

1 **The importance of considering the behavioural form of reconciliation in studies of conflict**
2 **resolution**

3

4 Richard McFarland^{a,b,*} & Bonaventura Majolo^a

5

6 ^aSchool of Psychology, University of Lincoln, Lincoln, U.K.

7 ^bSchool of Physiology, University of the Witwatersrand, Johannesburg, South Africa

8 *Correspondence: R McFarland, Brain Function Research Group, School of Physiology, Faculty
9 of Health Sciences, University of the Witwatersrand, Medical School, 7 York Road, Parktown,
10 Johannesburg 2193, South Africa. E-mail: richard.mcfarland@wits.ac.za, Tel: +27(0) 715
11 999709.

12 Word count (excluding references) = 3675, Pages = 26, Tables = 3, Figures = 4

13 **Abstract** (250 words)

14 Reconciliation is the most extensively studied conflict resolution mechanism in animal societies.
15 However, despite the extensive literature on this topic, behaviours considered to represent post-
16 conflict affiliation have not been consistent across studies of reconciliation. Critically,
17 reconciliation is usually defined as post-conflict contact affiliation (e.g. grooming) and the
18 importance of including inter-opponent distance regulation is often neglected. Moreover, to date,
19 no study has simultaneously investigated different behavioural forms of reconciliation. We
20 tested, in two groups of wild Barbary macaque (*Macaca sylvanus*), the relative importance of
21 post-conflict close-proximity and grooming in the mediation of two important costs of
22 aggression: damage to the opponent's social relationship and elevated post-conflict anxiety. We
23 provide evidence that close-proximity approaches function to resolve conflicts: close-proximity
24 approaches reduced the victim's post-conflict anxiety and were predicted by the quality of the
25 social relationship with the opponent. Moreover, post-conflict grooming alone, although
26 predicted by the quality of the opponent's social relationship, did not influence the victim's
27 elevated post-conflict anxiety. Our results suggest that inter-opponent distance regulation plays
28 an important role in reconciling the costs of aggression in Barbary macaques. We advocate that
29 further efforts should be made to test which behaviours play a role in conflict resolution in
30 different species. This is important as even closely related species may differ in the function of
31 behaviours that superficially appear to be rather similar. Moreover, the choice of behaviours used
32 to study conflict resolution determines the frequency with which reconciliation is observed and
33 can thus bias comparisons across species.

34 Key words: Aggression; Barbary macaques; Conciliatory tendency; Conflict management;
35 Proximity regulation; Social relationships

36 **Introduction**

37 Competition between conspecifics for food, social and mating partners is widespread in the
38 animal kingdom (van Schaik 1989). Such competition can often lead to aggression, which in
39 addition to posing a risk of physical injury, is commonly associated with a range of post-conflict
40 costs. These costs include, for example, renewed aggression, damage to the opponent's social
41 relationship and increased post-conflict anxiety (Aureli et al. 2002; McFarland & Majolo
42 2011a,b). There is comprehensive evidence that these costs of aggression can be mediated
43 through acts of reconciliation (Aureli & de Waal 2000; Aureli et al. 2002). Reconciliation is
44 defined as the exchange of friendly behaviour between former opponents in the minutes
45 immediately following a conflict (Aureli & de Waal 2000). The 'integrated hypothesis' (Aureli
46 1997) predicts that reconciliation serves to reduce the risk of renewed aggression, repair
47 damaged social relationships (i.e. is predicted by the quality of the opponent's social
48 relationship), and that high quality social partners will be more effective at alleviating post-
49 conflict anxiety through reconciliation compared to low quality social partners. Reconciliation is
50 the most studied behavioural mechanism in conflict resolution, and has been observed in a range
51 of group-living primate and non-primate species (Schino 2000; Aureli et al. 2002; Cordoni &
52 Palagi 2008; Cools et al. 2008; Fraser & Bugnyar 2011; McFarland & Majolo 2011a).

53 Despite the extensive literature on this topic, behaviours considered to represent
54 conciliatory post-conflict affiliation have not been consistent across studies of reconciliation.
55 This may partly be due to the fact that some forms of conciliatory behaviour are specific to a
56 particular species or higher taxonomic level (Aureli et al. 2002). For example, the use of soft
57 grunts is considered crucial in allowing former opponents to reconcile in chacma baboons (*Papio*
58 *ursinus*: Cheney et al. 1995, Silk et al. 1996) and chimpanzees (*Pan troglodytes*) have been

59 observed to use ‘kisses’ to reconcile after a conflict (de Waal & van Roosmalen 1979).
60 Moreover, the necessity to reconcile a conflict may also show marked variation across species.
61 For example, it has been suggested that the highly cooperative and cohesive group structure
62 observed in red-bellied tamarins (*Saguinus labiatus*) obviates the need for reconciliation, as a
63 conflict has no negative effects on their social relationships (Schaffner & Caine 2000).

64 Behaviours used in reconciliation have also been described as being either ‘explicit’ or
65 ‘implicit’ (de Waal and Ren 1988). These authors describe explicit forms of reconciliation as
66 behaviours rarely observed outside of a conciliatory context (e.g. ventro-ventral and hind-quarter
67 embraces in macaques: de Waal & Ren 1988; Arnold & Barton 2001). These behaviours are
68 thought to be observed more often in tolerant species (e.g. de Waal & Ren 1988; Arnold &
69 Barton 2001; Fraser & Aureli 2008) as context-specific behaviours are needed by the actor to
70 make their conciliatory intentions explicit. Conversely, implicit forms of reconciliation are
71 behaviours more widely used during affiliation (e.g. distance regulation: Call 2000, brushing
72 contact: de Waal 1989). These behaviours are thought to be sufficient in signalling reconciliation
73 in more despotic species (e.g. de Waal & Ren 1988; Aureli et al. 1993).

74 Within the same genus there are clear differences in the rate at which reconciliation
75 occurs. Among macaques, more tolerant species (Thierry 2000) have been observed to reconcile
76 more frequently than despotic species. However, even across studies of the same species
77 behaviours used to measure reconciliation have not always been consistent (e.g. macaques: Table
78 1). Such disparity across the literature is problematic for a number of reasons. The inconsistency
79 in the behavioural representation of reconciliation used across the literature makes comparative
80 studies, both between and within species, extremely difficult. Moreover, without independently
81 testing the role of specific behaviours for their conflict resolution function, one may

82 inadvertently over- or under-represent the frequency at which a species reconciles (i.e. its
83 corrected conciliatory tendency, CCT: de Waal & Yoshihara 1983; Veenema et al. 1994).

84

85 “Approximate location for Table 1”

86

87 Traditionally, studies on conflict resolution have investigated grooming, body-contact,
88 embraces and vocal/facial displays such as grunts, lip-smacking or teeth-chattering (de Waal &
89 van Roosmalen 1979; Cheney et al. 1995; Aureli 1997; Aureli et al. 2002) as forms of
90 reconciliation. Several authors have also suggested that inter-opponent distance regulation is
91 equivalent to using contact behaviours in restoring tolerance and reconciling a conflict (York &
92 Rowell 1988; Cords 1993; Call 1999; 2000; Patzelt et al. 2009; McFarland & Majolo 2011a,b).
93 However, while the theoretical issue of operationally defining reconciliation has previously been
94 addressed (in terms of the importance of mere proximity as a form of reconciliation: Cords
95 1993), evidence in support of this issue is limited to experimental testing of whether post-conflict
96 proximity regulation reduced a dyad’s latency to co-drinking (Cords 1993); whereby co-drinking
97 was considered to indicate that tolerance levels were restored to baseline levels following
98 aggression. To date, no study has simultaneously investigated different forms of behavioural
99 reconciliation.

100 Using data from wild Barbary macaques (*Macaca sylvanus*), we aimed to test and
101 exemplify this theoretical problem by analysing and comparing the effect that reconciliation, as
102 measured by either close-proximity approaches or grooming, has on the mediation of two
103 important post-conflict costs of aggression: damage to the opponent’s social relationship and the

104 victim's post-conflict anxiety (Aureli et al. 2002; McFarland & Majolo 2011a). We have
105 previously demonstrated (McFarland & Majolo 2011a) the occurrence of reconciliation in our
106 study animals and shown that victims of aggression, but not aggressors, experience elevated
107 post-conflict anxiety.

108 Following the 'integrated hypothesis' (Aureli 1997) and the suggestion that both close-
109 proximity and grooming serve a conciliatory function (York & Rowell 1988; Aureli et al. 2002),
110 we predicted that (1) post-conflict close-proximity approaches and grooming would
111 independently reduce the victim's post-conflict anxiety, and, (2) post-conflict close-proximity
112 approaches and grooming would be more likely to be observed between opponents sharing a
113 high quality relationship. Finally, if it is true that distance regulation is an important measure of
114 reconciliation (York & Rowell 1988; Cords 1993; Call 1999; 2000), we predicted that (3) the
115 CCT of our study animals would be higher when considering close-proximity approaches as a
116 measure of reconciliation, compared to grooming alone.

117

118 **Methods**

119 Study animals and field site

120 We studied 48 adult and sub-adult animals living in two groups (Group F and Group L) of wild
121 Barbary macaque in the Middle Atlas Mountains of Morocco (33° 24'N – 005° 12'W). At the
122 beginning of the study, group F consisted of 11 males and 8 females and group L consisted of 19
123 males and 10 females. We collected data daily between 06.00 and 19.00 hours from June 2008 to
124 September 2009. Study animals were fully habituated to the presence of human observers and
125 relied on a completely natural diet. The Commissariat aux Eaux et Forêts et à la Lutte Contre la

126 Désertification of Morocco provided research permission and the University of Lincoln Ethics
127 committee granted ethical approval. This study was entirely observational and did not affect the
128 welfare of our study animals.

129 Conflict and post-conflict data

130 We used the ‘post-conflict–matched-control method’ (de Waal & Yoshihara 1983; McFarland &
131 Majolo 2011a) to collect data. We recorded the identity and respective role of each of the
132 opponents anytime aggression (i.e. threat, lunge, charge, chase, slap, grab or bite) was observed.
133 The aggressor was defined as the initiator of the first aggressive display and the victim was
134 defined as the recipient of this aggression. A conflict was considered to be over when aggression
135 had not been exchanged for a period of ≥ 30 s. (Aureli 1997; Kutsukake & Castles 2001;
136 McFarland & Majolo 2011a,b). Of the 414 conflicts observed, we collected post-conflict data for
137 a duration of five minutes from either the victim (N=191) or the aggressor (N=223). We
138 considered a five minute window to collect post-conflict data as reconciliation usually occurs in
139 the first few minutes after a conflict (McFarland & Majolo 2011a).

140 During each post-conflict session we collected data on the occurrence of allo-grooming
141 (hereafter grooming) and close-proximity approaches (i.e. approaches where two individuals
142 remained within ≤ 1.5 m proximity without either animal being displaced or aggressed for at least
143 30s). Teeth-chattering, sandwich interactions (i.e. macaques facing each other in close ventro-
144 ventral contact), infant handling, close-proximity approaches and grooming exchanged by former
145 opponents have all been considered potential forms of reconciliation in Barbary macaques
146 (Hesler & Fischer 2008; Patzelt et al. 2009; McFarland & Majolo 2011a,b). However, only
147 close-proximity approaches (followed 16% of all conflicts) and grooming (6%) occurred at a

148 high enough frequency in our study for them to be analysed independently for their conciliatory
149 role (Table 2). Moreover, teeth-chattering, sandwich interactions and infant handling always
150 occurred immediately before, after or simultaneously with either grooming or close-proximity
151 approaches. All occurrences of grooming were preceded by a close-proximity approach. We
152 recorded all occurrences of self-scratching during post-conflict sessions to provide a measure of
153 anxiety for the victim or aggressor of the conflict (Maestriperi et al. 1992; Schino et al. 1996). A
154 bout of self-scratching was considered to be over when an animal had stopped scratching for
155 ≥ 10 s. We collected data during matched-control sessions following the same methodology
156 described for post-conflict sessions. We collected matched-controls within ≤ 2 weeks (mean=4.63
157 days, range=1–14 days) of their matched post-conflict session to control for seasonal variation in
158 the expression of contact affiliation. Matched-controls were not started until the focal subject had
159 not been involved in an aggressive interaction with another monkey for at least five minutes
160 prior to, or during the matched-control, and no other group member was within a ≤ 1.5 m
161 proximity to the matched-control focal subject.

162

163 “Approximate location for Table 2”

164

165 Social relationship quality

166 We used scan and focal sampling techniques to collect data on the social relationships between
167 all group member dyads across the entire study period. We collected scan samples every hour on
168 the activity of the study animals (i.e. resting, feeding, travelling, grooming and body contact), the
169 identity of social partners, and their ≤ 1.5 m proximity to other group members. An animal was

170 only sampled once in each scan. We used continuous 20 minute focal sessions to collect data on
171 the proportion of approaches exchanged between the study animals that resulted in close-
172 proximity (see above for definition). Each animal was sampled only once each day. We
173 randomized the order of each day's focal sessions and focal data were evenly distributed across
174 the study period and time of day.

175 Analyses were based on 414 conflicts, 792 scans and 1102 hours of focal data. We
176 measured the quality of each dyad's social relationship using a composite sociality index (CSI:
177 Silk et al. 2003):

$$178 \text{CSI} = \frac{\sum_{i=1}^3 \frac{x_i}{m_i}}{3}$$

179 x_i = the dyad's mean value for each of the three behavioural variables

180 m_i = the group's mean value for each of the three behavioural variables

181 Based on evidence that affiliation, tolerance and proximity are three important measures of social
182 relationship quality in non-human primates including Barbary macaques (Fraser et al. 2008;
183 Majolo et al. 2010; McFarland & Majolo 2011c), we entered the following variables into the
184 CSI: (1) Affiliation: the proportion of scans in which the dyad was grooming or in body contact,
185 (2) Proximity: the proportion of scans in which the dyad was within a ≤ 1.5 m proximity, and, (3)
186 the proportion of approaches between the two members of a dyad that resulted in close-proximity
187 (i.e. an approach not followed by aggression). Higher CSI values represent higher quality social
188 relationships. CSI values ranged from 0 to 8.15 (mean=1.32 CSI/dyad).

189 Conciliatory tendency

190 Our study animals' CCT was calculated when the form of reconciliation was considered both
191 inclusive and exclusive of close-proximity approaches. We used the 'post-conflict-matched-
192 control method' (de Waal & Yoshihara 1983) to analyse the occurrence of reconciliation by
193 comparing the latencies to affiliation in the post-conflict session to their corresponding matched
194 control. Conflicts were only considered in this calculation when both the corresponding post-
195 conflict and matched-control data were available. When affiliation occurred earlier in the post-
196 conflict session than the matched-control, the pair was considered 'attracted'. When affiliation
197 occurred earlier in the matched-control than the post-conflict session, it was considered
198 'dispersed'. Finally, if affiliation occurred at the same time, or did not occur in either the post-
199 conflict session or the matched-control, the pair was considered 'neutral'. Following the equation
200 proposed by Veenema et al. (1994): $(\text{attracted pairs} - \text{dispersed pairs}) / \text{all pairs}$, we calculated
201 our study animals CCT when the form of reconciliation was considered inclusive or exclusive of
202 close-proximity.

203 Statistical analysis

204 We used four generalised linear mixed models (GLMMs) to test our predictions. We ran our
205 analyses using each conflict as a single data point. We entered victim and aggressor ID as
206 random factors in all GLMMs to control for the non-independence of the data points, thus
207 avoiding the risk of pseudo-replication (Pinheiro & Bates 2000).

208 We found our dependent variable self-scratching rate to not be normally distributed (i.e.
209 $P < 0.05$) using Shapiro–Francia normality tests. Therefore, we ran two GLMMs with Poisson
210 distribution and log link (hereafter Poisson GLMM) to test our first prediction that close-

211 proximity approaches and grooming would both help mediate the victim's post-conflict anxiety.
212 We entered self-scratching as count data (i.e. number of occurrences in the post-conflict session).
213 We entered either close-proximity approaches or grooming (both binomial: yes, no) as our
214 independent variable. We also entered group ID (group F or L), the dyad's age (adult-adult,
215 subadult-subadult or adult-subadult) and sex combination (male-male, female-female or male-
216 female) and rank distance, as well as the occurrence of bystander affiliation (i.e. whether or not
217 the focal animal exchanged a friendly interaction with a bystander in the post-conflict session) as
218 control fixed factors because these variables may also affect post-conflict anxiety (Majolo et al.
219 2009; McFarland & Majolo 2012). We did not need to enter an 'exposure' variable into the
220 Poisson GLMMs as the time window for all observations were the same (i.e. 5min). We re-ran
221 the aforementioned Poisson GLMM analyses using negative binomial regression; an alternative
222 but equally appropriate method to analyse skewed data (i.e. self-scratching data included
223 multiple zero values). The results of the negative binomial regressions were virtually identical to
224 the Poisson GLMMs (i.e. the P values and coefficients were very similar and the significance
225 level remained unchanged). Therefore, the use of Poisson GLMMs in our study was robust
226 against skewed data. For the sake of brevity, we present here only the results of the Poisson
227 GLMMs.

228 We ran two GLMMs with binomial distribution and logit link (hereafter logistic GLMM)
229 to test our second prediction that the quality of the opponent's social relationship predicted the
230 occurrences of post-conflict close-proximity approaches and grooming. We entered either close-
231 proximity approaches or grooming as our dependent variable and dyad relationship quality (i.e.
232 CSI value) as our independent variable. We also entered group ID and they dyad's age and sex
233 combination and rank difference as control factors as they can affect the occurrence of

234 reconciliation (Majolo et al. 2009). GLMM analyses were performed using STATA v10.1
235 Software (StataCorp 2007). All figures (i.e. drop-line charts) were produced in IBM SPSS
236 Statistics Version 20. Drop-line charts display scores for each individual with lines extending
237 through each group of data points.

238 The proportions of ‘attracted’ and ‘dispersed’ pairs were compared using a Wilcoxon
239 signed-ranks test, run at the level of the individual. A one sample t-test was used to compare the
240 CCT% of our study animals when reconciliation was defined as either close-proximity
241 approaches or grooming.

242

243 **Results**

244 Post-conflict anxiety

245 In support of our first prediction, the victim’s mean rate of post-conflict self-scratching was
246 significantly lower for conflicts followed by close-proximity approaches (excluding cases
247 resulting in grooming), compared to those not followed by close-proximity approaches or
248 grooming (Poisson GLMM: Table 3(a), Fig. 1). However, in contrast to our first prediction, there
249 was no significant difference in the victim’s post-conflict self-scratching rate for conflicts
250 followed by grooming compared to those not (Poisson GLMM: Table 3(b), Fig. 2).

251

252 “Approximate location for Fig.1 and Fig. 2”

253

254 Relationship damage

255 In support of our second prediction, post-conflict close-proximity approaches (excluding cases
256 resulting in grooming) were more likely to occur following conflicts between opponents that
257 shared a high quality relationship (i.e. dyads with a high CSI value) compared to those with a
258 low quality relationship (Logistic GLMM: Table 3(c), Fig. 3). Similarly, post-conflict grooming
259 was significantly more likely to occur following conflicts between opponents that shared a high
260 quality relationship compared to those with a low quality relationship (Logistic GLMM: Table
261 3(d), Fig. 4).

262

263 “Approximate location for Fig.3 and Fig. 4”

264

265 Conciliatory tendency

266 Of the 61 post-conflict-matched-control pairs where close-proximity approaches were observed,
267 significantly more pairs were attracted (N=60) compared to those dispersed (N=1), giving a CCT
268 of 0.16, i.e. $(60-1)/381$ (Wilcoxon: $Z=-4.242$, $P<0.001$, $N = 24$ individuals). Of the 26 post-
269 conflict-matched-control pairs where grooming between former opponents was observed,
270 significantly more pairs were attracted (N=26) compared to those dispersed (N=0), giving a CCT
271 of 0.07, i.e. $26/381$ ($Z=-3.720$, $P<0.001$, $N = 17$ individuals). CCT was significantly higher when
272 reconciliation was defined as grooming and close-proximity approaches (16%) approaches,
273 compared to grooming alone (7%: $T_{380} = 3.729$, $P<0.001$).

274 **Discussion**

275 We provide evidence that close-proximity approaches are sufficient in reconciling the negative
276 consequences of aggression in wild Barbary macaques: close-proximity approaches reduced the
277 victim's post-conflict anxiety and were predicted by the quality of the opponent's social
278 relationship. Moreover, grooming alone (i.e. excluding post-conflict sessions with close-
279 proximity approaches only, but not grooming), although predicted by the quality of the
280 opponent's social relationship, did not have an impact on the victim's elevated post-conflict
281 anxiety despite the fact that they were preceded by close-proximity approaches.

282 Our findings do not dismiss the notion that grooming plays an important role in
283 mediating the consequences of aggression; there is comprehensive evidence that post-conflict
284 grooming is associated with reduced post-conflict anxiety in numerous animal species (Schino
285 2000; Aureli et al. 2002). However, our results do suggest that close-proximity approaches also
286 play a role in reconciling the costs of aggression in wild Barbary macaques. Our finding that
287 close-proximity approaches are enough to reconcile the negative consequences of aggression
288 suggests that implicit forms of reconciliation (de Waal & Ren 1988; Call 2000) are often used by
289 this species. This finding, in addition to the low CCT observed in our study (see below), appear
290 to contrast with the classification of the Barbary macaque as a relatively tolerant social species
291 (Thierry 2000). In fact, Grades 2 and 3 (sensu Thierry 2000) of the dominance style scale appear
292 to have mixed features shared with both dominant (Grade 1) and tolerant (Grade 4) species
293 (Balasubramaniam et al 2012).

294 Most importantly, our results exemplify the necessity to consider inter-opponent distance
295 regulation as a potential form of reconciliation. In the current study, for example, if close-
296 proximity was not investigated as a form of reconciliation, we would have failed to observe an
297 anxiety reducing function of reconciliation in our study species. These findings have important

298 implications for comparative studies and the modelling of conflict management styles across
299 primates. In studies of Old World monkeys, in particular macaques, the behavioural expression
300 of reconciliation has often been limited to contact affiliation (e.g. Table 1). Proximity regulation
301 as a social tool has more commonly been associated with primate species which may lack the
302 sophisticated dexterity required for social grooming or show fewer overt signs of affiliation, such
303 as patas monkeys (*Erythrocebus patas*: Rowell & Olson 1983; York & Rowell 1988). We predict
304 that previous studies that have failed to explore, or inconsistently used proximity regulation as a
305 measure of reconciliation, may have over- or under-estimated the occurrence of reconciliation in
306 their study species. This was apparent in our study as when we considered reconciliation
307 inclusive of close-proximity approaches our study animals had a CCT twice as high (16%) as
308 when we only considered grooming (7%). Such difference can affect the findings of studies
309 comparing social behaviour between species based on their tendency to reconcile (e.g. Thierry
310 2000).

311 Our findings add to the growing evidence that it is important to consider the conciliatory
312 role of inter-opponent distance regulation in studies of reconciliation in non-human primates
313 (Cords 1993; Call 2000). Our findings demonstrate the need to analyse species specific
314 behaviours independently for their role in mediating the costs of aggression, before they are used
315 as a representative form of reconciliation. Such continuity in the methodological approach to the
316 study of reconciliation will facilitate comparative research on post-conflict behaviour in different
317 species.

318 **Acknowledgements**

319 We would like to thank Mohamed Qarro for his support in the field, the Commissariat aux Eaux
320 et Forêts et à la Lutte Contre la Désertification of Morocco for research permission, and Chris

321 Young, Laëtitia Maréchal, Pawel Fedurek and Paolo Piedimonte for assistance in data collection.
322 We thank Joanna Setchell and two anonymous reviewers for their useful comments on our
323 manuscript.

324 **References**

- 325 Abegg, C., Thierry, B., & Kaumanns, W. (1996). Reconciliation in three groups of lion-tailed
326 macaques. *International Journal of Primatology*, 17(5), 803-816.
- 327 Arnold, K., & Barton, R. (2001). Postconflict behavior of spectacled leaf monkeys
328 (*Trachypithecus obscurus*). I. Reconciliation. *International Journal of Primatology*, 22, 243–266.
- 329 Aureli, F. (1997). Post-conflict anxiety in nonhuman primates: The mediating role of emotion in
330 conflict resolution. *Aggressive Behavior*, 23(5), 315-328.
- 331 Aureli, F., Cords, M., & van Schaik, C. P. (2002). Conflict resolution following aggression in
332 gregarious animals: A predictive framework. *Animal Behaviour*, 64(3), 325-343.
- 333 Aureli, F., & de Waal, F. B. M. (2000). *Natural conflict resolution*. Berkeley: University of
334 California Press.
- 335 Aureli, F., Das, M., Verleur, D., & van Hooff, J. A. (1994). Postconflict social interactions
336 among Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology*, 15, 471-485.
- 337 Aureli, F., Veenema, H. C., van Panthaleon van Eck, C.J., & van Hooff, J. A. (1993).
338 Reconciliation, consolation, and redirection in Japanese macaques (*Macaca fuscata*). *Behaviour*,
339 124, 1(2), 1-21.
- 340 Aureli, F., van Schaik, C. P., & van Hooff, J. A. (1989). Functional aspects of reconciliation
341 among captive long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*,
342 19(1), 39-51.

343 Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo
344 B, Ogawa, H., Schino, G., Thierry, B., & de Waal, F. B. M. (2012). Hierarchical steepness and
345 phylogenetic models: phylogenetic signals in *Macaca*. *Animal Behaviour*, 83: 1207-1218.

346 Call, J. (2000). Distance regulation in macaques: A form of implicit reconciliation? In F. Aureli,
347 & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 191-193). Berkeley: University of
348 California Press.

349 Call, J. (1999). The effect of inter-opponent distance on the occurrence of reconciliation in
350 stumptail (*Macaca arctoides*) and rhesus macaques (*Macaca mulatta*). *Primates*, 40(3), 515-523.

351 Castles, D., Aureli, F., & de Waal, F. B. M. (1996). Variation in conciliatory tendency and
352 relationship quality across groups of pigtail macaques. *Animal Behaviour*. 52, 389-403

353 Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The role of grunts in reconciling opponents
354 and facilitating interactions among adult female baboons. *Animal Behaviour*, 50(1), 249-258.

355 Cools, A. K. A., van Hout, A. J. M., & Nelissen, M. H. J. (2008). Canine reconciliation and
356 third-party-initiated postconflict affiliation: Do peacemaking social mechanisms in dogs rival
357 those of higher primates? *Ethology*, 114(1), 53-63.

358 Cooper, M. A., Aureli, F., & Singh, M. (2007). Sex differences in reconciliation and post-
359 conflict anxiety in bonnet macaques. *Ethology*, 113(1), 26-38.

360 Cooper, M. A., Bernstein, I. S., & Hemelrijk, C. K. (2005). Reconciliation and Relationship
361 Quality in assamese macaques (*Macaca assamensis*). *American Journal of Primatology* 65, 269-
362 282.

363 Cordoni, G., & Palagi, E. (2008). Reconciliation in Wolves (*Canis lupus*): New Evidence for a
364 Comparative Perspective. *Ethology*. 114, 298-308.

365 Cords, M. (1993). On operationally defining reconciliation. *American Journal of Primatology*,
366 29, 255-255.

367 de Waal, F. B. M. (1989). *Peacemaking among primates*. Cambridge, MA: Harvard University
368 Press

369 de Waal, F. B. M., & Ren, R. (1988). Comparison of the reconciliation behavior of stump-tail and
370 rhesus macaques. *Ethology*, 78, 129–142.

371 de Waal, F. B. M., & Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus
372 monkeys. *Behaviour*, 85, 224-241.

373 de Waal, F. B. M., & van Roosmalen, A. (1979). Reconciliation and consolation among
374 chimpanzees. *Behavioral Ecology and Sociobiology*, 5(1), 55-66.

375 Fraser, O. N., & Bugnyar, T. (2011). Ravens reconcile after aggressive conflicts with valuable
376 partners. *PLoS ONE*, 6(3), e18118.

377 Fraser, O., & Aureli, F. (2008). Reconciliation, consolation and postconflict behavioral
378 specificity in chimpanzees. *American Journal of Primatology*, 70, 1114–1123.

379 Fraser, O. N., Schino, G., & Aureli, F. (2008). Components of relationship quality in
380 chimpanzees. *Ethology*, 114(9), 834-843.

381 Hesler, N. & Fischer, J. (2008). Gestural communication in Barbary macaques (*Macaca*
382 *sylvanus*): An overview. In: J. Call., & M. Tomasello (Eds.). *The Gestural Communication of*
383 *Apes and Monkeys* (pp. 159-195). New Jersey: Lawrence Erlbaum Associates.

384 Kutsukake, N., & Castles, D. L. (2001). Reconciliation and variation in post-conflict stress in
385 Japanese macaques (*Macaca fuscata fuscata*): Testing the integrated hypothesis. *Animal*
386 *Cognition*, 4(3), 259-268.

387 Maestripietri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: Displacement
388 activities as an indicator of emotions in primates. *Animal Behaviour*, 44(5), 967-979.

389 Majolo, B., Ventura, R., & Schino, G. (2010). Asymmetry and dimensions of relationship quality
390 in the Japanese macaque (*Macaca fuscata yakui*). *International Journal of Primatology*, 31, 736-
391 750.

392 Majolo, B., Ventura, R. & Koyama, N. F. (2009). A statistical modelling approach to the
393 occurrence and timing of reconciliation in wild Japanese macaques. *Ethology*, 155(2), 152-166.

394 Majolo, B., & Koyama, N. (2006). Seasonal effects on reconciliation in *Macaca fuscata yakui*.
395 *International Journal of Primatology*, 27(5), 1383-1397.

396 McFarland, R., & Majolo, B. (2012). The occurrence and benefits of postconflict bystander
397 affiliation in wild Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, 84, 583–591.

398 McFarland, R., & Majolo, B. (2011a). Reconciliation and the costs of aggression in wild Barbary
399 macaques (*Macaca sylvanus*): a test of the integrated hypothesis. *Ethology*, 117, 928-937.

400 McFarland, R., & Majolo, B. (2011b). Grooming coercion and the post-conflict trading of social
401 services in wild Barbary macaques. *PLoS ONE*, 6, e26893. doi:10.1371/journal.pone.0026893.

402 McFarland, R., & Majolo, B. (2011c). Exploring the components, asymmetry and distribution of
403 relationship quality in wild Barbary macaques (*Macaca sylvanus*). *PLoS ONE*, 6, e28826.
404 doi:10.1371/journal.pone.0028826.

405 Patzelt, A., Pirow, R., & Fischer, J. (2009). Post-conflict affiliation in Barbary macaques is
406 influenced by conflict characteristics and relationship quality, but does not diminish short-term
407 renewed aggression. *Ethology*, 115(7), 658-670.

408 Petit, O., Abegg, C., & Thierry, B. (1997). A comparative study of aggression and conciliation in
409 three cercopithecine monkeys (*Macaca fuscata*, *Macaca nigra*, *Papio papio*). *Behaviour*, 134,
410 415-432.

411 Pinheiro, J. C., & Bates, D. M. (2000). *Mixed effects models in sand S-PLUS* (1st ed.). New
412 York: Springer-Verlag.

413 Rowell, T. E., & Olson, D. K. (1983). Alternative mechanisms of social organization in
414 monkeys. *Behaviour*, 86, 31-54.

415 Schaffner, C. M., & Caine, N. G. (2000). The peacefulness of cooperatively breeding primates.
416 In F. Aureli, & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 155–169). Berkeley:
417 California University Press.

418 Schino, G. (2000). Beyond the primates: Expanding the reconciliation horizon. In F. Aureli, & F.
419 B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 225-242). Berkeley: University of
420 California Press.

421 Schino, G., Perretta, G., Taglioni, A. M., Monaco, V., & Troisi, A. (1996). Primate displacement
422 activities as an ethopharmacological model of anxiety. *Anxiety*, 2, 186-191.

423 Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (1996). The form and function of post-conflict
424 interactions between female baboons. *Animal Behaviour*, 52(2), 259-268.

425 Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant
426 survival. *Science*, 302(5648), 1231-1234.

427 StataCorp (2007) *Stata Statistical Software: Release 10*. College Station, TX: Stata Press.

428 Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F.
429 Aureli, & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 106–128). Berkeley:
430 University of California Press.

- 431 van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In: V.
432 Standen (Eds.) Comparative socioecology: The behavioural ecology of humans and other
433 mammals (pp. 195–218). Oxford: Blackwell.
- 434 Veenema, H. C., Das, M., & Aureli, F. (1994). Methodological improvements for the study of
435 reconciliation. *Behavioural Processes*, 31(1), 29-37.
- 436 York, A. D., & Rowell, T. E. (1988). Reconciliation following aggression in patas monkeys,
437 *Erythrocebus patas*. *Animal Behaviour*, 36(2), 502-509.

438 **Figure legends**

439 **Fig. 1** – Drop-line chart showing the difference in victim post-conflict self-scratching in relation
440 to whether post-conflict close-proximity approaches occurred or not (circles represent individual
441 subjects)

442 **Fig. 2** – Drop-line chart showing the difference in victim post-conflict self-scratching in relation
443 to whether post-conflict grooming occurred or not (circles represent individual subjects)

444 **Fig. 3** – Drop-line chart showing the difference in opponent social relationship quality in relation
445 to whether post-conflict close-proximity approaches occurred or not (circles represent individual
446 subjects)

447 **Fig. 4** – Drop-line chart showing the difference in opponent social relationship quality in relation
448 to whether post-conflict grooming occurred or not (circles represent individual subjects)

449 **Tables and Table legends**

450 **Table 1** – Behaviours used to define reconciliation in previous studies of macaques

	<i>M.sylvanus</i> ¹	<i>M.sylvanus</i> ²	<i>M.sylvanus</i> ³	<i>M.mulatta</i> ⁴	<i>M.fascicularis</i> ⁵	<i>M.fascicularis</i> ⁶	<i>M.fuscata</i> ⁷	<i>M.fuscata</i> ⁸	<i>M.fuscata</i> ⁹	<i>M.fuscata</i> ¹⁰	<i>M.nemestrina</i> ¹¹	<i>M.arctoides</i> ⁴	<i>M.radiata</i> ¹²	<i>M.nigra</i> ¹⁰	<i>M.silenus</i> ¹³	<i>M.assamensis</i> ¹⁴
Allogrooming	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓			✓
Body contact	✓	✓	✓	✓	✓	✓	✓	✓			✓	✓	✓			✓
Huddling/embraces			✓		✓			✓			✓	✓	✓			✓
Mounting			✓	✓	✓	✓	✓	✓			✓	✓	✓			✓
Muzzle contact			✓		✓		✓	✓	✓		✓		✓			✓
Mutual lip-smacking/teeth-chattering	✓	✓	✓		✓	✓	✓	✓	✓		✓					
Playing			✓		✓		✓	✓								
Genital inspect/present			✓	✓	✓							✓	✓			
Passive contact						✓		✓					✓			
Inter-opponent distance	✓			✓	✓							✓				
Feeding in close-proximity		✓														
In-descriptive physical contact										✓				✓	✓	

451 ¹McFarland & Majolo 2011, ²Patzelt et al. 2009, ³Aureli et al. 1994, ⁴Call 1999, ⁵Aureli et al. 1989, ⁶Cords 1992, ⁷Aureli et al. 1993, ⁸Kutsukake & Castles 2001,

452 ⁹Majolo & Koyama 2006, ¹⁰Petit et al. 1997, ¹¹Castles et al. 1996, ¹²Cooper et al. 2007, ¹³Abegg et al 1996, ¹⁴Cooper et al. 2005

453 **Table 2** – The number and proportion of conflicts followed by different forms of friendly
 454 affiliation observed in two groups of wild Barbary macaque over a 15 month period

	N conflicts	% conflicts
Grooming	26	6.3
Sandwich interactions	1	0.2
Mutual teeth-chattering/lip-smacking	1	0.2
Infant handing	1	0.2
≤1.5m close-proximity approaches	67	16.2
<i>Total conflicts observed</i>	<i>414</i>	

455

456 **Table 3** – Poisson and logistic GLMM regression results

Dependent variable	Independent and control variables	$\beta \pm SE$	95% CIs	N	Z	P
(a) Victim post-conflict self-scratching	Post-conflict close-proximity approach	-0.70 \pm 0.33	-1.34 to -0.05	191	-2.12	0.03
	Group ID	-0.28 \pm 0.24	-0.76 to 0.20	191	-1.13	0.26
	Age combination	0.12 \pm 0.16	-0.20 to 0.43	191	0.73	0.47
	Sex combination	0.01 \pm 0.22	-0.42 to 0.45	191	0.07	0.95
	Rank difference	0.03 \pm 0.02	-0.01 to 0.07	191	1.42	0.16
	Bystander affiliation	-0.39 \pm 0.26	-0.91 to 0.12	191	-1.50	0.13
(b) Victim post-conflict self-scratching	Post-conflict grooming	-0.56 \pm 0.53	-1.59 to 0.47	191	-1.06	0.29
	Group ID	-0.21 \pm 0.24	-0.69 to 0.27	191	-0.87	0.39
	Age combination	0.09 \pm 0.16	-0.22 to 0.40	191	0.58	0.57
	Sex combination	0.04 \pm 0.22	-0.39 to 0.47	191	0.18	0.85

	Rank difference	0.02 ± 0.02	-0.01 to 0.06	191	1.19	0.23
	Bystander affiliation	-0.34 ± 0.26	-0.85 to 0.18	191	-1.29	0.20
(c) Post-conflict close-proximity approach	Relationship quality (CSI)	0.30 ± 0.10	0.11 to 0.49	414	3.07	0.002
	Group ID	-0.96 ± 0.35	-1.65 to -0.27	414	-2.74	0.01
	Age combination	-0.17 ± 0.23	-0.62 to 0.29	414	-0.72	0.47
	Sex combination	0.10 ± 0.33	-0.54 to 0.75	414	0.31	0.76
	Rank difference	0.07 ± 0.03	0.01 to 0.12	414	2.23	0.03
(d) Post-conflict grooming	Relationship quality (CSI)	0.29 ± 0.14	0.02 to 0.56	414	2.09	0.04
	Group ID	-0.81 ± 0.56	-1.91 to 0.29	414	-1.44	0.15
	Age combination	-0.48 ± 0.41	-1.28 to 0.33	414	-1.16	0.25
	Sex combination	0.14 ± 0.54	-0.92 to 1.19	414	0.25	0.80
	Rank difference	0.07 ± 0.04	-0.02 to 0.15	414	1.50	0.13

