Stress reduction through consolation in chimpanzees

Orlaith N. Fraser*, Daniel Stahl†, and Filippo Aureli**

*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 †Department of Biostatistics and Computing, Institute of Psychiatry, King's College, De Crespigny Park, London SE5 8AF, United Kingdom

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Consolation, i.e., postconflict affiliative interaction directed from a third party to the recipient of aggression, is assumed to have a stress-attenuating 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-attenuating 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. Compatibility is a measure of the tolerance 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 consolers. 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

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†To whom correspondence may be addressed. E-mail: f.aureli@ljmu.ac.uk or o.fraser@ljmu.ac.uk.

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simultaneous impact that all three components of the relationships between former opponents and between the recipient of aggression and potential consolers 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 consolers 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 similar, 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 [β = 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 (β = 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 (β = −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 (β = 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 consolers 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 (β = 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 (β = 0.21, 95% C.I.; −0.01, 0.02, P = 0.35; see Table S7).
Therefore, in this debate, our study lends support to the argument and attempts to ameliorate this state (20), and yet, until so-called “sympathetic concern,” i.e., concern about another’s postconflict stress, a bystander may be required to perceive the need for distress alleviation (22). To provide reassuring contact suggesting that they may be unable to perceive their offspring’s increase postconflict affiliative contacts with their offspring, when their offspring are targets of aggression nor do they fuscata affiliation has been demonstrated in stumptail macaques (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 *St 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 (hereafter referred to as the recipient). The outcome of the conflict was recorded as decided if there was a clear v 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’s (55) procedure, 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 submissions (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 that conflict. Although the location of the contact sector was the same in the corresponding PC and MC, 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 ± SD PC–MC pairs per recipient = 10.6 ± 5.7; range = 2–25).

Function of Consolation. Because the majority of postconflict affiliative interactive actions occurred in the first minute of the PC (G.N.F. and F.A., unpublished data), we considered this time as the beginning of the affiliative behavior 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 or both reconciliation and consolation occurring during the corresponding PC. The occurrence of consolation was defined as any adult subject not involved as an opponent of the recipient dyad with the highest intensity of aggression as the recipient of consolation 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 based on the presence or absence of consolation in the PC and MC. Consolations were defined as occurring either before or after the PC (PC–MC pair). The proportion of 5-sec blocks spent performing self-directed behavior after 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 the consolation took place. GLMMs were used to analyze the proportion of 5-sec blocks (bouts) in which self-directed behavior 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 components were operationally defined as affiliation occurring earlier in the PC than in the MC or only in the PC, they 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 interaction were considered undecided. Consolations were defined as having 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 the consolation took place. GLMMs were used to analyze the proportion of 5-sec blocks occurring 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.

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 affiliative participant 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 GLMMs allow the effects of each explanatory variable to be examined while control-
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. 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 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 α-level of 0.05 was adopted for all tests.

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

<table>
<thead>
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<th>Name</th>
<th>Type</th>
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<tr>
<td>TCT</td>
<td>Continuous</td>
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<tr>
<td>Fixed explanatory variables (relationship characteristics)</td>
<td></td>
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<tr>
<td>Value</td>
<td>Continuous</td>
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<tr>
<td>Compatibility</td>
<td>Continuous</td>
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<tr>
<td>Security</td>
<td>Continuous</td>
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<tr>
<td>Sex-dyad combination</td>
<td>Continuous</td>
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<td>Kinship</td>
<td>Dichotomous (1 = including males, 0 = no males)</td>
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<tr>
<td>Fixed explanatory variables (conflict characteristics)</td>
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<td>Outcome</td>
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<td>Reconciliation</td>
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