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

2

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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  $4.0 \pm 4.0$  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: $6.63 \pm 2.03$ , 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:  $0.04 \pm 0.07$  time/min and in baseline:  $0.01 \pm 0.01$ ), 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

**Ethical Note.** Research procedures were approved by the Ethics Committee of the Zoological Society of London and the Ministry of Environment and Tourism of Namibia (permit numbers 886/2005, 1039/2006, 1786/2013, and 1892/2014), and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

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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 <sup>a</sup>	No. females/males	V <sup>b</sup>	P-value <sup>b</sup>	No. (%) PC with affil <sup>c</sup>	No.(%) MC with affil <sup>d</sup>	Mean CCT $\pm$ SD
5min	18.8 $\pm$ 17.3	7.8 $\pm$ 8.3	181	23/31	107	<b>0.008</b>	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	<b>0.038</b>	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	<b>0.008</b>	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	<b>0.011</b>	28 (37.3)	16 (21.3)	23.5 $\pm$ 21.1

695

696

<sup>a</sup> Number of PC-MC pairs (=aggression events) available for the test.

697

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

698

<sup>c</sup> Number of PC observations including an affiliation between former opponents.

699

<sup>d</sup> 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 <sup>a</sup>	Rate of affiliation in baseline $\pm$ SD <sup>b</sup>	No. dyads	No. aggression <sup>c</sup>	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	<b>[0.90 ; 1.50]</b>	65.80	<b>0.002</b>
10min	0.04 $\pm$ 0.07	0.01 $\pm$ 0.02	151	223	1.15	0.10	<b>[0.90 ; 1.37]</b>	88.48	<b>0.002</b>
15min	0.03 $\pm$ 0.06	0.01 $\pm$ 0.02	146	210	1.11	0.09	<b>[0.89 ; 1.29]</b>	107.51	<b>0.002</b>
20min	0.04 $\pm$ 0.06	0.01 $\pm$ 0.02	136	191	1.11	0.09	<b>[0.90 ; 1.27]</b>	123.30	<b>0.002</b>

705

706 <sup>a</sup>The 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 <sup>b</sup>The 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 <sup>c</sup>Total number of PC observations.

710

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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

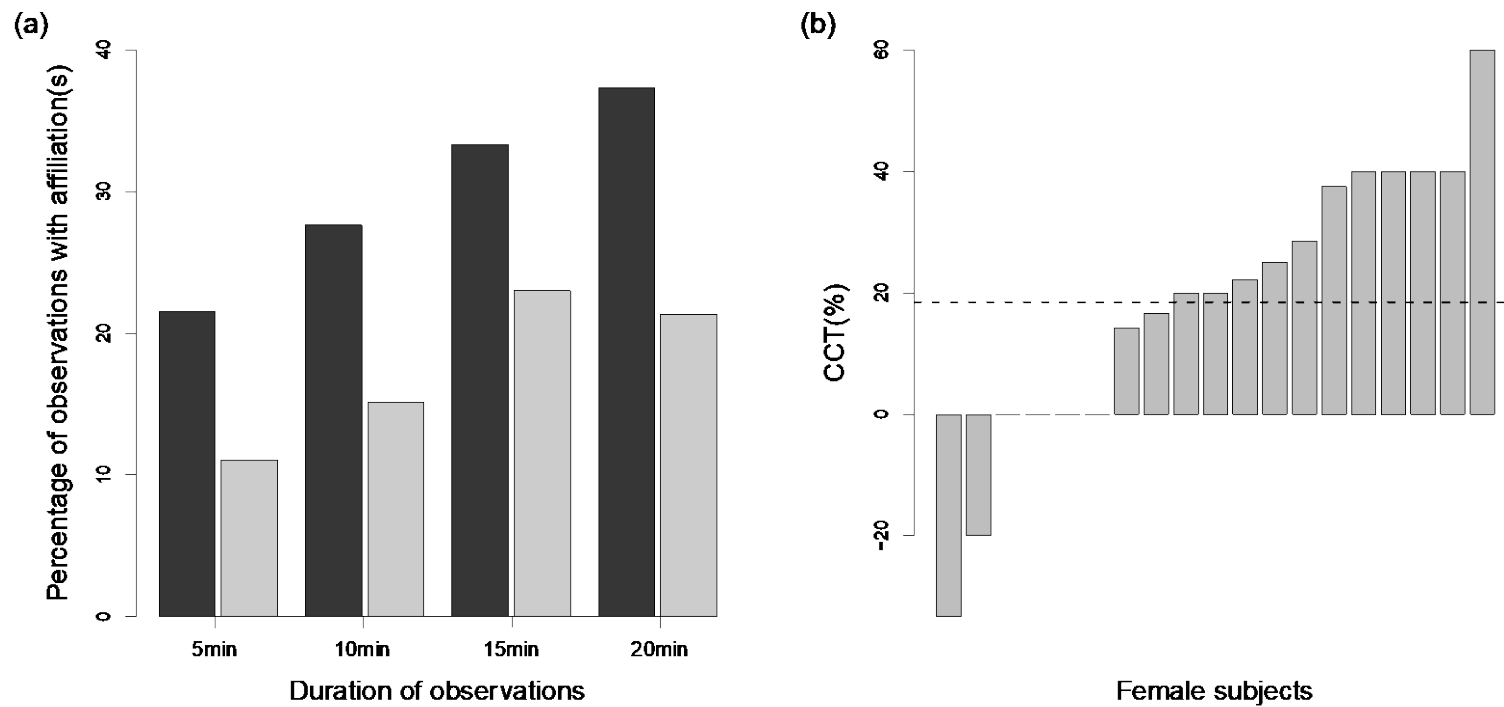
Response variable	Fixed factor	Levels	Estimate	SE	95% confidence interval	LRT	P-value
Number of affiliations exchanged between male-female dyads <sup>a</sup>	Type of observation	PC friend (ref: baseline friend)	1.00	0.27	<b>[0.43 ; 1.42]</b>	31.67	<b>0.002</b>
		PC non-friend (ref: baseline non-friend)	0.53	0.72	[-10.71 ; 1.54]		
		PC friend (ref: PC non-friend)	2.62	0.86	<b>[1.21 ; 12.86]</b>		
		Baseline friend (ref: baseline non-friend)	2.15	0.44	<b>[1.24 ; 3.15]</b>		
	Reproductive state <sup>b</sup>	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 <sup>a</sup> The duration (min) of observation of each dyad was fitted as an offset fixed factor, to control for variation in observation time across dyads.

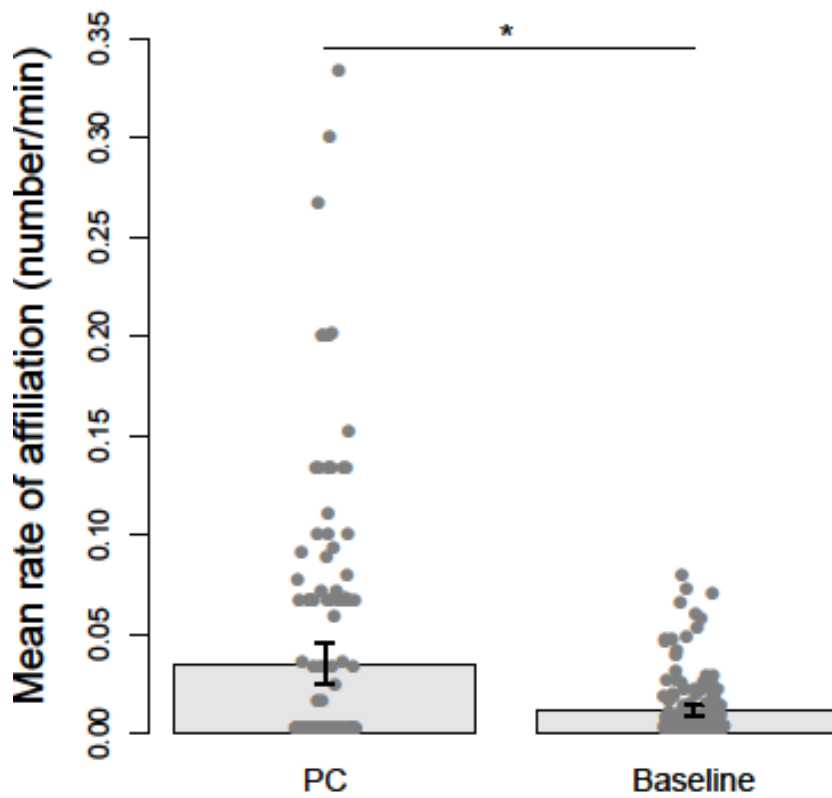
722 <sup>b</sup> Reference category: lactating

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.



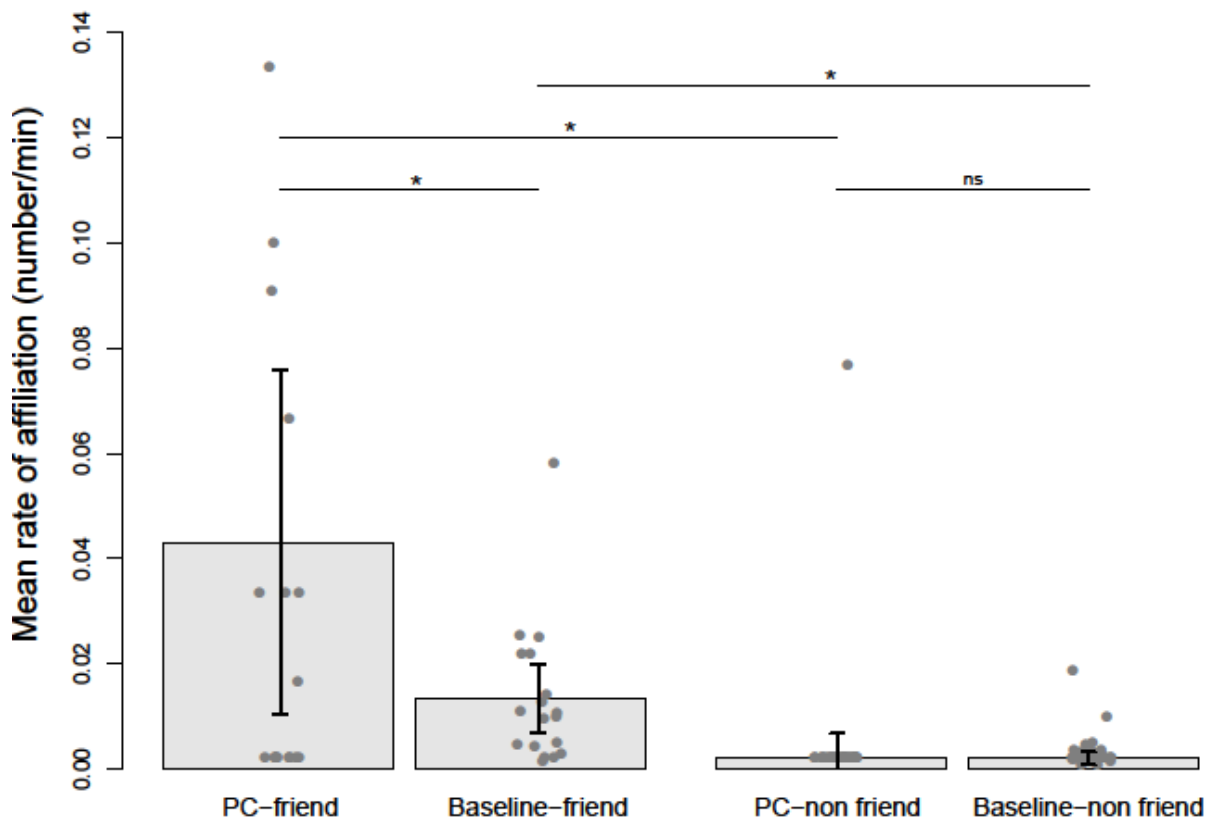
727

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