Consolation as possible expression of sympathetic concern among chimpanzees

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Chimpanzees are known to spontaneously provide contact comfort to recent victims of aggression, a behavior known as consolation. Similar behavior in human children is attributed to empathic or sympathetic concern. In line with this empathy hypothesis, chimpanzee consolation has been shown to reduce the recipient's state of arousal, hence to likely alleviate distress. Other predictions from the empathy hypothesis have rarely been tested, however, owing to small sample sizes in previous studies. An exceptionally large database of spontaneous consolation in two outdoor-housed groups of chimpanzees lends further support to the empathy hypothesis in that consolation occurred disproportionally between individuals that are socially close (i.e., kin and affiliation partners) and was more typical of females than males, which differences are also known of human empathy. These effects were demonstrated using generalized linear mixed models, which control multiple variables at once. An exception to the above pattern was formed by the highest-ranking males, which frequently offered consolation to victims of aggression, probably as part of their general policing function in chimpanzee society. Consolation occurred more frequently in the absence of reconciliation between former opponents, suggesting that actors are sensitive to the contact need of victims of aggression, which may be greater if the aggressor ignores them. That consolation is an integrated part of close mutual relationships is supported by the tendency for it being reciprocated.

empathy | *Pan troglodytes* | postconflict affiliation

Providing contact comfort to distressed others has been studied in human children, in whom it is generally classified as an expression of empathic or sympathetic concern for the other (1–3). The same behavior has received less attention in animal research, perhaps owing to its restricted distribution. Despite ample attention to postconflict behavior in more than 30 primate species, both in captivity and in the field (4–6), as well as several nonprimates (7–9), only a handful of species regularly shows reassurance of distressed conspecifics. The term *consolation* has been proposed for interactions in which an uninvolved bystander initiates friendly contact with a recent victim of aggression (10) (Fig. 1). This definition excludes other forms of postconflict contact, such as *reconciliation* (i.e., a reunion between former opponents) (10) and third-party contacts sought by the conflict participants themselves or made with the aggressor.

Thus defined, spontaneous consolation has been documented or suggested only for the great apes [*Pan troglodytes* (10–16), *P. paniscus* (17), *Gorilla gorilla* (18, 19)], canids [*Canis spp* (20, 21)], and corvids [*Corvus spp* (22, 23)] and has been studied with similar ethological methods in human children (24). That consolation has a much more limited distribution than some of the other forms of postconflict behavior has been related to the assumed underlying empathic capacity (11). If this behavior indeed serves to reassure distressed parties, as its label suggests, bystanders need to be affected by the distress of others and be inclined to provide succor. The reactions of chimpanzees to distressed others resemble those of humans in both social context and morphology (e.g., touching, hugging, kissing). Given the close genetic relation between both species, the most parsimonious assumption is a common motivation for both, hence to

apply to chimpanzees the same explanation as for human sympathetic concern, which is that of empathy with the predicament of another. At the same time, we realize that an observational study such as the present one cannot demonstrate underlying mechanisms.

Recent evidence has shown that chimpanzee consolation (*i*) reduces the recipient's stress, and (*ii*) is provided mainly by individuals socially close to the recipient (25, 26; but see ref. 15). Both findings are consistent with an empathy-based explanation given that similarity, familiarity, and social closeness are known to facilitate empathy in both humans and other animals (27–31). It remains unclear, however, whether other factors that facilitate or inhibit human empathy also modulate consolation in apes. Researchers have reported that human empathy and prosocial behavior tend to increase with age, at least up to adolescence, and that females are generally more empathic than males. Only two studies have examined the effect of these variables on consolation in other primates, however, and neither study reported an effect, perhaps owing to small sample sizes (11, 25).

It is assumed that empathy originally evolved in the context of maternal care, in which immediate reactions to the distress or alarm of others are highly adaptive (27, 32). This origin would explain the facilitating role of oxytocin on human empathy (33) as well as the generally greater sensitivity of women and girls to emotional signals. Indeed, using a wide range of assessments, human studies have consistently found females to score higher on empathy than males (34–36). For example, girls express more interpersonal concern and caring behaviors than do boys (37).

By reducing the stress of a victim of aggression, consolation confers benefits to another, as indicated for chimpanzees (25), while carrying the risk for the performer of getting drawn into the conflict that caused the recipient's distress (38). Consolation thus fits the definition of altruistic behavior, which is generally thought to evolve through kin selection or reciprocity. We therefore expect this behavior to be biased toward relatives and individuals inclined to return the favor. While evidence for kin selection in the evolution of altruistic behavior is strong (39), evidence for reciprocal altruism is weaker. Although consolation may be expected to be reciprocated or exchanged for other valuable services (31), no study has investigated correlations between given and received consolation.

The present study is unusual in its sample size, which is many times larger than that of any previous study of animal consolation, hence allowing an exploration of all of the above questions in a single analysis. In two large outdoor-living groups of chimpanzees (FS1 and FS2), a total of 3,003 aggressive conflicts and postconflict periods were recorded. This database served to investigate how consolation is affected by variables that typically modulate human
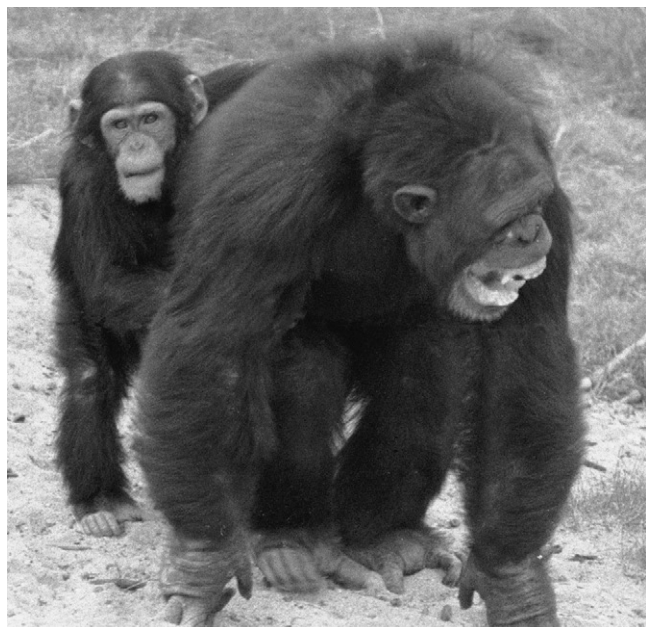
Fig. 1. Chimpanzees spontaneously console distressed individuals by means of friendly body contact. Loudly screaming after having lost a fight against a rival, an adult male (right) is approached by a juvenile who puts an arm around him. Photograph by Frans de Waal.

empathic responses, such as social closeness and actor sex. We also measured the characteristics of the previous conflict, the relation between conflict participants, and the conflict participants' relation with third parties, as well as the reciprocity of consolations (i.e., do chimpanzees preferentially console those individuals that console them most?).

Results

Social Determinants. The effects of a variety of variables on the likelihood of consolation (i.e., the first contact initiated by a bystander with an individual recently targeted by aggression, which individual will be called the "victim"; *Materials and Methods*) was measured using generalized linear mixed models (GLMM). Among

the characteristic of the previous conflict (*Materials and Methods* and Table 1), the only variables remaining in the best model were the occurrence of reconciliation between both opponents, and the victim's rank (Fig. 2 and Table S1). Consolation seemed to compete with or replace reconciliation between the opponents, in that consolation occurred more often after unreconciled conflicts (β = −0.781, P < 0.001). We also found that low-ranking victims of aggression were consoled significantly less often than high-ranking victims (high vs. low ranking: β = 0.724, P = 0.040; medium vs. low ranking: β = 0.849, P = 0.004).

Triadic Relations. Because consolation involves three parties (i.e., the consoling bystander and the two opponents, aggressor and victim, of the original conflict), there are three relationships to be considered. We investigated how relational variables between consoler and aggressor and between consoler and victim (Table 1) determine the occurrence of consolation by running GLMM (*Materials and Methods*). Whereas none of the aggressor's individual or relationship characteristics affected the occurrence of consolation, the variables kinship and affiliation between consoler and victim remained significant in the best model (Fig. 3 and Table S2). Consolation was directed more often at kin (β = 1.189, P < 0.001) and at unrelated individuals with whom the actor had a strong affinitive tie (strong vs. no-strong affiliation: β = 0.370, P = 0.005). Thus, victims of aggression were more likely to be consoled by individuals with whom they enjoyed a close social tie.

Sex Differences. Sex of the victim was not among the variables remaining in the best model, which suggests that male and female victims of aggression were consoled to a similar degree. On the actor's side, though, the sex of consolers and the interaction between the consoler's sex and rank remained in the best model (Table S2). Overall, female bystanders provided consolation more often than did males (β = 1.507, P < 0.001). This difference held only for individuals of medium and low rank, however, because high-ranking males offered significantly more affiliative contacts to victims of aggression than did females (Fig. 4 and Table S2).

Reciprocity. In both study groups, individuals disproportionally consoled individuals from whom they received consolation. This was measured by a rowwise matrix correlation (40) between consolation given and consolation received (i.e., between the consolation matrix and its transposition), which controls for in-

Table 1. Description of variables used in GLMM analyses

| Name	Type
Dependent variable	
Consolation behavior	Dichotomous (1 = yes, 0 = no)
Frequency of consolation	Continuous
Fixed explanatory variables	
Conflict characteristics	
Outcome	Dichotomous (1 = decided, 0 = undecided)
Intensity	Ordinal (1 = low, 2 = medium, 3 = high)
Directionality	Dichotomous (1 = unidirectional, 0 = bidirectional)
Reconciliation	Dichotomous (1 = yes, 0 = no)
Appeasement	Dichotomous (1 = yes, 0 = no)
Individual characteristics	
Sex	Dichotomous (1 = male, 2 = female)
Rank	Ordinal (1 = high, 2 = medium, 3 = low)
Relationship characteristics	
Kinship	Dichotomous (1 = kin, 0 = no kin)
Affiliation level	Dichotomous (1 = strong, 0 = no-strong)
Random variables	
Aggressor's, recipient's, and consoler's identity	Nominal
Group	Nominal
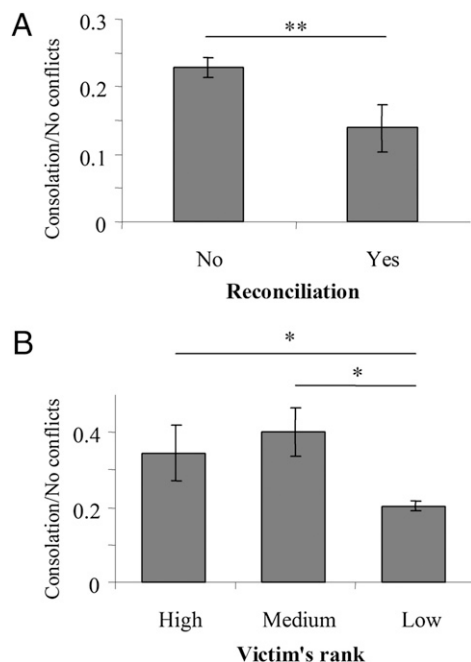
Fig. 2. Mean proportion of occurrence of consolation (±95% confidence intervals) corrected by the number of conflicts for each category in relation to (*A*) occurrence of reconciliation and (*B*) victim's dominance rank. *P < 0.05, **P < 0.001.

terindividual variation (FS1: τ_{rw} = 0.142, P = 0.002; FS2: τ_{rw} = 0.149, P < 0.0001). Because previous studies have shown that reciprocity may be affected by symmetrical aspects of the social relationship, such as proximity (41), we controlled for the proportion of scans samples in which two individuals were in close social contact (*Materials and Methods*) as well as for kinship
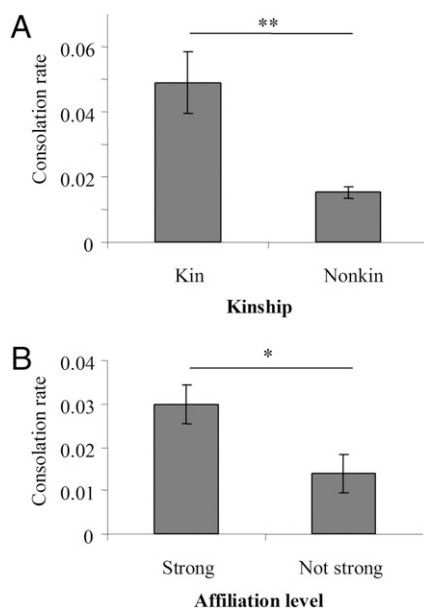
Fig. 3. Mean consolation rate (±95% confidence intervals) in relation to (*A*) genetic relationship and (*B*) affiliative relationship between consoler and recipient. Consolation rate was calculated as the number of consolations corrected for the total number of opportunities to receive consolation (*Materials and Methods*). *P < 0.05, **P < 0.001.
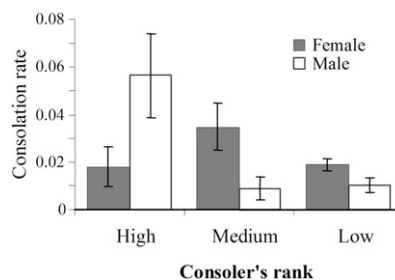
Fig. 4. Mean consolation rate (±95% confidence intervals) in relation to the sex and rank of consolers. Consolation rate was calculated as the number of consolations corrected by the total number of opportunities to receive consolation (*Materials and Methods*).

(entered in a separate 1/0 matrix). After having controlled for these variables, the partial correlation between given and received consolation remained significant in both study groups (FS1: $\tau_{rw;XY.ZW}$ = 0.101, P = 0.028; FS2: $\tau_{rw;XY.ZW}$ = 0.089, P = 0.047), suggesting that the observed reciprocity was unexplained by symmetrical aspects of the social relationships.

Discussion

According to our analysis, in which the effect of each variable on consolation was measured while controlling for the effects of all other variables, this behavior followed predictions from an empathy-based explanation in that it occurred disproportionately between socially close individuals and was more typical of females. Consolation also tended to be reciprocated, suggesting that it is an integrated part of mutually beneficial relationships.

Consistent with previous research (14, 17, 25), consolation was more often directed at victims who had not reconciled their conflict than at those who had. Although reconciliation is likely the most effective way to reduce relationship damage caused by aggression (4, 5), it has been argued that consolation provides advantages when reconciliation is either not beneficial or too risky (12). There is no evidence, however, that consolation is a true alternative to reconciliation, which serves to repair relationships (42, 43). Consolers might be reconciling with the victim "on behalf" of the aggressor, but then one would expect these bystanders to be close to the aggressor, such as immediate kin (44). Yet the relationship between aggressors and bystanders failed to affect consolation in the present study. Therefore, the more likely explanation focuses on the need for stress reduction in the victim, which need may be greater if reconciliation with the aggressor has failed to take place. As predicted if empathy is the main motivation, the increased rate of consolation in the absence of reconciliation may be a response to greater distress.

Consolation was more common if the victim of aggression was of high or medium rank. When dominant individuals find themselves on the receiving end of a fight, possibly losing to a subordinate (or a coalition of subordinates), they may show greater distress given that this is an unusual situation for them. Previous studies have shown that chimpanzee distress vocalizations, such as screams, can be flexibly modified and convey a rich array of social information (45), while also eliciting consolation by bystanders (14). Further studies are needed to evaluate how individuals modify the acoustic structure of their calls according to their emotional state and whether bystanders are responsive to the vocalizations or other distress behaviors when victims perceive the conflict outcome as a threat to their status. Such sensitivity has been suggested for a massive consolation response to a dethroned alpha male in a zoo colony (46).

Empathy is not equally aroused by the emotional signals of any individual, but rather is in both humans and other animals biased toward parties close to the observer (27, 28, 30). Empathy has

been proposed as the proximate mechanism of directed altruism, because its manifestations rather precisely follow predictions from kin selection and reciprocal altruism theories (31). That consolation in this study was disproportionally aimed at close social partners, including genetic relatives, fits the predictions of the empathy hypothesis, as did the only other chimpanzee study to analyze the effect of relationship quality (25). This may also hold for other species in which postconflict affiliation by bystanders is typically provided by close partners, such as mates in rooks (22) or individuals with a high degree of familiarity in wolves (*Canis lupus*) (21).

Another point in favor of the empathy hypothesis is the observed sex difference, which matches that found in human studies. Overall, female chimpanzees offered more consolation to recent victims of aggression than males, suggesting that females were particularly responsive to the distress of others. Furthermore, this postconflict pattern did not reflect typical sex differences in affiliation during nonconflict situations because in chimpanzee society in general (38, 47), and in our two study groups in particular, males are on average more affiliative than females (mean ± SD percentage of scan samples individuals spent grooming: females, 5.50 ± 0.81%; males, 7.10 ± 1.20%; ANOVA, $F_{1,25} = 62.28$, $P < 0.001$).

An unanticipated outcome was that the tendency of females to show more consolation behavior than males reversed when the analysis is limited to high-ranking individuals, because the most dominant males (e.g., alpha males) frequently reassured distressed parties. This may relate to the special political role of these males in a chimpanzee community, which is that of mediating and controlling open conflict. Adult male chimpanzees often intervene in ongoing conflicts and perform pacifying interventions (46, 48). Postconflict affiliative contacts by high-ranking males toward conflict participants may be part of these policing strategies, which reduce the probability of further aggression and/or social tensions within the group. In both study groups, high-ranking males not only affiliated frequently with recent victims of aggression, but also performed the vast majority of impartial interventions during ongoing conflicts (FS1: 63%; FS2: 68%). A recent experimental study on a different primate species showed that policing males exert a major positive effect on overall intragroup harmony (49).

An observational study cannot determine the exact empathy mechanism operative in chimpanzees. Researchers typically distinguish multiple levels (27). If perception of another's distress merely leads to a matching state in the observer, the latter is expected to selfishly seek alleviation of their own distress, probably turning away from the victim. This personal distress explanation does not seem to apply to our observations because it would preclude other-orientation. In contrast, when vicarious distress leads to sympathetic concern, observers are expected to seek out the other and perform prosocial acts. This explanation fits our observations in which the most typical chimpanzee consolation behaviors were grooming (28.1%), embracing (26.8%), gentle touching (19.2%), and kissing (9.5%). Future research should focus on the bystander's emotional state to evaluate their motivation to contact recipients of aggression. It should be kept in mind, however, that the first expressions of consolation in humans, around 1 y of age, have elements of both providing and receiving comfort (2), and that both elements may be also present in chimpanzee consolation.

Expressions of empathy are not immune to strategic decision making. Like all behavior, actors may learn about its costs and benefits, which in turn influence their propensity to show the behavior. Thus, consolation may become part of an exchange system among partners consistent with reciprocal altruism theory (31). In our data, significant reciprocity correlations persisted after controlling for symmetrical relationship characteristics, such as mutual association and kinship. This suggests that chimpan-

zees do not simply provide consolation to distressed others with whom they frequently interact but selectively offer this benefit to those partners that console them in return. The receipt of past favors may thus enter into the decision of whether consolation will be provided, which is consistent with experimental empathy studies on humans, in which the degree of empathy with others varies with the history of positive or negative interactions (50, 51).

In short, consolation among chimpanzees fits predictions derived from the empathy hypothesis. Until and unless contrary evidence is produced, this behavior should therefore be considered a likely expression of "sympathetic concern."

Materials and Methods

Study Population. The present study was conducted on two groups of chimpanzees (FS1 and FS2) housed at the field station of the Yerkes National Primate Research Center, Lawrenceville, GA. Each group had access to larger outdoor compounds (750 and 520 m²) connected to indoor areas. The demographic composition of groups varied slightly during the study period because of births, deaths, and several removals for veterinary reasons and management purposes. Most of the time, both groups included multiple adult males and at least twice as many adult females (26). The analysis has been limited to individuals at least 10 y old: a total of 8 males and 21 females.

Data Collection. Since the formation of the two groups, controlled observation sessions have been conducted with regularity (≈1 per week). Data presented here refer to a period from 1992 to 2000 for FS1 and from 1994 to 2000 for FS2. During 90-min observation sessions (52), affiliative and sexual interactions (including kiss, embrace, grooming, gentle touch, finger/hand-in-mouth, mounting) and 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) (53, 54) were recorded by a trained research technician, Mike Seres, using an all-occurrence sampling technique. Additionally, scan samples of state behaviors (e.g., contact-sitting, grooming, play) were taken at regular intervals (i.e., every 5 min through 1993 and every 10 min in the years thereafter).

Because the observation sessions were not designed to study postconflict interactions, formal postconflict and matched control observations were not conducted. However, because the observations were continuous, the behavior following aggression can be considered postconflict data (55). We focused on the immediate 10-min postconflict period on the basis of previous investigations (e.g., refs. 13, 14). Following de Waal and van Roosmalen (10), an interaction was considered 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 (53), and for each agonistic dyad the identities of the initial aggressor and recipient of aggression were recorded along with the intensity, directionality, and outcome of the conflict. The intensity was scored as low if the conflict included a threat, chase, and/or brusque rush, as medium if it included hit, punch, push, and pull, and as high if it involved trample or bite. A conflict was considered unidirectional if all aggressive behavior was directed toward the initial recipient of aggression and no counteraggression occurred. The outcome of the conflict was recorded as decided if only one of the parties showed signs of submission (e.g., screaming, teeth-baring, fleeing, or pant-grunt) and as undecided in the remaining cases.

Data Analysis. A total of 1,676 and 1,327 valid 10-min postconflict periods were collected for FS1 and FS2 groups, respectively. From postconflict 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. For the purpose of this study, reconciliation was operationally defined as the fist affiliative contact between former opponents after a conflict, appeasement as the first affiliative contact directed from a third party to the initial aggressor, and consolation as the first affiliative contact directed from a third party to the recipient of aggression. Third-party individuals were defined as those individuals who were neither involved in the conflict or in any agonistic interaction in a time window of ±2 min from the occurrence of the conflict.

To examine whether the occurrence of consolation was affected by several factors, GLMM with a binomial error structure and logit link function were used. When evaluating the effect of the characteristic of the previous conflict on the occurrence of consolation, the dependent variable was a binary term (binomial error structure) of whether consolation behavior was present

or absent. Conflict characteristics (i.e., intensity, directionality, outcome), sex and dominance rank of both opponents, relationship characteristics between aggressors and recipients, and the occurrence of reconciliation and appeasement were entered as fixed variables (Table 1). Dominance was defined by the direction of submissive signals, such as pant-grunt and bobbing movements, and by nonagonistic approach/retreat interactions. Rank was determined by the relative number of dominated individuals: individuals dominating at least 75% of group mates were classified as high ranking, those dominated by 75% of individuals as low ranking, and the remaining individuals as middle ranking. Kinship was based on maternal lineages, and only (grand)-mother-offspring and maternal siblings were considered related individuals. The affiliation level between dyads was categorized using a combined measure of four state behaviors collected during scans (i.e., contact sitting, sitting within arm's reach, grooming, and mutual grooming), and calculating the quartile points of dyadic scores for each focal individual. Only dyads with scores higher than the top quartile were considered to have a strong affiliative relationship. Because dominance rank and affiliative relationships could vary along years, we calculated dyadic values for each year independently. The identity of aggressors and recipients of aggression, as well as the study group name (i.e., FS1 and FS2) were entered as random variables.

A second set of analyses was performed to examine the effect of individual characteristics of participants and relationship characteristics between opponents and third parties on the occurrence of consolation. The dependent variable was the frequency of giving consolation corrected by the number of opportunities. In the first analysis, the frequency of giving consolation equaled the number of times each potential consoler initiated the affiliative interaction toward a particular recipient of aggression. To correct for the opportunity each potential consoler had to console the victim, we included as an offset variable the number of postconflicts in which one individual was the recipient, excluding those in which the partner was an involved individual in the conflict (i.e., the aggressor or a supporter of either opponent). GLMM was then run with individual characteristics of recipients of aggression and consolers (i.e., sex and rank) and relationship characteristics between recipients and potential consolers (i.e., kinship, affiliation level) as fixed terms (Table 1). In the second analysis, the frequency of consolation equaled the number of times each potential consoler offered consolation when a particular individual was the aggressor. We corrected for the opportunity to offer consolation, including as an offset variable the number of postconflicts in which one individual was the aggressor, excluding those in which the partner was an involved individual in the conflict (i.e., the recipient or a supporter of either opponent). Then, the GLMM was run including the aggressors' variables (Table 1). As random terms we included the identity of opponents and consolers and the group name.

For all GLMM analyses we used restricted maximum likelihood methods for model estimation. A step-up strategy (i.e., fixed factors were added to the model sequentially) was used, and the selection of the model was based on Akaike's information criterion (AIC). A model with a lower value of AIC is considered to be a better model. The assumptions of the GLMM analyses of the models were checked by visual inspection of the residuals and of predicted random variables. GLMM did not show overdispersion. GLMM analyses were run on R version 2.8.1 (56, 57) using the lmer function included in the lme4 package.

To test for reciprocity and interchange we used the rowwise matrix correlation method (40, 58), which is a distribution-free test taking into account that in interaction matrices data are not independent. The number of consolations received by third parties (corrected by the number of opportunities of receiving consolation) was entered into directional, square, interaction matrices. Interindividual proximity was defined by the percentage of scan samples during which a dyad was in close social contact (i.e., contact sitting, sitting within arm's reach, and grooming). Kendall's form of rowwise matrix correlations (τ_{rw}) and second-order partial rowwise matrix correlations ($\tau_{rw;XY.ZW}$) were used. The calculation was implemented in R software (57) with the recursive partial correlation formula, and exact probability values were calculated on the basis of 10,000 permutations. All analyses were two-tailed, and the significance level was set at 0.05.

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