

The submissive pattern of post-conflict affiliation in asymmetric relationships: a test in male and sexually coerced female baboons

Alice Baniel^{1,2,6}, Christine E. Webb^{3,6}, Guy Cowlshaw⁴, Elise Huchard^{5,7}

¹ Institute for Advanced Study in Toulouse, 21 allée de Brienne, 31015 Cedex 6, Toulouse, France.

² Department of Anthropology, Stony Brook University, Stony Brook, NY 11794, USA.

³ Department of Human Evolutionary Biology, Harvard University, 11 Divinity Avenue, Cambridge MA, 02138 USA

⁴ Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK.

⁵ Institute of Evolutionary Biology of Montpellier (ISEM), UMR 5554, Université de Montpellier, CNRS, IRD, EPHE, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France.

⁶ These authors contributed equally

Corresponding author. Alice Baniel. Department of Anthropology, Stony Brook University, (Social & Behavioral Sciences building, 5th floor), 100 Nicolls Road, Stony Brook, NY 11794, USA. Email: alice.baniel@gmail.com. Phone: +1 631-710-1293

Word count. 6033

1 **TITLE**

2 The submissive pattern of post-conflict affiliation in asymmetric relationships: a test in male
3 and sexually coerced female baboons

4

5 **ABSTRACT**

6 Reconciliation, or post-conflict (PC) affiliation between former opponents, is a widespread
7 conflict management strategy in animal societies, so-named for its relationship-repair
8 function. However, another possibility is that PC affiliation reflects a submissive response of
9 victims toward aggressors to limit conflict escalation when the power imbalance between the
10 opponents is large. Here we investigate this hypothesis in a highly asymmetric relationship
11 context: heterosexual wild chacma baboon (*Papio ursinus*) dyads involving sexually
12 receptive females, where sexual coercion by males is common. We found several lines of
13 support for the Submissive hypothesis in the context of sexual coercion. First, rates of sexual
14 and non-sexual PC affiliative interactions in these dyads exhibited significant and comparable
15 increases compared to baseline conditions (ca. three-fold). Second, the baseline strength of
16 the heterosexual social bond (outside of an aggressive context) did not predict the likelihood
17 of sexual and non-sexual PC affiliation. Third, mate-guarded females, who could not escape
18 the proximity of their aggressor (and faced high risks of renewed aggression), exhibited the
19 most PC affiliation with males. Finally, most PC affiliation sequences (74%) contained at
20 least one sexual act, and the first *sexual* affiliative act was primarily initiated by females via
21 presenting. This suggests that female victims affiliate in a submissive way by displaying
22 sexual compliance to aggressive males. Nevertheless, we cannot exclude the co-occurrence of
23 ‘true’ reconciliation: 26% of PC affiliations between males and receptive females were
24 exclusively non-sexual, and the first general affiliative act was equally initiated by males and
25 females. Overall, our results suggest a mixed PC affiliation strategy in which submission may

26 play an important role in highly asymmetric relationships, and indicate the function of PC
27 affiliation may vary from submission to reconciliation depending on the species, dyads,
28 individuals, and conflicts under consideration. Future research on PC interactions would
29 usefully consider this full spectrum.

30

31 **KEYWORDS**

32 aggression, chacma baboons, male-female associations, reconciliation, sexual coercion

33

34 **INTRODUCTION**

35 Two animals are said to have reconciled if, soon after an aggressive interaction between them,
36 they engage in friendly contact (de Waal & van Roosmalen, 1979). Several nonexclusive
37 hypotheses have been proposed to predict the distribution of reconciliation across opponent
38 dyads (Arnold, Fraser, & Aureli, 2010), with proximate or ultimate explanations emphasizing
39 its conciliatory nature (see Table 1). Friendly reunions following conflict may serve to repair
40 mutually beneficial (i.e., fitness-enhancing) relationships (the ‘Valuable Relationship’
41 hypothesis: Kappeler and van Schaik 1992; de Waal and Aureli 1997), attenuate uncertainty
42 or anxiety (the ‘Uncertainty Reduction’ hypothesis: Aureli, 1997; Aureli & van Schaik, 1991),
43 or communicate peaceful intentions between former opponents (the ‘Benign Intent’
44 hypothesis: Silk 1996). The ‘Integrated’ hypothesis combines the Uncertainty Reduction and
45 Valuable Relationship hypotheses by proposing that disruptions to valuable bonds are
46 particularly stressful for opponents, and therefore warrant stronger resolution attempts
47 (Aureli, 1997). Although they occasionally generate different predictions, these hypotheses
48 are generally treated as complementary, with expressions of benign intent serving to reduce
49 uncertainty about the conflict and thereby restore valuable relationships (Aureli, Cords, &
50 van Schaik, 2002; Cords & Aureli, 1996; Schaffner & Aureli, 2004). Tests of these

51 hypotheses have commonly focused on primates, where the frequency and patterning of
52 reconciliation varies according to the nature of the social systems and relationships under
53 study (Arnold et al., 2010).

54 Theory and research on reconciliation has previously emphasized variation in post-
55 conflict behaviour across different levels of dominance asymmetry, with more egalitarian
56 species showing higher conciliatory tendencies than despotic ones (Thierry, 2000; Thierry et
57 al., 2008). However, power imbalances have largely been considered at the level of the
58 species or social organization rather than the dyadic level. In more hierarchical relationship
59 contexts, two opponents may not ascribe equivalent fitness value to each other, and/or may
60 not share equally in their uncertainty or anxiety about renewed aggression. These
61 asymmetries highlight how the form, motive, and function of post-conflict behavior may vary
62 even within a dyad in ways not explicitly captured by existing reconciliation frameworks.
63 Reflecting the full spectrum and complexity of primate social relationships, post-conflict
64 interactions can either be more reciprocal and conciliatory, or hierarchical and coercive in
65 nature.

66 One intriguing possibility is that, in the context of highly asymmetrical relationships,
67 post-conflict affiliation represents a submissive response by victims towards their recent
68 aggressors (the 'Submissive' hypothesis) (de Waal, 1986; Kutsukake & Clutton-Brock,
69 2006). In other words, rather than expressing a motivation for peaceful and friendly
70 interactions, victims of aggression may affiliate out of fear in order to accede to aggressors'
71 demands by displaying submission/compliance in an attempt to limit conflict escalation and
72 injury. Several theoretical and experimental studies have emphasized the ubiquity of hidden
73 threats and punishment in animal societies, and their role in enforcing cooperation across a
74 range of contexts, particularly when the power imbalance between the opponents is
75 pronounced (Cant, 2010; Clutton-Brock & Parker, 1995a). We propose here that prolonged

76 intimidation and repeated aggression in a given dyad with high power asymmetry may yield
77 post-conflict interactions that are more characteristic of a submissive rather than conciliatory
78 scenario, even if it is taking the form of a typical affiliation (e.g., grooming).

79 At the ultimate level, the Submissive hypothesis and the Uncertainty Reduction
80 hypothesis may generate similar predictions, i.e., post-conflict affiliation functions to limit
81 renewed aggression and conflict escalation (Table 1). However, these hypotheses differ in at
82 least three important ways. First, at the proximate level, the underlying motivations for post-
83 conflict affiliation differ. In the Uncertainty Reduction hypothesis, both victims and
84 aggressors affiliate to reduce physiological stress and anxiety about future interactions (the
85 distress may come from the damage to a valuable relationship, or because opponents live in
86 proximity and may incur future costs - e.g., of increased vigilance or decreased tolerance - if
87 conflicts persist) (Aureli et al., 2002). In contrast, the Submissive hypothesis posits that
88 victims submit to comply with aggressors out of fear, often conferring immediate
89 social/sexual benefits upon aggressors. Second, the Submissive hypothesis posits that victims
90 affiliate to comply with their aggressor's demands, rather than to preserve a valuable
91 relationship (as clarified by the Integrated hypothesis). Consequently, the asymmetry of
92 power between opponents rather than the strength of their social bond (relationship value)
93 should predict the occurrence of PC affiliation. Third, the Submissive hypothesis predicts that
94 victims would be more likely to initiate post-conflict affiliation, in contrast to the Uncertainty
95 Reduction hypothesis, in which such distinctions are neither categorically made nor found
96 (Arnold et al., 2010).

97 Post-conflict interactions among heterosexual pairs have rarely been studied in wild
98 promiscuous primates, but represent an ideal context in which to explore this submissive
99 framework because of pronounced sexual dimorphism and power asymmetries between
100 males and females. Recent work has highlighted a previously underappreciated density and

101 complexity of primate heterosexual relationships (Archie, Tung, Clark, Altmann, & Alberts,
102 2014; Fürtbauer, Heistermann, Schülke, & Ostner, 2014; Machanda, Gilby, & Wrangham,
103 2013; Reddy & Mitani, 2020). On the one hand, males and females can form enduring bonds,
104 which enhance individual survival and reproductive success (Archie et al., 2014; Campos et
105 al., 2020; Palombit, 2000). On the other hand, heterosexual relationships can be violent since
106 males commonly attack sexually receptive females to achieve mating benefits, either
107 immediately (through forced copulation or sexual harassment) or subsequently (through
108 intimidation or punishment) (Clutton-Brock & Parker, 1995b; Muller, Kahlenberg, Emery
109 Thompson, & Wrangham, 2007; Smuts & Smuts, 1993). Sexual coercion usually targets the
110 most fertile females and can be costly in terms of stress and injury for the victims (Baniel,
111 Cowlshaw, & Huchard, 2017; Colmenares, Polo, & Herna, 2014; Kitchen et al., 2009;
112 Muller et al., 2007; Swedell et al., 2014). Females could thus benefit from evolving
113 behavioural strategies to decrease the chances of escalated or renewed aggression from
114 coercive males.

115 In the handful of studies to date that have investigated male-female post-conflict
116 affiliation, sexual behaviours have rarely been systematically analyzed. Generally, whereas
117 non-copulatory sexual behaviours (e.g., presenting and mounting) feature commonly in
118 studies of reconciliation, copulations have been omitted as a form of post-conflict affiliation
119 for a number of potential reasons (e.g., they do not occur among same-sex dyads or they do
120 occur but are not interpreted as affiliative acts). When sociosexual contacts are incorporated,
121 they are often aggregated with other affiliative contacts, precluding formal tests between
122 reconciliation and sexual coercion (but see Call et al. 1999). To our knowledge, bonobos are
123 the only species for which copulations and nonconceptive sexual behaviours are thought to
124 play a key role in conciliatory reunions (Clay & de Waal, 2014; Palagi, Paoli, & Tarli, 2004).
125 In less tolerant animal societies where aggression is more severe and asymmetric, it is

126 possible that post-conflict affiliations traditionally interpreted as conciliatory reunions in
127 some cases represent submissive responses to sexual (or other forms of) coercion. In
128 particular, sexual harassment - defined as repeated and costly aggressive mating attempts by
129 males that induce females to mate (Clutton-Brock & Parker, 1995b) - is operationally
130 identified by increases in males' chances to mate with their victims immediately following
131 aggression (compared to baseline chances). Thus, the conceptual frameworks supporting
132 reconciliation and sexual harassment make overlapping predictions regarding increased rates
133 of affiliation following conflicts, provided sexual behaviours count as affiliative interactions.
134 Yet the sexual coercion and reconciliation literatures rarely reference one another.

135 In this paper, we investigate the form and function of post-conflict (PC) affiliative
136 interactions among males and sexually receptive (i.e., swollen) females in wild chacma
137 baboons (*Papio ursinus*). Chacma baboons live in female-bonded societies, where immigrant
138 males fight to achieve dominance and monopolize swollen females through long (i.e., several
139 consecutive days) episodes of mate-guarding around ovulation (Bulger, 1993; Weingrill,
140 Lycett, Barrett, Hill, & Henzi, 2003). Such mate-guarding is coercive in the sense that
141 females cannot escape male proximity, and males regularly herd their consort females away
142 from rivals (Cheney & Seyfarth, 1977; Kitchen, Cheney, & Seyfarth, 2005; Kitchen et al.,
143 2009). While reconciliation has been documented in this species, the focus has predominantly
144 been on female-female dyads (Cheney, Seyfarth, & Silk, 1995; Silk, Cheney, & Seyfarth,
145 1996; Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007). Only one study has focused
146 on PC affiliation among heterosexual chacma baboon dyads, which found that reconciliation
147 commonly occurs between males and pregnant/lactating females when they are involved in a
148 'friendship', a long-term heterosexual social bond formed around an infant (Webb, Baniel,
149 Cowlshaw, & Huchard, 2019). Little is known about patterns of PC affiliation between
150 males and swollen females. Male aggression towards swollen females is common in this

151 species, inflicting frequent injuries to females (Baniel et al., 2017; Kitchen et al., 2009), and
152 functions as a form of sexual intimidation, where repeated aggression throughout the cycle
153 increases the aggressor's chances to consort with the female around ovulation (Baniel et al.,
154 2017). There is, however, no evidence for sexual harassment, where males harass females
155 until they accept matings, as there is no immediate increase in the rate of mating following
156 male aggression (Baniel et al., 2017). On a spectrum ranging from submission to
157 reconciliation, affiliation following conflicts between males and swollen females in this
158 coercive context may fall closer to the former. In this case, female victims would adopt a
159 compliant strategy to reduce the costs of conflict escalation (e.g., injury), while male
160 aggressors enact a coercive strategy to secure immediate or future mating opportunities
161 (Table 1).

162 Here, we test whether the pattern of post-conflict affiliation between heterosexual
163 pairs involving sexually receptive females could be explained by the Submission hypothesis
164 in the context of sexual coercion, via the following four predictions. First, we predicted that
165 increases in PC affiliation between males and swollen females would involve both sexual and
166 non-sexual affiliation (Prediction 1, P1), as intimidated females may use any behavioural
167 strategy at their disposal - e.g., sexual solicitations or grooming - to appease coercive males.
168 Second, we predicted that the rate of PC affiliation between a male and swollen female would
169 not reflect the strength of their social bond in baseline conditions (i.e., outside of an
170 aggressive context) (P2). Third, we predicted that the rate of PC affiliation would increase in
171 more coercive contexts; namely, mate-guarded females should display a higher rate of PC
172 affiliation than unguarded females, because they cannot escape the spatial proximity of their
173 aggressor and thus have a higher incentive to de-escalate conflicts with him (P3). Lastly, we
174 predicted asymmetrical patterns in who initiates PC affiliation, particularly when it comes to
175 sexual affiliations, where females should be mostly responsible for initiating the first

176 affiliative act (P4a) and/or the first sexual act of the PC affiliation sequence (P4b) in order to
177 display submission and propose positive sociosexual contacts to coercive males following
178 aggression.

179 This predictive framework differentiates itself from that generated by previous
180 hypotheses to explain post-conflict affiliation, including both the Sexual Harassment
181 hypothesis, and the Integrated hypothesis. According to the former, if patterns of affiliation
182 solely reflected sexual harassment, we would expect no support for P1 (rather, we would
183 expect only sexual PC affiliation to increase) or P4 (we would expect males rather than
184 females to initiate with copulations). According to the latter, if patterns of affiliation solely
185 reflected attempt to reduce anxiety and repair a valuable bond, we would expect no support
186 for P2 or P3 (because we would expect baseline affiliation rather than the power asymmetry
187 between opponents to predict PC affiliation).

188

189 **MATERIALS & METHODS**

190 **Data collection**

191 We studied two habituated groups of wild chacma baboons living at Tsaobis Nature Park, a
192 semi-arid environment in Namibia (Cowlshaw, 1997) over four field seasons (2005, 2006,
193 2013 and 2014) of variable length (5 to 9 months per year). Groups contained 3 to 11 adult
194 males and 9 to 19 adult females according to the period of study. Dominance ranks of adult
195 males and females were established using both ad libitum and focal observations of dyadic
196 agonistic interactions (see Supplementary text)

197 The reproductive state of each adult female was monitored daily and categorized as
198 pregnant, lactating, cycling swollen (i.e., sexually receptive with a perineal swelling), and
199 cycling non-swollen (i.e., between two swelling phases). Mate guarding episodes, defined as
200 periods when swollen females were constantly followed by a male that mated exclusively

201 with them and prevented others from doing so (Alberts, Altmann, & Wilson, 1996), were
202 monitored ad libitum on a daily basis, and confirmed or updated accordingly for each focal
203 observation. In the following analyses, we focused only on cycling swollen females and their
204 interactions with adult males.

205 Observers followed groups on foot daily from dawn to dusk, conducting 1-hour focal
206 observations on all adult females and males, spread equally across the day. In total, we
207 collected 1418 focal observations on 40 swollen females (mean \pm SD: 35.5 \pm 32.2 observations
208 per individual) and 524 observations on 25 males (21.0 \pm 8.8) (male focal observations were
209 only collected in 2013-14). During observations, we continuously recorded all occurrences of
210 male-female agonistic and affiliative interactions involving the focal individual, including the
211 partner's identity and the direction of the interaction. Agonistic interactions comprised
212 attacks (any aggressive physical contact), chases, and physical threats (including staring, head
213 bobbing, and ground sweeping while oriented toward the targeted individual) and approach-
214 avoid interactions (supplants, displacements). For the analysis of post-conflict affiliation, we
215 only used attacks, chases, and physical threats because more subtle agonistic interactions
216 such as displacements, supplants, or vocal threats are less likely to be stressful for the victim.
217 As expected on the basis of pronounced sexual dimorphism, 98% of aggression between
218 males and swollen females (i.e., 92 of 94 observed conflicts) were directed from males to
219 females. Affiliative interactions included grunts, positive facial expressions (come-here faces,
220 lip-smacks, sniff-mouths), positive physical contacts (touching, embracing, grooming,
221 sniffing or touching perineum, mounting, grasping pelvis) and sexual behaviour (presents,
222 copulations). Note that swollen females in this species invite males to copulate by presenting,
223 which can potentially directly lead to sex. A female's presenting behavior can be either
224 followed by a copulation (in which case, observers only noted the copulation and indicated
225 that the copulatory act was female-initiated) or not followed by a copulation when the male

226 ignores the female's initiative (in which case, observers only recorded the presenting bout).
227 For each copulation, we thus recorded if it was initiated by the female (via presenting) or by
228 the male (by approaching and usually grabbing the female's hindquarters).

229

230 **Statistical Analyses**

231 **Rate of sexual and non-sexual PC affiliation**

232 We first tested whether swollen females and males exhibit higher rates of affiliation
233 following male aggression (compared to baseline conditions), and whether any increase
234 detected in PC affiliation is primarily attributable to increases in sexual versus non-sexual
235 behaviours (P1). Using the collected focal observations of males and swollen females, and
236 following a statistical methodology previously validated in our study system (Webb et al.,
237 2019), we established the rate of (1) sexual affiliation (presenting and copulations) and (2)
238 non-sexual affiliation (e.g. grunts, grooming, etc) between a given heterosexual dyad
239 immediately after a conflict (i.e., the PC sexual and non-sexual affiliation rate) versus in the
240 absence of an immediate conflict (i.e., the baseline sexual and non-sexual affiliation rate).
241 Specifically, for each heterosexual dyad that exchanged at least one act of aggression, we
242 first identified all focal observations that were conducted on both individuals in a given year
243 and in which the female was swollen. Then, we split these observations into two categories.

244 First, the PC sample, in which we pooled all 15-minute observations following a
245 conflict between the same dyad together (i.e., dyads had between 1-5 conflicts, each of which
246 generated a 15-min observation period, so we pooled the corresponding 15-75 minutes of PC
247 observation together to calculate the rate of PC affiliation of a given dyad). We chose a
248 duration of 15 minutes following each conflict because our validation study identified this
249 time window as the best trade-off between the number of available PC observations (which
250 decreases as time period increases) and the strength of the reconciliation signal (which

251 increases as time period increases) (Webb et al., 2019). Incomplete PC observations (e.g.,
252 due to the focal individual going out of sight or the occurrence of another bout of aggression
253 shortly after the first one) were retained only if they lasted for at least 9 min without
254 interruption (mean \pm SD=12.1 \pm 1.6min, N=15 incomplete PC out of 94 total PC observations).
255 This 9 min threshold was chosen because the mean latency between aggression and the first
256 affiliative act was 4.5 \pm 4.2min (calculated over 37 occurrences of PC affiliation in complete
257 PC observations). We thus considered that 9 min would be enough time to capture - in most
258 cases - the potential occurrence of PC affiliation acts.

259 Second, for the baseline sample, we pooled the rest of the focal observations of the
260 dyad. To establish those baseline rates, we excluded each 15-minute period following a
261 conflict (i.e., the PC samples), as well as each 15-minute period at the start of the focal or
262 following its resumption after the focal individual briefly went out of sight (in case an
263 aggression occurred between the two members of the dyad when they were not visible).
264 Third, we tabulated the number of times that the two individuals affiliated sexually or non-
265 sexually in the PC and baseline samples, respectively, as well as the total observation time of
266 the corresponding (i.e., PC or baseline) sample.

267 We compared the strength of the PC affiliation signal between males and swollen
268 females when considering only sexual affiliations versus only non-sexual affiliations. We
269 thus ran two negative binomial GLMMs using the total number of affiliations exchanged
270 between each male and swollen female dyad as the response variable and including (1) only
271 sexual affiliations or (2) only non-sexual affiliations in the count. Fixed effects comprised the
272 type of observation (PC versus baseline samples) and the dominance ranks of the female and
273 male. The total observation time of the corresponding sample (PC or baseline) was log-
274 transformed and included as an offset variable. Random effects comprised the identity of the
275 female and male.

276

277 **Determinants of the occurrence of PC affiliation**

278 We then investigated the determinants of the presence (versus absence) of PC affiliation in
279 the subsequent 15 minutes following aggression (N=94 PC observations), namely with
280 respect to the strength of the affiliative relationship of the dyad in baseline conditions (i.e.,
281 outside of an aggressive context, P2) and female mate-guarding status (P3). We ran a
282 binomial GLMM using the occurrence of affiliation following an aggressive event (yes/no) as
283 the response variable. Fixed effects comprised the mate-guarding status of the swollen female
284 (unguarded versus mate-guarded by the aggressor), the dyad's baseline affiliation rate
285 (calculated via the occurrence of sexual and non-sexual behaviours in swollen periods),
286 female rank, male rank, and the type of aggression (chase, attack, threat). For both models,
287 random effects comprised the identities of the female and male. As supplementary analysis,
288 we also calculated the dyad's baseline affiliation rate using focal observations where the
289 female was non-swollen only.

290

291 **Pattern of initiation of PC affiliation**

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

295

296 All GLMMs were run using the glmer function of the lme4 package (Bates, Maechler, Bolker,
297 & Walker, 2014) in R version 3.5.2 (R Core Team, 2018). The significance of the fixed
298 factors was tested using a likelihood ratio test, LRT (assuming an asymptotic chi-square
299 distribution of the test statistic) via the drop1 function. We further computed the 95%
300 parametric bootstrap confidence intervals of fixed factors (using confint.merMod) and

301 checked that they did not cross zero. To validate models, we examined the distribution of
302 residuals and confirmed the absence of overdispersion by using the DHARMA package
303 (Hartig, 2018). Sample size is indicated for each model in the relevant output table.

304

305 **Ethical Note.** This study is strictly observational and relies on behavioural data collected
306 non-invasively on animals well-habituated to human observers. Our research procedures were
307 evaluated and approved by the Ethics Committee of the Zoological Society of London and
308 the Ministry of Environment and Tourism (MET), Namibia, and adhered to the ASAB/ABS
309 Guidelines for the Treatment of Animals in Behavioural Research and Teaching. Our
310 research was conducted under MET permit numbers 886/2005, 1039/2006, 1786/2013 and
311 1892/2014.

312

313 **RESULTS**

314 **Heterosexual dyads engage in sexual and non-sexual PC affiliation**

315 We observed 94 incidents of male aggression towards swollen females. Of these, 73 had a
316 documented context (as inferred by the observer): 42% were unprovoked (no apparent reason
317 for the male to attack the female), 25% were apparently triggered by the female leaving the
318 male's spatial proximity and may represent herding, 15% involved redirected aggression to
319 the female following an aggression received from a rival male, 10% occurred during feeding
320 bouts, and 7% occurred during intra-group male display (wahoo bouts) or inter-group
321 interactions. Of those 94 observed agonistic interactions, 43 (46%) were followed by at least
322 one affiliative act between the male and swollen female in the following 15 minutes. The
323 latency before the first affiliative act was 4.7 ± 4.2 min on average (range: 0-13min). As
324 expected under P1, the observed rates of affiliation between males and swollen females
325 following conflicts are significantly higher rates (~3 times more) than in baseline samples

326 when considering exclusively sexual behaviours (mean rate of affiliation \pm SD in PC:
327 0.033 \pm 0.054 events/min and in baseline: 0.010 \pm 0.011) (Table 2, Figure 1a). The same was
328 true when considering exclusively non-sexual behaviours (mean rate of affiliation \pm SD in PC:
329 0.044 \pm 0.069 events/min and in baseline: 0.013 \pm 0.017) (Table 2, Figure 1a). Females were
330 more likely to exhibit sexual affiliations (but not more non-sexual affiliations) with high-
331 ranking males in both PC and baseline conditions.

332

333 **PC affiliation peaks in dyads involving mate-guarded females**

334 Heterosexual dyads with strong affiliative relationships in baseline conditions were not more
335 likely to display affiliation following aggression (Table 3 and Table A1), consistent with P2.
336 Nonetheless, there were a high uncertainty around this effect, with a lot of variation across
337 dyads (Figure A1). According to P3, higher rates of PC affiliation are expected when females
338 are confined in close proximity to mate-guarding males. The need for PC affiliation under
339 these circumstances is highlighted by the finding that 38 of 41 recorded incidences of male
340 aggression toward mate-guarded females came directly from their consort male. As predicted,
341 males and swollen females involved in a mate-guarding consortship were more likely to
342 exhibit PC affiliation than when they were not involved in a consortship (Table 3 and Figure
343 1b).

344

345 **Swollen females initiate most sexual PC affiliations**

346 When PC affiliation occurred (N=43 cases), 32 (74%) incidences involved at least one sexual
347 behaviour and 11 (26%) involved exclusively non-sexual behaviours in the 15min sequence
348 following aggression. Among those 43 PC sequences, the first PC affiliative act was initiated
349 equally by males and females, contrary to P4a: males initiated 23 PC affiliations and females
350 initiated 20 PC affiliations (two-sided exact binomial test: p-value=0.761, 95% confidence

351 interval: 0.31-0.62; see Figure 2a and Table A2 for behavioural details on the first affiliative
352 act). However, when focusing on those 30 PC affiliations that contained at least one sexual
353 act (two sexual interactions had unknown initiators), the first sexual behaviour was initiated
354 21 times by the female - mostly via presenting - and nine times by the male, in accordance
355 with P4b (two-side exact binomial test: p -value=0.043, 95% confidence interval: 0.51-0.85;
356 Table A2, Figure 2b). In the 11 PC affiliations that remained exclusively non-sexual, three
357 were initiated by females and eight by males.

358

359 **DISCUSSION**

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

375

376 **PC affiliation reflects female submission to male intimidation**

377 The observed pattern of PC affiliation between male and female baboons does not reflect a
378 strict sexual harassment strategy, where males attack or persistently run after females until
379 they accept mating, as reported in some ungulates (Clutton-Brock & Parker, 1995b) and
380 orangutans (Fox, 2002; Knott, 2009). Indeed, male baboons seldom initiated copulations
381 following aggression (male-initiated copulations only represented 18% of the first affiliative
382 act and 30% of the first sexual act, see Table A2). Instead, females were mostly responsible
383 for initiating PC sexual behaviour by presenting to the male. Furthermore, the observed
384 increases in rates of non-sexual affiliation following conflicts were not expected under the
385 sexual harassment hypothesis, which exclusively focuses on sexual behaviour.

386 The fact that female baboons are primarily responsible for initiating the first sexual
387 act following aggression is more compatible with a scenario of long-term sexual intimidation,
388 where females would express sexual compliance towards males to appease them and limit
389 escalated aggression and future injuries. Males, on the other hand, may rarely pursue
390 immediate mating opportunities following aggression (and female presenting) to avoid
391 unnecessary matings, especially when the female is not in her ovulatory window (which can
392 be costly, e.g., sperm depletion) (Gesquiere, Wango, Alberts, & Altmann, 2007; Moscovice
393 et al., 2010; Weingrill, Lycett, & Henzi, 2000). Instead, they seem to use repeated aggressive
394 and affiliative behaviour to optimise their control of female spatial behaviour. In our
395 population, 42% of male attacks toward swollen females are unprovoked, sudden, and
396 probably unpredictable. Such randomly-timed attacks provide an effective means for the
397 aggressor to generate continuous anxiety, vigilance, and chronic stress in his victims (Silk,
398 2002). In line with this, half of our observed PC affiliation events happened in the context of
399 mate-guarding, where females have no choice but to stay in the proximity of their aggressor
400 and are thus likely to face renewed aggression. Mate-guarding episodes are particularly long

401 in chacma baboons (between 0.5 and 32 days, mean=9 days), and can last several consecutive
402 cycles (Baniel, Cowlshaw, & Huchard, 2016). Females might particularly benefit from
403 displaying their compliance in this context. Similar long-term sexual intimidation strategies is
404 also thought to occur in some chimpanzee (*Pan troglodytes*) populations: males who are
405 repeatedly aggressive toward particular females are more likely to mate with them during
406 ovulatory periods and more likely to sire their offspring (Feldblum et al., 2014; Muller,
407 Emery Thompson, Kahlenberg, & Wrangham, 2011; Muller et al., 2007; Muller, Kahlenberg,
408 & Wrangham, 2009).

409 The patterns of subordination observed in female chacma baboons immediately
410 following male aggression also resemble those seen in hamadryas baboons (*Papio*
411 *hamadryas*), where males use frequent aggression to enforce the spatial proximity of females
412 that are newly incorporated into their harem. New females spend more time affiliating with
413 their leader male than do resident females, and in particular groom him following aggression
414 (Swedell, 2015; Swedell & Schreier, 2009). In the long term, the aggression they face from
415 him decreases once their social bond is established and when females are "conditioned" (or
416 "abducted") to follow their leader male (Polo & Colmenares, 2012; Swedell, 2015; Swedell
417 & Schreier, 2009). Male aggression therefore specifically targets females that are weakly
418 bonded to the aggressor, presumably to dissuade them from dispersing or leaving male
419 proximity. The conditioning of female hamadryas baboons is probably similar to the pattern
420 we report in chacma baboons, particularly for consorting partners, where males may seek to
421 condition their female consorts to stay in proximity. It would be interesting to test if male
422 aggression toward female chacma baboons decreases once the mate-guarding episode is well-
423 established and as females become more compliant (the same heterosexual dyad often consort
424 during the receptive phase across several consecutive cycles), and if females' propensity to

425 propose sex following aggression decreases the chances of renewed aggression or conflict
426 escalation.

427

428 **Variation in the function of PC affiliation**

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

441 A subset of PC interactions may thus be conciliatory, an interpretation reinforced by
442 the existence of true reconciliation between new mothers and their male friends in the same
443 population (Webb et al., 2019), as well as among female-female dyads in this species
444 (Cheney et al., 1995; Silk et al., 1996; Wittig et al., 2007). This may also explain the
445 observed trend in the effect of baseline affiliation rates on rates of PC affiliation (Figure A1),
446 which may reflect this minority of conciliatory PC affiliation. We might expect the
447 occasional occurrence of reconciliation between swollen females and males on the basis that
448 a given male and cycling female dyad occasionally maintains a preferential relationship (in
449 terms of grooming or proximity) that may last across consecutive female cycles (Baniel et al.,

450 2016) and that may become a friendship when they conceive an offspring together, therefore
451 affording fitness benefits to both partners (Archie et al., 2014; Cheney, Silk, & Seyfarth,
452 2012). For a swollen female, reconciling with males may further enable immediate benefits
453 such as spatial association and tolerance, access to better food patches, and provide a buffer
454 against other aggressive groupmates. For males, reconciliation may encourage swollen
455 females to tolerate their proximity and therefore minimize the risk of extra-pair matings or
456 the loss of mate-guarding to rivals (Bercovitch, 1995; Smuts, 1985).

457

458 **Sex under coercion or affiliative ‘make-up’ sex?**

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

470 While female chacma baboons may occasionally choose to use sexual affiliations to
471 reconcile, such voluntary choice probably does not reflect the general pattern in our
472 population, where sexual affiliations are more likely to reflect sexual appeasement under
473 duress given the support we found for the Submissive hypothesis. So overall, although sexual
474 PC affiliation behaviour may appear similar in baboons and bonobos, the motivational and

475 emotional basis of PC affiliation likely differs for the initiator in most cases: whereas female
476 baboons may generally sexually submit out of fear, female bonobos may use sexual contacts
477 in a more symmetric way - though observations suggest that such contacts are not necessarily
478 always consensual (Zanna Clay and Martin Surbeck, pers. comm.). Interpretations concerning
479 both ultimate functions and proximate motivations for PC behaviours should thus reflect the
480 broader social dynamics of a given social system (such as power asymmetries between males
481 and females).

482

483 **Wider implications for the reconciliation literature**

484 The idea that PC affiliative behaviour, whether sexual or not, serves a submissive function
485 contrasts with previous hypotheses, which generally revolve around conciliatory explanations
486 (see Table 1) (Aureli & van Schaik, 1991; Kappeler & van Schaik, 1992; Silk, 1996). The
487 Uncertainty Reduction and Integrated hypotheses emphasize the symmetric function of PC
488 affiliation to alleviate anxiety and restore a damaged, reciprocal, and mutually beneficial
489 bond, whereas the Submission hypothesis highlights its asymmetry in dyads characterized by
490 pronounced power imbalances. While the reconciliation literature has occasionally alluded to
491 the submissive pattern of reconciliation (de Waal, 1986; Kutsukake & Clutton-Brock, 2006),
492 our study is the first to formally test its predictions and emphasize the full spectrum of
493 possible post-conflict patterns. In this study, we tested the Submissive hypothesis in the
494 specific context of coercive relationships between males and fertile female baboons, but it
495 may apply to any kind of asymmetric relationships, which are ubiquitous in animal societies.
496 By (re)framing the study of post-conflict behavior in the context of hierarchical relationships,
497 the Submissive hypothesis generates unique predictions from existing reconciliatory
498 frameworks, but does not exclude other hypotheses previously proposed to explain the

499 occurrence of PC affiliation; such hypotheses are complementary, rather than mutually
500 exclusive, within a given species or even dyad.

501 Taken together, our results emphasize the diversity of relationships possible within
502 and across dyads, where the function of PC affiliation may vary from reconciliation to
503 submission depending on the context and quality of the social bond. Attempts to separate
504 these two hypotheses at the species level may be oversimplistic given the sophistication of
505 social strategies and the individualized nature of social bonds within primate groups (Cheney
506 & Seyfarth, 2007; Smuts & Smuts, 1993).

507

508 **Conclusion**

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

522

523

524 **REFERENCES**

- 525 Alberts, S. C., Altmann, J., & Wilson, M. L. (1996). Mate guarding constrains foraging
526 activity of male baboons. *Animal Behaviour*, *51*(6), 1269–1277. Archie, E. A., Tung, J.,
527 Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters : both same-
528 sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings*
529 *of the Royal Society B-Biological Sciences*, *281*(1793), 20141261.
- 530 Albers, P. C. H., & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of
531 dominance strengths. *Animal Behaviour*, *61*(2), 489–495.
- 532 Arnold, K., Fraser, O. N., & Aureli, F. (2010). Postconflict reconciliation. In C. J. Campbell,
533 A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in*
534 *Perspective* (pp. 608–625). Oxford, UK: Oxford University Press.
- 535 Aureli, F. (1997). Post-conflict anxiety in nonhuman primates: The mediating role of emotion
536 in conflict resolution. *Aggressive Behavior*, *23*(5), 315–328.
- 537 Aureli, F., Cords, M., & van Schaik, C. P. (2002). Conflict resolution following aggression in
538 gregarious animals: A predictive framework. *Animal Behaviour*, *64*(3), 325–343.
- 539 Aureli, F., & van Schaik, C. P. (1991). Post-conflict behaviour in long-tailed macaques
540 (*Macaca fascicularis*): II. Coping with the uncertainty. *Ethology*, *89*(2), 101–114.
- 541 Baniel, A., Cowlshaw, G., & Huchard, E. (2017). Male violence and sexual intimidation in a
542 wild primate society. *Current Biology*, *27*(14), 2163-2168
- 543 Baniel, A., Cowlshaw, G., & Huchard, E. (2016). Stability and strength of male-female
544 associations in a promiscuous primate society. *Behavioral Ecology and Sociobiology*,
545 *70*(5), 761–775.
- 546 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: linear mixed-effects models
547 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)
548 [project.org/package=lme4](http://cran.r-project.org/package=lme4).

- 549 Bercovitch, F. B. (1995). Female cooperation, consortship maintenance, and male mating
550 success in savanna baboons. *Animal Behaviour*, *50*, 137–149.
- 551 Bulger, J. B. (1993). Dominance rank and access to estrous females in male savanna baboons.
552 *Behaviour*, *127*, 67–103.
- 553 Call, J., Aureli, F., & de Waal, F. B. M. (1999). Reconciliation patterns among stumptailed
554 macaques: A multivariate approach. *Animal Behaviour*, *58*(1), 165–172.
- 555 Campos, F. A., Villavicencio, F., Archie, E. A., Colchero, F., Alberts, S. C., & Alberts, S. C.
556 (2020). Social bonds , social status and survival in wild baboons: a tale of two sexes.
557 *Philosophical Transactions of the Royal Society B*, *375*, 20190621.
- 558 Cant, M. A. (2010). The role of threats in animal cooperation. *Proceedings of the Royal*
559 *Society B: Biological Sciences*, *278*(1703), 170–178.
- 560 Cheney, D. L., & Seyfarth, R. M. (1977). Behavior of adult and immature male baboons
561 during intergroup encounters. *Nature*, *269*, 404–406.
- 562 Cheney, D. L., & Seyfarth, R. M. (2007). *Baboon metaphysics - The evolution of a social*
563 *mind*. Chicago: The University of Chicago Press.
- 564 Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The role of grunts in reconciling
565 opponents and facilitating interactions among adult female baboons. *Animal Behaviour*,
566 *50*, 249–257.
- 567 Cheney, D. L., Silk, J. B., & Seyfarth, R. M. (2012). Evidence for intrasexual selection in
568 wild female baboons. *Animal Behaviour*, *84*, 21–27.
- 569 Clay, Z., & de Waal, F. B. M. (2014). Sex and strife: Post-conflict sexual contacts in bonobos.
570 *Behaviour*, *152*, 313–334.
- 571 Clutton-Brock, T. H., & Parker, G. A. (1995a). Punishment in animal societies. *Nature*, *373*,
572 209–216.
- 573 Clutton-Brock, T. H., & Parker, G. A. (1995b). Sexual coercion in animal societies. *Animal*

574 *Behaviour*, 49, 1345–1365.

575 Colmenares, F., Polo, P., & Herna, V. (2014). Male takeovers are reproductively costly to
576 females in hamadryas baboons: A test of the sexual coercion hypothesis. *PLoS ONE*,
577 9(3), e90996.

578 Cords, M., & Aureli, F. (1996). Reasons for reconciling. *Evolutionary Anthropology*, 2(5),
579 42–45.

580 Cowlishaw, G. (1997). Refuge use and predation risk in a desert baboon population. *Animal*
581 *Behaviour*, 54(2), 241–253.

582 de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *The*
583 *Quarterly Review of Biology*, 61(4), 459–479.

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

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

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

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

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

597 Fürtbauer, I., Heistermann, M., Schülke, O., & Ostner, J. (2014). Low female stress hormone
598 levels are predicted by same- or opposite-sex sociality depending on season in wild

599 Assamese macaques. *Psychoneuroendocrinology*, 48, 19–28.

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

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

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

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

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

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

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

622 Knott, C. D. (2009). Orangutans: sexual coercion without sexual violence. In M N Muller &
623 R. W. Wrangham (Eds.), *Sexual coercion in primates and humans: an evolutionary*

- 624 *perspective on male aggression against females* (pp. 81–111). Cambridge, Mass.:
625 Harvard University Press.
- 626 Kutsukake, N., & Clutton-Brock, T. H. (2006). Aggression and submission reflect
627 reproductive conflict between females in cooperatively breeding meerkats *Suricata*
628 *suricatta*. *Behavioral Ecology and Sociobiology*, 59(4), 541–548.
- 629 Machanda, Z. P., Gilby, I. C., & Wrangham, R. W. (2013). Male-female association patterns
630 among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *International*
631 *Journal of Primatology*, 34(5), 917–938.
- 632 Moscovice, L. R., Di Fiore, A., Crockford, C., Kitchen, D. M., Wittig, R., Seyfarth, R. M., &
633 Cheney, D. L. (2010). Hedging their bets? Male and female chacma baboons form
634 friendships based on likelihood of paternity. *Animal Behaviour*, 79, 1007–1015.
- 635 Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male
636 coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of*
637 *the Royal Society B: Biological Sciences*, 274(1612), 1009–1014.
- 638 Muller, M. N., Emery Thompson, M., Kahlenberg, S., & Wrangham, R. (2011). Sexual
639 coercion by male chimpanzees shows that female choice may be more apparent than real.
640 *Behavioral Ecology and Sociobiology*, 65, 921–933.
- 641 Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2009). Male aggression against
642 females and sexual coercion in chimpanzees. In M N Muller & R. W. Wrangham (Eds.),
643 *Sexual coercion in primates and humans: an evolutionary perspective on male*
644 *aggression against females* (pp. 184–217). Cambridge, Mass.: Harvard University Press.
- 645 Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdi, A.
646 Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of
647 progressive evaluation with Elo-rating. *Animal Behaviour*, 82, 911–921.
- 648 Palagi, E., Paoli, T., & Tarli, S. B. (2004). Reconciliation and consolation in captive bonobos

649 (*Pan paniscus*). *American Journal of Primatology*, 62(1), 15–30.

650 Palombit, R. A. (2000). Infanticide and the evolution of male-female bonds in animals. In C.

651 P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 239–

652 268). Cambridge: Cambridge University Press.

653 Polo, P., & Colmenares, F. (2012). Behavioural processes in social context: female

654 abductions, male herding and female grooming in hamadryas baboons. *Behavioural*

655 *Processes*, 90(2), 238–245.

656 R Core Team. (2018). R: A language and environment for statistical computing. In *R*

657 *Foundation for Statistical Computing*. Vienna, Austria. <http://www.r-project.org/>

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

659 affiliative, yet aggressive, relationships with females. *Journal of Human Evolution*, 144,

660 102813.

661 Schaffner, C. M., & Aureli, F. (2004). Conflict resolution. *International Journal of*

662 *Phytoremediation*, 21(1), 295–297.

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

664 Silk, J. B. (2002). Practice random acts of aggression and senseless acts of intimidation: The

665 logic of status contests in social groups. *Evolutionary Anthropology*, 11(6), 221–225.

666 Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (1996). The form and function of post-conflict

667 interactions between female baboons. *Animal Behaviour*, 52, 259–268.

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

669 Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in

670 nonhuman primates and other mammals: evidence and theoretical implications.

671 *Advances in the Study of Behavior*, 22, 1–63.

672 Swedell, L. (2015). *Strategies of sex and survival in female hamadryas baboons: Through a*

673 *female lens*. Upper Saddle River, NJ: Pearson Prentice Hall.

- 674 Swedell, L., & Schreier, A. (2009). Male aggression toward females in hamadryas baboons:
675 conditioning, coercion, and control. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual*
676 *coercion in primates and humans: an evolutionary perspective on male aggression*
677 *against females* (pp. 244–268). Cambridge, Massachusetts: Harvard University Press.
- 678 Swedell, L., Leedom, L., Saunders, J., Pines, M. (2014). Sexual conflict in a polygynous
679 primate: Costs and benefits of a male-imposed mating system. *Behavioral Ecology and*
680 *Sociobiology*, 68(2), 263–273.
- 681 Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In
682 Filippo Aureli & F. B. M. de Waal (Eds.), *Natural Conflict Resolution* (pp. 106–128).
683 Berkeley: University of California Press.
- 684 Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., & de Waal, F. B. M. (2008). A
685 comparative study of conflict resolution in macaques: Insights into the nature of trait
686 covariation. *Animal Behaviour*, 75(3), 847–860.
- 687 Webb, C. E., Baniel, A., Cowlshaw, G., & Huchard, E. (2019). Friend or foe: Reconciliation
688 between males and females in wild chacma baboons. *Animal Behaviour*, 151, 145–155.
- 689 Weingrill, T., Lycett, J. E., Barrett, L., Hill, R. A., & Henzi, S. P. (2003). Male consortship
690 behaviour in chacma baboons: the role of demographic factors and female conceptive
691 probabilities. *Behaviour*, 140, 405–427.
- 692 Weingrill, T., Lycett, J. E., & Henzi, S. P. (2000). Consortship and mating success in chacma
693 baboons (*Papio cynocephalus ursinus*). *Ethology*, 106(11), 1033–1044.
- 694 Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M., & Cheney, D. L. (2007). Kin-
695 mediated reconciliation substitutes for direct reconciliation in female baboons.
696 *Proceedings of the Royal Society B: Biological Sciences*, 274(1613), 1109–1115.

697 **Table 1.** Summary of the main proximate and ultimate hypotheses proposed to explain post-conflict affiliative behaviour.

Hypothesis	Explanation		Evidence (reviewed in Aureli et al. 2002; Arnold et al. 2010)
	Proximate	Ultimate	
Valuable Relationships (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 non-kin or non-affiliates
Uncertainty Reduction (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 behavior (SDB) in victims and aggressors following conflicts are decreased following reconciliation
Integrated (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
Benign Intent (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
Submissive (this study)	<i>Victims:</i> Fear and/or stress/anxiety about conflict escalation <i>Aggressors:</i> Motivation to obtain immediate social/sexual benefits, restore tolerance	<i>Victims</i> Reduce risks of renewed aggression and costs of conflict escalation (e.g., injury) <i>Aggressors:</i> Reap the benefits of subordination/compliance of the victim (e.g., secure grooming or mating opportunities)	Present study

698 **Table 2. Males and swollen females engage in both sexual and non-sexual PC affiliations.** Patterns of post-conflict (PC) and baseline
699 affiliation between males and swollen females when considering only (1) sexual behaviour or (2) non-sexual behaviour.

Response variable	Fixed factor	(1) only sexual behaviour						(2) only non-sexual behaviour					
		Estimate	SE	95% confidence interval	LRT	df	P-value	Estimate	SE	95% confidence interval	LRT	df	P-value
No. of affiliations exchanged between male-female dyads ^a	Intercept	-5.60	0.35	-	-	-	-	-5.9	0.71	-	-	-	-
	PC observation ^b	1.29	0.24	[0.78 ; 1.73]	27.1	1	<0.001	1.20	0.13	[0.98 ; 1.39]	68.3	1	<0.001
	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	[0.8 ; 2.57]	12.4	1	<0.001	0.77	0.64	[-0.53 ; 2.21]	1.44	1	0.230

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

702 ^b Reference category: baseline

703 Parameters and tests are based on 29 females, 27 males, 61 dyads and 94 aggressive events. The negative binomial GLMMs were performed controlling for
704 male and female identity. The 95% confidence intervals that do not cross zero and p-values of statistically significant results are highlighted in bold.

705 **Table 3. Mate-guarded swollen females display higher levels of post-conflict (PC) affiliation with males.**

Response variable	Fixed factor	Level	Estimate	SE	95% confidence interval	LRT	df	P-value
Occurrence of PC affiliation between males and swollen females (yes/no)	Intercept		-1.73	0.85	.	-	-	-
	Mate-guarding status	Mate-guarded	1.55	0.63	[0.46 ; 3.82]	7.48	1	0.006
	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]			

706 Parameters and tests are based on 28 females, 27 males, and 91 aggressive events (including 43 followed by PC affiliation). 53 of those aggressive events
707 involved unguarded swollen females, and 38 involved mate-guarded swollen females. For this model, we removed 3 observed aggressions where mate-
708 guarded females received aggression from a non-consort male. The baseline rate of affiliation of the dyad was calculated using focal observations collected
709 when the female was swollen and outside an aggressive context. Type of aggression refers to attack (“AT”, N=18), chase (“CH”, N=58), or threat (“TH”,
710 N=15). The binomial GLMM was performed controlling for male and female identity. The 95% confidence intervals that do not cross zero and p-values of
711 statistically significant results are highlighted in bold.

712

713 **Table A1. Determinants of the occurrence of PC affiliation between males and swollen females.** Contrary to Table 3, the baseline rate of
 714 affiliation was calculated over non-swollen periods only.

715

Response variable	Fixed factor	Level	Estimate	SE	95% confidence interval	LRT	df	P-value
Occurrence of PC affiliation between males and swollen females (yes/no)	Intercept		-0.53	0.64	-	-	-	-
	Mate-guarding status	Mate-guarded	1.75	0.61	[0.71 ; 4.03]	9.26	1	0.002
	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]			

716 Parameters and tests are based on 25 females, 26 males, and 80 aggressive events (including 38 followed by PC affiliation. The binomial GLMM was
 717 performed controlling for male and female identity. The baseline rate of affiliation of the dyad was calculated using focal observations collected when the
 718 female was non-swollen and outside an aggressive context. The 95% confidence intervals that do not cross zero and p-values of statistically significant results
 719 are highlighted in bold.

720 **Table A2. Behavioural details on the first affiliative act and the first sexual affiliative act.** Type and direction of (a) the first post-conflict
 721 (PC) affiliation act and (b) the first sexual PC affiliation act of a PC sequence (lasting 15 min in total) between males and swollen females. There
 722 were 43 PC sequences containing at least one PC affiliative act and 32 PC sequences containing at least one sexual act.

723

Behaviour	(a) First affiliative act		(b) First sexual act	
	Female initiates	Male initiates	Female initiates	Male initiates
Copulation	2	8	2 ^a	9 ^a
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

724

725 ^aTwo copulations had unknown initiator and are not reported here.

726 **FIGURE LEGENDS**

727

728 **Figure 1. Pattern of post-conflict (PC) affiliation between males and females.** (a) Mean
729 rate of affiliation between swollen females and males in PC versus baseline samples
730 according to whether only sexual affiliations (presenting and copulations) or only non-sexual
731 affiliations are included in the pool of affiliations. Error bars show the standard error of the
732 distribution. (b) Percentage of aggressive events followed by affiliation according to the
733 mate-guarding status of swollen females (unguarded vs mate-guarded by the aggressor).
734 *P<0.05.

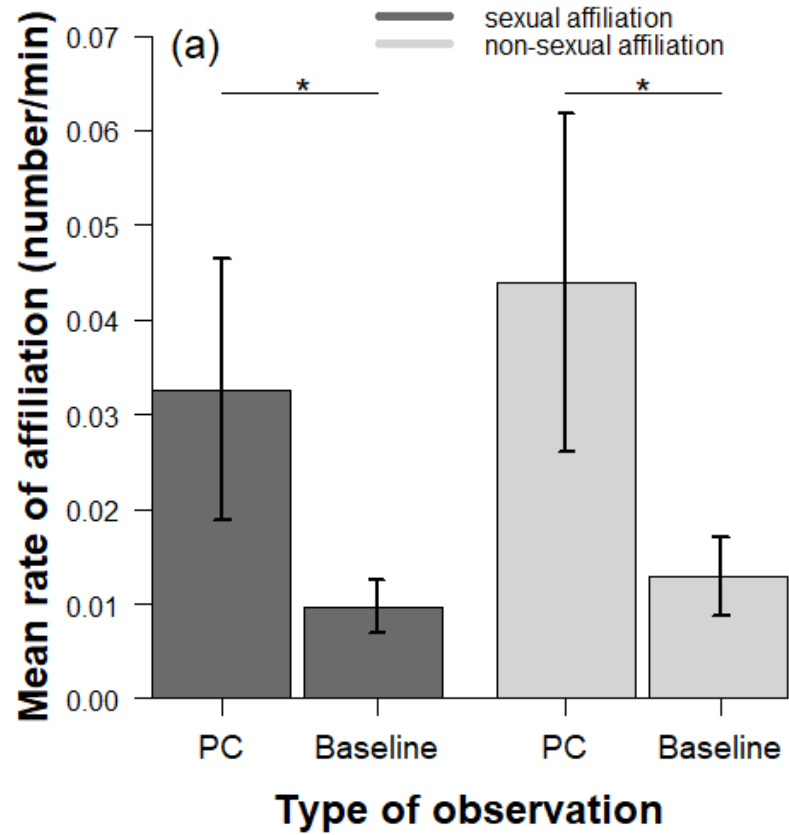
735

736 **Figure 2. Males and females are equally likely to initiate the first post-conflict (PC) act,**
737 **but swollen females initiate the first sexual PC act more often than males.** (a) Percentage
738 of the first PC affiliative act (both sexual and non-sexual behaviour combined) of the PC
739 sequence (lasting 15 minutes) initiated by females and males. (b) Percentage of the first
740 sexual PC affiliative act of the PC sequence initiated by females and males.

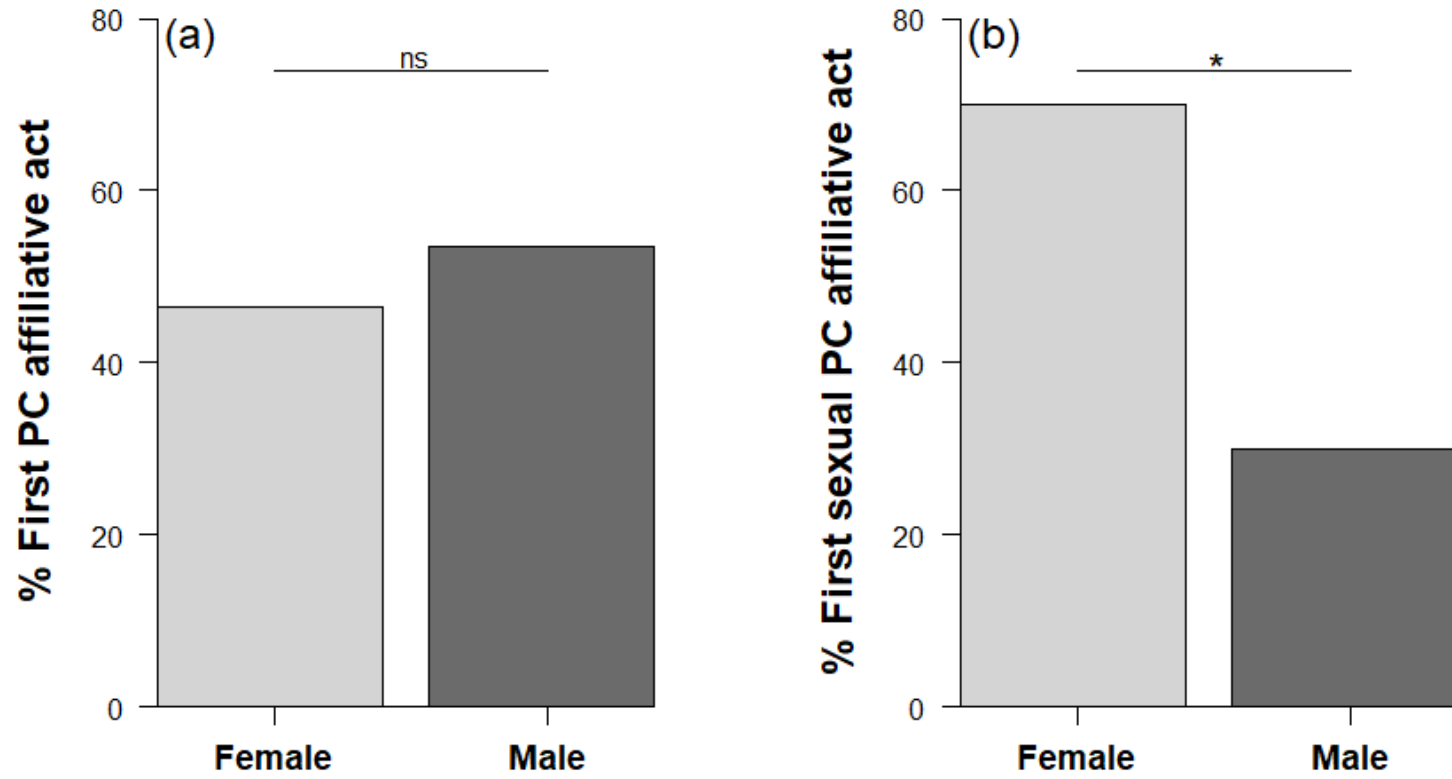
741

742 **Figure A1. The strength of the heterosexual relationship does not influence the**
743 **likelihood of post-conflict (PC) affiliation.** Occurrence of PC affiliation according to the
744 baseline rate of affiliation (i.e. outside of an aggressive context) of the dyad calculated over
745 the (a) swollen or (b) non-swollen period.

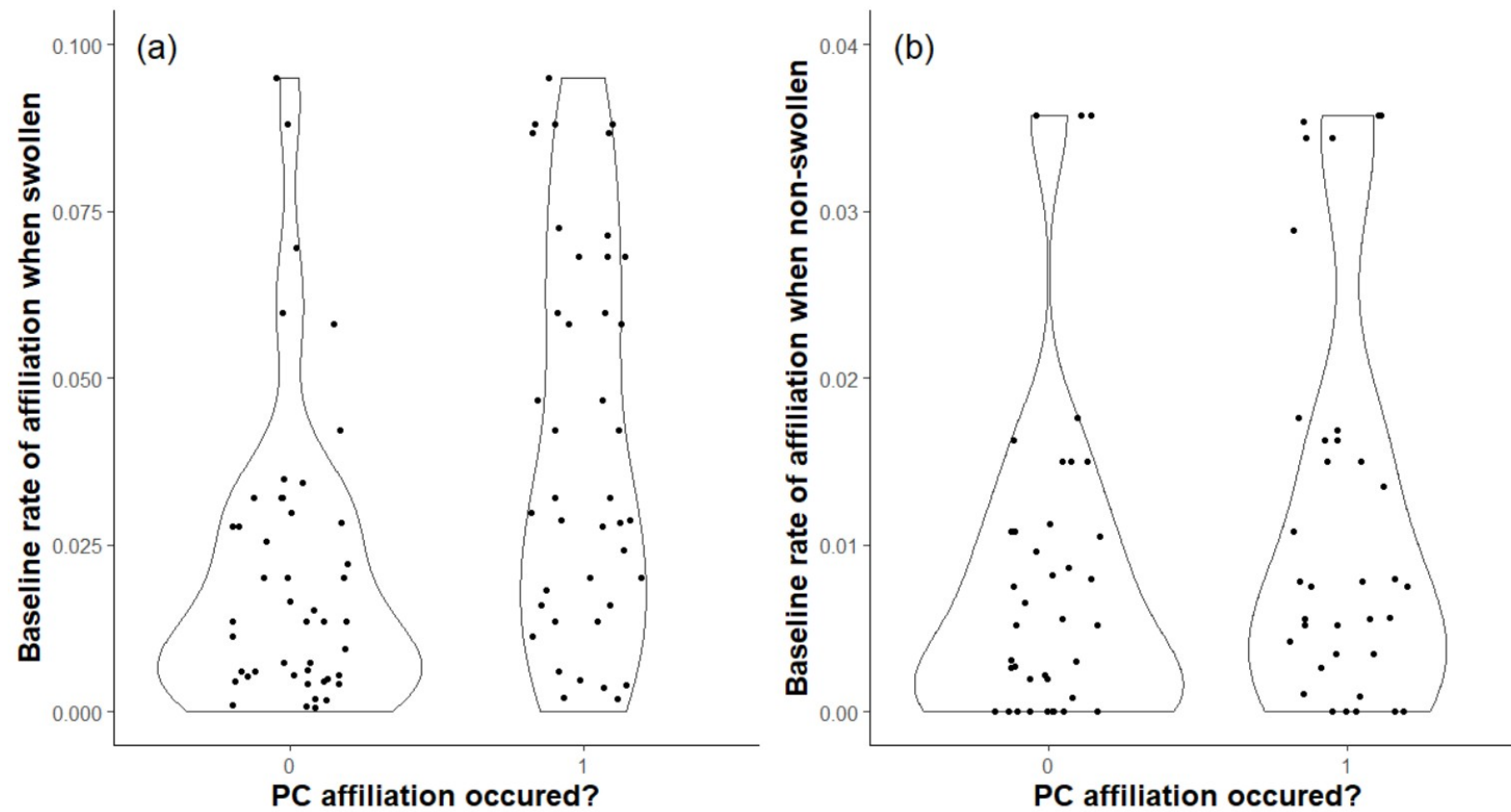
746 **Figure 1.**



747



750 **Figure A1.**



751

APPENDIX

752
753
754
755
756
757
758
759
760
761
762
763
764
765
766
767
768
769
770
771
772
773
774
775
776

Supplementary text. Dominance ranks of males and females

Individual dominance ranks were assessed through focal and *ad libitum* observations of approach-avoid interactions (supplants, when one animal actively displaces another to take its place; displacements, when one animal passes close to another and makes it move away) and agonistic interactions (attacks, any agonistic physical contacts including hits, bites, or grabbing movements; chases, when one animal chases another for a distance of at least 3 m; and threats, including staring, head bobbing, and ground sweeping while oriented toward the targeted individual). Female dominance hierarchies were calculated separately in each year using Matman 1.1.4 (Noldus Information Technology 2003) and were always linear ($N_{2005} = 412$ interactions, $N_{2006} = 576$, $N_{2013} = 367$, $N_{2014} = 1259$ in group L; $N_{2005} = 184$, $N_{2006} = 460$, $N_{2013} = 590$, $N_{2014} = 978$ in group J, Landau's linearity index h : $p < 0.05$ in all cases). In the analyses, we used relative female rank to control for variation in group size, where absolute ranks were standardised to vary between 0-1 using the formula: $1 - ((1-r)/(1-n))$, where r is the absolute rank of an individual (ranging from 1 to the group size, n). In contrast to females, the male hierarchies were much less stable within a year (Baniel et al., 2016), so male ranks were established using an Elo-rating procedure implemented in the R package EloRating (version 0.43) (Neumann et al., 2011). Compared to matrices of dyadic interactions where ranks are calculated over a given time period, an Elo-rating procedure continuously updates rankings according to the temporal sequence of interactions, and is better adapted to situations of unstable social dominance (Albers & de Vries, 2001; Neumann et al., 2011). This gives a score for each individual on each day of observation. We derived a daily standardised rank by scaling the Elo-rating score of each individual proportionally between 0 (corresponding to the minimal score and thus the lowest ranking male) and 1 (corresponding to the maximal score and the highest-ranking male).

Acknowledgments. We are very grateful to the Tsaobis Baboon Project volunteers (2005-06 and 2013-14) for help with data collection, the Tsaobis beneficiaries for permission to work at Tsaobis, the Gobabeb Research and Training Centre for affiliation, and the Snyman and Wittreich families for permission to work on their land. This paper is a publication of the ZSL Institute of Zoology's Tsaobis Baboon Project. Contribution ISEM 2020-339.

Data accessibility statement. The datasets necessary to run the analyses included in this paper have been deposited in the public depository GitHub at <https://github.com/AliceBaniel/The-Submissive-hypothesis>.

Author's contributions. A.B., C.E.W. and E.H. designed the study and performed the analyses. A.B and E.H collected the data. All authors contributed to draft the manuscript.

Funding. A.B. was supported by the Agence Nationale de la Recherche Labex IAST and C.E.W was supported by a Fyssen Foundation postdoctoral fellowship.

Competing interests. We have no competing interests.

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