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Witnessing reconciliation reduces arousal of bystanders in a baboon group (*Papio hamadryas hamadryas*)

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Reconciliation is the occurrence of friendly behaviour between opponents shortly after an aggressive conflict. In primate groups, reconciliation reduces aggression and postconflict arousal. Aggression within a group can also increase arousal of bystanders (e.g. increase bystanders' rates of self-directed behaviour). Since reconciliation reduces aggression between opponents, we tested whether it also reduces self-directed behaviour in bystanders. Following aggression in a captive group of hamadryas baboons, one observer conducted a focal sample on one of the combatants to document reconciliation and a second observer simultaneously conducted a focal sample on a randomly selected bystander. Matched control observations were then collected on the same individuals in a nonaggressive context to obtain baseline levels of behaviour. The self-directed behaviour of bystanders was elevated after witnessing a fight compared to baseline levels. If combatants reconciled aggression, bystander rates of self-directed behaviour significantly decreased. If combatants did not reconcile aggression, bystander rates of self-directed behaviour remained at elevated levels, significantly higher than after reconciliation. If combatants affiliated with partners other than their original opponent, bystander rates of self-directed behaviour did not decrease. The rate of bystander self-directed behaviour after a combatant affiliated with its opponent was significantly lower than the rate after a combatant affiliated with other animals. Witnessing aggression increased arousal in bystanders, and reconciliation between the combatants was accompanied by reduced bystander arousal. The reduction was specific to contexts in which former opponents interacted. We suggest that bystanders recognized the functional significance of this conflict-resolution mechanism when it occurred in their group.

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Sociality has evolved because individuals living in groups derive benefits such as increased foraging efficiency, cooperative protection against predators and increased defence against competitors (van Schaik & van Hooft 1983). Social living also has costs, however, as intragroup competition for resources inevitably produces aggressive conflicts (van Schaik 1989). To reduce the costs of such conflicts and maintain group cohesion, group-living animals have developed mechanisms to manage or resolve conflicts (Cords & Killen 1998). One such mechanism is reconciliation, in which animals involved in an aggressive conflict exchange affiliative contacts shortly after the fight (de Waal & van Roosmalen 1979). The mechanism is fairly widespread as reconciliation has been demonstrated in almost every primate species investigated (Aureli

et al. 2002) as well as several group-living nonprimate species (domestic dogs, *Canis lupus familiaris*: Cools et al. 2008; wolves, *Canis lupus*: Cordoni & Palagi 2008; hyaenas, *Crocuta crocuta*: Wahaj et al. 2001; horses, *Equus caballus*: Cozzi et al. 2010; domestic goats, *Capra aegagrus*: Schino 1998; bottlenose dolphins, *Tursiops truncatus*: Weaver 2003; ravens, *Corvus corax*: Fraser & Bugnyar 2011).

Research on the function of postconflict reunions between combatants has shown that the term 'reconciliation' is appropriate in that reconciliation restores disrupted relationships, decreases the likelihood of further aggression and reduces emotional arousal in the combatants (Aureli et al. 2002). Weaver & de Waal (2003) have emphasized the arousal reduction function of reconciliation and have proposed that reconciliation develops in young primates as an arousal control mechanism regulating emotional homeostasis after a conflict (see also Aureli & Smucny 2000). Rates of self-directed behaviour, such as scratching and self-touching, are reliable indices of arousal (Maestriperieri et al. 1992) and are typically used to assess the arousal reducing function of reconciliation. For example, a combatant's rates of self-directed behaviour are

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elevated over baseline immediately after a fight (Schino et al. 1988; Aureli et al. 1989) and return to baseline levels following reconciliation (Castles & Whiten 1998). The return to baseline is specific to affiliative contact with the former opponent as contacts with third parties not involved in the conflict do not typically reduce rates of self-directed behaviour to baseline levels (Das et al. 1998; Romero et al. 2009).

In complex societies, triadic interactions sometimes occur in which other group members become involved in dyadic aggressive encounters and influence the outcome. Third parties are likely to join a fight and either aggressively aid the aggressor or defend the victim (Cheney & Seyfarth 1986, 1989; Aureli & van Schaik 1991; Aureli et al. 1992). Uninvolved third parties are also likely to affiliate with the aggressor or the victim in the aftermath of a fight (reviewed in: Das 2000; Watts et al. 2000). Furthermore, the third parties that affiliate are often the kin or other close associates of one of the combatants (Judge 1991; Das et al. 1997; Call et al. 2002; Fraser et al. 2008; Wittig & Boesch 2010). Affiliative interactions of third parties with former combatants have been interpreted as 'appeasement' of aggressors, 'consolation' to the victim, or 'substitute reconciliation' for one of the opponents (de Waal & van Roosmalen 1979; Palagi et al. 2006; Wittig et al. 2007; Fraser & Aureli 2008; Fraser et al. 2008; Romero & de Waal 2010, 2011; Wittig & Boesch 2010). Caution should be used when applying such terms, however, since they imply unknown underlying motivations of the animals and they involve largely untested functions. Recent work has tested the appropriateness of such terms and the potential causes and consequences of triadic postconflict interactions (Koski & Sterck 2007, 2009; Fraser et al. 2009; Romero et al. 2009; Romero & de Waal 2010; Wittig & Boesch 2010). For our purposes, we have operationally defined any postconflict affiliative contact between a third party and an aggressor or victim as 'third-party affiliation' without suggesting any underlying function.

On another level, dyadic aggression also influences the aggressive and affiliative behaviour among uninvolved bystanders (Cheney & Seyfarth 1989; Judge & Mullen 2005). For example, in captive hamadryas baboons, *Papio hamadryas hamadryas*, a bystander was more likely to affiliate with another bystander immediately after witnessing a fight (Judge & Mullen 2005). Furthermore, the self-directed responses of the bystanders increased after witnessing a fight and decreased after affiliating with another bystander. The bystanders also tended to seek out their preferred social partners for affiliation. The interaction appears to be a mechanism for decreasing the negative arousal induced by witnessing a fight within one's group. Such interactions have been termed 'quadratic' interactions because they involve four individuals, two of which were not involved in the original conflict (Judge & Mullen 2005). The results have been replicated in Tonkean macaques, *Macaca tonkeana*, in that uninvolved bystanders were more likely to affiliate with preferred partners following aggression and scratching tended to decrease following the affiliative episode (De Marco et al. 2010). In contrast, another replication using geladas, *Theropithecus gelada*, found no increase in affiliation or self-directed behaviour in bystanders following aggression (Leone et al. 2010). The authors proposed that the difference may have been related to the likelihood that a dyadic aggressive interaction might escalate to include a bystander. They suggested that the likelihood of further escalation may have been low in this tolerant species and witnessing a fight may not have increased bystander arousal, as measured by self-directed behaviour.

We hypothesized that if bystander arousal is influenced by expectancies for escalated or continued aggression within a group, bystander arousal should be affected by the presence or absence of reconciliation between two combatants. As mentioned, reconciliation reduces the likelihood of further aggression (Aureli et al. 2002).

If a bystander recognizes the functional significance of reconciliation between two combatants, the interaction may signal a decreased likelihood of aggression and reduce a bystander's arousal. Therefore, we predicted that bystander rates of self-directed behaviour would increase after witnessing a fight and decrease if the combatants reconciled. If the combatants did not reconcile, we predicted that a bystander's self-directed behaviour would remain elevated. We also examined whether affiliation between a combatant and an uninvolved third party would influence the self-directed behaviour of a bystander. Although largely untested, some have suggested that third-party affiliative contacts with a combatant following a conflict may serve as a 'substitute' for reconciliation (Aureli & van Schaik 1991; Judge 1991; Wittig et al. 2007; Fraser & Aureli 2008; Wittig & Boesch 2010; Romero & de Waal 2011). If so, affiliative contacts between a combatant and any third party might reduce the likelihood of further aggression and be associated with reduced self-directed behaviour in bystanders. Conversely, a reduction in bystander self-directed behaviour might be specific to witnessing an act of reconciliation between former combatants, and affiliative interactions between a combatant and individuals other than the former opponent (i.e. third-party affiliation) would not lead to decreases in the self-directed behaviour of bystanders.

We used hamadryas baboons to test these predictions because virtually every pattern of postconflict interaction typically associated with reconciliation and third parties has been demonstrated in this species. Dyadic reconciliation has been found in hamadryas baboons, and combatants also interact with third parties significantly more following conflicts than during baseline periods (DeBolt 2003; Romero et al. 2009). Triadic postconflict interactions were bidirectional with both aggressors and victims initiating and receiving contacts from third parties. As mentioned above, the displacement activities of bystanders were elevated in the postconflict period in a hamadryas baboon group (Judge & Mullen 2005), indicating that bystanders were anxious after witnessing a conflict and are, therefore, poised to be influenced by a reconciliation between the combatants.

METHODS

Subjects and Housing

We conducted observations on a captive group of hamadryas baboons housed at Bucknell University in Lewisburg, Pennsylvania. The group contained 18 animals at the beginning of the study: one adult male, two subadult males, seven adult females, three juvenile males, four juvenile females and one male infant. Due to births, deaths and transfers to other facilities, the group contained 15 animals at the end of the study: one adult male, one subadult male, seven adult females, two juvenile males, two juvenile females and two male infants. All animals except the adult male were born into the group, which was originally established in 1968 from wild-caught animals. The adult male was introduced in 1996. The typical social structure of hamadryas baboons consists of several levels with the most basic level being a one-male unit consisting of an adult male, several females he recruits to form a harem, and their offspring (Abegglen 1984). Several one-male units, often with related males, are combined to form clans. Bands consist of several clans and bands may combine to form troops that often congregate at sleeping sites (Kummer 1968; Schreier & Swedell 2009). Within this four-tiered social structure, the group observed in this study would be considered a single one-male unit. We observed all individuals in the group as subjects except the infants because infants were rarely involved in conflicts. Furthermore, infants were not likely to have experienced the social cognitive development necessary to understand the social processes under investigation.

Animals were housed in an indoor/outdoor enclosure constructed of concrete and chain-link fencing. The outdoor enclosure measured $9 \times 11 \times 4.5$ m and contained a gravel substrate. Perches, hanging swings, climbing structures and other fixed objects were present to provide opportunities for naturalistic locomotion. The indoor quarters comprised two interconnected adjoining compartments measuring $10 \times 1 \times 3$ m each. The indoor compartments contained heated cement floors and each led to the outdoor enclosure via metal guillotine doors. During the winter months, the animals were housed in indoor quarters when temperatures were consistently below 4.4°C (40°F). Commercial monkey chow and water were available *ad libitum* and this diet was supplemented once daily with an assortment of fruits, vegetables, seeds and nuts. Enrichment objects for manual exploration and stimulation were continually available.

Procedure

We normally conducted observations while animals were in their outdoor enclosure with the doors to their indoor quarters closed. Observations were conducted from a location 1 m from one side of the outdoor enclosure consisting entirely of chain-link fencing. During the winter months when animals were locked indoors, observations were conducted from locations 0.33 m from barred doors that constituted one side of the indoor quarters. Observers took their posts 10 min prior to an observation session to habituate the animals, and all data were collected between 1000 and 1700 hours. Observation sessions typically lasted 1–2 h.

Data Collection

The data collection technique was a modified version of the well-established postconflict–matched control (PC–MC) method developed by *de Waal & Yoshihara (1983)* to test for reconciliation. Using the PC–MC method, an observer conducts a focal observation on either the initiator or recipient of aggression during a postconflict (PC) interval and then conducts a matched control (MC) focal observation on the same individual at the same time the following day to determine whether the animals are more likely to affiliate following aggression than during baseline periods. In our modification, once an aggressive interaction was observed, one observer began a postconflict observation on one of the combatants to monitor for reconciliation, while the second observer recorded the postconflict behaviour of a randomly selected bystander. The postconflict observations consisted of 5 min of focal animal sampling (*Altmann 1974*). A 5 min interval was used because reconciliation typically occurs approximately 1 min after a fight in hamadryas baboons (*DeBolt 2003; Romero et al. 2009*). Five minutes provided adequate additional time to observe bystander behaviour following a reconciliation.

The role of the observers to focus on combatants or bystanders was randomly assigned at the start of every observation period. The observer of a combatant alternated between selecting the victim and the aggressor as the focal subject. The bystander observer selected the first animal from a randomized list of animals with the conditions that the bystander was not involved in the aggressive encounter, was awake, and was oriented in the direction of the conflict. A further stipulation added for indoor observations, in which there were two compartments connected by a single small doorway (0.61×0.66 m), was that the bystander had to be in the same compartment in which the conflict occurred. If the animal at the top of the randomized list did not meet these criteria, we skipped that animal and selected the next animal on the list. As such, the process for selecting bystanders might be described as quasirandom. Both observers then simultaneously recorded the

behaviour of their respective focal subjects onto digital audio recorders noting the time within the 5 min interval that any behaviour occurred. Data were transcribed into computer files with focal observations on both animals synchronized by time, allowing a direct assessment of the bystander's behaviour relative to that of the combatant.

Behavioural responses recorded during focal observations were aggressive, affiliative and submissive interactions as well as instances of self-directed behaviour (Table 1). The identities of initiators and recipients of each response were also recorded. Interobserver reliability was maintained at 90% agreement or higher between all observers throughout the study as measured by Cohen's kappa. Aggression of moderate to high intensity was used to begin PC intervals because these interactions were conspicuous and/or produced screams from victims, increasing the likelihood that the interaction was witnessed by a bystander. Accordingly, aggressive behaviour was categorized into two levels of intensity, and, to begin a PC, a conflict had to involve either high-intensity aggression on the part of the aggressor (a chase or bite) or moderate-intensity aggression (rough behaviour or threat) accompanied by submissive screams from the victim (Table 1). Affiliative behaviour recorded included groom, contact, mount, play and touch (Table 1). Nonsocial self-directed behaviour recorded for assessing arousal included gravel-dig, manipulation, self-groom, self-scratch and self-touch (Table 1). These behavioural responses have been used as indicators of arousal in previous studies (*Maestriperi et al. 1992; Castles & Whiten 1998; Judge & Mullen 2005*). However, based on previous findings investigating arousal in bystanders witnessing conflicts (*Judge & Mullen 2005*), we did not expect all responses to fluctuate in response to combatants' behaviour.

If aggression occurred between the original opponents within 30 s of the initial conflict, we considered it as the same PC, however, when aggression occurred between the original combatants beyond the 30 s mark, we considered the interaction a new PC. We adopted this protocol because continuing conflict would interfere with combatants' participation in postconflict behaviour and the purpose of the study was to investigate the 5 min interval after aggression had ceased. We collected focal samples on bystander behaviour following aggressive interactions involving multiple animals, but discarded these samples from analysis due to the ambiguity of designating a primary aggressor and/or victim.

We conducted matched control observations on the next available observation day following the conflict for both combatants and bystanders and within 20 min of the time of day of the original aggressive interaction. Time of day was matched to control for possible diurnal variations in social activity. Both observers simultaneously collected MC observations on combatants and bystanders to ensure the comparability of MC data to PC data. We did not collect MC data unless both the combatant and the bystander were awake at the beginning of the observation period. In addition, MCs were collected only when at least 10 min had elapsed since an aggressive act had occurred in the group to ensure that the MC accurately represented behaviour occurring during a nonconflict period.

Data Analyses

Dyadic reconciliation

To confirm that reconciliation was occurring within the group, we compared the PC–MC pairs of combatants using the technique of *de Waal & Yoshihara (1983)* to identify pairs that were attracted (affiliation occurred between combatants earlier in PCs than in MCs or only in PCs), dispersed (affiliation occurred between combatants earlier in MCs than in PCs or only in MCs) and neutral (affiliation

Table 1
Ethogram of agonistic, affiliative and self-directed behaviour categories in hamadryas baboons

Behaviour category	Definition
Agonistic behaviour	
<i>Moderate intensity</i>	
Rough behaviour	Agonistic interactions involving slight physical contact and usually no facial component; may include nipping, grabbing, kicking, pulling, pushing, poking, slapping, pulling hair, butting and shoving
Threat	Agonistic interactions involving any of the following facial, vocal, or physical components: head thrust, open-mouth, raised eyebrows, teeth gnashing, lunge or pinning down
<i>High intensity</i>	
Chase	Pursuit past the location the recipient maintained at the start of the interaction
Bite	Forcibly clench the skin/limb of a recipient with the teeth, usually accompanied by head shaking; excludes 'nips', which consist of a brief pinch of the skin with the incisors
Submissive behaviour	
Scream	Usually repeated, loud, high-pitched vocalization occurring in a defensive or retreating context in which at least one component of noise is sustained for >1 s; bouts end with interruptions of 5 s
Affiliative behaviour	
Groom	Manipulation, licking or brushing of the fur of another animal with the hands or mouth for at least 5 s; bouts ended with interruptions of more than 5 s or when one individual moved >1 m away
Contact	Stationary contact (other than grooming) with another animal for more than 5 s; bouts ended with interruptions of 5 s or when one individual moved >1 m away
Mount	Foot-clasp, thrusting and apparent intromission; also included incomplete mounting and grasping the hips of another animal from behind; bouts ended with interruptions of 5 s or when one individual moved >1 m away
Play	Social interactions of 3 s or more characterized by low tension and usually accompanied by a 'play face', a facial gesture in which the mouth is open and the facial features are relatively relaxed; may have included any of the following: grunting, wrestling, sham-biting, jumping on, jumping over, chasing, fleeing, hiding and related activities; bouts were ended by interruptions of >10 s
Touch	Directed physical contact with another animal that did not include grooming, contact or mounting; physical contact during locomotion was scored as touch; touches lasting 5 s or longer were then scored as contact
Self-directed behaviour	
Gravel-dig	Pushing through gravel with hands, for at least two strokes, often accompanied by extraction of items from the gravel and placing them in the mouth; bouts ended with interruptions of >5 s
Manipulation	Investigating or handling food/cage/objects with hands, feet or mouth for at least 3 s; ingestion of food was not scored as manipulation; bouts ended with interruptions of >5 s
Self-groom	Manipulating or brushing own fur with hands or mouth, or licking of own fur for ≥ 5 s; bouts ended with cessation of activity for >5 s
Self-scratch	Usually repeated, movement of the hand or foot during which the finger/fingernails or toe/toenails were drawn across the fur or skin at least twice; bouts ended with interruptions of >3 s.
Self-touch	Contact to ones' own body with the hands, feet or mouth that did not meet the requirements of self-groom and self-scratch

between combatants occurred at the same time in PCs and MCs or in neither PCs nor MCs). For each animal, the proportions of attracted and dispersed pairs were determined by dividing the number of attracted pairs and the number of dispersed pairs by the total number of pairs (i.e. the sum of attracted, dispersed and neutral pairs). The proportion of attracted pairs was then compared to the proportion of dispersed pairs using a Wilcoxon signed-ranks test since a nonparametric test is appropriate for data converted to proportions. A significantly higher proportion of attracted pairs would confirm that reconciliation was occurring. The test for reconciliation was a manipulation check because we wished to document that reconciliation was occurring in the group more than expected by chance before we tested for the influence of reconciliation on bystander behaviour.

Self-directed behaviour

We made all comparisons of self-directed behaviour rates using two-tailed paired *t* tests evaluated for significance at $P < 0.05$. The only parametric assumption made when using paired *t* tests is that the difference scores are normally distributed. As such, we tested for violations of this assumption using the Shapiro–Wilk test for each comparison. In one test, there was a significant departure from normality (positive skew) that we corrected with a square-root transformation.

As a general test to determine whether bystanders increased their arousal after witnessing a fight, we compared bystander per minute rates of self-directed behaviour in PCs to rates in MCs. To determine whether bystander self-directed behaviour was influenced by the occurrence of reconciliation, rates of bystander self-directed behaviour in PCs in which reconciliation occurred were compared between the interval of time up to the point combatants reconciled and the time after reconciliation. We used 'per-second

rates' as a measure because sometimes a reconciliation would occur before a full minute elapsed and we needed a standard measure for pre- and postreconciliation comparisons. Each self-directed behaviour was compared individually before and after reconciliation to determine which were affected by reconciliation. Only any self-directed behavioural responses found to change significantly after reconciliation would be used for subsequent tests.

The pre- versus postreconciliation test was subject to a confound if bystander self-directed behaviour rates gradually declined throughout the postconflict interval after witnessing a fight regardless of whether reconciliation occurred between combatants. What might appear to be a decrease following reconciliation might be a natural decline in arousal over time. PCs in which combatants reconciled fairly soon after the conflict would be particularly susceptible to this potential confound because there would be longer periods for a natural decline to occur. As one control for a natural decline in self-directed behaviour, we compared the per-second rate of bystander self-directed behaviour before reconciliation to the per-second rate of self-directed behaviour for just 1 min after reconciliation. Using 1 min after reconciliation as a unit of measurement standardized the amount of time analysed after reconciliation and allowed us to create several other controls to test for a natural decline in arousal. In one control, each PC with reconciliation was paired with a PC in which no reconciliation occurred after matching for bystander identity, location (inside/outside) and time of day. Rates of self-directed behaviour in bystander PCs in which the conflict was reconciled were compared to corresponding rates in bystander PCs in which no reconciliation occurred. If a natural decline in arousal was occurring, the self-directed behaviour rate of bystanders in PCs with reconciliation should not differ from those without reconciliation. If witnessing reconciliation reduced arousal, then we

predicted that bystander self-directed behaviour rates would decline in the minute following reconciliation in the reconciled PCs, but there would be no corresponding decline in the nonreconciled PCs. To calculate self-directed behaviour rates in nonreconciled PCs that corresponded to the point before and after reconciliation in matched reconciled PCs, the point in time of reconciliation in its matching reconciled PC was identified and used to calculate a per-second rate of self-directed behaviour before and for the minute after that point in nonreconciled PCs (Fig. 1). The rate of self-directed behaviour in nonreconciled PCs before the corresponding point of reconciliation in its matching PC was then compared to the minute after the point of reconciliation in nonreconciled PCs. To ensure that there was no initial difference between reconciled and nonreconciled PCs, we calculated the per-second rates of bystander self-directed behaviour for PCs with reconciliation before reconciliation occurred and compared them to self-directed behaviour

rates in the matched nonreconciled PCs for the time before reconciliation occurred in each matching PC.

To determine the extent of any effect of witnessing reconciliation, we compared per-second rates of bystander self-directed behaviour in the minute after reconciliation in PCs with reconciliation to rates in the same minute in corresponding MCs (Fig. 1). The test would determine whether bystander self-directed behaviour returned to baseline levels after witnessing reconciliation. We conducted the same test for PCs with no reconciliation to determine whether rates of self-directed behaviour stayed elevated over baseline if bystanders did not witness reconciliation. Accordingly, rates of self-directed behaviour in PCs with no reconciliation during the minute that corresponded to the minute after reconciliation in matched reconciled PCs were compared to the same minute in the nonreconciled PC's corresponding MC.

As an additional control, we compared rates of self-directed behaviour by bystanders before and after the combatant affiliated with individuals other than its opponent to determine whether reductions in self-directed behaviour by bystanders were specific to witnessing a combatant affiliate with its former opponent (i.e. reconciliation), or whether witnessing affiliative contacts between the combatant and animals other than the opponent (i.e. third-party affiliation) reduced the self-directed behaviour of bystanders. We calculated per-second rates of bystander self-directed behaviour for the time before an uninvolved third party affiliated with the combatant and compared them to rates in the minute after the affiliative contact. The PCs used in this analysis were those in which a combatant affiliated only with a third party and not the former opponent (i.e. not reconciled PCs).

To confirm that combatants' self-directed behaviour was also influenced by conflict, we calculated per-second rates of self-directed behaviour and compared them between combatants' PCs and MCs. To test for a reduction in combatant self-directed behaviour following reconciliation in PCs with reconciliation, we compared per-second rates of combatants' self-directed behaviour between the time before and the minute after reconciliation.

As some categories of data used in comparisons were rather specific (e.g. average rate of bystander self-directed behaviour in PCs with reconciliation), and we could not control the number collected, some subjects had a low number of focal samples for some tests. To use a subject's data in an analysis, the subject had to have three or more of the required type of focal samples to compute an average. Removal of subjects from some tests, for this reason, resulted in variation in the sample sizes used in the *t* tests, which had a maximum *N* of 16.

RESULTS

During the course of the study, we collected 225 combatant/bystander postconflict focal sample pairs with corresponding matched controls on both the combatant and the bystander. The mean \pm SD number of focal samples collected on each subject as a combatant was 14.00 ± 7.08 (range 3–31) and the mean \pm SD number of focal samples collected on each subject as a bystander was 14.00 ± 3.97 (range 6–19). The number of combatant focal samples was not equal across all subjects because some individuals were more frequently the initiator or the target of aggression than others. The number of bystander focal samples was not equal across subjects because some animals were more prone to join conflicts than others and they were skipped more often on the randomized list of potential bystanders to observe, thereby accumulating fewer bystander focal samples. We also eventually biased our sampling towards observing victims in combatant focal samples because the alpha male harem leader started a high proportion of the conflicts (59.5%). We biased towards sampling victims when he initiated

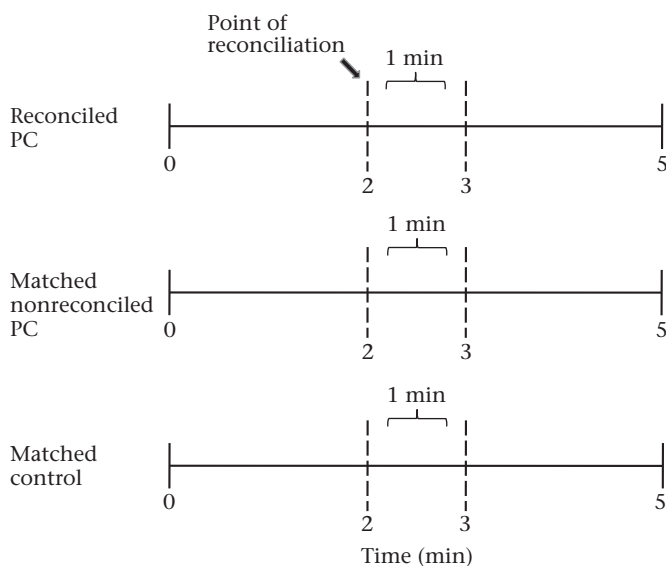


Figure 1. Diagram indicating the procedures used to calculate rates of self-directed behaviour in a reconciled postconflict (PC) interval, its matching nonreconciled PC and its matched control (MC), in hamadryas baboons. Horizontal lines represent 5 min of focal sampling on a bystander. The top line represents a 5 min PC focal sample taken on a bystander after two other animals became involved in a fight at time zero (0). In this example, the two combatants made affiliative contact 2 min into the focal sample (point of reconciliation), making the sample a 'reconciled PC' for the bystander. Rates of self-directed behaviour were calculated for the period up to the point of reconciliation (0–2) and for the 1 min interval following the point of reconciliation (2–3). The middle line represents a 5 min PC interval on a bystander in which two combatants fought at time zero but never made affiliative contact in the next 5 min (a 'nonreconciled PC'). To compare rates of self-directed behaviour in reconciled and nonreconciled PCs, we matched a reconciled PC to a nonreconciled PC and calculated rates of self-directed behaviour in the nonreconciled PC during the same corresponding time intervals used for the reconciled PC. In this example, we would have calculated rates of self-directed behaviour in the first 2 min of the nonreconciled PC and classified them as before the point of reconciliation. We would then calculate the rate of self-directed behaviour from min 2 to min 3 in the nonreconciled PC and classify that as corresponding to the minute after reconciliation in the matching reconciled PC. The lower line represents a 5 min matched control (MC) sample taken on a bystander in a nonaggressive context for comparison to a reconciled PC. To compare rates of self-directed behaviour in reconciled PCs and MCs, we again calculated rates of self-directed behaviour in the MC during the same corresponding time intervals used for the reconciled PC. In this example, we would have calculated the rate of self-directed behaviour during the first 2 min of the MC and classified it as before the point of reconciliation in its matching reconciled PC. We would then calculate the rate of self-directed behaviour from min 2 to min 3 in the MC and classify that as corresponding to the minute after reconciliation in the matching reconciled PC. The point of reconciliation was different for each reconciled PC, and the corresponding rates of self-directed behaviour extracted before and 1 min after reconciliation from matching nonreconciled PCs and MCs shifted accordingly.

fighters to reduce overrepresenting him as a focal subject. Thus, 67.4% of combatant focal samples were collected on victims and 32.6% on aggressors. However, for our purposes, it was important to document whether and when reconciliation occurred, not necessarily the role of the combatant (aggressor or victim) in the focal sample.

Dyadic Reconciliation

The outcome of each conflict was determined by comparing the timing of affiliative physical contact between combatants during the postconflict interval (PC) to that occurring during the baseline matched control interval (MC). Fifty-four of the 225 combatant PCs (23.9%) were classified as 'attracted', six were 'dispersed' and 165 were 'neutral'. The mean proportion of subjects' attracted pairs following conflicts (mean \pm SD = 0.21 \pm 0.15) was significantly higher than the mean proportion of subjects' dispersed pairs (0.03 \pm 0.04; Wilcoxon signed-ranks test: $T = 0.00$, $N = 13$, $P = 0.001$), demonstrating that reconciliation was occurring within the group.

Bystander Self-directed Behaviour

Total rates per min of bystander self-directed behaviour were significantly higher in PCs (mean \pm SD = 1.13 \pm 0.25) than in MCs (0.47 \pm 0.17; paired t test: $t_{15} = 8.16$, $N = 16$, $P < 0.001$), indicating that witnessing a fight increased arousal. To test whether witnessing reconciliation influenced bystanders' arousal, we classified any PC focal sample in which the combatants physically affiliated with each other (contact, groom, mount, play or touch) as a reconciled focal sample. Since the attracted versus dispersed pairs analysis indicated that reconciliation was occurring in the group, we considered any PC in which opponents affiliated with each other as a reconciled PC. Using this criterion, 54 focal samples were classified as reconciled focal samples and 171 were classified as nonreconciled focal samples. In reconciled PCs, total rates of bystander self-directed behaviour were significantly higher before reconciliation than after reconciliation (Table 2). The reduction was due to decreases in scratch and self-touch after reconciliation. As some responses rarely occurred (e.g. gravel-dig and self-groom) and were not performed by some subjects, they could not be compared with adequate power (e.g. $df = 3$). Since some self-directed behavioural responses were rare and others did not change after observing reconciliation, only scratch and self-touch were used as a measure of self-directed behaviour in the remainder of analyses. Any subsequent mention of 'self-directed behaviour' refers to a combined measure of self-scratch and self-touch.

The mean \pm SD time until reconciliation was 88.4 \pm 81.5 s. As most reconciliations occurred early in the 5 min PC period, if there was a gradual decline in the rate of self-directed behaviour by

bystanders after initially witnessing a fight, what might appear to be an effect of witnessing reconciliation might just be due to a natural decline in arousal over time. To control for this possibility, we compared the minute after reconciliation to the same minute in matching PCs with no reconciliation. When attempting to match reconciled PCs with nonreconciled PCs based on bystander identity, housing condition (inside/outside) and time of day, a pool of 39 of the 55 reconciled PCs could be matched adequately to PCs with no reconciliation. In this subsample of reconciled PCs, bystander rates of self-directed behaviour were still significantly higher before reconciliation than in the minute after reconciliation ($t_8 = 8.54$, $P < 0.001$; Fig. 2, comparison A), reconfirming the result found above on the entire sample of reconciled PCs. In nonreconciled focal samples, bystander rates of self-directed behaviour were not significantly different before the point of reconciliation in the matched reconciled PC than in the minute after the point of reconciliation ($t_8 = 0.87$, $P = 0.41$; Fig. 2, comparison B), demonstrating that the reduction in self-directed behaviour following reconciliation was not simply due to a passage of time. Bystander rates of self-directed behaviour in the minute after reconciliation in the reconciled PCs were significantly lower than in the minute after the point of reconciliation in the matched PCs with no reconciliation ($t_8 = 5.20$, $P = 0.001$; Fig. 2), providing additional evidence that the occurrence of reconciliation was associated with a decrease in self-directed behaviour. Furthermore, the bystander rate of self-directed behaviour before reconciliation was not significantly different than that before the point of reconciliation in matched PCs with no reconciliation ($t_8 = 0.79$, $P = 0.45$; Fig. 2), indicating that there was no fundamental difference in these two categories of postconflict focal sample up until the point of reconciliation.

Comparing self-directed behaviour before and 1 min after reconciliation in the PCs with reconciliation to the point before and after reconciliation in their corresponding MCs further demonstrated an influence of reconciliation. First, there was no significant difference in the rate of self-directed behaviour before and after the point of reconciliation in MCs ($t_8 = 0.13$, $P = 0.90$; Fig. 2, comparison C). The bystander rate of self-directed behaviour in the minute after reconciliation in PCs with reconciliation was not significantly different than in the minute after the time of reconciliation in MCs ($t_8 = 0.12$, $P = 0.91$; Fig. 2), indicating that, in the presence of reconciliation, bystander self-directed behaviour returned to baseline levels. In contrast, the bystander rate of self-directed behaviour was significantly higher in the minute after reconciliation in the matched PCs with no reconciliation than in MCs in the minute after reconciliation ($t_8 = 5.51$, $P = 0.001$; Fig. 2), indicating that, in the absence of reconciliation, bystander self-directed behaviour remained elevated over baseline levels.

Rates of self-directed behaviour by bystanders before the combatant affiliated with third parties other than its opponent were not significantly different from those in the minute after affiliative contact of a combatant with a third party ($t_{14} = 1.15$, $P = 0.27$; Fig. 2, comparison D). Furthermore, the rate of bystander self-directed behaviour in the minute after a reconciliation between combatants was significantly lower than the bystander rate in the minute after affiliative contact of a combatant with a third party ($t_8 = 2.98$, $P < 0.02$). Combatant affiliation with a third party was not accompanied by a reduction in the self-directed behaviour of bystanders. The reduction was specific to a reconciliation between a combatant and its former opponent.

Combatant Self-directed Behaviour

Combatant rates of self-directed behaviour were significantly higher in PCs (mean \pm SD = 0.02 \pm 0.01) than in MCs (0.01 \pm 0.00; $t_{10} = 10.86$, $P < 0.001$), indicating that involvement in a conflict

Table 2
Mean \pm SD rate per second of self-directed behaviour (SDB) by bystanders before and after combatants reconciled

SDB	Before reconciliation	After reconciliation	t test		
	Mean \pm SD	Mean \pm SD	t	df	P
Total SDB	0.039 \pm 0.027	0.006 \pm 0.004	4.42	10	0.001*
Gravel-dig	0.007 \pm 0.009	0.004 \pm 0.007	0.52	7	0.62
Manipulate	0.003 \pm 0.004	0.002 \pm 0.001	0.52	8	0.61
Self-groom	0.019 \pm 0.036	0.001 \pm 0.001	—	3	—
Self-scratch	0.012 \pm 0.003	0.001 \pm 0.001	4.52	10	0.001*
Self-touch	0.017 \pm 0.011	0.002 \pm 0.003	4.39	10	0.001*

Mean rates of individual behaviours do not add up to the total because some subjects did not perform some responses and means were calculated using different numbers of subjects. We did not calculate statistics for self-groom because too few subjects performed the response for meaningful analyses. We included the means because self-groom is often reported in similar studies of self-directed behaviour. * $P < 0.05$.

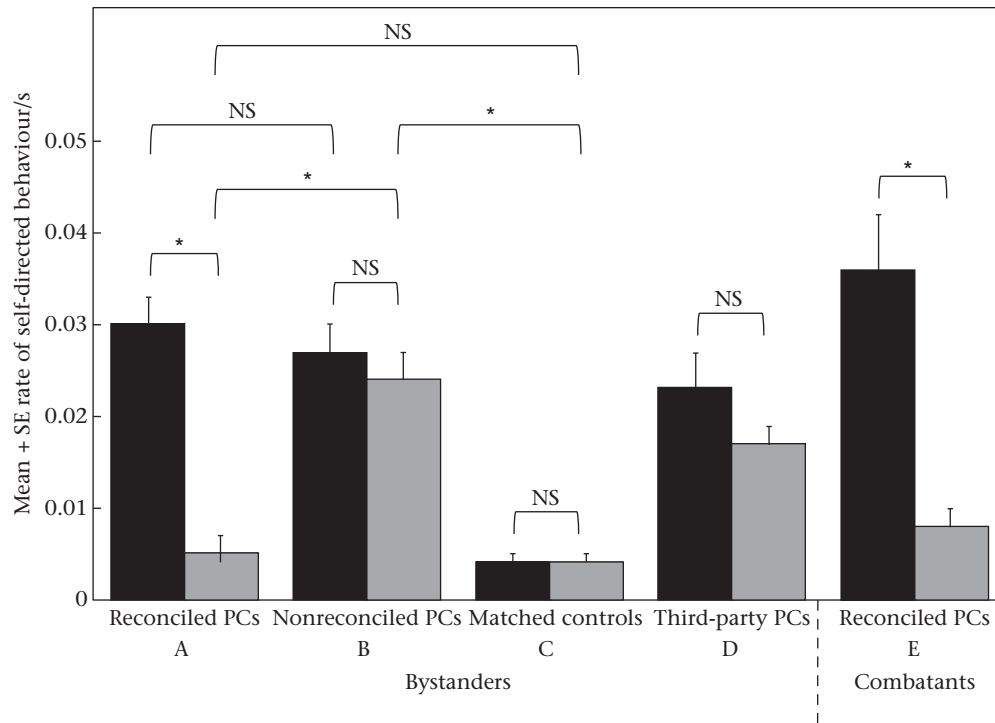


Figure 2. Mean + SE rate per second of bystander self-directed behaviour (scratch and self-touch) before (black) and 1 min after (grey) the point of reconciliation in reconciled PCs (comparison A), nonreconciled PCs (comparison B), matched controls (comparison C) and PCs with third-party affiliation (comparison D). Combatant rates of self-directed behaviour before and 1 min after reconciliation are also shown (comparison E). Brackets above the main statistical comparisons (A–E) indicate whether results of the before/after reconciliation tests were statistically significant ($*P < 0.05$). Additional brackets indicate the results of other comparisons mentioned in the text.

increased a combatant's arousal. To examine whether reconciliation also decreased the self-directed behaviour of combatants, for purposes of comparison, we tested for a change using the same parameters used to test for changes in bystander self-directed behaviour: we used only self-scratch and self-touch as the measure of self-directed behaviour and we tested the time before reconciliation against only the minute following reconciliation. Combatant rates of self-directed behaviour were significantly higher before reconciliation than after reconciliation ($t_7 = 5.02$, $P = 0.002$; Fig. 2, comparison E), indicating that reconciliation reduced arousal in combatants.

DISCUSSION

Consistent with previous findings (DeBolt 2003; Romero et al. 2009), hamadryas baboons exhibited dyadic reconciliation. Former opponents were attracted to one another in the 5 min following a conflict compared to baseline periods. Also consistent with previous findings on other primate species (Aureli & van Schaik 1991; Castles & Whiten 1998; Das et al. 1998; Kutsukake & Castles 2001), the self-directed behaviour of combatants decreased following reconciliation, indicating that reconciling a conflict reduced arousal. Results from Judge & Mullen (2005) on hamadryas baboons were also replicated in that rates of bystander self-directed behaviour were higher following a conflict than during matched control periods, indicating that witnessing a conflict in the group increased bystanders' arousal.

The main novel finding was that the elevated rates of bystanders' self-directed behaviour, as measured by self-scratch and self-touch, decreased after a reconciliation between combatants. The decrease in self-directed behaviour was not a general decrease in arousal due to a passage of time from onset of the observed conflict. The significant decrease occurred relatively quickly in just the minute

following the time of reconciliation. Furthermore, in matched non-reconciled PCs, there was no decrease in self-directed behaviour over the same corresponding time period, indicating that bystander rates of self-directed behaviour remained elevated over time when the conflict was not reconciled. These elevated rates of bystander self-directed behaviour in nonreconciled PCs were significantly higher than those in the minute following reconciliation in reconciled PCs. Furthermore, before the time of reconciliation, there was no significant difference in bystander rates of self-directed behaviour between PCs with reconciliation and PCs with no reconciliation. The lack of difference in self-directed behaviour before reconciliation in PCs with reconciliation and in PCs with no reconciliation, the significant difference after reconciliation and the lack of change before and after the time of reconciliation in nonreconciled PCs provide strong support that the difference in rates of self-directed behaviour resulted from the occurrence of reconciliation. A comparison of the rates of self-directed behaviour in PCs after reconciliation to MCs found no significant difference. Thus, not only does reconciliation by combatants correspond with a reduction in self-directed behaviour by bystanders, but it also appears to return bystander rates back to baseline levels. Finally, the reduction in bystander self-directed behaviour was specific to an affiliative interaction between the two original combatants after the fight (i.e. reconciliation). When a combatant affiliated with an animal other than its opponent, bystander rates of self-directed behaviour remained elevated. The specificity and timing of the effect lead us to conclude that bystanders were witnessing the reconciliation and reacting to the interaction. We should point out that, although bystanders were fairly well represented in the sample, most of the witnessed aggressive interactions involved the adult male (59.5%). Thus, the influence of reconciliation on bystander behaviour may not be representative of any aggressive dyad. However, even if the pattern of observed results was mostly influenced by reconciliations

involving the adult male, we do not think it reduces the import of the results.

Bystanders, like combatants, may show increased arousal after witnessing a fight because of the likelihood of escalated aggression. Many studies have shown that aggression is likely to spread to third parties following a fight, with the close associates of aggressors and victims, typically kin, supporting each other in conflicts (e.g. Massey 1977; Kaplan 1978; Aureli & van Schaik 1991). Combatants are also likely to attack the close associates of their opponents (Cheney & Seyfarth 1989; Aureli et al. 1992), and victims are likely to redirect aggression by attacking uninvolved group members (Aureli & van Schaik 1991; Aureli et al. 1993). Although the threat of aggression to bystanders was not directly assessed in this study, escalation was most likely a salient threat. Alpha male harem leaders frequently intervene in conflicts (Kummer 1968; Sigg 1980), posing a significant threat to all harem members. Furthermore, Gore (1994) found that triadic aggression of females in a captive group of hamadryas baboons was often an attempt to enlist the harem leader against other females. In fact, DeBolt (2003), who studied the same group of hamadryas baboons as in our present study, reported that approximately 19% of conflicts were due either to third parties becoming involved in fights or to aggression resuming between original opponents. Finally, in our study, the alpha male harem leader was the aggressor in the majority of conflicts. Witnessing reconciliation, particularly involving the alpha male, may have been especially stress relieving for a bystander. Also, we observed only one random bystander at a time. We presume that the occurrence of a reconciliation also influenced other bystanders, perhaps promoting a group-wide reduction in tension.

The reduction in bystander self-directed behaviour after witnessing reconciliation has important social cognitive implications as it suggests bystanders are recognizing its occurrence and, probably, its functional significance. Recall that the average time to reconciliation was approximately 1.5 min and that only affiliation between former opponents corresponded to a decrease in self-directed behaviour, not affiliation between combatants and other group members. To recognize that a reconciliation has occurred, a bystander must remember the two animals involved in the fight and subsequently recognize that they engage in a behavioural response (e.g. affiliative contact) that resolves the conflict. While it is possible that baboons could memorize the possible consequences of every type of social interaction that occurs with every combination of individuals within their group, this complex process is not an efficient method. Cheney & Seyfarth (2007) suggested that, while a baboon might learn all these associations by detailed observation over the course of an extended period, the task of comprehending social interactions would be made easier by the utilization of theories. By 'theories' they mean implicit expectations about how individuals interact with one another, or expectations of the outcome of novel combinations of individuals and behaviour based on previous examples (Cheney & Seyfarth 2007). From a survival standpoint the utilization of social 'theories' is adaptive. For example, an immigrant male with no knowledge of the group he is entering benefits from social concepts because they allow him to more rapidly grasp the relationships between group members and the outcomes of their interactions. Applying our case, an immigrant male that witnesses reconciliation between two animals shortly after aggression may understand that the two animals have resolved their conflict and further group disruption is unlikely even if he has never seen the two combatants fight before or interact positively afterward.

Utilization of 'theories' to explain primate social cognition is similar to a middle ground proposed by Tomasello & Call (1997) between one extreme view that social interactions are the product of simple operant conditioning without cognitive awareness and the opposite extreme that animals act with an understanding

of the intentional mental states of others (i.e. 'theory of mind'). These authors proposed that primates use inductive learning to understand the animacy and directedness of the behaviour of others without understanding their state of mind. In primates, the capacity is particularly developed in the domain of understanding third-party social relationships, in which knowledge of the interactions between two other individuals influences one's own behaviour. When witnessing reconciliation, hamadryas baboons may apply previously learnt associations to make predictions about group social interactions. In our case, they may understand that the conflict is resolved and that further aggression is less likely, thereby reducing their arousal.

Although we propose a social cognitive explanation for the results obtained based on a bystanders' assessment of the possibility for escalated aggression, there may be other explanations. In particular, one might suggest that bystanders' arousal is reduced after witnessing reconciliation because they empathize with the combatants' emotional state. For example, a bystander may perceive that the combatants' arousal is reduced after reconciliation and it, too, experiences a reduction in arousal. An empathy explanation would be somewhat controversial since it would suggest that a bystander understands the affective or emotional state of other monkeys and thus demonstrates theory of mind. Great Apes, such as chimpanzees, do seem to have limited abilities to understand the perception and knowledge of others and others' goals and intentions (Call & Tomasello 2008), and perhaps empathize with others' emotional states (Romero et al. 2010). Little evidence exists for these capacities in monkeys, however, particularly empathy. For example, rates of self-directed behaviour, and thus arousal, in Japanese macaque, *Macaca fuscata*, mothers do not increase after they observe their infants being attacked (Schino et al. 2004). Nakayama (2004) did find that Japanese macaques were responsive to the emotional cues of others as monkeys increased scratching when they witnessed a conspecific scratching. Contagious yawning in geladas has also been suggested as possible empathy in monkeys (Palagi et al. 2009). Such results are difficult to interpret, however, because one cannot know whether the witness is empathizing with the actor's emotional state or simply reacting to observed behaviour (Yoon & Tennie 2010). At the most basic level, our results may represent an 'emotional contagion' form of empathy (Preston & de Waal 2002) in which an animal perceives the emotional state of another and reflexively adopts the same state. In our case, a bystander becomes aroused by observing the combatants' increased arousal after a fight and bystander arousal declines when the combatants' arousal declines after reconciliation. Behavioural contagion, in which the behaviour of one animal serves as a releaser for the same behaviour in another animal (Zentall 2001), is a similar less mentalistic explanation for our results. Bystanders witnessing increased scratching by combatants after a fight may have increased their scratching, and bystanders witnessing decreased scratching by combatants after reconciliation may have decreased their scratching.

Concerning baboons, after 14 years of observing wild baboon behaviour, Cheney & Seyfarth (2007) remarked about the seeming lack of empathetic concern for others in their research group of chacma baboons, *Papio hamadryas ursinus*. They did, however, provide a multitude of evidence that baboons understand the causes and consequences of complex patterns of social interaction among the members of their group. As such, we would suggest recognition of the functional consequences of a reconciliation as the explanation of our results.

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