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

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23 Keywords: Reconciliation, post-conflict affiliation, aggression, male-female association,

24 chacma baboons

#### 26 INTRODUCTION

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

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

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

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

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

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

same period. Nonetheless, researchers have advocated for the use of baseline levels of
interaction over traditional PC-MC approaches for a variety of reasons (e.g., Aureli et al., 1989;
Cords, 1993; Kappeler & van Schaik, 1992; Veenema et al., 1994). Although these methods
typically yield complementary findings (Kappeler & van Schaik, 1992), they occasionally lead
to discrepant results (e.g., Kappeler 1993). At present, a combination of approaches is therefore
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 methodological approach in our study system, a population of wild chacma baboons. To date 108 109 the vast majority of research on reconciliation has been conducted on captive primate groups (reviewed in Arnold et al. 2010), although studies are increasingly carried out in naturalistic 110 settings. This bias likely stems in part from practical limitations associated with collecting 111 proper PC-MC data in non-captive/controlled settings. It may also reflect putative analytical 112 constraints on long-term data that were not explicitly collected to study reconciliation, wherein 113 appropriate post-conflict data are available but baseline/control observations must be 114 determined a posteriori. Since the time of reconciliation's first discovery in the late 1970s, 115 rather strict adherence to the conventional PC-MC protocol has persisted despite the emergence 116 of a host of sophisticated quantitative tools and techniques. Among them are multivariate 117 analyses that can simultaneously account for independent determinants of variation in 118 reconciliation rates across different dyads. These emphasize the utility of updating traditional 119 120 approaches with state-of-the-art statistical procedures. We thus aim to propose a practical method that will facilitate new research directions not only in our long-term field site, but for 121 similar longitudinal, individual-based, studies of wild animal populations. 122

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

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

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

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

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

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### 157 MATERIAL & METHODS

#### 158 (a) Data collection

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

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

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

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### 195 (b) Identification of heterosexual friendships

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

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

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### 227 (c) Statistical Analyses

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

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

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

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

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

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

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

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

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### 283 Method using baseline rate of affiliation

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

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

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

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

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

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

347

### 348 **RESULTS**

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

## 350 *Post-conflict matched-control method*

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

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### 367 Method using baseline rate of affiliation

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

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

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

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

388

#### 389 **DISCUSSION**

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

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

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

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

both victims/aggressors and restore tolerance in those dyads—is an area that warrants furtherinvestigation.

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

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

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

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

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

502

#### 503 CONCLUSION

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

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

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

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

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

<sup>d</sup> Number of MC observations including an affiliation between former opponents.

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

#### 

	Rate of Rate of affiliation in affiliation in		No.	No.					
	$PC \pm SD^a$	baseline $\pm SD^b$	dyads	aggression <sup>c</sup>	Estimate	SE	interval	LRT	P-value
5min	$0.04 \pm 0.09$	0.01±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±0.02	136	191	1.11	0.09	[0.90 ; 1.27]	123.30	0.002

<sup>a</sup> The rate of affiliation in PC is calculated as the total number of affinitive interactions observed in PC divided by the total time of PC observations <sup>b</sup> The baseline rate of affiliation is calculated as the total number of affinitive interactions observed in baseline divided by the total time of baseline observations

<sup>c</sup> Total number of PC observations.

**Table 3. Patterns of reconciliation between pregnant/lactating females and males.** PC: post-conflict observations. Parameters and tests are 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, and 73 events of aggression (mean $\pm$ SD aggression observed per dyad: 1.4 $\pm$ 0.8). Females have on average 20.0 $\pm$ 11.3 min of observation in PC and 867.0 $\pm$ 284.9 min of observation in baseline. The GLMM was performed controlling for male, female and dyad identity. P-values are used to test for the significance of each variable, while the 95% confidence intervals are used to test for the significance of each level of the qualitative variables. The confidence intervals and p-values of statistically significant results are highlighted in bold.

719

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

<sup>720</sup> 

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.

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

Figure 1. Patterns of reconciliation between males and females, as assessed by the post-conflict matched-control method. (a) Percentage of
observations containing at least one affiliation in the post-conflict (black bar) and matched-control (grey bar) sample. (b) Corrected conciliatory
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
CCT across females is indicated by the dotted line.





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



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

