



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.

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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,

& Kotschal, 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

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