The occurrence and benefits of post-conflict bystander affiliation in wild Barbary macaques (*Macaca sylvanus*)

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ABSTRACT

The majority of studies investigating conflict management in animal societies have focused on the role of reconciliation in mediating the costs of aggression. The function of bystander affiliation (i.e. the selective attraction between an opponent and a bystander in the minutes immediately following aggression) is less well understood.

The aim of the current study was to examine, in wild Barbary macaques (*Macaca sylvanus*), four potential functions of bystander affiliation with the victim of aggression: 1) bystander-initiated affiliation to reduce the victim's post-conflict (PC) anxiety (i.e. 'consolation'), 2) victim-initiated affiliation (i.e. 'solicited-consolation'), 3) victim- and bystander-initiated affiliation to avert re-directed aggression (i.e. self-protection), and 4) bystander-initiated affiliation to exploit grooming from the victim. We found partial support for the consolation function as bystander-initiated affiliation occurred more frequently between high quality social partners but had no effect on the victim's PC anxiety. In support of the solicited-consolation function, victim-initiated affiliation occurred more frequently between high quality social partners and also caused a reduction in the victim's PC anxiety. These findings suggest that solicited-consolation may substitute for the stress alleviation role of reconciliation. We found no support for a self-protective function as neither the bystander's or the victim's risk of receiving PC aggression was reduced following bystander affiliation with the victim. Finally, bystanders received significantly more PC grooming than victims, suggesting that grooming exploitation of the victim may drive the bystander's PC behaviour. Our results indicate that bystander affiliation holds different functions and benefits for the victim of

aggression and the bystander, and highlights the importance of considering which individual initiates this behaviour.

Key words: Conflict Management; Consolation; Grooming; Reconciliation; Solicited-Consolation; Third-Party Affiliation

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

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

occurrence of bystander affiliation in Old World monkeys (Watts et al. 2000). Moreover, the function of bystander affiliation is less well understood when compared to reconciliation (Aureli et al. 2002; Fraser et al. 2009).

Bystander affiliation can be beneficial for the bystander and the victim (Verbeek & de Waal 1997; Fraser et al. 2009). However, studies conducted so far have often failed to take into account the identity of both potential initiators of the affiliation (i.e. victim or bystander). Here we aim to analyse bystander affiliation in wild Barbary macaques (*Macaca sylvanus*) while taking into account the identity of the initiator of the affiliation. Specifically, we aim to test four main, non-mutually exclusive proximate functions of bystander affiliation: 1) Consolation (bystander-initiated), 2) Solicited-consolation (victim-initiated), 3) Self-protection (bystander or victim-initiated), and 4) Exploitation (bystander-initiated). To our knowledge, this is the first study to empirically test these functions of bystander affiliation in a wild non-ape species.

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

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

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

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

reconciliation) to gain grooming opportunities.

METHODS

Study subjects and field site

Between September 2008 and August 2009, data were collected daily from 48 individuals living in two groups ('Flat-face' and 'Large') of wild Barbary macaques, in the Middle Atlas Mountains of Morocco (33° 24'N – 005° 12'W). At the beginning of the study, group sizes were 19 (11 males, 8 females) and 29 (19 males, 10 females) adults and sub-adults for the 'Flat-face' and 'Large' group respectively. These groups were non-provisioned and relied on a completely natural diet. Study animals were fully habituated to the presence of researchers (i.e. they did not change their activity when we moved around the study group) and were individually identified via facial characteristics and body size. Permission to conduct our research was granted by the Haut Commissariat des Eaux et Forêts et à la Lutte Contre la Désertification of Morocco. This study complies with Moroccan and UK regulations regarding the ethical treatment of research subjects.

Data collection

Data were collected following the post-conflict - matched-control (PC-MC) method (de Waal & Yoshihara 1983; McFarland & Majolo 2011b). The identity and role of the opponents (i.e. aggressor or victim) were recorded anytime aggression was exchanged between two or more individuals. Aggression was recorded anytime at least one of the following behaviours was observed: threat, lunge, chase, slap, grab or bite. The aggressor was defined as the initiator of the first aggressive display. The victim was the recipient of

147 this aggression. Based on the outcome of unidirectional aggressive and submissive
148 interactions collected during baseline focal (see below) and *ad libitum* observations,
149 relative dominance positions (i.e. ranks) were determined for each group member using
150 MatMan 1.0 Software (de Vries et al. 1993). The role of the monkeys in a conflict
151 reflected their dominance relationships, as the aggressor was dominant over the victim in
152 96% of cases (N = 398 of 414 conflicts observed) and only 4% of conflicts involved
153 counter-aggression (i.e. a victim being aggressive towards the former aggressor, N = 17
154 conflicts observed).
155 PC data were collected from either the victim (N = 191) or the aggressor (N = 223)
156 of the conflict for five minutes. PC sessions were postponed if aggression between the
157 former opponents recommenced within 30 seconds of the initial conflict as the conflict
158 was considered to then still be in progress (Aureli 1997). PC data collected from the
159 victim were used to test the bystander-initiated consolation, victim-initiated solicited-
160 consolation, victim- and bystander-initiated self-protection, and the bystander-initiated
161 exploitation functions. PC data collected from the aggressor or the victim were used to
162 test whether bystanders were at risk of receiving PC aggression from the former
163 aggressor or victim of the conflict. During PC sessions we recorded the timing and
164 occurrence of any aggressive or friendly interaction exchanged between the focal
165 opponent and any other group member. We considered grooming, body-contact, mutual
166 teeth-chattering and successful ≤ 1.5m approaches (i.e. approaches that were not followed
167 by aggression or displacement for the first 30 seconds after the approach) as forms of
168 friendly affiliation (Hesler & Fischer 2008; McFarland & Majolo 2011a,b). The initiator
169 (e.g. victim or bystander) of the first PC friendly behaviour was recorded. We recorded

all occurrences of self-scratching and used this behaviour as a measure of anxiety. There is comprehensive behavioural, physiological and pharmacological evidence that self-scratching is a reliable measure of anxiety in primates (Schino et al. 1991, 1996; Maestripieri et al. 1992; Barros et al. 2000; Troisi 2002). Moreover, in a previous study on the same study subjects (McFarland & Majolo 2011b) we showed that the victim experienced elevated PC self-scratching rates when compared to MC conditions.

MCs were collected within ≤ two weeks (X = 4.63 days, range = 1 to 14 days) of the matched PCs to control for any variation in the expression of grooming, aggression and self-scratching across the year. To further standardise MC sessions, MCs were only started when, a) the MC focal subject had not been involved in an aggressive interaction with another monkey in the five minutes prior to a planned MC, or during the MC, and, b) no other group member was in close-proximity (i.e. ≤ 1.5m) to the MC focal subject. We collected the same data and followed the same methodology during MCs as previously described for the PCs.

Scan sampling and focal sampling were used 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 ≤ 1.5m proximity to other study subjects, and on the identity of their social partners. Scan data were collected on all subjects visible within ten minutes of the beginning of the scan. Moreover, across the entire study period twenty minute all-occurrences focal sessions were collected from our study animals to determine dyadic dominance relationships, and calculate the proportion of successful ≤ 1.5m approaches exchanged within each dyad. The order of focal sessions on the study animals was randomised each day and focal data

were evenly distributed across the study period and time of day. A monkey was never sampled more than once in a single day.

Data set and test variables

Of the 414 conflicts analysed, all but one adult male of the "Large group", and all "Flat-face group" members were targets of at least one PC session (X = 19, range = 1 – 31 PCs/monkey). 792 scan samples and 1,102 hours of focal observations were collected in the current study (X = 18.7, range = 4.7 – 50.9 hours/monkey). Bystander affiliation was defined as the first friendly behaviour (i.e. body-contact, teeth-chattering, grooming) exchanged between the victim and a bystander. Close-proximity approaches were also considered forms of bystander affiliation as there is evidence that close-proximity mediates the costs of aggression in Barbary macaques (McFarland & Majolo, in preparation; Patzelt et al. 2008; McFarland & Majolo 2011a,b). Of the 45 occurrences of bystander affiliation with the victim of aggression, 18 were followed by grooming and 27 followed by close-proximity approaches (in the absence of grooming). The occurrence of bystander affiliation was analysed using the 'PC-MC method' (de Waal & Yoshihara 1983) by comparing the timing of the first friendly behaviour exchanged between the bystander and victim in PC and MC sessions. If a friendly affiliation was not observed during the MC, a conservative latency of 300 seconds was estimated. This estimate was required because if no value was entered for the MC, the PC-MC would have been discarded from the analysis. When friendly behaviour occurred earlier in the PC than the MC (or only in the PC), the PC-MC pair was defined 'attracted'. When the interaction took place earlier in the MC than in the PC (or only in the MC), the PC-MC pair was

defined ‘dispersed’. If the friendly behaviour did not occur in the PC and MC, or if it occurred at the same time, the PC-MC pair was defined ‘neutral’. The proportions of ‘attracted’ and ‘dispersed’ pairs were compared using Wilcoxon signed-ranks tests.

When bystander affiliation resulted in grooming, we calculated the percentage of PC grooming received by the victim and bystander. Based on a hypothetical dyad of individual A and B, the percentage of grooming received by individual A (or B) in a grooming bout was calculated using the following equation: [grooming received by A / (grooming received by A + grooming received by B)] x 100. A composite sociality index (CSI) was used to measure the quality of the victim and bystander’s social relationship using the following formula (Silk et al. 2003; McFarland & Majolo 2011b):

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

x_i = Dyad’s mean value for each of the three behavioural measures.

m_i = Group’s mean 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. 2008b; Majolo et al. 2010; Silk et al. 2010; McFarland & Majolo 2011c). To calculate x_i for each dyad we combined data collected from each dyad member on: 1) the proportion of hourly scans each dyad member was exchanging friendly behaviour, 2) the proportion of hourly scans dyad members were within ≤ 1.5m proximity, and, 3) the proportion of successful ≤ 1.5m

237 approaches exchanged during the dyad's 20 minute focal sessions. The same three
238 variables were used to calculate medians at the group level to obtain m_i. The higher the
239 CSI value, the stronger the dyad relationship quality was. In this study the values of the
240 CSI ranged from 0 to 8.15 (X = 1.32 CSI/dyad).
241
242 *Statistical analysis*
243 We tested our predictions using non-parametric statistics and a series of generalised
244 linear mixed models (GLMMs). To test the consolation, solicited-consolation and self-
245 protection function of bystander affiliation we used three dependent variables in
246 GLMMs: self-scratching, bystander affiliation, and PC aggression received. Two
247 Shapiro-Francia normality tests showed that self-scratching and bystander affiliation
248 were not normally distributed, even after using a square-root transformation. Therefore,
249 these two dependent variables were entered as count data (i.e. N of occurrences in the
250 PC) in GLMMs with Poisson distribution and log link (hereafter Poisson GLMM). In
251 these Poisson GLMMs, the duration in seconds of the PC was the exposure variable in
252 the Poisson GLMM on PC scratching rate. The opportunity to bystander affiliation (i.e.
253 the total number of conflicts involving the victim, excluding those in which the bystander
254 was the opponent of the victim) was as our exposure variable in the Poisson GLMMs on
255 bystander affiliation. For our dichotomous dependent variable (i.e. PC aggression
256 received: yes, no) we used GLMMs with binomial distribution and logit link (hereafter
257 logistic GLMM). Poisson GLMMs do not control for the over-dispersion of the data.
258 Therefore, for each Poisson GLMM we ran a Vuong test (Vuong 1989) to compare the
259 'standard' Poisson GLMM with a zero-inflated Poisson regression. The Vuong tests

were all non-significant (see Results below) and thus the results of the Poisson GLMMs were not affected by over-dispersion.

GLMMs allow analysing the effect of a series of independent variables (i.e. fixed factors) on a continuous, count or categorical predictor variable (Pinheiro & Bates 2000). Moreover, GLMMs allow analyses to be run using each conflict dyad, or PC and MC session, as a single data point. This procedure is appropriate when using GLMMs, via the inclusion of random factors to the model. Random factors control for the non-independence of the data points (Pinheiro & Bates 2000) thus allowing analyses to be run at the level of the single observation (e.g. PC or MC session) while avoiding any bias due to pseudo-replication.

In all the GLMMs presented below, Subject IDs (i.e. victim, aggressor or bystander ID) were entered as 'crossed' random factors, thus controlling for pseudo-replication bias at both the individual subject and dyadic level. When comparing PC-MC data, we nested PC-MC pair ID inside Subject ID, as our random factor, so that each PC session was compared to its paired MC. The age combination of the opponents' dyad (adult-adult, subadult-subadult or adult-subadult), their sex combination (male-male, female-female or male-female), their rank distance, and the occurrence of reconciliation were used as 'control' fixed factors because these variables may also play a role in mediating the costs of aggression (Majolo et al. 2009; McFarland & Majolo 2011b). Group ID ('Flat-face' or 'Large' group) was also entered as a 'control' fixed factor. We used this procedure to control for Group ID (instead of entering Group ID as a third random factor with victim and aggressor ID or subject and PC-MC pair ID) because GLMMs could not generate an output for models with three random factors. Note here

that entering Group ID as a fixed factor allows testing the effect of an independent variable on a dependent variable while taking into account that the data came from monkeys belonging to different groups (Pinheiro & Bates 2000). For a complete list and description of variables used in GLMMS see Table 1. In each GLMM we entered our independent test variable/s together with our control variables. In light of this, we considered the presentation of full GLMM models more comprehensive and conservative to analyse bystander affiliation than the use model selection. All GLMMs were performed in STATA v10.1 software (StataCorp 2007). The exact Wilcoxon tests (Mundy & Fisher 1998) were performed in SPSS Software v17.

"Approximate location for Table 1"

Test models

Model 1: To test whether bystander affiliation reduces PC anxiety in the victim we used data from 191 victim PC sessions. We entered victim PC self-scratching as our dependent variable in a Poisson GLMM where the occurrences of bystander- and victim-initiated bystander affiliation (i.e. yes or no) were the test independent variables (control factors: group ID, dyad age and sex combination, rank difference and the occurrence of reconciliation and bystander-initiated affiliation, random factors: victim and aggressor ID).

Models 2 and 3: To test whether bystander affiliation occurs more frequently between high quality social partners we used data based on scores for each group member dyad (N= 450; only dyads with an opportunity of ≥ 1 for bystander affiliation were

306 included in the analysis). We entered either the bystander-initiated affiliation count
307 (Model 2) or the victim-initiated affiliation count (Model 3) as the dependent variable in
308 a Poisson GLMM and dyad relationship quality (i.e. CSI value) as the test independent
309 variable (control factors: group ID, dyad age and sex combination and rank difference,
310 random factor: subject ID,).

311 Models 4 and 5: Based on 200 PC-MC pairs we examined whether bystanders
312 faced an increased PC risk of receiving renewed aggression from the victim or the
313 aggressor compared to MCs. We used two logistic GLMMs on aggression received by
314 bystanders (dichotomous dependent variable, yes or no) from, respectively, the victim
315 (Model 4) or the aggressor (Model 5) and 'session' (i.e. PC or MC) as the test
316 independent variable (control factors: group ID, dyad age and sex combination, random
317 factors: PC-MC pair ID nested inside Subject ID).

318 Model 6: To further test the self-protection function we used the 191 PCs
319 collected from the victim and examined whether the occurrence of bystander affiliation
320 reduced re-directed aggression in the bystander or victim, respectively. For the bystander,
321 we ran a logistic GLMM on aggression received by the bystander from the victim (i.e.
322 yes or no) as our dependent variable, and bystander-initiated affiliation (i.e. yes or no) as
323 our test independent variable (control factors: group ID, dyad age and sex combination,
324 rank, reconciliation, victim-initiated affiliation; random factors: victim and aggressor ID).

325 Models 7 and 8: For the victim, we ran two logistic GLMMs on aggression
326 received by the victim from the bystander (Model 7) or the former aggressor (Model 8) as
327 our dependent variable, and victim-initiated affiliation (i.e. yes or no) as our test

328 independent variable (control factors: group ID, dyad age and sex combination, rank,
329 reconciliation, bystander-initiated affiliation; random factors: victim and aggressor ID).
330
331 RESULTS
332 *The occurrence of bystander affiliation*
333 Of the 191 PCs collected from the victim, 24% involved bystander affiliation with the
334 victim; 49% of which were initiated by the bystander, 38% by the victim and 13% were
335 considered to be mutually initiated (i.e. when the bystander and victim approached each
336 other simultaneously). Of the 22 PC-MC pairs involving bystander-initiated affiliation,
337 significantly more pairs were 'attracted' (N = 21) compared to those 'dispersed' (N = 1)
338 (Wilcoxon: N = 13 subjects, Z = -2.956, P = 0.002). Of the 17 PC-MC pairs involving
339 victim-initiated affiliation, significantly more pairs were 'attracted' (N = 17) compared to
340 those 'dispersed' (N = 0) (Wilcoxon: N = 11 subjects, Z = -3.022, P = 0.001). Therefore,
341 bystander affiliation initiated by the victim or the bystander did occur in Barbary
342 macaques.
343
344 *Consolation*
345 In contrast to our first prediction (i.e. consolation would reduce PC anxiety in the victim),
346 we found no significant difference in the victim's PC self-scratching following conflicts
347 that resulted in bystander-initiated affiliation or not (Model 1: $\beta \pm SE$ = -0.159 ± 0.314,
348 95% CIs = -0.774 – 0.456, Z = -0.51, N = 191, P = 0.613; Vuong test: z = 0.35, P = 0.36;
349 Fig 1; Table 2).
350

"Approximate location for Table 2"

"Approximate location for Figure 1"

In support of the consolation function, bystander-initiated affiliation was more likely to occur in bystander-victim dyads that shared high quality relationships than in those sharing low quality relationships (Model 2: $\beta \pm SE = 0.137 \pm 0.064$, 95% CIs = 0.012 – 0.262, $Z = 2.15$, $N = 450$, $P = 0.031$; Vuong test: z = 1.15, P = 0.09; Table 3). In this analysis, it is important to note that although the count score for bystander affiliation did not control for baseline levels of affiliation for each dyad (Fraser et al. 2008a), there was only one 'dispersed' PC-MC pair for bystander affiliation in our dataset. Therefore, it was not considered necessary to adjust these scores according to baseline levels of affiliation as has been done in previous studies (e.g. Fraser et al. 2008a).

"Approximate location for Table 3"

Solicited-consolation

The consolation and solicited-consolation functions shared similar predictions (see above) but differed in being, respectively bystander- or victim-initiated. Therefore, to analyse solicited-consolation we used the same 191 victim PC sessions and 450 group member dyad scores used to test for consolation and similarly structured (in terms of control fixed factors and random factors) Poisson GLMMs as described above.

In support of the prediction that victims would initiate affiliation with bystanders to reduce their own PC anxiety, the victim's PC self-scratching was significantly lower

374 when a conflict was followed by victim-initiated affiliation compared to when not (Model
375 1: β ± SE = -1.115 ± 0.519, 95% CIs = -2.132 – -0.098, *Z* = -2.15, *N* = 191, *P* = 0.032;
376 Vuong test: z = 0.42, P = 0.49; Fig 1; Table 2). Moreover, victims solicited-consolation
377 more frequently from bystanders with whom they shared high quality relationships
378 (Model 3: β ± SE = 0.158 ± 0.074, 95% CIs = 0.014 – 0.303, *Z* = 2.15, *N* = 450, *P* =
379 0.031; Vuong test: z = 1.06, P = 0.11; Table 4).
380
381 *Self-protection*
382 We found no significant difference between PC and MCs in the bystander's likelihood of
383 receiving aggression from the victim (Model 4: β ± SE = 3.052 ± 1.703, 95% CIs = -
384 6.390 – 0.286, *Z* = -1.79, *N* = 200, *P* = 0.073; Appendix 1) or the aggressor (Model 5: β
385 ± SE = 0.356 ± 0.491, 95% CIs = -1.318 – 0.606, *Z* = -0.73, *N* = 200, *P* = 468; Appendix
386 2). Therefore, bystanders might not need to affiliate for self-protection as they did not
387 face an increased risk of receiving re-directed aggression from the victim or aggressor.
388 This, however, might still be the case for victims, as victims are at risk of receiving
389 renewed PC aggression from the aggressor or bystander (McFarland & Majolo 2011b).
390 In contrast to the self-protection function, the risk of a bystander receiving re-
391 directed aggression from the victim was not significantly different in the presence or
392 absence of bystander-initiated affiliation (Model 6: β ± SE = 0.303 ± 0.808, 95% CIs = -
393 1.281 – 1.887, *Z* = 0.38, *N* = 191, *P* = 0.707; Appendix 3).
394 The occurrence of victim-initiated affiliation (i.e. yes or no) did not have a
395 significant effect on aggression received by the victim from the bystander (i.e. yes or no)
396 (Model 7: β ± SE = 0.594 ± 0.678, 95% CIs = -0.735 – 1.922, *Z* = 0.88, *N* = 191, *P* =

0.381; Appendix 4). Moreover, the victim's risk of receiving renewed aggression from the aggressor was not significantly different in the presence or absence of victim-initiated affiliation (Model 8: $\beta \pm SE = 1.458 \pm 0.875$, 95% CIs = -0.256 – 3.172, $Z = 1.67$, $N = 191$, $P = 0.096$; Appendix 5).

Exploitation

To test our two predictions for this function (i.e. more PC grooming would be received by the bystander from the victim than vice-versa, and bystanders would target subordinate victims) we used the 17 PCs in which bystander-initiated affiliation was followed by grooming between the victim and the bystander. In support of the exploitation function, bystanders received significantly more grooming than victims in the PC period (Wilcoxon: N = 18 victim subjects, Z = -2.111, $P = 0.002$). Moreover, out of all the occurrences of bystander affiliation (N = 45) we found that bystanders affiliated with subordinate victims significantly more often ($N = 39$, 87%) than they did with dominant victims ($N = 6$, 13%) in the PC period (Wilcoxon: N = 18 victim subjects, Z = -2.939, $P = 0.002$).

"Approximate location for Figure 2"

DISCUSSION

Our study is one of a few to have observed bystander affiliation with the victim outside of the great apes, and only the second to have observed this in a macaque species (Watts et al. 2000; Arnold & Barton 2001; Call et al. 2002). In fact, bystander affiliation was a

relatively common occurrence in the current study (24% of conflicts involving a focal victim). Through an exploration of four functions of bystander affiliation, we investigated the potential benefits that this PC behaviour offers both the bystander and the victim in the aftermath of a conflict. Unfortunately, kinship data were not available for our study animals and so kin relationships were not considered in our analyses; our results thus have to be interpreted with caution. However, primate social behaviour (e.g. grooming exchange, one of our measures of relationship quality) may be less affected by kinship than originally thought (Schino & Aureli 2010).

Why bystanders initiate affiliation with victims of aggression

Consolation is thought to be based on empathy, whereby a bystander initiates contact with a victim in response to the victim's emotional state following aggression (de Waal & van Roosmalen 1979; Fraser et al. 2008a). Acts of consolation are considered to reduce the victim's PC anxiety and to be positively predicted by the quality of the relationship shared by the victim and bystander (Aureli & Schaffner 2002; Fraser et al. 2008a). The current study is the first to directly test the consolation function of bystander affiliation (de Waal & van Roosmalen 1979) in a macaque species. In partial support of this hypothesis, bystanders initiated PC affiliation with victims with whom they shared high quality relationships more frequently than those with low quality relationships. However, we found no evidence that bystander-initiated affiliation reduced the victim's PC anxiety. In the absence of a stress-alleviation effect of bystander affiliation, our findings provide scarce support for the consolation function. This conclusion is in line with the suggestion that non-ape primates do not possess the cognitive capacity for empathy, and thus cannot

443 display consolatory behaviour (de Waal & Aureli 1996). However, bystanders may not
444 necessarily need to be empathic towards the victim's distress in order to affiliate them.
445 An innate response to social or non-social cues (e.g. a conflict or self-scratching) from
446 group companions could elicit bystander affiliation and its potential benefits for the
447 bystander or the victim. For example, the positive link between relationship quality and
448 bystander-initiated affiliation found in this study could result from a tendency for friends
449 (i.e. monkeys sharing a high quality relationship) to maintain proximity while moving,
450 feeding or engaging in other activities. If so, bystanders would be more likely to affiliate
451 victim friends because of their proximity and opportunity to attend to social and non-
452 social cues from the victim, which would elicit a response to such cues without any
453 empathic response.

454 We explored whether bystanders initiate affiliation with the victims of aggression
455 in order to gain grooming opportunities. Bystanders received proportionally more
456 grooming than victims after PC affiliation, similarly to what has previously been found
457 for the aggressor (McFarland & Majolo 2011a). Bystanders also affiliated more
458 frequently with subordinate victims and with victims with whom they shared a high
459 quality relationship. Therefore, exploitation of the victim for grooming appears to be a
460 selective PC tactic whereby bystanders attempt to maximise their grooming return from
461 victims; subordinate monkeys usually give more grooming than they receive (Schino
462 2001; Fruteau et al. 2011) and high quality social partners are generally more 'reliable' or
463 'profitable' grooming partners (Silk et al. 2006, 2010; Schino & Pellegrini 2009).

464 In the PC period when social tension is high, bystanders face an elevated risk of
465 receiving re-directed aggression from the victim. Victims of aggression can re-direct

aggression toward bystanders to alleviate stress (Aureli & van Schaik 1991) and deflect the attention of aggression away from themselves (de Waal & van Hooff 1981; Scucchi et al. 1988; Aureli & van Schaik 1991). Therefore, bystanders may affiliate the victim of aggression in order to protect themselves from re-directed aggression (Judge 1991; Aureli & van Schaik 1991; Das 2000; Call et al. 2002; Koski & Sterck 2007). The self-protection function of bystander-initiated affiliation does not explain bystander PC behaviour in wild Barbary macaques, as we found no significant effect of bystander affiliation on aggression received by the bystander.

Why victims initiate affiliation with bystanders

Reconciliation is considered to serve a stress alleviating function to the victim whereby exchanging friendly behaviour with their former opponent helps mediate their PC anxiety (Aureli et al. 2002; Mcfarland & Majolo 2011b). Alternatively, when the risk of receiving renewed aggression from their former opponent is too high, victims may solicit consolation from bystanders as an alternative strategy to mediate their PC anxiety (Watts et al. 2000; Wittig & Boesch 2003). This scenario may apply to our study, as the PC period, even after reconciliation took place, was associated with high rates of renewed inter-opponent aggression (McFarland & Majolo 2011a,b). We found evidence in support of the solicited-consolation function: victim-initiated affiliation reduced their PC anxiety and was predicted by the quality of their relationship with the bystander. Our study is the first to report a stress alleviating function of bystander affiliation in macaques. These novel findings may be due to the fact that we considered the stress alleviating function of bystander affiliation independently for bystander- and victim-initiated affiliation.

Whereas in chimpanzees a stress alleviating role of bystander affiliation has been observed in the victim following consolation (i.e. bystander-initiated; Fraser et al. 2008a, but see Koski & Sterck 2007), in Barbary macaques the stress alleviation in the victim is only observed following solicited-consolation (i.e. victim-initiated). Our findings thus evidence the need to consider the identity of the initiator of PC affiliation when exploring the stress alleviation function of bystander affiliation.

As for the bystander (see above), we found no evidence for a self-protection function of victim-initiated affiliation. Although victims experienced an increased risk of renewed PC aggression from their former aggressor or bystanders (McFarland & Majolo 2011b), victim-initiated affiliation did not reduce such risk. Overall, these findings suggest that bystander affiliation in Barbary macaques does not serve a self-protection function for either the victim or the bystander. Interestingly however, similarly to what has been observed during reconciliation in the same study population (McFarland & Majolo 2011b), solicited-consolation appeared to serve a stress alleviation function (see above) despite the fact that it does not reduce the victim's risk of receiving PC aggression.

Conclusions

Our findings highlight the importance of considering whether bystander affiliation is initiated by the victim or the bystander when exploring the function of this PC behaviour. Differences in dominance or resource-holding potential (RHP; Parker 1974) are thought to explain the asymmetric distribution of the costs and benefits of aggression between victims and aggressors (e.g. Schino et al. 2007; Cooper et al. 2007; Koski et al. 2007;

512 Schino et al. 2007; McFarland & Majolo 2011b) as well as their PC social tactics
513 (McFarland & Majolo 2011a). Similar asymmetries are expected to occur between the
514 bystander and the victim. Therefore, the decision-making processes made by the victim
515 or bystander to affiliate following a conflict, are potentially driven by different 'motives'
516 and benefits: victims attempt to reduce their PC anxiety whereas bystanders benefit from
517 grooming opportunities. Both benefits are more likely to be gained once the victim or the
518 bystander initiate PC affiliation with a high quality social partner. Although the
519 importance of considering the initiator of bystander affiliation has long been recognised
520 (de Waal & Aureli 1996; Verbeek & de Waal 1997; Fraser et al. 2008a), the majority of
521 previous studies have failed to account for this important parameter in studies of conflict
522 management. We propose that when testing for the occurrence bystander affiliation,
523 identifying the initiator of these interactions is crucial to further understanding of its
524 functional significance, as well as make sure the correct functional hypothesis is being
525 tested. Moreover, the lack of distinction between bystander-initiated and victim-initiated
526 affiliation in previous studies may explain the lack of evidence for the different functions
527 of bystander affiliation in animal societies (Fraser et al. 2009).
528 Bystander affiliation has been described as a mutualistic behaviour whereby
529 benefits are reciprocated between the victim and bystander (Aureli et al. in press). Our
530 findings support this view as bystander affiliation provides a stress-alleviation benefit to
531 the victim, and grooming benefits to the bystander. The adaptive value of bystander
532 affiliation appears to be two-fold. Bystander affiliation is used by the victim or bystander
533 to manage the costs of aggression and to maintain the benefits of high quality social
534 relationships, both of which impact on an individual's physiological well-being and

fitness (Keverne et al. 1989; van Schaik & Aureli 2000; Silk et al. 2003, 2009, 2010). Bystander affiliation also appears to be used by bystanders as a means to receive grooming and its social and hygienic benefits (Keverne et al. 1989; Zamma 2002; Dunbar 2010).

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REFERENCES

Arnold, K. & Barton, R. A. 2001. Postconflict behavior of spectacled leaf monkeys (*Trachypithecus obscurus*). II. contact with third parties. *International Journal of Primatology*, **22**, 267-286.

Aureli, F., Fraser, O. N., Schaffner, C. M. & Schino, G. The regulation of social relationships. In: *The evolution of primate societies* (Ed. by J. Mitani, J. Call, P. Kappeler, R. A. Palombit, & J. B. Silk). Chicago: University of Chicago Press. in press.

Aureli, F. & Schaffner, C. M. 2002. Relationship assessment through emotional mediation. *Behaviour*, **139**, 393-420.

Aureli, F., Cords, M. & van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: A predictive framework. *Animal Behaviour*, **64**, 325-343.

Aureli, F. & de Waal, F. B. M. 2000. *Natural conflict resolution*, Berkeley, California: University of California Press.

Aureli, F. & van Schaik, C. P. 1991. Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*). I. the social events. *Ethology*, **89**, 89-100.

Barros, M., Boere, V., Huston, J. P., & Tomaz, C. 2000. Measuring fear and anxiety in the marmoset (*Callithrix penicillata*) with a novel predator confrontation model: Effects of diazepam. *Behavioural Brain Research*, **108**, 205-211.

Call, J., Aureli, F. & de Waal, F. B. M. 2002. Postconflict third-party affiliation in stumptailed macaques. *Animal Behaviour*, **63**, 209-216.

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

Cordoni, G. & Palagi, E. 2008. Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. *Ethology*, **114**, 298-308.

Cordoni, G., Palagi, E. & Tarli, S. B. 2006. Reconciliation and consolation in captive western gorillas. *International Journal of Primatology*, **27**, 1365-1382.

Cozzi, A., Sighieri, C., Gazzano, A., Nicol, C. J. & Baragli, P. 2010. Post-conflict friendly reunion in a permanent group of horses (*Equus caballus*). *Behavioural Processes*, 85, 185-190.

Das, M. 2000. Conflict management via third parties; post-conflict affiliation of the aggressor. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 263–280. Berkeley, California: University of California Press.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. Matman: A programme for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, **125**, 157-175.

de Waal, F. B. M. & Aureli, F. 1996. Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. In: *Reaching into thought: The minds of the great apes* (Ed. By A. E. Russon, K. A. Bard & S. T. Parker), pp. 80-110. Cambridge, UK: Cambridge University Press.

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

de Waal, F. B. M. & van Hooff, J. A. 1981. Side-directed communication and agonistic interactions in chimpanzees. *Behaviour*, **77**, 164-198.

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

Dunbar, R. I. M. 2010. The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neuroscience and Biobehavioural Reviews*, **34**, 260-268.

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

Fraser, O. N. & Bugnyar, T. 2010. Do ravens show consolation? Responses to distressed others. *PloS ONE*, **5**, e10605.

Fraser, O. N., Stahl, D. & Aureli, F. 2008a. Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences*, **105**, 8557-8562.

Fraser, O. N., Schino, G. & Aureli, F. 2008b. Components of relationship quality in chimpanzees. *Ethology*, **114**, 834-843.

Fraser, O. N., Koski, S. E., Wittig, R. M. & Aureli, F. 2009. Why are bystanders friendly to recipients of aggression? *Communicative & Integrative Biology*, **2**, 285-291.

Fruteau, C., Lemoine, S., Hellard, E., van Damme, E. & Noë, R. 2011. When females trade grooming for grooming: testing partner control and partner choice models of cooperation in two primate species. *Animal Behaviour*, **81**, 1223-1230.

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

Judge, P. G. 1991. Dyadic and triadic reconciliation in pigtail macaques (*Macaca nemestrina*). *American Journal of Primatology*, **23**, 225-237.

Keverne, E. B., Martensz, N. D. & Tuite, B. 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, **14**, 155-161.

Koski, S. E. & Sterck, E. H. M. 2007. Triadic postconflict affiliation in captive chimpanzees: Does consolation console? *Animal Behaviour*, **73**, 133-142.

Koski, S. E., Koops, K. & Sterck, E. H. M. 2007. Reconciliation, relationship quality, and postconflict anxiety: Testing the integrated hypothesis in captive chimpanzees. *American Journal of Primatology*, **69**, 158-172.

622 **Maestripieri, D., Schino, G., Aureli, F. & Troisi, A.** 1992. A modest proposal:
623 Displacement activities as an indicator of emotions in primates. *Animal Behaviour*, **44**,
624 967-979.
625 **Majolo, B., Ventura, R. & Koyama, N. F.** 2009. Anxiety level predicts post-conflict
626 behaviour in wild Japanese macaques (*Macaca fuscata yakui*). *Ethology*, **115**, 986-995.
627 **Majolo, B., Ventura, R. & Schino, G.** 2010. Asymmetry and dimensions of relationship
628 quality in the Japanese macaque (*Macaca fuscata yakui*). *International Journal of*
629 *Primatology*, **31**, 736-750.
630 **McFarland, R. & Majolo, B.** 2011a. Grooming coercion and the post-conflict trading of
631 social services in wild Babrary macaques. *PLoS ONE*, **6(10)**, e26893.
632 doi:10.1371/journal.pone.0026893.
633 **McFarland, R. & Majolo, B.** 2011b. Reconciliation and the costs of aggression in wild
634 Barbary macaques (*Macaca sylvanus*): A test of the integrated hypothesis. *Ethology*, **117**,
635 928-937.
636 **McFarland, R. & Majolo, B.** 2011c. Exploring the components, asymmetry and
637 distribution of relationship quality in wild Barbary macaques (*Macaca sylvanus*). *PLoS*
638 *ONE*, **6(12**), e28826. doi:10.1371/journal.pone.0028826.
639 **Mundry, R. & Fischer, J.** 1998. Use of statistical programs for nonparametric tests of
640 small samples often leads to incorrect *P* values: examples from *Animal Behaviour*.
641 *Animal Behaviour*, **56,** 256-259.
642 **Palagi, E. & Cordoni, G.** 2009 Postconflict third-party affiliation in *Canis lupus*: do
643 wolves share similarities with the great apes? *Animal Behaviour*, **78**, 979-986.

Palagi, E., Paoli, T. & Tarli, S. B. 2004. Reconciliation and consolation in captive bonobos (*Pan paniscus*). *American Journal of Primatology*, **62**, 15-30.

Parker, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, **47**, 223-243.

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

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

Romero, T. & de Waal, F. B. M. 2010. Chimpanzee (*Pan troglodytes*) consolation: Third-party identity as a window on possible function. *Journal of Comparative Psychology*, **124**, 278-286.

Schino, G. 2001. Grooming, competition and social rank among female primates: A meta-analysis. *Animal Behaviour*, **62**, 265-271.

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

Schino, G. & Aureli, F. 2010. The relative roles of kinship and reciprocity in explaining primate altruism. *Ecology Letters*, **13**, 45 – 50.

Schino, G. & Pellegrini, B. 2009. Grooming in mandrills and the time frame of reciprocal partner choice. *American Journal of Primatology*, **71**, 884-888.

Schino, G., Troisi, A., Perretta, G., & Monaco, V. 1991. Measuring anxiety in nonhuman primates: Effect of lorazepam on macaque scratching. *Pharmacology Biochemistry and Behavior*, **38**, 889-891.

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

Schino, G., Rosati, L., Geminiani, S. & Aureli, F. 2007. Post-conflict anxiety in Japanese macaques (*Macaca fuscata*): Aggressor's and victim's perspectives. *Ethology*, **113**, 1081-1088.

Scucchi, S., Cordishi, C., Aureli, F. & Cozzolino, R. 1988. The use of redirection in a captive group of Japanese monkeys. *Primates*, **29**, 229-236.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2007. Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Current Biology*, **17**, 152-158.

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

Silk, J. B., Alberts, S. C., & Altmann, J. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) II. variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, **61**, 197-204.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B*, **276**, 3099-3104.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010. Female chacma baboons form

strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, **64**, 1733-1747.

StataCorp. 2007. Stata Statistical Software: Release 10. College Station, TX: Stata Press.

Troisi, A. 2002. Displacement activities as a behavioral measure of stress in nonhuman primates and human subjects. *Stress: The International Journal on the Biology of Stress,* **5**, 47-54.

van Schaik, C. P. & Aureli, F. 2000. The natural history of valuable relationships in primates In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 307-333. Berkeley, California: University of California Press.

Verbeek, P. & de Waal, F. B. M. 1997. Postconflict behavior of captive brown capuchins in the presence and absence of attractive food. *International Journal of Primatology*, 18, 703-726.

Vuong, Q. H. 1989. Likelihood ratio tests for model selection and non-nested hypotheses. *Econometrica,* 57, 307–333.

Watts, D. P., Colmenares, F. & Arnold, K. 2000. Redirection, consolation, and male policing; How targets of aggression interact with bystanders. In: *Natural conflict resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 281–301. Berkeley, California: University of California Press.

Wittig, R. M. & Boesch, C. 2003. The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour*, **140**, 1527-1559.

Zamma, K. 2002. Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates,* **43**, 41-49.

FIGURES

Figure 1. Box-plot (median, range, upper and lower quartiles) showing the victim's post-conflict self-scratching count in the presence or absence of bystander- or victim-initiated affiliation

Figure 2. Box-plot (median, range, upper and lower quartiles) showing the percentage of post-conflict grooming received by victims and bystanders

719 TABLES

720 Table 1. Variables used in the GLMMs (see Methods and Results for details on which

721 variables were used to test each prediction of this study).

Name	**Type**
Dependent variables	
PC self-scratching	Count
Bystander affiliation tendency (initiated by the victim or bystander)	Count
PC aggression received	Binomial (i.e. yes or no)
Independent variables	
Bystander-initiated affiliation	Binomial (i.e. yes or no)
Victim-initiated affiliation	Binomial (i.e. yes or no)
Composite sociality index	Continuous
PC-MC session	Binomial (i.e. PC or MC session)
Control variables	
Group	Binomial (i.e. 'Flat-face' or 'Large' group)
Age combination	Binomial (i.e. adult-adult or adult-subadult dyads)
Sex combination	Binomial (i.e. same sexed or different sexed dyads)
Rank difference	Continuous
Reconciliation	Binomial (i.e. yes or no)
Random factors	

Victim ID	Multinomial (ID number of the conflict victim)
Aggressor ID	Multinomial (ID number of the conflict aggressor)
Subject IDs	Multinomial (ID number of individuals in each group member dyad)
PC-MC pair	Multinomial (ID number of each PC-MC pair)

Table 2. GLMM Poisson-regression results for the relationship between victim post-conflict self-scratching count and bystander affiliation (initiated by the bystander or victim; N = 191) [Model 1]

	β ± SE	***Z***	***P***	**95% CIs**
Group	-0.2884 ± 0.2391	-1.21	0.228	-0.7570 - 0.1801
Age combination	0.1174 ± 0.1561	0.75	0.452	-0.1885 - 0.4234
Sex combination	0.0152 ± 0.2205	0.07	0.945	-0.4170 - 0.4473
Rank difference	0.0271 ± 0.0198	1.37	0.172	-0.0118 - 0.0659
Reconciliation	-0.7366 ± 0.3284	-2.24	0.025	-1.3802 - -0.0930
Bystander-initiated affiliation	-0.1588 ± 0.3140	-0.51	0.613	-0.7742 - 0.4565
Victim-initiated affiliation	-1.1147 ± 0.5188	-2.15	0.032	-2.1315 - -0.0979
Random effects				
Victim ID estimated variance ± SE = 0.1436 ± 0.3220				
Aggressor ID estimate variance ± SE = 0.00001 ± 0.2218				

Table 3. GLMM Poisson-regression results for the relationship between bystander-initiated affiliation count and bystander-victim relationship quality (N = 450) [Model 2]

	β ± SE	***Z***	***P***	**95% CIs**
Group	0.4410 ± 0.5957	0.74	0.459	-0.7266 - 1.6086
Age combination	-0.9262 ± 0.7530	-1.23	0.219	-2.4021 - 0.5497
Sex combination	0.1228 ± 0.5082	0.24	0.809	-0.8733 - 1.1188
Rank difference	0.04707 ± 0.0382	1.23	0.218	-0.0279 - 0.1220
Dyad relationship quality	0.1369 ± 0.0636	2.15	0.031	0.0122 - 0.2616
Random effects				
Victim ID estimated variance ± SE = 0.0947 ± 0.3283				
Aggressor ID estimated variance ± SE = 0.3231 ± 0.1781				

733 Table 4. GLMM Poisson-regression results for the relationship between victim-initiated
734 affiliation count and bystander-victim relationship quality (N = 450) [Model 3]
735

	β ± SE	***Z***	***P***	**95% CIs**
Group	0.0697 ± 0.6982	0.1	0.921	-1.2988 - 1.4381
Age combination	-0.4312 ± 0.7374	-0.58	0.559	-1.8765 - 1.0141
Sex combination	-0.3592 ± 0.5360	-0.67	0.503	-1.4098 - 0.6914
Rank difference	0.0809 ± 0.0437	1.85	0.064	-0.0046 - 0.1665
Dyad relationship quality	0.1584 ± 0.0737	2.15	0.031	0.0141 - 0.3026
Random effects				
Subject A ID estimated variance ± SE = 0.4248 ± 0.4222				
Subject B ID estimated variance ± SE = 0.4357 ± 0.4455				

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APPENDICES

Appendix 1. GLMM logistic-regression results for the relationship between aggression received by bystanders from victims and PC-MC session (N = 200) [Model 4]

	β ± SE	***Z***	***P***	**95% CIs**
Group	-2.6275 ± 3.2899	-0.8	0.424	-9.0757 - 3.8206
Age combination	-3.9583 ± 4.0410	-0.98	0.327	-11.8785 - 3.9619
Sex combination	-3.2627 ± 3.2304	-1.01	0.312	-9.5941 - 3.0687
PC-MC session	-3.0519 ± 1.7030	-1.79	0.073	-6.3897 - 0.2858
Random effects				
Subject ID (nested PC-MC pair ID) estimated variance ± SE = 8.1534 ± 3.5931				

Appendix 2. GLMM logistic-regression results for the relationship between aggression received by bystanders from aggressors and PC-MC session (N = 200) [Model 5]

	β ± SE	***Z***	***P***	**95% CIs**
Group	0.2864 ± 0.5038	0.57	0.57	-0.7009 - 1.2737
Age combination	0.5793 ± 1.1652	0.5	0.619	-1.7044 - 2.8630
Sex combination	-0.7432 ± 0.5947	-1.25	0.211	-1.9088 - 0.4224
PC-MC session	-0.3560 ± 0.4910	-0.73	0.468	-1.3182 - 0.606
Random effects				
Subject ID (nested PC-MC pair ID) estimated variance ± SE = 0.0009 ± 0.6976				

Appendix 3. GLMM logistic-regression results for the relationship between aggression received by bystanders from victims and bystander-initiated affiliation (N = 191) [Model 6]

	β ± SE	***Z***	***P***	**95% CIs**
Group	-0.8125 ± 0.7987	-1.02	0.309	-2.3780 - 0.7529
Age combination	-1.2780 ± 0.5999	-2.13	0.033	-2.4537 - -0.1022
Sex combination	0.2969 ± 0.6925	0.43	0.668	-1.0604 - 1.6541
Rank difference	0.09545 ± 0.0573	1.66	0.096	-0.0169 - 0.2079
Reconciliation	0.2346 ± 0.7280	0.32	0.747	-1.1922 - 1.6615
Bystander-initiated affiliation	0.3034 ± 0.8081	0.38	0.707	-1.2805 - 1.8873
Victim-initiated affiliation	1.4173 ± 0.7695	1.84	0.066	-0.0909 - 2.9254
Random effects				
Victim ID estimated variance ± SE = 0.9094 ± 0.4376				
Aggressor ID estimated variance ± SE = 0.4868 ± 0.6295				

Appendix 4. GLMM logistic-regression results for the relationship between aggression received by victims from bystanders and victim-initiated affiliation (N = 191) [Model 7]

	β ± SE	***Z***	***P***	**95% CIs**
Group	-1.0079 ± 0.6328	-1.59	0.111	-2.2481 - 0.2323
Age combination	-0.0508 ± 0.3821	-0.13	0.894	-0.7996 - 0.6980
Sex combination	-0.0937 ± 0.5334	-0.18	0.861	-1.1393 - 0.9518
Rank difference	0.04736 ± 0.0525	0.9	0.367	-0.0555 - 0.1502
Reconciliation	-0.3903 ± 0.7031	-0.56	0.579	-1.7683 - 0.9877
Bystander-initiated affiliation	-0.3546 ± 0.8258	-0.43	0.668	-1.9732 - 1.2640
Victim-initiated affiliation	0.5939 ± 0.6779	0.88	0.381	-0.7347 - 1.922
Random effects				
Victim ID estimated variance ± SE = 3.03e-09 ± 0.4033				
Aggressor ID estimated variance ± SE = 0.6383581 ± 0.4225				

Appendix 5. GLMM logistic-regression results for the relationship between aggression received by victims from aggressors and victim-initiated affiliation (N = 191) [Model 8]

	β ± SE	***Z***	***P***	**95% CIs**
Group	0.0412 ± 0.6698	0.06	0.951	-1.2715 - 1.3539
Age combination	-0.1594 ± 0.4364	-0.37	0.715	-1.0147 - 0.6960
Sex combination	-1.5156 ± 0.7389	-2.05	0.04	-2.9639 - -0.0673
Rank difference	0.0413 ± 0.059	0.7	0.483	-0.0741 - 0.1577
Reconciliation	1.2469 ± 0.6796	1.83	0.067	-0.0850 - 2.5788
Bystander-initiated affiliation	1.2027 ± 0.7943	1.51	0.13	-0.3542 - 2.7596
Victim-initiated affiliation	1.4580 ± 0.8746	1.67	0.096	-0.2562 - 3.1722
Random effects				
Victim ID estimated variance ± SE = 0.4836 ± 0.7469				
Aggressor ID estimated variance ± SE = 1.54e-06 ± 1.1251				