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The function of postconflict interactions: new prospects from the study of a tolerant species of primate☆

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Aggression can generate anxiety, create uncertainty about its aftermath and jeopardise social relationships. Postconflict interactions serve as conflict management strategies to mitigate these consequences. Whereas postconflict interactions are well characterized in many animals, their functions are still insufficiently investigated. Four functional hypotheses have been proposed: stress reduction, relationship repair, self-protection and benign intent. We aimed to test these hypotheses in females of a tolerant macaque species, the crested macaque, *Macaca nigra*, under natural conditions, for three postconflict interactions: reconciliation, affiliation and aggression with third parties. Our results provide meaningful contrasts compared with findings in other species. We found no evidence that aggression had consequences for individuals' behavioural indicators of anxiety, although it increased the likelihood of secondary aggression with third parties. There was little evidence for the stress reduction hypothesis as the occurrence of any of the three postconflict interactions investigated had little effect on the measured behavioural indicators of anxiety. Conflict and dyad characteristics also had limited influence on anxiety. The relationship repair function was only partly validated: dyads with stronger bonds or that exchanged more support did not reconcile more often, but dyads with attributes related to the symmetry, stability and predictability (i.e. security) within relationships did. Patterns of initiation and directionality of postconflict interactions in this study population suggest that reconciliation may constitute the signalling of appeasement and benign intent. Furthermore, we found that aggression towards third parties may serve as a source of self-protection and reassertion of the females' social status. The distinctive pattern of postconflict management strategies revealed in wild female crested macaques appears to be related to their typically tolerant social style. These results demonstrate the usefulness of concomitantly studying aggression, postconflict interactions and their functions, to understand conflict management strategies comprehensively, while taking into account the level of social tolerance characterizing the studied society.

A correlate of group living is the occurrence of conflicts of interests between group members, with their most conspicuous expression being overt aggression (Alexander, 1974). Aggression incurs costs such as injury or becoming the target of coalitions (Hand, 1986). Aggression increases anxiety, manifested through elevated scratching, restlessness, heart rate and stress hormone levels (nonhuman primates, Arnold & Aureli, 2006; mammals, Schino, 2000; king penguin, *Aptenodytes patagonicus*, Viblanc, Valette, Kauffmann, Malosse, & Groscolas, 2012; goose, *Anser anser*, Wascher, Scheiber, & Kotrschal, 2008). There are additional sources of anxiety linked to aggression: aggression creates 'uncertainty' about the social situation directly following a conflict in the sense that opponents are uncertain as to whether aggression will flare up again (Arnold & Aureli, 2006; Schino, 2000). Ultimately, aggression may jeopardise the benefits of a relationship between opponents (van Schaik & Aureli, 2000). Thus, in gregarious animals, conflict management strategies that mitigate the consequences of aggression have adaptive value and their study gives insight into how individuals balance competition and cooperation (de Waal, 1989, 2000).

To alleviate the consequences of aggression, for both the aggressor and the recipient, different postconflict management strategies are possible. Reconciliation is the exchange of positive behaviours between former opponents shortly after the end of aggression (de Waal & van Roosmalen, 1979). Secondary aggression

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is the reoccurrence of aggression, either between former opponents (renewed aggression) or between a noninvolved third party and one of the opponents (secondary aggression, Clutton-Brock & Parker, 1995; Kazem & Aureli, 2005). Affiliation with third parties or, more generally, mediation through a third party is the exchange of positive behaviour between a noninvolved third party and one of the previous opponents (Das, 2000; Watts, Colmenares, & Arnold, 2000; Yarn, 2000). However, even within the same dyad of individuals, not all conflicts are followed by postconflict interactions. Researchers have therefore shifted their attention from the characteristics of postconflict behaviour towards their potential functions and the factors influencing their occurrence.

Four main nonexclusive functional hypotheses have been formulated and tested. Generally, postconflict interactions serve to reduce the stress that opponents experience as a result of the conflict (stress reduction hypothesis; Aureli, 1997; Aureli, Fraser, Schaffner, & Schino, 2012), to mend relationships between partners (relationship repair hypothesis; Aureli, 1997; Aureli et al., 2012), to preserve oneself against further attacks or to reassert oneself in the social order of the group (self-protection hypothesis; Aureli et al., 2012), and/or to signal that the conflict has ended and that intentions are now peaceful (benign intent hypothesis; Silk, 1996). The common assumption of these hypotheses is that conflicts induce a negative emotional state in individuals (stress or anxiety). This can be because of the intrinsic properties of conflicts: more intense, longer or undecided conflicts are more stressful and thus should increase the likelihood of postconflict interactions (Arnold & Aureli, 2006). It can also be because the quality of the relationship between the two opponents is threatened (Arnold & Aureli, 2006; Aureli, 1997; Aureli et al., 2012). In addition, the quality of a relationship can influence the degree of anxiety experienced by interacting partners: higher relationship quality means heightened anxiety. Therefore, repairing relationships also helps to decrease anxiety (‘integrated hypothesis’; nonhuman primates, Aureli, 1997; Koski, Koops, & Sterck, 2007; McFarland & Majolo, 2012; humans, Worthington, 2004, 2006). In this context, Cords and Aureli (2000) distinguished between three components of a relationship: value (in terms of fitness or wellbeing benefits), security (i.e. how predictable or stable the relationship is) and compatibility (i.e. the general tenor of a relationship). It could then be shown that more ‘valuable’ partners such as kin or friends do indeed reconcile more often than less ‘valuable’ partners (Aureli et al., 2012; Cords & Aureli, 2000). Different postconflict interactions do not necessarily have different functions. The differences in function can be inherent to the identity of the initiator and receiver of the behaviour, and to their role, or absence thereof, in the previous conflict, i.e. aggressor, recipient or a third party (Table 23.1 in Aureli et al., 2012). In this study, we specifically investigated the function of three postconflict interactions from the opponents’ perspective.

Among primates, macaque societies are well studied with respect to their conflict management strategies and their functions (Aureli, Das, Verleur, & van Hooff, 1994; Aureli, Veenema, van Panthaleon van Eck, & van Hooff, 1993; Demaria & Thierry, 2001; Judge, 1991; Majolo, Ventura, & Koyama, 2009a; Patzelt, Pirow, & Fischer, 2009; Thierry et al., 2008; de Waal & Aureli, 1996, 1997). Females, the philopatric sex, form the core of the group and they develop long-lasting relationships. More interestingly, the different macaque species show variation in conciliatory tendencies, degree of power asymmetries, kin bias in social interactions and levels of social tolerance between individuals (Thierry et al., 2008). Macaques that are said to be tolerant display lower conflict intensity, higher rates of retaliation and higher conciliatory tendencies than macaques that are said to be despotic. In general, tolerant macaques seem to form large and diverse affiliative networks, which are more independent of dominance and kinship, in contrast to more despotic species in which individuals form highly clustered social relationships with a substantial preference for kin (Thierry, 2007; Thierry et al., 2008). We can therefore expect tolerant macaques to contrast with more despotic ones in regard to the functions of postconflict interactions. This is because some assumptions, such as the influence of conflict characteristics on anxiety, may not fit with the social style of tolerant macaques. For example, on the one hand, conflicts in tolerant macaques could theoretically induce little stress because they are mainly of low intensity but, on the other hand, they could involve significant costs or stress because they include a high amount of counteraggression (Duboscq et al., 2013; Petit, Abegg, & Thierry, 1997). However, in comparison to more despotic macaque species, tolerant macaque species remain largely understudied, especially under natural conditions. In particular, the potential functions of postconflict interactions have never been fully investigated in the most tolerant species, the Sulawesi macaques. In addition, the different strategies of postconflict management are often addressed separately in a given species (but see Call, Aureli, & de Waal, 1999; Koski, de Vries, van den Tweel, & Sterck, 2007; Logan, Emery, & Clayton, 2012; Wittig & Boesch, 2003), although different postconflict interactions may not be independent of each other and may even occur concurrently (Koski, de Vries, et al., 2007).

The aims of this study were two-fold: (1) to analyse the consequences of aggression in general and in relation to conflict and dyad characteristics, and (2) to test hypotheses regarding the function of postconflict interactions in wild female crested macaques, *Macaca nigra*, a species characterized by a tolerant style of social relationships (Duboscq et al., 2013; Petit et al., 1997). For this purpose, we investigated relations between characteristics of conflicts and interacting dyads, behavioural indicators of anxiety (hereafter anxiety), and the occurrence of three postconflict interactions: reconciliation, affiliation with and aggression towards a third party, in order to test their functions. From the opponents’ perspective, the following general predictions, which can overlap between hypotheses, can be drawn (more specific ones are listed in Tables 1 and 2).

(1) Consequences of aggression: (a) in general, the occurrence of aggression should increase the opponents’ anxiety and the likelihood of further aggression; (b) conflict and dyad characteristics should influence the degree of anxiety experienced by opponents.

(2) Stress reduction hypothesis: (a) affiliative postconflict interactions, either between opponents or with a third party, should decrease the opponents’ anxiety and the likelihood of further aggression; (b) redirection (i.e. aggression from the initial recipient

Table 1
Details of predictions and summary of results on the consequence of aggression for the restlessness index and scratching levels

Predictions	Results
The occurrence of aggression increases:	
Scratching	No
Restlessness	No
Secondary aggression	Yes
Conflicts generate more scratching and higher restlessness when they are:	
More intense	Scratching: no – restlessness: no
Longer	Scratching: no – restlessness: no
Undecided	Scratching: no – restlessness: yes
Conflicts generate more scratching and higher restlessness when within:	
Dyads with higher CSI	Scratching: no – restlessness: no
Dyads with more frequent support	Scratching: no – restlessness: no
Dyads with more symmetric relationships	Scratching: no – restlessness: no
Dyads with more constant temporal exchange of grooming	Scratching: no – restlessness: no
Dyads with less counteraggression	Scratching: no – restlessness: no
Dyads with less aggression	Scratching: no – restlessness: no
Dyads with a smaller rank difference	Scratching: no – restlessness: no

towards a third party) should decrease the anxiety of the initiator of redirection; (c) if certain conflict characteristics generate more anxiety than others, conflicts with these characteristics should be preferentially followed by postconflict interactions to alleviate this anxiety.

(3) Relationship repair hypothesis: we formulated predictions in the specific framework of this hypothesis only for reconciliation as we are presently not aware of the kin relationships of all individuals in the group, and could not identify all the juveniles involved in third-party interactions. Reconciliation should be more likely after conflicts among dyads with special relationships, that is, between individuals that are strongly bonded and/or that particularly benefit from being associated.

(4) Self-protection hypothesis: (a) the initial recipient of aggression should initiate postconflict interactions more often than the aggressor because she is theoretically more at risk of receiving new bouts of aggression; (b) the occurrence of postconflict affiliation between any parties should lower the risk of further aggression to/from any parties; (c) in secondary aggression, opponents should target mainly third-party individuals that are lower ranking than themselves, to reassert the opponents' social status.

(5) Benign intent hypothesis: (a) the opponent with more motivation to signal the end of the conflict (e.g. the one more likely to escalate aggression by retaliating or the one more 'stressed' by the event, most likely the recipient) should be the one to initiate the first interaction; (b) noncontact affiliative behaviours should precede contact behaviours as a signal that re-establishing contact with the former opponent will have no immediate negative consequences.

METHODS

Data Collection

Crested macaques are endemic to the island of Sulawesi, Indonesia (Sugardjito et al., 1989). The study population inhabits the Tangkoko-Batuangus Nature Reserve (1°33′N, 125°10′E; see Duboscq et al., 2013), broadly classified as a lowland rainforest with seasonal variation in rainfall and fruit abundance (O'Brien & Kinnaird, 1997). We studied two well-habituated nonprovisioned groups, 'PB' and 'R1', comprising about 60 and 80 individuals respectively. All adults could be individually identified based on physical characteristics. Observation conditions were excellent because the monkeys are semiterrestrial, spending approximately 60% of their time on the ground (O'Brien & Kinnaird, 1997). This research adheres to all legal requirements and guidelines of the German and Indonesian governments and institutions and to the ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching.

Each study group was followed from dawn (ca. 0530 hours) to dusk (ca. 1800 hours) every day between October 2008 and May 2010. We collected behavioural data on all adult females (15–18 in PB, 21–24 in R1) using focal animal sampling (Martin & Bateson, 1993). We observed focal females until 30 activity point samples were collected. We recorded their activity (feeding, foraging, socializing, travelling, resting, self-grooming) every minute and the identity of neighbours (in body contact, within one body length and within five body lengths) every second minute. We also counted scratching bouts per min (Table 3). We recorded focal social events continuously, including the start and end time of interactions, the sequence of all of the females' behaviours, and the identity and behaviours of all social partners. During the course of the study, the adult female cohort changed slightly as one old female disappeared and six young females reached adulthood. For clarity and simplicity, we included in the analyses only adult females that were continuously present in the groups throughout the study. In total, this study included 2480 h of focal data from 36 females (PB, $N = 15$: median 68 h/female, range 65–78; R1, $N = 21$: median 66 h/female, range 59–71). Interobserver reliability was calculated with Cohen's kappa for categorical data and a set of Pearson correlations for continuous data (Martin & Bateson, 1993). Overall,

Table 2
Details of predictions and summary of results on the four potential functions of three postconflict interactions

Predictions	Results		
	Reconciliation	Affiliation with third party	Aggression with third party
Stress reduction			
Interaction decreases:			
Scratching	No	Yes	No
Restlessness	No	No	No
Renewed and secondary aggression	No	No	
Interaction is more likely to occur after:			
Intense conflicts	No	No	No
Undecided conflicts	Yes	No	No
Longer conflicts	No	No	No
Social context conflicts	Yes	Yes	No
Conflicts with unexpected direction	Trend	No	No
Relationship repair			
Interaction is more likely to occur after conflicts within:			
Dyads with higher CSI	No	No	No
Dyads with more frequent support	No	No	No
Dyads with more symmetric relationships	No	No	No
Dyads with more constant temporal exchange of grooming	No	No	No
Dyads with less counteraggression	Yes	No	No
Dyads with less aggression	No	No	No
Dyads with a smaller rank difference	No	Yes	No
Self-protection			
Recipients initiate more interaction than aggressors	No (59%)	No (53%)	No (30%)
Interaction initiated by opponents targets more often lower-ranking individuals		Yes (81%)	Yes (83%)
Aggression with third-party occurs less often with reconciliation or affiliation with third-party			No
Benign intent			
Recipients initiate reconciliation more often than aggressors	No (41%)		
Higher-ranking females initiate reconciliation more often than lower-ranking females	Yes (64%)		
Noncontact affiliation precedes contact affiliation	Yes (69%)		

Table 3
Summary of behavioural variables, their definitions, units and scales (see text for details)

Variables	Definitions	Unit/scale
Consequences of aggression		
Scratching bout	One episode of scratching the same body area. A new bout started with changes in body area or breaks of more than 5 s	No. per min
Aggression	Aggression between a third party and one of the opponents (secondary aggression) or between the two opponents again (renewed aggression, only if >1 min after PC started).	No. per min
Restlessness	An index of changes in activity. The higher the index the more restless the individual	Continuous
Postconflict interaction characteristics		
Affiliation	Frequency of affiliation between opponents or with third parties, controlling for proximity scans (<5 body lengths)	No. per dyadic proximity scan
Presence in proximity	Frequency of proximity scan with opponent present	No. per focal proximity scan
Aggression	Frequency of aggression between opponents or with third parties, controlling for proximity scans (<5 body lengths)	No. per dyadic proximity scan
Initiation	Initiation of reconciliation, affiliation and aggression with a third party	By aggressor/recipient or by opponent/a third party
Conflict characteristics		
Intensity	Occurrence of physical contact (hit, grab, push, bite)	Yes/no
Duration	Difference between the onset and offset of the aggressive interaction	s
Decidedness	Identification of a clear winner (e.g. recipient avoids aggressor)	Yes/no
Polyadic	Involvement of individuals other than the two original opponents	Yes/no
Redirection	The recipient of aggression directs aggressive behaviour(s) towards third-party individual(s) within 30 s after the original conflict	Yes/no
Context	Divided into food-related: conflict occurring during feeding or foraging; and socially related: conflict occurring over access to an infant, a grooming or mating partner or consisting of an aggressive intervention	Food/social
Dyadic characteristics		
Grooming	Duration of grooming given and received	Min. per dyad per observation-hour
Approach frequency	Frequency of approaches in close proximity (≤ 1 body length)	No. per dyad per observation-hour
Positive approach	Frequency of close proximity approaches followed by affiliation	No. per dyad per observation-hour
Grooming variation	Coefficient of variation of grooming duration across the 19 months of the study	Continuous
Absolute Elo difference	Difference in Elo ratings of the aggressor and recipient	Continuous
Sign rank difference	Sign of the difference in Elo ratings	Positive/negative
Affiliation symmetry index	Average symmetry index in grooming and approach	Continuous
CSI scores	Based on grooming, approach within one body length and positive approach	Continuous
Support	Mean frequency of support and peaceful intervention	No./dyad per observation-hour
Aggression	Frequency of aggressive interactions	No./dyad per observation-hour
Counteraggression	Frequency of bidirectional aggressive interactions	No./dyad per observation-hour
Components of a relationship		
Value	Support	
Security	Affiliation asymmetry index, grooming variation, counteraggression frequency	
Compatibility	CSI, aggression frequency, Elo difference	

reliability was good to excellent ($\kappa = 0.69-0.90$, correlation coefficients between behavioural variables $= 0.79-0.98$, all $Ps < 0.05$).

Data Processing

We defined and recognized a bout of aggression, or conflict, whenever an individual displayed aggressive behaviour (threat, hit, grab, push, bite; Duboscq et al., 2013) towards another one, who responded with either aggressive or nonaggressive (avoidance) behaviour (Duboscq et al., 2013). Aggression was terminated when females had stopped exchanging aggressive behaviour for more than 1 min (Petit et al., 1997). Similarly, an affiliation was defined and recognized as any active affiliative behaviour (grooming, embracing, touching, lipsmacking, grunting), directed towards an observable target (Duboscq et al., 2013; Thierry et al., 2000). The individual that started the behaviour was the initiator of the interaction and the target of this behaviour was the recipient.

Postconflict Observation Periods

Postconflict observations (PC) were extracted a posteriori from focal protocols. PCs started right after the last exchange of aggressive behaviours between the focal female and her opponent, and ideally lasted for 10 min (median 10 min, range 2–10 min). If aggression flared up again within 1 min of the start of a PC, the PC was postponed until the bout of aggression had definitely stopped, or discarded if it was not possible to postpone it. Traditionally, PCs are subsequently paired with matched-control observation periods (MC). MCs are standard observation protocols often conducted the day after or, according to observation conditions, as soon as possible after the specific bout of aggression has occurred, controlling for opponents' proximity, the group's activity and/or the period of the day (de Waal & Yoshihara, 1983). However, this procedure was traditionally designed for captive studies in which group composition and activity are more stable and predictable throughout the day than under natural conditions. Using this method substantially reduced our data set (285 PC–MC against 450 PCs in total) because we did not always find suitable MCs to match PCs (e.g. previous opponents were not found in proximity within a fixed timeline after the specific bout of aggression). To be able to analyse our complete data set, we followed the procedure of Patzelt et al. (2009), who applied a derivative of the time rule method (Aureli, van Schaik, & van Hooff, 1989). Females in this study affiliated with each other on average 2.5 times/h and were aggressive to each other on average 0.4 times/h (Duboscq et al., 2013), meaning that an interaction occurring within 10 min was above the average probability of interacting (24 min for affiliation and 150 min for aggression) and was therefore counted as a postconflict interaction. When calculating the frequency of aggressive and affiliative interactions in PC and the baseline (i.e. the entire observation period, see Data Analyses), we nevertheless controlled for the number of scans the dyad spent in proximity (see Data Analyses). The results based on this definition of postconflict interactions and those obtained through the PC–MC method were identical.

Behavioural Variables and Indices

Definitions of variables are summarized in Table 3 (see Duboscq et al., 2013 for more details).

Restlessness and scratching were used as behavioural indicators of anxiety. Restlessness is the rate of change in activity or behaviour; the higher the value the more restless the individual is. This is a symptom in the generalized anxiety disorder in humans (e.g. Kavan, Elsasser, & Barone, 2009). It was positively correlated with scratching in rhesus macaques, *Macaca mulatta* (Higham, Heistermann, & Maestripieri, 2011) and in the females of this study (Pearson correlation: $r_{34} = 0.625$, $P < 0.001$). We based our index on feeding, foraging, resting, travelling and self-grooming activities. For each 1 min observational scan, we coded 1 when a change in activity occurred (for example, the female foraged then rested) or 0 when no change occurred (the female kept foraging). We then calculated the number of changes (i.e. number of 1s) for all activity scans, i.e. the total number of 1s and 0s, per focal female in PCs and the baseline (i.e. the entire observation period).

To account for differences in dominance between females, we used the Elo rating, a recently developed index which reflects individuals' success in agonistic interactions (Albers & de Vries, 2001; Neumann et al., 2011). Calculations were based on sequences of agonistic interactions with a clear winner and loser (aggressive interactions in which the recipient leaves, or displacement interactions; see Duboscq et al., 2013; Neumann et al., 2011). At the beginning of the observation period, each individual in a group starts with a rating of 1000, which is updated after each agonistic interaction in which an individual is involved. The updating process increases or decreases the Elo rating of each individual, according to the outcome of the interaction and a determined factor, k (here $k = 100$ as in Neumann et al., 2011): the winner's Elo rating increases and the loser's decreases. Furthermore, an expected outcome (higher-rated individual wins) brings smaller changes in individual Elo ratings than an unexpected one (lower-rated individual wins). One of the advantages of this method is that ratings are updated continuously and can be extracted at any point in time. Since the Elo rating is a new method in behavioural ecology and biology, we ordered females according to their Elo ratings (higher Elo rating first) and verified that this order was identical to the one obtained through the I&SI method which establishes the optimal rank order fitting a linear hierarchy (de Vries, 1998). We calculated the Elo ratings of the aggressor and the recipient retrospectively the day before the conflict occurred. We then subtracted the Elo rating of the recipient of aggression from the Elo rating of the aggressor to get the absolute difference in Elo ratings between the two opponents. We tabulated the sign of the difference as an extra variable (e.g. higher-ranking female as the initiator = positive difference).

Relationships can be described by three components representing different relationship qualities: value, i.e. the benefits partners provide (e.g. support in aggression); security, i.e. how stable, symmetric or predictable the exchange of social behaviour is; and compatibility, i.e. the general tenor of relationships (Cords & Aureli, 2000). Researchers have operationally defined these three components by reducing a pool of dyadic variables into three relationship components through principal component analysis (Fraser & Bugnyar, 2010; Fraser, Schino, & Aureli, 2008; Majolo, Ventura, & Schino, 2010; McFarland & Majolo, 2011). However, our data were not adequate for this procedure (low Kaiser–Meyer–Olkin index of sampling adequacy, low communalities and variables loading on different factors that were difficult to interpret). To study the influence of dyadic relationship characteristics, we therefore selected a set of variables most representative of social relationships (see Table 3), consistent with the framework of Cords and Aureli (2000) and with those used by other researchers (e.g. Fraser & Bugnyar, 2011; Majolo, Ventura, & Koyama, 2009b; McFarland & Majolo, 2012).

To quantify the strength of the social bond of a dyad, we pooled different affinitive behaviours into a single index, the composite sociality index (CSI), following Silk, Altmann, and Alberts (2006). This index measures the extent to which a dyad deviates from the average dyad in the group. It is built on matrices of correlated social behaviours, grooming duration, frequency of approach in close proximity and percentage of positive approaches (Table 3). High values represent dyads that had stronger social bonds than the average dyad in their group. Although the strength of bonds may be related to fitness components and wellbeing in female mammals (primates, Silk, 2007b; mammals, Silk, 2007a), we have no evidence of this pattern in our study population yet. Thus, this index, together with the frequency of aggression, represented the general tenor of relationships or their compatibility (Cords & Aureli, 2000; Fraser & Bugnyar, 2010; Fraser et al., 2008; McFarland & Majolo, 2011). Using Elo ratings (see above), we also controlled for rank difference which can influence the frequency of social exchanges, such as females that are closer in rank interacting more often with each other than females that are further apart in the dominance hierarchy (Schino, 2001; Seyfarth, 1977). This variable also represented the compatibility of a relationship. The sign of the difference was included because lower-ranking females can also initiate aggression against higher-ranking ones (Duboscq et al., 2013), which is a particular feature of tolerant macaque species and which might influence postconflict events.

We also selected diverse indices or interactions measuring symmetry (ASI, see below and Table 3), stability (CV, see below and Table 3) and predictability (counteraggression because it is related to undecided outcomes in aggression, see Table 3) in behavioural exchanges, which together represented the security in relationships (Cords & Aureli, 2000; Fraser & Bugnyar, 2010; McFarland & Majolo, 2011). The affiliation symmetry index (ASI) shows how much each member of the dyad contributes to the relationship. A value of 0 indicates complete symmetry (equal exchange between individuals within the dyad), and 1 complete asymmetry. The index is based on the absolute difference between what is given by individual A to individual B, and what is given by individual B to individual A, over the sum of what is exchanged between A and B (Majolo et al., 2010). To take into account a more substantial part of females' relationships and because one dyad was never observed grooming, we calculated the ASI both for grooming duration and for the number of approaches in close proximity. The two were highly correlated. We then averaged the two indices to compute a mean dyadic ASI. The grooming variation index (CV) measures the temporal variation in grooming duration exchanged within a dyad (Majolo et al., 2010). Grooming duration within a dyad was calculated for each month (range 0–3011 s). The grooming variation index was then computed by dividing the standard deviation by the mean of the 19 months of the study for each dyad. A small coefficient of variation indicates that, within a dyad, grooming was exchanged consistently month after month.

Value was represented by support in aggressive interactions (Cords & Aureli, 2000; Fraser & Bugnyar, 2010; Majolo et al., 2010) as it is often related to fitness advantages through rank-related benefits and access to resources (Harcourt, 1989; Harcourt & de

Waal, 1992), and it was reciprocated among females in our study (J. Duboscq, M. Agil, D. Perwitasari-Farajallah, B. Thierry & A. Engelhardt, unpublished data). Support in aggression included both aggressive support in favour of a female and peaceful interventions (Petit & Thierry, 1994a). In the former, the focal female either gave or received support to/from another female in an ongoing aggressive interaction. In the latter, the focal female directed affiliation to one or both of the opponents, of which at least one was female, or the focal female received affiliation from another female during an aggressive interaction. Frequencies were calculated over the total number of aggressive interactions in which each member of the dyad was separately involved, to account for support opportunities.

Data Analyses

For the entire observation period, we calculated the frequency of baseline behaviour per min of focal observation time for each female. We also calculated PC frequencies over the duration of PCs. Although PC events were not excluded from baseline calculations, they represent only 2.7% of the total observation time; thus baseline calculations were conservative. We computed dyadic frequencies over total dyadic observation time and focal frequencies over focal observation time.

Consequences of aggression

We compared the amount of scratching and level of restlessness between PC periods without any kind of interaction and baseline to assess the influence of the occurrence of aggression on anxiety. To investigate the consequences of aggression more directly, we studied the overall effect of conflict and fighting dyad characteristics on (1) restlessness, (2) scratching and (3) the occurrence of secondary aggression (Appendix Table A1, Models 1a–c).

Occurrence of postconflict interactions

To show that postconflict interactions were specific to postconflict periods, we compared the frequency of specific interactions (affiliation between opponents, affiliation and aggression between one of the opponents and third parties) between PC periods and baseline (Appendix Table A1, Models 2a–c). We also report the attributes of actors and receivers of the first interaction of the PC (opponents' role in the previous conflict, relative rank and strength of the dyadic bond between opponent and interaction partner when possible).

Functions of postconflict interactions

Stress reduction hypothesis (Appendix Table A1, Models 2a–c and 3a, b). We investigated the effect of postconflict interactions on scratching, restlessness and the occurrence of secondary aggression, while taking into account, among other variables, conflict and fighting dyad characteristics.

Relationship repair hypothesis (Appendix Table A1, Models 3a and 4). We first tested the effect of fighting dyad characteristics on the occurrence of postconflict affiliation between opponents at the conflict level. We then investigated the influence of dyadic characteristics on the general dyadic propensity to reconcile. Since we could not reliably calculate Veenema's corrected conciliatory tendency for each dyad owing to the number of conflicts per dyad being too low (minimum necessary = 3; Veenema, Das, & Aureli, 1994), we analysed the number of dyadic conflicts followed by affiliation between opponents, which was controlled for the total number of conflicts per dyad over the observation period.

Self-protection hypothesis (Appendix Table A1, Models 2c and 3a, b). We tested whether recipients initiated or received postconflict interactions more often than aggressors. We also investigated

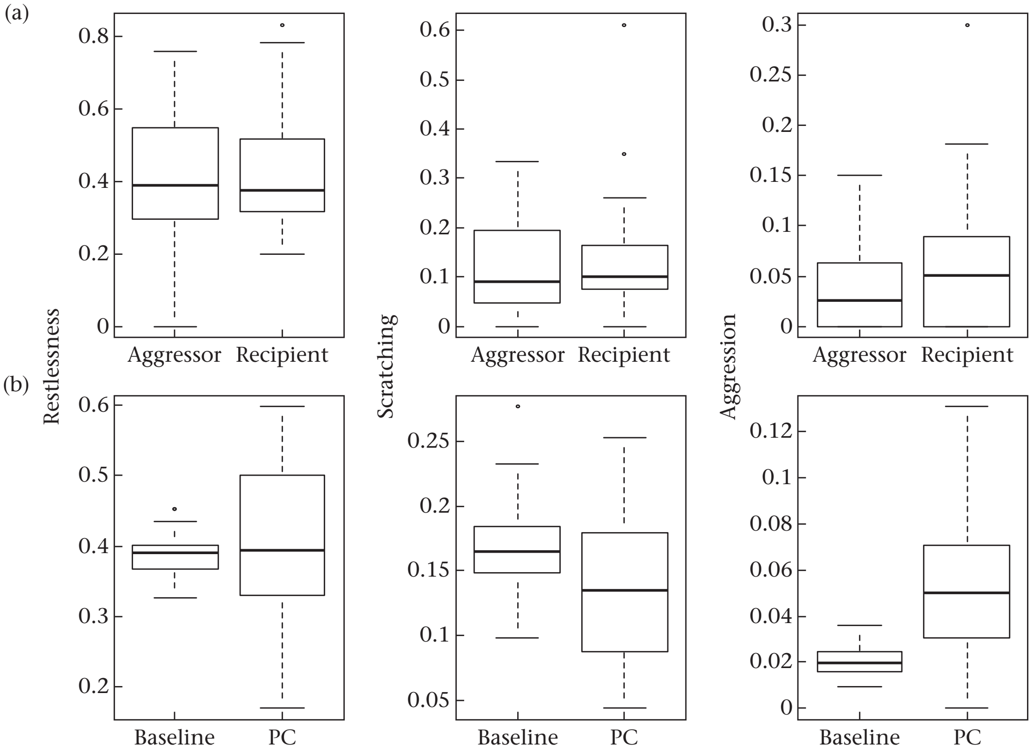

Figure 1. Restlessness index, scratching frequency (no./min) and secondary aggression frequency (no./h) (a) according to role of focal female in initial aggression, aggressor or recipient, and (b) in postconflict periods (PC) and baseline (median, interquartiles and 1.5 times interquartile range (circles represent values outside the 1.5 times interquartile range), $N = 36$, see text for test results).

whether affiliative postconflict interactions reduced the likelihood of secondary aggression. When possible, we looked at the relative rank of targets of secondary aggression compared to the initiator.

Benign intent hypothesis (Appendix Table A1, Model 3a). We analysed the initiation of reconciliation in regard to the opponents' role in the previous conflict. We also investigated whether the initiator of reconciliatory affiliation used noncontact behaviours systematically before contact behaviours to signal peaceful intent.

Statistical Analyses

All analyses were conducted with R version 2.14.1 (R Development Core Team, 2011). Alpha was set at 0.05. Wilcoxon tests were executed with the package 'exactRankTests' (Hothorn & Hornik, 2011). To test the effects of postconflict interactions, conflict characteristics and dyadic characteristics, we ran generalized linear mixed models (GLMMs; Bolker et al., 2008) as they allowed us to take single conflicts as the basis of analysis while accounting for repeated measurements. Random factors included aggressor, recipient or focal female, and group, depending on the model. In Model 4, an 'offset' term was introduced to take into account the total number of conflicts per dyad (Appendix Table A1). We also included various interactions between our different variables, especially between different conflict characteristics, between the role of the opponent and conflict characteristics or between dyadic characteristics. None of the interactions tested contributed significantly to our models (likelihood ratio tests (LRT), full versus reduced model, all Ps > 0.05); hence we excluded them all from the analyses. We transformed continuous variables to improve normality whenever necessary and standardized them to a mean of 0 and a standard deviation of 1 to make estimates comparable. GLMMs, with Gaussian, binomial or Poisson error structures, were implemented with the function 'lmer' from the package 'lme4' (Bates, Maechler, & Bolker, 2011). For all models, we checked the assumption that residuals were normally distributed and/or homogeneous by visually inspecting plots of the residuals and of the residuals against fitted values (Field, Miles, & Field, 2012). We also checked for model stability by excluding data points one by one and compared the resulting estimates with those obtained from the full model (Field et al., 2012). Variance inflation factors were derived using the function 'vif.mer' and were considered acceptable because all were below 4 (Field et al., 2012). Since we aimed to test general hypotheses about the influence of a set of predictor variables, rather than the influence of single predictor variables, on the response variable, we tested the full model (including all fixed effects and random effects) against a null model (including only the intercept, random factors and, when specified, control factors) using a likelihood ratio test (function 'anova' with argument test 'Chisq'). P values from GLMMs with Gaussian error structure were calculated based on Markov Chain Monte Carlo sampling and derived using the function 'pvals.fnc' of the package 'languageR' (Baayen, 2007). Whenever the full model was not statistically different from the null model, we report the estimates and standard errors but omit the P values. For details of the different models see Appendix Table A1 and for their full results see Appendix Tables A2–A5.

RESULTS

We based our analyses on 450 conflicts (PB: 173, median per female 7, range 6–20; R1: 277, median per female 12, range 6–24) on 207 of 315 dyads (PB: 76, median per dyad 2, range 1–8; R1: 141, median per dyad 2, range 1–9). In half of the cases ($N = 226$), the focal female was the recipient of aggression. Results are summarized in Tables 1 and 2.

Consequences of Aggression

Whether females were the aggressor or the recipient did not significantly affect the mean focal restlessness index, scratching frequency and secondary aggression frequency (Wilcoxon signed-ranks tests: restlessness: $V = 237$, $N = 32$, $P = 0.625$; scratching: $V = 245$, $N = 32$, $P = 0.733$; aggression: $V = 190$, $N = 32$, $P = 0.258$; Fig. 1a).

There was no significant difference in female mean restlessness and mean scratching frequency between PCs with no interaction and baseline (Wilcoxon test: restlessness: $V = 276$, $N = 36$, $P = 0.380$; scratching: $V = 271$, $N = 32$, $P = 0.205$; Fig. 1b). There was also no significant difference between mean scratching frequencies in PCs with interactions (of any kind) and PCs without interactions (Wilcoxon test: $V = 177$, $N = 32$, $P = 0.168$). Female mean aggression frequency was higher in PCs compared to the baseline (Wilcoxon test: $V = 10$, $N = 36$, $P < 0.001$; Fig. 1b).

Females were more likely to scratch after low-intensity conflicts, and were more restless when conflicts were undecided (Table A2, Models 1a, b). None of the conflict characteristics had a significant influence on the occurrence of secondary aggression (Table A2, Model 1c). Similarly, there was no evidence that fighting within a specific dyad had any effect on anxiety and on the likelihood of secondary aggression (Table A2, Models 1a–c).

Occurrence of Postconflict Interactions

Postconflict affiliation between opponents

Females affiliated with their opponent in 47% of PC periods. Female opponents affiliated and remained within proximity of each other significantly more often during PCs than baseline (Table A3, Models 2a, b).

Postconflict affiliation between opponents and third parties

Female opponents affiliated with a third-party individual in 62% of PCs. The overall frequency of affiliation with third-party individuals in PCs was significantly higher than baseline affiliation levels (Table A3, Model 2c). However, females gave and received affiliations equally often in PCs and baseline (Wilcoxon tests: affiliation given: PC $= 0.07 \pm 0.09$ per min, baseline $= 0.06 \pm 0.05$, $V = 304$, $N = 36$, $P = 0.658$; affiliation received: PC $= 0.05 \pm 0.06$, baseline $= 0.04 \pm 0.04$, $V = 341$, $N = 36$, $P = 0.907$). Previous opponents initiated 57% of affiliations with third parties. Females were more likely to affiliate with a third party when they had previously affiliated with their opponent (73% versus 54%; Table A4, Models 3a, b).

Postconflict aggression between opponents and between opponents and third parties

We observed a total of 205 bouts of secondary aggression occurring in 36% of PC periods. Aggression occurred more frequently in PCs than overall aggression during baseline (Wilcoxon test: $V = 10$, $N = 36$, $P < 0.001$). Females both gave and received more aggression in PCs than baseline (Wilcoxon tests: aggression given: PC $= 0.05 \pm 0.03$ per min, baseline $= 0.02 \pm 0.01$, $V = 83$, $N = 36$, $P < 0.001$; aggression received: PC $= 0.04 \pm 0.03$, baseline $= 0.01 \pm 0.00$, $V = 55$, $N = 36$, $P < 0.001$). Aggression flared up again between the two previous opponents in only 8% of all cases (renewed aggression, $N = 15$); in half of these cases, renewed aggression occurred despite reconciliation having already taken place. Recipients redirected aggression in 13% of PCs (redirection, $N = 58$). In 56% of these cases, females simultaneously left the proximity of their aggressor, thereby ending the initial conflict. Of the bouts of secondary aggression other than renewed aggression and redirection ($N = 132$), 56% were initiated by one of the opponents.

Functions of Postconflict Interactions

Stress reduction hypothesis

Females were not less likely to scratch or to be less restless when reconciliation occurred than when it did not occur (Table A2, Models 1a–c). Females affiliating with third-party individuals scratched less, but were not less restless (Table A2, Models 1a–c). Scratching and restlessness were not influenced by the reoccurrence of aggression (Table A2, Models 1a, b; for redirected aggression: Wilcoxon tests: restlessness: $V = 82$, $N = 20$, $P = 0.409$; scratching: $V = 108$, $N = 20$, $P = 0.352$; secondary aggression: $V = 190$, $N = 20$, $P = 0.257$).

Females reconciled significantly more often when conflicts occurred in a social context (58% versus 21%), when conflicts were undecided (70% versus 30%) or shorter (35% of above-mean duration versus 51% of below-mean duration), and when redirected aggression did not occur (48% versus 36%; Table A4, Model 3a). Females affiliated significantly more often with third-party individuals when conflicts occurred in a social context (73% versus 37%; Table A4, Model 3b). There was no evidence that conflict characteristics influenced the occurrence of secondary aggression (Table A2, Model 1c).

Relationship repair hypothesis

There was a large variation in the dyadic proportion of reconciled conflicts: 20% of dyads that had conflicts ($N = 207/315$) never reconciled, and 23% always reconciled. Overall, dyads reconciled after 45% of their conflicts. At the conflict level, we found that dyads with a higher asymmetry in affiliation (48% for dyads with an above-mean symmetry versus 46%), or that exchanged less counteraggression (51% for dyads with a below-mean counteraggression frequency versus 46%) were more likely to reconcile compared to other dyads (Table A4, Model 3a). In addition, in general, dyads with a higher asymmetry in affiliation, a lower variation in grooming duration over time and a smaller frequency of aggressive interactions showed more reconciliation after conflicts than other dyads (Table A5, Model 4).

Females did not affiliate more often with female third parties with which they had a higher than average CSI score (mean $\mathrm{CSI}_{\mathrm{third\ party}} = 1.81 \pm 0.95$, mean $\mathrm{CSI}_{\mathrm{baseline}} = 1.58 \pm 0.97$; one-sample Wilcoxon signed-ranks tests: $V = 2\,534$, $N = 92$, $P = 0.124$), but they did affiliate more often with female third parties closer in Elo rating than the average difference (mean $\mathrm{Elo}_{\mathrm{third\ party}} = 641 \pm 471$, mean $\mathrm{Elo}_{\mathrm{baseline}} = 849 \pm 576$; one-sample Wilcoxon tests: $V = 1033$, $N = 92$, $P < 0.001$). Secondary aggression between females occurred regardless of their CSI score or their Elo rating difference (one-sample Wilcoxon tests: mean $\mathrm{CSI}_{\mathrm{third\ party}} = 1.88 \pm 1.11$, mean $\mathrm{CSI}_{\mathrm{baseline}} = 1.58 \pm 0.97$, $V = 848$, $N = 53$, $P = 0.241$; mean $\mathrm{Elo}_{\mathrm{third\ party}} = 785 \pm 580$, mean $\mathrm{Elo}_{\mathrm{baseline}} = 849 \pm 576$, $V = 536$, $N = 53$, $P = 0.112$).

Self-protection hypothesis

Overall, the role of the focal female in the initial bout of aggression did not significantly influence the occurrence of reconciliation, third-party affiliation or secondary aggression (Table A2, Model 1c, Table A4, Models 3a, b). Recipients did not initiate significantly more affiliation with third parties than aggressors (Wilcoxon test: $V = 211$, $N = 36$, $P = 0.657$). Furthermore, aggressors initiated significantly more aggression towards third parties than recipients (Wilcoxon test: $V = 409$, $N = 36$, $P < 0.001$).

Female recipients redirected aggression towards lower-ranking individuals in 98% of all instances (juveniles: 75% of cases; females: 23% of cases (all of a lower rank than the recipient); males: 2%). Secondary aggression from opponents towards third parties was generally directed down the hierarchy (83% of instances directed at lower-ranking individuals than the opponents).

The occurrence of postconflict affiliation did not significantly lower the likelihood of secondary aggression (Table A2, Model 1c). Reconciliation was less likely when redirection occurred (Table A4, Model 3a). Females were more likely to affiliate with a third party when they also redirected aggression (67% versus 62%) or, in general, when they were involved in secondary aggression (70% versus 59%; Table A4, Model 3b).

Benign intent hypothesis

Recipients did not initiate significantly more reconciliation than aggressors (59% of reconciliations initiated by recipients; Wilcoxon test: $V = 259$, $N = 36$, $P = 0.930$). Higher-ranking females initiated significantly more reconciliation than lower-ranking females (64% initiated by the higher-ranking female; Wilcoxon test: $V = 419$, $N = 36$, $P < 0.001$). Reconciliation tended to be more likely when lower-ranking females had initiated the previous conflict (77% versus 40%; Table A4, Model 3a). Of first contact affiliations, 59%, which was significantly higher than chance (proportion test: $N_{\mathrm{initiator}} = 75$, $N_{\mathrm{total}} = 127$, 95% $\mathrm{CI} = 0.50–0.68$, $P = 0.051$), were preceded by a noncontact affiliative behaviour such as lipsmacking or grunting.

DISCUSSION

The study of postconflict interactions in the females of a wild population of tolerant macaques provides a novel perspective on their functions. The occurrence of aggression did not increase the measured level of anxiety in opponents, but it did increase the likelihood of further aggression in the subsequent period. Conflict and dyad characteristics had little influence either on the tested behavioural indicators of anxiety or on the occurrence of any of the three postconflict interactions investigated. The patterns uncovered in wild female crested macaques thus indicate different functions of postconflict interactions in this population, compared to other macaques in particular and, to our knowledge, other animal societies in general.

The fact that the occurrence of aggression did not increase behavioural indicators of anxiety in aggressors or in recipients stands in stark contrast with what is generally found in other animals. Thus, although scratching has been linked to anxiety in numerous species, including humans (Maestripieri, Schino, Aureli, & Troisi, 1992; Schino, Perretta, Taglioni, Monaco, & Troisi, 1996), it is possible that scratching and anxiety levels are weakly correlated in tolerant species (see De Marco, Cozzolino, Dessi-Fulgheri, & Thierry, 2010, 2011; but also Aureli & Yates, 2010). Recording of other displacement activities and/or physiological parameters such as heart rate, blood pressure or stress hormones could provide a more detailed anxiety profile. Another possible explanation for this pattern could be that females were ‘too busy to scratch’ given that postconflict interactions occurred overall in 63% of PCs, and happened quickly and in rapid succession. In contrast, in more despotic macaques, affiliation after conflicts is rarer, leaving room for the expression of anxiety (Cooper & Bernstein, 2008; Majolo et al., 2009a; Thierry et al., 2008). More significantly, since conflict characteristics had little influence on behavioural indicators of anxiety, it seems that conflicts between the study females were not overly costly or were not perceived as risky. In comparison to despotic species, conflicts were of lower intensity (i.e. with less biting) so the risk of being wounded was indeed lower (Duboscq et al., 2013;

Thierry et al., 2008). Since crested macaque females also showed high rates of counteraggression, a fair amount of aggressive interactions were undecided, that is, without a clear winner and loser, and power asymmetries were moderate (Duboscq et al., 2013). The low reactivity of females to potentially stressful events, i.e. conflicts, thus seems to be related to the mild nature of these conflicts, making it plausible that social exchanges are less stressful (Aureli & Schaffner, 2006; de Waal, 1986, 1996). These patterns are mostly consistent with existing results from captive crested macaques (Petit & Thierry, 1994b; Petit et al., 1997) and other tolerant Sulawesi macaques (semifree-ranging Tonkean macaques, *Macaca tonkeana*, Demaria & Thierry, 2001; wild Moor macaques, *Macaca maurus*, Matsumura, 1996), which suggests that the function of postconflict interactions depends on the social style of the species.

Our results show contrasting patterns not only with regard to the consequences of aggression, but also with regard to our predictions about the functions of postconflict events. There was little evidence for the stress reduction hypothesis. Female opponents affiliating with third parties saw their scratching levels reduced compared to baseline, but otherwise, the occurrence of postconflict interactions had little effect on the opponents' behavioural indicators of anxiety. The occurrence of positive postconflict interactions also did not seem to prevent the reoccurrence of aggressive ones. This is at odds with most of the literature in nonhuman primates (Arnold & Aureli, 2006; Aureli et al., 2012) and other mammals (e.g. domestic goat, *Capra hircus*, Schino, 1998). None the less, these particular findings are understandable given that aggression had no effect on behavioural indicators of anxiety in the first place, and in the light of crested macaques' conflict characteristics, that is, low intensity and high frequency of bidirectional aggression.

Again, contrary to what we expected and to what has been reported in many other animal species (nonhuman primates, Arnold & Aureli, 2006; Aureli et al., 2012; canids, Cools, van Hout, & Nelissen, 2008; Cordoni & Palagi, 2008; common raven, *Corvus corax*, Fraser & Bugnyar, 2011) and in humans (Fry, 2000), partners with a higher CSI ('friends', i.e. dyads that associated and groomed above average), a lower rank difference (potential kin) and a higher frequency of support ('valuable' partners) did not reconcile more often than those with 'weaker' relationships. Female opponents affiliated more frequently with female third parties that were close to them in dominance rank, but this may be a general effect in female primates (Schino, 2001), not specific to postconflict interactions. Overall, these findings may be related to the large affinitive networks these females form, where they largely distribute their grooming and approaches in proximity among their female partners (Duboscq et al., 2013). Thus, in contrast with the expectation of the relationship repair hypothesis, female crested macaques may work at mending a majority of their relationships, and not only the stronger, more compatible or more valuable ones in the sense of Cords and Aureli (2000). However, we did not investigate long-term benefits of postconflict interactions on social relationships. It is possible that reconciliation promotes reciprocity in grooming, or lowers the probability of aggression in future interactions (Koyama, 2001; Silk, Cheney, & Seyfarth, 1996). Alternatively, our results shed light on other relationship characteristics that female crested macaques may value: dyads with more asymmetric affinitive interactions but less aggression and a more consistent exchange of grooming throughout the study period were more likely to reconcile. This may seem paradoxical at first glance. On the one hand, a predictable and stable relationship, however asymmetric, should be worth preserving. On the other hand, regardless of the stability/predictability of the relationship, reconciling asymmetrical relationships may underlie the high motivation to reconcile of both the dyad member most responsible for maintaining the relationship and the member receiving the benefits of the relationship. Altogether, these results stress the importance of considering all aspects of a relationship since the different components may have different weights for the individuals in species with different social styles.

Since the two major functions of postconflict interactions could not be readily confirmed in females of this population of crested macaques, the self-protection and benign intent hypotheses remain as potential explanatory functions. Related to a self-protection function, the risk of renewed aggression between opponents was low, and reconciliation did not prevent the reoccurrence of hostility between them. In addition, given that, in general, positive interactions did not prevent the reoccurrence of negative ones, affiliative postconflict interactions were unlikely to serve a self-protection function (but see below on the benign intent hypothesis). Aggressors were more often the initiators of secondary aggression towards third parties. They also received more affiliation from third parties than recipients, although not significantly, suggesting that third parties could intervene to appease aggressors. However, since affiliation with third parties was not associated with less secondary aggression from/to third parties, an appeasing effect was unlikely. Aggression towards third parties was mainly directed at lower-ranking individuals, especially redirected aggression, which is consistent with a majority of findings in other animals (Kazem & Aureli, 2005). From the recipient's perspective, these results thus support a self-protection effect of aggression towards third parties in the sense that redirection may serve to reverse a 'loser effect', thereby helping to re-establish social status or to 'score psychological victories' (Aureli et al., 2012; Watts et al., 2000). Additionally, given that redirection stopped the initial conflict in more than half of the cases, the initial recipients may also initiate secondary aggression when it is less costly or more beneficial to leave the conflict, for example, to avoid escalating aggression (Thierry, 1985). From the aggressor's perspective, directing aggression towards third parties, especially lower-ranking ones, may serve the function of reinforcing a 'winner effect' (Aureli et al., 2012). This makes sense in crested macaques considering that there is no obvious signal of submission which females can rely on to assess their status (Duboscq et al., 2013; Petit et al., 1997; Thierry et al., 2000).

Lastly, consistent with a benign intent function, more than half of the first reconciliatory affiliations with contact started with a noncontact affiliative behaviour such as lipsmacking. Similarly, in chacma baboons, *Papio ursinus*, and chimpanzees, *Pan troglodytes schweinfurthii*, opponents were more successful at engaging in reconciliation if they 'signalled' their peaceful intentions with vocalizations during or before initiating affiliative body contact (Arnold & Whiten, 2001; Cheney, Seyfarth, & Silk, 1995; Silk et al., 1996). In addition, higher-ranking females initiated reconciliation more frequently than lower-ranking ones. Reconciliation was also more likely to follow aggression with unexpected directionality, that is, from lower- to higher-ranking females. The elevated risk of counteraggression in crested macaques could thus produce a strong incentive for higher-ranking individuals to be conciliatory in order to avoid subsequent escalation, potential coalition formation or long harmful conflicts. This may indicate a self-protection function of reconciliation for the higher-ranking females, in addition to signalling benign intent. These findings are indeed also in line with the prediction that when retaliation is likely to happen, as is the case with female crested macaques, recipients should initiate postconflict contact to signal their peaceful intent and their willingness to avoid escalation (Silk, 1996).

Finally, the co-occurrence of different types of postconflict interactions was not explained by the sequence of interactions: affiliation with a third party did not necessarily follow secondary aggression and thus did not constitute a reconciliation episode between one of the opponents and the third party. Also, on average, secondary aggression occurred later than affiliation with a third party and the partners involved were rarely the same. This co-occurrence of different kinds of interactions with different partners could reflect a general response to the arousal induced by the initial conflict. This explanation has been proposed, for instance, to account for the occurrence of quadratic affiliations, that is, affiliative interactions arising between bystanders right after a conflict they were not involved in (De Marco et al., 2010; Judge & Mullen, 2005). This finding is consistent with the idea that the occurrence of postconflict interactions is driven by emotional arousal, which would trigger mechanisms to restore tolerance and to re-establish cooperation between partners (Aureli & Schaffner, 2013; Aureli & Schino, 2004).

Overall, postconflict interactions in wild female crested macaques show a different profile from those in a majority of other macaque and primate species. From the opponents' point of view, our results do not substantiate the stress reduction hypothesis and only partly support the relationship repair hypothesis. This does not, however, undermine the value of these hypotheses for other species. The patterns uncovered in this population make sense in light of its tolerant social style. In contrast to more despotic ones, individuals from tolerant species are subjected to fewer hierarchical and nepotistic constraints and they interact with numerous and diverse partners (Duboscq et al., 2013; Sueur et al., 2011). These extended social networks may allow individuals of tolerant species to maintain group cohesion and to enhance information transmission at a low cost through elaborate and efficient social exchanges (de Waal, 1986).

The present conclusions, although drawn from the study of a single population of wild crested macaques, highlight the need for further systematic investigations, especially in nonprimate species, to achieve a more comprehensive understanding of conflict management strategies in animal societies. Many gregarious animals form social units with permanent or recurrent membership, and individualized relationships (Aureli, Cords, & van Schaik, 2002). In this context, individuals benefit from having mechanisms to maintain or to restore tolerance between group members and, ultimately, to preserve the benefits of sociality (e.g. spotted hyaenas, *Crocuta crocuta*, Hofer & East, 2000; toothed whales, Samuels & Flaherty, 2000). From this perspective, factoring in the level of despotism versus tolerance in social structure appears to be a valuable analytical tool to unravel the full range of mechanisms and functions of conflict management strategies in animal societies.

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Appendix

Table A1
Lists of generalized linear mixed models, with number of cases (*N*), response variable, its state (category) and transformation (only given once per variable), main and control fixed-effect factors and their levels if categorical, and random-effect factors

	N	Responses	Category (transformation)	Main fixed factors (transformation)	Control fixed factors	Random factors
Model 1						
1a	450	Occurrence scratching	Binomial	Affiliation opponents: yes/no Affiliation 3rd party: yes/no CSI (4th root) |Elo difference| (square root) Sign Elo difference: +/− ASI CV (4th root) Aggression (4th root) Counteraggression (4th root) Support (4th root) Aggression duration (log) Intensity: display/contact Decided: yes/no Polyadic: yes/no Context: social/food Redirection: yes/no [a,b]Renewed: yes/no	Focal recipient: yes/no	Aggressor, recipient Group
1b	424	Restlessness	Continuous			
1c	450	Occurrence aggression	Binomial			
Model 2						
2a	210	Affiliation opponent	Continuous/square root	Session: PC/baseline	Focal recipient: yes/no	Focal group
2b	210	Proximity opponent	Continuous/log			
2c	283	Affiliation opponent/ third party	Continuous/log			
Model 3						
3a	450	Occurrence affiliation opponent	Binomial	[a,b]Affiliation 3rd party: yes/no [c]Affiliation opponent: yes/no CSI |Elo difference| Sign Elo difference: +/− ASI CV Aggression Counteraggression Support Aggression duration Intensity: display/contact Decided: yes/no Polyadic: yes/no Context: social/food Redirection: yes/no [c]Renewed: yes/no	Focal recipient: yes/no	Aggressor, recipient, group
3c	450	Occurrence affiliation opponent/3rd party	Binomial			
Model 4						
	270	No. of reconciled conflicts	Count	|Elo difference| CSI ASI CV Aggression Counteraggression Support	Offset term: no. of bouts of aggression per dyad	Member 1, member 2, group

CSI, ASI, CV = see Methods. Letters in superscript a, b and c refer to model in the same category in which the superscripted variable is included (for example, Model 3a, 3b or 3c).

Table A2
Influence of affiliation between opponents, affiliation with third parties, conflict and dyad characteristics on the occurrence of scratching (Model 1a), the restlessness index (Model 1b) and the occurrence of secondary aggression (Model 1c)

		Model 1a			Model 1b			Model 1c	
	LRT test Full vs null	$\chi^2_{17} = 29,\ P = 0.034$			$\chi^2_{17} = 382,\ P < 0.001$			$\chi^2_{16} = 13,\ P = 0.685$	
Factors	Variables	β	SE	*P*	β	SE	P_{MCMC}	β	SE
Fixed	Intercept	−0.943	0.569	0.098	0.013	0.265	0.943	−1.104	0.565
	Affiliation with opponent (y)	−0.384	0.289	0.183	0.079	0.136	0.606	−0.241	0.301
	Affiliation with 3rd party (y)	−0.530	0.268	0.048	−0.195	0.127	0.127	0.531	0.283
	CSI	−0.059	0.163	0.717	0.159	0.084	0.116	0.097	0.168
	|Elo difference|	0.119	0.144	0.407	0.078	0.067	0.278	−0.056	0.147

Table A2 (*continued*)

		Model 1a			Model 1b			Model 1c	
	LRT test Full vs null	$\chi^2_{17} = 29,\ P = 0.034$			$\chi^2_{17} = 382,\ P < 0.001$			$\chi^2_{16} = 13,\ P = 0.685$	
Factors	Variables	β	SE	*P*	β	SE	P_{MCMC}	β	SE
	Sign Elo (+)	0.381	0.351	0.278	0.287	0.165	0.096	0.154	0.354
	ASI	−0.006	0.136	0.963	−0.047	0.066	0.569	0.058	0.137
	CV	−0.027	0.144	0.851	−0.078	0.071	0.220	0.087	0.146
	Aggression	−0.014	0.135	0.917	−0.076	0.067	0.395	−0.012	0.140
	Counteraggression	−0.061	0.136	0.656	0.012	0.062	0.773	0.001	0.135
	Support	0.010	0.151	0.948	−0.053	0.068	0.357	−0.113	0.156
	Context (social)	0.216	0.352	0.506	−0.157	0.148	0.269	0.534	0.337
	Intensity (n)	1.044	0.395	0.008	0.172	0.169	0.376	−0.266	0.369
	Decided (y)	0.169	0.252	0.603	−0.315	0.151	0.047	0.139	0.330
	Polyadic (y)	−0.002	0.310	0.996	0.132	0.149	0.401	−0.096	0.321
	Duration	0.061	0.129	0.635	−0.064	0.061	0.295	−0.027	0.134
	Redirection (y)	0.059	0.385	0.878	0.159	0.180	0.369	−0.819	0.432
	Secondary aggression (y)	−0.248	0.254	0.329	−0.029	0.119	0.787		
Control	Focal (recipient)	0.041	0.243	0.866	−0.047	0.114	0.689	−0.105	0.667
Random	Aggressor/group	0.000	0.000		0.028	0.168		0.013	0.106
	Recipient/group	0.001	0.013		0.000	0.000		0.000	0.000

When the full model is not different from the null model, only the estimates and standard errors are given. See Methods for details and acronyms.

Table A3

Differences between PC and baseline levels of opponent affiliation per proximity scans (Model 2a), opponent presence in proximity (Model 2b) and frequency of opponent/third party affiliation (Model 2c)

		Model 2a			Model 2b			Model 2c		
	LRT test Full vs null	$\chi^2_1 = 124,\ P < 0.001$			$\chi^2_1 = 474,\ P < 0.001$			$\chi^2_1 = 124,\ P < 0.001$		
Factors	Variables	β	SE	P_{MCMC}	β	SE	P_{MCMC}	β	SE	P_{MCMC}
Fixed	Intercept	0.502	0.019	0.001	−0.403	0.009	0.001	2.367	0.047	0.001
	Session (PC)	0.241	0.020	0.001	0.450	0.010	0.001	0.479	0.040	0.001
Control	Focal (recipient)	0.024	0.021	0.252	−0.017	0.011	0.133	−0.007	0.043	0.898
Random	Focal/group	0.001	0.024		0.000	0.000		0.029	0.170	

See Methods for details and acronyms.

Table A4

Influence of conflict and dyadic characteristics on the occurrence of affiliation between opponents (Model 3a) and the occurrence of affiliation with third parties (Model 3b)

		Model 3a			Model 3b		
	Full vs null LRT test	$\chi^2_{16} = 110,\ P < 0.001$			$\chi^2_{16} = 55,\ P < 0.001$		
Factors	Variables	β	SE	*P*	β	SE	*P*
Fixed	Intercept	0.686	0.619	0.268	−0.471	0.584	0.420
	Affiliation between opponents (y)				0.595	0.311	0.056
	Affiliation with 3rd parties(y)	0.557	0.313	0.076			
	CSI	0.253	0.193	0.190	0.086	0.182	0.637
	|Elo difference|	−0.277	0.179	0.122	−0.130	0.155	0.404
	Elo sign (+)	−0.814	0.432	0.061	−0.257	0.390	0.510
	ASI	0.352	0.166	0.033	0.135	0.152	0.375
	CV	−0.093	0.178	0.599	−0.206	0.156	0.189
	Aggression	−0.015	0.162	0.926	0.150	0.149	0.314
	Counteraggression	−0.458	0.166	0.006	0.249	0.162	0.125
	Support	0.011	0.182	0.951	−0.028	0.164	0.863
	Context (social)	1.413	0.381	0.001	1.075	0.325	0.001
	Intensity (n)	−0.484	0.420	0.249	−0.029	0.404	0.943
	Decided (y)	−1.518	0.358	0.001	−0.136	0.355	0.702
	Poly (y)	0.045	0.361	0.901	0.113	0.339	0.740
	Duration	−0.304	0.153	0.047	0.139	0.144	0.334
	Redirection (y)	−1.102	0.458	0.016	0.838	0.433	0.054
	Secondary aggression (y)	−0.264	0.302	0.383	0.518	0.279	0.095
Control	Focal (recipient)	0.066	0.288	0.818	−0.059	0.263	0.821
Random	Aggressor/group	0.000	0.000		0.000	0.000	
	Recipient/group	0.016	0.125		0.000	0.000	

See Methods for details and acronyms.

Table A5
Influence of dyad characteristics on the dyadic number of reconciled conflicts (Model 4)

	Full vs null LRT test	$\chi^2_7 = 94,\ P < 0.001$		
Factors	Variables	β	SE	*P*
Fixed	Intercept	0.562	0.092	0.001
	CSI	0.054	0.071	0.442
	|Elo difference|	−0.123	0.071	0.084
	CV	−0.169	0.073	0.020
	ASI	0.197	0.058	0.001
	Aggression	−0.505	0.052	0.001
	Counteraggression	0.012	0.061	0.841
	Support	0.114	0.077	0.135
Random	Member 1/group	0.017	0.131	
	Member 2/group	0.033	0.182	

See Methods for details and acronyms.