

# Stress reduction through consolation in chimpanzees

Orlaith N. Fraser<sup>\*†</sup>, Daniel Stahl<sup>‡</sup>, and Filippo Aureli<sup>\*†</sup>

<sup>\*</sup>Research Centre in Evolutionary Anthropology and Palaeoecology, School of Biological and Earth Sciences, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, United Kingdom; and <sup>‡</sup>Department of Biostatistics and Computing, Institute of Psychiatry, King's College, De Crespigny Park, London SE5 8AF, United Kingdom

Communicated by Frans B. M. de Waal, Emory University, Atlanta, GA, May 1, 2008 (received for review November 10, 2007)

**Consolation, i.e., postconflict affiliative interaction directed from a third party to the recipient of aggression, is assumed to have a stress-alleviating function. This function, however, has never been demonstrated. This study shows that consolation in chimpanzees reduces behavioral measures of stress in recipients of aggression. Furthermore, consolation was more likely to occur in the absence of reconciliation, i.e., postconflict affiliative interaction between former opponents. Consolation therefore may act as an alternative to reconciliation when the latter does not occur. In the debate about empathy in great apes, evidence for the stress-alleviating function of consolation in chimpanzees provides support for the argument that consolation could be critical behavior. Consistent with the argument that relationship quality affects their empathic responses, we found that consolation was more likely between individuals with more valuable relationships. Chimpanzees may thus respond to distressed valuable partners by consoling them, thereby reducing their stress levels, especially in the absence of reconciliation.**

empathy | *Pan troglodytes* | postconflict behavior | social relationships

Conflicts of interest may arise frequently in group-living species over access to resources, dominance ranks, or decisions about courses of action such as direction of travel or change of group activity. The escalation of a conflict of interest into an aggressive conflict can be costly; potential costs include risk of injury, increased stress, and damage to the relationship between opponents (1). We should therefore expect forms of conflict management to mitigate the negative consequences of aggressive escalation. Reconciliation, i.e., postconflict affiliative interaction between former opponents (2), occurs in many primate species and some nonprimate species (1, 3–5). Reconciliation apparently repairs any damage to relationships between opponents disturbed by the previous conflict and reduces postconflict stress levels (1, 6–9). A separate category of postconflict interactions is affiliation directed from a third party toward the recipient of aggression, known as consolation (2), which has received attention because of its possible relevance for the cognitive uniqueness of great apes and humans (10, 11).

Consolation has been demonstrated convincingly only in the great apes [*Pan troglodytes* (2, 10, 12–15), *Pan paniscus* (16), and *Gorilla gorilla* (17, 18)]. De Waal and Aureli (10) have speculated that consolation may reflect a level of empathy unique to humans and apes. Following Preston and de Waal's (19) discussion of the mechanisms and levels of empathy, consolation may represent an intermediate level that corresponds with "sympathetic concern" in developmental psychology (20). Monkeys seem to lack this particular level (21, 22), but intriguingly, there is suggestive evidence for consolation in large-brained birds (23) and dogs (24).

The present study, however, is not about the mechanisms of consolation but about its effect and possible function, which, as its name suggests, is postconflict stress alleviation in recent recipients of aggression (2, 25, 26). The only study that has tested this hypothesis found no support for a stress-alleviating effect (15). Although reconciliation is beneficial in reducing postconflict stress and repairing interopponent relationships, approaching a former opponent soon after a conflict carries the risk of

renewed aggression (5, 9). Also, one party may not be interested in reconciliation because the relationship might not be worth repairing (9, 27). A further hypothesis, therefore, advocates that consolation may serve as a substitute for reconciliation, provided that consolation alleviates postconflict stress (12, 14, 21). The substitute-for-reconciliation hypothesis has received some indirect support because consolation was more likely to occur in the absence of reconciliation in some studies on chimpanzees and bonobos (12, 14, 16) but not in others (15). Thus, overall, there is no empirical evidence that consolation serves to reduce stress and only some indirect evidence that consolation serves as a substitute for reconciliation. Some researchers therefore prefer the more neutral label "triadic postconflict affiliation" (13, 15). Here, because we specifically aimed to test the hypothesis that triadic postconflict affiliation has a calming function, and because we investigated only affiliative interactions directed toward the initial recipient of aggression, we used the term "consolation."

The quality of the relationship between former opponents, in addition to the characteristics of the preceding conflict, may affect the occurrence of consolation (21). Cords and Aureli (27) suggested that the quality of a relationship between two individuals consists of three separate components: value, compatibility, and security. The value of the relationship refers to the advantages (or fitness benefits) that it affords. Compatibility is a measure of the tolerance and affiliation between the two partners. The security of the relationship indicates its predictability or consistency over time. The influence of relationship quality and, in particular, relationship value on reconciliation has been the subject of numerous studies, although measures of relationship quality and interpretation of its effects have varied (1, 4, 5, 9, 28). The effect of relationship quality on consolation, however, has received much less attention. Only two studies, both on chimpanzees, have examined the determinants of consolation. Both investigated the effects of the relationship value and compatibility and those of several characteristics of conflicts on the probability of consolation. Koski *et al.* (29) found no significant predictors of consolation, whereas Wittig and Boesch (12) found that chimpanzees were more likely to receive consolation after conflicts between same-sex partners, after conflicts between partners who provided only limited benefits to each other, and after conflicts where relatively few competitors were present. Although both studies incorporated some aspect of relationship quality into their analyses, both focused on the relationship between the former opponents and not on the relationship with potential consolars. Although some effort has been made in recent studies of postconflict behavior to distinguish between the effects of each of the components of relationship quality (i.e., value, compatibility, and security) on reconciliation (15, 28, 30), no study has examined the

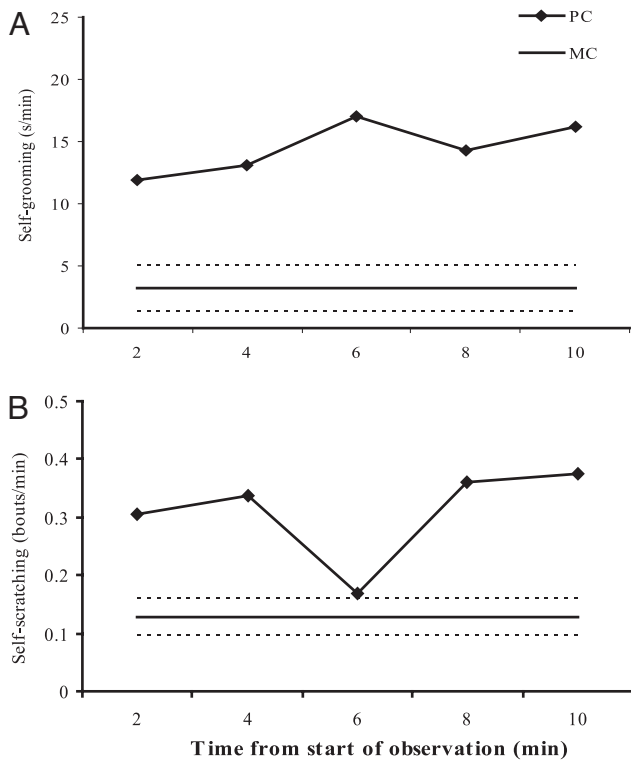
Author contributions: O.N.F. and F.A. designed research; O.N.F. performed research; D.S. contributed new reagents/analytic tools; O.N.F. and D.S. analyzed data; and O.N.F., D.S., and F.A. wrote the paper.

The authors declare no conflict of interest.

<sup>†</sup>To whom correspondence may be addressed. E-mail: f.aureli@ljamu.ac.uk or o.fraser@ljamu.ac.uk.

This article contains supporting information online at [www.pnas.org/cgi/content/full/0804141105/DCSupplemental](http://www.pnas.org/cgi/content/full/0804141105/DCSupplemental).

© 2008 by The National Academy of Sciences of the USA



**Fig. 1.** Mean self-grooming (A) and self-scratching (B) levels during post-conflict periods without reconciliation or consolation, where more than one PC–MC pair was available per individual. For PC data, means for every second minute are used. Means for the whole 10 min are used for MC data, with 95% confidence intervals.

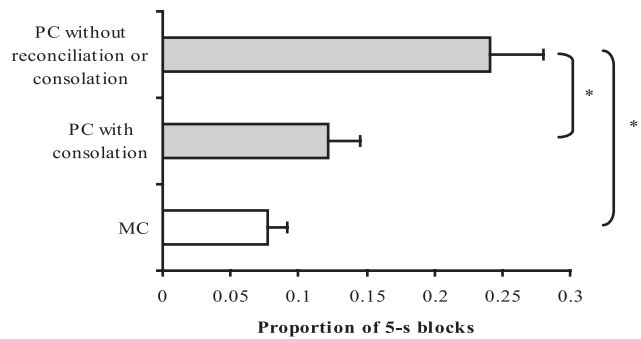
simultaneous impact that all three components of the relationships between former opponents and between the recipient of aggression and potential consoler has on the occurrence of consolation.

In this study, we investigated the function of consolation in a large zoo group of chimpanzees by testing the prediction that consolation reduces postconflict stress. We used self-directed behaviors, such as self-scratching and self-grooming, as indicators of stress because these are known to increase in primates under stressful conditions (31, 32). The link between self-directed behaviors and stress levels is further supported by pharmacological evidence (33). Reconciliation reduces postconflict rates of self-directed behaviors to baseline levels (6, 34, 35). If consolation also has a stress-reducing function, rates of self-directed behaviors should decrease after its occurrence.

Our second aim was to examine the social determinants of consolation, studying the effects of conflict characteristics, reconciliation and interopponent relationship quality on the occurrence of consolation. Lastly, we investigated the effect of relationship quality between the initial recipient of aggression and potential consoler on the rate of consolation.

## Results

**Function of Consolation.** Levels of self-grooming and self-scratching were elevated above baseline [matched-control observations (MCs)] for the entire 10 min of postconflict observations (PCs) without reconciliation or consolation (Fig. 1), suggesting that aggressive conflict raised stress levels and that they remained raised for the full PC if no reconciliation or consolation occurred. These results were confirmed when analyses were conducted while controlling for individual variation by using linear mixed models (LMMs). Because the patterns for time spent self-grooming and rates of self-scratching were sim-



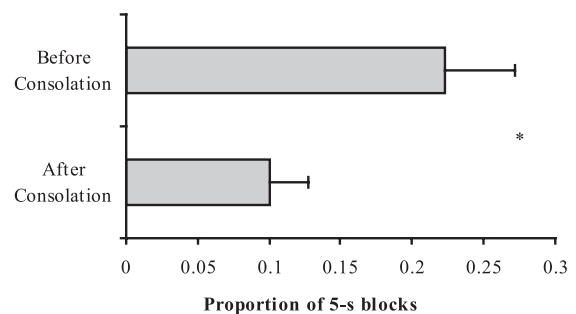
**Fig. 2.** Mean (+SE) proportion of 5-sec blocks spent performing self-directed behavior during minutes 2–10 of PCs without consolation or reconciliation and PCs with consolation and during MCs. \*,  $P < 0.05$

ilar, the following LMM analyses were conducted on a combined measure of self-directed behavior and focused on minutes 2–10 because consolation and reconciliation occurred mostly in the first minute of PCs (see *Methods*). Levels of self-directed behavior for PCs without reconciliation and consolation were higher than levels for MCs [ $\beta = 0.17$ , 95% C.I.; 0.08, 0.25,  $P < 0.001$ ; see Fig. 2 and [supporting information \(SI\) Table S1](#)].

Levels of self-directed behavior were not significantly different for PCs after consolation and MCs ( $\beta = 0.04$ , 95% C.I.;  $-0.02$ , 0.10,  $P = 0.139$ ; see Fig. 2; and [Table S2](#)). PCs after consolation had a significantly lower level of self-directed behavior than PCs without consolation or reconciliation ( $\beta = -0.12$ , 95% C.I.;  $-0.21$ ,  $-0.03$ ,  $P = 0.009$ ; see Fig. 2 and [Table S3](#)). In addition, levels of self-directed behavior before consolation were found to be significantly higher than levels after consolation had taken place ( $\beta = 0.12$ , 95% C.I.; 0.01, 0.22,  $-0.03$ ,  $P = 0.009$ ; see Fig. 3 and [Table S4](#)).

**Determinants of Consolation.** Generalized linear mixed models (GLMMs) were used to identify factors affecting the occurrence of consolation (operationally defined as “attracted” pairs; see *Methods*) at the PC level. In the best model ([Table S5](#)), reconciliation had a negative effect on consolation (odds ratio = 0.43, 95% C.I.; 0.22, 0.85,  $P = 0.013$ ), indicating that consolation was more likely to occur in the absence of reconciliation.

To examine the impact of the quality of the relationship between the initial recipient of aggression and possible consoler on the occurrence of consolation, we used LLMs with the consolation index as a dependent variable (see *Methods*). The only variable remaining in the best model was the value of the relationship between the recipient of aggression and the consoler ( $\beta = 0.01$ , 95% C.I.;  $<0.01$ , 0.02,  $P = 0.018$ ; see [Table S6](#)). This result was confirmed when the triadic contact tendency (TCT) (see *Methods*) was used as the dependent variable ( $\beta =$



**Fig. 3.** Mean (+SE) proportion of 5-sec blocks spent performing self-directed behavior before consolation and after consolation. \*,  $P < 0.05$

0.01, 95% C.I.; 0.01, 0.02,  $P = 0.002$ ; see Table S6). Thus, recipients of aggression were more likely to be consoled by individuals with whom they had a more valuable relationship.

## Discussion

The present study provides evidence that consolation calms recipients of aggression. Our findings support the notion that consolation can be an alternative to reconciliation as a stress-alleviation mechanism. Consolation was more likely to be offered by valuable partners, providing further support for its beneficial nature.

Chimpanzees spent less time engaged in self-directed behavior after conflicts when consolation occurred than when it did not, and levels of self-directed behavior after consolation were not different from baseline levels. Furthermore, levels of self-directed behavior were higher before consolation than after consolation. These results imply that consolation had a stress-alleviating effect. Because levels of self-directed behavior are an indirect measure of stress, the use of additional measures of stress is recommended in future studies to confirm our findings. High levels of postconflict stress may be experienced by recipients of aggression due to uncertainty caused by possible disruption of interopponent relationships and loss of associated benefits in addition to risks of renewed aggression (6). Long-term high stress levels may have negative consequences (36) that may thus be mitigated by consolation. The only other study that has investigated the stress-alleviating function of consolation, also in captive chimpanzees, focused only on self-scratching rates before and after consolation and found no support for this function (15).

Consolation was more likely to occur when reconciliation did not, a result that confirms previous studies (14, 16). Consolation therefore may function as an alternative to reconciliation for stress alleviation. Consolation, however, is likely to act only as a partial alternative to reconciliation, because the latter also serves to repair the relationship between opponents (7, 8). Consolation may be preferable to reconciliation only if the relationship between opponents is of low value and/or the risks of approaching the former opponent are too high and thus reconciliation is not worthwhile (12).

The cognitive mechanisms underlying consolation may explain the interspecific variation found in the occurrence of consolation in primates. Consolation has been documented in great apes, but not in monkeys. Although third party-initiated affiliation has been demonstrated in stump-tail macaques (*Macaca arctoides*), it seems to be behaviorally different from consolation among apes and has been suggested to serve a protective or appeasement function [i.e., prevention of further aggression (37)]. Interspecific variation in consolation patterns might reflect differences in the perception of distress, that is, apes may be more sensitive to or more accurate in evaluating the stress levels of others (10, 25). Japanese macaque (*Macaca fuscata*) mothers, for example, do not display signs of distress when their offspring are targets of aggression nor do they increase postconflict affiliative contacts with their offspring, suggesting that they may be unable to perceive their offspring's need for distress alleviation (22). To provide reassuring contact to a recipient of aggression, thus helping the recipient reduce its postconflict stress, a bystander may be required to perceive the distress of the recipient and act empathically. Many mammals may be capable of basic empathy, such as emotional contagion (19), but there is an ongoing debate about the level reached by chimpanzees, which seems to exceed this level (19, 20, 38–42). Consolation may be one of the best documented examples of so-called “sympathetic concern,” i.e., concern about another's state and attempts to ameliorate this state (20), and yet, until now, there was no evidence that consolation reduces distress. Therefore, in this debate, our study lends support to the argu-

ment that consolation is a critical behavior. The bystander's behavior and emotional state, however, are critical areas for further research to evaluate whether the consoler contacts the recipient primarily to reduce their own or the recipient's distress.

The flexibility in behavior according to relationship quality allows individuals to maximize the benefits and minimize the costs of each relationship (43, 44). Aureli and Schaffner (45) suggested that the quality of relationship between individuals is likely to affect their empathic response. Indeed, studies on both mice (*Mus musculus*) and humans have found that similarity and closeness between individuals promotes empathy (19, 46, 47). Similarly, we found that consolation was more likely between individuals with a valuable relationship (while controlling for kinship), suggesting that chimpanzees are particularly responsive to the distress of valuable partners. Although this has not previously been shown in primates, postconflict third-party affiliation has been reported between valuable partners, such as mates, in rooks (*Corvus frugilegus*) (23).

Because consolation was more likely to occur between valuable partners, it is likely that bystanders derived greater benefits from consoling valuable partners than from consoling other individuals. Consolation may be part of a behavioral exchange between partners, possibly through reciprocity or interchange (48, 49), and thus, the consoler may derive benefits by receiving consolation or other valuable behavior in the future. It has also been suggested that consolation reduces the likelihood of further attacks among all group members and is therefore advantageous to both consoler and recipient (14). Koski (50) suggested that consolation in chimpanzees may serve a protection function by specifically reducing the risk of the consoler's becoming the target of further aggression from the original recipient of aggression. Given how rare redirected aggression (i.e., further aggression initiated by the recipient of aggression and directed toward a third party) is among chimpanzees (51–53), the “protection hypothesis” (50) is, however, unlikely to account for the primary function of consolation. Furthermore, because in our study, consolation was more likely to be provided by valuable partners, these partners are unlikely targets of redirected aggression. Indeed the high value of the relationship between the recipient and consoler makes it more likely that consolation is a mutualistic behavior, providing distress alleviation and improving well being, thus maintaining the benefits afforded by the relationship to both parties.

The results of this study suggest that chimpanzees console valuable partners who are recipients of aggression, thus reducing recipients' postconflict stress levels, particularly when reconciliation fails to occur. In the debate about the degree of empathic tendencies in great apes, these findings provide support for the argument that consolation is a critical behavior. Further research should focus on consolation, not simply as a postconflict event, but also as a possible empathic behavior mediated by variation in relationship quality and emotional state.

## Methods

**Study Subjects and Housing.** The study was conducted on a well established group of chimpanzees at the Chester Zoo (Chester, U.K.). During the study period, the group size varied from 26 to 32, with 17 adult females, 5 adult males and 4–10 juveniles and infants. All adults were present throughout the study and constituted the study subjects. For further details, see *SI Text*.

**Data Collection.** Data were collected from January 2005 to September 2006. The chimpanzees were observed throughout the day while they were in the indoor or outdoor enclosures. All instances of aggressive conflict between adults were recorded, when visible. Aggressive conflict was defined as any interaction involving a bite, hit, brusque rush, trample, chase, or threat in addition to screaming (54). The identities of the initial recipients of aggression and the aggressors were recorded along with the intensity, directionality, and outcome as well as whether the conflict started with a bluff display (i.e., charging behavior with piloerection and pant-hoot vocalizations). The inten-



sity was recorded as low if the conflict involved a threat and/or hit, as medium if it included chase or brusque rush, and as high if it involved trample or bite. Directionality was scored as bidirectional if both participants engaged in aggressive behavior and as unidirectional if all aggressive behavior was directed toward the initial recipient. Because chimpanzees frequently engage in bidirectional aggression, both partners can become "victims" of aggression, and thus, we conducted our analyses on the initial recipient of aggression (heretofore referred to as the recipient). The outcome of the conflict was recorded as decided if there was a clear victor (the initial aggressor in 74% and the initial recipient in 10% of conflicts) and as undecided if neither participant of a bidirectional conflict showed signs of submission (e.g., pant-grunt greetings, flight, bared-teeth, or screaming). In polyadic conflicts, the aggressor-recipient dyad with the highest intensity of aggression was chosen for postconflict observations.

Following de Waal and Yoshihara (55), we conducted PC observations on the initial recipient of aggression for 10 min immediately after the end of an aggressive conflict. During this time, all self-directed behaviors and social interactions were recorded. Self-directed behaviors were recorded as the duration of self-grooming and frequency of self-scratching, where a new scratching bout was recorded if scratching resumed after an interval of at least 5 sec. Social interactions included affiliative (kiss, embrace, grooming, finger-in-mouth, gentle touch, or play) and aggressive behaviors in addition to submissive pant-grunt greetings (54, 56). If the conflict was renewed within 2 min of the start of the PC, the PC was abandoned and restarted once the conflict ceased.

MCs were conducted on the same individual by following the same procedure at the same time on the next possible day after the corresponding PC. If the focal individual was involved in an aggressive conflict within 10 min before the planned MC, the MC was postponed until at least 10 min after the end of the conflict, up to a maximum of 1 h after the time of the corresponding PC. The outdoor enclosure was visually mapped into six sectors following the patterns of vegetation on the island, and the indoor enclosure was counted as a seventh sector. Within each sector, all individuals were visible and audible to each other. MCs were conducted only when the recipient was within the same sector of the enclosure as the aggressor and was clearly visible to the observer. If these conditions were not met, the MC was postponed until the next day for a maximum of 1 week.

**Data Analysis.** A total of 234 PC-MC pairs was collected on 22 recipients of aggression involving 129 distinct aggressor-recipient dyads (mean  $\pm$  SD PC-MC pairs per recipient =  $10.6 \pm 5.7$ ; range = 2–25).

**Function of Consolation.** Because the majority of postconflict affiliative interactions occurred in the first minute of the PC (O.N.F. and F.A., unpublished data), PCs with consolation were operationally defined as those in which an affiliative behavior was initiated by a third party toward the recipient of aggression in the first minute. Initiators were the individuals starting the affiliative contact. If affiliative contact was preceded by offering a hand, the partner offering the hand was considered to be the initiator. Third parties were defined as any adult subject not involved as an opponent of the recipient of aggression in the preceding conflict, including supporters of the original aggressor. PCs in which both reconciliation and consolation occurred in the first minute were not included in the analyses ( $n = 6$ ). In addition, PC-MC pairs in which the initiator of the first affiliative interaction between the recipient and a third party was unclear in either the PC or the MC were removed ( $n = 62$ ). PCs with no reconciliation or consolation were those in which neither postconflict interaction occurred in the entire PC period.

Postconflict stress levels were assessed by using self-directed behaviors (31, 32). In particular, we used rates of self-scratching (bouts per minute) and the duration of self-grooming (seconds per minute), both previously used in postconflict studies (6). To determine whether aggressive conflict leads to increased postconflict stress levels, individual mean rates of self-scratching and mean durations of self-grooming for each minute of PCs without reconciliation or consolation were compared with individual mean levels (and 95% C.I.s) of self-scratching and self-grooming across the whole 10-min MC. This allowed us to define a time window in which the PC values differed from baseline values (6). Because the postconflict patterns of self-grooming and self-scratching were similar, a combined measure of self-directed behavior was used for the ensuing analyses. The presence or absence of either self-directed behavior was scored for each 5-sec block in each PC and MC. The level of self-directed behavior was thus calculated as the proportion of 5-sec blocks in which self-grooming, self-scratching, or both occurred.

Given the operational definition of consolation (i.e., occurrence in the first PC minute), mean proportions of 5-sec blocks spent performing self-directed behavior in the time window in which PC values differed from MCs, but

excluding the first minute, were used to determine the effects of consolation. Such values for PCs with consolation and PCs without consolation or reconciliation were compared with mean MC levels for the whole 10 min. LMMs were used for these comparisons. LMMs allow both fixed and random variables to be fitted to a model. The inclusion of random variables allowed us to model residual correlations due to the repeated observations of the same individual (57). The level of self-directed behavior was entered as a continuous dependent variable, and the identity of the initial recipient of aggression was entered as a random variable in the initial model. In addition, we included the random variable PC-MC pair, for which each PC and its corresponding MC were given a unique number. The occurrence of consolation (PC with consolation = 1, and PC without consolation or reconciliation = 0) or type of observation (PC = 1, and MC = 0) was entered as a fixed explanatory variable depending on the analysis. The best model was selected by using Akaike's information criteria (58) (see *SI Text* for further details).

These analyses were further supported by an additional comparison between the proportion of 5-sec blocks spent performing self-directed behavior before and after consolation. Because the operational definition of consolation in which affiliation must occur within the first minute of the PC would leave little opportunity for self-directed behavior to occur before consolation, the operational definition of PCs with consolation was expanded to include all "attracted PCs." Following de Waal and Yoshihara's (55) procedure, PC-MC pairs were labeled attracted if affiliative interaction occurred earlier in the PC than in the MC or only in the PC. Neutral pairs had no affiliative interaction in either the PC or the MC or at the same time in both. Pairs in which affiliative interaction occurred earlier, or only in the MC, were labeled dispersed. For reconciliation, the affiliative interaction was between the former opponents, and for consolation, the affiliative interaction was directed from a third party to the initial recipient of aggression. PC-MC pairs in which it was unclear who had initiated the contact were not considered. Consolation was considered to have taken place when the PC-MC pair was attracted. A similar operational definition for reconciliation was used. For these analyses, neutral or dispersed pairs indicated an absence of reconciliation or consolation.

The proportion of 5-sec blocks in which self-directed behavior occurred before consolation was compared with the proportion of 5-sec blocks in which self-directed behavior occurred after consolation, excluding the 5-sec block in which consolation took place, by using LMMs. PCs in which consolation occurred in the first 10 sec of the observation were not included in the analyses, because the opportunity for self-directed behavior to be performed before consolation was considered to be too small. The level of self-directed behavior was entered as a continuous dependent variable, with its occurrence relative to consolation as a fixed explanatory variable (1 = before consolation, 0 = after consolation). The identity of the recipient and "PC observation" (i.e., each PC observation was given a unique number to link self-directed behavior levels before and after consolation) were entered as random variables.

**Determinants of Consolation.** Measures of each of the components of relationship quality were obtained by using methods commonly used to assess mother-infant relationships (59). Three components were derived from nine behavioral variables by using principal-components analysis. Because the loadings of the different behavioral variables on each emerging component appeared to match the characteristics of the relationship quality components proposed by Cords and Aureli (27), they were labeled value, compatibility, and security (60). The component value consisted of high positive loadings of variables including the proportion of time spent grooming, the frequency of food sharing, and frequency of agonistic support. Negative loadings from variables representing the rate of counterintervention, aggression, and negative responses to approaches characterized the second component, compatibility. Security consisted of high positive loadings from variables describing the consistency of affiliation and symmetry in proportion of time spent grooming. This method allows components of relationship quality to be assessed independently without relying on assumptions of the relationship quality of clusters of individuals, such as different age-sex classes or kinship combinations.

Factors affecting the occurrence of consolation were investigated by using GLMMs, an extension of LMMs, which enable models to be fitted with dichotomous dependent variables, in this case the presence or absence of consolation. For the purpose of this analysis, consolation and reconciliation were operationally defined as affiliation occurring earlier in the PC than in the MC (attracted pairs, see above). Conflict characteristics (directionality, outcome, intensity, and initiation with a bluff display), characteristics of the relationship between the recipient and the aggressor (value, compatibility, security, kinship, and sex combination), and the occurrence of reconciliation were entered as fixed variables (see Table 1 for descriptions of variables). Because (G)LMMs allow the effects of each explanatory variable to be examined while control-

**Table 1. Variables used in GLMM (dichotomous dependent variables) and LMM (continuous dependent variables) analyses for the determinants of consolation**

| Name  | Type  |
|---|---|
| <b>Dependent variables</b>  |   |
| Consolation   | Dichotomous (1 = yes, 0 = no)                                     |
| Consolation index   | Continuous  |
| TCT   | Continuous  |
| <b>Fixed explanatory variables (relationship characteristics)</b> |   |
| Value   | Continuous  |
| Compatibility   | Continuous  |
| Security  | Continuous  |
| Sex-dyad combination  | Dichotomous (1 = including males, 0 = no males)                   |
| Kinship   | Dichotomous (1 = yes, 0 = no)                                     |
| <b>Fixed explanatory variables (conflict characteristics)</b>     |   |
| Outcome   | Dichotomous (1 = decided, 0 = undecided)                          |
| Intensity   | Ordinal (1 = low, 2 = medium, 3 = high)                           |
| Directionality  | Dichotomous (1 = bi-directional, 0 = unidirectional)              |
| Bluff   | Dichotomous (1 = starts with bluff display, 0 = no bluff display) |
| Reconciliation  | Dichotomous (1 = yes, 0 = no)                                     |
| <b>Random variables</b>   |   |
| Recipient   | Nominal   |
| Aggressor   | Nominal   |
| Consoler  | Nominal   |

ling for the effects of the other explanatory variables, they ensure that any effect of value, compatibility or security, on the dependent variable is not due solely to the effects of kinship or certain sex combinations. The identities of the recipients and aggressors were evaluated as random variables. We used GLMMs with binomial error structures and a logit-link function (57).

To investigate the effects of the characteristics of the relationship between third parties and recipients on the occurrence of consolation, the following consolation index was devised for each dyad: frequency of consolation/opportunity to console. The frequency of consolation was the number of times each potential consoler initiated the first affiliative interaction directed toward the recipient of aggression. The opportunity to console was the number of PCs in which one individual was the recipient, excluding those in which the partner was an aggressor. A LMM was run with the consolation index as a continuous dependent variable. Relationship characteristics (value, compatibility, security, sex-dyad combination, and kinship) between potential consolers and recipients were input as fixed variables, and the identities of potential consolers and recipients were entered as random variables (Table 1).

Because the consolation index does not control for baseline levels of

affiliation between partners, a further analysis was conducted by using the TCT (37) for the recipient and each potential consoler. The TCT was calculated for each dyad as follows: (attracted pairs – dispersed pairs)/(attracted + dispersed + neutral pairs). PC–MC pairs in which it was unclear who had initiated the contact were not considered for that dyad. The LMM was then rerun by using TCT as the continuous dependent variable. TCT is based on the first affiliative interaction between the recipient and each potential consoler, regardless of whether affiliative interaction has already occurred with another partner, but the function and demonstration of consolation are based only on the first affiliative interaction initiated by any third party. Hence, we cannot know whether further contacts function as consolation. This analysis is thus viewed as complementary to the LMM by using the consolation index (above). An  $\alpha$ -level of 0.05 was adopted for all tests.

**ACKNOWLEDGMENTS.** We thank the Chester Zoo for permission to conduct this study; Clare Caws and Sonya Hill for their help; and Frans de Waal, Nicola Koyama, Maria Teresa Romero, Colleen Schaffner, David Watts, and an anonymous reviewer for comments and discussion. This project was supported by the Leakey Trust.

- de Waal FBM (2000) Primates—a natural heritage of conflict resolution. *Science* 289:586–590.
- de Waal FBM, van Roosmalen A (1979) Reconciliation and consolation among chimpanzees. *Behav Ecol Sociobiol* 5:55–66.
- Silk JB (2002) The form and function of reconciliation in primates. *Ann Rev Anthropol* 31:21–44.
- Judge PG (2003) Conflict resolution. *Primate Psychology*, ed Maestriperi D (Harvard Univ Press, Cambridge, MA), pp 41–68.
- Arnold K, Aureli F (2007) Postconflict reconciliation. *Primates in Perspective*, eds Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (Oxford Univ Press, Oxford), pp 592–608.
- Aureli F, van Schaik CP (1991) Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): II. Coping with uncertainty. *Ethology* 89:101–114.
- Cords M (1992) Post-conflict reunions and reconciliation in long-tailed macaques. *Anim Behav* 44:57–61.
- Koyama NF (2001) The long-term effects of reconciliation in Japanese macaques *Macaca fuscata*. *Ethology* 107:975–987.
- Aureli F, Cords M, van Schaik CP (2002) Conflict resolution following aggression in gregarious animals: A predictive framework. *Anim Behav* 64:325–343.
- de Waal FBM, Aureli F (1996) Consolation, reconciliation and a possible cognitive difference between macaques and chimpanzees. *Reaching into Thought: The Minds of Great Apes*, eds Russon AE, Bard KA, Taylor Parker S (Cambridge Univ Press, Cambridge, UK), pp 80–110.
- Castles DL (2000) Triadic versus dyadic resolutions: Cognitive implications. *Natural Conflict Resolution*, eds Aureli F, de Waal FBM (Univ of California Press, Berkeley), pp 289–291.
- Wittig RM, Boesch C (2003) The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour* 140:1527–1559.
- Kutsukake N, Castles DL (2004) Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates* 45:157–165.
- Palagi E, Cordoni G, Borgognini Tarli S (2006) Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). *Am J Phys Anthropol* 129:105–111.
- Koski SE, Sterck EHM (2007) Triadic postconflict affiliation in captive chimpanzees: Does consolation console? *Anim Behav* 73:133–142.
- Palagi E, Paoli T, Borgognini Tarli SM (2004) Reconciliation and consolation in captive bonobos (*Pan paniscus*). *Am J Primatol* 62:15–30.
- Cordoni G, Palagi E, Tarli S (2006) Reconciliation and consolation in captive western gorillas. *Int J Primatol* 27:1365–1382.
- Mallavarapu S, Stoinski TS, Bloomsmith MA, Maple TL (2006) Postconflict behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*). *Am J Primatol* 68:789–801.
- Preston SD, de Waal FBM (2002) Empathy: Its ultimate and proximate bases. *Behav Brain Sci* 25:1–72.
- de Waal FBM (2008) Putting the altruism back into altruism: The evolution of empathy. *Ann Rev Psychol* 59:1–22.
- Watts DP, Colmenares F, Arnold K (2000) Redirection, consolation and male policing: How targets of aggression interact with bystanders. *Natural Conflict Resolution*, eds Aureli F, de Waal FBM (Univ of California Press, Berkeley), pp 281–301.
- Schino G, Geminiani S, Rosati L, Aureli F (2004) Behavioral and emotional response of Japanese macaque (*Macaca fuscata*) mothers after their offspring receive an aggression. *J Comp Psychol* 118:340–346.
- Seed AM, Clayton NS, Emery NJ (2007) Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Curr Biol* 17:152–158.
- Cools AKA, Van Hout AJM, Nelissen MHJ (2008) Canine reconciliation and third-party-initiated postconflict affiliation: Do peacemaking social mechanisms in dogs rival those of higher primates? *Ethology* 114:53–63.
- Aureli F (1997) Post-conflict anxiety in nonhuman primates: The mediating role of emotion in conflict resolution. *Agg Behav* 23:315–328.

26. de Waal FBM, Aureli F (1997) The integrative neurobiology of affiliation. *Ann NY Acad Sci* 807:317–328.
27. Cords M, Aureli F (2000) Reconciliation and relationship qualities. *Natural Conflict Resolution*, eds Aureli F, de Waal FBM. (Univ of California Press, Berkeley), pp 177–198.
28. Watts DP (2006) Conflict resolution in chimpanzees and the valuable-relationships hypothesis. *Int J Primatol* 27:1337–1364.
29. Koski SE, de Vries H, van den Tweel SW, Sterck EHM (2007) What to do after a fight? The determinants and inter-dependency of post-conflict interactions in chimpanzees. *Behaviour* 144:529–555.
30. Cooper MA, Bernstein IS, Hemelrijk CK (2005) Reconciliation and relationship quality in Assamese macaques (*Macaca assamensis*). *Am J Primatol* 65:269–282.
31. Maestripieri D, Schino G, Aureli F, Troisi A (1992) A modest proposal—displacement activities as an indicator of emotions in primates. *Anim Behav* 44:967–979.
32. Troisi A (2002) Displacement activities as a behavioural measure of stress in nonhuman primates and human subjects. *Stress* 5:47–54.
33. Schino G, Perretta G, Taglioni A, Monaco V, Troisi A (1996) Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety* 2:186–191.
34. Castles DL, Whiten A (1998) Post-conflict behaviour of wild olive baboons II: Stress and self-directed behaviour. *Ethology* 104:148–160.
35. Kutsukake N, Castles DL (2001) Reconciliation and variation in post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): Testing the integrated hypothesis. *Anim Cognit* 4:259–268.
36. Sapolsky, R. M (2004) Social status and health in humans and other animals. *Ann Rev Anthropol* 33:393–418.
37. Call J, Aureli F, de Waal FBM (2002) Postconflict third party affiliation in stump-tailed macaques. *Anim Behav* 63:209–216.
38. Povinelli DJ, Nelson KE, Boysen ST (1992) Comprehension of role reversal in chimpanzees: evidence of empathy? *Anim Behav* 43:633–640.
39. Silk JB, et al. (2005) Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437:1357–1359.
40. Jensen K, Hare B, Call J, Tomasello M (2006) What's in it for me? Self-regard precludes altruism and spite in chimpanzees *Proc R Soc London Ser B* 273:1013–1021.
41. Warneken F, Hare B, Melis AP, Hanus D, Tomasello M (2007) Spontaneous altruism by chimpanzees and young children. *PLoS Biol* 5:1414–1420.
42. Penn DC, Povinelli DJ (2007) On the lack of evidence that non-human animals possess anything remotely resembling a “theory of mind”. *Phil Trans R Soc London Ser B* 2:731–744.
43. Kummer H (1978) On the value of social relationships to nonhuman primates: A heuristic scheme. *Soc Sci Inform* 17:697–705.
44. Aureli F, Schaffner C (2002) Relationship assessment through emotional mediation. *Behaviour* 139:393–420.
45. Aureli F, Schaffner C (2002) Empathy as a special case of emotional mediation of social behavior. *Behav Brain Sci* 25:23–24.
46. Cialdini RB, Brown SL, Lewis BP, Luce C, Neuberg SL (1997) Reinterpreting the empathy–altruism relationship: When one into one equals oneness. *J Pers Soc Psych* 73:481–494.
47. Langford D, et al. (2006) Social modulation of pain as evidence for empathy in mice. *Science* 312:1967–1970.
48. de Waal FBM (1997) The chimpanzee's service economy: Food for grooming. *Evol Hum Behav* 18:375–386.
49. Watts DP (2002) Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* 139:343–370.
50. Koski SE (2007) Chimpanzees, conflicts and cognition: Functions and mechanisms of chimpanzee conflict resolution. PhD dissertation. (Utrecht Univ, Utrecht, The Netherlands).
51. de Waal FBM, Hoeksstra JA (1980) Contexts and predictability of aggression in chimpanzees. *Anim Behav* 28:929–937.
52. de Waal FBM, van Hooff JARAM (1981) Side-directed communication and agonistic interactions in chimpanzees. *Behaviour* 77:164–198.
53. Arnold K, Whiten A (2001) Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo forest, Uganda. *Behaviour* 138:649–690.
54. van Hooff JARAM (1974) A structural analysis of the social behaviour of a semi-captive group of chimpanzees. *Social Communication and Movement*, eds von Cranach M, Vine I. (Academic, London), pp 75–162.
55. de Waal FBM, Yoshihara D (1983) Reconciliation and redirected affection in rhesus monkeys. *Behaviour* 85:224–241.
56. Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behaviour* (Belknap, Cambridge, MA).
57. Brown H, Prescott R (1999) *Applied Mixed Models in Medicine* (Wiley, Chichester, UK).
58. Pinheiro JC, Bates DM (2000) *Mixed Effects Models in S and S-Plus* (Springer, New York).
59. Schino G, D'Amato FR, Troisi A (1995) Mother–infant relationships in Japanese macaques—sources of interindividual variation. *Anim Behav* 49:151–158.
60. Fraser ON, Schino G, Aureli F (2008) Components of relationship quality in chimpanzees. *Ethology*, in press.