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Chimpanzee (*Pan troglodytes*) Consolation: Third-Party Identity as a Window on Possible Function

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Consolation, that is, postconflict affiliative contact by a bystander toward a recipient of aggression, has acquired an important role in the debate about empathy in great apes because it has been proposed that the reassuring behavior aimed at distressed parties reflects empathetic arousal. However, the function of this behavior is not fully understood. The present study tests specific predictions about the identity of bystanders on the basis of a database of 1102 agonistic interactions and their corresponding postconflict periods in two outdoor-housed groups of captive chimpanzees (*Pan troglodytes*). We found that recipients of aggression were more likely to be contacted by their own "friends" than by "friends" of the aggressor and that frequent targets of aggression were not more likely to offer consolation than were nontargets of aggression. These findings support the stress reduction hypothesis rather than two proposed alternatives, that is, the opponent relationship repair hypothesis and the self-protection hypothesis. Our results provide further support for relationship quality as a fundamental underlying factor explaining variation in the occurrence of consolation.

Keywords: consolation, postconflict behavior, chimpanzees, *Pan troglodytes*, relationship quality

The first systematic study of postconflict interactions described the occurrence of affiliative exchanges between former opponents as well as between recipients of aggression and uninvolved bystanders in the aftermath of agonistic conflicts in a zoo colony of chimpanzees (*Pan troglodytes*; de Waal & van Roosmalen, 1979). During the following three decades, research on conflict management, especially by means of postconflict interactions, has produced evidence that these strategies are critical components of the social systems of many different animals (e.g., bottlenose dolphins, *Tursiops truncatus*: Weaver, 2003; capuchin monkeys, *Cebus paella*: Verbeek & de Waal, 1997; domestic goats: *Capra hircus*, Schino, 1998; macaques, *Macaca spp*.: de Waal & Ren, 1988; spotted hyenas, *Crocuta crocuta*: Wahaj, Guse, & Holekamp, 2001; and rooks, *Corvus frugilegus*: Seed, Clayton, & Emery, 2007). However, researchers have concentrated most of their efforts on the study of one type of postconflict contact, that is, affiliative reunions between former opponents, also known as *reconciliation* (reviewed by Arnold & Aureli, 2007; Aureli, Cords, & van Schaik, 2002; de Waal, 2000). Other types of interactions have received far less attention.

Only recently, investigations have begun to focus on postconflict third-party affiliation (i.e., affiliation between conflict participants and uninvolved bystanders or third parties) carrying on deeper analyses than the mere establishment of their presence or absence (e.g., Das, 2000; Fraser, Stahl, & Aureli, 2008; Koski & Sterck, 2007; Palagi, Cordoni, & Borgognini Tarli, 2006; Romero, Colmenares, & Aureli, 2008; Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007). Part of this renewed interest in third-party postconflict behavior is due to the underlying cognitive and emotional mechanisms that have been suggested for some of these interactions (Castles, 2000; de Waal & Aureli, 1996; Preston & de Waal, 2002).

The postconflict interaction labeled *consolation* has been defined as affiliative contact made by an uninvolved bystander toward the former recipient of aggression (see below). Consolation has been amply demonstrated in great apes (chimpanzees: de Waal & Aureli, 1996; de Waal & van Roosmalen, 1979; Koski & Sterck, 2007; Kutsukake & Castles, 2004; Palagi et al., 2006; Wittig & Boesch, 2003; gorillas, *Gorilla spp.*: Cordoni, Palagi, & Borgognini Tarli, 2006; Mallavarapu, Stoinski, Bloomsmith, & Maple, 2006; Watts, 1995; and bonobos, *Pan paniscus*: Palagi, Paoli, & Borgognini Tarli, 2004) but thus far not in monkeys (de Waal & Aureli, 1996; Schino, Geminiani, Rosati, & Aureli, 2004; Watts, Colmenares, & Arnold, 2000; but see Wittig et al., 2007). De Waal and Aureli (1996) proposed that different cognitive and empathetic abilities might be at the basis of the observed variation in consolation. In human children (*Homo sapiens*), consolation has been extensively studied and is generally attributed to "sympathetic

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concern," an expression of empathy (e.g., Eisenberg, 2000; Zahn-Waxler & Radke-Yarrow, 1990; Zahn-Waxler, Hollenbeck, & Radke-Yarrow, 1984) that may be present in apes (e.g., de Waal, 2008; Preston & de Waal, 2002) but not in monkeys. Interestingly, consolation has recently also been suggested for large-brained birds (rooks, *Corvus frugilegus*: Seed et al., 2007) and has been demonstrated in dogs (*Canis familiaris*: Cools, van Hout, & Nelissen, 2008).

The term *consolation* is a functional term originally proposed by de Waal and van Roosmalen (1979) implying distress alleviation of the recipient of aggression. Since then, this term is applied mostly to a highly specific category of third-party contacts, namely, unsolicited friendly contacts made by bystanders with victims of aggression, thus excluding contacts with aggressors, contacts lacking in friendly behavior, or contacts initiated by the conflict participants themselves (Aureli, 1997; de Waal & Aureli, 1997). Although researchers have suggested more descriptive terms such as *bystander affiliation* or *triadic affiliation* (e.g., Fraser, Koski, Wittig, & Aureli, 2009; Kutsukake & Castles, 2004), we use *consolation* throughout this article because we test predictions derived from the initial functional hypothesis and also because none of the alternative terms excludes some quite different types of postconflict affiliation (e.g., Das, 2000; Romero, Colmenares, & Aureli, 2009), which are not the focus of the present study.

Only two studies in chimpanzees have formally tested the implied stress-mitigating function of consolation. Both studies used self-directed behavior (e.g., self-scratching and self-grooming) as a behavioral indicator of stress. Whereas Koski and Sterck (2007) failed to find support for a stress-alleviating effect, because recipients of consolation showed no decline in self-directed behavior, Fraser et al. (2008) did find such an effect and concluded that consolation serves to calm down distressed parties.

A second functional hypothesis proposes that consolation serves as a substitute for reconciliation when the latter fails to take place (Palagi et al., 2006; Watts et al., 2000; Wittig & Boesch, 2003). It has been demonstrated that reconciliation is beneficial in repairing the relationship between former opponents and in reducing postconflict stress (reviewed by Arnold & Aureli, 2007; Aureli et al., 2002). However, approaching a former opponent may be risky because aggression may resume (Aureli & van Schaik, 1991). Hence, alternative postconflict strategies may be preferable (Koski, de Vries, van den Tweel, & Sterck, 2007; Wittig & Boesch, 2003). If consolation functions as an alternative for reconciliation, it should produce effects similar to those of reconciliation, such as restoration of the opponents' relationship to baseline levels or reduction of postconflict anxiety. Recent findings on chimpanzees and bonobos indirectly support the opponent relationship repair hypothesis (Fraser et al., 2009). In some studies, consolation was found to occur more often in the absence of reconciliation than in its presence (chimpanzees: Fraser et al., 2008; Palagi et al., 2006; bonobos: Palagi et al., 2004), whereas other studies failed to find a connection between the two (chimpanzees: Koski & Sterck, 2007).

Even though both above hypotheses predict that consolation alleviates the distress of the recipient of aggression, they predict different third parties as consolers. If consolation mainly serves to alleviate the victim's distress and rests on empathetic arousal in the actor, it should involve individuals with whom the recipient has a close relationship, given that empathy is greatly facilitated by similarity, familiarity, and social closeness between individuals (Anderson & Keltner, 2002; Aureli & Schaffner, 2002; de Waal, 2008; Fraser et al., 2008; Preston & de Waal, 2002). On the other hand, if the main function of consolation is to substitute for reconciliation, and hence is part of relationship-mending tactics, consolation should be provided mostly by the former aggressor's friends or kin, who by contacting the victim provide a triadic reconciliation similar to those documented for Cercopithecine primates (Cheney & Seyfarth, 1989; Judge, 1991; Wittig et al., 2007). To date, only one ape study has investigated the relationship between conflict participants and third parties that provide consolation (Fraser et al., 2008). This study, however, failed to address how consolers relate to the individual that had caused the recipient's distress, that is, the former aggressor.

As a third hypothesis, it has been proposed that the postconflict behavior provides direct and immediate benefits to the consoler, such as reducing their likelihood of becoming the target of further aggression by the former recipient of aggression (Koski & Sterck, 2007, 2009). According to this hypothesis, consolation should be performed mostly by frequent targets of aggression as a form of appeasement to protect themselves. Support for this self-protection hypothesis comes from a study on captive chimpanzees in which third parties selectively directed affiliation to those conflict participants who more often gave further aggression to them, and postconflict affiliation was associated with low levels of further aggression (Koski & Sterck, 2009). However, because of sample size limitations, the data of aggressors and recipients of aggression was combined in some analyses, and the implied causal relation (i.e., third-party contacts reduce further aggression) was not proven and could well be reversed (i.e., third-party contacts are preferentially made when the chance of further aggression is low).

Overall, there seems to exist partial empirical support for each of the three suggested hypotheses, and consequently the function of consolation remains unclear. Here, we aim to shed light on the function of consolation in chimpanzees by investigating specific predictions about the identity of third parties, which are summarized in Table 1.

Method

Subjects and Housing

Our chimpanzees (*Pan troglodytes*) lived in two social groups (FS1 and FS2) at the field station of the Yerkes National Primate Research Center, Atlanta, Georgia. Each group had access to indoor areas and a large outdoor compound (750 and 520 m^2, respectively). The compounds were equipped with vertical climbing structures and visual barriers, as well as plastic barrels, large tires, and a variety of toys. Water and primate chow were available ad libitum. The number of individuals per group varied slightly during the study period because of births, deaths, and several removals for veterinary reasons and management purposes. At any time, both groups consisted of at least one adult male and several adult females. A more detailed description of the study subjects can be found in Table 2.

Table 1
Predictions Derived From the Alternative Hypothesis About the Function of Consolation

Hypothesis	Effect	Prediction
Stress reduction	Reduction of recipients' postconflict anxiety	Bystanders should direct affiliation to close social partners
Opponent relationship repair	Restoration of the opponents' relationship, reduction of recipients' postconflict anxiety, or both	Affiliation to recipients should be initiated by kin and friends of the aggressor
Self-protection	Reduction of bystanders likelihood of becoming the target of further aggression	Bystanders should direct affiliation to recipients that are bystanders' frequent aggressors

Observation Methods

Since the formation of the two groups, controlled observation sessions have been conducted with regularity (approximately 1 per week). Data analyzed here refer to the period of time from 1992 to 2000 for FS1 and from 1994 to 2000 for FS2. All data were collected by one trained research technician, Mike Seres, during 90-min observation sessions (described in detail by de Waal, 1989). A total of 1320 and 618 observation hours were recorded for FS1 and FS2, respectively. During observation sessions, affiliative and sexual interactions (including kiss, embrace, grooming, gentle touch, finger or hand in mouth, and mounting) as well as agonistic interactions (which by definition include at least one of the following behavior elements: tug, brusque rush, trample, bite, grunt-bark, shrill-bark, flight, crouch, shrink/flinch, or bared-teeth scream; de Waal & van Hooff, 1981; van Hooff, 1974) were recorded with an all-occurrence sampling technique. All of these behaviors were recorded in the triplet format "who does what to whom" with an associated time stamp in seconds since the start of the protocol. Additionally, scan samples of state behaviors (e.g., contact-sitting, grooming, and playing) were taken at regular intervals (i.e., every 5 min through 1993 and every 10 min in the years thereafter).

Because the observations were continuous, the behavior of the opponents after aggression represents postconflict (PC) data (cf. de Waal & Yoshihara, 1983). Because previous investigations in chimpanzees have shown that differences in behavior between PC and baseline data are typically limited to the first 10 min after a conflict (Arnold & Whiten, 2001; Kutsukake & Castles, 2004; Palagi et al., 2006; Preuschoft, Wang, Aureli, & de Waal, 2002), our analysis focused on the immediate 10-min PC period. Following de Waal & van Roosmalen (1979), we considered an interaction an agonistic conflict if at least one of the strictly agonistic patterns previously listed occurred. Polyadic conflicts (i.e., those involving more individuals than the two original opponents) were divided into dyadic components (cf. de Waal & van Hooff, 1981), and for each agonistic dyad the initial aggressor and the initial recipient of aggression were identified. A matched control (MC) observation of the same duration as the PC was chosen, a posteriori, to extract baseline information. Periods of at least 10 min during which the focal individual was not involved in aggressive interaction were selected as MC periods. Each PC was matched with a MC period recorded on the nearest observation day within a time window of ±7 days. Third parties were defined as those individuals who were

Table 2
Sex, Age, and Kinship Relationships of Study Subjects From FS1 and FS2 Groups

FS1				FS2			
Subject	Sex	D.O.B.	D.O.R.	Subject	Sex	D.O.B.	D.O.R.
Jimoh	M	01/1964[a]	09/1996	Phineas	M	01/1966[a]	
Marilyne	F	01/1971	11/1993	Amos	M	11/1981	
Reinette[b]	F	12/1987		Chip	M	03/1989	
Gwennie	F	01/1969	03/1999	Magnum	M	07/1989	
Socrates[b]	M	01/1987		Erika	F	10/1973	
Claus[b]	M	12/1992		Virginia[b]	F	04/1991	
Mai	F	01/1964[a]		Tai	F	01/1967[a]	
Natasha[b]	F	12/1987		Daisy[b]	F	10/1989	
Borie	F	01/1964[a]		Waga	F	03/1982	
Georgia[b]	F	08/1980		Barbi	F	06/1976	
Kathy[c]	F	10/1989		Sean[b]	M	03/1992	
Rita[b]	F	07/1987		Cynthia	F	06/1980	
Atlanta	F	08/1965	12/2000	Vivianne	F	07/1974	
Rhett[b]	M	04/1989		Pollynna	F	02/1989	
Peony	F	01/1968					
Anja[b]	F	01/1980					
Bjorn[c]	M	07/1988					
Dona[b]	F	04/1990					

Note. All dates are month/year. M = male; F = female; D.O.B. = date of birth; D.O.R. = date of removal or death.
[a] Approximate date of birth. [b,c] Offspring of females are indicated by a superscript letter next to the subject's name (e.g., Reinette is the daughter of Marilyne; Kathy is the daughter of Georgia).

neither involved in the conflict or in any agonistic interaction in a time window of ±2min from the occurrence of the conflict. Only interactions involving individuals ages 8 years or older were considered in the present analysis.

Data Analysis

From PC and MC periods we extracted the information concerned with all interactions involving the opponents as well as the time of the interaction, the identity of the interaction partners, and the identity of the initiator of the interactions. Initiators were the individuals starting the interaction.

To detect the occurrence of consolation in the two study groups, we followed the PC–MC method (de Waal & Yoshihara, 1983). A PC–MC pair was considered attracted if the affiliation directed from a bystander toward the recipient of aggression occurred only or earlier in the PC than in the MC, dispersed if it occurred earlier or only in the MC, and neutral if the affiliation occurred at the same time in both or did not occur in either the PC or the MC. For each focal individual we compared the proportion of attracted and dispersed PC–MC pairs via the Wilcoxon signed-ranks test. Mann–Whitney *U* test was used to compare the triadic contact tendency (TCT) between the two groups and between male and female recipients. We calculated TCT for a particular dyad according to the following formula: 100 ∗ [(attracted pairs − dispersed pairs)/total number of PC–MC pairs] (cf. Call, Aureli, & de Waal, 2002).

To test the predictions about the identity of third parties, we classified postconflict contacts according to the affiliative level of the involving individuals. Because consolation is a triadic interaction (i.e., aggressor–recipient–third party), we kept that triadic character in the analyses by classifying postconflict contacts not only according to the relationship between the third party and the recipient but also according to the relationship between the third party and the aggressor.

Friends and nonfriends. We first categorized the overall level of affiliation within dyads using a combined measure of four state behaviors collected during scan sampling (i.e., contact sitting, sitting within arm's reach, grooming, and mutual grooming) and calculating the quartile points of dyadic scores per focal individual. Dyads with scores within the top quartile were labeled *friends* and all remaining dyads as *nonfriends*. Then, third parties were categorized as *aggressors' friends* if the third party involved in the interaction was a friend of the aggressor but not of the recipient; *recipients' friends* if it was a friend of the recipient but not of the aggressor; *friends of both* if the third party was a friend of both the aggressor and the recipient, and *nonfriends* if the third party did not maintain a close relationship with either opponent.

Targets and nontargets. Similarly, dyads were classified according to their aggression level. A dyad (between individuals A and B) was named *target of A* if the rate of aggression directed by A against B was in the top quartile of A's aggressive scores. Otherwise, the dyad was labeled *nontarget*. Then, bystanders were classified as *aggressors' targets* if the third party was an aggressor's target of aggression but not a target of the recipient; *recipients' targets* if the bystander was a recipient's target but not an aggressor's target; *target of both* if the third party received high rates of aggression from both the aggressor and the victim; or n*ontarget* if the third party was not a target of aggression of either opponent. Because overall affiliation and aggression levels between dyads could vary over time, we calculated dyadic levels of affiliation and aggression for each year independently.

We evaluated the predictions about the identity of bystanders offering consolation by fitting generalized linear mixed models (GLMM) with a binomial error structure and logit link function. Each postconflict opportunity of offering consolation for each of the different affiliative (or aggressive) categories was entered as a data point into the model. The dependent variable was the occurrence (i.e., yes or no) of consolation. We followed the operational definition of consolation by including only the first affiliative interaction directed by a bystander to the former recipient of aggression within the 10 min following the conflict. Affiliation (or aggression) level was set as a fixed factor and bystander availability (i.e., number of potential third parties available for a particular affiliative or aggressive category during the postconflict period) as an offset variable. As random terms we included the group (i.e., to account for any similarities among members of the same group) and the identity of opponents and PCs. When random terms did not have a statistical effect, we excluded them from the model.

Although the previous GLMM analysis took into account the triadic character of the postconflict affiliation, it did not control for baseline levels of affiliation between each dyad. Thus, we ran a second set of analyses using the TCT as a dependent variable. TCT analyses were based on the first affiliative interaction between the recipient of aggression and each potential consoler regardless of the identity of the aggressor. Thus, levels of affiliation were limited to bystander–recipient dyads that were either friends or nonfriends, and levels of aggression were limited to bystander–recipient dyads that were either targets or nontargets. Linear mixed models (LMM) were run with the TCT as a continuous dependent variable, the affiliation (or aggression) level as a fixed term, and the identity of the recipient of aggression and the bystander as well as the group as random variables. For all GLMM and LMM analyses we used restricted maximum likelihood methods. Nonparametric statistics were run in SPSS version 16.0 and GLMM and LMM in R version 2.8.1 (R Development Core Team, 2008) using the lmer function included in the lme4 package. All analyses were two tailed, and the significance level was set at 0.05.

Results

A total of 593 and 509 valid 10-min PC–MC pairs were collected on 18 and 14 adult recipients of aggression for Groups FS1 and FS2, respectively. All adults in both groups served as bystanders at least once.

Occurrence of Consolation

We confirmed the occurrence of consolation as a postconflict strategy in both study groups of chimpanzees. The proportion of attracted pairs significantly exceeded the proportion of dispersed pairs in FS1 (mean ± *SD* proportion of attracted pairs = 19.3% ± 10.9%, dispersed pairs = 10.9% ± 10.1%; Wilcoxon signed-ranks test: $N = 18$, $z = -2.18$, $p = .027$) and FS2 groups (attracted pairs = 20.6% ± 11.4%, dispersed pairs = 13.3% ± 10.8%; Wilcoxon signed-ranks test: $N = 14$, $z = -2.23$, $p = .025$). The mean group TCTs for FS1 and FS2 did not significantly differ from each other (FS1: 16.5% ± 15.6%; FS2: 10.8% ± 6.5%;

Mann–Whitney U test: $U = 111$; $N_1 = 18$; $N_2 = 14$, $p = .580$). TCTs for adult male recipients of aggression (FS1: 19.2% ± 21.1%; FS2: 10.6% ± 2.9%) was not significantly different from those of female recipients of aggression (FS1: 15.7% ± 12.5%; FS2: 9.2% ± 2.9%; Mann–Whitney U test: FS1: $U = 24.5$, $N_1 = 4$, $N_2 = 14$, $p = .741$, FS2: $U = 16$, $N_1 = 5$, $N_2 = 9$, $p = .438$).

Consolation and Affiliation Level Between Recipients and Bystanders

The results of the GLMM revealed that consolation was affected by the level of affiliation between the opponents and the third parties. After a conflict, friends of the former recipient of aggression offered consolation significantly more often than did friends of the original aggressor and nonfriends (Table 3; Figure 1). Furthermore, the aggressor's friends and nonfriends were significantly less likely to console victims than were friends of both opponents (Table 3; Figure 1).

Because the previous analysis did not correct for baseline levels of affiliation, it could be argued that the observed pattern is just a mirror of a general affiliative pattern among individuals. However, we can discard this possibility, because the result of the LMM analysis showed that the TCT, a measure that controls for baseline affiliation, was significantly higher for friend dyads than for nonfriend dyads (see Table 4).

Consolation and Aggression Level Between Recipients and Bystanders

Postconflict third-party interactions were also classified according to the identity of the third party in terms of the rate of aggression that third parties received. We defined individuals as a "target" of a particular subject A if the rate of aggression received from A was in the top quartile of A's aggressive scores. Otherwise, individuals were classified as nontargets of A. During the postconflict period, nontarget third parties directed affiliative contact at victims significantly more often than did frequent targets of the former aggressor (Table 5; Figure 1). Frequent targets of the original victim of aggression did not offer consolation more often than did any other types of third parties (Table 5; Figure 1). This result was confirmed by the LMM analysis, which revealed that TCT was not affected by the aggression level between the victim of aggression and third parties (see Table 4).

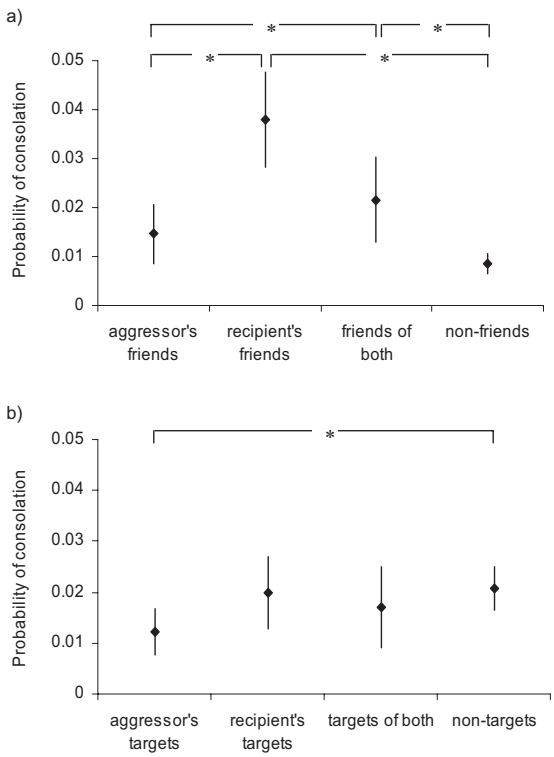

Figure 1. Mean probability (±95% Confidence Interval) of consolation behavior according to the (a) affiliation level and (b) aggression level between opponents and bystanders. * $p < .05$.

Discussion

This study first of all confirms the occurrence of consolation (i.e., postconflict affiliative contact by a bystander toward a recip-

Table 3
Results of GLMM Analyses in Which the Effect of Affiliation Level Between Opponents and Bystanders on the Occurrence of Consolation Were Tested

Affiliation	β	*SE*	*Z*	*p*	Odds ratio	95% CI
Fixed effect						
Intercept	−4.594	0.223	−20.543	<0.0001		
Friend of both–aggressor's friend	0.660	0.272	2.426	0.015	1.93	1.13–3.29
Nonfriend–aggressor's friend	−0.197	0.229	−0.859	0.390	0.82	0.52–1.28
Recipient's friend–aggressor friend	0.997	0.227	4.383	<0.0001	2.71	1.73–4.23
Nonfriend–friend of both[a]	−0.857	0.232	−3.694	0.0002	0.42	0.27–0.67
Recipient's friend–friend of both[a]	0.337	0.226	1.492	0.135	1.40	0.89–2.18
Recipient's friend– nonfriend[a]	1.195	0.178	6.711	<0.0001	3.30	2.32–4.68
Random effect						
Recipient	variance	0.293				
Aggressor	variance	0.045				

Note. GLMM = generalized linear mixed models; *SE* = standard error; CI = confidence interval.
[a] Nonorthogonal comparisons were calculated by rerunning the GLMM and changing the order of levels.

Table 4
Results of LMM Analyses Using the Triadic Contact Tendency as the Dependent Variable

Variable	β	*SE*	95% CI	*t*	*p*
Affiliation level					
Fixed effects					
Intercept	0.029	0.003	0.023–0.034	8.62	<0.001
Friends–nonfriends	0.021	0.003	0.026–0.015	6.23	<0.001
Random effects					
Recipient	variance	<0.001			
Third party	variance	<0.001			
Residual	variance	0.003			
Aggression level					
Fixed effects					
Intercept	0.015	0.002	0.011–0.018	5.778	<0.001
Target–nontarget	−0.003	0.003	−0.008–0.002	−1.042	0.297
Random effects					
Recipient	variance	<0.001			
Aggressor	variance	<0.001			
Residual	variance	0.003			

Note. Separate analyses were conducted for affiliation and aggression level. *SE* = standard error; CI = confidence interval.

ient of aggression) as a postconflict interaction in two captive groups of chimpanzees. Uninvolved third parties were more likely to direct affiliative behavior toward victims of aggression soon after the end of a conflict in comparison with matched control periods. The overall TCT values for both study groups of chimpanzees (FS1: 16.5, FS2: 10.8) did not differ and were within the range of values previously reported for other captive ape populations (chimpanzees: Fraser & Aureli, 2008; Koski & Sterck, 2007; bonobos: Palagi et al., 2004; gorillas: Cordoni et al., 2006).

Possible functions of consolation in chimpanzees were investigated by testing predictions about the identity of the adult third parties that initiated such contacts. Both study groups showed clear patterns in the distribution of consolatory contacts according to the levels of affiliation between the conflict participants and third parties. After a conflict, chimpanzee victims of aggression were more likely to be contacted by their own friends than by the aggressor's friends. Furthermore, levels of aggression received by third parties from the recipient of aggression did not seem to affect their participation in consolatory contacts. During postconflict periods, frequent targets of aggression were neither more nor less likely to offer consolation than were nontargets.

The fact that in both study groups, recipients' friends were significantly more likely to act as third parties during postconflict periods lends support to the stress reduction hypothesis rather than to the substitution for reconciliation hypothesis. The first hypothesis suggests that the main function of consolation is to reassure recent recipients of aggression by reducing postconflict stress (Aureli, 1997; de Waal & Aureli, 1997; de Waal & van Roosmalen, 1979). This hypothesis proposes that consolers perceive the recipient's distress and react empathically. Because empathic responses are more easily activated in relation to those with whom individuals have a close or positive relationship (de Waal, 2008), friends and kin of the victim of aggression are expected to be frequent consolers, as is demonstrated here. If this behavior indeed reflects empathetic activation, it would be one of the best documented examples of "sympathetic concern" in great apes (e.g., de

Table 5
Results of GLMM Analyses in Which the Effect of Aggression Level Between Opponents and Bystanders on the Occurrence of Consolation Were Tested

Aggression level	β	*SE*	*z*	*p*	Odds ratio	95% CI
Fixed effect						
Intercept	−4.598	0.207	−22.151	<0.0001		
Target of both–aggressor's target	0.068	0.288	0.236	0.813	1.07	0.60–1.88
Nontarget–aggressor's target	0.487	0.203	2.400	0.016	1.63	1.09–2.42
Recipient's target–aggressor target	0.371	0.248	1.496	0.135	1.45	0.89–2.35
Nontarget–target of both[a]	0.419	0.251	1.672	0.094	1.52	0.93–2.48
Recipient's target–target of both[a]	0.303	0.287	1.053	0.292	1.35	0.77–2.37
Recipient's target–nontarget[a]	−0.116	0.200	−0.582	0.561	0.89	0.60–1.31
Random effect						
Recipient	variance	0.264				
Aggressor	variance	0.043				

Note. GLMM = generalized linear mixed models; *SE* = standard error; CI = confidence interval.
[a] Nonorthogonal comparisons were calculated by rerunning the GLMM and changing the order of levels.

Waal, 2008; Preston & de Waal, 2002). Results from independent studies on wild and captive chimpanzees further support this idea, because it has been shown that consolation reduces the recipients' distress (Fraser et al., 2008) and, as in this study, is provided mainly by individuals with whom the victim of aggression has a close social bond (Fraser et al., 2008; Kutsukake & Castles, 2004).

The alternative hypothesis proposes that consolation functions as an alternative mechanism for reconciliation, not only alleviating the recipient's stress but also repairing the relationship between opponents (e.g., Wittig et al., 2007). This would be expected to apply mostly when bystanders have a close bond with the aggressor. The findings of the present study, however, do not support this hypothesis because third parties bonded to the aggressor were less likely to offer consolation to victims of aggression than were friends of either the victim or both opponents. Furthermore, if postconflict triadic affiliation serves as a substitution for reconciliation, one would expect the victims of aggression to seek contacts with bystanders rather than the other way around, because they would stand to gain more benefits (i.e., relationship repair) than third parties (Fraser & Aureli, 2008). Studies on chimpanzee postconflict behavior, however, have consistently failed to demonstrate solicited consolation (i.e., postconflict affiliative contacts made by the victims of aggression with uninvolved third parties; Fraser & Aureli, 2008; Koski & Sterck, 2007; Kutsukake & Castles, 2004; Wittig & Boesch, 2003). Thus, although consolation may occasionally be an alternative postconflict strategy to reconciliation, this is unlikely to be its main function.

The nature of the relationship between individuals has been shown to be a critical factor affecting the occurrence of several postconflict behaviors. For example, previous studies have reported that the frequency of reconciliation varies greatly between group members, and that the factor that best accounts for that variation is the quality of the relationship between the opponents (reviewed by Arnold & Aureli, 2007; Aureli et al., 2002). Thus, reconciliation occurs more often between individuals with high-quality relationships (e.g., Aureli, Das, & Veenema, 1997; Cools et al., 2008; Cooper, Bernstein, & Hemelrijk, 2005; de Waal, 1986, 2000; Kappeler, 1993). Other studies have also illustrated the importance of bond strength between interacting individuals in postconflict triadic interactions. For instance, in hamadryas baboons, most aggressor-initiated postconflict affiliation involved third parties with whom the aggressor maintained an affiliative relationship (Romero et al., 2008). In mountain gorillas, adult female victims of female aggression affiliate with the alpha male (Watts, 1995). Indeed, the only other study that analyzed the effect of the relationship quality between recipients of aggression and third parties found that consolation was more frequent between individuals with a high-quality relationship and, in particular, with valuable partners (Fraser et al., 2008). In the present study, we also found that relationship quality affects the occurrence of consolation, because third parties with close bonds with the recipients of aggression were frequent consolers. Our results therefore provide further support for relationship quality being a fundamental factor explaining variation in many aspects of postconflict interactions.

If relationship quality affects the expression of postconflict behaviors, individuals should show a great flexibility in the frequency and quality of interactions with various group members. An individual, therefore, will engage in friendly postconflict reunions depending on the quality of the relationship with the other individual. For instance, it is known that primates engage in higher frequencies of reconciliation with individuals with whom they interchange high rates of friendly behavior at baseline than with other individuals (reviewed by Arnold & Aureli, 2007; Aureli et al., 2002). It has been suggested that emotional differences could be at the basis of the observed variation in social interactions (Aureli & Schaffner, 2002) and that relationship quality between individuals would affect empathic responses (de Waal, 2008). Indeed, humans and other animals exhibit a robust effect of familiarity, social closeness, and positive experience with the other in their empathic responses (reviewed by Preston & de Waal, 2002). In a similar way, we found that friends of the recipient of aggression were frequent consolers during postconflict periods, suggesting that chimpanzees are particularly sensitive to the distress of individuals with whom they maintain a close relationship. Further studies, however, are needed to evaluate whether different levels of recipient's distress are associated with different consoler's responses.

We found no evidence for the protective function of consolation for bystanders. In social groups, aggression can spread far beyond the two original opponents, and bystanders may become the target of further aggression from the original recipient of aggression (i.e., redirected aggression; Aureli & van Schaik, 1991; Das, 2000; Watts et al., 2000). The self-protection hypothesis suggests that affiliating with the victim of aggression could provide protection for bystanders by reducing their likelihood of redirected aggression (Koski & Sterck, 2007, 2009). Thus, individuals that frequently receive aggression from recipients would be expected to offer consolation to reduce their risk of becoming the target of further aggression. Our results, however, did not support this prediction, because in both study groups of chimpanzees, recipients' frequent targets of aggression were not more likely to affiliate with victims of aggression during postconflict periods.

Furthermore, in contrast to cercopithecine species in which former recipients of aggression frequently redirect aggression to bystanders, rates of redirected aggression are in fact extremely low among chimpanzees (Arnold & Whiten, 2001; de Waal & van Hooff, 1981). In the present study, for instance, bystanders received redirected aggression on average in less than 0.5% of postconflict periods (FS1: 0.3%, FS2: 0.4%). Hence, the protective hypothesis is unlikely to be the main function of this postconflict behavior, although we cannot exclude the possibility that bystanders gain indirect benefits from consoling the recipient of aggression, for example, by reducing tensions in the group as a whole.

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