

1 **Friend or foe: Reconciliation between males and females in wild chacma baboons**

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1 **Abstract**

2 Male aggression towards females is a common and often costly occurrence in species that live
3 in bisexual groups. But preferential heterosexual relationships are also known to confer
4 numerous fitness advantages to both sexes—making it of interest to explore how aggression is
5 managed among male-female dyads through strategies like reconciliation (i.e., post-conflict
6 affiliative reunions between former opponents). In this study, we build on traditional PC-MC,
7 time-rule, and rate methods to validate a novel methodological approach that tests for the
8 presence and form of reconciliation between male and female wild chacma baboons (*Papio*
9 *ursinus*). We show that heterosexual opponents exhibit friendly post-conflict reunions, further
10 demonstrating that reconciliation occurs almost exclusively between males and
11 pregnant/lactating females who form tight social bonds. Such ‘friendships’ represent stable
12 associations offering proximate and ultimate benefits to both parties—mainly improving
13 (future) offspring survival. This aligns our findings with the Valuable Relationship Hypothesis,
14 which predicts rates of reconciliation to increase with the fitness consequences of the
15 opponents’ bond. Moreover, patterns concerning the initiative to reconcile reveal that males
16 are as likely as females to initiate reconciliation, suggesting that males play a heretofore
17 underappreciated role in maintaining heterosexual friendships. Beyond proposing a
18 multivariate methodological technique applicable to other long-term observational datasets, the
19 present research illuminates how male-female aggression in promiscuous societies may be
20 mitigated via relationship-repair strategies like reconciliation, the balance in those efforts
21 between partners shedding new light on the mutual investment in such bonds.

22

23 **Keywords:** Reconciliation, post-conflict affiliation, aggression, male-female association,
24 chacma baboons

25

26 **INTRODUCTION**

27 Conflict is an inherent yet often detrimental consequence of group living in animals. Its
28 potential fitness costs include injury, stress, resource loss, and perhaps above all—irreparable
29 damage to social relationships. It is therefore of great interest to understand the mechanisms
30 by which animals manage and mitigate conflict. One such strategy is *reconciliation*, or friendly
31 reunions between former opponents occurring soon after conflicts (de Waal & van Roosmalen,
32 1979). Since its inception, research in this area has sought to identify the factors that predict
33 variation in reconciliation's occurrence. Paramount among these factors is the nature of the
34 relationship between opponents (de Waal & Aureli, 1997). Approaching a recent conflict
35 opponent entails a certain risk, and thus partners should reconcile when they stand more to lose
36 if they do not repair their damaged bond. Accordingly, the Valuable Relationship Hypothesis
37 (VRH) posits that reconciliation should occur whenever the quality of the relationship has
38 important fitness consequences for the opponents (de Waal & Aureli, 1997; Kappeler & van
39 Schaik, 1992). This hypothesis generates key insights to animal sociality at different levels of
40 analysis.

41 At one level, tests of the VRH have shed light on how social relationships vary across
42 different types of social organization. This is exemplified by studies assessing rates of
43 reconciliation between and within sexes. For example, conciliatory tendencies are highest
44 between females in female-bonded macaque societies where matrilineal kin play an important
45 role in rank acquisition and maintenance (Cooper, Bernstein, & Hemelrijk, 2005; Schino,
46 Rosati, & Aureli, 1998). On the contrary, in chimpanzees, strong male intrasexual alliances
47 due to male philopatry are thought to promote higher reconciliation rates between male
48 opponents (de Waal, 1986; Koski, Koops, & Sterck, 2007; Watts, 2006; *cf* Fraser, Stahl, &
49 Aureli, 2010). In mountain gorillas and hamadryas baboons, females often reconcile with the
50 adult male of their social unit, who commonly provides protection and agonistic support

51 (Romero, Colmenares, & Aureli, 2008; Watts, 1995). As this brief overview illustrates, the vast
52 majority of reconciliation research has focused on primates (see Romero & Aureli, 2007, Table
53 1). Though limited by comparison, systematic studies of reconciliation in non-primate animal
54 societies, including canids (Cools, Van Hout, & Nelissen, 2008; Cordoni & Palagi, 2008),
55 cetaceans (Weaver, 2003), marsupials (Cordoni & Norscia, 2014), hyenas (Wahaj, Guse, &
56 Holekamp, 2001), domestic horses (Cozzi, Sighieri, Gazzano, Nicol, & Baragli, 2010) and
57 goats (Schino, 1998), corvids (Fraser & Bugnyar, 2011), and fish (Bshary & Würth, 2001) have
58 revealed that post-conflict affiliative behaviours are by no means limited to primate or even
59 mammalian taxa, and have provided new insights to the VHR. For example, reconciliation is
60 thought to be largely absent in cooperative breeders because valuable partners (i.e., the
61 breeding pair) rarely engage in aggression (Logan, Emery, & Clayton, 2012; Seed, Clayton, &
62 Emery, 2007). Further, in the only evidence to date of interspecies reconciliation, cleaner
63 wrasse fish reconcile with their valuable client reef partners, underscoring the fundamental role
64 such relationships play in this symbiotic dynamic (Bshary & Würth, 2001). By and large, this
65 work highlights how patterns of reconciliation reflect and underpin animal social structure.

66 At another level, tests of the VRH have been instrumental in revealing the nature of
67 individualized relationships within animal social groups. For instance, Wittig and Boesch
68 (2003) found that chimpanzee dyads who support one another and share food reconcile more
69 often than those who do not. Likewise, coalitionary support predicts post-conflict affiliation in
70 wolves (Cordoni & Palagi, 2008), whereas familiarity may facilitate reconciliation in dogs
71 (Cools et al., 2008). In a number of primate species, dyads characterized by more frequent
72 affiliation—e.g., as indexed by grooming and proximity measures—are known to exhibit
73 higher conciliatory tendencies than less affiliative dyads (reviewed in Romero & Aureli 2017).
74 Similarly, Fraser and Bugnyar (2011) found that reconciliation in pairs of ravens is positively
75 related to durations of allopreening and contact-sitting (measures that further relate to agonistic

76 support). In the only experimental test of the VRH to date, pairs of long-tailed macaques were
77 trained to cooperate in order to obtain food rewards. Reconciliation was three times more likely
78 to occur (relative to baseline rates) in those dyads whose relationships had been artificially
79 enhanced (Cords & Thurnheer, 1993). Through such direct measures and manipulations of
80 relationship value, tests of the VRH highlight which social bonds are most worthy of repair
81 following disruption by conflict.

82 A basic tenet of studies on reconciliation is that interaction patterns in post-conflict
83 periods differ in a meaningful way from interaction patterns at other times. To achieve this,
84 researchers have employed various methodologies, each with its own advantages and
85 shortcomings (reviewed in Kappeler & van Schaik 1992; Cords 1993; Veenema et al. 1994).
86 By far the most common approach is the ‘PC-MC method’ (de Waal & Yoshihara, 1983),
87 wherein the timing of the first affiliative interaction between former opponents during a post-
88 conflict (PC) sample is compared with that of a corresponding matched-control (MC), usually
89 sampled within one week of the conflict. One advantage of comparing a particular PC reunion
90 to a single control observation matched within this temporal window is that it accounts for
91 potential fluctuations in dyad members’ social bond over time. At the same time, this method
92 can generate noisy data, as stochasticity in the selection of a single MC observation means that
93 it may not be representative of the baseline affiliation characterizing a given dyad (Cords,
94 1993). This problem is partially circumvented by methodologies that compare PCs to a wider
95 subset of control observations, such as the ‘time-rule method,’ wherein the frequency
96 distribution of the first affiliative interaction as a function of time in aggregate PCs is compared
97 with the equivalent distribution in aggregate MCs (see Aureli, van Schaik, & van Hooff, 1989),
98 or the ‘rate method,’ which compares the distribution of the mean rate of affiliation in PCs and
99 MCs (see Judge, 1991). However, because these observations are not time-matched, such
100 methods may be less robust if there are temporal fluctuations in social relationships over the

101 same period. Nonetheless, researchers have advocated for the use of baseline levels of
102 interaction over traditional PC-MC approaches for a variety of reasons (e.g., Aureli et al., 1989;
103 Cords, 1993; Kappeler & van Schaik, 1992; Veenema et al., 1994). Although these methods
104 typically yield complementary findings (Kappeler & van Schaik, 1992), they occasionally lead
105 to discrepant results (e.g., Kappeler 1993). At present, a combination of approaches is therefore
106 considered the most reliable way to test for reconciliation's presence (Veenema, 2000).

107 In the current research, we apply—and build on—these methods to validate a novel
108 methodological approach in our study system, a population of wild chacma baboons. To date
109 the vast majority of research on reconciliation has been conducted on captive primate groups
110 (reviewed in Arnold et al. 2010), although studies are increasingly carried out in naturalistic
111 settings. This bias likely stems in part from practical limitations associated with collecting
112 proper PC-MC data in non-captive/controlled settings. It may also reflect putative analytical
113 constraints on long-term data that were not explicitly collected to study reconciliation, wherein
114 appropriate post-conflict data are available but baseline/control observations must be
115 determined *a posteriori*. Since the time of reconciliation's first discovery in the late 1970s,
116 rather strict adherence to the conventional PC-MC protocol has persisted despite the emergence
117 of a host of sophisticated quantitative tools and techniques. Among them are multivariate
118 analyses that can simultaneously account for independent determinants of variation in
119 reconciliation rates across different dyads. These emphasize the utility of updating traditional
120 approaches with state-of-the-art statistical procedures. We thus aim to propose a practical
121 method that will facilitate new research directions not only in our long-term field site, but for
122 similar longitudinal, individual-based, studies of wild animal populations.

123 We apply this methodology to test the VRH in an original and meaningful context—
124 that is, to study patterns of reconciliation between males and females within a promiscuous
125 primate society. On one level, we first sought to test whether adult heterosexual partners engage

126 in friendly post-conflict reunions. Thus far most research on the fitness benefits of animal social
127 bonds have focused on same-sex relationships (e.g., McDonald 2007; Yee et al. 2008; Silk et
128 al. 2010; Stanton & Mann 2012), but relationships between males and females also have a
129 documented impact on individual fitness (Archie, Tung, Clark, Altmann, & Alberts, 2014;
130 Cheney, Silk, & Seyfarth, 2012). Research on reconciliation in chacma baboons to date may
131 reflect this imbalance, focusing exclusively on post-conflict behaviour amongst adult female
132 opponents (e.g., Cheney et al. 1995; Silk et al. 1996; Wittig et al. 2007). It is therefore of
133 interest to investigate whether heterosexual opponent dyads also reconcile, particularly given
134 the high frequency of male aggression towards females in this species (Baniel, Cowlshaw, &
135 Huchard, 2017). The presence of reconciliation between males and females would further
136 elucidate the nature and value of adult heterosexual bonds in promiscuous societies, including
137 how those bonds are sustained despite conflict being a common occurrence.

138 On another level, we were interested in applying the VRH to test differentiated
139 relationships within these heterosexual dyads. Namely, chacma baboons live in large
140 multimale-multifemale societies where females are philopatric and dispersing males compete
141 for reproductive opportunities. It is common for pregnant and lactating females to associate
142 with the father of their offspring, and such ‘friendships’ may enhance the fitness of both
143 partners via paternal care (Baniel, Cowlshaw, & Huchard, 2016; Huchard et al., 2010, 2013;
144 Moscovice et al., 2010; Palombit, Seyfarth, & Cheney, 1997). Thus, using friendship as a direct
145 measure of relationship quality, we sought to test the VRH across different heterosexual
146 opponent pairs.

147 Our predictions were that: (1) male-female baboons would engage in post-conflict
148 affiliation at higher rates than expected from baseline affiliative patterns, thereby providing
149 evidence for reconciliation; (2) the occurrence of reconciliation would be more frequent
150 between male-female friends than non-friends, as the former should be motivated to maintain

151 mutual fitness benefits that might otherwise be disrupted by conflict; and (3) females would
152 initiate reconciliations more frequently than their male friends, as spatial proximity between
153 friends appears to be almost exclusively maintained by females (Huchard et al., 2010;
154 Palombit, Cheney, & Seyfarth, 2001; Palombit et al., 1997), who therefore seem to play the
155 primary role in sustaining these mutually beneficial bonds.

156

157 **MATERIAL & METHODS**

158 **(a) Data collection**

159 Data were collected in 2005-06 and 2013-14 from two habituated groups of wild chacma
160 baboons living at Tsaobis Nature Park (22°22'S 15°44'E), Namibia (for details of the site and
161 population, see (Cowlshaw, 1997)). Group composition and study periods are given in Table
162 S1. Males were considered adult when they reached eight years of age (Alberts & Altmann,
163 1995) and females when they reached menarche (Altmann & Alberts, 2003). Dominance ranks
164 of adult males and females were established using both *ad libitum* and focal observations of
165 dyadic agonistic interactions (see Appendix 1 in Supplementary Materials). The reproductive
166 state of each female was monitored daily and categorised as follows: (1) pregnant, where
167 pregnancy was determined *post hoc* following infant birth, and encompassed the six months
168 since the conceptive cycle; (2) lactation, if she had a dependant infant and had not yet resumed
169 cycling, (3) cycling oestrous, if she was sexually receptive with a perineal swelling, and (4)
170 cycling non-oestrous otherwise.

171 Observers on foot followed groups daily from dawn to dusk, conducting 1-hour focal
172 observations (mean duration \pm SD: 59.9 \pm 3.6 min) on all adult females and males (male
173 observations were only collected in 2013-14), spread equally across the day. In total, we
174 collected 3541 focal observations on 54 females (mean \pm SD: 65.6 \pm 45.5 observations per
175 individual) and 524 observations on 25 males (21.0 \pm 8.8). During observations, we

176 continuously recorded all occurrences of male-female agonistic and affiliative interactions
177 involving the focal individual, noting the partner's identity and the direction of the interaction.
178 Agonistic interactions comprised attacks (any aggressive physical contact including bites, hits,
179 grabbing), chases, and threats (including staring, head bobbing, and ground sweeping while
180 oriented toward the targeted individual). As expected on the basis of pronounced sexual
181 dimorphism, 97% of conflicts were directed from males to females (351/361 conflicts).
182 Affiliative interactions included grunts, positive facial expressions (come-here faces, lip-
183 smacks, sniff-mouths), positive physical contacts (touching, embracing, grooming, touching
184 perineum, mounting, grasping pelvis), and socio-sexual interactions (presenting hindquarters
185 to another individual across sexual and nonsexual contexts, copulating). Greetings frequently
186 involved a sequence of several affiliative interactions in short succession, so affiliative
187 interactions occurring within 30 seconds of each other in the same dyad were considered as
188 non-independent and we only retained the first interaction to avoid pseudoreplication. We also
189 monitored approaches and leaves continuously within one meter between the focal individual
190 and other adults of the group to establish the time spent in close proximity. Finally, we
191 conducted proximity scans every five minutes to record the identity and distance of the nearest
192 adult male (in the case of female observations) or female (in the case of male observations)
193 neighbour.

194

195 **(b) Identification of heterosexual friendships**

196 The male friend(s) of each pregnant and lactating female (i.e., the male(s) with whom they had
197 a particularly strong social bond) was identified using a combination of spatial proximity and
198 grooming allocation indices, following an established method (Baniel et al., 2016). Note that
199 cycling oestrous and non-oestrous females usually do not form such long-lasting friendships
200 with males. First, we calculated dyadic proximity and grooming scores between all pregnant

201 or lactating females and resident males. The grooming allocation index was calculated as the
202 number of grooming bouts that a female gave to a male divided by the total number of
203 grooming bouts given by that female to any male of the group. The dyadic spatial proximity
204 index was calculated as the number of scans in which the male was the female's nearest
205 neighbour divided by the total number of scans collected for that female. Second, for each
206 behavioural index we investigated if one or two males had an outstandingly high score
207 compared to other males, hereafter referred as the “preferred male(s).” We ranked males from
208 the highest to the lowest score, then calculated the ratio of the highest index divided by the
209 second highest index, and the ratio of the second highest index divided by the third highest
210 index. If the first ratio was higher than two (i.e., the male with the highest index had twice as
211 many interactions with the female than the second male), we assigned only one preferred
212 male—the one with the highest score—to the female. If the second ratio was also higher than
213 two, we assigned two preferred males—the ones with the first and second highest indices—to
214 the female. If no male had a highly differentiated score compared to the others, we considered
215 the female to have no preferred male for this reproductive state. Thus, pregnant/lactating
216 females could have one, two, or no preferred male(s). Third, we compared the preferred male(s)
217 designated by each behavioural index and considered as "male friend" the male that was
218 preferred according to both grooming and proximity indices. Using this criterion, a female
219 would have either one or two male friend(s) or, in the case of undifferentiated relationships
220 with males, no friend. Friendship assignment was conducted separately for lactating females
221 who had an infant that was younger *versus* older than six months. This is because infanticide
222 risk decreases considerably after this age (Palombit et al., 1997) and mothers show weaker
223 associations with their male friend and/or occasionally terminate associations (by switching
224 male partners) after this critical period (Baniel et al., 2016). Overall, we identified at least one
225 male friend for 83% of pregnant and lactating females.

226

227 **(c) Statistical Analyses**

228 **1. Validating a novel method to study reconciliation**

229 We tested for patterns of reconciliation between former male and female opponents by
230 implementing two complementary methods: (1) the *post-conflict matched-control* ('PC-MC')
231 method (de Waal & Yoshihara, 1983; Veenema, 2000), which has so far been the conventional
232 approach to establish the occurrence of reconciliation in animals, and (2) a new method which
233 builds on the *time-rule* and *rate methods* (Aureli et al., 1989; Cords, 1993; Judge, 1991;
234 Kappeler & van Schaik, 1992; Veenema et al., 1994), which have been less widely used but
235 are more practical for long-term observational datasets from wild populations that were not
236 explicitly collected to analyze reconciliation patterns (Kutsukake & Castles, 2004; Silk et al.,
237 1996; Wittig & Boesch, 2003). As a first step, we thus aimed to validate this new method using
238 a large sample of conflicts from our study system, ensuring that results corresponded with those
239 generated by a more traditional PC-MC approach.

240

241 ***Post-conflict matched-control method***

242 We used an extended matched-control analysis (de Waal & Yoshihara, 1983) to test whether
243 individuals were more likely to affiliate with a former opponent within 5-20 minutes after a
244 conflict. After each instance of intersexual aggression (chase, attack or threat), we selected the
245 x ($x=5, 10, 15$ and 20) following minutes of the focal observation, hereafter called the post-
246 conflict ('PC') observation, and assessed whether at least one affiliation occurred with the
247 opponent (no: 0; yes: 1). When it occurred, we also recorded the timing, type and direction of
248 the first affiliation. When another conflict happened within x minutes of the first conflict, we
249 excluded the first PC observation from the dataset, and only retained the x minutes following
250 the second conflict.

251 To each PC observation, we matched an observation of the same duration x , referred to
252 as the matched-control ('MC') observation. MC observations were paired to PC observations
253 following four criteria: (1) they involved the same focal individual and its former opponent,
254 (2) no aggression occurred between the focal subject and its former opponent during the x
255 minutes preceding the start of the MC observation, (3) they occurred less than seven days apart
256 and (4) the female was in the same reproductive state (pregnant, lactating, oestrous or cycling
257 non-oestrous) (see Appendix 2 in Supplementary Materials for more details about the selection
258 of MC observations). In order to gather enough MC observations that met these four selection
259 criteria, it was necessary to accept MC observations that were collected at different times of
260 day from the corresponding PC observation. However, we ensured that selecting MC
261 observations randomly did not bias the data in any particular direction for time of day (see
262 Figure S1). We then assessed whether the focal individual affiliated with its former opponent
263 in the MC observation (no: 0; yes: 1).

264 We subsequently determined, for each PC-MC pair, whether it was 'attracted' (i.e.,
265 affiliation occurred earlier or exclusively in the PC observation), 'dispersed' (affiliation
266 occurred earlier or exclusively in the MC observation) or 'neutral' (affiliation did not occur in
267 either observation, or occurred at the same time). A Wilcoxon matched-pair signed-rank test
268 that compared the proportion of attracted and dispersed pairs for each individual female was
269 used to test for a signal of reconciliation. Only females involved in at least five aggressive acts
270 (mean \pm SD: 7.9 \pm 2.5 for the 5-min dataset) were included. We also calculated the corrected
271 conciliatory tendency (CCT) for each focal female defined as 'the number of attracted minus
272 dispersed pairs in which an individual is involved, divided by its total number of PC-MC pairs'
273 (Veenema et al., 1994).

274 Using approaches and leaves occurring within 1m of the focal subject, we also
275 calculated for each PC-MC pair the average time that the male and female spent in close

276 proximity in the PC and MC observation. We tested whether opponents were in closer
277 proximity in PC than in MC observations using a Wilcoxon matched-pair signed-rank test, as
278 such a difference could bias results towards more affiliation in PC observations. Opponents
279 spent the same amount of time within 1m in PC and MC observations (Table S2, except for the
280 5-min dataset), indicating that PC and MC observations were directly comparable for the 10,
281 15 and 20-min datasets.

282

283 *Method using baseline rate of affiliation*

284 We implemented a second method (adapted from the time-rule and rate methods described in
285 Aureli et al., 1989; Cords, 1993; Judge, 1991; Kappeler & van Schaik, 1992; Veenema et al.,
286 1994), that uses baseline levels of affiliation among members of a dyad and compares multiple
287 PC observations to multiple control observations. Using our large body of focal observations,
288 we began by establishing the rate of affiliation between a given pair of individuals (1) in the x
289 (x= 5, 10, 15 and 20) minutes following aggression between them (i.e., the post-conflict
290 samples) and (2) when no aggression occurred in the x preceding minutes (i.e., the baseline
291 samples). This involved a three-step process. First, for each heterosexual dyad that exchanged
292 at least one act of aggression, we identified all focal observations (i) that were conducted on
293 both individuals in a given year and (ii) where the female was in a given reproductive state
294 (non-oestrus, oestrus, pregnant, lactating). Second, we split these observations into two
295 categories: the post-conflict sample, where we pooled all observations that followed a conflict
296 between the dyad members, and the baseline sample, where we pooled all observations that
297 were not preceded by a conflict. In some cases, PC observations were incomplete (e.g., because
298 the focal individual went out of sight or another aggression occurred). We therefore retained
299 only PC observations that lasted at least 3, 6, 9 and 12 min for the 5, 10, 15 and 20-min datasets,
300 respectively (i.e., $\geq 60\%$ of the observation time). For each baseline observation, we removed

301 x minutes of observation at the start of the focal observation and after the focal individual went
302 out of sight for a couple of minutes (in case an aggression occurred between the two members
303 of the dyad as they were out of sight). Third, we tabulated the number of times that the two
304 individuals affiliated in the respective post-conflict and baseline sample, as well as the total
305 observation time of the corresponding sample, thus generating the rates of affiliation in each
306 case.

307 We analysed the difference in the mean rate of affiliation between the post-conflict and
308 baseline samples across male-female dyads using a generalised linear mixed-effect model
309 (GLMM) with a Poisson error structure. The number of affiliations exchanged by each male-
310 female dyad was fitted as the response variable. The total observation time of the corresponding
311 sample (post-conflict or baseline) was log-transformed and included as an offset variable to
312 model a rate of affiliation. The fixed effects comprised the type of observation (post-conflict
313 samples: 1, baseline samples: 0). Random effects comprised the identity of the female, male,
314 and dyad. In this analysis, females were included regardless of their number of observed
315 conflicts since GLMMs can account for unbalanced samples, and do not rely on categorizing
316 each dyad as attracted or dispersed (as in the PC-MC method) but simply evaluate whether
317 affiliations are more common after a conflict.

318 All GLMMs were run using the glmer function of the lme4 package (Bates, Maechler,
319 Bolker, & Walker, 2014) in R version 3.4.1 (R Core Team, 2017). The significance of the fixed
320 factors was tested by computing their 95% bootstrap confidence intervals (using
321 confint.merMod) and checking that they did not cross zero. Their p-values were calculated by
322 using the PBmodcomp function from the pbkrtest package (Halekoh & Højsgaard, 2014),
323 which compares a model with and without the variable using a parametric bootstrap method.
324 To test for differences between all levels of multilevel categorical variables, we changed the
325 reference category sequentially and refitted the model (Pinheiro & Bates, 2000).

326

327 **2. Reconciliation between males and pregnant/lactating females**

328 After validating the new method (see results), we then investigated in more detail patterns of
329 reconciliation between males and non-cycling females (i.e., pregnant and lactating), especially
330 in relation to their friendship status. Using the previously established dataset, we ran a GLMM
331 with a Poisson error structure using the number of affiliations exchanged between male and
332 female dyads as the response variable, but selecting only heterosexual dyads involving
333 pregnant and lactating females. We chose the dataset looking at 15-min after aggression for
334 this analysis, because the sample size was reasonably high and the strength of the reconciliation
335 signal was maximal in this dataset (see Results). As above, the total observation time of the
336 corresponding sample (post-conflict or baseline) was log-transformed and included as an offset
337 variable to model a rate of affiliation. Random effects comprised the identity of the female,
338 male, and dyad. Fixed effects included the social context, i.e., a categorical variable recording
339 whether (i) the male and female of the dyad were friends and (ii) the observation was post-
340 conflict or not, with four levels: PC & friend, baseline & friend, PC & non-friend, baseline &
341 non-friend. We created this variable to avoid fitting an interaction between two qualitative
342 variables (here, the type of observation and the friendship status of the dyad), which are hard
343 to estimate statistically and pose challenges for interpreting results. The reproductive state of
344 the female of the dyad (pregnant or lactating), the relative rank of the female, and the relative
345 rank of the male (averaged over the period of observation used to estimate the corresponding
346 affiliation rate) were additionally entered as fixed effects.

347

348 **RESULTS**

349 **1. Validating a novel method to study reconciliation**

350 *Post-conflict matched-control method*

351 Consistent with our prediction that heterosexual dyads would exhibit reconciliation, males and
352 females were more likely to affiliate after an aggression than by chance (Table 1, Figure 1a).
353 The reconciliation signal was significant at 5, 10, 15 and 20 min, and peaked at 20-min, where
354 37% of conflicts were reconciled. The downstream figures were nevertheless estimated from
355 the 15 min dataset, which includes a relatively high rate of reconciliation (33% of conflicts)
356 alongside a larger number of conflicts (N=126 versus 75 in the 20 min dataset), thereby offering
357 higher statistical resolution. The average duration between aggression and the first affiliative
358 contact was 4.0 ± 4.0 min (mean \pm SD, calculated over 42 conflicts followed by affiliation in the
359 15 min dataset). Of these 42 reconciled conflicts, the first affiliation was initiated 22 times by
360 the male (52%) and 20 times by the female (48%). The four most common first post-conflict
361 affiliative acts used to reconcile were presenting (36%), one or more grunts (19%), a grooming
362 initiation (14%), and a copulation (12%). Individual females differed highly in their tendency
363 to reconcile with the opposite sex (Table 1, Figure 1b), with some subjects who never
364 reconciled, and others who reconciled up to 60% of their conflicts – though this figure is based
365 on a relatively low number of conflicts per individual (mean \pm SD: 6.63 ± 2.03 , min-max: 5-12).

366

367 *Method using baseline rate of affiliation*

368 Male-female dyads were found to affiliate at higher rates in the PC samples than in the baseline
369 samples, regardless of whether 5, 10, 15 or 20 min of PC samples were selected (Table 2,
370 Figure 2). This is in accordance with the results of the PC-MC method, showing that this
371 method is appropriate for investigating patterns of reconciliation.

372

373 **2. Reconciliation between males and pregnant/lactating females**

374 Friend dyads affiliated at much higher rates after a conflict than in baseline observations (rate
375 of affiliation \pm SD in PC: 0.04 ± 0.07 time/min and in baseline: 0.01 ± 0.01), although with high

376 levels of variation across dyads. In contrast, non-friend dyads affiliated at comparable rates
377 across post-conflict and baseline observations (rate of affiliation \pm SD in PC: 0.00 \pm 0.01 and in
378 baseline: 0.00 \pm 0.00) (Table 3, Figure 3). As predicted, friend dyads also affiliated significantly
379 more than non-friend dyads after a conflict. Counter to our prediction that females would be
380 the more frequent initiators of reconciliation, out of 32 aggressive events observed between
381 friend dyads, 10 were reconciled, and the first affiliation was initiated by the male in half of
382 these cases (n=5). Out of 41 aggressive interactions observed between non-friend dyads, only
383 one was reconciled (initiated by the female). Overall, these results indicate that reconciliation
384 between pregnant/lactating females and males occurs only if they are friends. Unsurprisingly,
385 we also found that friends affiliated more than non-friends across baseline observations.
386 Female reproductive state (pregnant or lactating) and male and female rank did not influence
387 dyadic rates of affiliation.

388

389 **DISCUSSION**

390 We validate a new methodological approach to study reconciliation patterns using long-term
391 datasets, and implement it to test the VRH in a novel context, that of reconciliation between
392 male and female chacma baboons. Our analyses indicate affiliative reunions occur following
393 conflicts between adult heterosexual pairs. Further, we demonstrate that such reconciliation
394 regularly occurs between males and pregnant/lactating females who are engaged in friendships
395 (who also exchange higher baseline levels of affiliation) but is virtually absent among males
396 and pregnant/lactating females who are not friends. Such ‘friendships’ are strong, stable
397 associations that are mutually beneficial at both a proximate and ultimate level (see below),
398 and evidently worthy of reconciling in the face of conflict. These findings thus lend further
399 credence to the overall value of heterosexual bonds in this species, whose role is often

400 overlooked in structuring the social organization of baboon societies (Archie et al., 2014;
401 Baniel et al., 2016; Cheney et al., 2012).

402 According to the VRH, reconciliation should be present when any resulting damage to
403 the relationship has important fitness consequences (de Waal & Aureli, 1997; Kappeler & van
404 Schaik, 1992). In this case, the potential fitness costs of disrupted male-female relationships
405 are manifold. For males, they may lead to a direct loss of mating opportunities and/or of
406 grooming partners, which can be contingent on the quality of male-female social relationships
407 (Smuts, 1985). Whenever they have sired their friend's offspring, males who lose their female
408 friend also lose an opportunity to invest in their own descent (Buchan, Alberts, Silk, &
409 Altmann, 2003; Huchard et al., 2010; Moscovice et al., 2010). A disruption of the mother-
410 father relationship may consequently weaken the father-offspring bond during weaning, which
411 can in turn impair infant survival and nutritional benefits obtained through paternal care
412 (Charpentier, Van Horn, Altmann, & Alberts, 2008; Huchard et al., 2013). For females with
413 infants, disrupted relationships to males may translate into a loss of paternal care, and notably
414 to a higher infanticide risk (Buchan et al., 2003; Huchard et al., 2013; Palombit et al., 1997).
415 Damaged relationships with males may also result in females losing males' protection, and
416 potentially incurring subsequent harassment from dominant females and aggression from other
417 resident males (Lemasson, Palombit, & Jubin, 2008; Nguyen, Van Horn, Alberts, & Altmann,
418 2009), and of associated costs such as injuries (Baniel et al., 2017) and increased risks of
419 miscarriages (Zipple et al., 2017). Friendships with males also buffer females against elevated
420 stress levels during periods of group instability, such as when a new male immigrates (e.g.,
421 Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2005). Considering these myriad fitness
422 benefits, the presence of post-conflict conciliatory interactions between males and females
423 underscores the adaptive value of repairing the adverse consequences of at least some conflicts
424 in these relationships.

425 That in the present work the overwhelming majority of conflicts were directed by males
426 towards females does not necessarily indicate commensurate asymmetry in who initiates
427 reconciliation. In fact, contrary to expectations, the initiation of post-conflict affiliation in these
428 male-female dyads exhibited near symmetry, inviting us to speculate that the motivation behind
429 repairing these valuable relationships is not purely one-sided. Heterosexual friendships are
430 characterized by a strong asymmetry in the maintenance of proximity among partners—where
431 only females actively contribute (Huchard et al., 2010; Lemasson et al., 2008; Palombit et al.,
432 1997)—which has long raised questions over males’ motivations for such bonds. The initiative
433 of males in relationship-repair strategies like reconciliation provides a new form of evidence
434 that males are indeed motivated to maintain relationships to female friends. This adds further
435 nuance to the present study’s support for the VRH, in that the fitness consequences of such
436 relationships may be more jointly motivating than previously assumed. More generally, it sheds
437 new light on how patterns of reconciliation can be revelatory for understanding shared
438 investments in social bonds in ways that proximity measures alone do not capture.

439 In wild olive baboons, Castles and Whiten (1998b) found that conflicts increased stress
440 for both victims and aggressors, as evidenced by elevated rates of self-directed behaviours in
441 PC periods. Reconciliation served to reduce this stress, but only amongst individuals involved
442 in bilateral conflicts in which both parties exchanged aggression. Unilateral victims of conflict,
443 particularly in despotic species like chacma baboons, may be reluctant to approach recent
444 aggressors. Nonetheless, females in our study did not appear constrained in the initiative to
445 reconcile compared to their male aggressor counterparts, indicating that the benefits of
446 initiating reconciliation might outweigh the risks of receiving renewed aggression.
447 Nonetheless, the extent to which males and females are differentially stressed by these
448 asymmetrical conflicts—and further whether reconciliation actually serves to reduce stress in

449 both victims/aggressors and restore tolerance in those dyads—is an area that warrants further
450 investigation.

451 An additional prospective line of research concerns the relative rates of reconciliation
452 across different relationships and individuals. Notably, the rates of reconciliation reported here
453 (nearly one third of all conflicts) are consistently higher than those reported by Silk and
454 colleagues' (1996) research on female-female chacma baboons, who often grunt to reconcile
455 with former opponents (13% of all cases). In fact, whereas the likelihood of approaches and
456 grunts increased following conflicts in Silk et al.'s (1996) study, other affiliative behaviours
457 generally decreased. The discrepancy between these results and ours may be a consequence of
458 the present study's inclusion of a wider repertoire of potential post-conflict behaviours. It could
459 further be attributable to differences in the way conflict and PC data were extracted: whereas
460 in their study it is unclear whether successive bouts of aggression were counted as one or more
461 conflict(s), our study focused only on the most recent conflict in a series of aggressions. This
462 may have contributed to Silk et al.'s (1996) finding that rates of aggression between former
463 opponents were higher in PC than in MC samples, whereas our study design prevented us from
464 observing such a contrast, as aggression rates between opponents in PC samples were set to 0
465 by construction. Acknowledging such differences is not to overlook the distinct possibility that
466 male-female dyads indeed reconcile more frequently than do female-female dyads, particularly
467 given the pronounced evolutionary stakes.

468 That some subjects in our study rarely reconciled, while others did so rather frequently,
469 is an area that also warrants further study. Individual variation may reflect the variable quality
470 of the relationships of different individuals (with higher reconcilers having more valuable
471 bonds) or stable individual differences, as recently emphasized by work incorporating conflict
472 management skills as a component of broader animal personality (Webb, Franks, Romero,
473 Higgins, & de Waal, 2014; Webb, Romero, Franks, & de Waal, 2017; Webb & Verbeek, 2016).

474 Our results further revealed that even among friendship dyads there is considerable variation
475 in the tendency to reconcile, which is not simply explained by variation in male and female
476 dominance ranks. It would be interesting to disentangle the causes and consequences of
477 observed variations in reconciliation rates across dyads and individuals by determining whether
478 having better social bonds leads to higher reconciliation, or, alternatively, having higher
479 reconciliation tendencies facilitates better social bonds. In the first case, we would expect
480 relationship quality to predict the likelihood of reconciliation independently of individual
481 factors. In the second case, we would expect relationship quality and reconciliation tendency
482 to be predicted by the same individual factors.

483 Finally, studies like this might further our understanding of heterosexual reconciliatory
484 patterns across species, and in turn help to elucidate the nature of male-female associations
485 across other social/mating systems. It would be especially interesting to consider where
486 reconciliation is absent in this regard. Studies of cooperative breeders have found little
487 evidence for reconciliation, even within the breeding pair for whom the relationship has clear
488 fitness value for both partners (reviewed in Schaffner & Caine, 2000). In red-bellied tamarins,
489 for example, reconciliation is thought to be absent largely because conflicts of interest seldom
490 escalate into overt aggression with the potential to damage relationships (Schaffner, Aureli, &
491 Caine, 2005, *cf* Peñate et al., 2009). The pair-bonded nature of most bird species, in which
492 mates seldom fight, may also preclude the need for reconciliation (see Logan, Emery, &
493 Clayton, 2012; Seed, Clayton, & Emery, 2007), though post-conflict affiliation occurs in
494 valuable relationships outside of the pair bond (Fraser & Bugnyar, 2011). Differences in avian
495 and mammalian reconciliation behavior have been attributed not merely to the lower incidence
496 of aggression in monogamous relationships, but to the fluidity of avian social systems which
497 may facilitate post-conflict dispersal (Fraser & Bugnyar, 2011; Seed et al., 2007). Overall,
498 reconciliation may be most frequent in societies with low average kinship among group

499 members like those of promiscuous mammals, where conflicts of interests are common and
500 require individuals to develop complex strategies to manage differentiated and fitness-
501 enhancing relationships with non-kin (Lukas & Clutton-Brock, 2018).

502

503 **CONCLUSION**

504 Post-conflict interactions among heterosexual pairs have rarely been studied in wild
505 promiscuous social systems, despite growing knowledge that males and females form long-
506 term associations marked by clear fitness consequences for both partners. Our study reveals
507 that male and female baboons engage in affiliative post-conflict reunions at higher rates than
508 expected from baseline measures of affiliation—that is, they engage in reconciliation. The
509 present research shows that reconciliation rates are high among friends and absent among non-
510 friends, and further reveals that males and females are equally likely to initiate reconciliation.
511 This sheds new light on the shared investment of heterosexual friends in their relationship, a
512 picture which is more consistent with the mutual benefits obtained from such bonds.

513

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691

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692 **Table 1. Results of the post-conflict matched-control method, for four different time periods.** PC: post-conflict observations, MC: matched-
 693 control observations. Significant p-values are highlighted in bold.

694

	Mean percentage of attracted pairs \pm SD	Mean percentage of dispersed pairs \pm SD	Sample size ^a	No. females/males	V ^b	P-value ^b	No. (%) PC with affil ^c	No.(%) MC with affil ^d	Mean CCT \pm SD
5min	18.8 \pm 17.3	7.8 \pm 8.3	181	23/31	107	0.008	39 (21.5)	20 (11.0)	11.0 \pm 18.0
10min	23.4 \pm 18.3	10.5 \pm 12.0	152	22/30	161	0.038	42 (27.6)	23 (15.1)	12.9 \pm 24.0
15min	30.5 \pm 19.3	12.1 \pm 14.1	126	19/27	107	0.008	42 (33.3)	29 (23.0)	18.5 \pm 23.2
20min	35.2 \pm 19.8	11.7 \pm 12.7	75	12/24	72	0.011	28 (37.3)	16 (21.3)	23.5 \pm 21.1

695

696

^a Number of PC-MC pairs (=aggression events) available for the test.

697

^b Statistic of a Wilcoxon matched-pairs signed-rank test that compares the difference between the proportion of attracted and dispersed pairs.

698

^c Number of PC observations including an affiliation between former opponents.

699

^d Number of MC observations including an affiliation between former opponents.

700 **Table 2. Results of the baseline affiliation method, for four different time periods.** PC: post-conflict observations. We present the estimate
 701 and significance of the variable “Type of observation” (PC versus baseline samples) for the four GLMMS corresponding to the four different time
 702 periods (5, 10, 15 and 20 min). GLMMs were performed controlling for male, female and dyad identity. The 95% confidence intervals and p-
 703 values of statistically significant results are highlighted in bold.

704

	Rate of affiliation in PC \pm SD ^a	Rate of affiliation in baseline \pm SD ^b	No. dyads	No. aggression ^c	Estimate	SE	95% confidence interval	LRT	P-value
5min	0.04 \pm 0.09	0.01 \pm 0.02	163	256	1.23	0.16	[0.90 ; 1.50]	65.80	0.002
10min	0.04 \pm 0.07	0.01 \pm 0.02	151	223	1.15	0.10	[0.90 ; 1.37]	88.48	0.002
15min	0.03 \pm 0.06	0.01 \pm 0.02	146	210	1.11	0.09	[0.89 ; 1.29]	107.51	0.002
20min	0.04 \pm 0.06	0.01 \pm 0.02	136	191	1.11	0.09	[0.90 ; 1.27]	123.30	0.002

705

706 ^aThe rate of affiliation in PC is calculated as the total number of affiliative interactions observed in PC divided by the total time of PC observations

707 ^bThe baseline rate of affiliation is calculated as the total number of affiliative interactions observed in baseline divided by the total time of baseline
 708 observations

709 ^cTotal number of PC observations.

710

711

712

713 **Table 3. Patterns of reconciliation between pregnant/lactating females and males.** PC: post-conflict observations. Parameters and tests are
714 based on 31 females, 22 males, and 52 dyads (including 29 with a pregnant female and 23 with a lactating female). There were 18 friend dyads,
715 and 73 events of aggression (mean±SD aggression observed per dyad: 1.4±0.8). Females have on average 20.0±11.3 min of observation in PC and
716 867.0±284.9 min of observation in baseline. The GLMM was performed controlling for male, female and dyad identity. P-values are used to test
717 for the significance of each variable, while the 95% confidence intervals are used to test for the significance of each level of the qualitative
718 variables. The confidence intervals and p-values of statistically significant results are highlighted in bold.

719

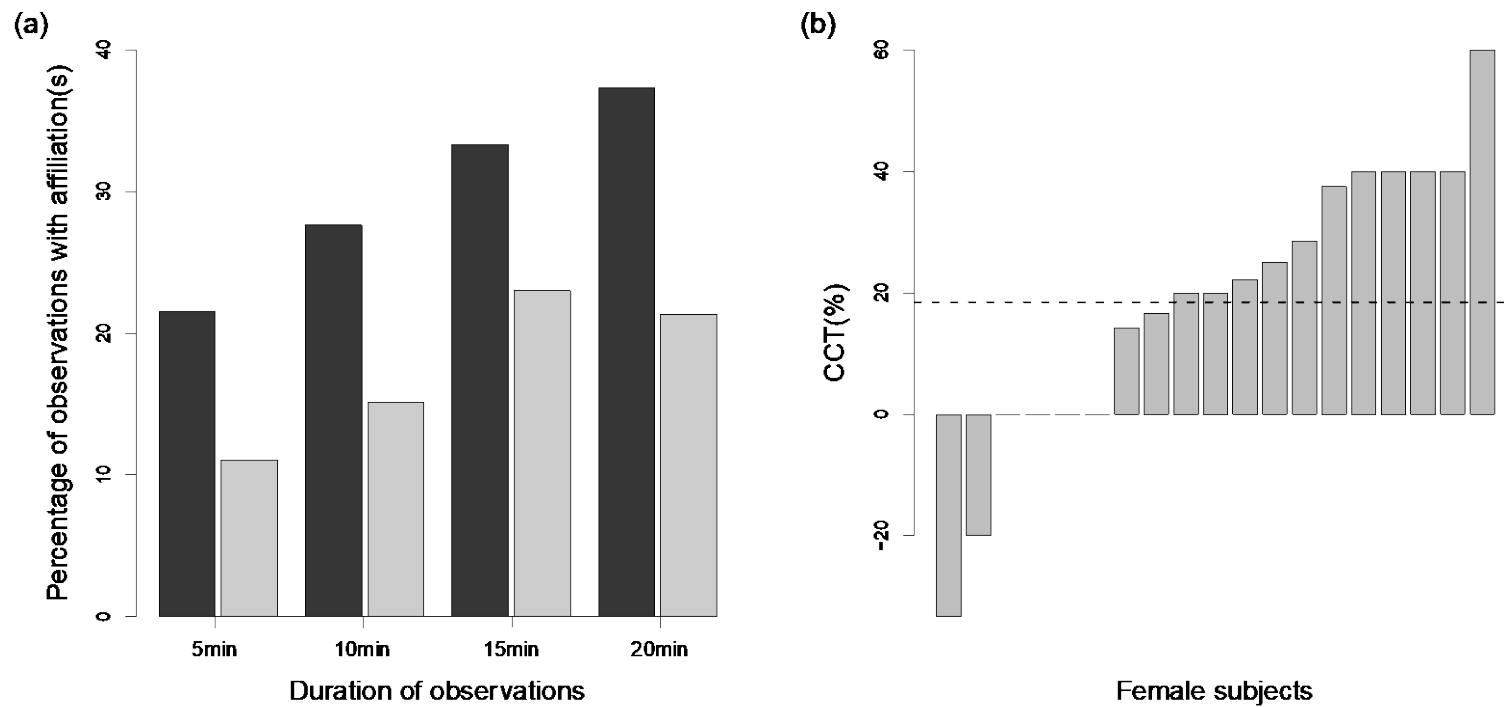
Response variable	Fixed factor	Levels	Estimate	SE	95% confidence interval	LRT	P-value
Number of affiliations exchanged between male-female dyads ^a	Type of observation	PC friend (ref: baseline friend)	1.00	0.27	[0.43 ; 1.42]	31.67	0.002
		PC non-friend (ref: baseline non-friend)	0.53	0.72	[-10.71 ; 1.54]		
		PC friend (ref: PC non-friend)	2.62	0.86	[1.21 ; 12.86]		
		Baseline friend (ref: baseline non-friend)	2.15	0.44	[1.24 ; 3.15]		
	Reproductive state ^b	Pregnant	0.20	0.39	[-0.53 ; 0.96]	0.27	0.634
		Female rank	0.85	0.61	[-0.44 ; 2.20]	1.59	0.252
		Male rank	-0.43	0.81	[-2.51 ; 1.21]	0.27	0.643

720

721 ^a The duration (min) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

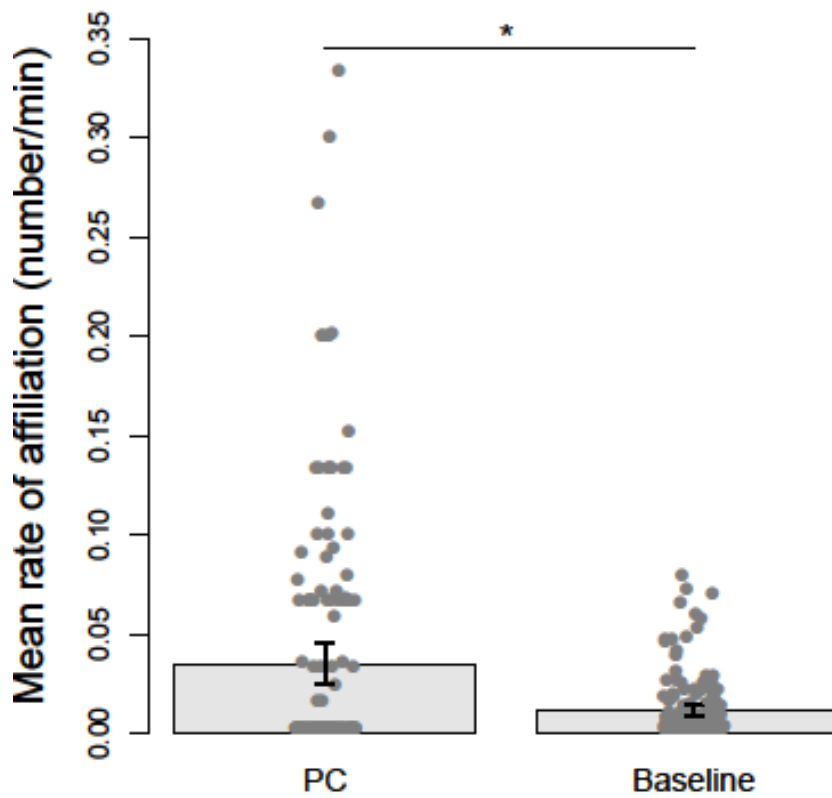
722 ^b Reference category: lactating

723 **Figure 1. Patterns of reconciliation between males and females, as assessed by the post-conflict matched-control method. (a)** Percentage of
724 observations containing at least one affiliation in the post-conflict (black bar) and matched-control (grey bar) sample. **(b)** Corrected conciliatory
725 tendency (CCT) for each individual female (N=19 females, including four with a CCT of zero that are invisible for the 15-min dataset). The average
726 CCT across females is indicated by the dotted line.



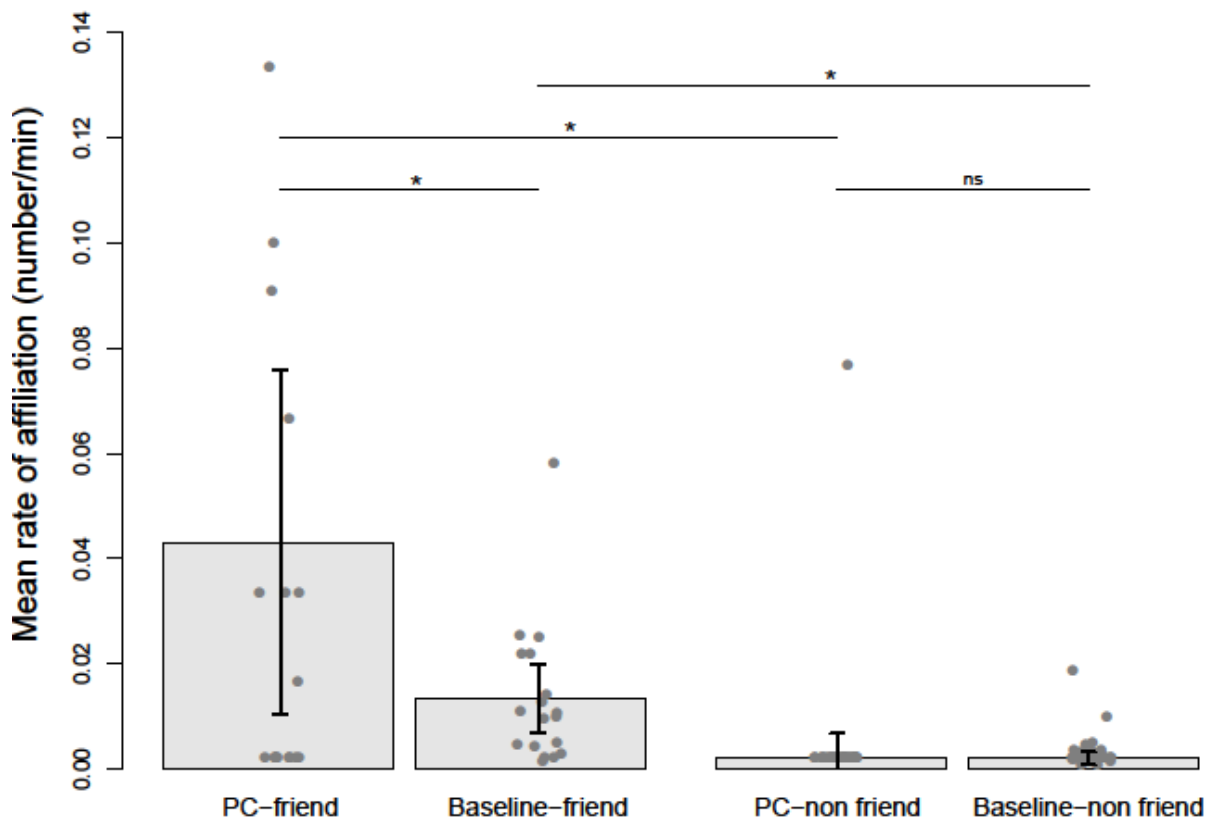
727

728 **Figure 2. Patterns of reconciliation between males and females, as assessed by the baseline**
729 **affiliation method.** Mean rate of affiliation in post-conflict (PC) versus baseline samples
730 across male-female dyads. Data are shown for 15-min observations. Black bars represent the
731 standard error and grey dots represent the raw mean of each dyad.
732



733

734 **Figure 3. Patterns of reconciliation between males and pregnant/lactating females, as**
735 **assessed by the baseline affiliation method.** Mean rate of affiliation between
736 pregnant/lactating female and a male, according to the context (PC versus baseline) and to their
737 friendship status (friend/non-friend). Data are shown for 15-min observations. Black bars
738 represent the standard error and grey dots represent the raw mean of each dyad. The
739 significance of the difference between all levels of categorical variables is evaluated by
740 changing contrasts in GLMMs. * $P < 0.05$.



741