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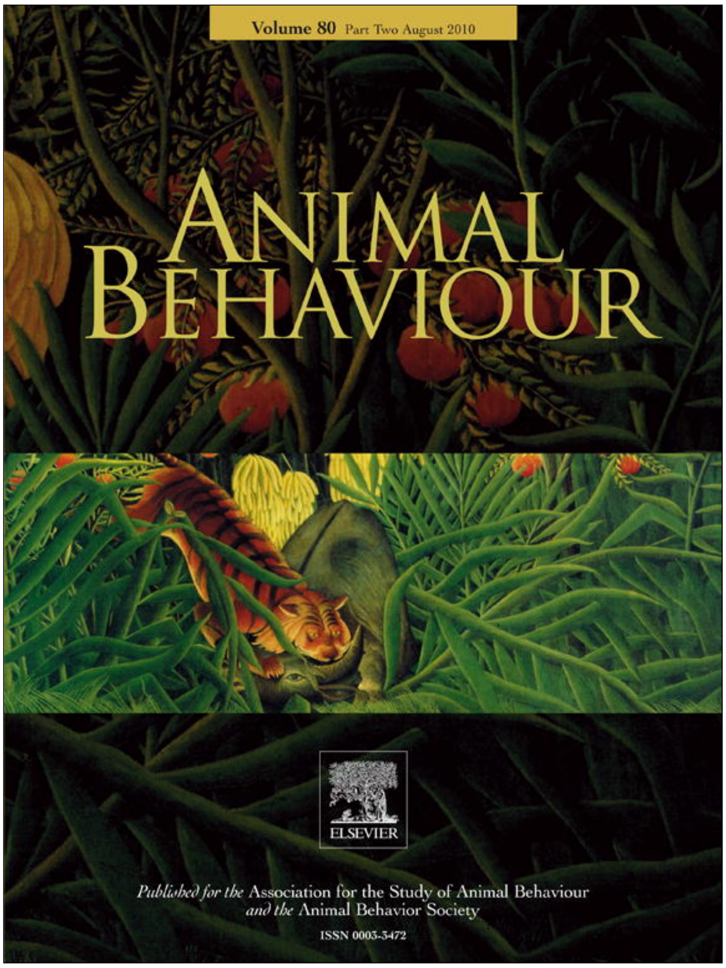
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Conflicts induce affiliative interactions among bystanders in a tolerant species of macaque (*Macaca tonkeana*)

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Aggression is potentially disruptive for social groups. Although individuals witnessing a conflict are not directly threatened by aggressive interactions, the aftermath of aggression appears to be a period of social instability. We expected bystanders to respond to conflicts by affiliating with other group members and so reducing social tension. To test this hypothesis we collected data on two captive groups of Tonkean macaques, *Macaca tonkeana*. After an agonistic interaction, the behaviours of focal individuals uninvolved in the conflict were recorded over 5 min postconflict periods, for comparison with baseline periods. The results showed that bystanders were more likely to show affiliation during postconflict periods than in baselines. We found that affiliation occurred more frequently between individuals linked by friendship, whereas no significant effect of kinship appeared, which may be related to the open social relationships reported in Tonkean macaques. Females initiated affiliation sooner than males and conflicts involving physical contact were more quickly followed by affiliation between bystanders. Rates of scratching tended to decrease after the first affiliative interaction. None the less, few signs of anxiety were observed in bystanders. Our results reflect the high propensity of Tonkean macaques to appease others and stop aggression. This study demonstrates that postconflict affiliation occurs between bystanders in a species characterized by tolerant social relationships. It could be a pervasive means of social cohesion among primates.

Conflicts are potentially disruptive for the cohesion of social groups. They can escalate and propagate among group members. They can also damage social relationships and generate social tension. In many species it is common to see third parties intervene to support one of the opponents aggressively in agonistic interactions (nonhuman primates: Chapais 1995; dolphins, *Tursiops* sp.: Connor et al. 1992; spotted hyaenas, *Crocuta crocuta*: Engh et al. 2005; corvids: Emery et al. 2007). In baboons and macaques, opponents enlist partners, redirect aggression or take revenge (Aureli et al. 1992; Ehardt & Bernstein 1992; Noë 1992; Silk 1992; Watts et al. 2000). In chimpanzees, *Pan troglodytes*, adversaries display side-directed behaviours towards bystanders to seek reassurance and take refuge (de Waal & van Hooff 1981; Fraser et al. 2008). On the other hand, several mechanisms may reduce the spread of aggression (Aureli & de Waal 2000). Greeting contacts between individuals help reduce social tension outside the agonistic context (Smuts & Watanabe 1990; Kutsukake et al. 2006), and some interventions are specifically designed to control outbursts of aggression. In policing interactions, for instance, dominant males stop fights by acting against aggressors, while in peaceful interventions third parties appease opponents (Petit & Thierry 2000; Watts et al. 2000).

Another way to reduce social disruption is to repair the damage induced by aggression. Reconciliation is a major tool in postconflict management. It is defined as the affiliative contact occurring after conflict between former opponents (de Waal & van Roosmalen 1979). Several studies have shown that reconciliation reduces tension in both opponents and decreases the probability of renewed aggression; it also has the potential to restore disrupted social relations between individuals (Aureli et al. 2002). Although third parties can spread conflicts by joining the fight to support allies, they can also buffer the consequences of aggression by addressing appeasing behaviours to the adversaries of their allies

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(Judge 1991). In several primate species, triadic affiliative interactions occur between opponents and other group members initially uninvolved in the conflict (Das 2000; Watts et al. 2000; Koski & Sterck 2007; Fraser et al. 2008). Opponents can interact with their own kin, the opponent's kin and nonkin members of the group. Postconflict contacts involving opponents' kin have been called substitute reconciliation because they could indirectly restore relationships between former opponents, thus producing similar effects to reconciliation (Aureli & van Schaik 1991a, b). Third-party affiliation with nonkin has been alternatively interpreted as a means to recruit support, to alleviate distress and appease, or to strengthen alliances and reinforce the dominance hierarchy (Das 2000).

Most studies to date have focused on interactions involving opponents. Given the potentially negative consequences of aggression on any group members, however, we may expect bystanders also to react to disturbances and interact with each other. Although relationships between bystanders are not damaged by conflicts, the aftermath of aggression appears to be a period of increased risk for every group member. Judge & Mullen (2005) argued that observing fights may produce a state of anxiety, and that even individuals uninvolved in conflicts may alleviate emotional arousal and uncertainty by affiliating with each other following a conflict. These authors termed such affiliation 'quadratic interaction' because it involves four individuals: two opponents plus two individuals not involved in the conflict. It is commonly assumed that individual recognition and good memory are sufficient to reconcile (Kappeler & van Schaik 1992; Castles 2000), but engaging in postconflict interactions involving several individuals no doubt requires more elaborate cognitive skills. There is substantial evidence that not only do primates know their own affiliative bonds and dominance relationships with others, but they are also aware of relationships among other group members (Cheney & Seyfarth 1980; Dasser 1988; Tomasello & Call 1997; Silk 1999). This makes quadratic interactions very possible given the cognitive abilities of monkeys.

The study of behaviour in bystanders can help complete our knowledge about the range of possible postconflict resolution strategies. To date, only one study has investigated quadratic affiliative interactions. Judge & Mullen (2005) studied a group of hamadryas baboons, *Papio h. hamadryas*, and found that rates of affiliative contacts increased between bystanders after aggression, and that levels of displacement activities associated with stress decreased following such contacts. Whereas quadratic interactions occurred both between kin and between nonkin partners, they were more frequent when bystanders were relatives of opponents. Social relations in hamadryas baboons are characterized by rather fierce aggression and a steep dominance hierarchy (Kummer 1968; Abegglen 1984). A main question is whether quadratic affiliation is an outcome of the stress experienced by individuals in the system of relationships peculiar to hamadryas baboons, or whether this is a commonly occurring phenomenon in monkeys. In Tonkean macaques, *Macaca tonkeana*, patterns of triadic interactions are influenced by the intensity of conflicts (Petit & Thierry 1994). It may be asked whether quadratic interactions would be affected in a similar way by the characteristics of conflicts. Moreover, since patterns of interactions are related to the system of relationships peculiar to each species, the influence of friendship and kinship could differ according to the specific social organization.

Our aim in the present study was to document the occurrence of quadratic interactions among Tonkean macaques, and to investigate their determinants. This species displays relaxed dominance and a weaker influence of kin networks on the behaviours of individuals compared to other macaque species (Thierry 2000, 2007). Aggression is usually low intensity; correspondingly, a majority of conflicts involve protests or counterattacks by the victim, and most are followed by reconciliations showing rates significantly higher than in most other macaque species (Thierry 1985; Demaria & Thierry 2001). Tonkean macaques show a high propensity to prevent the escalation of conflicts: appeasement is frequent at the dyadic level (Thierry 1985), and third parties can successfully stop aggression by addressing appeasement signals to adversaries (Petit & Thierry 1994). Since tolerant social relationships create room for negotiation and reduce fear in tense situations, we wanted to establish whether Tonkean macaque bystanders would need affiliation following a conflict, and whether these quadratic interactions would alleviate signs of tension in bystanders. Given that Tonkean macaques exhibit low kin bias, we predicted that quadratic interactions would occur regardless of kinship among group members.

METHODS

Subjects

The study was carried out on two captive groups of Tonkean macaques. The first group was housed in an enclosure approximately 120 m^2 and 4 m high at the Orangerie Zoo of Strasbourg, France. It was founded 20 years before our observations and consisted of 20 individuals, including four adult males, four adult females, three subadult males, two subadult females, two juvenile males, three juvenile females and two infants. The second group was maintained in an enclosure about 1000 m^2 and 5 m high at the Giardino faunistico di Piano dell'Abatino Rescue Centre in Rieti, Italy. It was founded 4 years before our study and consisted of 10 individuals, including three adult males, two adult females, one subadult male, one subadult female, one juvenile male, one juvenile female and one infant. Two and one infants were born during the study in the Strasbourg and Rieti groups, respectively. Subadults were defined as those individuals 4 and 5 years of age, and juveniles as those individuals 1–3 years old. Enclosures were furnished with perches, slides, wooden structures, ropes and platforms. Monkeys were fed every day with commercial monkey diet pellets. They received fresh fruit and vegetables, but not during observations. Water was available ad libitum.

Observational Methods

Data were collected by A.D.M. every day between 0900 and 1400 hours from May to November 2006 in the Strasbourg group, and from January to July 2007 in the Rieti group. An agonistic interaction was defined as the display of an aggressive behaviour by one individual (in increasing order of intensity: vocal or facial threat, chasing/lunging, slapping/grabbing, biting) and an aggressive or nonaggressive response by the receiver of the aggression (avoidance, lipsmack, screaming vocalization, fleeing, counteraggression). The observer collected details of conflicts between adults, subadults and juveniles using all-occurrence sampling (Altmann 1974). She recorded the identity of adversaries and their behaviours. She also recorded the duration of the conflict and the occurrence of interventions.

Immediately after an agonistic interaction, the observer followed one of the animals uninvolved in the conflict over a 5 min postconflict (PC) observation. The 13 adults and subadults present in the Strasbourg group and the seven adults and subadults present in the Rieti group served as focal subjects. The observer selected the focal animal from a randomized list of potential bystanders, depending on whether it was awake and if it witnessed the conflict. If the bystander was involved in an agonistic interaction during the 5 min focal period, that focal sample was discarded. For each PC focal observation, a 5 min matched-control (MC) observation was conducted on the next possible day at approximately the same time. During PC and MC periods, behaviours and interactions involving the focal animal were recorded. Affiliative behaviours included sitting in contact, social grooming, social play, mount, embrace and facial displays (lipsmack and bared-teeth; in Tonkean macaques the latter facial expression signals the animal's peaceful intentions, see Thierry et al. 1989; Preuschoft 1995). Scored displacement behaviours consisted of scratching and yawning. Ten agonistic interactions and PC/MC periods were collected for each bystander.

Two additional types of data were collected to assess social relationships between individuals. To quantify affiliation between group members, the observer recorded sitting in contact every 30 min (except during ongoing focal samples) using instantaneous scan sampling (Altmann 1974). To assess dominance relationships, she also collected the supplantations spontaneously occurring during observations (excluding PC periods), and those performed during drinking competition tests (see Thierry et al. 1994 for further information).

Data Analysis

To investigate whether bystanders tended to perform affiliative interactions sooner in PC than in MC periods, we compared PC and MC observations using the method described by de Waal & Yoshihara (1983). A PC/MC pair was considered 'attracted' when the first affiliative interaction occurred during the PC periods but not during the MC ones, or earlier in the PC than in the MC periods. PC/MC pairs were defined as 'dispersed' if the first affiliative interaction occurred during the MC periods but not during the PC ones, or earlier in the MC than in the PC periods. 'Neutral' pairs were those in which no affiliative interaction occurred in either the PC or MC periods, or when the first affiliation occurred at the same time during both PC and MC periods. Numbers of attracted and dispersed pairs were calculated for each bystander, and the number of attracted pairs was compared to the number of dispersed pairs. We carried out separate analyses for (1) interactions between a bystander and one of the opponents or interveners (triadic interactions), and (2) interactions between a bystander and another bystander (quadratic interactions; Fig. 1). For triadic interactions, we compared the first affiliative interaction of the focal bystander with one of the opponents or interveners within a PC period to the first affiliative interaction of the same individual with either of those triadic partners within the paired MC. For quadratic interactions, we compared the first affiliative interaction of the focal bystander with another bystander in a PC period to the first affiliative interaction of the focal bystander with any group member other than opponents and interveners in the paired MC.

To measure whether quadratic interactions occurred more frequently than triadic ones, we calculated the 'affiliation tendency' of each bystander using the index defined by Veenema et al. (1994) for reconciliations: number of attracted pairs minus number of dispersed pairs divided by the total number of pairs (see Judge & Mullen 2005). We also calculated the duration of bystanders' affiliative interactions across all partners by measuring this duration within each minute. We then compared durations in PC periods to those in MC periods. Since the same number of PC and MC periods was collected on each subject ($N = 10$), we report attracted and dispersed pairs as mean frequencies rather than percentages.

We investigated whether a bystander affiliated with a preferred social bystander (i.e. a 'friend') after a conflict. Using data from instantaneous sampling, we calculated the number of times per hour each bystander was observed sitting in contact with each group

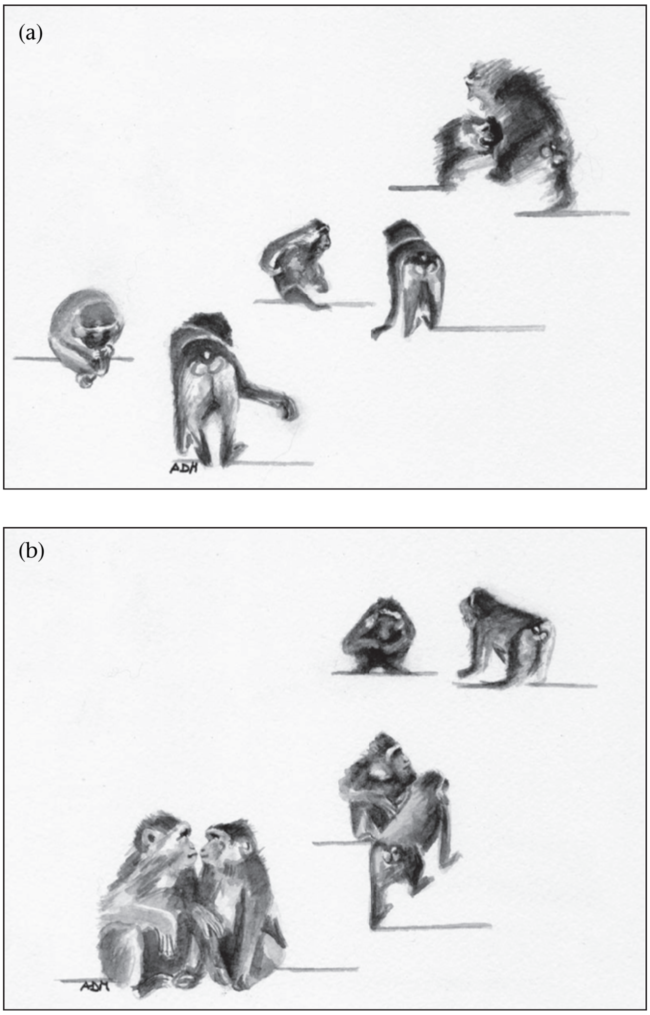

Figure 1. Conflict and postconflict interactions: (a) bystanders witness a conflict; (b) quadratic affiliative interaction between bystanders. Drawings: A. De Marco.

member (hereafter referred to as 'contact frequency'). Bystanders' preferred partners were defined as those whose contact frequency scored above the mean contact frequency of all group members with this bystander. For each bystander, we compared the percentages of quadratic interactions involving a preferred partner after conflict to those occurring in control periods.

To test whether bystanders affiliated more with kin bystanders after conflict, we calculated for each bystander the percentages of quadratic interactions with a kin bystander (defined from a maternal relatedness coefficient of 0.50). We compared these percentages across PC and MC periods. Given the small number of subjects in the Rieti group, the effect of friendship and kinship was only tested in the Strasbourg group.

To compare the frequencies of displacement behaviours in PC and MC periods, we split each PC or MC period into two intervals, namely those before and those after a quadratic interaction. For each focal individual, we calculated in each interval the frequency per minute at which it performed scratching and yawning. We discarded periods in which there was no affiliative contact during the 5 min of observation because there were too few (see Table 1) for statistical analyses. To avoid any influence upon bystanders' interactions by opponents' and interveners' behaviours, we did not use PC intervals before affiliation in which triadic interactions preceded quadratic ones. Similarly, we discarded PC intervals after affiliation in which any triadic interactions occurred.

Table 1
Occurrence percentages of the different types of postconflict affiliative interactions between a bystander and other partners in the Strasbourg and Rieti groups

Types of partner	Strasbourg group	Rieti group
Bystander	52.3	44.3
Opponent	2.3	4.3
Intervener	0	0
Both bystander and opponent	17.7	21.4
Both bystander and intervener	10.0	7.1
Both opponent and intervener	0.8	1.4
Opponent, bystander and intervener	2.3	7.1
No affiliation	14.6	14.3

Statistical comparisons between PC and MC periods were based on the exact Wilcoxon signed-ranks test. We used SPSS software version 16 (SPSS Inc., Chicago, IL, U.S.A.) to run statistical tests.

The effect of independent variables on the timing of the first quadratic affiliation during postconflict was assessed with a generalized linear mixed model (GLMM) with Gaussian distribution using the SAS software version 9.1 (SAS Institute Inc., Cary, NC, U.S.A.). We tested a model made of variables related to the characteristics of conflicts and bystanders (see Table 2). We applied it to the interactions where focal subjects initiated an affiliative contact with another bystander. We discarded the interactions in which no contact occurred during the 5 min of observation since we could not tell whether focal subjects were active or passive performers. Subject identity and groups were introduced as random factors in the model to control for the nonindependence of the samples.

To assess dominance relationships, we built a matrix of interactions from supplantation records and used MatMan software version 1.0 (Noldus Information Technology, Wageningen, The Netherlands) to rank individuals in a dominance hierarchy.

All probabilities were two tailed. The significance level was set at 0.05.

RESULTS

We collected data for 130 conflicts in the Strasbourg group and 70 in the Rieti group, of which 72.3% and 65.7%, respectively, involved more than two individuals. Table 1 provides the occurrence percentages of the different types of postconflict affiliative interactions by bystanders.

Postconflict Affiliative Interactions

For each bystander, we calculated frequencies from the number of quadratic interactions within each minute of PC and MC periods. In both groups, frequencies of the first affiliative interaction between bystanders were higher during the first minute of PC periods compared to MC periods (Fig. 2). The first affiliative interaction of a bystander with another bystander occurred sooner after conflict than in the control period; the number of attracted pairs was significantly higher than the number of dispersed pairs in the PC period both in the Strasbourg group (attracted pairs: mean ± SD = 6.5 ± 1.4 per subject; dispersed pairs: 2.6 ± 1.5; Wilcoxon test: $T = 1$, $N = 13$, $P < 0.001$) and the Rieti group (attracted: 7.0 ± 1.6; dispersed: 1.1 ± 0.7; $T = 0$, $N = 7$, $P = 0.016$). For triadic interactions, we found more attracted pairs (3.3 ± 1.5) than dispersed pairs (1.00 ± 0.8) between a bystander and an opponent in Rieti ($T = 0$, $N = 7$, $P = 0.031$), whereas no significant difference was observed in Strasbourg (attracted pairs: 1.9 ± 1.6; dispersed pairs: 1.7 ± 1.3; $T = 33$, $N = 13$, $P = 1$). The first affiliative interaction of a bystander with an intervener did not differ between PC and MC periods in either group (Strasbourg: attracted pairs: 0.2 ± 0.2; dispersed pairs: 0.1 ± 0.1; $T = 13.5$, $N = 13$, $P = 0.166$; Rieti: attracted pairs: 0.2 ± 0.2; dispersed pairs: 0.1 ± 0.1; $T = 2$, $N = 7$, $P = 0.188$).

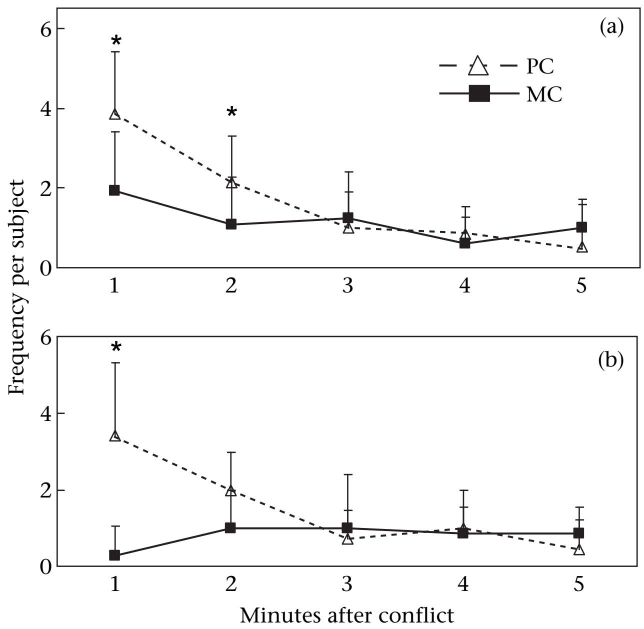

Figure 2. Mean + SD frequency of occurrence of the first affiliative interaction between bystanders during postconflict (PC) and matched-control (MC) observations in the (a) Strasbourg ($N = 13$) and (b) Rieti ($N = 7$) groups. *$P < 0.05$; Wilcoxon test.

The affiliation tendency between bystanders (Strasbourg: 0.4 ± 0.3; Rieti: 0.6 ± 0.2) was significantly higher than that observed between bystanders and opponents (Strasbourg: 0.02 ± 0.2; $T = 1.5$, $N = 13$, $P = 0.003$; Rieti: 0.2 ± 0.2; $T = 1$, $N = 7$, $P = 0.031$), or between bystanders and interveners (Strasbourg: 0.01 ± 0.03; $T = 1$, $N = 13$, $P < 0.001$; Rieti: 0.02 ± 0.03, $T = 0$, $N = 7$, $P = 0.016$), which indicates that bystanders engaged in contact more frequently with each other than with participants of conflicts.

We calculated the duration of affiliative behaviours between bystanders within each minute of PC and MC periods. Durations per individual were significantly higher in PC than in MC periods for the majority of minute intervals in both groups (Fig. 3).

After conflict, bystanders could use various behaviours to initiate an affiliative interaction with another bystander (Fig. 4). In the Strasbourg group, the comparison of PC and MC periods showed higher percentages of sitting in contact following conflict ($T = 0$, $N = 13$, $P < 0.001$), and lower percentages of social play ($T = 0$, $N = 13$, $P = 0.004$) and facial displays ($T = 10$, $N = 13$,

Table 2
Independent variables entered into the GLMM

Variable name	Variable definition	Type
Duration	Conflict duration (s)	Continuous
Intensity	Contact or noncontact aggression between opponents	Categorical
Extension	Dyadic or polyadic conflict	Categorical
Adulthood	Conflict involving only adults or both adult and immature (i.e. juvenile or subadult) individuals	Categorical
Sex	Male or female	Categorical
Age	Age in years	Ordinal
Dominance	Three-tier dominance status (higher rank, intermediate rank, lower rank)	Categorical

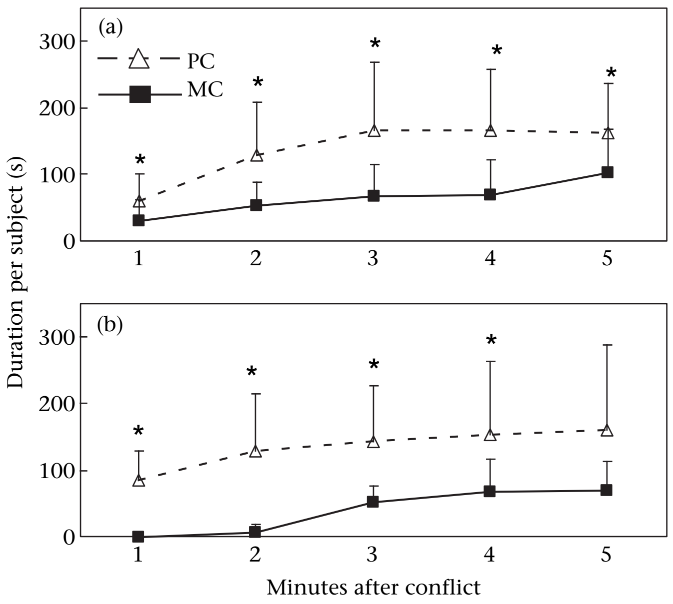

Figure 3. Mean + SD duration of affiliative interactions between focal subject and bystander within each minute of postconflict (PC) and matched-control (MC) observations in the (a) Strasbourg ($N = 13$) and (b) Rieti ($N = 7$) groups. *$P < 0.05$; Wilcoxon test.

$P = 0.040$). Other comparisons did not yield statistically significant differences (Fig. 4).

We compared the mean percentages in the Strasbourg group of PC and MC periods in which a bystander affiliated with a preferred partner in a quadratic interaction. Bystanders increased affiliation with friends after conflict (0.68 ± 0.11) relative to control periods (0.52 ± 0.19; $T = 2.5$, $N = 13$, $P = 0.001$). Similar comparisons based on kinship revealed that bystanders' rates of quadratic affiliation with maternal kin did not change following conflict (0.23 ± 0.22) compared to control periods (0.29 ± 0.32; $T = 29$, $N = 13$, $P = 0.748$).

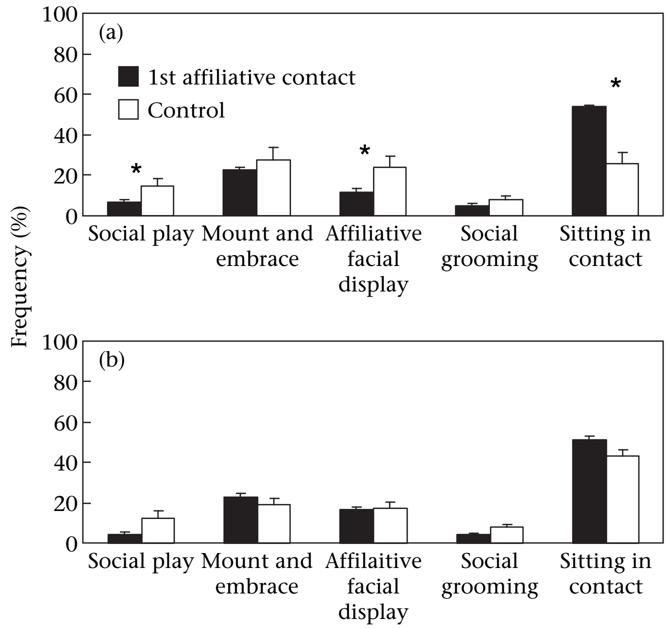

Figure 4. Mean + SD frequency of behaviour patterns of the first affiliative interaction in postconflict (PC) and matched-control (MC) observations in the (a) Strasbourg ($N = 13$) and (b) Rieti ($N = 7$) groups. *$P < 0.05$; Wilcoxon test.

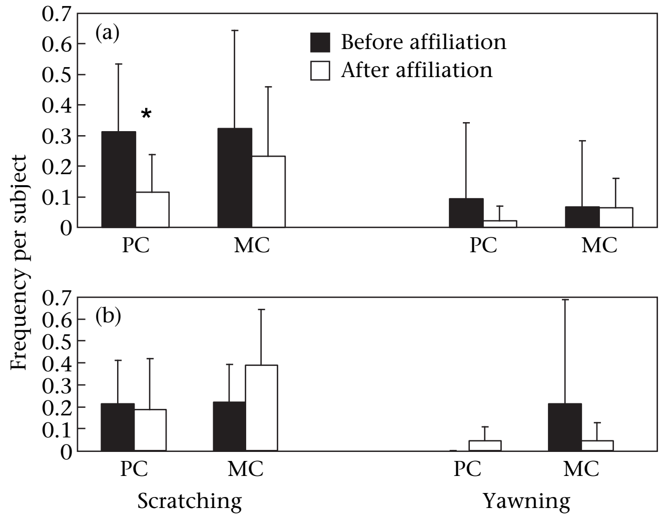

Figure 5. Mean + SD frequency per minute of scratching and yawning performed by bystanders before and after an affiliative interaction in postconflict (PC) and matched-control (MC) periods in the (a) Strasbourg and (b) Rieti groups.

Displacement Behaviours

We compared the displacement behaviour frequencies per minute in PC and MC periods before and after the first occurrence of an affiliative quadratic interaction. Bystanders showed significantly lower frequencies per minute of scratching after the first occurrence of a postconflict quadratic affiliation in the Strasbourg group (before affiliation: 0.31 ± 0.22; after affiliation: 0.11 ± 0.12; $T = 9$, $N = 13$, $P = 0.008$). Other comparisons did not produce significant differences (Fig. 5).

Determinants of Quadratic Interactions

The results of the GLMM analysis are provided in Table 3. The timing of the first quadratic affiliation initiated by focal subjects was related to the intensity of aggression; conflicts involving physical contact were more quickly followed by affiliation between bystanders. Sex emerged as a significant factor in the model, indicating that females affiliated sooner than males after aggression. The analysis also indicated that the higher the rank of the individuals, the sooner they affiliated with others, but this trend did not reach significance (Table 3).

DISCUSSION

We found evidence in Tonkean macaques that aggression influenced behaviours of those individuals uninvolved in agonistic interactions. Bystanders were more likely to take part in affiliative interactions during postconflict periods compared to baselines. It has already been established that some bystanders

Table 3
Effect of variables on the timing of the first quadratic affiliation initiated by focal subjects (GLMM, $N = 86$)

Variable	*df*	*F*	*P*
Duration	1, 63	0.15	0.696
Intensity	1, 63	5.79	0.020
Quality	1, 63	0.45	0.505
Extension	1, 63	1.40	0.241
Sex	1, 63	7.09	0.001
Age	1, 63	1.07	0.305
Dominance	2, 63	2.88	0.063

interact with opponents following conflict to appease them, bring support, or confirm bonds and strengthen alliances (Das 2000; Watts et al. 2000). The present results add that most group members show some response to the conflict, which is consistent with a previous study of hamadryas baboons (Judge & Mullen 2005). Whereas it is known that in Tonkean macaques third individuals commonly display affiliative behaviours towards opponents during conflict to appease them (Petit & Thierry 1994), our results emphasize that, as in hamadryas baboons (Judge & Mullen 2005), Tonkean macaque bystanders were more often involved in quadratic affiliation than in triadic affiliation after conflict.

In group-living animals, individuals manage to prevent conflicts of interest arising, but sometimes escalation leads to overt fights (Aureli & de Waal 2000). Once aggression occurs some costs are unavoidable. Opponents have to assume the cost of negative ecological consequences, for example by spending less time on feeding and monitoring activities (Aureli 1992). The spread of conflicts to other individuals can extend negative effects to the entire group. Processes of conflict resolution are necessary to counteract these effects and preserve the benefits of group living. From an adaptive perspective, the selective attraction that leads to reconciliation stops hostility between former opponents and reduces the probability of further attack (de Waal & van Roosmalen 1979; Aureli et al. 2002). Quadratic affiliation appears to be a response to the periods of social instability induced by aggression. In Tonkean macaques, not only did bystanders affiliate early after conflict, but they continued to affiliate throughout the full 5 min postconflict periods. Long-lasting affiliation between bystanders can reassure individuals, creating a positive milieu throughout the group. By seeking relief, bystanders would indirectly contribute to group cohesion.

In some primates, individuals reconcile through explicit gestures which are not frequently performed in other contexts, whereas in other species common behaviours such as grooming or sitting in contact are used instead (Arnold & Aureli 2007). In Tonkean macaques, former opponents show conspicuous behavioural patterns such as facial displays, mounts and clasps when reconciling (Demaria & Thierry 2001). It is likely that bystanders are less emotionally aroused than those individuals that have just participated in conflicts, leading to relatively less demonstrative quadratic interactions. Bystanders used behaviours that were regularly observed in other contexts; sitting in contact occurred more often in postconflict than in control periods in the Strasbourg group, and to a lesser degree in the Rieti group.

After conflict, bystanders engaged in higher frequencies of affiliation with friend bystanders than with other group members. Quadratic interactions occurred regardless of kinship bonds between bystanders. This result may be related to the open social relationships reported in Tonkean macaques where the degree to which females prefer relatives in affiliative contact, social grooming and support in conflicts is less pronounced than in other macaque species (Thierry 2000, 2007). The study of reconciliation in Tonkean macaques also showed that kinship did not significantly influence the occurrence of reconciliation between previous opponents, in contrast with other macaque species in which the matrilineal structure is more prominent (Thierry et al. 2008). It would be worth investigating whether quadratic interactions are more influenced by kinship than friendship in macaques that have a strong kin bias.

In hamadryas baboon bystanders, the rates of some displacement activities were higher in postconflict periods, then decreased after affiliative contact between bystanders. This led Judge & Mullen (2005) to conclude that observing a conflict induces a state of tension throughout the group. In the Strasbourg group, we also found that rates of scratching decreased after affiliative contact in the postconflict period, while a nonsignificant tendency was observed in the Rieti group. It should be stressed, however, that we did not find clear evidence of stress among bystanders in Tonkean macaques, since rates of scratching and yawning did not differ significantly between postconflict and control periods. Rates of yawning were no more contrasted between periods in hamadryas baboons (Judge & Mullen 2005). The study of reconciliation has shown that opponents display higher rates of scratching following conflict, and that the occurrence of an affiliative contact between them decreases these rates, thus reducing tension levels (Das et al. 1998; Kutsukake & Castles 2001; Cooper et al. 2007; Arnold & Aureli 2007; Romero et al. 2009). As previously noted, bystanders are presumably less aroused than opponents, and signs of tension consequently show limited variation. This may be especially true for Tonkean macaques, which are characterized by relaxed dominance relationships and high levels of social tolerance (Thierry et al. 1994; Thierry 2000). This is consistent with between- and within-species comparisons which indicate that postconflict responses vary according to the emotional profile of individuals (Thierry 2007; Majolo et al. 2009b).

The likelihood and timing of reconciliation are known to be influenced by the characteristics of conflicts, that is, duration, intensity, occurrence of intervention, decidedness of outcome, and those of the opponents, that is, sex, age and dominance rank (Aureli et al. 1989; Call et al. 1999; Arnold & Aureli 2007; Majolo et al. 2009a). A multivariate approach showed that quadratic affiliation in Tonkean macaques occurred earlier after conflicts involving physical contact. It is understandable that serious aggression and possible escalation induced social tension, thus promoting affiliative behaviours in bystanders. The finding that females performed quadratic interactions sooner than males indicates that female Tonkean macaques were more sensitive to social tension.

Our study demonstrated that responses to agonistic events are not limited to individuals involved in conflicts; they extend to most group members. This broadens the conclusions of Judge & Mullen (2005) drawn from the study of a more despotic species, the hamadryas baboon. This also shows that quadratic affiliation can contribute to individual reassurance in primates such as macaques and baboons, regardless of their style of social relationships. Although anxiety levels seem lower in Tonkean macaques than in hamadryas baboons, postconflict affiliation between individuals witnessing a conflict appears to be a powerful mechanism promoting cohesion among group members, even in a species displaying a high propensity to appease others and stop aggression (Petit & Thierry 1994; Demaria & Thierry 2001). The two social groups studied here differed in both the number of individuals and their demographic composition, which could explain some of the differences found in our results. Future research should investigate which factors (e.g. levels of nepotism and social tolerance) are liable to determine the occurrence of quadratic affiliation in a further sample of groups and species.

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