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The occurrence and benefits of postconflict bystander affiliation in wild Barbary macaques, *Macaca sylvanus*

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The majority of studies investigating conflict management in animal societies have focused on the role of reconciliation in mediating the costs of aggression. The function of bystander affiliation (i.e. the selective attraction between an opponent and a bystander in the minutes immediately following aggression) is less well understood. We examined, in wild Barbary macaques, four potential functions of bystander affiliation with the victim of aggression: (1) bystander-initiated affiliation to reduce the victim's postconflict (PC) anxiety (i.e. 'consolation'), (2) victim-initiated affiliation (i.e. 'solicited consolation'), (3) victim- and bystander-initiated affiliation to avert redirected aggression (i.e. self-protection), and (4) bystander-initiated affiliation to exploit grooming from the victim. We found partial support for the consolation function as bystander-initiated affiliation occurred more frequently between high-quality social partners but had no effect on the victim's PC anxiety. In support of the solicited-consolation function, victim-initiated affiliation occurred more frequently between high-quality social partners and also caused a reduction in the victim's PC anxiety. These findings suggest that solicited consolation may substitute for the stress alleviation role of reconciliation. We found no support for a self-protective function as neither the bystander's nor the victim's risk of receiving PC aggression was reduced following bystander affiliation with the victim. Finally, bystanders received significantly more PC grooming than victims, suggesting that grooming exploitation of the victim may drive the bystander's PC behaviour. Our results indicate that bystander affiliation has different functions and benefits for the victim of aggression and the bystander, and highlights the importance of considering which individual initiates this behaviour.

In group-living species, conflict between group members is sometimes inevitable as individuals strive for dominance and compete for valuable resources. Opponents experience a number of costs in the minutes immediately following aggression, including, for example, an increased risk of receiving renewed aggression from a former opponent or bystander, elevated postconflict (PC) anxiety, and reduced feeding opportunities or grooming exchange (Schino 2000; Aureli et al. 2002; McFarland & Majolo 2011b). Therefore, analysing the mechanisms used to mediate the costs of aggression is fundamental to our understanding of how social relationships are maintained in animal societies.

Reconciliation, the PC exchange of friendly behaviour between the victim and aggressor (Aureli & de Waal 2000), mediates the costs of aggression by repairing the opponents' social relationship damaged by the conflict, and by reducing their PC anxiety and risk of receiving renewed aggression (Aureli & de Waal 2000). Reconciliation has been demonstrated in over 30 primates (Aureli & de Waal 2000) and several nonprimate species (e.g. domestic goats, *Capra hircus*: Schino 2000; wolves, *Canis lupus*: Cordoni & Palagi 2008; ravens, *Corvus corax*: Fraser & Bugnyar 2011). Postconflict bystander affiliation may also be effective at mediating the opponent's costs of aggression (Fraser et al. 2009). Bystander affiliation is defined as the exchange of friendly behaviour between an opponent and a bystander (i.e. an animal not involved in the former conflict) in the minutes immediately following aggression (Judge 1991). It has been demonstrated in apes (Fraser et al. 2009), wolves (Palagi & Cordoni 2009), ravens (Fraser & Bugnyar 2010), rooks, *Corvus frugilegus* (Seed et al. 2007) and horses, *Equus caballus* (Cozzi et al. 2010). However, to date, numerous studies have failed to provide support for the occurrence of bystander affiliation in Old World monkeys (Watts et al. 2000). Moreover, the function of bystander affiliation is less well understood when compared to reconciliation (Aureli et al. 2002; Fraser et al. 2009).

Bystander affiliation can be beneficial for the bystander and the victim (Verbeek & de Waal 1997; Fraser et al. 2009). However, studies conducted so far have often failed to take into account the

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identity of both potential initiators of the affiliation (i.e. victim or bystander). In this study, we aimed to analyse bystander affiliation in wild Barbary macaques while taking into account the identity of the initiator of the affiliation. Specifically, we aimed to test four main, nonmutually exclusive proximate functions of bystander affiliation: (1) consolation (bystander-initiated), (2) solicited consolation (victim-initiated), (3) self-protection (bystander- or victim-initiated), and (4) exploitation (bystander-initiated). To our knowledge, this is the first study to test these functions of bystander affiliation empirically in a wild nonape species.

Consolation describes the PC scenario whereby bystanders respond to the anxiety of the victim and thus initiate affiliation to appease them (de Waal & Aureli 1996). Despite being a rather anthropomorphic term, consolation might be an innate response in the bystander, elicited by behavioural signs of anxiety in the victim (i.e. self-scratching), that do not involve empathy. We predicted that consolation would reduce PC anxiety in the victim (de Waal & Aureli 1996; Aureli 1997; Wittig & Boesch 2003; Palagi et al. 2004). Moreover, we predicted that consolation would occur more frequently between high-quality social partners (i.e. between individuals exchanging high rates of affiliation), as bystanders should be more responsive to the signs of anxiety of their friends (Aureli & Schaffner 2002; Fraser et al. 2008a; Fraser & Bugnyar 2010; Romero & de Waal 2010).

When testing the solicited-consolation function, we predicted that victims would initiate affiliation with bystanders to reduce their own PC anxiety (de Waal & Aureli 1996; Verbeek & de Waal 1997). We also predicted that victims would solicit consolation from bystanders with whom they shared high-quality relationships, as these individuals may be more effective at reducing their PC anxiety (Aureli & Schaffner 2002; Fraser et al. 2008a). Therefore, the consolation and solicited-consolation functions shared similar predictions but differed in the identity of the initiator of PC affiliation (bystander or victim, respectively).

For the self-protection functions, we first analysed whether bystanders face an increased risk of receiving redirected aggression from the victim or aggressor in the PC period (we have previously shown that the victim is at risk of receiving renewed PC aggression from the aggressor or bystander: McFarland & Majolo 2011b). If the bystander or the victim was at risk of receiving PC aggression from each other or from the aggressor (Koski & Sterck 2007), we predicted that the bystander or the victim, respectively, would affiliate in order to reduce such risk.

To our knowledge, the exploitation function has never been tested before (Fraser et al. 2009). For this function, we predicted that more PC grooming would be received by the bystander from the victim, than vice versa, and that bystanders would target subordinate victims more often than dominants (as subordinate group members tend to give more grooming: Schino 2001; Fruteau et al. 2011). This scenario would be similar to what we found in a previous study (McFarland & Majolo 2011a), showing that, in Barbary macaques, the aggressor often initiates PC affiliation with the victim (i.e. reconciliation) to gain grooming opportunities.

METHODS

Study Subjects and Field Site

Between September 2008 and August 2009, data were collected daily from 48 individuals living in two groups ('Flat-face' and 'Large') of wild Barbary macaques, in the Middle Atlas Mountains of Morocco (33°24′N – 005°12′W). At the beginning of the study, group sizes were 19 (11 males, eight females) and 29 (19 males, 10 females) adults and subadults for the 'Flat-face' and 'Large' group, respectively. These groups were not provisioned and relied on a completely natural diet. Study animals were fully habituated to the presence of researchers (i.e. they did not change their activity when we moved around the study group) and were individually identified via facial characteristics and body size. Permission to conduct our research was granted by the Haut Commissariat des Eaux et Forêts et à la Lutte Contre la Désertification of Morocco. This study complies with Moroccan and U.K. regulations regarding the ethical treatment of research subjects.

Data Collection

Data were collected following the postconflict–matched-control (PC–MC) method (de Waal & Yoshihara 1983; McFarland & Majolo 2011b). The identity and role of the opponents (i.e. aggressor or victim) were recorded whenever aggression was exchanged between two or more individuals. Aggression was recorded when at least one of the following behaviours was observed: threat, lunge, chase, slap, grab or bite. The aggressor was defined as the initiator of the first aggressive display. The victim was the recipient of this aggression. Based on the outcome of unidirectional aggressive and submissive interactions collected during baseline focal (see below) and ad libitum observations, relative dominance positions (i.e. ranks) were determined for each group member using MatMan 1.0 Software (de Vries et al. 1993). The role of the monkeys in a conflict reflected their dominance relationships, as the aggressor was dominant over the victim in 96% of cases ($N = 398$ of 414 conflicts observed) and only 4% of conflicts involved counteraggression (i.e. a victim being aggressive towards the former aggressor, $N = 17$ conflicts observed).

PC data were collected from either the victim ($N = 191$) or the aggressor ($N = 223$) of the conflict for 5 min. PC sessions were postponed if aggression between the former opponents recommenced within 30 s of the initial conflict, as the conflict was then considered to be still in progress (Aureli 1997). PC data collected from the victim were used to test the bystander-initiated consolation, victim-initiated solicited-consolation, victim- and bystander-initiated self-protection and the bystander-initiated exploitation functions. PC data collected from the aggressor or the victim were used to test whether bystanders were at risk of receiving PC aggression from the former aggressor or victim of the conflict. During PC sessions we recorded the timing and occurrence of any aggressive or friendly interaction exchanged between the focal opponent and any other group member. We considered grooming, body contact, mutual teeth chattering and successful $\leq$1.5 m approaches (i.e. approaches that were not followed by aggression or displacement for the first 30 s after the approach) as forms of friendly affiliation (Hesler & Fischer 2008; McFarland & Majolo 2011a, b). The initiator (e.g. victim or bystander) of the first PC friendly behaviour was recorded. We recorded all occurrences of self-scratching and used this behaviour as a measure of anxiety. There is comprehensive behavioural, physiological and pharmacological evidence that self-scratching is a reliable measure of anxiety in primates (Schino et al. 1991, 1996; Maestripieri et al. 1992; Barros et al. 2000; Troisi 2002). Moreover, in a previous study on the same animals (McFarland & Majolo 2011b) we showed that the victim experienced elevated PC self-scratching rates when compared to MC conditions.

MCs were collected within $\leq$2 weeks (mean = 4.63 days, range 1–14 days) of the matched PCs to control for any variation in the expression of grooming, aggression and self-scratching across the year. To standardize MC sessions further, we started MCs only when (1) the MC focal subject had not been involved in an aggressive interaction with another monkey in the 5 min prior to a planned MC, or during the MC, and (2) no other group member was in close proximity (i.e. $\leq$1.5 m) to the MC focal subject. We collected the