



**HAL**  
open science

## The submissive pattern of postconflict affiliation in asymmetric relationships: a test in male and sexually coerced female baboons.

Alice Baniel, Christine Webb, Guy Cowlshaw, Elise Huchard

### ► To cite this version:

Alice Baniel, Christine Webb, Guy Cowlshaw, Elise Huchard. The submissive pattern of postconflict affiliation in asymmetric relationships: a test in male and sexually coerced female baboons.. *Animal Behaviour*, 2021, 175, pp.87-97. 10.1016/j.anbehav.2021.02.014 . hal-03192677

**HAL Id: hal-03192677**

**<https://hal.science/hal-03192677v1>**

Submitted on 10 Jun 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Published in final edited form as:

2 *Animal Behaviour* (2021), 175: 87-97. <https://doi.org/10.1016/j.anbehav.2021.02.014>

3

4 **The submissive pattern of postconflict affiliation in asymmetric**  
5 **relationships: a test in male and sexually coerced female baboons**

6

7 **Alice Baniel<sup>1,2,6,\*</sup>, Christine E. Webb<sup>3,6</sup>, Guy Cowlshaw<sup>4</sup>, Elise Huchard<sup>5,7</sup>**

8

9 <sup>1</sup> Institute for Advanced Study in Toulouse, Toulouse, France.

10 <sup>2</sup> Department of Anthropology, Stony Brook University, Stony Brook, NY, U.S.A.

11 <sup>3</sup> Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, U.S.A.

12 <sup>4</sup> Institute of Zoology, Zoological Society of London, London, U.K.

13 <sup>5</sup> Institute of Evolutionary Biology of Montpellier (ISEM), UMR 5554, Université de  
14 Montpellier, CNRS, IRD, EPHE, Montpellier, France

15 <sup>6</sup> These authors contributed equally

16 **\*Corresponding author.**

17 E-mail: [alice.baniel@gmail.com](mailto:alice.baniel@gmail.com)

18 **ABSTRACT**

19 Reconciliation, or postconflict (PC) affiliation between former opponents, is a widespread  
20 conflict management strategy in animal societies, so-named for its relationship–repair  
21 function. However, another possibility is that PC affiliation reflects a submissive response of  
22 victims towards aggressors to limit conflict escalation when the power imbalance between the  
23 opponents is large. Here we investigated this hypothesis in a highly asymmetric relationship  
24 context: heterosexual wild chacma baboon, *Papio ursinus*, dyads involving sexually receptive  
25 females, where sexual coercion by males is common. We found several lines of support for  
26 the submissive hypothesis in the context of sexual coercion. First, rates of sexual and  
27 nonsexual PC affiliative interactions in these dyads exhibited significant and comparable  
28 increases compared to baseline conditions (ca. three-fold). Second, the baseline strength of  
29 the heterosexual social bond (outside of an aggressive context) did not predict the likelihood  
30 of sexual and nonsexual PC affiliation. Third, mate-guarded females, which could not escape  
31 the proximity of their aggressor (and faced high risks of renewed aggression), exhibited the  
32 most PC affiliation with males. Finally, most PC affiliation sequences contained at least one  
33 sexual act, and the first sexual affiliative act was primarily initiated by females via  
34 presenting. This suggests that female victims affiliate in a submissive way by displaying  
35 sexual compliance to aggressive males. Nevertheless, we cannot exclude the co-occurrence of  
36 ‘true’ reconciliation: a quarter of PC affiliations between males and receptive females were  
37 exclusively nonsexual, and the first general affiliative act was equally initiated by males and  
38 females. Overall, our results suggest a mixed PC affiliation strategy in which submission may  
39 play an important role in highly asymmetric relationships and indicate the function of PC  
40 affiliation may vary from submission to reconciliation depending on the species, dyads,  
41 individuals and conflicts under consideration. Future research on PC interactions would  
42 usefully consider this full spectrum.

43 **KEYWORDS**

44 aggression, chacma baboon, male–female association, reconciliation, sexual coercion

45

46 **INTRODUCTION**

47 Two animals are said to have reconciled if, soon after an aggressive interaction between  
48 them, they engage in friendly contact (de Waal & van Roosmalen, 1979). Several  
49 nonexclusive hypotheses have been proposed to predict the distribution of reconciliation  
50 across opponent dyads (Arnold, Fraser, & Aureli, 2010), with proximate or ultimate  
51 explanations emphasizing its conciliatory nature (see Table 1). Friendly reunions following  
52 conflict may serve to repair mutually beneficial (i.e. fitness-enhancing) relationships (the  
53 ‘valuable relationship’ hypothesis: Kappeler and van Schaik 1992; de Waal and Aureli 1997),  
54 attenuate uncertainty or anxiety (the ‘uncertainty reduction’ hypothesis: Aureli, 1997; Aureli  
55 & van Schaik, 1991), or communicate peaceful intentions between former opponents (the  
56 ‘benign intent’ hypothesis: Silk 1996). The ‘integrated’ hypothesis combines the uncertainty  
57 reduction and valuable relationship hypotheses by proposing that disruptions to valuable  
58 bonds are particularly stressful for opponents, and therefore warrant stronger resolution  
59 attempts (Aureli, 1997). Although they occasionally generate different predictions, these  
60 hypotheses are generally treated as complementary, with expressions of benign intent serving  
61 to reduce uncertainty about the conflict and thereby restore valuable relationships (Aureli,  
62 Cords, & van Schaik, 2002; Cords & Aureli, 1996; Schaffner & Aureli, 2004). Tests of these  
63 hypotheses have commonly focused on primates, where the frequency and patterning of  
64 reconciliation vary according to the nature of the social systems and relationships under study  
65 (Arnold et al., 2010).

66 Theory and research on reconciliation have previously emphasized variation in  
67 postconflict (PC) behaviour across different levels of dominance asymmetry, with more

68 egalitarian species showing higher conciliatory tendencies than despotic ones (Thierry, 2000;  
69 Thierry et al., 2008). However, power imbalances have largely been considered at the level of  
70 the species or social organization rather than the dyadic level. In more hierarchical  
71 relationship contexts, two opponents may not ascribe equivalent fitness value to each other,  
72 and/or may not share equally in their uncertainty or anxiety about renewed aggression. These  
73 asymmetries highlight how the form, motive and function of PC behaviour may vary even  
74 within a dyad in ways not explicitly captured by existing reconciliation frameworks.  
75 Reflecting the full spectrum and complexity of primate social relationships, PC interactions  
76 can either be more reciprocal and conciliatory or hierarchical and coercive in nature.

77         One intriguing possibility is that, in the context of highly asymmetrical relationships,  
78 PC affiliation represents a submissive response by victims towards their recent aggressors  
79 (the ‘submissive’ hypothesis; de Waal, 1986; Kutsukake & Clutton-Brock, 2006). In other  
80 words, rather than expressing a motivation for peaceful and friendly interactions, victims of  
81 aggression may affiliate out of fear in order to accede to aggressors’ demands by displaying  
82 submission/compliance in an attempt to limit conflict escalation and injury. Several  
83 theoretical and experimental studies have emphasized the ubiquity of hidden threats and  
84 punishment in animal societies, and their role in enforcing cooperation across a range of  
85 contexts, particularly when the power imbalance between the opponents is pronounced (Cant,  
86 2010; Clutton-Brock & Parker, 1995a). We propose here that prolonged intimidation and  
87 repeated aggression in a given dyad with high power asymmetry may yield PC interactions  
88 that are more characteristic of a submissive rather than conciliatory scenario, even if it takes  
89 the form of a typical affiliation (e.g. grooming).

90         At the ultimate level, the submissive hypothesis and the uncertainty reduction  
91 hypothesis may generate similar predictions, i.e. PC affiliation functions to limit renewed  
92 aggression and conflict escalation (Table 1). However, these hypotheses differ in at least

93 three important ways. First, at the proximate level, the underlying motivations for PC  
94 affiliation differ. In the uncertainty reduction hypothesis, both victims and aggressors affiliate  
95 to reduce physiological stress and anxiety about future interactions (the distress may come  
96 from the damage to a valuable relationship, or because opponents live in proximity and may  
97 incur future costs, for example of increased vigilance or decreased tolerance, if conflicts  
98 persist; Aureli et al., 2002). In contrast, the submissive hypothesis posits that victims submit  
99 to comply with aggressors out of fear, often conferring immediate social/sexual benefits upon  
100 aggressors. Second, the submissive hypothesis posits that victims affiliate to comply with  
101 their aggressor's demands, rather than to preserve a valuable relationship (as clarified by the  
102 integrated hypothesis). Consequently, the asymmetry of power between opponents rather than  
103 the strength of their social bond (relationship value) should predict the occurrence of PC  
104 affiliation. Third, the submissive hypothesis predicts that victims would be more likely to  
105 initiate PC affiliation, in contrast to the uncertainty reduction hypothesis, in which such  
106 distinctions are neither categorically made nor found (Arnold et al., 2010).

107 PC interactions among heterosexual pairs have rarely been studied in wild  
108 promiscuous primates but represent an ideal context in which to explore this submissive  
109 framework because of pronounced sexual dimorphism and power asymmetries between  
110 males and females. Recent work has highlighted a previously underappreciated density and  
111 complexity of primate heterosexual relationships (Archie, Tung, Clark, Altmann, & Alberts,  
112 2014; Fürtbauer, Heistermann, Schülke, & Ostner, 2014; Machanda, Gilby, & Wrangham,  
113 2013; Reddy & Mitani, 2020). On the one hand, males and females can form enduring bonds,  
114 which enhance individual survival and reproductive success (Archie et al., 2014; Campos et  
115 al., 2020; Palombit, 2000). On the other hand, heterosexual relationships can be violent since  
116 males commonly attack sexually receptive females to achieve mating benefits, either  
117 immediately (through forced copulation or sexual harassment) or subsequently (through

118 intimidation or punishment; Clutton-Brock & Parker, 1995b; Muller, Kahlenberg, Emery  
119 Thompson, & Wrangham, 2007; Smuts & Smuts, 1993). Sexual coercion usually targets the  
120 most fertile females and can be costly in terms of stress and injury for the victims (Baniel,  
121 Cowlshaw, & Huchard, 2017; Colmenares, Polo, & Herna, 2014; Kitchen et al., 2009;  
122 Muller et al., 2007; Swedell et al., 2014). Females could thus benefit from evolving  
123 behavioural strategies to decrease the chances of escalated or renewed aggression from  
124 coercive males.

125         In the handful of studies that have investigated male–female PC affiliation, sexual  
126 behaviours have rarely been systematically analysed. Generally, whereas noncopulatory  
127 sexual behaviours (e.g. presenting and mounting) feature commonly in studies of  
128 reconciliation, copulations have been omitted as a form of PC affiliation for a number of  
129 potential reasons (e.g. they do not occur among same-sex dyads or they do occur but are not  
130 interpreted as affiliative acts). When sociosexual contacts are incorporated, they are often  
131 aggregated with other affiliative contacts, precluding formal tests between reconciliation and  
132 sexual coercion (but see Call et al. 1999). To our knowledge, bonobos, *Pan paniscus*, are the  
133 only species for which copulations and nonconceptive sexual behaviours are thought to play a  
134 key role in conciliatory reunions (Clay & de Waal, 2014; Palagi, Paoli, & Tarli, 2004). In less  
135 tolerant animal societies where aggression is more severe and asymmetric, it is possible that  
136 PC affiliations traditionally interpreted as conciliatory reunions in some cases represent  
137 submissive responses to sexual (or other forms of) coercion. In particular, sexual harassment,  
138 defined as repeated and costly aggressive mating attempts by males that induce females to  
139 mate (Clutton-Brock & Parker, 1995b), is operationally identified by increases in males’  
140 chances of mating with their victims immediately following aggression (compared to baseline  
141 chances). Thus, the conceptual frameworks supporting reconciliation and sexual harassment  
142 make overlapping predictions regarding increased rates of affiliation following conflicts,

143 provided sexual behaviours count as affiliative interactions. Yet the sexual coercion and  
144 reconciliation literatures rarely reference one another.

145         In this study, we investigated the form and function of PC affiliative interactions  
146 among males and sexually receptive (i.e. swollen) females in wild chacma baboons, *Papio*  
147 *ursinus*. Chacma baboons live in female-bonded societies, where immigrant males fight to  
148 achieve dominance and monopolize swollen females through long (i.e. several consecutive  
149 days) episodes of mate guarding around ovulation (Bulger, 1993; Weingrill, Lycett, Barrett,  
150 Hill, & Henzi, 2003). This mate guarding is coercive in the sense that females cannot escape  
151 male proximity, and males regularly herd their consort females away from rivals (Cheney &  
152 Seyfarth, 1977; Kitchen, Cheney, & Seyfarth, 2005; Kitchen et al., 2009). While  
153 reconciliation has been documented in this species, the focus has predominantly been on  
154 female–female dyads (Cheney, Seyfarth, & Silk, 1995; Silk, Cheney, & Seyfarth, 1996;  
155 Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007). Only one study has focused on PC  
156 affiliation among heterosexual chacma baboon dyads, which found that reconciliation  
157 commonly occurs between males and pregnant/lactating females when they are involved in a  
158 ‘friendship’, a long-term heterosexual social bond formed around an infant (Webb, Baniel,  
159 Cowlshaw, & Huchard, 2019). Little is known about patterns of PC affiliation between  
160 males and swollen females. Male aggression towards swollen females is common in this  
161 species, inflicting frequent injuries to females (Baniel et al., 2017; Kitchen et al., 2009), and  
162 functions as a form of sexual intimidation, where repeated aggression throughout the cycle  
163 increases the aggressor’s chances of consorting with the female around ovulation (Baniel et  
164 al., 2017). There is, however, no evidence for sexual harassment, where males harass females  
165 until they accept matings, as there is no immediate increase in the rate of mating following  
166 male aggression (Baniel et al., 2017). On a spectrum ranging from submission to  
167 reconciliation, affiliation following conflicts between males and swollen females in this



168 coercive context may fall closer to the former. In this case, female victims would adopt a  
169 compliant strategy to reduce the costs of conflict escalation (e.g. injury), while male  
170 aggressors enact a coercive strategy to secure immediate or future mating opportunities  
171 (Table 1).

172         Here, we tested whether the pattern of PC affiliation between heterosexual pairs  
173 involving sexually receptive females could be explained by the submission hypothesis in the  
174 context of sexual coercion, via the following four predictions. First, we predicted that  
175 increases in PC affiliation between males and swollen females would involve both sexual and  
176 nonsexual affiliation (Prediction 1, P1), as intimidated females may use any behavioural  
177 strategy at their disposal, for example sexual solicitations or grooming, to appease coercive  
178 males. Second, we predicted that the rate of PC affiliation between a male and swollen  
179 female would not reflect the strength of their social bond in baseline conditions (i.e. outside  
180 an aggressive context; P2). Third, we predicted that the rate of PC affiliation would increase  
181 in more coercive contexts; namely, mate-guarded females should display a higher rate of PC  
182 affiliation than unguarded females, because they cannot escape the spatial proximity of their  
183 aggressor and thus have a higher incentive to de-escalate conflicts with him (P3). Lastly, we  
184 predicted asymmetrical patterns in who initiates PC affiliation, particularly when it comes to  
185 sexual affiliations, where females should be mostly responsible for initiating the first  
186 affiliative act (P4a) and/or the first sexual act of the PC affiliation sequence (P4b) in order to  
187 display submission and propose positive sociosexual contacts to coercive males following  
188 aggression.

189         This predictive framework differentiates itself from that generated by previous  
190 hypotheses to explain pos-conflict affiliation, including both the sexual harassment  
191 hypothesis, and the integrated hypothesis. According to the former, if patterns of affiliation  
192 solely reflected sexual harassment, we would expect no support for P1 (rather, we would

193 expect only sexual PC affiliation to increase) or P4 (we would expect males rather than  
194 females to initiate copulations). According to the latter, if patterns of affiliation solely  
195 reflected attempt to reduce anxiety and repair a valuable bond, we would expect no support  
196 for P2 or P3 (because we would expect baseline affiliation rather than the power asymmetry  
197 between opponents to predict PC affiliation).

198

## 199 **METHODS**

### 200 **Data Collection**

201 We studied two habituated groups of wild chacma baboons living at Tsaobis Nature Park, a  
202 semiarid environment in Namibia (Cowlshaw, 1997) over four field seasons (2005, 2006,  
203 2013 and 2014) of variable length (5–9 months per year). Groups contained 3–11 adult males  
204 and 9–19 adult females according to the period of study. Dominance ranks of adult males and  
205 females were established using both ad libitum and focal observations of dyadic agonistic  
206 interactions (see Appendix 1)

207         The reproductive state of each adult female was monitored daily and categorized as  
208 pregnant, lactating, cycling swollen (i.e. sexually receptive with a perineal swelling) and  
209 cycling nonswollen (i.e. between two swelling phases). Mate-guarding episodes, defined as  
210 periods when swollen females were constantly followed by a male that mated exclusively  
211 with them and prevented others from doing so (Alberts, Altmann, & Wilson, 1996), were  
212 monitored ad libitum daily, and confirmed or updated accordingly for each focal observation.  
213 In the following analyses, we focused only on cycling swollen females and their interactions  
214 with adult males.

215         Observers followed groups on foot daily from dawn to dusk, conducting 1 h focal  
216 observations on all adult females and males, spread equally across the day. In total, we  
217 collected 1418 focal observations on 40 swollen females (mean±SD: 35.5±32.2 observations

218 per individual) and 524 observations on 25 males ( $21.0 \pm 8.8$ ; male focal observations were  
219 only collected in 2013–2014). During observations, we continuously recorded all occurrences  
220 of male–female agonistic and affiliative interactions involving the focal individual, including  
221 the partner’s identity and the direction of the interaction. Agonistic interactions comprised  
222 attacks (any aggressive physical contact), chases and physical threats (including staring, head  
223 bobbing and ground sweeping while oriented towards the targeted individual) and approach–  
224 avoid interactions (supplants, displacements). For the analysis of PC affiliation, we only used  
225 attacks, chases and physical threats because more subtle agonistic interactions such as  
226 displacements, supplants or vocal threats are less likely to be stressful for the victim. As  
227 expected on the basis of pronounced sexual dimorphism, 98% of aggression between males  
228 and swollen females (i.e. 92 of 94 observed conflicts) were directed from males to females.  
229 Affiliative interactions included grunts, positive facial expressions (come-here faces, lip-  
230 smacks, sniff-mouths), positive physical contacts (touching, embracing, grooming, sniffing or  
231 touching perineum, mounting, grasping pelvis) and sexual behaviour (presents, copulations).  
232 Note that swollen females in this species invite males to copulate by presenting, which can  
233 potentially directly lead to sex. A female’s presenting behaviour can be either followed by a  
234 copulation (in which case, observers only noted the copulation and indicated that the  
235 copulatory act was female initiated) or not followed by a copulation when the male ignores  
236 the female’s initiative (in which case, observers only recorded the presenting bout). For each  
237 copulation, we thus recorded whether it was initiated by the female (via presenting) or by the  
238 male (by approaching and usually grabbing the female’s hindquarters).

239

## 240 **Statistical Analyses**

### 241 ***Rate of sexual and nonsexual PC affiliation***

242 We first tested whether swollen females and males exhibit higher rates of affiliation  
243 following male aggression (compared to baseline conditions), and whether any increase  
244 detected in PC affiliation is primarily attributable to increases in sexual versus nonsexual  
245 behaviours (P1). Using the collected focal observations of males and swollen females, and  
246 following a statistical methodology previously validated in our study system (Webb et al.,  
247 2019), we established the rate of (1) sexual affiliation (presenting and copulations) and (2)  
248 nonsexual affiliation (e.g. grunts, grooming, etc) between a given heterosexual dyad  
249 immediately after a conflict (i.e. the PC sexual and nonsexual affiliation rate) versus in the  
250 absence of an immediate conflict (i.e. the baseline sexual and nonsexual affiliation rate).  
251 Specifically, for each heterosexual dyad that exchanged at least one act of aggression, we  
252 first identified all focal observations that were conducted on both individuals in a given year  
253 and in which the female was swollen. Then, we split these observations into two categories.

254 First, the PC sample, in which we pooled all 15 min observations following a conflict  
255 between the same dyad together (i.e. dyads had between one to five conflicts, each of which  
256 generated a 15 min observation period, so we pooled the corresponding 15–75 min of PC  
257 observation to calculate the rate of PC affiliation of a given dyad). We chose a duration of 15  
258 min following each conflict because our validation study identified this time window as the  
259 best trade-off between the number of available PC observations (which decreases as time  
260 period increases) and the strength of the reconciliation signal (which increases as time period  
261 increases; Webb et al., 2019). Incomplete PC observations (e.g. due to the focal individual  
262 going out of sight or the occurrence of another bout of aggression shortly after the first one)  
263 were retained only if they lasted for at least 9 min without interruption (mean $\pm$ SD=12.1 $\pm$ 1.6  
264 min,  $N=15$  incomplete PC of 94 total PC observations). This 9 min threshold was chosen  
265 because the mean latency between aggression and the first affiliative act was 4.5 $\pm$ 4.2 min  
266 (calculated over 37 occurrences of PC affiliation in complete PC observations). We thus

267 considered that 9 min would be enough time to capture, in most cases, the potential  
268 occurrence of PC affiliation acts.

269 Second, for the baseline sample, we pooled the rest of the focal observations of the  
270 dyad. To establish these baseline rates, we excluded each 15 min period following a conflict  
271 (i.e. the PC samples), as well as each 15 min period at the start of the focal observation or  
272 following its resumption after the focal individual briefly went out of sight (if an aggression  
273 occurred between the two members of the dyad when they were not visible). Third, we  
274 tabulated the number of times that the two individuals affiliated sexually or nonsexually in  
275 the PC and baseline samples, respectively, as well as the total observation time of the  
276 corresponding (i.e. PC or baseline) sample.

277 We compared the strength of the PC affiliation signal between males and swollen  
278 females when considering only sexual affiliations versus only nonsexual affiliations. We thus  
279 ran two negative binomial generalized linear mixed models (GLMMs) using the total number  
280 of affiliations exchanged between each male and swollen female dyad as the response  
281 variable and including (1) only sexual affiliations or (2) only nonsexual affiliations in the  
282 count. Fixed effects comprised the type of observation (PC versus baseline samples) and the  
283 dominance ranks of the female and male. The total observation time of the corresponding  
284 sample (PC or baseline) was log transformed and included as an offset variable. Random  
285 effects comprised the identity of the female and male.

286

### 287 *Determinants of the occurrence of PC affiliation*

288 We then investigated the determinants of the presence (versus absence) of PC affiliation in  
289 the subsequent 15 min following aggression ( $N=94$  PC observations), namely with respect to  
290 the strength of the affiliative relationship of the dyad in baseline conditions (i.e. outside an  
291 aggressive context, P2) and female mate-guarding status (P3). We ran a binomial GLMM

292 using the occurrence of affiliation following an aggressive event (yes/no) as the response  
293 variable. Fixed effects comprised the mate-guarding status of the swollen female (unguarded  
294 versus mate-guarded by the aggressor), the dyad's baseline affiliation rate (calculated via the  
295 occurrence of sexual and nonsexual behaviours in swollen periods), female rank, male rank  
296 and the type of aggression (chase, attack, threat). For both models, random effects comprised  
297 the identities of the female and male. As supplementary analysis, we also calculated the  
298 dyad's baseline affiliation rate using focal observations where the female was nonswollen  
299 only.

300

### 301 *Pattern of initiation of PC affiliation*

302 We tested for asymmetry in the pattern of initiation of the first PC affiliative act (P4a) and of  
303 the first sexual act of a PC sequence (P4b) between male and female opponents using two-  
304 tailed exact binomial tests.

305

306 All GLMMs were run using the glmer function of the lme4 package (Bates, Maechler,  
307 Bolker, & Walker, 2014) in R version 3.5.2 (R Core Team, 2018). The significance of the  
308 fixed factors was tested using a likelihood ratio test, LRT (assuming an asymptotic chi-square  
309 distribution of the test statistic) via the drop1 function. We further computed the 95%  
310 parametric bootstrap confidence intervals of fixed factors (using confint.merMod) and  
311 checked that they did not cross zero. To validate models, we examined the distribution of  
312 residuals and confirmed the absence of overdispersion by using the DHARMA package  
313 (Hartig, 2018). Sample size is indicated for each model in the relevant output table.

314

### 315 *Ethical Note*

316 This study was strictly observational and relied on behavioural data collected noninvasively  
317 on animals well habituated to human observers. Our research procedures were evaluated and  
318 approved by the Ethics Committee of the Zoological Society of London and the Ministry of  
319 Environment and Tourism (MET), Namibia, and adhered to the ASAB/ABS Guidelines for  
320 the Treatment of Animals in Behavioural Research and Teaching. Our research was  
321 conducted under MET permit numbers 886/2005, 1039/2006, 1786/2013 and 1892/2014.

322

## 323 **RESULTS**

### 324 *Rate of sexual and nonsexual PC affiliation*

325 We observed 94 incidents of male aggression towards swollen females. Of these, 73 had a  
326 documented context (as inferred by the observer): 42% were unprovoked (no apparent reason  
327 for the male to attack the female), 25% were apparently triggered by the female leaving the  
328 male's spatial proximity and may represent herding, 15% involved redirected aggression to  
329 the female following aggression received from a rival male, 10% occurred during feeding  
330 bouts and 7% occurred during intragroup male display (wahoo bouts) or intergroup  
331 interactions. Of these 94 observed agonistic interactions, 43 (46%) were followed by at least  
332 one affiliative act between the male and swollen female in the following 15 min. The latency  
333 before the first affiliative act was  $4.7 \pm 4.2$  min on average (range 0–13 min). As expected  
334 under P1, the observed rates of affiliation between males and swollen females following  
335 conflicts were significantly higher (about three times more) than in baseline samples when  
336 considering exclusively sexual behaviours (mean rate of affiliation  $\pm$ SD in PC:  $0.033 \pm 0.054$   
337 events/min; in baseline:  $0.010 \pm 0.011$ ; Table 2, Fig. 1a). The same was true when considering  
338 exclusively nonsexual behaviours (mean rate of affiliation  $\pm$ SD in PC:  $0.044 \pm 0.069$   
339 events/min; in baseline:  $0.013 \pm 0.017$ ; Table 2, Fig. 1a). Females were more likely to exhibit

340 sexual affiliations (but not more nonsexual affiliations) with high-ranking males in both PC  
341 and baseline conditions.

342

### 343 *Determinants of the occurrence of PC affiliation*

344 Heterosexual dyads with strong affiliative relationships in baseline conditions were not more  
345 likely to display affiliation following aggression (Table 3, Appendix 2, Table A1), consistent  
346 with P2. Nevertheless, there was a high uncertainty around this effect, with a lot of variation  
347 across dyads (Appendix 2, Fig. A1). According to P3, higher rates of PC affiliation are  
348 expected when females are confined in close proximity to mate-guarding males. The need for  
349 PC affiliation under these circumstances is highlighted by the finding that 38 of 41 recorded  
350 incidences of male aggression towards mate-guarded females came directly from their  
351 consort male. As predicted, males and swollen females involved in a mate-guarding  
352 consortship were more likely to exhibit PC affiliation than when they were not involved in a  
353 consortship (Table 3, Fig. 1b).

354

### 355 *Pattern of initiation of PC affiliation*

356 When PC affiliation occurred ( $N=43$  cases), 32 (74%) cases involved at least one sexual  
357 behaviour and 11 (26%) involved exclusively nonsexual behaviours in the 15 min sequence  
358 following aggression. Among these 43 PC sequences, the first PC affiliative act was initiated  
359 equally by males and females, contrary to P4a: males initiated 23 PC affiliations and females  
360 initiated 20 PC affiliations (two-tailed exact binomial test:  $P=0.761$ ; 95% confidence interval:  
361 0.31–0.62; see Fig. 2a and Appendix 2, Table A2 for behavioural details on the first  
362 affiliative act). However, when focusing on those 30 PC affiliations that contained at least  
363 one sexual act (two sexual interactions had unknown initiators), the first sexual behaviour  
364 was initiated 21 times by the female, mostly via presenting, and nine times by the male, in



365 accordance with P4b (two-tailed exact binomial test:  $P=0.043$ ; 95% confidence interval:  
366 0.51–0.85; Appendix 2, Table A2, Fig. 2b). In the 11 PC affiliations that remained  
367 exclusively nonsexual, three were initiated by females and eight by males.

368

## 369 **DISCUSSION**

370 The present study reveals that in highly asymmetrical relationship context, like those  
371 characterizing heterosexual dyads in chacma baboons, PC affiliation may frequently  
372 correspond to a submissive response from victims to a powerful opponent, rather than  
373 reflecting a conciliatory pattern. The evidence for submission by sexually receptive females  
374 to aggressive males in chacma baboons in response to sexual coercion is fourfold. First, the  
375 frequency of sexual interactions increased three-fold following aggression, just like the  
376 frequency of nonsexual affiliation (compared to baseline conditions). Second, the baseline  
377 strength of the heterosexual social bond (i.e. the ‘value’ of their relationship) did not predict  
378 the likelihood of PC affiliation. Third, dyads involving males and mate-guarded females, who  
379 faced high risks of renewed aggression due to the permanent proximity of their aggressor,  
380 exhibited the highest rates of PC affiliation. Finally, most PC affiliation sequences (74%)  
381 contained at least one sexual act, and the first sexual affiliative act was primarily initiated by  
382 females via presenting. This suggests that receptive female victims often affiliate in a  
383 submissive way by displaying sexual compliance (i.e. proposing matings) to coercive males  
384 to limit the chances of escalated aggression.

385

### 386 ***PC Affiliation Reflects Female Submission to Male Intimidation***

387 The observed pattern of PC affiliation between male and female baboons does not reflect a  
388 strict sexual harassment strategy, where males attack or persistently run after females until  
389 they accept mating, as reported in some ungulates (Clutton-Brock & Parker, 1995b) and

390 orangutans (Fox, 2002; Knott, 2009). Indeed, male baboons seldom initiated copulations  
391 following aggression (male-initiated copulations only represented 18% of the first affiliative  
392 act and 30% of the first sexual act; see Appendix 2, Table A2). Instead, females were mostly  
393 responsible for initiating PC sexual behaviour by presenting to the male. Furthermore, the  
394 observed increases in rates of nonsexual affiliation following conflicts were not expected  
395 under the sexual harassment hypothesis, which exclusively focuses on sexual behaviour.

396         The fact that female baboons are primarily responsible for initiating the first sexual  
397 act following aggression is more compatible with a scenario of long-term sexual intimidation,  
398 where females would express sexual compliance towards males to appease them and limit  
399 escalated aggression and future injuries. Males, on the other hand, may rarely pursue  
400 immediate mating opportunities following aggression (and female presenting) to avoid  
401 unnecessary matings, especially when the female is not in her ovulatory window (which can  
402 be costly, e.g. sperm depletion; Gesquiere, Wango, Alberts, & Altmann, 2007; Moscovice et  
403 al., 2010; Weingrill, Lycett, & Henzi, 2000). Instead, they seem to use repeated aggressive  
404 and affiliative behaviour to optimize their control of female spatial behaviour. In our  
405 population, 42% of male attacks towards swollen females are unprovoked, sudden and  
406 probably unpredictable. Such randomly timed attacks provide an effective means for the  
407 aggressor to generate continuous anxiety, vigilance and chronic stress in his victims (Silk,  
408 2002). In line with this, half of our observed PC affiliation events happened in the context of  
409 mate guarding, where females have no choice but to stay in the proximity of their aggressor  
410 and are thus likely to face renewed aggression. Mate-guarding episodes are particularly long  
411 in chacma baboons (between 0.5 and 32 days, mean=9 days), and can last several consecutive  
412 cycles (Baniel, Cowlshaw, & Huchard, 2016). Females might particularly benefit from  
413 displaying their compliance in this context. Similar long-term sexual intimidation strategies  
414 are also thought to occur in some chimpanzee, *Pan troglodytes*, populations: males that are

415 repeatedly aggressive towards particular females are more likely to mate with them during  
416 ovulatory periods and more likely to sire their offspring (Feldblum et al., 2014; Muller,  
417 Emery Thompson, Kahlenberg, & Wrangham, 2011; Muller et al., 2007; Muller, Kahlenberg,  
418 & Wrangham, 2009).

419         The patterns of subordination observed in female chacma baboons immediately  
420 following male aggression also resemble those seen in hamadryas baboons, *Papio*  
421 *hamadryas*, where males use frequent aggression to enforce the spatial proximity of females  
422 that are newly incorporated into their harem. New females spend more time affiliating with  
423 their leader male than do resident females, and in particular groom him following aggression  
424 (Swedell, 2015; Swedell & Schreier, 2009). In the long term, the aggression they face from  
425 him decreases once their social bond is established and when females are ‘conditioned’ (or  
426 ‘abducted’) to follow their leader male (Polo & Colmenares, 2012; Swedell, 2015; Swedell &  
427 Schreier, 2009). Male aggression therefore specifically targets females that are weakly  
428 bonded to the aggressor, presumably to dissuade them from dispersing or leaving male  
429 proximity. The conditioning of female hamadryas baboons is probably similar to the pattern  
430 we report in chacma baboons, particularly for consorting partners, where males may seek to  
431 condition their female consorts to stay in proximity. It would be interesting to test whether  
432 male aggression towards female chacma baboons decreases once the mate-guarding episode  
433 is well established and as females become more compliant (the same heterosexual dyad often  
434 consort during the receptive phase across several consecutive cycles), and whether females’  
435 propensity to propose sex following aggression decreases the chances of renewed aggression  
436 or conflict escalation.

437

438 ***Variation in the Function of PC Affiliation***

439 The observed pattern of affiliation is not fully compatible with true conciliatory tendencies,  
440 under which we would expect an effect of relationship quality (i.e. baseline rates of  
441 affiliation) between the two opponents on the probability of PC affiliation. In addition, we  
442 would not expect any effect of mate-guarding episodes on the probability of PC affiliation.  
443 However, we cannot exclude the occasional occurrence of ‘true’ reconciliation, alongside  
444 submission. Specifically, 26% of affiliations following conflicts between males and sexually  
445 receptive females were exclusively nonsexual, with nonsexual affiliative behaviours  
446 occurring three times more frequently than expected in baseline contexts, and symmetry in  
447 initiation patterns (of the first general affiliative act) suggesting that males and females were  
448 equally motivated to reconcile. It is noteworthy that had we only tested for a reconciliation  
449 signal, following the conventions of the reconciliation literature, we would have interpreted  
450 these findings as evidence of a conciliatory tendency.

451 A subset of PC interactions may thus be conciliatory, an interpretation reinforced by  
452 the existence of true reconciliation between new mothers and their male friends in the same  
453 population (Webb et al., 2019), as well as among female–female dyads in this species  
454 (Cheney et al., 1995; Silk et al., 1996; Wittig et al., 2007). This may also explain the  
455 observed trend in the effect of baseline affiliation rates on rates of PC affiliation (Appendix 2,  
456 Fig. A1), which may reflect this minority of conciliatory PC affiliation. We might expect the  
457 occasional occurrence of reconciliation between swollen females and males on the basis that  
458 a given male and cycling female dyad occasionally maintains a preferential relationship (in  
459 terms of grooming or proximity) that may last across consecutive female cycles (Baniel et al.,  
460 2016) and that may become a friendship when they conceive an offspring together, therefore  
461 affording fitness benefits to both partners (Archie et al., 2014; Cheney, Silk, & Seyfarth,  
462 2012). For a swollen female, reconciling with males may further enable immediate benefits  
463 such as spatial association and tolerance, access to better food patches, and provide a buffer

464 against other aggressive groupmates. For males, reconciliation may encourage swollen  
465 females to tolerate their proximity and therefore minimize the risk of extrapair matings or the  
466 loss of mate guarding to rivals (Bercovitch, 1995; Smuts, 1985).

467

#### 468 *Sex under Coercion or Affiliative ‘Make-up’ Sex?*

469 The mixed function of PC affiliation observed in this study, encompassing both submissive  
470 and true conciliatory behaviour, raises an interesting possibility: that when female chacma  
471 baboons mate with males following aggression, this may occasionally reflect a voluntary  
472 choice of females to use sex to reconcile with males, rather than the submissive acceptance of  
473 the sexual advances of males under coercion. In bonobos, sociosexual behaviours also occur  
474 in socially tensed situations, and although their tension alleviation function remains unclear  
475 (Hohmann, Mundry, & Deschner, 2009) such sexual interactions in PC contexts are  
476 conventionally considered friendly and conciliatory (‘make-up sex’) (Clay & de Waal, 2014;  
477 de Waal, 1987; Palagi et al., 2004). Importantly, however, these interactions predominantly  
478 occur in the context of female–female bonds and have a variety of documented  
479 nonconceptive functions (Hohmann & Fruth, 2000).

480 While female chacma baboons may occasionally choose to use sexual affiliations to  
481 reconcile, such voluntary choice probably does not reflect the general pattern in our  
482 population, where sexual affiliations are more likely to reflect sexual appeasement under  
483 duress given the support we found for the submissive hypothesis. So overall, although sexual  
484 PC affiliation behaviour may appear similar in baboons and bonobos, the motivational and  
485 emotional basis of PC affiliation probably differs for the initiator in most cases: whereas  
486 female baboons may generally sexually submit out of fear, female bonobos may use sexual  
487 contacts in a more symmetric way, although observations suggest that such contacts are not  
488 necessarily always consensual (Z. Clay and M. Surbeck, personal communication).

489 Interpretations concerning both ultimate functions and proximate motivations for PC  
490 behaviours should thus reflect the broader social dynamics of a given social system (such as  
491 power asymmetries between males and females).

492

### 493 *Wider Implications for the Reconciliation Literature*

494 The idea that PC affiliative behaviour, whether sexual or not, serves a submissive function  
495 contrasts with previous hypotheses, which generally revolve around conciliatory explanations  
496 (see Table 1; Aureli & van Schaik, 1991; Kappeler & van Schaik, 1992; Silk, 1996). The  
497 uncertainty reduction and integrated hypotheses emphasize the symmetric function of PC  
498 affiliation to alleviate anxiety and restore a damaged, reciprocal and mutually beneficial  
499 bond, whereas the submission hypothesis highlights its asymmetry in dyads characterized by  
500 pronounced power imbalances. While the reconciliation literature has occasionally alluded to  
501 the submissive pattern of reconciliation (de Waal, 1986; Kutsukake & Clutton-Brock, 2006),  
502 our study is the first to formally test its predictions and emphasize the full spectrum of  
503 possible PC patterns. In this study, we tested the submissive hypothesis in the specific context  
504 of coercive relationships between males and fertile female baboons, but it may apply to any  
505 kind of asymmetric relationships, which are ubiquitous in animal societies. By (re)framing  
506 the study of PC behaviour in the context of hierarchical relationships, the submissive  
507 hypothesis generates unique predictions from existing reconciliatory frameworks but does not  
508 exclude other hypotheses previously proposed to explain the occurrence of PC affiliation;  
509 such hypotheses are complementary, rather than mutually exclusive, within a given species or  
510 even dyad.

511 Taken together, our results emphasize the diversity of relationships possible within  
512 and across dyads, where the function of PC affiliation may vary from reconciliation to  
513 submission depending on the context and quality of the social bond. Attempts to separate

514 these two hypotheses at the species level may be oversimplistic given the sophistication of  
515 social strategies and the individualized nature of social bonds within primate groups (Cheney  
516 & Seyfarth, 2007; Smuts & Smuts, 1993).

517

### 518 ***Conclusion***

519 Primate societies are a mosaic of social bonds, ranging from the most coercive/hierarchical to  
520 the most egalitarian/reciprocal in nature (de Waal, 1986). Conflict resolution patterns reflect  
521 this spectrum, with a higher frequency of PC affiliation in more tolerant species compared to  
522 more despotic ones (Thierry, 2000; Thierry et al., 2008). Our results further suggest that, on  
523 top of its frequency, the very function of PC affiliation similarly varies across and within  
524 populations, and hypotheses pertaining to proximate and ultimate explanations for the  
525 observed behavioural patterns should account for such variation. On the egalitarian end of the  
526 spectrum, reconciliation may be required after conflicts to restore the relationship to baseline  
527 levels of tolerance and affiliation. On the hierarchical end, reconciliation may facilitate the  
528 avoidance of injury through submissive behaviour rather than repairing social bonds. Overall,  
529 a more balanced view of the functions of PC affiliation is warranted. Animal social  
530 relationships are multifaceted and involve a mixture of coercive and sociopositive  
531 interactions, a reality that research on PC behaviour should reflect.

532

### 533 **Author Contributions**

534 A.B., C.E.W. and E.H. designed the study and performed the analyses. A.B and E.H collected  
535 the data. All authors contributed to drafting the manuscript.

536

### 537 **Data Availability**

538 The data sets necessary to run the analyses included in this paper have been deposited in the  
539 public depository GitHub at <https://github.com/AliceBaniel/The-Submissive-hypothesis>.

540

#### 541 **Declaration of Interest**

542 We have no competing interests.

543

#### 544 **Acknowledgments**

545 We are very grateful to the Tsaobis Baboon Project volunteers (2005–2006 and 2013–2014)  
546 for help with data collection, the Tsaobis beneficiaries for permission to work at Tsaobis, the  
547 Gobabeb Research and Training Centre for affiliation, and the Snyman and Wittreich families  
548 for permission to work on their land. This paper is a publication of the ZSL Institute of  
549 Zoology’s Tsaobis Baboon Project. Contribution ISEM 2020-339. A.B. was supported by  
550 the Agence Nationale de la Recherche Labex IAST and C.E.W was supported by a Fyssen  
551 Foundation postdoctoral fellowship.

552

553

#### 554 **REFERENCES**

- 555 Albers, S. C., Altmann, J., & Wilson, M. L. (1996). Mate guarding constrains foraging  
556 activity of male baboons. *Animal Behaviour*, *51*(6), 1269–1277. Archie, E. A., Tung, J.,  
557 Clark, M., Altmann, J., & Albers, S. C. (2014). Social affiliation matters : both same-  
558 sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings*  
559 *of the Royal Society B: Biological Sciences*, *281*(1793), 20141261.
- 560 Albers, P. C. H., & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of  
561 dominance strengths. *Animal Behaviour*, *61*(2), 489–495.
- 562 Arnold, K., Fraser, O. N., & Aureli, F. (2010). Postconflict reconciliation. In C. J. Campbell,



563 A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in*  
564 *Perspective* (pp. 608–625). Oxford, U.K.: Oxford University Press.

565 Aureli, F. (1997). Post-conflict anxiety in nonhuman primates: The mediating role of emotion  
566 in conflict resolution. *Aggressive Behavior*, 23(5), 315–328.

567 Aureli, F., Cords, M., & van Schaik, C. P. (2002). Conflict resolution following aggression in  
568 gregarious animals: A predictive framework. *Animal Behaviour*, 64(3), 325–343.

569 Aureli, F., & van Schaik, C. P. (1991). Post-conflict behaviour in long-tailed macaques  
570 (*Macaca fascicularis*): II. Coping with the uncertainty. *Ethology*, 89(2), 101–114.

571 Baniel, A., Cowlshaw, G., & Huchard, E. (2017). Male violence and sexual intimidation in a  
572 wild primate society. *Current Biology*, 27(14), 2163-2168

573 Baniel, A., Cowlshaw, G., & Huchard, E. (2016). Stability and strength of male-female  
574 associations in a promiscuous primate society. *Behavioral Ecology and Sociobiology*,  
575 70(5), 761–775.

576 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: linear mixed-effects models  
577 using Eigen and S4. R package version 1.1-7. *R Package Version 1.1-7*. [http://cran.r-](http://cran.r-project.org/package=lme4)  
578 [project.org/package=lme4](http://cran.r-project.org/package=lme4).

579 Bercovitch, F. B. (1995). Female cooperation, consortship maintenance, and male mating  
580 success in savanna baboons. *Animal Behaviour*, 50, 137–149.

581 Bulger, J. B. (1993). Dominance rank and access to estrous females in male savanna baboons.  
582 *Behaviour*, 127, 67–103.

583 Call, J., Aureli, F., & de Waal, F. B. M. (1999). Reconciliation patterns among stumptailed  
584 macaques: A multivariate approach. *Animal Behaviour*, 58(1), 165–172.

585 Campos, F. A., Villavicencio, F., Archie, E. A., Colchero, F., Alberts, S. C., & Alberts, S. C.  
586 (2020). Social bonds , social status and survival in wild baboons: a tale of two sexes.  
587 *Philosophical Transactions of the Royal Society B*, 375, 20190621.

- 588 Cant, M. A. (2010). The role of threats in animal cooperation. *Proceedings of the Royal*  
589 *Society B: Biological Sciences*, 278(1703), 170–178.
- 590 Cheney, D. L., & Seyfarth, R. M. (1977). Behavior of adult and immature male baboons  
591 during intergroup encounters. *Nature*, 269, 404–406.
- 592 Cheney, D. L., & Seyfarth, R. M. (2007). *Baboon metaphysics—The evolution of a social*  
593 *mind*. Chicago, IL: The University of Chicago Press.
- 594 Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The role of grunts in reconciling  
595 opponents and facilitating interactions among adult female baboons. *Animal Behaviour*,  
596 50, 249–257.
- 597 Cheney, D. L., Silk, J. B., & Seyfarth, R. M. (2012). Evidence for intrasexual selection in  
598 wild female baboons. *Animal Behaviour*, 84, 21–27.
- 599 Clay, Z., & de Waal, F. B. M. (2014). Sex and strife: Post-conflict sexual contacts in  
600 bonobos. *Behaviour*, 152, 313–334.
- 601 Clutton-Brock, T. H., & Parker, G. A. (1995a). Punishment in animal societies. *Nature*, 373,  
602 209–216.
- 603 Clutton-Brock, T. H., & Parker, G. A. (1995b). Sexual coercion in animal societies. *Animal*  
604 *Behaviour*, 49, 1345–1365.
- 605 Colmenares, F., Polo, P., & Herna, V. (2014). Male takeovers are reproductively costly to  
606 females in hamadryas baboons: A test of the sexual coercion hypothesis. *PLoS One*,  
607 9(3), e90996.
- 608 Cords, M., & Aureli, F. (1996). Reasons for reconciling. *Evolutionary Anthropology*, 2(5),  
609 42–45.
- 610 Cowlishaw, G. (1997). Refuge use and predation risk in a desert baboon population. *Animal*  
611 *Behaviour*, 54(2), 241–253.
- 612 de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *The*

613 *Quarterly Review of Biology*, 61(4), 459–479.

614 de Waal, F. B. M. (1987). Tension regulation and non-reproductive functions of sex in  
615 captive bonobos. *National Geographic Research*, 3, 318–335.

616 de Waal, F. B. M., & Aureli, F. (1997). Conflict resolution and distress alleviation in  
617 monkeys and apes. In C. S. Carter, B. Kirkpatrick, & I. Lenderhendler (Eds.), *The*  
618 *Integrative Neurobiology of Affiliation* (Vol. 807, pp. 317–328). New York: Annals of  
619 the New York Academy of Sciences.

620 de Waal, F., & van Roosmalen, A. (1979). Reconciliation and consolation among  
621 chimpanzees. *Behavioral Ecology and Sociobiology*, 5(1), 55–66.

622 Feldblum, J. T., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Paiva, T., Cetinkaya-  
623 Rundel, M., Pusey, A.E., Gilby, I. C. (2014). Sexually coercive male chimpanzees sire  
624 more offspring. *Current Biology*, 24(23), 2855–2860.

625 Fox, E. A. (2002). Female tactics to reduce sexual harassment in the Sumatran orangutan  
626 (*Pongo pygmaeus abelii*). *Behavioral Ecology and Sociobiology*, 52(2), 93–101.

627 Fürtbauer, I., Heistermann, M., Schülke, O., & Ostner, J. (2014). Low female stress hormone  
628 levels are predicted by same- or opposite-sex sociality depending on season in wild  
629 Assamese macaques. *Psychoneuroendocrinology*, 48, 19–28.

630 Gesquiere, L. R., Wango, E. O., Alberts, S., & Altmann, J. (2007). Mechanisms of sexual  
631 selection: sexual swellings and estrogen concentrations as fertility indicators and cues  
632 for male consort decisions in wild baboons. *Hormones and Behavior*, 51, 114–125.

633 Hartig, F. (2018). DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)  
634 Regression Models. R package version 0.2.0. [https://CRAN.R-](https://CRAN.R-project.org/package=DHARMA)  
635 [project.org/package=DHARMA](https://CRAN.R-project.org/package=DHARMA).

636 Hohmann, G., & Fruth, B. (2000). Use and function of genital contacts among female  
637 bonobos. *Animal Behaviour*, 60(1), 107–120.

638 Hohmann, G., Mundry, R., & Deschner, T. (2009). The relationship between socio-sexual  
639 behavior and salivary cortisol in bonobos: Tests of the tension regulation hypothesis.  
640 *American Journal of Primatology*, 71(3), 223–232.

641 Kappeler, P. M., & van Schaik, C. P. (1992). Methodological and evolutionary aspects of  
642 reconciliation among primates. *Ethology*, 92(2), 51–69.

643 Kitchen, D. M., Beehner, J. C., Bergman, T. J., Cheney, D. L., Crockford, C., Engh, A. L.,  
644 Fischer, J., Seyfart, R.M., Wittig, R. M. (2009). The causes and consequences of male  
645 aggression directed at female chacma baboons. In M N Muller & R. W. Wrangham  
646 (Eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male*  
647 *aggression against females* (pp. 128–156). Cambridge, MA: Harvard University Press.

648 Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2005). Contextual factors mediating  
649 contests between male chacma baboons in Botswana: effects of food, friends and  
650 females. *International Journal of Primatology*, 26(1), 105–125.

651 Knott, C. D. (2009). Orangutans: sexual coercion without sexual violence. In M N Muller &  
652 R. W. Wrangham (Eds.), *Sexual coercion in primates and humans: an evolutionary*  
653 *perspective on male aggression against females* (pp. 81–111). Cambridge, MA: Harvard  
654 University Press.

655 Kutsukake, N., & Clutton-Brock, T. H. (2006). Aggression and submission reflect  
656 reproductive conflict between females in cooperatively breeding meerkats *Suricata*  
657 *suricatta*. *Behavioral Ecology and Sociobiology*, 59(4), 541–548.

658 Machanda, Z. P., Gilby, I. C., & Wrangham, R. W. (2013). Male-female association patterns  
659 among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *International*  
660 *Journal of Primatology*, 34(5), 917–938.

661 Moscovice, L. R., Di Fiore, A., Crockford, C., Kitchen, D. M., Wittig, R., Seyfarth, R. M., &  
662 Cheney, D. L. (2010). Hedging their bets? Male and female chacma baboons form

663 friendships based on likelihood of paternity. *Animal Behaviour*, 79, 1007–1015.

664 Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male  
665 coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of*  
666 *the Royal Society B: Biological Sciences*, 274(1612), 1009–1014.

667 Muller, M. N., Emery Thompson, M., Kahlenberg, S., & Wrangham, R. (2011). Sexual  
668 coercion by male chimpanzees shows that female choice may be more apparent than  
669 real. *Behavioral Ecology and Sociobiology*, 65, 921–933.

670 Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2009). Male aggression against  
671 females and sexual coercion in chimpanzees. In M N Muller & R. W. Wrangham (Eds.),  
672 *Sexual coercion in primates and humans: an evolutionary perspective on male*  
673 *aggression against females* (pp. 184–217). Cambridge, MA: Harvard University Press.

674 Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdi, A.  
675 Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of  
676 progressive evaluation with Elo-rating. *Animal Behaviour*, 82, 911–921.

677 Palagi, E., Paoli, T., & Tarli, S. B. (2004). Reconciliation and consolation in captive bonobos  
678 (*Pan paniscus*). *American Journal of Primatology*, 62(1), 15–30.

679 Palombit, R. A. (2000). Infanticide and the evolution of male-female bonds in animals. In C.  
680 P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 239–  
681 268). Cambridge, U.K.: Cambridge University Press.

682 Polo, P., & Colmenares, F. (2012). Behavioural processes in social context: female  
683 abductions, male herding and female grooming in hamadryas baboons. *Behavioural*  
684 *Processes*, 90(2), 238–245.

685 R Core Team. (2018). R: A language and environment for statistical computing. Vienna,  
686 Austria: R Foundation for Statistical Computing.. <http://www.r-project.org/>

687 Reddy, R., & Mitani, J. (2020). Adolescent and young adult male chimpanzees form

688 affiliative, yet aggressive, relationships with females. *Journal of Human Evolution*, 144,  
689 102813.

690 Schaffner, C. M., & Aureli, F. (2004). Conflict resolution. *International Journal of*  
691 *Phytoremediation*, 21(1), 295–297.

692 Silk, J. B. (1996). Why do primates reconcile? *Evolutionary Anthropology*, 5(2), 39–42.

693 Silk, J. B. (2002). Practice random acts of aggression and senseless acts of intimidation: The  
694 logic of status contests in social groups. *Evolutionary Anthropology*, 11(6), 221–225.

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

697 Smuts, B. B. (1985). *Sex and friendship in baboons*. Hawthorne, NY: Aldine Publishing.

698 Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in  
699 nonhuman primates and other mammals: evidence and theoretical implications.  
700 *Advances in the Study of Behavior*, 22, 1–63.

701 Swedell, L. (2015). *Strategies of sex and survival in female hamadryas baboons: Through a*  
702 *female lens*. Upper Saddle River, NJ: Pearson Prentice Hall.

703 Swedell, L., & Schreier, A. (2009). Male aggression towards females in hamadryas baboons:  
704 conditioning, coercion, and control. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual*  
705 *coercion in primates and humans: an evolutionary perspective on male aggression*  
706 *against females* (pp. 244–268). Cambridge, MA: Harvard University Press.

707 Swedell, L., Leedom, L., Saunders, J., Pines, M. (2014). Sexual conflict in a polygynous  
708 primate: Costs and benefits of a male-imposed mating system. *Behavioral Ecology and*  
709 *Sociobiology*, 68(2), 263–273.

710 Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In  
711 Filippo Aureli & F. B. M. de Waal (Eds.), *Natural Conflict Resolution* (pp. 106–128).  
712 Berkeley, CA: University of California Press.

- 713 Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., & de Waal, F. B. M. (2008). A  
714 comparative study of conflict resolution in macaques: Insights into the nature of trait  
715 covariation. *Animal Behaviour*, *75*(3), 847–860.
- 716 Webb, C. E., Baniel, A., Cowlshaw, G., & Huchard, E. (2019). Friend or foe: Reconciliation  
717 between males and females in wild chacma baboons. *Animal Behaviour*, *151*, 145–155.
- 718 Weingrill, T., Lycett, J. E., Barrett, L., Hill, R. A., & Henzi, S. P. (2003). Male consortship  
719 behaviour in chacma baboons: the role of demographic factors and female conceptive  
720 probabilities. *Behaviour*, *140*, 405–427.
- 721 Weingrill, T., Lycett, J. E., & Henzi, S. P. (2000). Consortship and mating success in chacma  
722 baboons (*Papio cynocephalus ursinus*). *Ethology*, *106*(11), 1033–1044.
- 723 Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M., & Cheney, D. L. (2007). Kin-  
724 mediated reconciliation substitutes for direct reconciliation in female baboons.  
725 *Proceedings of the Royal Society B: Biological Sciences*, *274*(1613), 1109–1115.

726 **Table 1.** Summary of the main proximate and ultimate hypotheses proposed to explain postconflict affiliative behaviour.

Hypothesis	Explanation		Evidence  (reviewed in Aureli et al. 2002; Arnold et al. 2010)
	Proximate	Ultimate	
<b>Valuable relationships</b> (de Waal & Aureli, 1997; Kappeler & van Schaik, 1992)	Usually not clarified	Repair valuable (i.e. fitness enhancing) social bond	Kin or close affiliates (e.g. as indexed by frequency of grooming, proximity, cooperation, agonistic support) more likely to reconcile than nonkin or nonaffiliates
<b>Uncertainty reduction</b> (Aureli & van Schaik, 1991)	Motivation to reduce stress/anxiety due to uncertainty about the social situation	Reduce risk of renewed aggression, alleviate more subtle social risks, prevent negative consequences of chronic stress	Elevated rates of self-directed behaviour (SDB) in victims and aggressors following conflicts are decreased following reconciliation
<b>Integrated</b> (Aureli, 1997)	Motivation to reduce stress/anxiety due to uncertainty about the social situation	Repair valuable social bond	Aggression between opponents with more valuable bonds results in higher SDB and reconciliation rates
<b>Benign intent</b> (Silk, 1996)	Signal friendly intentions (that the conflict has ended) in order to restore tolerance	Achieve benefits of resumed interaction (e.g. short-term objectives like grooming or access to resources)	Grunts between female–female baboons serve as signals of friendly intent and facilitate infant handling
<b>Submissive</b> (this study)	Victims: fear and/or stress/anxiety about conflict escalation Aggressors: motivation to obtain immediate social/sexual benefits, restore tolerance	Victims: reduce risks of renewed aggression and costs of conflict escalation (e.g. injury) Aggressors: reap the benefits of subordination/compliance of the victim (e.g. secure grooming or mating opportunities)	Present study



727 **Table 2.** Rate of postconflict (PC) and baseline affiliation between males and swollen females when considering only sexual behaviour or  
 728 nonsexual behaviour.

Fixed factor	Only sexual behaviour						Only nonsexual behaviour					
	Estimate	SE	95% confidence interval	LRT	df	<i>P</i>	Estimate	SE	95% confidence interval	LRT	df	<i>P</i>
Intercept	-5.60	0.35	-	-	-	-	-5.9	0.71	-	-	-	-
PC observation <sup>a</sup>	1.29	0.24	<b>[0.78 ; 1.73]</b>	27.1	1	<b>&lt;0.001</b>	1.20	0.13	<b>[0.98 ; 1.39]</b>	68.3	1	<b>&lt;0.001</b>
Female rank	-0.20	0.33	[-0.84 ; 0.44]	0.31	1	0.580	0.69	0.97	[-1.29 ; 2.99]	0.49	1	0.480
Male rank	1.59	0.44	<b>[0.8 ; 2.57]</b>	12.4	1	<b>&lt;0.001</b>	0.77	0.64	[-0.53 ; 2.21]	1.44	1	0.230

729 The response variable is number of affiliations exchanged between male–female dyads. The duration (min) of observations for each dyad (in PC or in  
 730 baseline) was fitted as an offset fixed factor, to control for variation in observation time across dyads. Parameters and tests are based on 29 females, 27 males,  
 731 61 dyads and 94 aggressive events. The negative binomial GLMMs were performed controlling for male and female identity. LRT: likelihood ratio test. The  
 732 95% confidence intervals that do not cross zero and *P* values of statistically significant results are highlighted in bold.

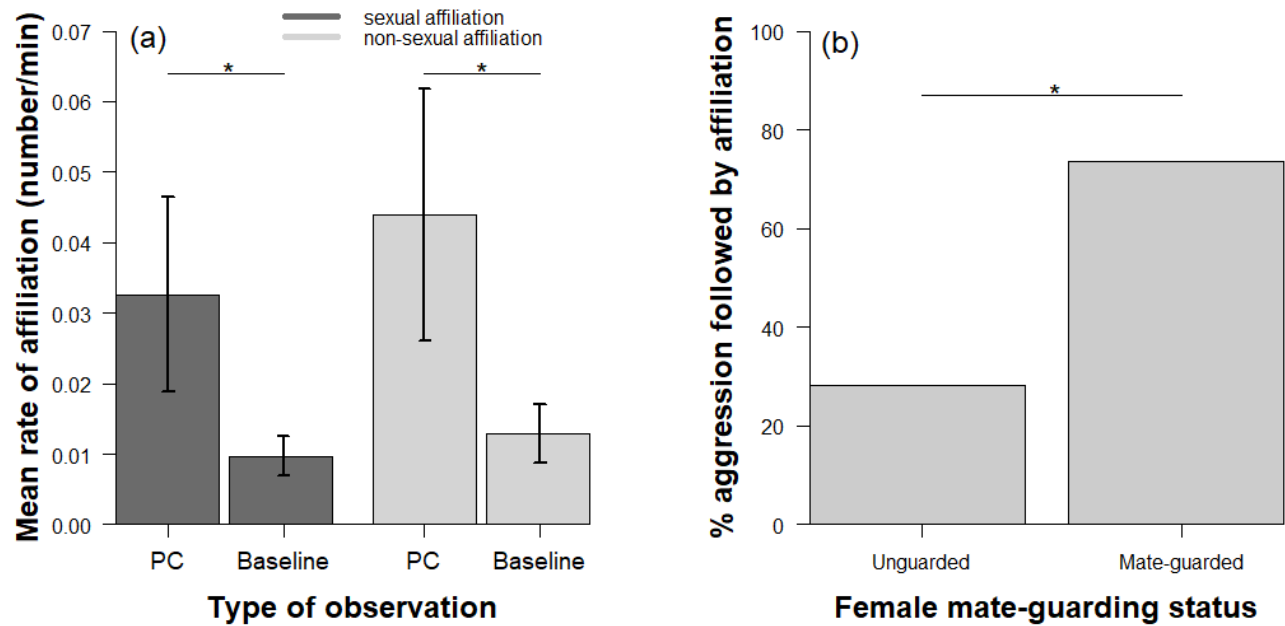
733 <sup>a</sup> Reference category: baseline.

734 **Table 3.** Determinants of the occurrence of postconflict (PC) affiliation between males and swollen females.

Fixed factor	Level	Estimate	SE	95% confidence interval	LRT	<i>df</i>	<i>P</i>
Intercept		-1.73	0.85	-	-	-	-
Mate-guarding status	Mate guarded	1.55	0.63	<b>[0.46 ; 3.82]</b>	7.48	1	<b>0.006</b>
Baseline rate of affiliation		14.85	11.7	[-9.75 ; 53.98]	1.6	1	0.206
Female rank		-0.37	0.84	[-2.49 ; 1.47]	0.2	1	0.653
Male rank		0.47	0.81	[-1.54 ; 2.78]	0.34	1	0.563
Type of aggression	CH (ref: AT)	0.85	0.68	[-0.47 ; 2.83]	3.74	2	0.154
	TH (ref: AT)	-0.46	0.96	[-4.42 ; 1.65]			
	TH (ref: CH)	-1.31	0.84	[-9.89 ; 0.18]			

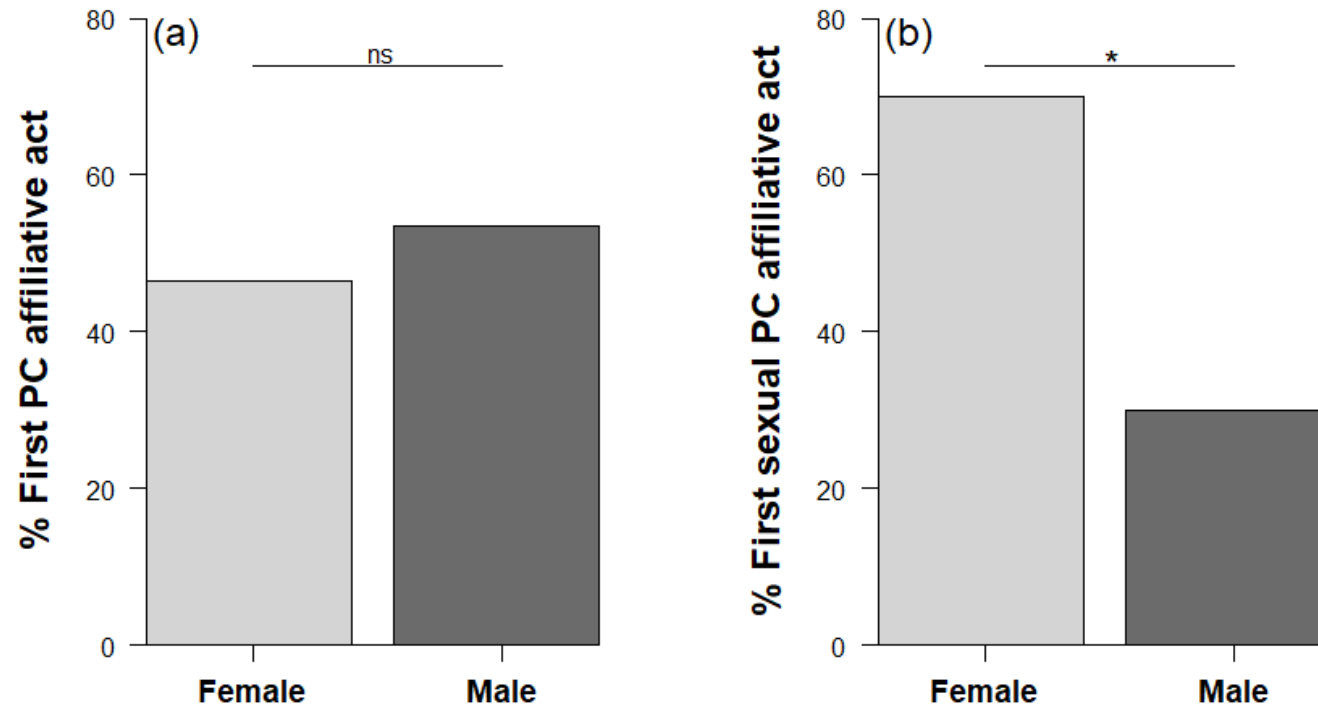
735 The response variable is the occurrence of PC affiliation between males and swollen females (yes/no). Parameters and tests are based on 28 females, 27  
736 males, and 91 aggressive events (including 43 followed by PC affiliation). Of these aggressive events 53 involved unguarded swollen females, and 38  
737 involved mate-guarded swollen females. For this model, we removed three observed aggressive events where mate-guarded females received aggression from  
738 a nonconsort male. The baseline rate of affiliation of the dyad was calculated using focal observations collected when the female was swollen and outside an  
739 aggressive context. Type of aggression refers to attack ('AT', *N*=18), chase ('CH', *N*=58), or threat ('TH', *N*=15). The binomial GLMM was performed  
740 controlling for male and female identity. The 95% confidence intervals that do not cross zero and *P* values of statistically significant results are highlighted in  
741 bold.

742 **Figure 1.** Pattern of postconflict (PC) affiliation between males and females. (a) Mean rate of affiliation between swollen females and males in  
743 PC versus baseline observations according to whether only sexual affiliations (presenting and copulations) or only nonsexual affiliations are  
744 included in the pool of affiliations. Error bars show the standard error of the distribution. (b) Percentage of aggressive events followed by  
745 affiliation according to the mate-guarding status of swollen females (unguarded versus mate guarded by the aggressor). \* $P < 0.05$ .



746

747 **Figure 2.** Pattern of initiation of the first postconflict (PC) act and the first sexual PC act by females and males. (a) Percentage of the first PC  
748 affiliative act (both sexual and nonsexual behaviour combined) of the PC sequence (lasting 15 min) initiated by females and males. (b)  
749 Percentage of the first sexual PC affiliative act of the PC sequence initiated by females and males. \* $P < 0.05$ .



750

## 751 **Appendix 1**

752 Individual dominance ranks were assessed through focal and ad libitum observations of  
753 approach–avoid interactions (supplants, when one animal actively displaces another to take  
754 its place; displacements, when one animal passes close to another and makes it move away)  
755 and agonistic interactions (attacks, any agonistic physical contacts including hits, bites or  
756 grabbing movements; chases, when one animal chases another for a distance of at least 3 m;  
757 and threats, including staring, head bobbing and ground sweeping while oriented towards the  
758 targeted individual). Female dominance hierarchies were calculated separately in each year  
759 using Matman 1.1.4 (Noldus Information Technology, Wageningen, The Netherlands) and  
760 were always linear ( $N_{2005} = 412$  interactions,  $N_{2006} = 576$ ,  $N_{2013} = 367$ ,  $N_{2014} = 1259$  in group  
761 L;  $N_{2005} = 184$ ,  $N_{2006} = 460$ ,  $N_{2013} = 590$ ,  $N_{2014} = 978$  in group J, Landau's linearity index  $h$ :  
762  $P < 0.05$  in all cases). In the analyses, we used relative female rank to control for variation in  
763 group size, where absolute ranks were standardized to vary between 0 and 1 using the  
764 formula:  $1 - ((1-r)/(1-N))$ , where  $r$  is the absolute rank of an individual (ranging from 1 to the  
765 group size,  $N$ ). In contrast to females, the male hierarchies were much less stable within a  
766 year (Baniel et al., 2016), so male ranks were established using an Elo-rating procedure  
767 implemented in the R package EloRating (version 0.43; Neumann et al., 2011). Compared to  
768 matrices of dyadic interactions where ranks are calculated over a given time period, an Elo-  
769 rating procedure continuously updates rankings according to the temporal sequence of  
770 interactions and is better adapted to situations of unstable social dominance (Albers & de  
771 Vries, 2001; Neumann et al., 2011). This gives a score for each individual on each day of  
772 observation. We derived a daily standardized rank by scaling the Elo-rating score of each  
773 individual proportionally between 0 (corresponding to the minimal score and thus the lowest  
774 ranking male) and 1 (corresponding to the maximal score and the highest-ranking male).

775 **Appendix 2**

776 **Table A1.** Determinants of the occurrence of postconflict (PC) affiliation between males and swollen females.

777

Fixed factor	Level	Estimate	SE	95% confidence interval	LRT	df	P
Intercept		-0.53	0.64	-	-	-	-
Mate-guarding status	Mate guarded	1.75	0.61	<b>[0.71 ; 4.03]</b>	9.26	1	<b>0.002</b>
Baseline rate of affiliation		-10.62	26.67	[-70.61 ; 47.62]	0.16	1	0.690
Female rank		-0.65	0.81	[-2.64 ; 1.1]	0.64	1	0.424
Male rank		0.73	0.8	[-1.12 ; 2.66]	0.84	1	0.360
Type of aggression	CH (ref: AT)	0.66	0.65	[-0.77 ; 2.37]	2.60	2	0.273
	TH (ref: AT)	-0.42	0.91	[-14.88 ; 1.73]			
	TH (ref: CH)	-1.08	0.78	[-3.39 ; 0.42]			

778 The response variable is the occurrence of PC affiliation between males and swollen females (yes/no). Parameters and tests are based on 25 females, 26  
 779 males, and 80 aggressive events (including 38 followed by PC affiliation). Type of aggression refers to attack ('AT', N=18), chase ('CH', N=58), or threat  
 780 ('TH', N=15). The binomial GLMM was performed controlling for male and female identity. In contrast to Table 3, the baseline rate of affiliation of the dyad  
 781 was calculated using focal observations collected when the female was nonswollen and outside an aggressive context. The 95% confidence intervals that do  
 782 not cross zero and *P* values of statistically significant results are highlighted in bold.

783 **Table A2.** Behavioural details on the first affiliative act and the first sexual affiliative act.

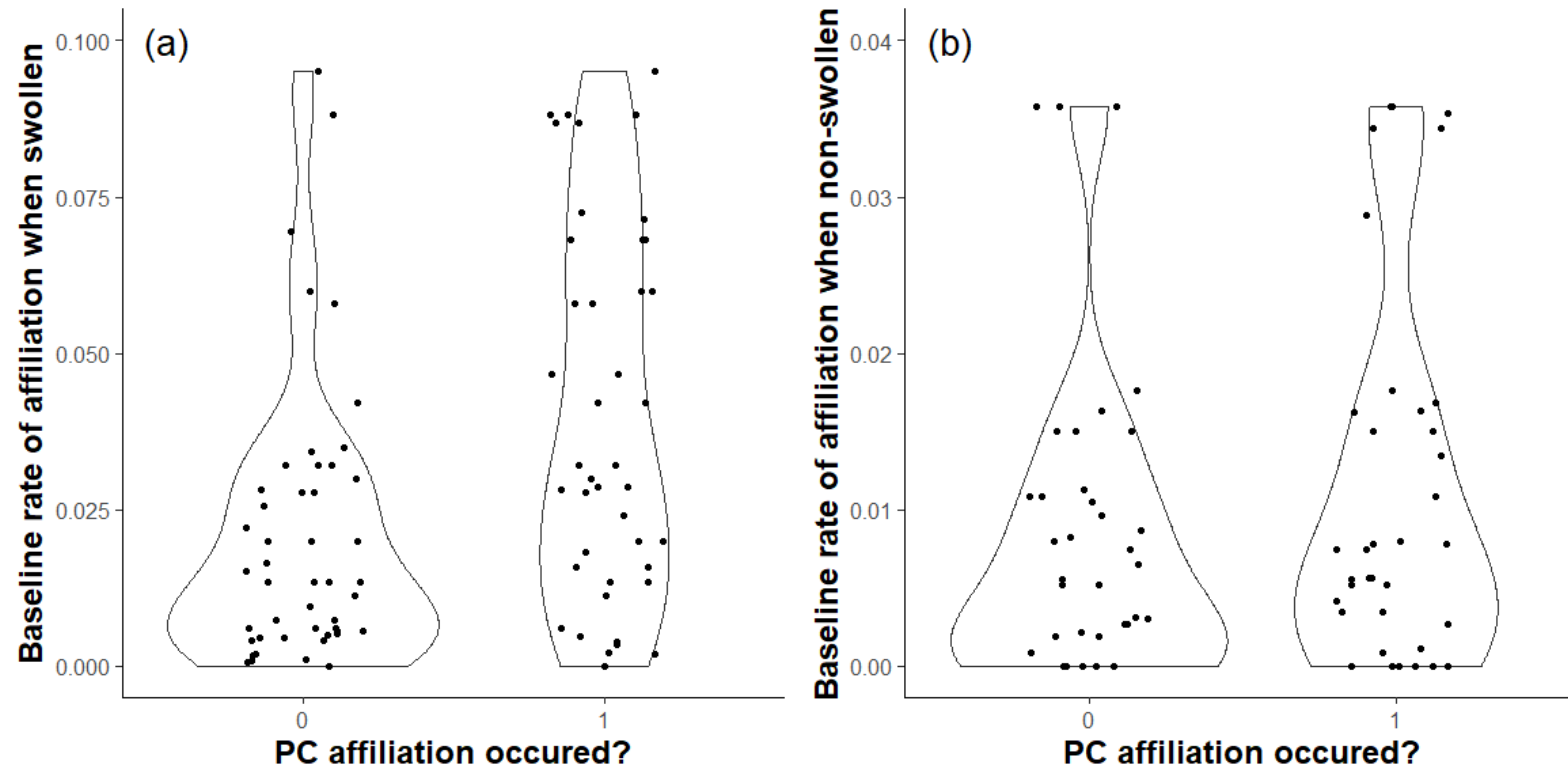
784

Behaviour	First affiliative act		First sexual act	
	Female initiates	Male initiates	Female initiates	Male initiates
Copulation	2	8	2 <sup>a</sup>	9 <sup>a</sup>
Presenting	11	NA	19	NA
Grooming	5	3		
Grunt	0	6		
Lip-smack	0	4		
Sniffing perineum	0	2		
Sniffing mouth	1	0		
Come-here face	1	0		
Total	20	23	21	9

785 NA: not applicable. The table shows the type and direction of the first postconflict (PC) affiliation act and the first sexual PC affiliation act of a PC sequence  
786 (lasting 15 min in total) between males and swollen females. There were 43 PC sequences containing at least one PC affiliative act and 32 PC sequences  
787 containing at least one sexual act.

788 <sup>a</sup>Two copulations had unknown initiator and are not reported here.

789 **Fig. A1.** Occurrence of postconflict (PC) affiliation according to the baseline rate of affiliation (i.e. outside an aggressive context) of the  
790 malefemale dyad calculated over the (a) swollen or (b) nonswollen period. The violin plots (created using `geom_violin` from the `ggplot2`  
791 package, [cran.r-project.org/package=ggplot2](http://cran.r-project.org/package=ggplot2)) show the kernel probability density of the data at different y values.



792