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# Postconflict third-party affiliation in stumptailed macaques

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Stumptailed macaques, *Macaca arctoides*, are characterized by high levels of postconflict affiliative contacts between opponents. We investigated the occurrence of postconflict affiliative contacts between opponents and third parties that were not involved in the original conflict. We collected 10-min focal observations during postconflict and control periods in which we recorded all aggressive and affiliative behaviours between opponents and third parties. We distinguished three types of third parties depending on the relationship with the focal animal: own kin, opponent's kin and individuals unrelated to both opponents. We analysed the interactions with third parties separately, while distinguishing two classes of affiliative behaviours: (1) allogrooming and contact sitting and (2) sociosexual behaviours (e.g. genital inspection). The macaques showed differences between postconflict and control periods in their affiliative contacts with third parties. Aggressors received more postconflict grooming and contact sitting from their opponents' kin, received more sociosexual behaviour from their own kin and unrelated individuals, and directed more sociosexual behaviour to unrelated individuals. Victims received and directed less postconflict grooming from and towards their own kin. They received more postconflict sociosexual behaviour from all partners except their own kin and directed more sociosexual behaviour to all partners except the opponent's kin. This study establishes the occurrence of multiple postconflict triadic affiliation in stumptailed macaques, and is the first to show that victims receive contacts from third parties in a cercopithecine species, a behaviour previously described only in chimpanzees. It also highlights the importance of analysing the different affiliative behaviours separately in postconflict situations. Otherwise, many of the patterns we report, especially those involving victims, would have been missed.

The majority of cercopithecine primates live in socially complex groups within which they form extensive networks of affiliation and competition. One way to investigate these complex networks is to study dyadic interactions between individuals. For instance, dyadic allogrooming has been used to investigate the depth of friendship and extent of networks (Dunbar 1991; Castles et al. 1996; see also Henzi & Barrett 1999). Another complementary way to investigate social networks consists of observing triadic interactions, that is individual A interacts with individual B after an interaction between B and C. For instance, when individuals A and B have a conflict, we can infer who their respective 'friends' and 'enemies' are by observing who receives support and who receives aggression from whom (Aureli et al. 1992; Silk 1992; de Waal & Lutrell 1998).

Postconflict third-party affiliation, defined as postconflict affiliative contacts between opponents and bystanders (Judge 1991), has been described in various species (for reviews see Das 2000; Watts et al. 2000), and can also be used to study social networks. In particular, aggressors of various species of primates increase their contacts with different classes of individuals such as their own kin, the opponent's kin and unrelated individuals (de Waal & Yoshihara 1983; Judge 1991; Das et al. 1997; Arnold & Barton 2001). There is also some evidence that victims of aggression increase their contacts with third parties (de Waal & van Roosmalen 1979; Petit & Thierry 1994a; Watts 1995; Arnold & Barton 2001; also in New World monkeys: Verbeek & de Waal 1997). However, with the exception of chimpanzees, *Pan troglodytes*, it is

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the victim who is responsible for these contacts (de Waal & Aureli 1996; but see Petit & Thierry 1994a). Nevertheless, those studies that have found triadic postconflict affiliation are few compared with those that have found dyadic interactions between former opponents (see Aureli & de Waal 2000). This scant data set may give the impression that triadic postconflict affiliative interactions, especially those in which the victim receives affiliation from third parties (i.e. 'consolation' as defined in de Waal & van Roosmalen 1979), are relatively rare among cercopithecine primates.

One possibility for this lack of evidence is that all studies have treated different types of affiliative contact behaviours as if they were equivalent. Support for this claim comes from the study of dyadic reconciliation, defined as postconflict affiliative contacts between former opponents (de Waal & van Roosmalen 1979). Call et al. (1999) found that pooling various affiliative behaviours may not be the best strategy because different behaviours may be used for different functions. When evaluating the occurrence of dyadic reconciliation in stumptailed macaques, *Macaca arctoides*, for instance, de Waal & Ren (1988) treated allogrooming and hold-bottom as equivalent (de Waal & Ren 1988). However, Call et al. (1999) found that postconflict affiliative behaviours between opponents in this species could be classified into two main clusters. Cluster 1 was formed by allogrooming and contact sitting whereas cluster 2 consisted of sociosexual behaviours such as genital inspect, hold-bottom, mounting, gentle touching and passing contact. These two clusters differed in two main dimensions. First, they differed in the temporal occurrence of the behaviours within each cluster. In particular, a greater proportion of behavioural patterns belonging to cluster 2 occurred earlier than those belonging to cluster 1, a difference that was especially pronounced during the first minute after the conflict. Second, the degree of friendship and kinship between opponents best predicted the use of behaviours belonging to cluster 1 in postconflict reunions, whereas initial interopponent distance in postconflict periods produced the best fit for cluster 2. These results led us to hypothesize that behaviours in cluster 1 and cluster 2 accomplished different functions during postconflict periods. In particular, postconflict allogrooming and contact sitting may be used for the maintenance of valuable relationships, whereas sociosexual behaviours may be used more indiscriminately by any pair of opponents as a buffering mechanism to prevent immediate reoccurrence of aggression.

Since the distinction of different behaviours at the dyadic level appears to have functional implications for reunions between opponents, it is conceivable that distinguishing these patterns can also be important at the triadic level, that is, for contacts between opponents and third parties. In this study we investigated the affiliative contacts between opponents and third parties that were not involved in the original conflict. We analysed the interactions of former aggressors and victims separately with three classes of individuals: own kin, opponent's kin and unrelated individuals. In the analyses, we used the two clusters of behaviours we had found in our previous study (Call et al. 1999) because different affiliative behaviours may be exchanged depending on the type of relationship between opponents and third parties to achieve different functions. In addition, we included new analyses of the behaviour between opponents (i.e. reconciliation) for comparative purposes.

## METHODS

### Subjects and Housing

Our subjects were the same group of stumptailed macaques that were used in Call et al. (1999). There were eight adult males, all of which were born in the group, 17 adult females and 13 juveniles from at least 11 matrilines. For housing and maintenance, see Call et al. (1999).

### Data Collection

J.C. conducted 143 h of behavioural observations from an observation tower from October 1993 to January 1995. The macaques were locked outdoors for the observation sessions, and no observation was made within 90 min of food being provisioned. We collected 10-min focal animal observations during postconflict (PC) and matched-control (MC) periods based on the PC/MC method (de Waal & Yoshihara 1983) in which we recorded all aggressive and affiliative behaviours between the focal animal and other group members (see Call et al. 1999 for additional details on data collection methods). We distinguished three types of third parties depending on the relationship with the focal animal: own kin, opponent's kin and individuals unrelated to both opponents. Two individuals were considered kin if they belonged to the same matriline.

In the postconflict period, either the aggressor or the victim was selected as the focal animal and followed for 10 min. Matched-control observations were carried out the next possible day after the conflict. A PC was started only when an aggressive interaction included one of the following patterns (in increasing order of intensity): chasing, grabbing or slapping, and biting. Affiliative contacts included: allogrooming, contact sitting, genital inspection, gentle touching, smelling (brief mouth to fur touch or muzzle–muzzle contact), mounting, contact passing (walking by and brushing against the opponent) and hold-bottom (clasping at an individual's hip with both hands). Our previous study (Call et al. 1999) had indicated that these behaviours could be classified into two main clusters. Cluster 1 consisted of allogrooming and contact sitting and cluster 2 consisted of genital inspection, gentle touching, mounting, contact passing, and hold-bottom (an additional cluster 3 including 'smelling' was found but its sample size was too small for analyses; see Table 1).

### Data Analysis

We collected data on 215 conflicts. These conflicts produced a total of 251 PC–MC opponent pairs (36 of

**Table 1.** Frequency of the various behaviours shown by aggressors and victims towards each of the classes of partners in postconflict (PC) and matched-control (MC) periods

| | PC | | | | MC | | | |
|---|---|---|---|---|---|---|---|---|
| | Opponent | Own kin | Opponent's kin | Unrelated | Opponent | Own kin | Opponent's kin | Unrelated |
| **Aggressor** | | | | | | | | |
| Cluster 1 | | | | | | | | |
| Allogrooming | 35 | 77 | 45 | 193 | 22 | 74 | 19 | 176 |
| Contact sitting | 20 | 17 | 9 | 61 | 13 | 26 | 4 | 77 |
| Cluster 2 | | | | | | | | |
| Gentle touching | 14 | 8 | 1 | 41 | 8 | 9 | 4 | 27 |
| Genital inspect | 10 | 3 | 12 | 18 | 1 | 1 | 3 | 20 |
| Hold bottom | 14 | 1 | 0 | 4 | 0 | 0 | 0 | 3 |
| Passing contact | 2 | 1 | 0 | 7 | 2 | 2 | 0 | 12 |
| Mounting | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 1 |
| Cluster 3 | | | | | | | | |
| Touch smelling | 5 | 1 | 4 | 10 | 0 | 1 | 0 | 9 |
| **Victim** | | | | | | | | |
| Cluster 1 | | | | | | | | |
| Allogrooming | 62 | 63 | 10 | 143 | 26 | 106 | 23 | 148 |
| Contact sitting | 29 | 18 | 3 | 30 | 16 | 35 | 9 | 34 |
| Cluster 2 | | | | | | | | |
| Gentle touching | 20 | 18 | 6 | 34 | 3 | 7 | 3 | 17 |
| Genital inspect | 13 | 5 | 5 | 22 | 0 | 2 | 0 | 6 |
| Hold bottom | 1 | 0 | 1 | 3 | 1 | 0 | 0 | 1 |
| Passing contact | 3 | 1 | 1 | 9 | 2 | 2 | 1 | 5 |
| Mounting | 2 | 0 | 2 | 0 | 0 | 1 | 0 | 1 |
| Cluster 3 | | | | | | | | |
| Touch smelling | 4 | 2 | 1 | 10 | 1 | 1 | 1 | 7 |

which were the result of multiple opponent pairs in polyadic conflicts) from 32 focal individuals (mean number of PC–MC pairs per individual=6.7). The minimum required number of PC–MC pairs per focal animal was one. Five individuals contributed only to the aggressor data set, two only to the victim data set, and 25 to both aggressor and victim data sets. We investigated two aspects of triadic contacts: occurrence and direction of these contacts. Occurrence consisted of whether contacts occurred more in PC than MC periods; direction consisted of who made the contact (the focal animal could either give or receive a contact). We excluded from the data set those contacts in which the third party was related to both the aggressor and the victim. For comparative purposes, we also included contacts between opponents that were the focus of our previous study (Call et al. 1999), but here we did separate analyses according to whether the former aggressor or the former victim was the focal animal.

We used the method pioneered by de Waal & Yoshihara (1983) to test whether attracted pairs were more frequent than dispersed pairs, where an attracted pair was defined as those in which affiliative contacts occurred earlier in the PC than in the MC observations, whereas dispersed pairs were defined as those pairs in which affiliative contacts occurred earlier in the MC than the PC observations. Neutral pairs were those in which no contact occurred in either the PC or MC, or contact occurred in the same minute in the PC and MC observations. We used Veenema et al.'s (1994) measure of conciliatory tendency (CT), defined as attracted minus dispersed pairs divided by the total number of PC–MC pairs, for dyadic reconciliation. In the case of postconflict third-party affiliation, we did a similar calculation but we labelled it 'triadic contact tendency' (TCT). We tested and calculated CT and TCT with this methodology for both all affiliative acts (i.e. without distinguishing between clusters as previous studies have done) and the two clusters of behaviours separately. In this latter case, for each cluster we scored an attracted pair when any of the behaviours belonging to that cluster occurred earlier in the PC than in the MC period and, conversely, a dispersed pair when they occurred first in the MC period. The occurrence of all other behaviours (including those from other clusters) was ignored. We obtained CT or TCT for each of the two clusters used and for each of the four types of partner (opponent, own kin, opponent's kin and unrelated individual). Of special interest was the direction of the contacts between individuals. We investigated the direction of contacts between opponents and their partners by splitting the data into contacts received and given by the focal animal, and comparing each of them between the PC and MC periods. Note that the direction of the contacts does not necessarily reflect who takes the initiative; it simply indicates who is responsible for the contact. We conducted all analyses at the individual level to avoid results being affected by the possible excessive contribution of a few individuals to the data set. We used the Wilcoxon matched-pair signed-ranks test (two tailed) to assess differences between the PC and MC periods; our data were unsuitable for the use of parametric statistics because of the small sample size and lack of normality.

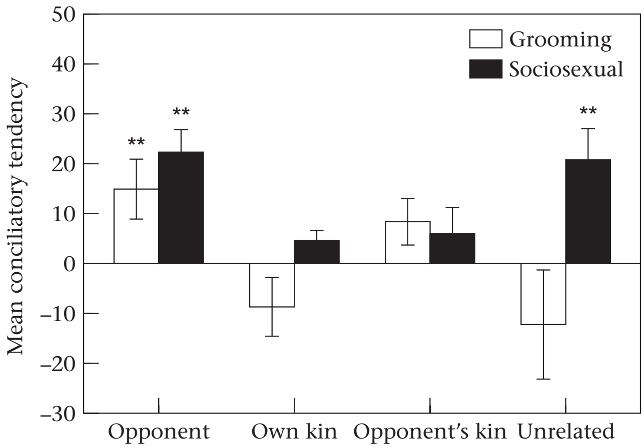

**Figure 1.** Conciliatory tendency±SEM of aggressors for the grooming and sociosexual clusters as a function of the type of partner. $^{**}P<0.01$.

## RESULTS

### Aggressors

Figure 1 presents the aggressor's CT and TCT for each of the two clusters of behaviours. Aggressors had more attracted than dispersed pairs with their opponents when only grooming and contact sitting were considered ($T=22.5$, $N=15$, $P=0.002$). Furthermore, aggressors also had more postconflict sociosexual behaviours with both their opponents ($Z=3.74$, $N=18$, $P<0.001$) and unrelated individuals ($Z=2.80$, $N=18$, $P=0.005$).

Focusing on the directionality of the dyadic and triadic contacts for each of the clusters of behaviours, aggressors received more postconflict grooming from their opponent's kin ($T=1$, $N=7$, $P=0.031$; Fig. 2a). Aggressors also received more sociosexual behaviour from their own kin ($T=0$, $N=6$, $P=0.031$) and unrelated individuals ($Z=2.28$, $N=16$, $P=0.022$; Fig. 2b). Furthermore, aggressors also directed more sociosexual behaviour towards their opponents ($Z=3.74$, $N=18$, $P<0.001$) and unrelated individuals ($T=0$, $N=10$, $P=0.002$; Fig. 2b).

### Victims

Figure 3 presents the victim's CT and TCT for each of the two clusters of behaviours. Victims had fewer attracted than dispersed pairs with their kin when only behaviours of cluster 1 were considered ($T=9$, $N=15$, $P=0.009$). Furthermore, victims showed more postconflict sociosexual behaviours with all classes of individual (opponent: $T=0$, $N=14$, $P<0.001$; own kin: $T=0$, $N=8$, $P=0.008$; opponent's kin: $T=0$, $N=10$, $P=0.002$; unrelated: $Z=3.27$, $N=17$, $P=0.001$).

Focusing on the directionality of the dyadic and triadic contacts for each cluster of behaviours, victims both received ($T=4$, $N=12$, $P=0.003$) and directed ($T=10$, $N=14$, $P=0.005$) less grooming from and towards their own kin (Fig. 4a). Victims received more sociosexual behaviour both from their opponents ($T=0$, $N=11$, $P=0.001$), their opponent's kin ($T=0$, $N=10$, $P=0.002$) and unrelated individuals ($T=0$, $N=13$, $P<0.001$; Fig. 4b). Victims also directed more sociosexual behaviour towards their opponents ($T=0$, $N=7$, $P=0.016$), their own kin ($T=0$, $N=6$, $P=0.031$) and unrelated individuals ($T=13.5$, $N=12$, $P=0.042$; Fig. 4b).

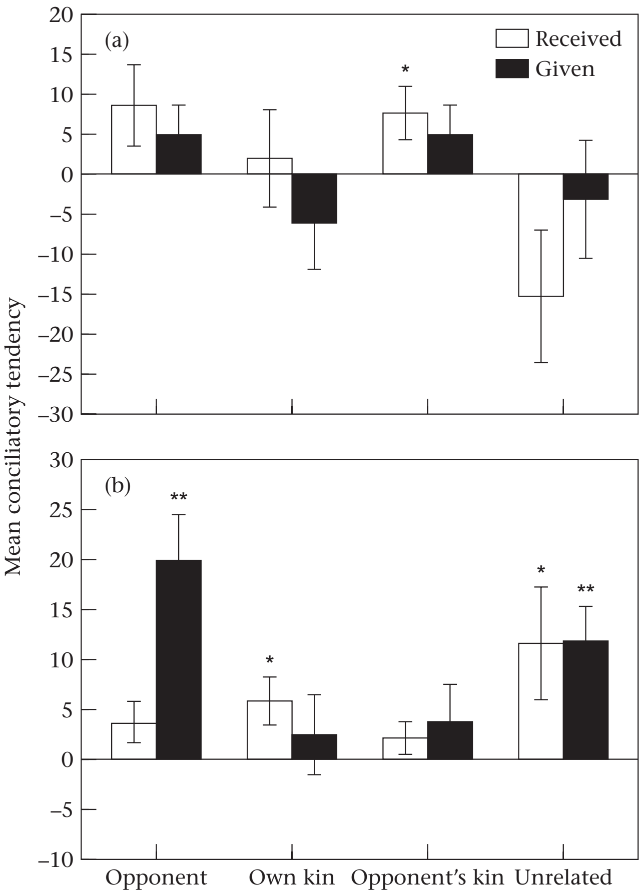

**Figure 2.** Directionality of the conciliatory tendency±SEM of aggressors for the (a) grooming and (b) sociosexual cluster as a function of the type of partner. $^{*}P<0.05$; $^{**}P<0.01$.

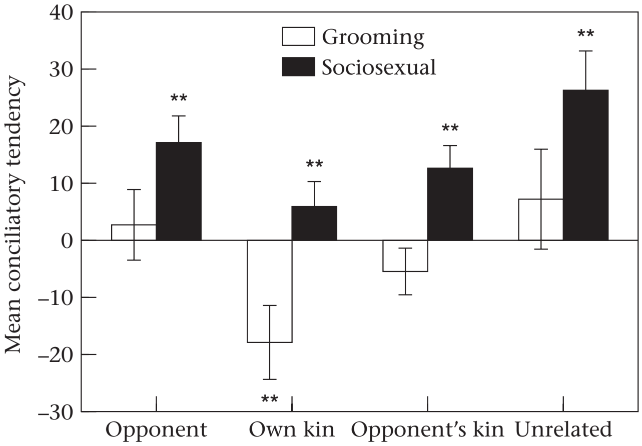

**Figure 3.** Conciliatory tendency±SEM of victims for the grooming and sociosexual clusters as a function of the type of partner. $^{*}P<0.05$; $^{**}P<0.01$.

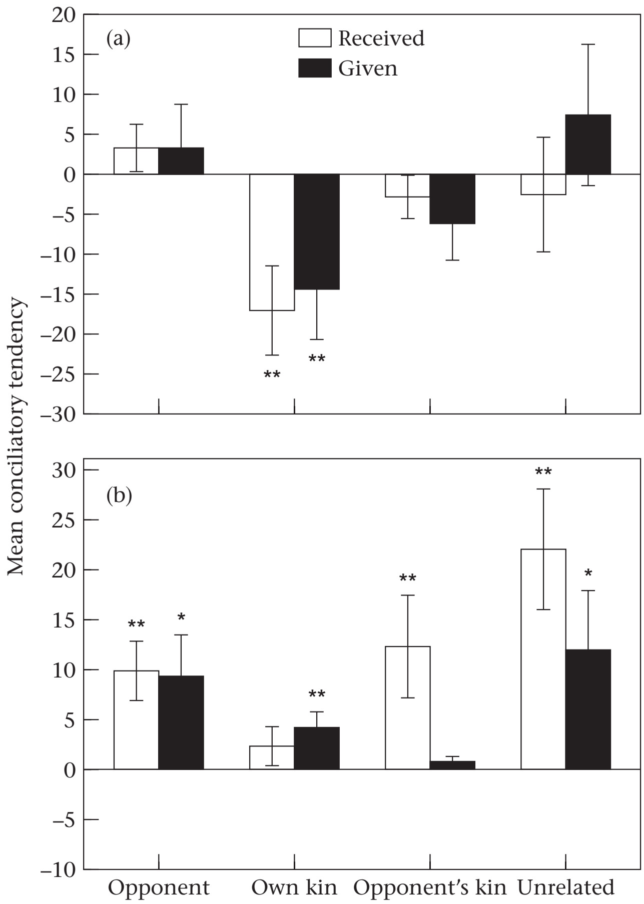

**Figure 4.** Directionality of the conciliatory tendency±SEM of victims for the (a) grooming and (b) sociosexual cluster as a function of the type of partner. **P*<0.05; ***P*<0.01.

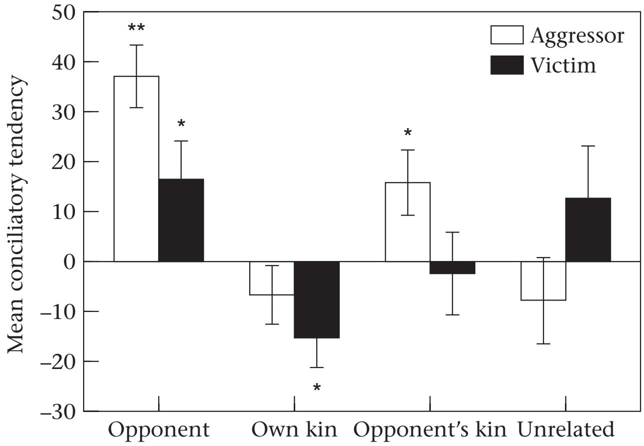

**Figure 5.** Conciliatory tendency±SEM of aggressors and victims as a function of the type of partner. **P*<0.05; ***P*<0.01.

For purposes of comparison with previous studies, Fig. 5 presents the dyadic and triadic contacts for each of the four classes of partners of the aggressor and the victim disregarding both the directionality and the type of contact. In the aggressor data set, there were more attracted than dispersed pairs with the former opponent ($Z$=4.03, $N$=21, $P$<0.001) and with the opponent's kin ($T$=19, $N$=14, $P$=0.035). Similarly, in the victim data set there were more attracted than dispersed pairs with former opponents ($Z$=2.23, $N$=18, $P$=0.026). In contrast, more dispersed pairs were found between victims and their own kin ($T$=15, $N$=14, $P$=0.017). No other significant difference was found.

## DISCUSSION

Stumptailed macaques showed differences between postconflict and matched-control affiliative contacts both with their opponents and third parties who had not been involved in their previous conflict. Classifying the various affiliative contacts into two clusters (allogrooming cluster and sociosexual cluster) rather than treating all contacts equally, and analysing each cluster separately, was instrumental in finding specific interactions that would otherwise have been missed. The nature and the direction of these contacts depended on the role individuals had in the previous conflict (i.e. aggressors or victims).

Aggressors received more postconflict grooming and contact sitting from their opponents' kin, received more sociosexual behaviour from their own kin and unrelated individuals, and directed more sociosexual behaviour to their opponents and unrelated individuals. These results corroborate those of studies on pigtailed and longtailed macaques in which aggressors also showed more postconflict contacts with both their opponent's kin and unrelated individuals (Judge 1991; Das et al. 1997; see also Das 2000). In addition, the patterns of the two clusters of behaviours received by aggressors from different partners found in our study may indicate that postconflict allogrooming and sociosexual behaviours accomplish different functions as hypothesized by Call et al. (1999). Although it is conceivable that aggressors received grooming from their opponents and their opponents' kin as a mechanism of relationship repair (i.e. triadic reconciliation, Aureli & van Schaik 1991; Judge 1991), it is unclear why they also received sociosexual behaviour from their own kin. In our previous study (Call et al. 1999) we had hypothesized that sociosexual behaviours between opponents were used as a buffering mechanism to prevent further aggression. Yet, given that macaque aggressors do not seem to attack their own kin preferentially after conflicts with third parties (or vice versa; see Watts et al. 2000), a buffering mechanism may not be needed in the first place. A more plausible explanation is that kin may direct sociosexual behaviours towards the aggressor to show their support after a conflict with third parties.

Victims received and directed less postconflict grooming from and towards their own kin than in control periods (Fig. 4a). This result confirms Aureli et al.'s (1993, 1994) findings of a lower postconflict tendency of the victim to associate with own kin in Japanese, *Macaca fuscata*, and Barbary macaques, *Macacus sylvanus*. More importantly, victims received more postconflict sociosexual behaviour from all partners except their own kin and directed more sociosexual behaviour to all partners except the opponent's kin (Fig. 4b). The majority of previous studies, including one on stumptailed macaques (de Waal & Ren 1988), failed to find more postconflict contacts between victims and third parties in several species of primates (see Watts et al. 2000, for a review), the only exceptions being Guinea baboon, *Papio papio*, victims increasing contacts with their own kin (Petit & Thierry 1994a), and capuchin monkeys, *Cebus apella* (Verbeek & de Waal 1997), spectacled langurs, *Trachypithecus obscurus* (Arnold & Barton 2001), chimpanzees, *Pan troglodytes* (de Waal & van Roosmalen 1979; de Waal & Aureli 1996) and mountain gorillas, *Gorilla gorilla beringei* (Watts 1995) increasing their contacts with third parties in general. In all these species, except chimpanzees, victims were responsible for these triadic contacts. In contrast, our study is the first to show that victims were also the recipients of contacts from third parties in a monkey species even though several studies have investigated this topic in various species of monkeys (Watts et al. 2000; but see Petit & Thierry 1994a). It is important to emphasize that responsibility for contacts (directionality) should not be equated with taking the initiative in a contact. It is very likely that individuals use noncontact signals to initiate interactions that may or may not end with physical contact between individuals. Furthermore, those individuals who use a signal in the first place may not always be the ones establishing the contact with their partners. Whereas the study of directionality between individuals is straightforward, the study of who takes the initiative is more problematic because individuals may use subtle signals to initiate interactions that observers may easily miss.

Triadic postconflict affiliation directed to the victim from third parties had only been described previously for chimpanzees with the label of consolation (de Waal & van Roosmalen 1979) and has been hypothesized to reflect empathy (de Waal & Aureli 1996). Whether third party contacts with the victim in stumptailed macaques represent cases of consolation and empathy is still unclear. It is noteworthy that in our study all these contacts were due to sociosexual behaviours. Allogrooming should be a candidate behaviour for PC contacts with a third party if their primary function is to calm down the victim, as the term consolation implies, because receiving allogrooming reduces heart rate and tension-related activities (Schino et al. 1998; Aureli et al. 1999).

One explanation for our result is that postconflict third-party affiliation based on sociosexual behaviours does not serve to console but to prevent aggression by the victim. In a previous study we argued that PC sociosexual behaviours between stumptailed opponents may act as a buffer against further aggression whereas PC allogrooming may be implicated in repairing damaged relationships (Call et al. 1999). Similarly, the higher rates of sociosexual behaviours in triadic postconflict situations may also indicate that at least in stumptailed macaques postconflict third-party affiliations, unlike their dyadic counterparts, do not function to repair damaged relationships, as the term 'triadic reconciliation' (Judge 1991) may imply. Das et al.'s (1997, 1998) findings on longtailed macaques provide some support for the idea of different functions between dyadic and triadic PC contacts. Das et al. found that whereas contacts with opponents decreased the aggressor's stress level, contacts with third parties did not (note that these authors did not conduct separate analyses for different clusters of behaviours nor did they deal with contacts between victims and third parties).

There is evidence that in macaques victims redirect aggression against other group members soon after being attacked (Scucchi et al. 1988; Aureli & van Schaik 1991; Aureli et al. 1993) and that they target in particular vulnerable individuals, including opponents' kin (Judge 1982; Aureli et al. 1992). Postconflict sociosexual behaviour could function in reducing the likelihood of redirection. In our study, we found no evidence that victims (or aggressors) redirected aggression towards third parties after conflicts, including their opponents' kin. In contrast, we found that victims were more likely to receive aggression from third parties during the postconflict period than during the matched-control period ($T=16.5$, $N=15$, $P=0.01$).

It is important to emphasize that had we not split the various affiliative contacts into two clusters, we would have obtained results comparable to other studies on postconflict triadic affiliation as our analyses in Fig. 5 showed. In particular, we would have found only higher PC contacts between the aggressor and the opponent's kin (as in Judge 1991; Das et al. 1997), no evidence of higher PC contacts between the victim and third parties (as reviewed in Watts et al. 2000), and lower postconflict tendency to associate with victim's kin (as in Aureli et al. 1993, 1994). It is therefore important to distinguish between the various affiliative behaviours because they may serve different functions and pooling them may obscure potential differences with control conditions. Thus, future studies should investigate how different patterns are distributed. This is especially important for those species that have a large postconflict behavioural repertoire such as chimpanzees, black macaques, *Macaca nigra*, and stumptailed macaques (de Waal & van Roosmalen 1979; de Waal & Ren 1988; Petit & Thierry 1994b). Those species with broader postconflict repertoires are also more tolerant species (as opposed to despotic; cf. de Waal 1989). It is conceivable that a more tolerant system includes subtleties and more room for negotiation than the more rigid and despotic systems (Thierry 1986, 2000; de Waal & Ren 1988; Aureli et al. 1997; Petit et al. 1997). Therefore, more tolerant species may be the best candidates to find the more complex patterns of triadic interaction, once behavioural patterns are distinguished. In addition, in more tolerant species third parties are more likely to associate with victims soon after an aggressive conflict without the risk of being involved in further aggression by the former aggressor as the social constraints hypothesis predicts (de Waal & Aureli 1996).

A conflict has repercussions not only at the dyadic level for the former opponents, but also at a triadic level. Many conflicts involve directly other individuals in the form of aggressive coalitions, peaceful interventions, or redirections, and these interactions reflect the patterns of affiliation within the group (Aureli et al. 1992; Harcourt & de Waal 1992; Petit & Thierry 2000; Thierry 2000; Watts et al. 2000). In addition, various studies, including the present one, have shown that even when third parties are not involved in the aggressive conflict, they may play an important role in the postconflict period. These triadic patterns are a reflection of the complex social networks found in at least some primates. Further insight into these complex networks could be gained by observing the aggressor and the victim simultaneously after conflicts. These data may shed some light on the decisions that each partner makes with regard to each other and with regard to third parties. Also more research on triadic patterns in other taxa would increase our understanding of how widespread these networks are in animal societies.

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