CALMING AN AGGRESSOR THROUGH SPONTANEOUS POST-CONFLICT TRIADIC CONTACTS: APPEASEMENT IN *MACACA TONKEANA*

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ABSTRACT

Peaceful third-party interventions usually occur after an aggressive encounter and can be directed towards the victim or the aggressor. *Macaca tonkeana*, a cercopithecine species characterized by high levels of tolerance, frequently engage in consolatory contacts, which both calm the victim and reduce the probability of further attacks against him/her. Other post-conflict affiliative interventions such as reconciliation and quadratic affiliation are also common in this species. However, little attention has been given to contacts directed towards the aggressor. Here, we explore the role of bystander affiliative interventions towards the aggressor in influencing the affective state of the aggressor and the consequences of triadic interventions at group level. We found that triadic post-conflict affiliation occurred independently from the intensity of the conflict and that it was more frequent in absence of the conciliatory contact between the opponents (reconciliation). Bystanders showed a higher amount of post-conflict affiliation towards low ranking aggressors. Post-conflict triadic affiliation functioned as a tension reduction mechanism by lowering the arousal of the aggressor, which less frequently engaged in renewed aggression. All these findings suggest that post-conflict triadic contacts in Tonkean macaques can be considered as a strategic mechanism to calm the aggressor and reduce the risk of retaliatory aggression.

INTRODUCTION

Conflict in social species may be disruptive not only for the opponents, but also for other group members because they create uncertainty at the group level (Aureli, 1997; Castles & Whiten, 1998; Das, Penke, & van Hooff, 1998). Unresolved conflicts can escalate into renewed attacks towards subjects not involved in the previous conflict, which increase their anxiety rate (De Marco, Cozzolino, Dessi-Fulgheri & Thierry, 2010; Judge & Mullen, 2005) and their motivation to aggressively interact (Pallante, Stanyon & Palagi, 2016). Reconciliation is a post-conflict process that restores the relationship between opponents (de Waal & Roosmalen, 1979) and mitigates negative consequences of conflicts (Arnold & Aureli, 2007; Aureli, Cords, & van Schaik, 2002; Kazem & Aureli, 2005). Conflict management strategies may also involve a third subject, who spontaneously offers a friendly contact to one of the two opponents after the aggression ("unsolicited third-party affiliation" or "unsolicited bystander affiliation"). Post-conflict spontaneous affiliation may be directed towards the victim of a conflict (macaques: Palagi, Dall'Olio, Demuru, & Stanyon, 2014; chimpanzees: Fraser & Aureli, 2008; Palagi, Cordoni, & Borgognini, 2006; Romero & de Waal, 2010; Romero, Castellanos, & de Waal., 2010; Wittig & Boesch, 2003, 2010; gorillas: Cordoni & Palagi, 2007; bonobos: Clay & de Waal, 2013; Palagi & Norscia, 2013; Palagi, Paoli, & Tarli, 2004; humans, Fujisawa, Kutsukake, & Hasegawa, 2006). This kind of contact can be considered as "consolation" when it is directed towards strong bonded partners and when it reduces anxiety in the victim (Fraser & Aureli, 2008; Palagi & Norscia, 2013; Palagi et al., 2014; Romero & de Waal, 2010). Contacting a victim after an agonistic encounter is also thought to provide benefits to the consoler, as the probability that the victim redirects aggression towards other group members is reduced (Call, Aureli, & de Waal, 2002; Koski & Sterck, 2009; Schino & Marini, 2012).

Third-party affiliation towards the aggressor has often been neglected in the study of post-conflict mechanisms. The aggressor can represent a danger, because he/she may reiterate their aggressive contacts (Cordoni & Palagi, 2015; Das, 2000; Petit & Thierry, 1994; Romero, Castellanos, & de Waal, 2011). Van Hooff (1967) defined "appeasement" as every affiliative contact provided by a

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third-party to limit the aggressor arousal and its tendency to renew aggression. Similarly, Das (2000) used the term "appeasement" when post-conflict affiliation reduced the risk of further attacks. The calming function deriving from the third-party contact towards the aggressor was demonstrated only in a few cases (Cordoni & Palagi, 2015; Palagi, Chiarugi, & Cordoni, 2008; Romero et al., 2011). However, none of these studies focused on the potential role of third-party affiliation in reducing arousal in the aggressor (Das et al., 1998).

Previous reports have concluded that *Macaca tonkeana* are sensitive to variations in the affective states of other group members (Palagi et al., 2014; Scopa & Palagi, 2016). In this species, opponents show a high rate of reconciliation (Demaria & Thierry, 2001) and third parties are reactive to conflicts that occur in the group, thus increasing the reciprocal affiliative interactions (De Marco et al., 2010). Tonkean macaques spontaneously provide post-conflict affiliation to the victims (Palagi et al., 2014; Puga-Gonzalez, Butovskaya, Thierry, & Hemelrijk, 2014). Palagi et al. (2014) found that Tonkean macaques appear to be sensitive to the distress experienced by the victim. After a conflict, female victims showed the highest distress rates (measured by self-directed behaviors *sensu* Troisi, 2002) and were the preferred targets of triadic post-conflict affiliation. Triadic post-conflict affiliation followed an empathic gradient, since it was directed more frequently towards the victim who shared a strong bond with the bystander. Moreover, after the triadic post-conflict affiliation, the level of self-directed behaviors of the victim was significantly reduced. All these findings led Palagi et al. (2014) to interpret this post-conflict mechanism as consolation. In a parallel study carried out on a different colony of Tonkean macaques, Puga-Gonzalez et al. (2014) concluded that spontaneous triadic post-conflict affiliation was driven by social facilitation (e.g., lowering the reaction threshold in the third-party) rather than empathy due to the similar frequency of spontaneous and solicited contacts recorded after a conflict. The different results of the two studies could be ascribed to several factors such as i) the different approaches (a purely empirical approach by Palagi et al. 2014 and a combined model-empirical approach by Puga-Gonzalez et al. 2014), ii) the different sample size of PC-MC pairs (876 PCs-MCs by Palagi et al., 2014 vs 83 PCs-MCs by Puga-Gonzalez et al. 2014) and iii) the behavioral

variability and composition typical of different social groups (Thoiry group in Palagi et al., 2014 and Strasbourg group in Puga-Gonzalez et al. 2014).

Tonkean macaques also affiliatively contact the aggressor (Petit & Thierry, 1994). Thierry (1984) reported that a bystander may contact the aggressor during a conflict, intervening with an affiliative behavior that can stop the ongoing aggression (Thierry, 1984). The affiliative contact can be expressed through clasping, a form of tactile communication consisting of grasping or embracing an individual (Thierry, 1984). Interveners are usually dominant over both the opponents although this intervention seems not to be linked to an increase of the social rank of the third subject. The interaction between the intervener during a conflict and the aggressor continues even after the end of the conflict, since aggressor and interveners frequently engage in a grooming session (Petit & Thierry, 1994). The high level of social tolerance of Tonkean macaques permits us to test whether the unsolicited triadic affiliation towards the aggressor has an appeasement function, and is informative about the motivation of the bystander to limit further aggression by the previous aggressor.

Third-party affiliative interventions towards the aggressor are particularly frequent during high intensity conflicts, probably due to the victim's vocalizations that attract the attention of other group members (Petit & Thierry, 1994). During conflicts, the presence of vocalizations may induce third-party interventions because high-pitch sounds convey information about the intensity of the aggression and elicit the attention of bystanders, thus inducing them to interact (Gouzoules, Gouzoules, & Marler, 1984; Gouzoules, Gouzoules, & Marler, 1986; Palagi et al., 2006; Petit & Thierry, 1994; Thierry, 1985). To test this hypothesis, we investigated how Tonkean macaques adjust their tendency to provide affiliation towards the aggressor according to the intensity of the agonistic contact.

Prediction 1 - Post-conflict triadic contact towards the aggressor

According to the *Substitute for Reconciliation Hypothesis*, the presence of triadic post-conflict resolution mechanisms may act as an alternative when the two opponents fail to reconcile. Triadic contacts towards the victim are more likely to occur in the absence of reconciliation (Aureli et al.,

2002). In chimpanzees, Romero et al. (2011) reported the same result for the triadic affiliation towards the aggressor. Thus, if in Tonkean macaques affiliation towards the aggressor is sensitive to the conflict management strategies employed by the opponents (e.g., reconciliation), according to the *Substitute for Reconciliation Hypothesis* we expect the presence of reconciliation to reduce the probability of post-conflict triadic contacts towards the aggressor.

Prediction 2 - The importance of the ranking status of the aggressor

A non-resolved conflict may lead to an increased rate of renewed aggression by the aggressor (Kazem & Aureli, 2005; Romero et al., 2011). Approaching one of the two opponents may be potentially dangerous for a third-party (gorillas: Palagi et al., 2008; wolves: Cordoni & Palagi, 2015). Interacting with a dominant individual entails a higher risk: therefore, we expect that when the aggressor occupies a high ranking position the amount of triadic post-conflict affiliation will be reduced.

Prediction 3 – Arousal reduction in the aggressor

Previous results show that aggression can increase of the arousal/anxiety levels in both victims and aggressors (Aureli & van Schaik, 1991; Castles & Whiten, 1998; Das et al., 1998; Kutsukake & Castles, 2001; Palagi et al., 2014). In non-human primates, the terms arousal and anxiety are often used in an interchangeable way by different scholars (for an extensive review see van Hooff & Aureli, 1994). In non-human and human primate research, both phenomena can be measured by the rates of self-directed behaviors (e.g., yawning, object shaking, scratching, self-grooming; Aureli & de Waal, 1997; De Marco et al., 2010; Judge & Bachmann, 2013; Maestripieri, Schino, Aureli, & Troisi, 1992; Thierry et al., 2000; Zannella, Stanyon, & Palagi, 2017). In this study, we define arousal as the variation of the emotional state experienced by the aggressor immediately after a conflict (Leavens, Aureli, Hopkins, & Hyatt, 2001; Judge, Evans, Schroepfer, & Gross, 2011; van Hooff, 1967). No data exist on the emotional arousal relief of the aggressor after a spontaneous third-party contact. If post-conflict affiliation towards the aggressor functions to reduce arousal we would expect that behavior which is indicative of this affective state in the aggressor will decrease after spontaneous post-conflict third-party affiliation.

153 *Prediction 4 - Effect of triadic post-conflict affiliation on the renewed aggression*

154 After a conflict, aggressors may renew aggression towards both the previous victim and other group

155 members (Kazem & Aureli, 2005; Romero et al., 2011). If post-conflict affiliation towards the

156 aggressor functions to protect the victim, according to the *Victim Protection Hypothesis* (Palagi &

157 Norscia, 2013), we would expect that third-party affiliation limits renewed aggression towards the

158 victim (Prediction 4a). According to the *Tension Reduction Hypothesis* (Palagi et al., 2006), post-

159 conflict affiliation towards the aggressor limits its motivation to reiterate agonistic interactions

160 towards other group members. Thus, we expect that in Tonkean macaques renewed aggression

161 towards other group members will be reduced when the aggressor receives a spontaneous affiliative

162 contact by a third-party (Prediction 4b).

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164 **METHODS**

165 **Ethic Statements**

166 The research complied with current laws of France, Italy, and the European Community. The

167 University of Pisa waived the need for a permit since the study was purely observational.

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169 **Subjects, Housing & Data Collection**

170 The colony of Tonkean macaques was hosted at the Parc Zoologique de Thoiry (France) and was

171 composed of 29 adult males, 1 sub-adult male (4.5-6 years; sexually active animals without the full-

172 size typical of the adult), 29 adult females, 2 sub-adult females (4.5-6 years) and 6 immatures (1-4

173 years old) (see Table S1 for details). Kinship was not known. The colony was set in an enclosure with

174 an indoor ($182m^2$) and an outdoor ($3900m^2$) facility. The outdoor grass enclosure was provided with

175 environmental enrichments such as rope structures, branches, trees, bushes and pools. Tonkean

176 macaques were fed with fruits and pellets, twice a day at 11.45 a.m. and at 6.00 p.m. Water was

177 available *ad libitum*. Observations were carried out outdoor when all the animals were constantly

visible. We collected data on adult and sub-adult subjects for a total of six months divided between two years: from August to October in 2010 and 2011.

Individual identification was based on age, sex and external features (scars, size, pattern and missing of fur patches, fur color and facial traits). Three observers carried out the data collection through the aid of video cameras and tape recorders during working days, thus limiting the influence of visitors in the holidays and weekends. Observations were divided into two sessions: from 8.00 a.m. to 1.00/2.30 p.m. and from 1.00/2.30 p.m. to 5.00/6.00 p.m., for a total of about 8 hours a day. Before starting the systematic data collection, the observers underwent a period of about 90h to learn how to collect data through all occurrences, focal-animal sampling (Altman, 1974) and Post-Conflict/Match-Control method (PC-MC) (de Waal & Yoshihara, 1983). During the training period the observers simultaneously followed the same animal, then the data were compared and discussed. The training was considered over when the Cohen's kappa was higher than 0.75 for each behavioral pattern observed. The reliability was checked at the beginning of each month and values below 0.75 were never obtained.

Via focal animal sampling we collected 547 hours of observations ($N_{subjects}$= 61, individual mean of hours 8.96 $\pm$ 1.41 SE). A single focal session lasted 10 minutes and each subject was followed every day at different time to obtain balanced data covering the entire day. To acquire information on the relationship between the focal animal and other subjects, focal data were used to record contact sitting and grooming sessions in which the focal animal was involved.

Via all occurrences sampling we collected 380 hours of observations to record all the agonistic encounters. We recorded the identity of the victim and the aggressor and the characteristics of the conflict. A high intensity conflict included physical agonistic actions (e.g. aggressive pushing, pulling, biting, stamping and grabbing) and a low intensity agonistic interaction included patterns without physical contact such as threats, chasing, charging, avoiding and fleeing. The aggressor was defined as the initiator of the conflict who performed charging, chasing, aggressive pulling/pushing, slapping, biting, stamping, aggressive facial expressions (staring, threat open mouth display, scalp

retraction) and vocalizations (bark). The victim was the target of the aggression and was defined as the subject showing submissive behaviors such as fleeing, avoiding, submissive crouching, fear facial expressions (bared teeth display) and vocalizations (screaming).

Only dyadic aggressive interactions were considered for the post-conflict analyses. Post-Conflict observations (PCs) began at the end of the agonistic interactions (de Waal & Yoshihara, 1983). During the PC observation, the aggressor was followed for the subsequent five minutes, then the PC was compared with a Matched-Control focal observation (MC), conducted on the same subject the next day at approximately the same time as the original PC. MCs were carried out when two conditions were met: 1. no conflict in the five minutes before the beginning of the observations and 2. the opportunity for the focal animal to interact with the opponent of the conflict of the correspondent PC (opponents within 15m one to the other) and with other group members (< 15 m). During PCs and MCs observers recorded all the affiliative interactions of the aggressor with the victim (reconciliation) and with third subjects (third-party contact). Affiliative patterns of the PCs were then compared with those of the MCs. For both PCs and MCs the observers recorded: 1) the identity of the aggressor, the victim and the third subjects with whom the aggressor interacted; 2) the starting time of the observations; 3) the exact minute in which the aggressor had an interaction with the victim or with a third-party; 4) who first initiated the affiliative contact. After the end of a conflict the aggressor may engage in an affinitive contact towards the victim (reconciliation) or towards a third-subject not involved in the previous conflict (third-party affiliation). We distinguished solicited third-party affiliation from unsolicited third-party affiliation. In the solicited third-party affiliation the aggressor initiated the interaction with a third-party (aggressor's approach); in unsolicited third-party affiliation a third subject spontaneously affiliated with the aggressor without any solicitation by the aggressor to interact (bystander's approach) (Cordoni, Palagi, & Borgognini Tarli, 2006; Palagi & Norscia, 2013; Palagi et al., 2006; Palagi et al., 2014; Verbeek & de Waal, 1997). Since it was difficult to exclude the possibility that some subtle forms of invitation occurred, we discarded all occurrences when a facial expression or a vocalization was emitted by the aggressor.

Because the aim of this study was to explore the effect of spontaneous triadic contacts on the affective state of the aggressor and its possible consequences, we limited our analyses to unsolicited third-party affiliation.

Statistical Analysis

Presence of unsolicited third-party affiliation - To assess the presence of unsolicited third-party affiliation, the interactions between third subjects and the aggressor recorded during PCs-MCs were compared to determine the number of attracted, dispersed and neutral pairs. A pair was attracted if the affiliative contact occurred earlier in PC than in MC or if it was not present in MC. A pair was considered dispersed when the contact was provided by the third-party earlier in MC than in PC or if it was not performed at all in PC. In neutral pairs the affiliative contact occurred at the same minute of PC and MC, or did not occur in either of the two conditions. Third-party post-conflict contacts included all the affiliative interactions that a bystander spontaneously offered to the aggressor during PC observations (or MCs). The affiliative interactions considered in this study were contact sitting, grooming, touching, embracing, playful contacts, mounting, manipulating genitals, copulations, kissing, mouthing, face sniffing, cheek-to-cheek, holding face. Only the subjects with at least three PC-MC observations were considered for the analysis. The Triadic Contact Tendency value (TCT), a measure used to evaluate the entity of the phenomenon, was calculated through the difference between attracted pairs and dispersed pairs divided by the sum of attracted, dispersed and neutral pairs. The TCT was calculated at a dyadic level, considering the identity of the third subject and the aggressor. To determine the exact time-window in which third-party contact occurred we compared attracted and dispersed pairs at each minute via two-pair sample t randomization test. We evaluated whether the intensity of aggression affected the frequency of post-conflict triadic affiliation (measured via TCT) and whether the presence of reconciliation affected the occurrence of unsolicited third-party affiliation via the same test. We used randomization procedures to avoid pseudoreplication

due to the non-independence of data. All the randomization tests were employed with a number of 10,000 permutations using the software Resampling Procedures 1.3 (David C. Howell, freeware).

Calculation of the dominance relationships - For each year of observation (2010-2011), we evaluated hierarchical relationships on the basis of only dyadic and decided conflicts. For each conflict, data were entered into a winner/loser socio-matrix used to assess the rank by Normalized David's Scores (Table S1). Normalized David's scores (NDS) were calculated on the basis of a dyadic dominance index (Dij) in which the observed proportion of wins (Pij) is corrected for the chance occurrence of the observed outcome. The chance occurrence of the observed outcome was calculated on the basis of a binomial distribution with each animal having an equal chance of winning or losing in every dominance encounter (de Vries, Stevens & Vervaecke, 2006). The correction is necessary when, as in the case of our study groups, the interaction numbers greatly differed between dyads (Table S1). Rank hierarchies were calculated including the subjects for each period independently. In our colony, males and females did not differ in their NDS values (independent randomization t-test: t=0.001; $N_{females}$=31; N_{males}=30; P=1.000). Therefore, the variable NDS and SEX do not covariate.

Relationship quality - The quality of the relationship between the subjects forming each dyad (A-B) was determined by counting how many times A groomed B and dividing these events by the total hours of observation of A, in order to obtain the hourly frequency of grooming directed by A to B. This number was then divided by the hourly frequency of the total grooming performed by A to each other subject of the group.

Evaluation of post-conflict aggressive arousal - We measured the level of arousal by recording the events of self-directed behaviors (scratching and self-grooming), yawning and object shaking, (Maestripieri et al., 1992; Palagi & Norscia, 2011; van Hooff & Aureli, 1994; Zannella et al., 2017). We considered scratching a repeated movement of the hand or foot during which the fingertips are drawn across the individual's fur. We counted as a new scratching event when the scratched body part changed or when scratching was resumed after more than 5s. A self-grooming event was defined as every self-oriented grooming session that lasted at least 10 seconds. A new self-grooming session

began after 5 seconds from the end to the previous one. During object shaking the animal performed a repeated movement of an object or jumped on the ground or on a wood platform where animals could climb or walk. To be included in the analysis, a new shaking event should need to occur at least 5 seconds after the previous episode.

We evaluated whether i) the presence of aggression not followed by a triadic post-conflict contact led to an increase in aggressors' arousal and whether ii) the presence of a third-party affiliation restored the arousal of the aggressor to its baseline levels. Firstly, arousal behavior was compared between PC-no contact and MC; secondly, it was compared between PC-contact and MC. Reconciled PCs and individuals with less than two PCs were not included in the analysis. For all these analyses we applied two-pair sample t randomization test.

Assessment of renewed aggression events. To evaluate whether the post-conflict triadic contact reduced the aggressors' subsequent agonistic interactions towards the victim and towards other subjects, we quantified the new aggressive events occurring in three different conditions: PC-no contact, PC-contact and MC. We classified as a new aggressive event every aggressive pattern (charging, chasing, aggressive pulling/pushing, slapping, biting, stamping, aggressive facial expressions, bark) that the aggressor performed 10s after the end of the previous conflict. Since reconciliation could reduce the occurrence of subsequent attacks from the aggressor, we excluded the reconciled PCs from the analysis. We then compared the frequency of renewed aggression via two-pair sample t randomization test in the conditions PC-no contact/MC and PC-contact/MC in the post-conflict five-min time window.

Statistical Model Analysis - We ran a multi-model comparison of Generalized Linear Mixed Models (GLMM) to determine what variables affected the levels of third-party affiliation towards the aggressor. In the model, the dependent variable was the TCT (Gamma distribution, Log-link function; Anderson-Darling, ns, EasyFit 5.5 Professional). The fixed and random factors are listed and defined in Table 1.

306 To be conservative, we used robust estimation to handle violations of model assumptions during

307 GLMM (Yau & Kuk, 2002). The GLMM was applied to determine what variables could affect the

308 levels of third-party affiliation toward the aggressor. We tested models for each combination

309 involving the five variables of interest (Table 1), spanning a single-variable model to a model

310 including all the fixed variables (full model). The tested models were 18. Mixed-effects modeling

311 protects against problems of non-independence of data (asphericity). In particular, random effects are

312 effective in the analysis of repeated measurement data with crossed subjects, in our case aggressor

313 and bystander (Baayen, Davidson, & Bates, 2008).

314 To select the best model, we used the Akaike's corrected information criterion (AICc), which corrects

315 the Akaike's information criterion (AIC) for small sample sizes. As the sample size increases, the

316 AICc converges to AIC. To measure how much better the best model is compared to the next best

317 models, we calculated the difference (ΔAICc) between the AICC value of the best model and the

318 AICC value for each of the other models. As a coarse guide, models with ΔAICc values less than 2

319 are considered to be essentially as good as the best model (also defined as "substantial", Burnham &

320 Anderson, 1998, p. 70) and models with ΔAICc up to 7 should probably not be discounted (also

321 defined as "considerably less", Burnham & Anderson, 1998, p. 70). Moreover, to assess the relative

322 strength of each candidate model, we employed ΔAICc to calculate the evidence ratio and the Akaike

323 weight (*w*i). The *w*i (ranging from 0 to 1) is the weight of evidence or probability that a given model

324 is the best model, taking into account the data and set of candidate models (Symonds & Moussalli,

325 2011).

326

327 **RESULTS**

328 We collected 488 PC/MC (132 in 2010 and 356 in 2011) (*N*=54; mean individual value = $8.41_{pc/mc}$

329 $\pm 0.75SE$). To exclude the PC-MCs characterized by conciliatory contacts we tested the presence and

330 timing of reconciliation. Reconciliation was significant only at the first minute of the post-conflict

331 period (attracted pairs > dispersed pairs; two-pair sample randomization test t_{1min} = 7.668, *N* = 54, P

= 0.0001). Spontaneous third-party post-conflict affiliation towards the aggressor (in absence of reconciliation) was significant in the first post-conflict minute (attracted pairs > dispersed pairs; two-pair sample randomization test t_{1min} = 4.84, N = 38, P = 0.0001; t_{2min}=1.657; N =37; P=0.159; t_{3min}=1.463; N=37; P=0.198; t_{4min}=0.297; N =32; p=0.882; t_{5min}=0.779; N =31; p=0.573; Figure 1).

The TCT levels were not affected by the intensity of the conflict ($TCT_{low\ intensity} \sim TCT_{high\ intensity}$; two-pair sample randomization test t = 0.703, N =31, P =0.502). In this analysis, we included only those aggressors that were involved in both high and low intensity conflicts.

The presence of reconciliation affected the occurrence of unsolicited third-party affiliation towards the aggressor (two-pair sample randomization test t = 2.988, N =47, P =0.003).

Then we moved our attention to the frequency of the post-conflict triadic contacts towards the aggressor measured by Triadic Contact Tendency (TCT) at a dyadic level. In the model, we included TCT as dependent variable and evaluated which fixed factors (Table 1) influenced its distribution. The selection of the fixed factors was made on the basis of previous findings. Previous studies indicated that sex, rank, and bonding can affect the distribution of triadic contacts (measured through TCT) between the bystander and the aggressor not only in primates but also in non-primate species (Cordoni & Palagi, 2015; Palagi & Norscia, 2013; Romero et al., 2010; Schino & Marini, 2012). We found two competing models as best models (Table 2). The first one included the variables $NDS_{aggressor}$ and $SEX_{aggressor}$ (AICc=112.368) and explained about 57.01% of the distribution. The second model included the variables $NDS_{aggressor}$, $SEX_{aggressor}$ and BONDING (AICc=113.10) and explained about 39.59% of the distribution. The ΔAICc between the first and the second model was 0.729. The AICc of intercept only was 140.72.

We investigated the function of the triadic post-conflict affiliative contacts on the affective state of the aggressor. Three different conditions were considered: absence of spontaneous post-conflict third-party affiliation (PC-no contact), presence of spontaneous post-conflict third-party affiliation (PC-contact) and matched-control (MC). We found that yawning and object shaking were more frequently performed by the aggressor in the first three minutes in PCs-no contact than in the MCs ($t_{PC1-MC1}$ =

358 7.766, $N = 44$, P = 0.0001; $t_{PC2-MC2}$ = 4.157, $N = 34$, P = 0.0001; $t_{PC3-MC3}$ = 2.535, $N = 31$, P = 0.0001;

359 $t_{PC4-MC4}$ = 0.393, $N = 27$, P = 0.719; $t_{PC5-MC5}$ = 0.351, $N = 27$, P = 0.730; Figure 2a). No difference in

360 the rate of aggressors' arousal was found between PCs-contact and MC ($t_{PC1-MC1}$ = 1.00, $N = 15$, P =

361 0.999; $t_{PC2-MC2}$ = 1.00, $N = 15$, P = 1.000; $t_{PC3-MC3}$ = 1.193, $N = 15$, P = 0.503; $t_{PC4-MC4}$ = 0.716, $N =$

362 15, P = 0.249; $t_{PC5-MC5}$ = 0.619, $N = 15$, P = 1.00; Figure 2b).

363 Scratching and self-grooming (self-directed behaviors) were significantly higher in the first three

364 minutes of the PCs-no contact than in the MCs conditions (t $t_{PC1-MC1}$ = 8.321, $N = 44$, P = 0.0001;

365 $t_{PC2-MC2}$ = 4.601, $N = 34$, P = 0.0001; $t_{PC3-MC3}$ = 3.72, $N = 31$, P = 0.0001; $t_{PC4-MC4}$ = 1.876, $N = 27$, P

366 = 0.073; $t_{PC5-MC5}$ = 1.648, $N = 27$, P = 0.110; Figure 3a). No difference in the aggressors' scratching

367 and self-grooming rates was found between the PCs-contact and MC conditions (Prediction 3

368 supported, $t_{PC1-MC1}$ = 1.417, $N = 15$, P = 0.212; $t_{PC2-MC2}$ = 0.807, $N = 15$, P = 0.376; $t_{PC3-MC3}$ = 0.323,

369 $N = 15$, P = 1.00; $t_{PC4-MC4}$ = 1.036, $N = 15$, P = 0.283; $t_{PC5-MC5}$ = 0.401, $N = 15$, P = 0.641; Figure 3b).

370 We tested the rate of renewed aggression performed by the aggressor towards the previous victim and

371 the other subjects of the group. The analysis was carried out considering three conditions (PC-contact,

372 PC-no contact, MC). We did not find any difference in the renewed aggression towards the victim

373 between PC-no contact and MC (PCs-no contact *vs* MCs; two-pair sample randomization test t_{PC1-}

374 $_{MC1}$ = 0.571, $N = 45$, P = 0.628; $t_{PC2-MC2}$ = 1.383, $N = 34$, P = 0.189; $t_{PC3 -MC3}$ = 1.00, $N = 32$, P =

375 0.998; $t_{PC4-MC4}$ = 1.00, $N = 27$, P = 1.00; $t_{PC5-MC5}$ = 1.005, $N = 27$, P = 0.989) (Prediction 4a not

376 supported).

377 In absence of any affiliative contact by a third-party, the aggressor significantly renewed aggression

378 towards other subjects (excluding the victim) in the first two minutes after the previous conflict (PCs-

379 no contact *vs* MCs; two-pair sample randomization test $t_{PC1-MC1}$ = 2.014, $N = 45$, P = 0.042; $t_{PC2-MC2}$

380 = 2.338, $N = 34$, P = 0.007; $t_{PC3-MC3}$ = 1.612, $N = 32$, P = 0.258; $t_{PC4-MC4}$ = 1.981, $N = 27$, P = 0.089;

381 $t_{PC5-MC5}$ = 1.439, $N = 27$, P = 0.298). In the presence of the affiliative contact by a third-party towards

382 the aggressor we never recorded any renewed attack in the five-minute time window after the previous

383 conflict (Prediction 4b supported).

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Discussion

Our results show that in Tonkean macaques post-conflict affiliation towards the aggressor plays a role in conflict management. Post-conflict affiliation towards the aggressor reduced both self-directed behaviors in the aggressor and the rate of renewed aggression of the aggressor towards other group members.

The occurrence of post-conflict affiliation towards the aggressor was limited to the first minute of the PC period. The phenomenon was independent from the intensity of the conflict and negatively affected by the presence of reconciliation. When we focused our attention on the rates of third-party affiliation (measured via Triadic Contact Tendency, TCT) we found that contact was affected by rank and sex of the aggressor and the bonding shared between aggressors and bystanders. Specifically, triadic post-conflict affiliation seems to be mainly provided to low ranking aggressors (Figure S1) and preferentially to females (Figure S2). Bystanders also seem to provide spontaneous affiliation to those aggressors that share a weak bond with bystanders (Figure S3). Aggression implied an increase of aggressors' arousal, which was restored to its baseline levels after the aggressor was spontaneously contacted by a third-party. While aggressors did not show any escalation in their conflicts towards the previous victim, they tended to reiterate their aggression towards other subjects not involved in the previous conflict. This tendency disappeared when the aggressor received a third-party post-conflict affiliation.

The intensity of the conflict can make post-conflict affiliation more or less risky for bystanders. When the intensity is particularly high, the risk for the third-party to affiliate with the aggressor can be even higher. In gorillas, a strongly despotic species, post-conflict third-party affiliation towards the aggressor was less likely as the intensity of the conflict increased, thus suggesting that apes are able to adjust their behavior according to circumstances (Palagi et al., 2008). In this low tolerant species, redirection (males) and retaliation (females) are two common phenomena (Watts, 1995). In gorillas, triadic post-conflict affiliation can be considered as a service, which is particularly important when

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dominance relationships between females are often undecided and retaliation between opponents is common. For this reason, third parties are particularly attentive to the social conditions in which the conflict occurs (mountain gorillas: Watts, 1995; lowland gorillas: Palagi et al., 2008). In chimpanzees, high intensity conflicts predict the occurrence of triadic affiliation (Palagi et al., 2006) and prevent the occurrence of other post-conflict strategies such as reconciliation, which, conversely to triadic affiliation, takes place less frequently after high intensity aggression (Wittig & Boesch, 2003). Tonkean macaques are one of the most tolerant macaque species. In our study group, the intensity of aggression did not affect the outcome of triadic post-conflict affiliation towards the aggressor. This result probably indicates that the immediate potential danger was not sufficient to inhibit the behavior. This hypothesis finds support in the fact that post-conflict third-party affiliation in *M. tonkeana* occurred more frequently in absence of reconciliation. Hence, the two post-conflict strategies are functionally distinct and post-conflict third-party affiliation can be considered as a substitute for reconciliation.

We found the relationship quality shared by bystanders and previous aggressors had an effect on the distribution of third-party affiliation (measured via TCT values). This finding suggests that the post-conflict affiliation towards the aggressor is predominantly driven by a strategic rather than an emotional motivation of the bystander. This conclusion is supported by the fact that such affiliation appears more frequent between weakly bonded subjects. The empathic basis of triadic post-conflict affiliation towards the aggressor was also excluded by Puga-Gonzalez et al. (2014), who found that social facilitation rather than empathic motivation drove the phenomenon. This interpretation is also supported by the fact that the amount of third-party affiliation in our colony was higher when the aggressor was a low ranking subject. This result could be interpreted as a long-term strategy. In tolerant species both high and low ranking bystanders are interested in maintaining control over the arousal of the aggressor. In despotic species, the levels of post-conflict affiliation are low (Thierry, 1985) and contacting a high ranking aggressor, even though much riskier, may provide benefits to the bystander in terms of resource access, tolerance, and possible future alliances (Das, 2000; Romero

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et al., 2011). In tolerant species, where reversal of dominant positions is not so rare, affiliation directed to low ranking aggressors can limit the possibility that they can improve their dominance status and, consequently, to destabilize social relationships. This hypothesis finds support in the results of the analysis of renewed aggression directed from the previous aggressor towards other group members, who received fewer attacks only when the previous aggressor was the target of an affiliative contact from a bystander. Affiliating with the aggressor may thus be interpreted as strategic behavior that benefits at first the bystander and then, as a by-product, promotes the stability of the group. The finding that bystanders evaluate the ranking position of the aggressor supports the interpretation that the aggressor post-conflict affiliation is a self-serving behavior aimed at reducing the probability that the by-stander will be attacked. The decrease in the escalation of aggressive behaviors may depend on the affective state that individuals experience immediately after the conflict (Norscia & Palagi, 2013; Palagi et al., 2014). In Tonkean macaques, arousal was significantly reduced in the aggressor by the presence of the third-party affiliation, which had a calming effect. Hence, the unsolicited third-party affiliation played a role in the arousal relief. Consequently, the term "appeasement" seems appropriate for Tonkean macaques. This is a novel result, which should induce researchers to use the term "appeasement" when two conditions are met: the aggressors significantly reduce their self-directed behaviors and their tendency to engage in renewed aggression.

The level of tolerance of a given species may affect the outcome of the study of triadic post-conflict affiliation, especially when an affective variation in the subjects (here, the aggressor) is implied. It seems reasonable to suppose that in tolerant societies subjects are less inhibited about intervening after a conflict. Therefore, triadic interventions may be fairly frequent and successful (Palagi et al., 2014). Studies on tolerant species and comparisons with more rigid hierarchical species provide an opportunity to better understand the complex behavioral roles of the third subjects.

Acknowledgments

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Figure legends

Figure 1 - Temporal distribution of the attracted (A) and dispersed (D) pairs (mean ±SE) of spontaneous triadic contacts across five minutes of observation via two-pair sample randomization test.

Figure 2 - Temporal distribution (mean ±SE) of yawning and object shaking in PC and MC context. (a) PCs no-contact are compared with MCs via two-pair sample randomization test; (b) PCs contact are compared with MCs via two-pair sample randomization test.

Figure 3 - Temporal distribution (mean ±SE) of self-directed behaviors (scratching and self-grooming) in PC and MC context. (a) PCs no-contact are compared with MCs via two-pair sample randomization test; (b) PCs contact are compared with MCs via two-pair sample randomization test

Figure S1 - Scatterplot showing the frequency of triadic contact towards the aggressor as a function of the rank of the aggressor (measured via Normalized David's Scores, NDS).

Figure S2 - Frequency of triadic contact towards the aggressor (mean ±SE) as a function of the sex of the aggressor.

Figure S3 - Scatterplot showing the frequency of triadic contact towards the aggressor as a function of the bonding shared between the aggressor and the bystander.
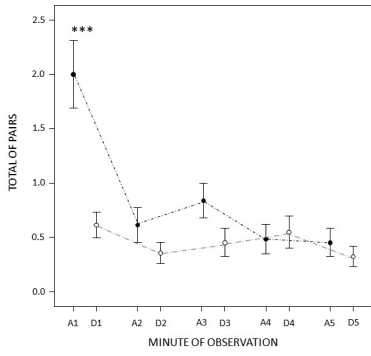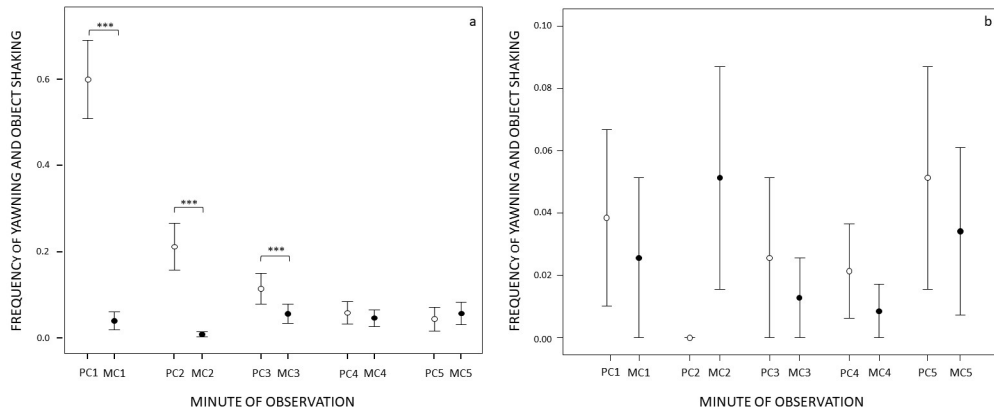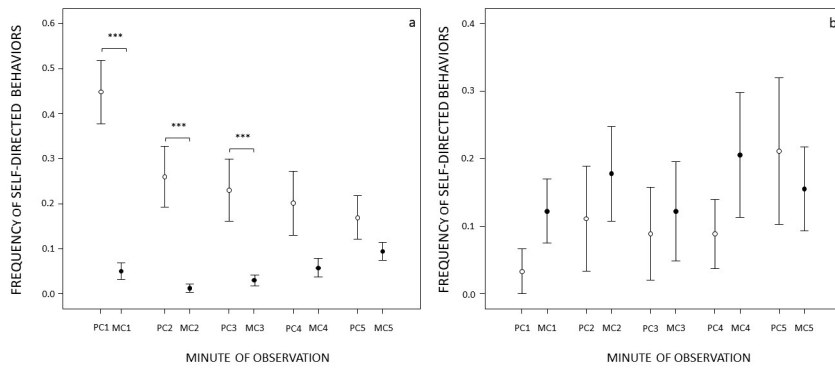
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Figure 1

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Figure 2

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