Post-Conflict Non-Aggressive Behaviours may be neither Friendly nor Conciliatory: Conflict Management of Male Hamadryas Baboons

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Abstract

The relational model of conflict resolution predicts that after an aggressive conflict there should be a motivational shift from aggression to attraction. Most tests of the reconciliation hypothesis assume, however, that all non-aggressive post-conflict behaviours between former opponents are motivationally homogeneous and qualify as friendly reunions. In fact, although the hypothesis predicts an increased occurrence of friendly contacts after conflicts, in practice, however, post-conflict reunions often include a mixture of contact and non-contact behaviours. Most reconciliation studies either (often) assume a conciliatory function for post-conflict reunions or (less often) test functional predictions. Finally, the valuable relationships hypothesis predicts that conciliatory rates should be relatively higher between friends and allies than between non-friends/allies. In this paper, we use data on non-aggressive interactions following conflicts between adult male hamadryas baboons that are neither friends nor allies to assess the implications of all these important but largely overlooked issues. The analyses of the rate and temporal relation of non-contact greeting (NCTG) to anxiety-related behaviours and side-directed aggression as well as of the behaviours used during non-aggressive interactions with male and female third-parties suggest that the NCTG used by males after conflicts were neither motivationally friendly nor functionally conciliatory. We point out that the gestures exchanged during these post-conflict NCTG can be interpreted as formalized signals of equal status and that the rate and form of the greetings used by male opponents are indicative of high relationship insecurity and incompatibility respectively. We conclude that although male hamadryas' post-conflict NCTG are not conciliatory they may serve to assess their opponents' attitude and to negotiate the restoring of their pre-conflict levels of peaceful but non-amicable co-existence.

Introduction

de Waal & van Roosmalen (1979) reported that aggressive conflicts between chimpanzees living in a large colony in captivity were often followed by friendly contacts between the combatants, and de Waal & Yoshihara (1983) designed a controlled procedure, known as the PC–MC method, to determine if such friendly contacts were more likely during post-conflict observations than during control periods in which there had been no preceding aggression. de Waal hypothesized that such friendly post-conflict contacts would serve a conciliatory function (i.e. *reconciliation hypothesis*, e.g. de Waal &

van Roosmalen 1979; de Waal & Yoshihara 1983; de Waal 1989, 1993). After almost three decades of research on conflict management and resolution in more than 30 species of non-human primates and in a few others of non-primates, there exists a general consensus that the rate of friendly contacts between former opponents is significantly higher soon after an aggressive confrontation than during matched-control periods not preceded by aggression (Aureli & de Waal 2000; Aureli et al. 2002; Arnold & Aureli 2007; Colmenares 2006).

The reconciliation hypothesis holds two core assumptions. First, it states that after aggression former opponents experience attraction rather than continued antagonism towards each another. It is argued that soon after an agonistic incident antagonists experience a motivational switch from aggression to affiliation (de Waal 1986, 1989, 1993, 2000a). The empirical prediction to test this assumption is that former opponents will seek and make friendly contacts with each other at much higher rate not longer after conflicts than at other times (i.e. *friendly reunion* prediction). The second assumption is that these friendly post-conflict reunions serve a conciliatory function, that is, they reduce the probability of renewed aggression, mend relationships potentially damaged by conflicts, and alleviate the levels of stress experienced by both antagonists (Aureli 1997; Aureli & de Waal 2000; Aureli et al. 2002; Arnold & Aureli 2007). The empirical prediction to test this assumption is that conflicts that are followed by friendly reunions between former opponents (i.e. reconciled conflicts) are expected to decrease the probability of re-aggression, restore pre-conflict levels of tolerance and cooperation, and reduce the rate of stress-related behaviours (i.e. *conciliatory function* prediction).

Early empirical and theoretical studies of reconciliation emphasized that for a post-conflict interaction to qualify as a *reunion*, former opponents should make *contact* with each other and such contact should be motivationally *friendly* (e.g. de Waal & van Roosmalen 1979; de Waal & Yoshihara 1983). [The conflict research literature also uses the terms *affinitive*, *affiliative* or *peaceful* interchangeably to refer to this one motivation (Kappeler & van Schaik 1992; Aureli & de Waal 2000; Aureli et al. 2002; Silk 2002; Arnold & Aureli 2007.] In practice, however, adherence to this double criterion has not been really systematic, many researchers have combined proximity and friendly behaviours involving *or* lacking actual body contact between former opponents into one single category (see Colmenares 2006, Table III), without assessing the motivational nature and homogeneity of such behaviours. Thus, the implicit assumption that the behaviour patterns subsumed into the 'friendly body contact' category are motivational homogeneous has not been formally tested, despite the fact that it appears to be critical for understanding the nature and diversity of the processes that drive the strategies of conflict management and resolution. The relation between the motivation of post-conflict behaviours and their function thus remains an open issue that deserves to be addressed.

It is a well-established fact that conciliatory tendencies vary widely across dyads within groups (and species) (Kappeler & van Schaik 1992; Cords & Aureli 2000; van Schaik & Aureli 2000; Aureli et al. 2002; Arnold & Aureli 2007; Watts 2006). de Waal argued that, in group-living species, rivalry and fights often take place among friends and allies, that is, between partners that represent critical social resources worth maintaining and servicing if fitness is to be maximized (i.e. the Relational Model, for example, de Waal 2000a,b; also see de Waal 1986, 1989, 1993, 1996). So, the valuable relationships hypothesis, as it has come to be labelled, predicts that conflicts are more likely to be reconciled if the opponents maintain friendly or mutually valuable relationships (Aureli et al. 2002; Arnold & Aureli 2007).

In the present study, we use data on aggressive conflicts between male hamadryas baboons (*Papio hamadryas hamadryas*), collected with the PC/MC paradigm, to address three important issues in conflict management research. First, we test the assumption that non-aggressive post-conflict behaviours (NAPBs) are *motivationally* friendly. Second, we test the prediction that NAPBs are *functionally* conciliatory. Finally, we test the prediction from the valuable relationships hypothesis that the rate of NAPBs is higher between friends and allies, that is, between antagonists that maintain mutually valuable bonds.

In an early study of aggression and greeting behaviour between male hamadryas baboons, Colmenares (1990) hypothesized that greetings among male hamadryas baboons, especially those not involving body contact, were motivationally ambivalent (Colmenares et al. 2000); Colmenares (1990) stated that such greetings 'may be regarded as 'quasi-aggressive' behaviour... rather than as a category of affiliative or friendly behaviour' (p. 110). If this were the case, we should expect non-contact greeting (NCTG) among males to be particularly high soon after conflicts, when the former opponents' aggressive motivation is most likely to remain elevated. Colmenares' hypothesis was based mainly on

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the analysis of the form and rate of the greeting exchanges, its context of occurrence (e.g. rivalry over the possession of females), and the nature of the changing relationship between the incumbent males (e.g. a leader–follower relationship turning into a leader–leader relationship). Recent studies, however, have disputed this view or have reported mixed evidence (Guinea baboons: Whitham & Maestripieri 2003; hamadryas baboons: Fraser & Plowman 2007). In none of these studies, however, the PC/MC paradigm was used, and the original hypothesis remains untested.

The majority of the conflict resolution studies has only tested the friendly post-conflict reunion prediction and has readily assumed that NAPBs have a conciliatory function (Arnold & Aureli 2007). We believe that the motivation and the function of NAPBs are different issues that should be addressed separately. Our stance here is that NAPBs may or may not be motivationally friendly and, in addition, they may or may not be functionally conciliatory. So, in this paper, in addition to test the presumed friendly motivation of NAPBs, we provide a test of its function regarding the possible effects on post-conflict behavioural indicators of anxiety.

Hamadryas baboons are cross-sex bonded, mate polygynously, and form multilevel societies (Kummer 1984; Colmenares 2004; Swedell 2005). Although clan males (including their followers) can profit from their spatial association with one another compared with males from single units (Colmenares et al. 2006), the evidence for active cooperation between males, even within clans, is poor at best (Colmenares, unpubl. data). Given the lack of evidence for male bonding and active alliances between adult males, especially when they hold reproductive units, one would expect a reduced rate of NAPBs between adult males, if the valuable relationships hypothesis is correct. Of course, this prediction would not need to follow if NAPBs were driven by non-friendly motivations and/or fulfilled functions not envisaged by the predominant version of the valuable relationships hypothesis.

Methods

Subjects and Housing

The study reported here was conducted on the colony of hamadryas baboons (*P. h. hamadryas*) housed at the Parque Lecocq Zoo, Montevideo, Uruguay. The colony was established in 1980 and at the time this study was carried out it consisted of 55 subjects, all of whom were individually identifiable. The colony was found to display the basic patterns of social organization that have been described for this species in the wild (Kummer 1968; Abegglen 1984; Zinner et al. 2001; Swedell 2002) and in other large colonies in captivity (Colmenares 1992, 2004), that is, multiple one-male/multi-female social units or OMUs (Silveira et al. 2001). The subjects of this study were the eight sexually mature males of the colony. Following Colmenares (1990), they were classified as followers (i.e. owning no female), young leaders (i.e. owning nulliparous females), prime leaders (i.e. owning primiparous and multiparous females), and old leaders (i.e. post-prime males that have started to lose their females to younger males). There were three young leaders, four prime leaders, and one old leader (one of the males changed his status from follower to young leader during the study). The colony was housed in a grassy dome-shaped outdoor corral of 2750 m^2, which contained large piles of natural rocks. They were fed once, in the morning, and water was available *ad libitum*.

Data Collection

The second author collected all the data between 08:45 and 12:30, from Sept. 1995 to Aug. 1997 (Silveira 1999). Spontaneously occurring agonistic conflicts in which both antagonists were adult males were the focus of the study. When more than one conflict took place at one time, the observer chose for close observation the one of the greatest intensity and involving the one dyad that had contributed the least amount of data. To increase data independence no dyad was sampled more than once per day. Agonistic conflicts were dyadic (or polyadic) interactions in which at least one of the antagonists directed aggressive behaviours at his opponent; these could vary along a continuum of intensity from screaming against the opponent to actual physical combat (e.g. sparring and jaw fencing) (Colmenares 1996). In addition to the behavioural content of the agonistic conflict and the direction of the behaviours that were exchanged, information on the identity of the initial antagonists and, whenever possible, of the role they played in the conflict, i.e. aggressor or victim, were also noted. The aggressor was the animal who initiated the aggressive interaction (unless it used screaming), or who exhibited the aggressive behaviour of the highest intensity. There were 23 (2.45%) conflicts in which the role of the participants could not be established, and of these, only 6 (3.77%) were conflicts followed by some

non-aggressive interaction. Where applicable, these were dropped from the analyses. We then used the standard method developed by de Waal & Yoshihara (1983) that involves the collection of observations during post-conflict periods and during matched-control periods. When the aggressive exchanges between the former opponents stopped for, at least, 1 min, a 10-min focal sample of both opponents was recorded (i.e. post-conflict period or PC). If aggression between the opponents reoccurred within the first min of the PC period, the session was aborted and restarted immediately after the aggression ceased again. The next possible observation day (1 wk at most), and at approximately the same time of day, a matched control focal observation of the two former antagonists was conducted (i.e. matched-control period or MC). MC observations were postponed if any of the focal partners was engaged in an aggressive conflict within 10 min before a planned MC. Also, MC observations were aborted if both members of the focal dyad initiated an agonistic interaction with each other. The simultaneous collection of both antagonists' behaviour was possible and reliable because the observer (F. S.) had been watching and collecting data on the colony for over 2 yr before the beginning of this study and because the observation conditions were excellent. In addition, before the beginning of the study, the senior author (F. C.) assessed the reliability of the procedure to be used by the second author. During the focal sampling of the antagonists (both during PC and MC observation periods), all the non-aggressive and agonistic interactions in which at least one of the antagonists participated as initiator or recipient were noted. Finally, all the events of self-grooming, self-scratching, and 'sweeping' that were performed by any of the former antagonists during PC or MC observations were also recorded (Silveira 1999). During sweeping, the individual scratched (with the fingers) and/or rubbed (with open hand) the ground repeatedly and from side to side, the manner of the movements being often exaggerated and highly conspicuous. All the observations were collected on check sheets, using continuous recording methods (Altmann 1974; Martin & Bateson 1993). We collected 243 conflicts (i.e. PC/MC pairs) from the 28 male–male dyads. We recorded an average of 8.6 conflicts per dyad (range: 3–12) and 30.4 per individual (range: 24–34).

Behavioural Measures and Data Analysis

In the present paper, we analyse the non-aggressive, agonistic, and stress-related behaviours that occurred during PC and MC observations. Non-aggressive behaviours were classified into three mutually exclusive categories: NCTG, which included lip-smacking, ear-flattening, approaching and retreating, presenting (Colmenares 1990); contact greeting (CTG), which consisted of touching or grasping the opponent's hindquarters or genitalia, and mounting (Colmenares 1990); and grooming (GRO). The following agonistic behaviours were recorded during post-conflict observations: re-aggression by the aggressor (RA), counter aggression by the victim (CA), side-directed aggression by the aggressor (SDA), redirected aggression by the victim (RDA), and aggressive intervention by a third-party (AI). Behavioural indicators of post-conflict anxiety included self-grooming, self-scratching and sweeping. Data from another hamadryas study have showed that they are all temporally associated with one another and tend to co-occur during stressful situations in which individuals appear to be motivationally agitated and uncertain about what may happen next (Romero & Colmenares 2005).

We analysed whether NAPBs between former opponents and between former opponents and third-parties (initiated by former opponents or by third-parties) occurred only or earlier in the PC than the corresponding MC period. In all cases, the difference between PC and MC scores of each category of post-conflict non-aggressive behaviour was required to reach statistical significance for accepting that NAPBs were more likely after aggressive encounters than during periods not preceded by aggression (i.e. rejecting the null hypothesis). At this stage, and given that our first goal was to test if NAPBs qualified as friendly reunions, we avoided labelling such interactions as reconciliations, triadic affiliations and peaceful interventions. To work out standardized indices of the tendency for non-aggressive interactions between former opponents or between former opponents and third-parties, we adapted the method developed by Veenema et al. (1994) to work out corrected indices of conciliatory tendency, CCT, i.e. V = (attracted pairs−dispersed pairs)/(total number of pairs). In our study, we developed two indices, the CTt, defined as the corrected tendency for non-aggressive behaviours between former opponents, and the CTTt, defined as the corrected tendency for non-aggressive behaviours between former opponents and third-parties, initiated by the former. 'Attracted' pairs were pairs in which the behavioural interaction criterion was reached earlier or only in the PC compared with the MC period, and 'dispersed' pairs were pairs in which it was reached

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earlier or only in the MC compared with the PC observation period. The behavioural interaction criterion was the occurrence of any of the non-aggressive behaviours mentioned above [i.e. (NCTG), (CTG), or (GRO)].

We also used the *time rule* method (Aureli et al. 1989) to determine the time window during which there were statistically significant differences in the cumulative frequency of the first non-aggressive behaviour between the former opponents during PC vs. MC observations. This time window was later used to test one of the functional predictions of the reconciliation hypothesis, that is, that after a post-conflict non-aggressive interaction the frequency of stress-related behaviours decreases significantly. To do so, we compared the rate of anxiety-related behavioural measures recorded during two types of PC samples. PCs(+) and PCs(−) were PC samples in which there was or there was not a non-aggressive interaction between the former opponents respectively. In fact, we first determined the time window for the occurrence of non-aggressive interactions between former opponents, which happened to be the first minute after the conflict (i.e. PC1, see below), and then compared the time window from minute 2 through 10 of PCs(+) vs. PCs(−). We could not test the functional prediction that NAPBs reduce the probability of renewed aggression by the former aggressor as there were very few PC samples with re-aggression.

All the analyses presented here were based on data from dyads (n = 28) and involved the comparison of each dyad's scores across two conditions (e.g. PC vs. MC observations) or across behaviour categories. We used dyads instead of individuals in the analyses because it is a well-established fact that an individual's behaviour varies widely as a function of whom he or she is interacting with (Hinde 1983); in other words, dyads are unique. Thus, pooling data from the different dyads to which any given individual contributes may have two undesirable and largely uncontrolled effects. First, each individual's data are somehow entered again in the summary data of their multiple partners. Second, the dyadic singularities may be diluted and distorted by combining inter-dyad scores. Finally, the most widely tested hypothesis to understand variation in post-conflict affiliation, that is, the valuable relationships hypothesis, is actually a hypothesis about inter-*dyad* variation in the occurrence of reconciliation (e.g. Watts 2006). Although we collected data from the two opponents simultaneously, their behaviours were never double-counted as the behavioural measures analysed focused on dyadic outcomes (e.g. was the aggressive conflict in any given dyad followed by a non-aggressive interaction? How many aggressive conflicts were followed by a non-aggressive exchange for any given dyad? Who (aggressor or victim) initiated the non-aggressive interaction?) rather than on the separate contribution of each individual partner.

We used the Wilcoxon signed matched-pairs test (Siegel & Castellan 1988; Zar 1999) throughout. Although the number of dyads was always 28, the degrees of freedom for the test varied across the different analyses because paired scores that were equal are discarded (i.e. n = total number of non-zero differences). All tests were two-tailed and differences were considered statistically significant when $p \leq 0.05$. To circumvent problems of lack of independence in the data and of assumptions about the theoretical distribution of scores, we report exact p-values that are based on permutation tests. We used SPSS version 15.0 (SPSS Inc., Chicago, IL, USA). Although Wilcoxon tests rest on the comparison of differences in medians rather than means, our graphs present information on means (and SEs), just for illustrative purposes. We confirmed, however, that if medians were reported it would not affect the interpretation of the graphs.

Results

Post-Conflict Non-Aggressive Behaviour

Males tended to engage in some kind of non-aggressive interaction (i.e. a category made of (NCTG), (CTG), and (GRO) with their former opponents far more often soon after an aggressive conflict than during a peaceful matched-control period ($T = 0$, $n = 28$, $p < 0.001$, Fig. 1). The mean corrected tendency for non-aggressive interactions between former opponents (CTt) was 63.65% (SE = ± 4.07%).

Male opponents also tended to initiate non-aggressive interactions with third-parties more often during post-conflict periods than during control periods ($T = 64.5$, $n = 23$, $p = 0.023$, Fig. 1). The mean corrected triadic tendency for non-aggressive behaviour (CTTt) was 13.39% (SE = ±7.87). However, when separate analyses were conducted for aggressors and victims, we found that only victims showed such a significant inclination to initiate non-aggressive interactions with bystanders (victims: $T = 91$, $n = 27$, $p = 0.016$; aggressors: $T = 143$, $n = 26$, ns, Fig. 1). We found no evidence for non-aggressive interactions initiated by bystanders ($T = 124$, $n = 23$, ns);

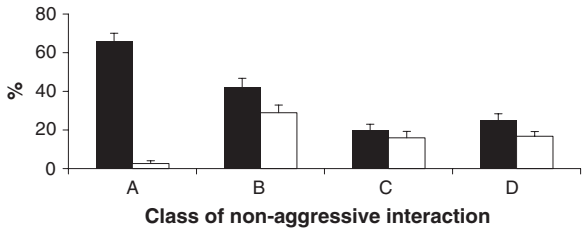

Fig. 1: Percentage (mean + SE) of 'attracted' (filled bars) vs. 'dispersed' (open bars) pairs for four classes of non-aggressive interactions during post-conflict and during matched-control observations. (A) Interactions between former opponents. (B) Interactions initiated by former opponents towards third-parties. (C) Interactions initiated by aggressors towards third-parties. (D) Interactions initiated by victims towards third-parties.

the mean tendency for this class of interaction was −2.72% (SE = ±4.96%). We also found that the corrected tendency for non-aggressive interactions between former opponents was far higher than the corrected tendency for non-aggressive interactions with third-parties (mean CTt = 63.65% vs. mean CTTt = 13.39%, T = 17, n = 25, $p < 0.001$).

Non-Aggressive Interactions between Former Opponents

The previous analyses indicate that non-aggressive interactions were especially frequent between former opponents as compared with those between opponents and third-parties. A closer look at the data reveals that, in fact, the majority of these interactions involved a single class of non-aggressive behaviour, i.e. NCTG. In effect, of the three non-aggressive behaviours recorded and analysed, NCTG occurred in 149 PC samples vs. 28 MC samples (i.e. 61.32% vs. 7% respectively), whereas CTG occurred only in 15 PC samples vs. 1 MC sample (i.e. 6.17% vs. 0.41% respectively), and GRO occurred only in 10 PC samples vs. no MC sample (4.11% vs. 0 respectively). According to the standard, more conservative approach, NCTG occurred earlier or only in an average of 59.73% PCs vs. 2.17% MCs (T = 0, n = 28, $p < 0.001$). A similar analysis of the category made of the two low-frequency non-aggressive behaviours (i.e. CTG + GRO) also yielded a statistically significant result, although in this case only 7 of 28 dyads did actually contribute data (6.53% attracted pairs vs. 0.44% dispersed pairs, T = 0, n = 7, p = 0.016). Even in these seven dyads, the scores of NCTG were significantly higher than the scores of CTG + GRO (mean 42.86% vs. 14.29% respectively, T = 0, n = 6, p = 0.028). The mean corrected tendencies for NCTG and CTG + GRO were CTnctg = 57.56% (SE = ± 3.53%) and CTcgt + gro = 6.1% (SE = ± 2.3%) respectively. In 59% of the conflicts, it was the aggressors who initiated the NCTG towards the victims, however, the difference did not reach statistical significance (T = 92, n = 24, p = 0.09).

The three non-aggressive behaviours analysed here showed very distinctive patterns of co-occurrence. Thus, CTG occurred in 15 PC samples and in 16 intervals (i.e. in one of the samples it occurred twice), and in 15 of those intervals it co-occurred with NCTG. In contrast, GRO was recorded in 10 samples and 47 intervals, however, GRO only shared one sample and one interval with NCTG and CTG.

Non-Aggressive Behaviour Directed at Third-Parties

When male opponents targeted male third-parties, they were far *more* likely to use NCTG than either CTG or GRO (95% vs. 4% of PC samples: T = 3, n = 28, $p < 0.001$; 95% vs. 1%: T = 0, n = 27, $p < 0.001$ respectively; Fig. 2). In contrast, when male opponents targeted female third-parties, they were far *less* likely to use NCTG than either CTG or GRO (77% vs. 2%, in both cases, T = 44, n = 21, p = 0.009 and T = 38, n = 20, p = 0.01 respectively; Fig. 2).

Aggression vs. Non-Aggression During Post-Conflict Observations

The analysis of the post-conflict aggressive interactions recorded revealed that the percentages of PC samples in which RA, CA, or AI occurred were very low indeed (i.e. 4.9%, 2.47%, 8.64% respectively).

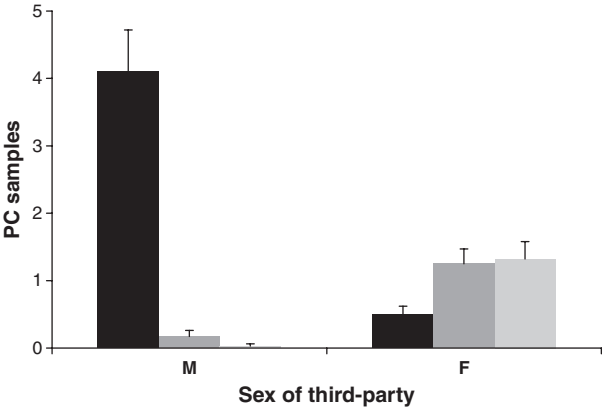

Fig. 2: Number of PC samples (mean + SE) in which male opponents directed each class of non-aggressive behaviour towards third-parties as a function of the latter's sex (M, male; F, female). Black bars, NCTG; grey bars, CTG and shaded bars, GRO.

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In contrast, the percentages of PC samples with RDA or with SDA were relatively elevated (i.e. 21.40% and 18.10% respectively). In any case, the percentage of PC samples in which NCTG occurred was far higher than the percentage of PC samples in which any of the other behaviours, either non-aggressive or aggressive, were displayed (Fig. 3).

Post-Conflict Stress-Related Behaviours

The category made of self-scratching, self-grooming and sweeping occurred significantly more often during post-conflict samples than during the corresponding matched-control samples (59.67% PCs vs. 22.76% MCs, $T = 1.5$, $n = 26$, $p < 0.001$). During PCs, the stress-related scores of aggressors and victims were roughly the same (41% vs. 43% respectively; $T = 99.5$, $n = 20$, ns).

Post-Conflict Non-Aggressive Behaviour and Stress-Related Behaviours

The comparison of the frequency of the first NCTG throughout the 10 min of the two sampling periods (i.e. PCs vs. MCs) shows that most NCTG occurred during the very first minute following the aggressive conflict (PC1 vs. MC1, $T = 0$, $n = 25$, $p < 0.001$; Fig. 4). In fact, both NCTG and anxiety-related behaviours tended to co-occur during the first minute following a conflict (PCs1 vs. PCs2-10; NCTG: $T = 53.5$, $n = 27$, $p < 0.001$; anxiety-related behaviours: $T = 3$, $n = 28$, $p < 0.001$ respectively). The critical test of the anxiety-reduction hypothesis, that is, the comparison of the rate of stress-related behaviours during min 2–10 of PCs[+] and PCs[−] yielded non-significant differences ($T = 151.50$, $n = 25$, $p = 0.76$, Fig. 5). Although CTG + GRO occurred as first non-aggressive behaviour in very few PCs (i.e. 8 or 3.2%) and was performed only by 10 of 28 dyads, most of it also occurred in the first minute (PC1 = 12 vs. MC1 = 0, $T = 0$, $n = 6$, $p = 0.031$). CTG + GRO was recorded in 23 conflicts, however, we could not find any association between its occurrence and the occurrence of stress-related behaviours. Thus, stress-related behaviours were recorded in 15 of these conflicts and in nine of them (or 60%) these behaviours were observed *after* the occurrence of CTG + GRO.

Fig. 3: Percentage of post-conflict samples in which the three non-aggressive behaviours and the five aggressive behaviours were recorded. NCTG, non-contact greeting; CTG, contact greeting; GRO, grooming; RA, re-aggression; CA, counter-aggression; AI: aggressive intervention; RDA, redirected aggression; SDA, side-directed aggression.

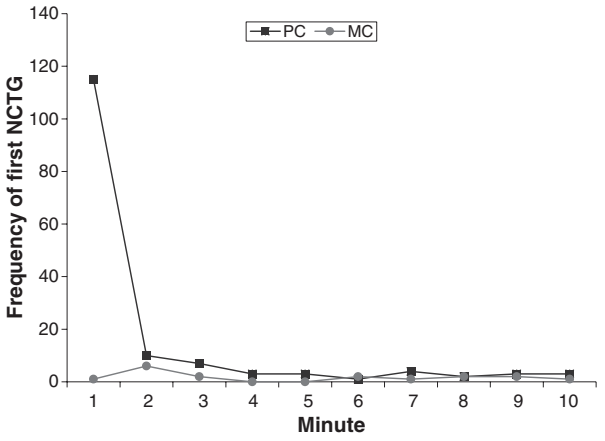

Fig. 4: Temporal distribution of the frequency of the *first* NCTG across the 10 min of the PC and MC sample periods.

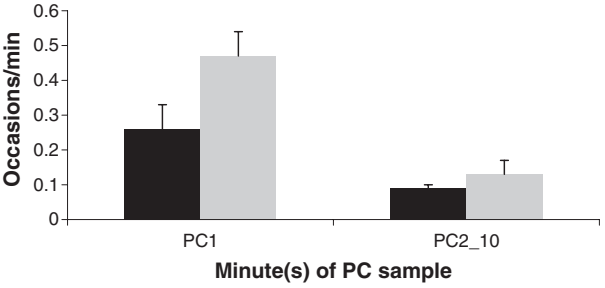

Fig. 5: Rate (mean + SE) of anxiety-related behaviours performed during the first minute (PC1) and during min 2 to 10 (PC2-10) of post-conflict samples with vs. without non-contact greeting (black bars and grey bars respectively). Rates are measured as number of occasions per minute.

Discussion

Is All Post-Conflict Non-Aggressive Behaviour Motivationally Friendly?

Although the first assumption of the reconciliation hypothesis holds that post-conflict reunions should

be *friendly* and involve *contact* between former opponents, in practice, however, researchers have not been very strict when applying this criterion (Colmenares 2006). The behavioural measures used by studies in Table 1 to assess post-conflict reunions and hence conciliatory tendencies after male–male conflicts in a number of species may illustrate this point. Although some of these studies only used contact behaviours (Kutsukake & Castles 2004; Cooper et al. 2007; Wittig & Boesch 2005), however, many others explicitly (or probably) included non-contact behaviours as well (e.g. lipsmack: Petit et al. 1997; Schino et al. 1998; Majolo et al. 2005; Berman et al. 2006; Castles & Whiten 1998; present: Berman et al. 2006; Arnold & Whiten 2001; approach: Arnold & Whiten 2001). Cooper & Bernstein (2002) recorded 'affiliative contacts', however, they did not describe the actual behavioural measures which were included in that category. Anyway, except in Berman et al.'s (2006) study, in none of these reports was there a quantitative analysis of the different non-aggressive behaviours used by males after aggressive confrontations. This means that we can neither assess the motivational nature and homogeneity of the behaviours that were used during post-conflict reunions nor evaluate their individual contribution to the overall mean conciliatory tendencies reported (Table 1). The present study has shown that the analysis of a single category made of non-aggressive contact and non-contact behaviours may convey a distorted picture. Thus, whereas the overall mean CTt for non-aggressive interactions after male–male conflicts in our hamadryas study was 63.65%, however, the corrected tendencies obtained for NCTG and for CTG plus GRO were 57.56% and 6.1% respectively. In other words, the two behavioural categories were probably motivationally heterogeneous. In fact, we found that whereas CTG tended to co-occur with NCTG, GRO was not associated with either.

The findings from the present analysis, based on the PC/MC methodology, lend support to Colmenares's (1990) hypothesis that NCTG between male hamadryas baboons are tense and motivationally ambivalent interactions: they appear to be neither agonistic nor friendly. Several further indicators of this motivational ambivalence are provided by this study. First, NCTG were very frequent following the occurrence of an aggressive conflict. Second, these interactions tended to occur during the very first minute following the conflict, when a full motivational switch to affiliation is most unlikely, especially between individuals who avoid one another's proximity and rarely interact affiliatively during peaceful periods. Third, NCTG typically involves a slow approach immediately followed by a quick retreat (Colmenares 1990; Colmenares et al. 2000), that is, although the distance is initially reduced (i.e. reunion component), the final outcome involves increased distance (i.e. separation component). Fourth, the type of non-aggressive behaviour exhibited by antagonists during triadic post-conflict interactions is very revealing: male targets received *non-contact* greeting whereas female targets received *contact* greeting and/or GRO. Finally, the relatively high rate of side-directed aggressive interactions initiated by aggressors and victims might also reflect the antagonists' persisting aggressive motivation during post-conflict periods. We believe that for a post-conflict interaction to qualify as a reunion, the

Table 1: Mean corrected conciliatory tendencies (CCTs) reported in studies of reconciliation for conflicts in male-male dyads

Species	Setting	Social system	Mating system	CCT	Reference
Macaca fuscata	C	FB	Promiscuous	30.3	Petit et al. (1997)
Macaca fuscata	C	FB	Promiscuous	9.7	Schino et al. (1998)
Macaca fuscata	W	FB	Promiscuous	31	Majolo et al. (2005)
Macaca assamensis	F	FB	Promiscuous	17.6	Cooper & Bernstein (2002)
Macaca thibetana	W	FB	Promiscuous	31	Berman et al. (2006)
Macaca radiata	F	FB	Promiscuous	30.2	Cooper et al. (2007)
Papio h. papio	C	FB	Polygynous[a]	8.8	Petit et al. (1997)
Papio h. anubis	W	FB	Promiscuous	11	Castles & Whiten (1998)
Pan troglodytes	W	MB	Promiscuous	32.8	Arnold & Whiten (2001)
Pan troglodytes	W	MB	Promiscuous	13.7	Kutsukake & Castles (2004)
Pan troglodytes	W	MB	Promiscuous	14.5	Wittig & Boesch (2005)
Papio h. hamadryas	C	CSB	Polygynous	6.1	This study

C, captivity; W, wild; F, free-ranging, provisioned; FB, female-bonded; MB, male bonded; CSB, cross-sex bonded.

[a]See Maestripieri et al. (2007).

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former opponents should be shown to be able to *maintain* non-aggressive proximity, at the very least.

Is Post-Conflict Non-Aggressive Behaviour Functionally Conciliatory?

In this study, we set out to test two functional predictions of the reconciliation hypothesis, that is, that non-aggressive post-conflict reunions (or reconciliations) reduce both the probability of renewed aggression by aggressors and the rate of the antagonists' stress-related behaviours (anxiety-reduction hypothesis) (Arnold & Aureli 2007). We could not test the first prediction, as the rate of re-aggression was very low in this study (i.e. 4.9% of PC samples), and although the majority of non-aggressive post-conflict interactions between former opponents were non-friendly, i.e. they were NCTG, we tested whether they reduced the antagonists' level of anxiety, anyway. The rate of post-conflict stress was especially elevated in the first PC minute and although it declined thereafter, the decrease was not related to the occurrence or absence of NCTG. The very few cases recorded of post-conflict contact greeting and GRO also confirmed the lack of any association between post-conflict non-aggression and stress alleviation. Therefore, our observations failed to support the stress alleviation prediction and indicate that non-aggressive post-conflict interactions between males were not functionally conciliatory.

Non-Contact Greeting between Non-Friends and Non-Allies

According to the valuable relationships hypothesis, friendly post-conflict reunions should be the highest between individuals that maintain relatively high baseline rates of affiliative behaviours (they are friends), and that depend on one another's agonistic support (they are allies) to gain access to fitness-related services and resources (Cords 1997; Arnold & Aureli 2007). Even when male hamadryas baboons stay on in their natal bands and form clans and leader–follower associations with male kin (Abegglen 1984; Colmenares 1992, 2004), there is very little evidence that they develop bonds or alliances that resemble those reported for species that are strongly male-philopatric and male-bonded (e.g. chimpanzees; see Mitani et al. 2000). The two highest corrected conciliatory tendencies for male–male conflicts in the *Macaca* species described in Table 1 occur in species in which grooming (bonds) and agonistic (alliances) between males were reported (*Macaca fuscata yakui*: Majolo et al. 2005; *Macaca thibetana*: Berman et al. 2006). In contrast, GRO between adult male hamadryas baboons is extremely rare (Abegglen 1984; this study: 9 PC samples or 3.79%, and zero occasions during MC observations), especially if they have established one-male units; and although Colmenares et al. (2006) reported that leader males from clans gained a competitive advantage over leader males from single OMUs in a context of contest competition for food, the evidence for active cooperation (as opposed to passive tolerance) between clan males is meagre at most (in this study, agonistic interventions only occurred in 8.64% of PC samples).

If we acknowledge that the two non-aggressive behaviours involving body contact were acceptable indicators of friendly reunions, then our findings are consistent with the valuable relationships hypothesis, as a corrected tendency for CTG + GRO of 6.1% falls clearly within what one would expect for a species in which males do not form bonds and alliances with one another (van Hooff 2001). In any case, we are still left with an intriguing question: if male hamadryas baboons are neither friends nor allies, why should they be so inclined to engage in non-conciliatory NCTG after conflicts?

The reconciliation hypothesis holds that there is a quick motivational transition from aggression and fear to attraction and affiliation (e.g. de Waal 2000a,b). This is built upon the idea that combatants are assumed to be friends and/or allies and that friendly post-conflict reunions serve to restore their mutually valuable bonds. However, does this necessarily mean that non-friends/allies should not be expected to manage their conflicts in a peaceful way? In their relationships with other unit leaders, males have to manage the uncertainty as to whether and when they will be challenged and eventually lose females to their rivals, and, rather than making friends or allies with other unit leaders, males appear to concentrate on not making enemies (also see Wittig & Boesch 2005). If we take a broader view of functional reconciliation, it can be argued that NCTG between males perhaps contributes to restore previous levels of non-hostile interactions between individuals that are neither friends nor allies.

The results of the analysis presented in this study regarding the behaviours used by male antagonists during triadic affiliation as a function of the third-party's sex lend support to the view that links GRO to high relationship compatibility (between males and females) and NCTG to high relationship incompatibility (between males) (Kummer 1975; Zaragoza

& Colmenares 2002). In general, any sign of tension or anxiety during the course of an interaction could be a candidate measure of relationship security (Cords & Aureli 2000; Arnold & Aureli 2007). Again, our results indicate the existence of a close temporal relationship between stress-related behaviours and NCTG between former opponents, thus suggesting that NCTG can be used as a valid index of (low) relationship security (also see Kummer et al. 1974, 1978; Colmenares 1991).

Recently, Flack & de Waal (2004) have proposed the existence of formal signals of equal status to refer to those signals that may be exchanged by partners who have symmetrical agonistic relationships. The fairly even responsibility for the initiation of NCTG between aggressors and victims that we found in this study as well as the finding that both antagonists experienced similar rates of post-conflict stress appear consistent with this view. Thus, the reciprocal gestures exchanged by male hamadryas during the performance of post-conflict NCTG (Colmenares 1990) could well qualify as formalized signals of equal status.

In sum, this study of conflict management among male hamadryas baboons has shown that after male–male conflicts, unit leaders tended to engage in NCTG with their opponents. We suggest that the gestures exchanged during these NCTG can be interpreted as formalized signals of equal status (cf. Flack & de Waal 2004) and that the rate and form of the greetings used by male opponents are indicative of relationship insecurity and incompatibility (Zaragoza & Colmenares 2002). We argue that the NCTG patterns used by unit males after conflicts reflect motivational ambivalence and do not qualify as friendly behaviours (Colmenares 1990). We conclude that male hamadryas baboons' post-conflict NCTG are not conciliatory but probably serve to assess their opponents' attitude and to negotiate the restoring of their pre-conflict levels of peaceful but *non-amicable* co-existence (Colmenares 1991).

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