Reconciliation and the costs of aggression in wild Barbary macaques (*Macaca sylvanus*): a test of the integrated hypothesis

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Abstract

The ‘integrated hypothesis’ predicts that reconciliation (the post-conflict friendly interaction between former opponents observed in various group-living species) functions to reduce anxiety and the risk of aggression from the former opponent or a bystander in the aftermath of a conflict. It also predicts that relationship quality between opponents affects the occurrence of reconciliation and modulates the anxious response of the opponents after a conflict. Due to the asymmetric nature of aggressive interactions, the cost of aggression is likely to differ between the victim and the aggressor. The aim of this study was to test the predictions of the ‘integrated hypothesis’ independently for the victim and the aggressor of a conflict. We collected data on two wild groups of Barbary macaques. This study represents, to our knowledge, the first systematic test of the integrated hypothesis on wild, non-provisioned animals. Victims of aggression were at a greater risk of receiving aggression from the former opponent or a bystander after a conflict and showed elevated anxiety. We found no such costs for the aggressor. Reconciliation reduced anxiety in the victim but did not reduce their risk of receiving aggression. Finally, relationship quality affected the occurrence of reconciliation but did not modulate post-conflict anxiety. The results of our study show that the costs of aggression are asymmetrically distributed between the victim and the aggressor. Such differences are likely to lead to different social tactics used by the victim and the aggressor in the aftermath of a conflict.

Introduction

In group-living animals, aggression amongst group members is sometimes unavoidable and often occurs as a result of competition over valuable resources such as food, social or mating partners (van Schaik 1989). In addition to the risk of physical injury, aggressive interactions often lead to an increase in the anxiety of the opponents in the first few minutes after a conflict (Aureli & van Schaik 1991a). Reconciliation (the friendly interaction exchanged between former opponents in the first few minutes after their conflict; de Waal & Yoshihara 1983) is a post-conflict mechanism that functions to control for the risk that aggression between group members has on renewed aggression, anxiety and social relationships. Reconciliation has been observed in a range of group-living species (Schino 2000; Aureli et al. 2002).

Studies on post-conflict behaviour and reconciliation have evidenced some consistent findings across species. The 'valuable-relationship hypothesis' (Kappeler & van Schaik 1992; de Waal & Aureli 1997) views reconciliation as a key mechanism to restore and maintain friendly relationships with group members that are beneficial for individual fitness (Silk et al. 2003). Supporting this hypothesis, reconciliation is more often observed between individuals that share high quality relationships (i.e. social partners that exchange high rates of affiliative behaviour, e.g. Koski et al. 2007; Majolo et al. 2009) because a non-reconciled conflict would have more dramatic consequences for them than for individuals that share a low quality relationship (i.e. social partners that exchange low rates of affiliative behaviour: de Waal 1986; Cords & Aureli 2000; Koyama 2001). Moreover, the 'uncertainty-reduction hypothesis' (Aureli & van Schaik 1991a) predicts that the primary function of reconciliation is to reduce the anxious response that former opponents experience in the aftermath of a

conflict, due to the risk of renewed aggression. Indeed, empirical data show that former opponents are more at risk of receiving aggression from one another or from a bystander, and have an increased level of anxiety in the first few minutes after a conflict than in a control condition (Aureli & van Schaik 1991a; Aureli 1997; Kutsukake & Castles 2001). The 'integrated hypothesis' (Aureli 1997) combines the 'valuable-relationship' and the 'uncertainty-reduction' hypotheses, predicting that the occurrence of reconciliation should reduce the risk of receiving renewed aggression from the former opponent, and decrease their post-conflict anxiety in comparison to non-reconciled conflicts. Moreover, it predicts that the increase in post-conflict anxiety should be higher the higher the quality of the relationship between the opponents is, as the more costly the effect of the conflict is on their relationship.

Only a small number of studies have tested the 'integrated hypothesis' (Kutsukake & Castles 2001; Koski et al. 2007), despite it providing a clear framework predicting post-conflict behaviour (Aureli et al. 2002). Moreover, the 'integrated hypothesis' does not make distinct predictions for the post-conflict behaviour of the victim and aggressor (Aureli 1997). However, aggression is often an asymmetric event where the costs and benefits may differ for the opponents, eliciting different behavioural responses. For example, although post-conflict anxiety has been observed in both the victim and aggressor (Castles & Whiten 1998; Das et al. 1998), victims have been observed to show higher rates of anxiety than aggressors in various studies (Cooper et al. 2007; Koski et al. 2007; Schino et al. 2007). Also, in the few studies that have analysed post-conflict behaviour according to the role of the opponents, it was found that the aggressor did not have an elevated risk of receiving aggression in the post-conflict period (Castles & Whiten 1998; Das et al. 1998). These findings suggest that differences in the post-conflict aggression received by opponents should be controlled

for when evaluating the emotional response of opponents to damaged social relationships. Moreover, these findings highlight the importance of analysing post-conflict behaviour independently for the victim and aggressor.

The aims of this study were to test the predictions of the 'integrated hypothesis' in two wild groups of Barbary macaques (*Macaca sylvanus*) and to analyse the cost of aggression, in terms of risk of renewed aggression and increased anxiety, independently for the aggressor and the victim of aggression. In particular, we predicted that: 1) Victims would be more at risk of receiving aggression from the former opponent or a bystander, and would show an increase in anxiety after a conflict. In addition, we predicted no such costs for the aggressor due to the expected asymmetry in the cost of aggression for the victim and the aggressor; 2) Reconciliation would function to reduce the risk of receiving aggression, from the former opponent or a bystander, and to reduce post-conflict anxiety in the victim but not in the aggressor, as we predicted no post-conflict increase of aggression and anxiety for the aggressor (see prediction 1); 3) Reconciliation would be more likely to be observed after conflicts between opponents sharing higher quality relationships. Moreover, the anxious response due to the lack of reconciliation would be higher for opponents sharing a high quality relationship.

This is the first study to analyse post-conflict behaviour in wild Barbary macaques. Moreover, to our knowledge it is the first comprehensive test of the 'integrated hypothesis' on a wild, non-provisioned species.

Methods

a) Study subjects

Subjects of this study were 48 adult or sub-adult monkeys (30 males and 18 females) living in two groups of wild Barbary macaques. These two groups (named 'Flat-face' and 'Large' group) inhabited the deciduous cedar and oak forest near the city of Azrou (33° 24'N – 005° 12'W), in the Middle-Atlas Mountains of Morocco, at an altitude between 1600 and 2000 metres a.s.l. Both groups relied on a completely natural diet. At the beginning of the study, the 'Flat-face' group consisted of 29 individuals (10 adult males, 1 sub-adult male, 8 adult females, 5 juveniles and 5 infants) while the 'Large' group consisted of 39 individuals (16 adult males, 3 sub-adult males, 10 adult females, 7 juveniles and 3 infants).

b) Data collection

RM was responsible for the data collection with the help of four research assistants. Data were collected daily between 06.00 and 19.00 hours from June 2008 to September 2009. Data were only collected when inter-observer reliability was above 95%. Observers conducted parallel observations on a randomly selected focal animal every month. Data were then compared to ensure inter-observer agreement in the data collected.

We used the post-conflict - matched-control (PC-MC) method to analyse the post-conflict behaviour of our study animals, following a well established methodology (de Waal & Yoshihara 1983; Aureli 1997). Anytime we observed aggression (i.e. threat, lunge, charge, chase, slap, grab or bite) exchanged between two or more monkeys, we collected data on the identity of the animals involved and on their role (i.e. aggressor or victim, the aggressor being defined as the initiator of the first aggressive display and the victim as the recipient of this aggression). We also collected data on the intensity of the conflict, on its result (decided or undecided, where a conflict was

134 defined as ‘decided’ if one of the opponents displayed submission (i.e. give ground,
135 make-room, flee), and on whether more than two opponents were involved in the
136 conflict. As soon as the conflict was over, we collected focal data on the victim or the
137 aggressor of the conflict for five minutes. We postponed a PC focal session if
138 aggression between the former opponents recommenced within 30 seconds since the
139 initial conflict was considered to then still be in progress (Aureli 1997; Kutsukake &
140 Castles 2001). During PC focal sessions we recorded the timing and occurrence of
141 any aggressive (i.e. threat, lunge, charge, chase, slap, grab or bite) or friendly
142 interaction between our focal animal and any other group member. We considered
143 successful ≤1.5 metres approaches (i.e. approaches that were not followed by
144 aggression or displacement for the first 30 seconds after the approach), allo-grooming,
145 body-contact and teeth-chattering as forms of friendly affiliation (Hesler & Fischer
146 2008). We recorded the occurrence of self-scratching and used this behaviour as a
147 measure of the anxiety of our focal animal. There is comprehensive pharmaceutical,
148 physiological and behavioural evidence that self-scratching is a reliable measure of
149 anxiety in primates (Maestripieri et al. 1992; Schino et al. 1996). We recorded
150 ambient temperature and relative humidity (using a 3500 Kestrel Pocket Weather
151 Station) because these two climatic variables may affect the rate of self-scratching in
152 macaques (Ventura et al. 2005).
153 On the next possible day, we collected five minute MC focal sessions on the same
154 focal monkey targeted in the matched PC session. In the MC sessions we collected the
155 same data and followed the same procedure and sampling method described for the
156 PC sessions above. Moreover, a MC session was only started when the distance
157 between the focal animal and the former opponent was matching the distance between
158 the same two monkeys at the beginning of the PC session. Two MCs were collected

for each PC. The first MC session (MC1) gave us a reliable measure of baseline latency to friendly interaction and of aggression for each dyad (Veenema et al. 1994). However, they could give us biased data with respect to baseline self-scratching. For example, if the focal animal was involved in a grooming session or in a conflict during a MC such social interactions could, respectively, decrease or increase the occurrence of self-scratching (Maestripieri et al. 1992). Therefore, we collected a second MC focal session (MC2) for each PC to effectively analyse whether PC self-scratching differed from baseline self-scratching. To obtain a reliable baseline measure of self-scratching, we started these MCs only if the focal animal was not involved in a grooming or aggressive interaction with another monkey in the five minutes prior to a planned MC, or during the MC. There was no significant difference in average daily temperature and humidity recorded between PC and MC sessions (paired-sample t-tests, PC-MC1 temperature: $t_{(129)} = 0.12$, $p = 0.91$, PC-MC2 temperature: $t_{(129)} = 0.23$, $p = 0.82$, PC-MC1 humidity: $t_{(129)} = 0.68$, $p = 0.50$, PC-MC2 humidity: $t_{(129)} = 0.90$, $p = 0.37$). The two MC sessions did not differ for any of the other criteria or sampling method described above. To control for the temporal and seasonal variation in the expression of grooming, aggression and self-scratching across the year, the two MC sessions were collected within two weeks of the matched PCs (mean days ± SE = 4.63 ± 0.78). If it was not possible to collect the two MCs following these criteria within two weeks from the relevant PC, the PC session was discarded.

We used scan sampling and focal sampling to collect data on the baseline level of affiliation for each dyad. Scan samples were collected every hour on the activity of the study animals (i.e. resting, feeding, allo-grooming, body contact), their ≤ 1.5 metre proximity to other study subjects, and on the identity of their social partners.

Moreover, we collected 20 minute focal sessions on our study animals to calculate the proportion of successful ≤1.5 metres approaches (see above for definition) exchanged within each dyad. For each study monkey the order of focal observations was evenly distributed across the study period and time of day. A monkey was never sampled more than once in a single day.

c) Data analysis

Analyses were based on 414 PC-MC pairs (Table 1). All but one adult male of the 'Large' group, and all of the study monkeys from the 'Flat-face' group were represented in at least one PC-MC observation (mean PC-MC pairs per monkey ± SE = 17.6 ± 2.2). Moreover, we also collected 792 scan samples and 1,101.9 hours of focal observations (mean hours/monkey ± SE = 18.71 ± 2.10).

A conflict was considered to be reconciled if the opponents exchanged a friendly behaviour (i.e. body-contact, teeth-chattering or grooming) within the five minutes PC observation (Cords 1993; Call 1999; Aureli et al. 2002). In addition, we considered close-proximity approaches as a PC friendly behaviour as there is evidence that close proximity functions to reconcile in the Barbary macaque (McFarland & Majolo, in preparation; Patzelt et al. 2009). The occurrence of reconciliation was demonstrated using the 'PC-MC method' (de Waal & Yoshihara 1983) which compared the timing of the first friendly behaviour exchanged between opponents in PC and MC sessions. When friendly behaviour occurs earlier in the PC than the MC, the PC-MC pair is considered 'attracted'. When the interaction takes place earlier in the MC, the PC-MC pair is considered 'dispersed'. If they occur at the same time the PC-MC pair is considered 'neutral'. The proportion of 'attracted' and 'dispersed' pairs was compared using a Wilcoxon signed-ranks test.

We used a composite sociality index (CSI) to measure relationship quality for each dyad following the formula (Silk et al. 2003):

$$\frac{\sum_{3}^{3} \frac{x_i}{m_i}}{3}$$

x_i = Individual's mean value for each of the three behavioural measures.

m_i = Group's median value for each of the three behavioural measures.

Three behavioural variables were entered into this index (exchange of friendly behaviour [i.e. grooming or body-contact], proximity, and tolerance) as they represent three key measures of relationship quality in non-human primates (Fraser et al. 2008; Majolo et al. 2010; Silk et al. 2010). To calculate x_i for each dyad we collapsed together the proportion of hourly scans in which the two members of a dyad were exchanging friendly behaviour or were within ≤ 1.5 metre proximity, and the proportion of successful ≤1.5 metre approaches exchanged between them collected during the 20 minute focal sessions. The same three variables were used to calculate medians at the group level to obtain m_i. The higher the CSI value, the stronger the dyad relationship quality. In this study the values of the CSI ranged from 0 to 8.15 (mean CSI per dyad ± SE = 1.32 ± 0.06).

Data were analysed using a series of generalised linear mixed models GLMMs). GLMMs allow analysing the effect of a series of independent variables (i.e. fixed factors) on a continuous or categorical variable (Pinheiro & Bates 2000). Moreover, GLMMs allow analyses to be run using each PC or MC session as a single data point. This is because the inclusion of random factors to the model can control for non-independence of the data points (due, for example, to the fact that the same monkey was represented in multiple PC-MC pairs; Pinheiro & Bates 2000). Therefore, in all the analyses presented below we entered the victim and aggressor ID

as two random factors. To test our predictions we entered, as fixed factors, 'PC-MC session' (i.e. whether each data point was collected in a PC or in a MC session), 'reconciliation' (i.e. whether a conflict was reconciled during the PC or not) or 'relationship quality' (i.e. CSI value). When testing the integrated hypothesis, we calculated the 'PC augment of self-scratching' by subtracting MC2 self-scratching rates from PC self-scratching rates. This figure gave us a measure of the relative increase in PC self-scratching rates while controlling for the individual's baseline level (Majolo et al. 2009a).

When analysing the effects of fixed factors 'reconciliation' and 'relationship quality', we entered, as 'control' fixed factors, group ID ('Flat-face' or 'Large' group), age combination of the dyad (adult-adult, subadult-subadult or adult-subadult), their sex combination (male-male, female-female or male-female), and their rank distance because these variables can affect the occurrence of reconciliation and PC anxiety (Majolo et al. 2009b). We also entered 'bystander affiliation' (i.e. whether or not the focal animal exchanged a friendly interaction with a bystander in the PC session) as a control fixed factor as it may play a role in mediating the costs of aggression (de Waal & Aureli 1996). Finally, when analysing the fixed factor 'PC-MC session', the opponent's sex (male or female) and age (adult or subadult) were entered as 'control' fixed factors. PC-MC pairs that involved reconciliation or bystander affiliation were removed from the analyses comparing rates of aggression and anxiety between PCs and MCs.

Results for the control fixed factors are not shown here for the sake of brevity (see electronic appendices for complete GLMM results). GLMM analyses were performed using STATA v10.1 Software (StataCorp 2007).

Results

The occurrence of reconciliation in our study groups were confirmed using the 'PC-MC method'. There was a significantly higher proportion of 'attracted' pairs (98%) than 'dispersed' pairs (2%; Wilcoxon: $z = -7.554$, $p < 0.001$, N of dyads = 61). Moreover, the mean latency to affiliation was significantly shorter in the PC (mean ± SE = 62.66s ± 8.88) than the MC sessions (mean ± SE = 276.93s ± 8.15) (β ± SE = 214.28 ± 11.82, 95% CIs = 191.12 – 237.44, $z = 18.14$, N = 61, $p < 0.001$; Appendix 1). A survival curve (Fig 1) showed that reconciliation was most likely to occur in the first two minutes after a conflict. Therefore, we ran the analyses on a five minutes PC time window to fully investigate the consequences of aggression before and after the occurrence of reconciliation.

a) The costs of aggression

In support of our first prediction, the mean rate of opponent aggression received by the victim was significantly higher in the PCs than in the MCs (β ± SE = -0.01 ± 0.004, 95% CIs = -0.02 – -0.002, $z = -2.35$, N = 99, $p < 0.05$; Table 2, Appendix 2). Moreover, there was no significant difference in the mean rate of opponent aggression received by the aggressor between the PCs and the MCs (β ± SE = -0.004 ± 0.004, 95% CIs = -0.01 – -0.004, $z = -0.99$, N = 100, $p = 0.324$; Table 2, Appendix 3).

The mean rate of bystander aggression received by the victim was significantly higher in the PCs compared to MCs (β ± SE = -0.02 ± 0.006, 95% CIs = -0.04 – -0.01, $z = -4.37$, N = 99, $p < 0.001$; Table 2, Appendix 4). Moreover, we found no significant difference in the mean rate of bystander aggression received by the aggressor between PCs and MCs (β ± SE = -0.004 ± 0.005, 95% CIs = -0.01 – 0.007, $z = -0.72$, N = 100, $p = 0.473$; Table 2, Appendix 5).

The victim's mean rate of self-scratching was significantly higher in the PCs compared to MCs ($\beta \pm SE = -0.04 \pm 0.02$, 95% CIs = -0.08 – -0.01, $z = -2.38$, $N = 99$, $p < 0.05$; Table 2, Appendix 6). Moreover, there was no significant difference between the PC and MC mean rate of self-scratching for the aggressor ($\beta \pm SE = -0.03 \pm 0.03$, 95% CIs = -0.08 – 0.03, $z = -1.01$, $N = 100$, $p = 0.315$; Table 2, Appendix 7).

b) The role of reconciliation in reducing the costs of aggression

In contrast to our second prediction, the mean rate of PC opponent aggression received by the victim was significantly higher following reconciled conflicts compared to non-reconciled conflicts ($\beta \pm SE = 0.13 \pm 0.04$, 95% CIs = 0.05 – 0.20, $z = 3.36$, $N = 410$, $p < 0.01$; Table 2, Appendix 8). There was no significant difference in the rate of PC bystander aggression received by the victim following reconciled or non-reconciled conflicts ($\beta \pm SE = -0.01 \pm 0.07$, 95% CIs = -0.14 – 0.12, $z = -0.14$, $N = 190$, $p = 0.889$; Table 2, Appendix 9). In support of our second prediction, the victim's mean rate of PC self-scratching was significantly lower following reconciled conflicts compared to non-reconciled conflicts ($\beta \pm SE = -0.07 \pm 0.04$, 95% CIs = -0.15 – -0.004, $z = -2.06$, $N = 190$, $p < 0.05$; Table 2, Appendix 10).

In support of our second prediction, there was no significant difference in the rate of PC opponent or bystander aggression received by the aggressor following reconciled or non-reconciled conflicts (opponent aggression: $\beta \pm SE = 0.47 \pm 0.02$, 95% CIs = -0.001 – 0.10, $z = 1.92$, $N = 410$, $p = 0.055$; Table 2, Appendix 11, bystander aggression: $\beta \pm SE = -0.06 \pm 0.04$, 95% CIs = -0.15 – 0.02, $z = -1.40$, $N = 220$, $p = 0.161$; Table 2, Appendix 12). Moreover, there was no significant difference in the aggressor's mean rate of PC self-scratching following reconciled or non-reconciled conflicts ($\beta \pm SE = -0.07 \pm 0.04$, 95% CIs = -0.15 – -0.007, $z = -1.79$, $N =$

220, p = 0.073; Table 2, Appendix 13). The non-significant effect of reconciliation on aggression and anxiety in the aggressor confirmed the view that a conflict is not costly for the aggressor (see above).

c) Relationship quality and post-conflict behaviour

Supporting the 'integrated hypothesis', reconciliation was more likely to occur following conflicts between opponents that shared a high quality relationship (i.e. high value of their CSI) compared to those with a low quality relationship ($\beta \pm SE$ = 0.30 ± 0.10, 95% CIs = 0.11 – 0.49, $z = 3.07$, $N = 414$, $p < 0.01$; Fig 2, Appendix 14). Finally, there was no significant main effect of relationship quality on the 'PC augment of self-scratching' of the victim ($\beta \pm SE$ = -0.01 ± 0.01, 95% CIs = -0.03 – 0.007, $z = -1.25$, $N = 110$, $p = 0.212$; Appendix 15) or the aggressor ($\beta \pm SE$ = -0.006 ± 0.01, 95% CIs = -0.03 – 0.02, $z = -0.45$, $N = 121$, $p = 0.651$; Appendix 16).

Discussion

We showed that aggression is costly (in terms of renewed aggression and anxiety) for the victim but not for the aggressor of a conflict. Our results provided partial support for the predictions of the 'integrated hypothesis' in the victim, as reconciliation reduced PC anxiety but not aggression. Moreover, reconciliation was more likely to occur after conflicts between monkeys with a stronger social bond, as predicted by the 'integrated hypothesis', but relationship quality did not mediate emotional response in non-reconciled conflicts.

Our study supports the view that, for the victim of aggression, the PC period represents a time of high risk and uncertainty (Aureli 1997; Kutsukake & Castles 2001). Receiving renewed aggression from the former opponent can be a consequence

of the reduced tolerance and disruption of the social relationship elicited by the conflict (Aureli & van Schaik 1991a; Cords 1992; Wittig & Boesch 2005). Moreover, bystander aggression to the victim of a conflict may be an opportunistic strategy adopted by bystanders to strengthen their social bond with the former aggressor (Johnstone & Dugatkin 2000) or to establish, or confirm their dominance over the former victim as explained by the 'loser effect' (the increased chance of winning a fight against a previously defeated individual; Chase 1974; Hsu et al. 2006). Elevated anxiety in the PC period may be related to the risk of aggression from the former aggressor or a bystander (Aureli & van Schaik 1991b; Kutsukake & Castles 2001). The absence of observed PC aggression received by the aggressor in the current study may explain why the aggressor does not show elevated anxiety in the aftermath of a conflict.

The anxiety level of the victim was significantly reduced when a conflict was reconciled, a finding that supports the calming effect of reconciliation as predicted by the 'integrated hypothesis' (Aureli & van Schaik 1991b; Das et al. 1998). However, in contrast to previous studies (Aureli & van Schaik 1991a; Das et al. 1998), we found that the risk of opponent aggression was higher for the victim in reconciled compared to non-reconciled conflicts. Moreover, there was no evidence that reconciliation reduced the victim's risk of receiving aggression from bystanders. These results are congruent with what has been recently found in a study on captive Barbary macaques (Patzelt et al. 2009). In support of the 'integrated hypothesis', these results suggest that reconciliation functions to reduce anxiety in the victim despite the fact that reconciliation is positively associated with receiving PC aggression. The results of the current study highlight that the damage caused to the social relationship of the opponents, and not the risk of renewed aggression, is likely to be the main factor

causing elevated PC anxiety in the victim. Together with its calming effect, reconciliation functions to repair relationships as relationship quality between opponents was an important predictor of reconciliation in Barbary macaques. It is important to note that this result is consistent with what has been found in other species (Kappeler & van Schaik 1992; Koski et al. 2007; Majolo et al. 2009b), although we used a CSI to measure relationship quality and not grooming alone. Incorporating multiple, potentially inter-correlated variables into a CSI might inflate the absolute values calculated from the index. However, such potential inflation should not affect the magnitude of the differences in relationship quality between individuals. Moreover, a CSI gives a more comprehensive measure of relationship quality than a single behaviour (e.g. grooming).

If PC anxiety is the result of the damage caused by the conflict to the social relationship of the opponents, the 'integrated hypothesis' predicts that damage to high quality relationships would elicit a stronger anxious response compared to damaged low quality relationships (Aureli 1997). However, in the current study PC anxiety was not affected by relationship quality. One explanation for this might be that reconciliation occurs earlier between opponents who share a high quality relationship than between opponents with a low quality relationship (Koski et al. 2007; Majolo et al. 2009b). Therefore, if this was the case, PC self-scratching data would involve a shorter 'uncertainty' time window (i.e. the time from the end of aggression to the onset of reconciliation) for opponents in dyads that share high quality relationships. Therefore, the shorter 'uncertainty' time window for opponents in high quality relationships may counter-balance their expected stronger anxious response as predicted by the 'integrated hypothesis'.

Our findings, together with previous studies of conflict resolution, highlight the importance of analysing PC behaviour and its associated costs independently for the victim and aggressor. An important factor that may help explain why victims and aggressors experience differential costs of aggression could be the difference in value each opponent attributes to their social relationship. Social relationships are often asymmetric due to differences in resource-holding potential and dominance between the two members of a dyad (Cords & Aureli 2000). For example, Japanese macaques show large differences in both the type and frequency of friendly behaviour exchanged within a dyad (Majolo et al. 2010). In general, dominant individuals are more valuable than subordinates in terms of tolerance and agonistic support for example (van Schaik & Aureli 2000). Therefore, the cost of damaging a social relationship with a dominant social partner is likely to be higher than with a subordinate social partner. As a result, the uncertainty (i.e self-scratching) after a conflict is likely to be higher for the victim than the aggressor, as observed in this and other studies (Cooper et al. 2007; Koski et al. 2007; Schino et al. 2007). Moreover, the diverse costs of aggression experienced by the former opponents may drive an individual's social tactics and subsequent PC behaviour differently. For example, victims of aggression who experience an increase in anxiety in the PC period may be less able to reconcile (Majolo et al. 2009a) and this may have negative consequences on their social relationships. It is interesting to observe such a different PC emotional response and risk of aggression between the aggressor and victim in Barbary macaques. This species is considered relatively 'tolerant' according to Thierry's grading system (Thierry 2000), characterised by a high frequency of counter-aggression, which should lead to a similar response to aggression in both opponents. Our results contrast with this picture, probably due to the low frequency of counter-

aggression observed in our study (i.e. 4% of conflicts; Table 1), and stress the importance of independently analysing the behaviour of the victim and aggressor.

The importance of asymmetry in shaping social relationships and the costs of aggression is likely to have a significant impact on the post-conflict tactics used by the opponents. In order to directly compare the asymmetric PC costs for the opponents, data should be collected simultaneously from both the victim and aggressor. Most importantly, if there are indeed asymmetries in the costs of damaging relationships to the victim and aggressor, it would be useful to provide a measure of the relative value an individual poses on their social relationship. For example, calculating an index of relationship quality which controls for the number and quality of additional/alternative relationships an opponent holds in their group, would shed important light on the asymmetric costs of damaging a social relationship through aggression.

Our study on wild Barbary macaques evidences some clear similarities with the PC behaviour of captive con-specifics (Aureli 1997; Patzelt et al. 2009), but demonstrates differences in the pattern of aggression and the costs of aggression experienced by the victim and aggressor. In conclusion, our study was the first comprehensive test of the 'integrated hypothesis' in a wild macaque species. Our study stresses the role of asymmetry in shaping social relationships and highlights the importance of analysing PC behaviour independently for the victim and aggressor of a conflict.

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551 Table 1. Description of variables and number of conflicts collected in the PC-MC

552 sessions.

Variable	Category	Number of conflicts
Focal animal role	Victim	191
	Aggressor	223
Focal animal sex	Male	202
	Female	212
Dyad sex combination	Male - Male	91
	Female - Female	128
	Male - Female	195
Number of opponents	Dyadic	376
	Polyadic	38
Result of conflict	Decided	392
	Undecided	22
Direction of aggression	Uni-directional	399
	Counter-aggression	15
Intensity of aggression	Threat	178
	Lunge or charge	186
	Chase, slap, grab or bite	50
Total		414

553

554 Table 2. Frequency (mean events/minute ± SE) of opponent or bystander aggression received by, and anxiety level of the focal animal in the PC

555 or MC sessions, and in reconciled or non-reconciled conflicts.

Variable	**Focal animal**	**PC**	**MC**	**Reconciled conflict**	**Non-reconciled conflict**
Opponent aggression	Victim	0.02 ± 0.01	0.004 ± 0.003	0.19 ± 0.05	0.07 ± 0.01
	Aggressor	0.01 ± 0.003	0.005 ± 0.003	0.06 ± 0.03	0.03 ± 0.01
Bystander aggression	Victim	0.03 ± 0.01	0.004 ± 0.003	0.10 ± 0.05	0.13 ± 0.03
	Aggressor	0.01 ± 0.004	0.005 ± 0.003	0.00 ± 0.00	0.07 ± 0.02
Anxiety (i.e. self-scratching)	Victim	0.14 ± 0.02	0.09 ± 0.02	0.07 ± 0.03	0.12 ± 0.01
	Aggressor	0.18 ± 0.02	0.13 ± 0.02	0.08 ± 0.02	0.15 ± 0.02

Figure 1. Survival curve showing the decreasing likelihood of the occurrence of reconciliation over the five minute post-conflict period

Figure 2. Relationship quality of opponents in reconciled and non-reconciled conflicts (mean ± SE)