	0.06	NS
				large	125	4.8	−0.61	3.92	*
Independent variables	**C. Normal Interaction**								
	Wald	df	*p*	parameter	*N*	f_p%	β	Wald	*p*
Conflict duration	8.81	1	**	continuous	545	$\downarrow^2$	−1.29	8.81	**
Sex combination	5.11	1	*	m-m	148	23.6	0.29	5.11	*
				f-f	160	33.1	0.29		
				m-f	194	17.0	−0.29		
				f-m	43	23.3	−0.29		

Presented are the significant variables of the best models, their parameters (including frequency of occurrence f_p and estimate-coefficients β) and the Wald-statistics.
Model A (aggressive PCIs *vs* affiliative PCIs): [1] longer conflicts preceding aggressive PCIs than preceding affiliative PCIs.
Model B (no PCI *vs* all interactions): $\bar{f}_{\text{no PCI}} = 8.4\%$.
Model C (normal interaction *vs* PCIs): $\bar{f}_{\text{normal interaction}} = 24.0\%$; [2] shorter conflicts preceding normal interactions.
Significance levels: $^{**} < 0.01$; $^{*} < 0.05$; $(^{*}) < 0.1$; NS = non-significant. Wald: Wald-statistics; $f_p\%$ = frequency in percent of the dependent variable after conflicts with particular parameter; β: estimate-coefficient; $\bar{f}$ = overall frequency of dependent variable.

20.1, $N = 414$, $p < 0.001$; Table 4A). Reconciliation was equally initiated by winners and losers of conflicts (winner: 41.7%, loser: 58.3%; Goodness of fit: $\chi^2_1 = 3.14$, $N = 115$, NS). After non-contact aggression losers significantly increased their proportion of initiation of reconciliation with conflict intensity, while after contact aggression (parameters 4 and 5) the proportion of losers as initiators was not significantly different from average (GLZ: $LR\chi^2_7 = 24.2$, $N = 115$, $p < 0.01$; Table 4B). Furthermore, while losers were more likely than winners to initiate reconciliation after conflicts over food, winners showed a tendency to initiate more reconciliation in social and sex contexts (Table 4B).

Reconciliation was thus preferred among mixed sex partners and among opponents with highly valuable relationships. Losers initiated reconciliation following conflicts over food, and their initiation frequency increased with conflict intensity, yet neither conflict partner was more initiative in reconciliation after contact aggression.

Offered consolation

Taï chimpanzees received consolation more often after conflicts with same sex partners, with partners of low benefit or when only a few competitors were present (GLZ: $LR\chi^2_5 = 12.8$, $N = 414$, $p < 0.05$; Table 4C). Offered consolation and reconciliation occurred after almost complementary conflict situations (Fig. 3). Moreover, consolation was received after significantly longer conflicts as compared to reconciled conflicts (Wilcoxon exact one-tailed: $T = 93$, $N = 15$, $p < 0.05$; Fig. 2).

Renewed aggression

Renewed aggression did not show any distinct predictors in the multivariate analysis (GLZ: $LR\chi^2_1 = 2.68$, $N = 414$, $p < 0.2$). However, after conflicts ending in a draw, conflict partners were more likely to initiate renewed aggression than any other PCI (9 of 21 draws resulted in renewed aggressions, while 96 times renewed aggression was chosen of 418 conflict partner initiated interactions; Goodness of fit: $\chi^2_1 = 4.76$, $N = 21$; $p < 0.05$).

Renewed aggression was more likely to be initiated by winners than losers of conflicts (winner: 74.4%, loser: 25.3%, Goodness of fit: $\chi^2_1 = 21.25$, $N = 87$, $p < 0.0001$). Losers, however, renewed aggression when they had initiated the conflict, or when they were the dominant partner (GLZ: $LR\chi^2_{10} = 57.1$, $N = 87$, $p < 0.0001$; Table 5A).

Therefore, renewed aggression seemed to be the preferred PCI following draws, while dominant initiators renewed aggression when they unexpectedly lost a conflict.

Redirected aggression

Aggression was redirected slightly more often after initiators won the conflict (GLZ: $LR\chi^2_2 = 6.73$, $N = 414$, $p < 0.05$; Table 5B). However this predictor was only marginally significant.

Third party aggression

Third parties reacted more often with aggression after very long or very intense conflicts or when the conflicts were in a social context (GLZ: $LR\chi^2_{11} =$

TABLE 4. *Factors affecting the choice of affiliative post-conflict interactions in Taï chimpanzees*

Independent variables	A. Reconciliation								
	Wald	df	p	parameter	N	f_p%	β	Wald	p
Association index	4.64	1	*	rare	267	25.5	−0.26	4.64	*
				frequent	147	36.1	0.26		
Relationship benefit	6.76	2	*	low	142	23.2	−0.29	2.74	(*)
				medium	201	27.9	−0.22	1.85	NS
				high	71	45.1	0.51	6.76	**
Sex combination	4.02	1	*	m-m	113	26.5	−0.24	4.02	*
				f-f	107	19.6	−0.24		
				m-f	161	34.8	0.24		
				f-m	33	42.4	0.24		

Independent variables	B. Initiator of reconciliation									
	Wald	df	p	parameter	N	WI f_p%	LO f_p%	β^1	Wald	p
Conflict context	9.18	2	*	social	57	49.1	50.9	0.66	3.74	(*)
				sex	26	50	50	0.70	2.95	(*)
				food	32	21.9	78.1	−1.36	8.93	**
Conflict intensity	10.66	4	*	1	26	57.7	42.3	1.34	5.54	*
				2	27	40.7	59.3	−0.22	0.22	NS
				3	32	28.1	71.9	−1.44	7.97	**
				4	22	36.4	63.6	−0.08	0.02	NS
				5	8	62.5	37.5	0.40	0.29	NS

TABLE 4. *(Continued)*

Independent variables	C. Offered Consolation								
	Wald	df	p	parameter	N	f_p%	β	Wald	p
Competitor proportion	7.78	2	*	few	61	34.4	0.36	5.84	*
				some	209	24.4	−0.02	0.02	NS
				many	144	18.8	−0.34	6.98	**
Relationship Benefit	7.54	2	*	low	142	30.1	0.28	4.96	*
				medium	201	19.9	−0.24	3.77	(*)
				high	71	21.1	−0.04	0.08	NS
Sex combination	3.96	1	*	m-m	113	29.2	0.18	3.96	*
				f-f	107	26.2	0.18		
				m-f	161	19.9	−0.18		
				f-m	33	18.2	−0.18		

Presented are the significant variables of the best models, their parameters (including frequency of occurrence f_p and estimate-coefficients β) and the Wald-statistics.
Model A (reconciliation *vs* other PCIs): $\bar{f}_{\text{reconciliation}} = 29.2\%$.
Model B (winner *vs* loser initiation of reconciliation): $\bar{f}_{\text{winner}} = 41.7\%$ (WI); $\bar{f}_{\text{loser}} = 58.3\%$ (LO); [1] positive β = effect in favour of winner.
Model C (offered consolation *vs* other PCIs): $\bar{f}_{\text{offered consolation}} = 23.9\%$.
Significance levels: $^{**} < 0.01$; $^{*} < 0.05$; $^{(*)} < 0.1$; NS = non-significant. Wald: Wald-statistics; f_p% = frequency in percent of the dependent variable after conflicts with particular parameter; β: estimate-coefficient; $\bar{f}$ = overall frequency of dependent variable; WI = winner; LO = loser.

48.2, $N = 414$, $p < 0.0001$; Table 5C). However this PCI was less frequently observed after the most intense non-contact aggression.

Discussion

Taï chimpanzees applied five of the initially six identified PCIs and likely 'no PCI' for post-conflict management. We have summarised the results of the choice of PCI in Fig. 4, in order to provide an accessible overview of the post-conflict management related PCIs. This suggests that Taï chimpanzees show a clear-cut evaluation process in selecting a PCI. Conflict participants avoided further interactions after conflicts over non-monopolisible resources or among rare associates. Very short conflicts did not require post-conflict management, as Taï chimpanzees continued with business as usual. Below, we discuss the influence of the advantages and disadvantages on the choice

TABLE 5. *Factors affecting the choice of aggressive post-conflict interactions in Taï chimpanzees*

Independent variables	A. Initiator of renewed aggression									
	Wald	df	p	parameter	N	WI f_p%	LO f_p%	β^1	Wald	p
Initiator's victory outcome[2]	14.49	1	***	winner	77	83.1	16.9	3.76	14.49	***
				loser	10	10	90	−3.76		
Winner's rank	3.96	1	*	dominant	70	84.3	15.7	1.35	3.96	*
				subordinate	17	35.3	64.7	−1.35		

Independent variables	B. Redirected aggression								
	Wald	df	p	parameter	N	f_p%	β	Wald	p
Initiator's victory outcome	4.68	2	(*)	winner	347	18.8	0.83	4.46	*
				loser	42	9.5	0.05	0.01	NS
				draw	25	4	−0.88	1.56	NS

Independent variables	C. Third party aggression								
	Wald	df	p	parameter	N	f_p%	β	Wald	p
Conflict context	14.15	2	***	social	203	10.3	1.19	9.22	**
				sex	73	1.4	−0.60	0.77	NS
				food	138	4.3	−0.59	1.56	NS
Conflict duration	11.12	1	***	continuous	414	↑[3]	2.08	11.11	***
Conflict intensity	10.07	4	*	1	84	6.0	−0.01	0.01	NS
				2	97	5.2	0.36	0.71	NS
				3	101	2.0	−1.38	5.13	*
				4	67	7.5	0.04	0.01	NS
				5	65	16.9	0.99	7.56	**

Presented are the significant variables of the best models, their parameters (including frequency of occurrence f_p and estimate-coefficients β) and the Wald-statistics.

Model A (winner *vs* loser initiation of renewed aggression): $\bar{f}_{\text{winner}} = 73.9\%$ (WI); $\bar{f}_{\text{loser}} = 26.1\%$ (LO); [1] positive β = effect in favour of winner; [2] draws were excluded, since we tested winner *vs* loser.

Model B (redirected aggression *vs* other PCIs): $\bar{f}_{\text{redirected aggression}} = 16.9\%$.

Model C (third party aggression *vs* other PCIs): $\bar{f}_{\text{third party aggression}} = 6.8\%$; [3] longer conflicts preceding third party aggression.

Significance levels: *** < 0.001; ** < 0.01; * < 0.05; (*) < 0.1; NS = non-significant. Wald: Wald-statistics; f_p% = frequency in percent of the dependent variable after conflicts with particular parameter; β: estimate-coefficient; $\bar{f}$ = overall frequency of dependent variable; WI = winner; LO = loser.

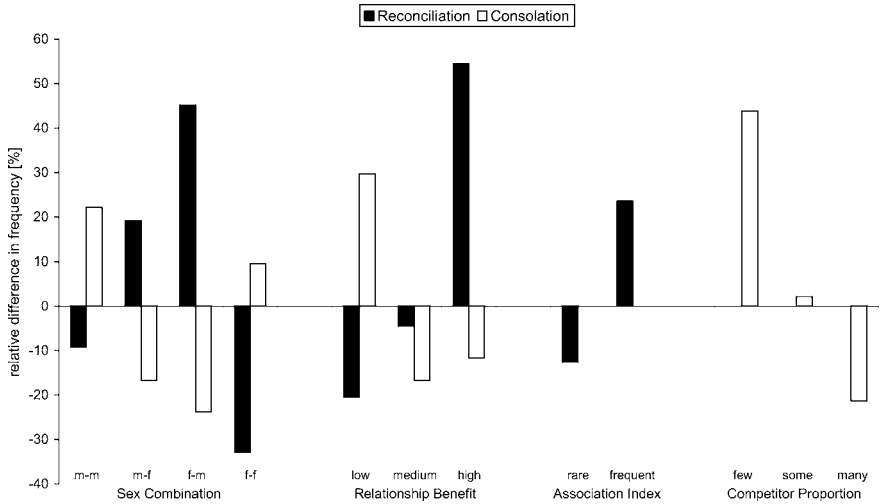

Fig. 3. Comparison between the tendencies to initiate reconciliation and consolation in Taï chimpanzees. The relative difference in frequency of each parameter $((f_p - \bar{f})/\bar{f})$ is shown for the significant variables, separately for reconciliation (■) and consolation (□). Positive relative differences indicate a positive effect of the parameter on the frequency of the PCI, while negative relative differences point out a negative effect.

of PCI and compare the post-conflict management of Taï chimpanzees with those of other mammals. Finally we extract general rules for the evaluation process and discuss their validity.

Solicited consolation was to the only possible PCI that did not serve a function in the post-conflict management of Taï chimpanzees. As solicited consolation followed very short conflicts and it was indistinguishable from normal interactions it seems likely that any costs were minimal after very short conflicts. Moreover, conflict partners were able to interact non-aggressively after shorter conflicts while longer conflicts led to aggressive PCIs, and the longest conflicts usually resulted in attacks by third parties. In fact there was almost a linear relationship between increasing length of conflict and likelihood of further aggression as well as the level of escalation. On the one hand this may reflect the motivation for escalation to aggression within the dyad and therefore within the party. Competition over beneficial resources was more likely to lead to aggression than less beneficial ones (Janson, 1988a; Preuschoft & van Schaik, 2000; Wittig & Boesch, 2003b) and the length of the conflict was dependent on the value of the resource (Wittig & Boesch, 2003a). On the other hand this may also suggest that

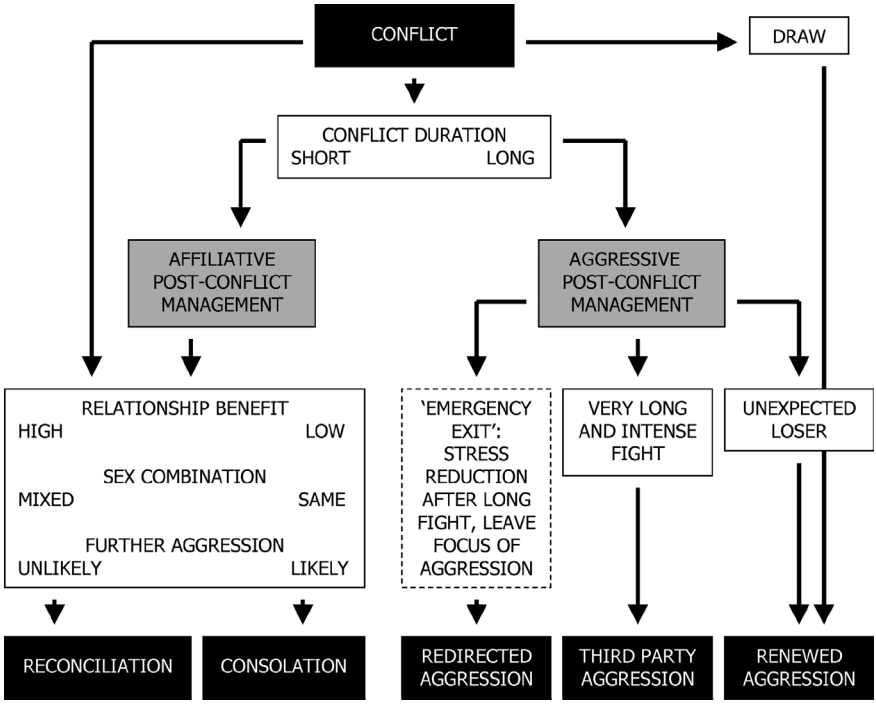

Fig. 4. Schematic depiction of the evaluation process for post-conflict management in Taï chimpanzees. Several factors influence the optimal choice of PCI between the conflict (starting point: black, on top) and five post-conflict interactions (end points: black, at bottom). Affiliative PCIs are arranged on the left side, while aggressive PCIS are grouped on the right side of the figure (marked in grey). Some post-conflict interactions can be reached following several different effects. Dashed box indicates that effect is one possible conclusion.

stress and tension created by the conflict increased with conflict duration. Although some studies have tried to find relationships between post-conflict stress and conflict intensity (contact *vs* non-contact aggression), but failed to detect them (*Macaca fascicularis*: Aureli, 1997; *Macaca fuscata*: Kutsukake & Castles, 2001; *Papio anubis*: Castles & Whiten, 1998b), they all neglected conflict duration as a possible predictor. It remains unclear whether or not there is also a positive correlation between conflict duration and stress or tension, besides the correlation with escalation to aggression. We suggest that conflict duration is possibly a good predictor for the level of induced stress.

While Taï chimpanzees continued with business as usual after a seemingly negligible stress response, they avoided any further interaction after fighting

over non-limited resources. Although non-limited resources do not usually cause conflicts, aggression can arise in situations where many competitors are present (Janson, 1988b; Wittig & Boesch, 2003b). Usually, with a non-limited resource, the possible disadvantages of engaging on a PCI are likely to out weigh the possible benefits gained. Therefore, moving to a different feeding spot or engaging in other activities (*e.g.* resting, travelling) seems to be a reasonable post-conflict reaction. Whether or not the avoidance of any further interaction was dependent on the preceding conflict, was not possible to test with the time-rule method. Thus we can neither definitely include nor exclude 'no PCI' from the conflict management. Although Taï chimpanzees sometimes avoided interactions or continued with business as usual after conflicts, most of the conflicts required a PCI.

Reconciliation

Taï chimpanzees reconciled more often with cooperative partners and frequent associates. This is strong evidence that the choice for reconciliation was due to its advantage of relationship repair. Reconciliation with high value partners is common in many primate species, such as among cooperative partners (*e.g.* Cords & Thurnheer, 1993), alliance partners (*e.g.* Watts, 1995a), kin (*e.g.* York & Rowell, 1988; Cheney & Seyfarth, 1989; Kappeler, 1993; Castles & Whiten, 1998a), partners of affiliation (*e.g.* Cords & Aureli, 1993; Watts, 1995a; Castles *et al.*, 1996; Schino *et al.*, 1998; Call *et al.*, 1999), and frequent associates (*e.g.* de Waal & Yoshihara, 1983; Aureli *et al.*, 1989). Wild chimpanzees in Budongo, Uganda, preferably reconciled with mating partners (Arnold & Whiten, 2001). Taï chimpanzees might even consider potential mating partners as valuable since they reconciled more often in mixed sex dyads.

Reconciliation was also more likely when further aggression seemed to be less likely. The result suggests that the disadvantage of risking recurring aggression, when approaching the former opponent, also shaped the choice for reconciliation. Similar results were found in other studies, where low intensity conflicts (non-contact aggression) were reconciled more often than high intensity ones (*e.g. Eulemur fulvus*: Kappeler, 1993; *Pan troglodytes* (Budongo): Arnold & Whiten, 2001). Furthermore, when Budongo chimpanzees accepted the outcome of conflicts by emitting greetings, they were

more likely to reconcile afterwards (Arnold & Whiten, 2001). Tufted capuchins (*Cebus apella*) reconciled only after non-food conflicts although almost 90% of their conflicts were over clumped food (Verbeek & de Waal, 1997). This might show that tufted capuchins do not dare to reconcile when the chance of further aggression is high. Since macaques and baboons reconciled less after food than after non-food conflicts (*Macaca fascicularis*: Aureli, 1992; *Macaca maurus*: Matsumura, 1996; *Papio anubis*: Castles & Whiten, 1998a), Aureli *et al.* (2002) argued that food conflicts may not damage the relationship of opponents and therefore there is less need for reconciliation. However our multivariate analysis for Taï chimpanzees showed that the occurrence of reconciliation was not different between food and social context.

Losers initiated more reconciliation after food conflicts, while the initiation rates of winners and losers were equal in social and sex contexts. After food conflicts losers appeared to be the main profiteers of reconciliation. Taï chimpanzees, as well as Budongo chimpanzees (Arnold & Whiten, 2001), probably tried to access food with a second attempt after they calmed the former opponent. In contrast after social and sex conflicts the social leverage of subordinates seemed to be similar to those of dominants (Hand, 1986; Lewis, 2002). Since both potential mating partners can avoid copulation, and the support of a high value partner might be needed in future conflicts with other individuals, both partners should have an interest in repair the relationship after social and sex conflicts. However losers initiated more reconciliation with increasing conflict intensity, but after contact aggression neither conflict partner showed an initiation preference. This suggests that losers are more restricted by increasing conflict intensity than dominants. Since subordinate partners risk more in approaching the former opponent than their dominant partners, they may decrease their initiation rate when the dominant partners is highly motivated to fight again. A conflict partner using contact aggression, however, might signal a willingness to risk more to gain the benefit of the resource. Losers, therefore, may be more hesitant to approach the former opponent for reconciliation than after non-contact aggression. The results suggest that increasing conflict intensity increasingly disturbed the relationship of opponents in Taï chimpanzees. The advantages of relationship repair and of accessing the resource through affiliation as well as the disadvantage of further aggression shaped the proportion of loser to winner

initiated reconciliations. Different proportions of victim initiated reconciliation among species might be explained by inter-specific differences in the risk of further aggression or the advantage of cooperation or affiliation (more aggressor initiated: *e.g. Cebus capucinus*: Leca *et al.*, 2002; *Papio anubis*: Castles & Whiten, 1998a; *Carpa hircus*: Schino, 1998; no difference: *e.g. Macaca fuscata*: Aureli *et al.*, 1993; *Macaca silenus*: Abegg *et al.*, 1996; *Papio papio*: Petit & Thierry, 1994; more victim initiated: *e.g. Colobus guereza*: Björnsdotter *et al.*, 2000; *Macaca arctoides*: de Waal & Ren, 1988; *Crocuta crocuta*: Wahaj *et al.*, 2001).

Consolation

Consolation was offered in almost the contrary conflict situations as compared to reconciliation (Fig. 3). Taï chimpanzees seemed to offer consolation when reconciliation was either not beneficial or was too risky for conflict participants. Since low benefit partners were those that did not share food and did not support each other, opponents would gain little from relationship repair. Similarly same sex dyads would not provide much benefit in terms of potential mating partners. Additionally, same sex opponents probably have a higher tendency for further aggression than mixed sex opponents, as competing aggressively over the same resource again might be very unlikely when the resource provides different benefits to each opponent. Indeed same sex dyads in Taï chimpanzees fought more often than mixed sex dyads (Wittig & Boesch, 2003a). Since the risk of further aggression increased with length of conflict and consolation followed longer conflicts more than reconciliation, consolation was probably offered when approaching former opponents was too risky. Thus consolation may have been substituted for reconciliation when further aggression was more likely. In gorillas (*Gorilla gorilla*) consolation might also be a substitute for reconciliation for the same reason. Consolation mostly occurred after conflicts among gorilla females (Watts, 1995b), three quarters of which were conflicts ending without any submissive sign that showed the acceptance of the outcome (Watts, 1994). This preference for consolation when conflicts could be followed by further aggression might explain why female gorillas mainly sought consolation from males (Watts, 1995b).

Renewed aggression

Undecided conflicts in Taï chimpanzees were usually followed by renewed aggression. In addition losers of conflicts mostly initiated renewed aggression when they were dominant losers or initiators that lost, and thus they had a good chance of winning the new conflict (Wittig & Boesch, 2003a). The advantage of accessing the resource in a second aggressive attempt thus seemed to be a main factor for the choice of renewed aggression. However, why did so many winners renew the aggression? In contrast to Taï chimpanzees, redfronted lemurs (*Eulemur fulvus*) had a higher tendency to reconcile, when the conflict was undecided (Kappeler, 1993). Reconciliation is the only other PCI that allows possible access to the resource but in addition excludes costs of aggression. Redfronted lemurs might face a lower risk of further aggression than chimpanzees, which enables them to arrange undecided conflicts peacefully while chimpanzee winners might react aggressively when the former opponent, aiming to reconcile, approaches too early. For other mammals there is no evidence that undecided conflicts result in any specific PCI (*e.g.* *Cercopithecus athiops*: Cheney & Seyfarth, 1989; *Lemur catta*: Kappeler, 1993; *Capra hircus*: Schino, 1998).

Redirected aggression

Redirected aggression was the only PCI in the post-conflict management of Taï chimpanzees that showed an ambiguous pattern. Taï chimpanzees redirected aggression marginally more often when the initiator won, so after expected outcomes (see: renewed aggression). This casts doubts on the idea that individuals would redirect their frustration to third parties. However, redirected aggression is the only aggressive PCI with evidence for stress reduction (Aureli & van Schaik, 1991b). Since preceding conflicts of aggressive PCIs were longer than those of affiliative PCIs, Taï chimpanzees might use redirected aggression as a kind of 'emergency exit' to reduce their stress after long conflicts, where either reconciliation or consolation were too risky, and to sneak out of the focus of aggression. Thus the 'emergency-exit' strategy pays for all dyads that engaged in long conflicts regardless of their relationship. Other primate species might also employ the 'emergency exit', since redirected aggression is usually not affected by the relationship of opponents (not affected: *Gorilla berengei*: Watts, 1995b; *Macaca fuscata*: Aureli *et al.*, 1993; *Macaca sylvanus*: Aureli *et al.*, 1994; *Papio anubis*: Castles

& Whiten, 1998a; but, affected: *Cercopithecus athiops*: Cheney & Seyfarth, 1989).

Third party aggression

Third party aggression occurred after the longest and the most intense conflicts in Taï chimpanzees. On one hand, individuals might support their coalition partners after the conflict has already been decided (winner-support: de Waal, 1978) or general high arousal within the party might induce general escalation of aggression (*e.g.* Aureli & van Schaik, 1991b; Cords, 1992; Preuschoft & van Schaik, 2000). On the other hand conflict partners, especially losers, were probably weakened after such long and intense fights. These vulnerable individuals would be easy targets of aggression for their frequent competitors, for example rank neighbours. Since third party aggression also occurred more often after social conflicts, we were unable to rule out any of these possibilities.

General discussion and final conclusion

Following the post-conflict management found in Taï chimpanzees (Fig. 4) we try to extrapolate generalised rules for the choice of PCIs: Reconciliation appeared to be chosen when a disturbed relationship is costly and further aggression is unlikely. However when initiation of reconciliation appears to be too risky, consolation seems to substitute for reconciliation. In situations where losing partners perceive a chance to access the resource by further aggression, they might renew aggression to gain the benefit of the resource in a second attempt. If the social tension has reached a level where attempting peaceful post-conflict management is too risky, conflict partners might take the 'emergency-exit' and redirect aggression to deflect aggressive attention to third parties. When conflict partners seem to be weakened, third parties might seize the opportunity to defeat a frequent competitor.

The interaction of advantages and disadvantages of PCIs might explain why despotic macaque species reconcile less often than egalitarian ones (Thierry, 2000). As both select usually high value partners for reconciliation (*Macaca arctoides*: de Waal & Ren, 1988; *Macaca fascicularis*: Aureli *et al.*, 1989; *Macaca fuscata*: Aureli *et al.*, 1997; *Macaca mulatta*: de Waal & Yoshihara, 1983; *Macaca nemestrina*: Judge, 1991), relationship repair seems to be important in both hierarchy types. However the approach of

former opponents in despotic macaques is likely to carry higher risks of further aggression, as tolerance levels in despotic societies are less clear-cut. Therefore approaching a former opponent can be easily mistaken as a counterattack and lead to further aggression. Additionally aggression in egalitarian macaques is milder and less costly for the victim (Thierry, 1986, 2000). Therefore a failed reconciliation attempt in despotic macaques is more costly than in egalitarian ones. Following the generalised rules, we would expect consolation to substitute for reconciliation in despotic macaques. However consolation seems not to be part of the macaque repertoire (Watts *et al.*, 2000), probably due to social or cognitive constraints (de Waal & Aureli, 1996). Despotic macaque species probably use redirected aggression instead to deflect the disadvantages of aggression to third parties and perhaps to reduce their own stress (*e.g. Macaca fascisularis*: Aureli & van Schaik, 1991b; Aureli, 1992; *Macaca fuscata*: Aureli *et al.*, 1993). In egalitarian species, however, redirected aggression is either less frequent (Thierry, 1985; Thierry *et al.*, 2000) or is not observed at all (*e.g. Macaca sylvanus*: Aureli *et al.*, 1994), as they reconcile more likely.

In consequence our results indicate that Taï chimpanzees have a clear-cut evaluation process as they seem to weigh carefully advantages against disadvantages to select the best PCI to the experienced conflict situation. Conflict management in Taï chimpanzees appears to take into account both cost and benefit before escalating a conflict of interest (Wittig & Boesch, 2003a) and selecting the best PCI to handle remaining costs. Since both conflict partners have the possibility to vary their post-conflict cost, conflict management opens the door for negotiation to lessen the consequences of conflicts. Thus post-conflict management seems to be an important negotiation tool for social mammals to enable advantageous social living despite the existing conflicts of interest.

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