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4 **Male violence and sexual intimidation in a wild primate society**

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6

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24 **SUMMARY**

25 Sexual violence occurring in the context of long-term heterosexual relationships, such as
26 sexual intimidation, is widespread across human populations [1–3]. However, its evolutionary
27 origins remain speculative because few studies have investigated the existence of comparable
28 forms of sexual coercion in animals [4,5], where repeated male aggression towards a female
29 provides the aggressor with delayed mating benefits [6]. Here, we test whether male
30 aggression towards females functions as sexual coercion in wild chacma baboons (*Papio*
31 *ursinus*). We found support for all three main predictions of the sexual coercion hypothesis
32 [7]: male aggression (1) is greatest against cycling females, (2) is costly and represents the
33 main source of injuries for cycling females, and (3) increases male mating success with their
34 victims in the future. Detailed analysis of chronological sequences between aggression and
35 matings ruled out other coercive mechanisms, such as short-term harassment and punishment,
36 by showing that aggression and matings are temporally decoupled. This decoupling may
37 explain why some forms of sexual violence have been largely overlooked in well-studied
38 animal populations despite their likely impact on the fitness of both sexes. Finally, we found
39 no support for alternative hypotheses such as a female preference for aggressive males [8,9].
40 This new, detailed study of the forms and intensity of sexual intimidation in a wild primate
41 suggests that it may be widespread across mammalian societies, with important implications
42 for understanding the evolution of mate choice and sexual conflict in mammals, as well as the
43 origins of human sexual violence.

44

45 **KEYWORDS:** sexual conflict, sexual coercion, intersexual aggression, coercive mate-
46 guarding, intimidation, promiscuous mating, injury.

47

48 RESULTS

49 Animal studies of sexual conflict have focused on its more conspicuous forms, including
50 infanticide [10,11], forced copulations [12,13], and sexual harassment [14–16]. Pioneering
51 studies exploring more discreet forms of sexual coercion, such as sexual intimidation in
52 chimpanzees (*Pan troglodytes*), have reported that males who direct repeated aggression
53 towards cycling females are more likely to mate with them around ovulation [17–20]. Besides
54 this work and some anecdotal reports [7,21,22], the prevalence and evolutionary importance
55 of sexual intimidation in wild primates remain largely unknown. Here, we investigate the
56 occurrence and forms of sexual coercion in wild chacma baboons (*Papio ursinus*). Chacma
57 baboons live in stable multimale-multifemale groups, where females are philopatric while
58 males disperse and compete for reproductive opportunities [23]. Females develop perineal
59 swellings during their oestrus cycle and mate with multiple males [24], but are often mate-
60 guarded by a dominant male when approaching ovulation [25], which increases their
61 likelihood of paternity [26,27]. First, we tested the three main predictions of the sexual
62 coercion hypothesis [7]: (1) cycling females face higher rates of aggression from males than
63 non-cycling females ('cycling' refers to all cycling females, with and without swellings), (2)
64 aggression directed by males to cycling females translates into a higher rate of injury, and (3)
65 males achieve higher mating success with those females toward whom they are more
66 aggressive. Second, we characterized the forms of coercion by investigating chronological
67 associations between aggression and matings, in order to differentiate between short-term
68 sexual harassment (where mating immediately follows aggression), punishment (where
69 mating with a rival is immediately followed by aggression), and sexual intimidation (where
70 matings and aggression are temporally decoupled). Finally, we also tested an alternative
71 hypothesis to sexual coercion, postulating that the association between male aggression and
72 mating is driven by a female preference for aggressive males, which may provide direct or
73 indirect fitness benefits to females [8,9].

74

75 **1. Does male aggression target cycling females?**

76 We investigated whether the reproductive state of females, defined as swollen (sexually
77 receptive), non-swollen (non-sexually receptive, the non-fertile phase of the cycle), pregnant,
78 or lactating, influenced their chances of receiving aggression from males using a generalized
79 linear mixed model ('GLMM', see Experimental Procedures and Table S1). We found that
80 males preferentially targeted cycling females [swollen: mean±standard deviation: 0.13±0.19
81 time per hour, i.e., once every 8h; non-swollen: 0.12±0.19, 1/9h] and directed much less
82 aggression towards non-cycling females [pregnant: 0.03±0.08, 1/32h; lactating: 0.03±0.08,
83 1/32h] (Table S2, Figure 1a). Cycling females could also attract male aggression if they
84 generate frequent conflicts because males regularly intervene in conflicts [5,28]. However,
85 cycling females do not initiate more aggression towards other group members than non-
86 cycling females (Appendix 1 and Table S3).

87

88 **2. Are cycling females likely to be injured by male aggression?**

89 Of the few female injuries with an observed cause, 78% were inflicted by adult males
90 (N=17/22). We tested whether the risk of injury is higher in cycling than non-cycling females
91 using a GLMM (see Experimental procedures and Table S1). Daily rates of female injury
92 varied across the reproductive cycle, and mirrored the rate of male aggression: swollen
93 females received most injuries (0.014±0.022 injuries per day, i.e., 1 injury every 73 days),
94 followed by non-swollen females (0.009±0.016, 1/115), lactating females (0.005±0.010,
95 1/191), and pregnant females (0.005±0.009, 1/208) (Table S4, Figure 1b). We also found that,
96 within a given cycle, females that faced higher rates of aggression from males suffered more
97 injuries (Table 1, Fig. 2a,b).

98

99 **3. Does aggression by males increase their likelihood of mating with the recipient?**

100 **3a. Do males use short-term sexual harassment?**

101 To test whether a male was more likely to copulate with a female within 5, 10, 15 or 20
102 minutes of assaulting her, we used a matched-control analysis [29]. We tested the difference
103 in the proportion of observations containing copulations with the aggressor in the post-
104 aggression ('PA') and matched-control ('MC') (no aggressive event) observations, using
105 McNemar's Chi-squared tests (see Appendix 2). We found no support for short-term sexual
106 harassment: the probability of copulation did not increase in the 5-20 minutes following male
107 aggression, for either unguarded (Table S5a) or mate-guarded females (Table S5b).

108

109 **3b. Do males use punishment?**

110 We used a similar approach to investigate whether the probability of females receiving male
111 aggression increased within 5, 10 or 15 minutes after copulating with a rival male. We tested
112 the difference in the proportion of aggression received from males who had not mated with
113 the focal female in the post-copulation ('PC') and MC (no copulation) observations (see
114 Appendix 3). We found no evidence for punishment either by non-mated males for
115 unguarded females (Table S5a) or by the consort male for guarded females (Table S5b).

116

117 **3c. Do males use sexual intimidation?**

118 We tested whether a male's probability of mate-guarding a female at her peak fertility (i.e.,
119 during her peri-ovulatory period, called 'POP') increased as a function of the mean hourly
120 rate of aggression received by the female from this male *prior* to her POP, during the same
121 oestrus cycle (calculated using focal observation data). We found that a female who received
122 more aggression from a male throughout her cycle was more likely to be mate-guarded by
123 him during her ovulatory window at the end of that cycle (Table 2, Fig. 2c,d). Overall,

124 females received aggression through their cycle from their future male consort at a rate of
125 0.04 ± 0.09 times/h compared to 0.01 ± 0.05 times/h from other males. Similar results were
126 found when estimating the rate of male-female aggression using *ad libitum* data (Table S6).

127

128 **4. Do females prefer aggressive males?**

129 This last set of results could possibly result from a female preference for aggressive males,
130 rather than from sexual coercion [8,9]. Under this scenario, we would expect some males to
131 express aggressive phenotypes, and females to express a preference for these aggressive
132 phenotypes. To test this alternative hypothesis, we included an additional fixed effect in the
133 GLMM described above, a proxy of male general propensity to aggression, estimated as the
134 *ad libitum* daily rate of male aggression initiated toward any individual of the group per year.
135 In contrast to the dyadic rate of aggression received by a female from a male during an
136 oestrus cycle, a male's general rate of aggression was not found to influence his probability
137 of mate-guarding that female (Table 2, Table S6) .

138

139 **DISCUSSION**

140 Our study extends previous work on sexual coercion in mammals in three ways. First, our
141 results present new evidence supporting the use of sexual intimidation by wild chacma
142 baboons. Such behaviour, previously reported only in chimpanzees [17–20], may therefore
143 occur in a wider range of primates and strengthens the case for an evolutionary origin of
144 human sexual intimidation [2,3]. Earlier work in baboons has underlined the importance of
145 conditioning aggression by male hamadryas baboons, typically expressed when females leave
146 their spatial proximity [30–32], and has also reported higher rates of male aggression against
147 cycling (versus non-cycling) females in chacma baboons [33–36]. Our results further link
148 male-female aggression to mating rates, in support of a core prediction of the sexual coercion

149 hypothesis. By attacking females repeatedly in the weeks preceding ovulation, males appear
150 to increase their chances of monopolizing sexual access to females around ovulation, which
151 in turn increases their probability of successful reproduction [26,27]. Although we cannot
152 demonstrate the causality of this link using correlative data, our analyses rule out several
153 alternative hypotheses, including the proposal that cycling females receive more male
154 aggression than non-cycling females because they are more aggressive, and the proposal that
155 females prefer to mate with aggressive males.

156 Second, we conducted a detailed characterization of the mechanisms of sexual
157 coercion through an analysis of behavioural sequences that reveals the temporal decoupling
158 between aggression and matings. Our results suggest that direct coercion is more important
159 than indirect coercion (i.e., males attempt to increase their own mating rates rather than to
160 decrease those of others), by showing that males rarely punish females who mate with rivals,
161 although it may not be possible to fully disentangle these effects because one aggressive act
162 may simultaneously encourage a female to mate and discourage her to leave.

163 Third, our study points to important fitness costs of sexual intimidation for females.
164 Previous evidence has been limited to the finding that fertile female chimpanzees experience
165 higher stress levels than non-fertile females [17]. Here we show that sexual violence is an
166 important source of injuries for fertile females, which can compromise their survival (Fig 2b).
167 Our study may therefore offer an evolutionary explanation for the co-variation between
168 female injury rates and fertility cycles that has been reported from a range of mammals [37–
169 42], including baboons [43,44].

170 Several factors may favour the use of sexual intimidation in baboons and
171 chimpanzees, including the coexistence of males and females in large groups for long periods
172 of time, their sexual dimorphism in body size and armaments, and long-term memory of
173 previous interactions [45,46]. Sexual intimidation may occur in other mammals sharing these

174 traits, but could have easily gone undocumented due to the temporal decoupling between
175 aggression and matings [6]. Recognizing the importance of discreet forms of sexual coercion,
176 by examining their taxonomic distribution and fitness consequences, should become an
177 important focus for future research. The widespread use of sexual intimidation by males may
178 help to explain core aspects of reproductive strategies with consequences for the evolution of
179 mate choice, social structure and sexual dimorphism [47,48].

180

181 **EXPERIMENTAL PROCEDURES**

182 *(a) Study site and population*

183 We studied wild chacma baboons at Tsaobis Nature Park, a semi-arid environment in
184 Namibia [49]. We collected data on two habituated groups. Group composition and periods of
185 data collection are given in Table S7. Only adults were included in the study (see Table S7 for
186 definition), and all were recognizable. Dominance ranks were based on both focal and *ad*
187 *libitum* observations of approach-avoid and agonistic interactions (see Appendix 4).

188

189 *(b) Female reproductive state & mate-guarding patterns*

190 Female reproductive state was recorded daily as pregnant (determined *a posteriori*) if a
191 female gave birth within six months after the day of observation, lactating if she had a
192 dependant infant and had not yet resumed cycling, swollen if she was sexually receptive with
193 a perineal swelling, and non-swollen otherwise. For each cycle, we defined the POP as the 5-
194 day period preceding the day of swelling detumescence, during which ovulation generally
195 occurs [50,51]. Mate-guarding episodes were monitored *ad libitum*.

196

197 *(c) Behavioural data*

198 We conducted one-hour focal animal samples on all adults. We conducted 3439 focal
199 observations on 53 females distributed across reproductive states (Table S8) during which we
200 recorded 222 chases or attacks led by males. Supplants, displacements, and threats were
201 excluded because they are likely to be less stressful for females. We also recorded 520 focal
202 observations of 25 adult males, with 79 chases or attacks towards adult females. In addition,
203 we recorded *ad libitum* agonistic interactions, with 1579 chases or attacks involving an
204 identified adult male/female.

205

206 *(d) Observations of injuries*

207 From 2013 onwards, injuries were recorded daily, including the date, type of wound (open
208 cuts, punctures of the skin, abnormal skin swelling, limps), freshness (presence of wet/dry
209 blood), and likely cause when known. We recorded 101 injuries on 31 adult females. For
210 analyses, we omitted injuries inflicted by adult females and juveniles where known (N=5/22).

211

212 *(e) Statistical analysis*

213 We ran a combination of GLMMs (summarized in Table S1), described below, and matched-
214 control analyses (described in Appendix 2 and 3). For technical details on GLMM
215 procedures, see Appendix 5.

216

217 **Male aggression and female reproductive state**

218 A binomial GLMM with a logit link function was run, using the probability that a female
219 receives male aggression during a one-hour focal observation (yes/no) as the response
220 variable. Reproductive state was fitted as a fixed factor together with the following control
221 variables: female dominance rank, female parity (nulliparous or parous), group sex ratio (the
222 number of adult females divided by the number of adult males, in case females receive more

223 male aggression when the sex ratio is more male-biased), year, and group identity. Random
224 factors comprised female identity and the date of focal sampling.

225

226 **Male aggression and rate of injury**

227 The number of injuries received by a female in a given reproductive state was modelled as a
228 GLMM with a Poisson error structure. The number of days spent in each reproductive state
229 was log-transformed and included as an offset variable. Fixed effects comprised: female
230 reproductive state, dominance rank, parity, group sex ratio, year, and group identity. Female
231 identity was included as a random effect.

232 To test whether females who experience more male aggression during their oestrus
233 cycle suffer more injuries, we ran a second GLMM with a Poisson error structure using the
234 number of injuries received in a given cycle as the response variable. The log-transformed
235 number of days spent in each cycle was fitted as an offset variable. The mean rate (number
236 per hour) of aggressive acts received from any adult male by the female throughout her cycle
237 (calculated using female focal observations) was fitted as a fixed effect. Other fixed and
238 random effects were similar to the previous model, except that the operational sex ratio (the
239 number of cycling females divided by the number of adult males) was fitted instead of the
240 group sex ratio. We included a cycle only if we had >5 focal observations for a female in that
241 cycle.

242

243 **Sexual intimidation and male mating success**

244 We ran a binomial GLMM using the probability that each resident male mate-guards the
245 female during her POP (yes/no) as the response variable. Fixed factors comprised the mean
246 rate of aggression received by the female from the male during the entire cycle, but *prior to*
247 her POP, calculated as the total number of aggressive acts received during focal observations

248 divided by the number of observation hours, prior to her POP; female dominance rank and
249 parity; male dominance rank (to control for increased access of dominant males to receptive
250 females); operational sex ratio; year; and group identity. To test the alternative hypothesis of
251 female preference for aggressive male phenotypes, we included an additional fixed effect: the
252 rate of male aggression toward any individual of the group (total number of *ad libitum*
253 aggressive acts initiated by a male per year divided by the time spent in the group that year
254 and by the number of individuals in the group to control for differences in group size).
255 Random effects comprised the female and male identities, and cycle identity. Only cycles for
256 which we had >5 focal observations of a given female were included.

257 This analysis was replicated using *ad libitum* records of male-female aggression to
258 ensure our estimated rates of aggression reliably captured variation across dyads. We ran the
259 same model as above but calculating the mean daily rate of aggression received by the female
260 from the male during her entire cycle, but *prior to* her POP, as the total number of *ad libitum*
261 aggressive acts received divided by the number of days observed in the cycle. We only
262 included cycles for which >10 days of group observations were available.

263

264 **AUTHOR CONTRIBUTIONS**

265 A.B. and E.H. collected the data and designed the study, A.B ran the analyses, and all authors
266 contributed to draft the manuscript.

267

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278

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412 female reproductive quality and fertility in colony-living baboons (*Papio h. anubis*) in
413 relation to ensuring paternal investment. *Am. J. Primatol.* 71, 529–538.

414 **Table 1.** Influence of the mean hourly rate of male aggression received by females (calculated from focal observations) on their daily rate of
 415 injury. Parameters and tests are based on the observation of 30 injuries and 119 aggressive acts, distributed among 64 cycles of 30 different
 416 females (number of focals per cycle: mean±sd:11.2±5.0). Significant variables appear in bold. SE: Standard Error, LRT: statistic of a likelihood
 417 ratio test, df: degrees of freedom.

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Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Number of injuries received in a given cycle ^a	Rate of male aggression during cycle		2.53	1.11	[0.36 ; 4.70]	4.74	1	0.029
	Female rank		1.04	0.57	[-0.08 ; 2.17]	3.51	1	0.061
	Female parity ^b	nulliparous	0.35	0.4	[-0.45 ; 1.14]	0.70	1	0.402
	Operational sex ratio		0.15	1.28	[-2.36 ; 2.66]	0.01	1	0.905
	Group ^c	L	-0.64	0.57	[-1.76 ; 0.48]	1.31	1	0.253
	Year ^d	2014	-0.38	0.53	[-1.43 ; 0.66]	0.52	1	0.470

419

^a The number of days of the cycle observed fitted as an offset fixed factor, which modelize a daily rate of injury

420

^b Reference category: parous

421

^c Reference category: J group

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^d Reference category: 2013. Injuries were only collected in 2013 and 2014.

423 **Table 2.** Influence of the mean hourly rate of aggression received from a male by an unguarded female throughout her oestrus cycle but prior to
 424 peri-ovulatory period (POP) (calculated from focal observations) on the same male's probability of mate-guarding her during her subsequent
 425 POP. Parameters and tests are based on 58 cycles and 74 male-female aggressive acts, distributed among 30 females (number of focal
 426 observations per cycle: mean±sd:16.07±12.00, number of mate-guarding males per cycle: 1.20±0.72, range: [0-4]), and 39 males, and analysed
 427 using a GLMM. Significant variables appear in bold. SE: Standard Error, LRT: statistic of a likelihood ratio test, df: degrees of freedom. LRT
 428 tests are used to test for the significance of each variable, while the confidence intervals are used to test for the significance of each level of the
 429 qualitative variables.

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Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Probability that a male mate-guards a female during her POP (0/1)	Rate of male-female aggression during cycle		5.22	2.03	[1.24 ; 9.19]	7.47	1	0.006
	Rate of male aggression toward all individuals		47.44	50.35	[-51.25 ; 146.13]	0.85	1	0.356
	Female rank		-0.87	0.48	[-1.81 ; 0.06]	3.37	1	0.066
	Female parity^a	nulliparous	-0.96	0.43	[-1.80 ; -0.12]	5.82	1	0.016
	Male rank		2.30	0.63	[1.06 ; 3.54]	12.01	1	0.001
	Operational sex ratio		0.89	0.99	[-1.05 ; 2.84]	0.83	1	0.364
	Group ^b	L	0.24	0.38	[-0.50 ; 0.98]	0.39	1	0.533
	Year^c	2006	0.61	0.61	[-0.57 ; 1.80]	8.41	3	0.038
	2013	-1.10	0.78	[-2.63 ; 0.43]				
	2014	-0.80	0.75	[-2.26 ; 0.66]				

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^a Reference category: parous

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^b Reference category: J group

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^c Reference category: 2005. LRT tests are used to test for significance of the whole variable “Year”, while the confidence intervals are used to test for significance of each level of the variable.

434

FIGURES LEGENDS

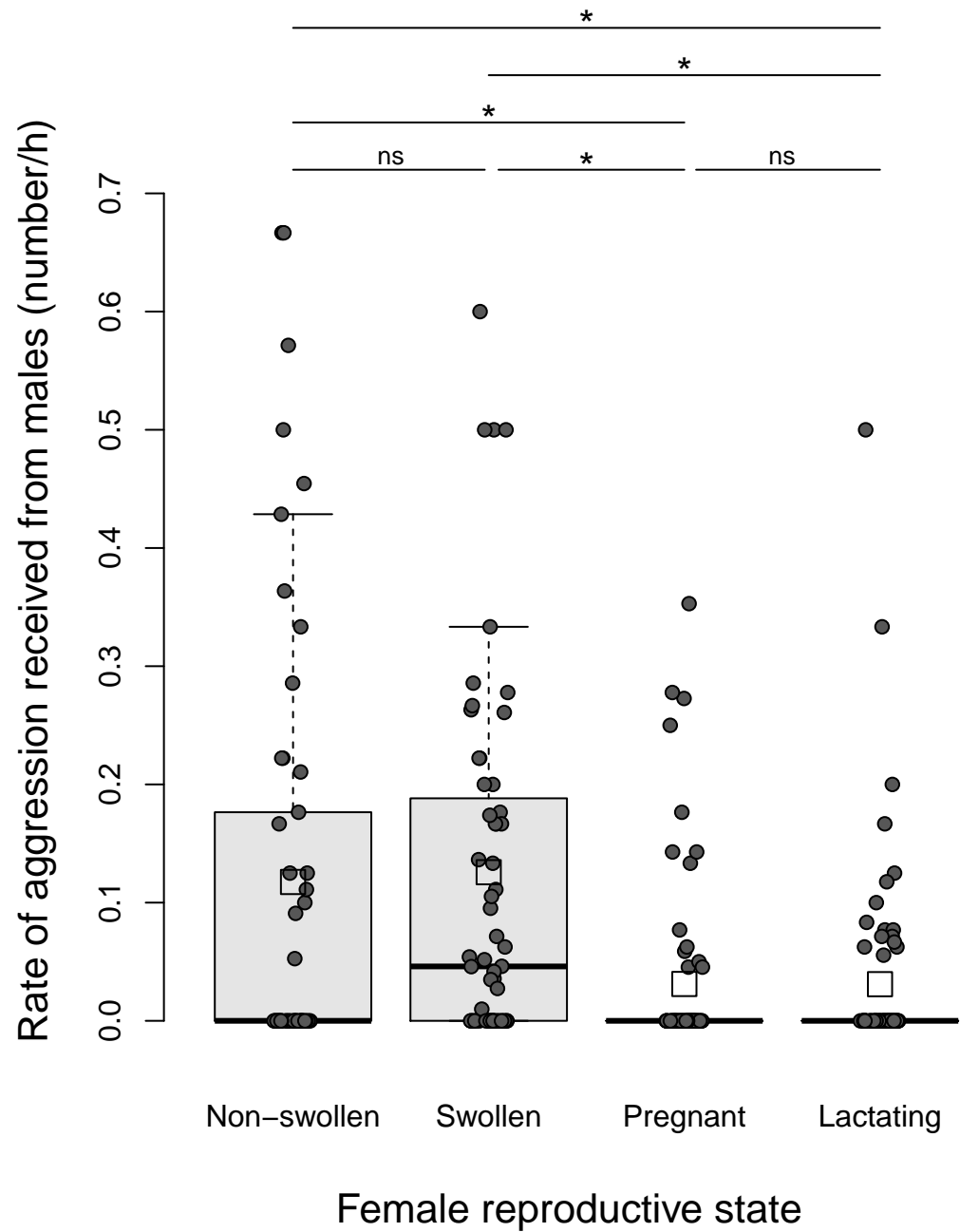
Figure 1. Cycling females receive more aggression from males and more injuries than non-cycling females.

Distribution of the (a) mean rate of male aggression against females (related to Table S2) and (b) mean rate of female injuries (related to Table S4) across female reproductive states. Boxplots are drawn from the raw individual means per year (represented by black dots). The bottom and top of the box respectively represent the 25th and 75th quartiles, and the bold horizontal line the median. Whiskers include the interquartile range. Open squares represent the mean of the distribution. Note that the boxes representing the rate of aggression received by pregnant and lactating females are not visible because the median, the 25th and 75th quartiles are equal to zero. Comparisons are denoted by "*" if significant and by "ns" otherwise.

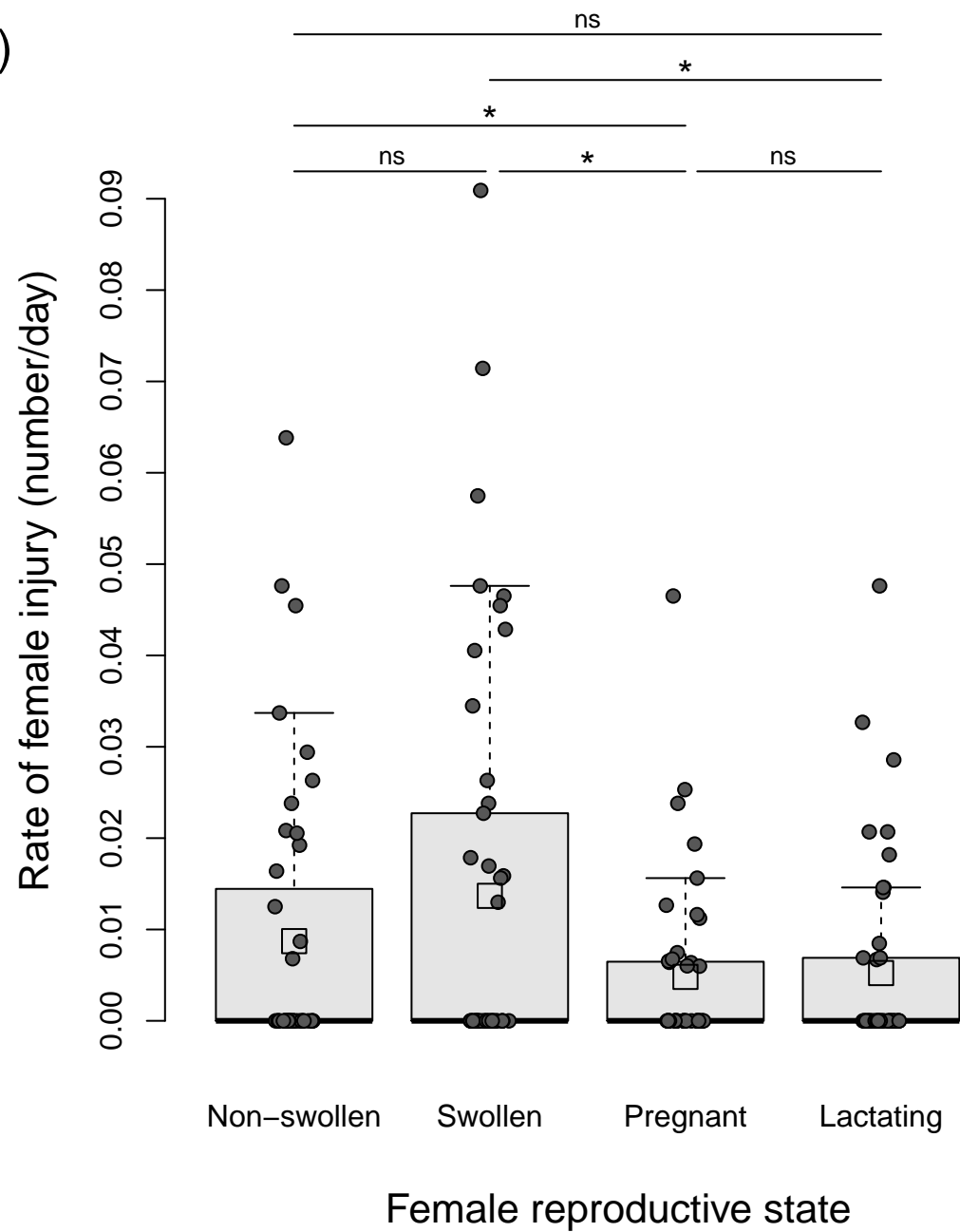
Figure 2. Male-female aggression predicts future mating success for males and risk of injury for females.

(a) Partial residual plot of the number of injuries incurred by cycling females during a cycle in relation to the mean rate of male aggression received during the same cycle (calculated from focal observations). Black dots represent partial residuals of the GLMM, the black line is the model prediction, and the grey area the confidence intervals. The prediction line is drawn holding all other fixed effects constant, using the median for numeric variables and most common category for factors (i.e., for a multiparous female, of rank 0.6, cycling over 38 days, in L group, when there were 9 adult males present, in 2014). Related to Table 1. (b) A female injured three times by her mate-guarding male on the head, who died for unknown reasons 6 months later. (c) Partial residual plot of the probability of establishing a mate-guarding episode with a male in the POP of a cycle in relation to the mean rate of aggression received from him throughout the cycle (calculated from focal observations). The prediction line is drawn for a multiparous female, of rank 0.5, a male of rank 0.5 and an overall rate of aggression of 0.005 time/day, in L group, in 2014. Related to Table 2. (d) A male directs aggression towards a female. Photo credit: Alecia Carter.

(a)



(b)



Supplemental Tables

Table S1. Summary of the statistical analyses explained in the Experimental Procedures. SW: swollen, NSW: non-swollen, P: pregnant, L: lactating

Predictions	Females included	Response variable	Model type	Fixed factors	Random factors	No of models	Tables & Figures
1. Males target cycling females	- all	Probability of receiving male aggression during a focal observation	Binomial	- Reproductive state (NSW, SW, P, L) - Female rank - Female parity - Group sex ratio - Group & Year	- Female ID - Date of focal observation	1	Table S2 Fig 1a
2a. Cycling females are at higher risk of injury	- all	Number of injuries received in a given reproductive state	Poisson	- Reproductive state (NSW, SW, P, L) - Female rank - Female parity - Group sex ratio - Group & Year - Number of days in reproductive state (offset)	- Female ID	1	Table S4 Fig 1b
2b. Cycling females experiencing more aggression from males suffer more injuries	-cycling (SW+NSW)	Number of injuries received in a given oestrus cycle	Poisson	- Mean hourly rate of aggression received by males throughout the cycle using focal observation data - Female rank - Female parity - Operational sex ratio - Group & Year - Number of observation days of the cycle (offset)	- Female ID	1	Table 1 Fig 2a
3a. Males use harassment	- unguarded SW - guarded SW	Matched control analysis comparing the probability of copulation of a male-female dyad after the male has attacked or chased the female <i>vs</i> in the absence of such aggression				8	Table S5
3b. Males use punishment	- unguarded SW - guarded SW	Matched control analysis comparing the probability of aggression of a male-female dyad after the female has copulated with another male <i>vs</i> in the absence of such a copulation				6	Table S5
3c. Males use sexual intimidation	-cycling (SW+NSW)	Probability of mate-guarding a given female during her POP	Binomial	- Mean rate of aggression received from a given male prior to POP throughout the cycle using focal observation data or <i>ad lib</i> data - Mean rate of aggression emitted by the male toward all individuals using <i>ad lib</i> data - Female rank - Female parity - Male rank - Operational sex ratio - Group & Year	- Female ID - Male ID - Cycle ID	2	Table 2 (focal) Fig 2c (focal) Table S6 (<i>ad lib</i>)

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5 **Table S2.** Influence of female reproductive state on the probability that she receives male aggression during a one-hour focal observation. Parameters and tests are based on
6 3439 focal observations (including 172 observations with aggression) distributed among 53 females. Significant variables appear in bold. SE: Standard Error, LRT: statistic of
7 a likelihood ratio test, df: degrees of freedom. LRT tests are used to test for the significance of each variable, while the confidence intervals are used to test for the significance
8 of each level of the qualitative variables. Related to main-text results, section 1.
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Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Probability of receiving aggression from males (0/1)	Reproductive state	Swollen (ref: non-swollen)	-0.14	0.21	[-0.55 ; 0.28]	32.53	3	<0.001
		Pregnant (ref: non-swollen)	-1.02	0.27	[-1.56 ; -0.48]			
		Lactating (ref: non-swollen)	-1.26	0.31	[-1.86 ; -0.65]			
		Swollen (ref: pregnant)	0.89	0.25	[0.41 ; 1.37]			
		Swollen (ref: lactating)	1.12	0.28	[0.57 ; 1.67]			
		Pregnant (ref: lactating)	0.23	0.32	[-0.39 ; 0.86]			
	Female rank		0.08	0.28	[-0.47 ; 0.63]	0.08	1	0.778
	Female parity ^a	nulliparous	0.13	0.21	[-0.28 ; 0.54]	0.37	1	0.541
	Sex ratio		-0.04	0.21	[-0.46 ; 0.38]	0.03	1	0.853
	Group ^b	L	-0.13	0.21	[-0.55 ; 0.29]	0.36	1	0.551
Year^c	2006	-0.42	0.35	[-1.10 ; 0.26]	74.41	3	<0.001	
	2013	-1.00	0.45	[-1.88 ; -0.12]				
	2014	1.14	0.29	[0.57 ; 1.71]				

11 ^a Reference category: parous

12 ^b Reference category: J group

13 ^c Reference category: 2005

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15 **Table S3.** Influence of female reproductive state on the probability of initiating aggression toward any individual of the group during a one-hour focal observation. Parameters
 16 and tests are based on 3439 focal observations (including 843 observations with aggression) distributed among 53 females. Significant variables appear in bold. SE: Standard
 17 Error, LRT: statistic of a likelihood ratio test, df: degrees of freedom. LRT tests are used to test for the significance of each variable, while the confidence intervals are used to
 18 test for the significance of each level of the qualitative variables. Related to main-text results, section 1.
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Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Probability of initiating an aggression toward any individual (0/1)	Reproductive state	Swollen (ref: non-swollen)	0.03	0.14	[-0.25 ; 0.30]	7.39	3	0.060
		Pregnant (ref: non-swollen)	0.33	0.15	[0.03 ; 0.62]			
		Lactating (ref: non-swollen)	0.09	0.15	[-0.22 ; 0.39]			
		Swollen (ref: pregnant)	-0.30	0.12	[-0.54 ; -0.06]			
		Swollen (ref: lactating)	-0.06	0.13	[-0.30 ; 0.19]			
		Pregnant (ref: lactating)	0.24	0.13	[-0.02 ; 0.50]			
	Female rank		2.30	0.18	[1.95 ; 2.64]	70.10	1	<0.001
	Female parity ^a	nulliparous	0.19	0.13	[-0.06 ; 0.44]	2.13	1	0.145
	No of individuals in group		-0.02	0.01	[-0.04 ; -0.01]	9.05	1	0.003
	Group ^b	L	-0.15	0.13	[-0.40 ; 0.10]	1.31	1	0.252
Year^c	2006	0.46	0.18	[0.11 ; 0.81]	101.47	3	<0.001	
	2013	1.12	0.26	[0.61 ; 1.63]				
	2014	2.19	0.27	[1.67 ; 2.71]				

22 ^a Reference category: parous

23 ^b Reference category: J group

24 ^c Reference category: 2005

25 **Table S4.** Influence of female reproductive state on the daily rate of injury. Parameters and tests are based on the observation of 96 injuries distributed among 39 females.
 26 Significant variables appear in bold. SE: Standard Error, LRT: statistic of a likelihood ratio test, df: degrees of freedom. LRT tests are used to test for the significance of each
 27 variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables. Related to main-text results, section 2.
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Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Number of female injuries ^a	Reproductive state	Swollen (ref: non-swollen)	0.46	0.29	[-0.11 ; 1.03]	15.85	3	0.001
		Pregnant (ref: non-swollen)	-0.73	0.34	[-1.39 ; -0.07]			
		Lactating (ref: non-swollen)	-0.37	0.33	[-1.01 ; 0.27]			
		Swollen (ref: pregnant)	1.19	0.31	[0.59 ; 1.79]			
		Swollen (ref: lactating)	0.83	0.3	[0.24 ; 1.42]			
		Pregnant (ref: lactating)	-0.36	0.31	[-0.98 ; 0.25]			
	Female rank		-0.37	0.48	[-1.31 ; 0.58]	0.59	1	0.442
	Female parity ^b	nulliparous	0.04	0.40	[-0.74 ; 0.82]	0.01	1	0.928
	Sex ratio		-0.26	0.67	[-1.57 ; 1.06]	0.15	1	0.701
	Group ^c	L	0.43	0.32	[-0.20 ; 1.06]	1.75	1	0.186
Year ^d	2014	0.40	0.28	[-0.15 ; 0.95]	2.08	1	0.150	

29 ^a The number of days spent in the reproductive state was fitted as an offset fixed factor, which modelize a daily rate of injury

30 ^b Reference category: parous

31 ^c Reference category: J group

32 ^d Reference category: 2013. Injuries were only collected in 2013 and 2014.

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34 **Table S5.** Results of the matched-control analyses testing for sexual harassment and punishment from (a) any male for unguarded females and (b) male consorts for mate-
 35 guarded females. For sexual harassment, we tested the difference between the proportion of copulations during post-aggression (PA) and matched-control (MC) observations
 36 using McNemar's Chi-squared tests for 4 different time periods. For punishment, we tested the difference between the proportion of aggressive acts during post-copulation
 37 (PC) and MC observations using McNemar's Chi-squared tests for 3 different time periods. Significant p-values are set at 0.007 due to Bonferroni correction. Related to main-
 38 text results, section 3a&b.

		(a) Unguarded females							(b) Mate-guarded females						
		N. cop in PA ^a / agg in PC ^b	N. cop/agg in MC ^c	Sample size ^d	X ²	df	P- value ^e	Median time of observation	N. cop in PA ^a / agg in PC ^b	N. cop/agg in MC ^c	Sample size ^d	X ²	df	P- value ^e	Median time of observation
Harassment	05 min	1	3	52	0.25	1	0.617	5	9	3	45	3.13	1	0.077	5
	10 min	1	2	52	0.00	1	1.000	10	10	4	45	2.08	1	0.149	10
	15 min	2	0	51	0.50	1	0.480	15	11	9	43	0.08	1	0.773	15
	20 min	2	1	47	0.00	1	1.000	17	12	10	41	0.08	1	0.773	20
Punishment	05 min	2	8	1334	2.50	1	0.114	5	1	0	31	0.00	1	1.000	5
	10 min	3	8	1062	1.78	1	0.182	10	1	0	31	0.00	1	1.000	10
	15 min	4	14	771	5.06	1	0.024	13	1	0	31	0.00	1	1.000	15

42 ^a Number of PA observations including a copulation with the male aggressor (for harassment)

43 ^b Number of PC observations where aggression was received from a non-copulating male after a copulation (for punishment).

44 ^c Number of MC observations with a copulation (for harassment) or with an aggressive act (for punishment).

45 ^d Number of PA-MC or PC-MC pairs available for the test.

46 ^e McNemar's Chi-squared test.

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48 **Table S6.** Influence of the mean daily rate of aggression received from a male by an unguarded female throughout her oestrus cycle but prior to her peri-ovulatory period
49 (POP) (calculated from *ad libitum* data) on the same male's probability of mate-guarding her during her subsequent POP. Parameters and tests are based on 78 cycles, 309
50 male-female aggressive acts, 2240 total aggressive acts from males, distributed among 34 females (number of days of observation per cycle: mean±sd:29.0±14.1, number of
51 mate-guarding males per cycle: 1.10±0.69, range: [0-4]),) and 39 males, and performed using a GLMM controlling for female identity, male identity and cycle identity (fitted
52 as random factors). Significant variables appear in bold. SE: Standard Error, LRT: statistic of a likelihood ratio test, df: degrees of freedom. LRT tests are used to test for the
53 significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables. Related to main-text results, section
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Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Probability that a male mate-guards a female during her POP (0/1)	Rate of male-female aggression during cycle		10.65	2.39	[5.96 ; 15.34]	27.02	1	<0.001
	Rate of male aggression toward all individuals		5.54	44.77	[-82.21 ; 93.29]	0.01	1	0.907
	Female rank		-0.66	0.43	[-1.50 ; 0.19]	2.31	1	0.128
	Female parity^a	nulliparous	-0.88	0.36	[-1.58 ; -0.18]	6.77	1	0.009
	Male rank		2.34	0.60	[1.17 ; 3.52]	13.75	1	<0.001
	Operational sex ratio		0.40	0.73	[-1.03 ; 1.83]	0.30	1	0.583
	Group ^b	L	0.34	0.36	[-0.36 ; 1.05]	0.91	1	0.34
	Year^c	2006	0.81	0.64	[-0.43 ; 2.06]	11.69	3	0.009
	2013	-1.10	0.69	[-2.46 ; 0.26]				
	2014	-0.49	0.71	[-1.88 ; 0.90]				

58 ^a Reference category: parous

59 ^b Reference category: J group

60 ^c Reference category: 2005

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62 **Table S7.** Demography of J and L groups in the study periods: June-December 2005, May 2006-January 2007, June-October 2013 and May-November 2014. Demography
63 varies due to migrations, births, disappearances, and life-history transitions (i.e. from juvenile to adulthood). Age was estimated from a combination of known birth dates and
64 dental patterns of tooth eruption and wear, examined during prior captures [1]. Related to main-text Experimental Procedures.
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Year	Number of adult males ^a		Number of adult females ^b		Number of subadults and juveniles ^c	
	J group	L group	J group	L group	J group	L group
2005	6-9	3	17	9	26	5-9
2006	4-5	4-5	17	9-11	36	18
2013	7-10	9-11	17	18-19	29-32	31-33
2014	7-8	9	18	17-19	35	29

68 ^a Males are considered adult when they reach eight years of age [2].

69 ^b Females are considered adult when they reach menarche [3].

70 ^c Males are considered subadult between 4 and 8 years old, and juveniles below 4 years old [2].
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Table S8. Sample size of behavioural focal observations. Related to main-text, Experimental Procedures.

	Reproductive state	Number of focal observations	Number of individuals	Number of focal observations per individual (mean±sd ; [min-max])
Adult females	Lactating	884	45	19.6±10.5 ; [1-45]
	Pregnant	714	47	15.2±9.7 ; [1-46]
	Non-swollen	469	36	13.0±9.7 ; [1-40]
	Swollen mate-guarded	491	32	15.3±14.5 ; [1-53]
	Swollen unguarded	881	39	22.6±21.5 ; [1-81]
Adult males		520	25	20.8±8.9 ; [4-37]

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Supplemental Experimental Procedures

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Appendix 1. Description of the analysis testing the influence of female reproductive state on the probability that females initiate aggression toward any individual of the group

We investigated whether the reproductive state of females influenced their propensity to initiate aggression. A binomial GLMM with a logit link function was run, using the probability that a female initiates aggression towards any group member during a one-hour focal observation (yes/no) as the response variable. In this model, we include any type of aggression (supplant, displacement, threat, chase and attack). Reproductive state (non-swollen, swollen, pregnant, or lactating) was fitted as a fixed factor together with the following control variables: female dominance rank, female age, the number of individuals in the group (since females may be more likely to initiate aggression when more individuals are present), year, and group identity. Random factors comprised female identity and the date of focal sampling. Results of this model are given in Table S3.

Appendix 2. Description of the matched-control analysis of sexual harassment

Using both male and female focal observations, we tested whether an adult male was more likely to copulate with a female after he attacked her across 4 different time intervals ($x=5, 10, 15$ and 20 minutes). We did not have enough matched-control observations to investigate longer time intervals. After each incidence of male-female aggression during a focal follow, we selected the x following minutes of observation, hereafter the post-aggression (PA) observation, and assessed whether a copulation occurred with the male aggressor (no: 0; yes: 1). To each PA observation, we matched an observation of the same length of time for the same female, where no male aggression occurred during the previous x minutes, hereafter the matched-control (MC) observation, and assessed whether she copulated with the male aggressor of the PA observation. We compared the difference in the proportions of observations including copulations between the post-aggression (PA) and matched-control (MC) observations using McNemar's Chi-squared tests.

Matched control (MC) observations corresponding to a particular post-aggression (PA) observation were chosen from 60-minutes focal observations of (1) the same female, who was (2) in the same consortship status as in the PA observation (unguarded, or guarded by the same male), and (3) in the same cycle and located less than 7 days apart from the PA observation. For PA observations that had several possible MC observations, we paired MC and PA observations in a way that minimized the number of times each MC observation was reused. For models investigating periods of x minutes post-aggression (x taking a range of values from 5 to 20, with increments of 5), the first x minutes of each MC observation were discarded in case an event of male-female aggression occurred immediately before the start of the focal. Within suitable 60-minutes MC observations, the time period selected as an MC sample (which was less than the duration of the entire focal observation) was chosen randomly. Some focal observations were used to draw more than one MC sample (for example, minutes 15-20 and then minutes 45-50 of a 60-minutes focal observation). In such cases, we attempted to sample non-overlapping time periods within the 60-minutes observation. When this was not possible (e.g. the same 60-minutes observation was used to draw three MC samples for the dataset looking at intervals of 20 minutes), we randomly deleted some PA observations relying on this 60-minutes observation in order to keep only independent PA/MC pairs. In the PA samples, when the x minutes were incomplete (e.g. when a second incidence of male-female aggression occurred within the same time interval or when the focal observation finished before the end of the time interval), we reduced the time interval of the matched MC sample accordingly so that the matched PA and MC samples are of similar duration. However, we only kept aggressive acts that were followed by at least 1 minute of observation (see Table S4 for the median observation time after aggressive acts for each analysis). Note that across the 4 different datasets (i.e. 5, 10, 15, 20 min), the same PA-MC pairs were kept but the random sampling of MC samples within 60-minutes observations was rerun for each dataset (in order to optimize the sample size in each dataset).

We ran these analyses separately for unguarded and mate-guarded females, since we may expect different coercion strategies from males not involved in mate-guarding or from male consorts (who already have sexual access to females and may not benefit from harassment).

Appendix 3. Description of the matched-control analysis of punishment

We tested whether an adult male was more likely to attack a female after she has copulated with a rival using a similar matched-control analysis across 3 different time intervals ($x=5, 10, 15$ minutes). We did not have enough matched-control observations to investigate longer time intervals. After each copulation, we determined whether the female received aggression from a male who was not involved in the copulation, within a given time interval. For these post-copulation (PC) observations, we selected MC observations, without a copulation event, as

137 described in the Appendix 2. Although this analysis focuses on adult male aggression, we included copulations
138 with juvenile males because adult males may punish females who mate with juveniles.

139 We similarly ran these analyses separately for unguarded and mate-guarded females, to test for
140 punishment both from any male for unguarded females and from the male consort for mate-guarded females.
141 Extra-pair copulations during mate-guarding are rare in chacma baboons, but still occur in 4% of cases in our
142 dataset (31 out of 726 copulations).

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145 **Appendix 4. Dominance ranks of males and females**

146 Individual ranks were assessed through focal and *ad libitum* observations of approach-avoid interactions
147 (supplants, when one animal actively displaces another to take its place, and displacements, when one animal
148 passes close to another and makes it move away) and agonistic interactions: attacks (any agonistic physical
149 contacts including hits, bites, or grabbing movements), chases (when one animal chases another for a distance of
150 at least 3 m) and threats (including staring, head bobbing, and ground sweeping while oriented toward the
151 targeted individual).

152 Our approach to the female dominance hierarchy was contingent upon the demographic stability of the
153 study period. In 2005-2006 there were few demographic changes, so a single hierarchy was calculated by
154 pooling the aggression matrix across years. In 2013-14 there were several demographic changes, so a separate
155 hierarchy was calculated for each year. We used Matman 1.1.4 (Noldus Information Technology 2003) in all
156 cases. The female dominance hierarchies were always linear (interactions in group L: $N_{05-06} = 1190$, $N_{13} = 367$,
157 $N_{14} = 1259$; interactions in group J: $N_{05-06} = 1173$, $N_{13} = 590$, $N_{14} = 978$; Landau's linearity index h : $P < 0.05$ in all
158 cases). All analyses presented here use the female's relative rank (a standardization of absolute rank between 0
159 and 1), to control for differences in group size. This was calculated using the formula: $1 - ((1-r)/(1-n))$, where r is
160 the absolute rank of an individual (ranging from 1 to the group size, n).

161 In contrast to the female hierarchy, the male hierarchy was much less stable [4]. Thus, male ranks were
162 established for each study period using an Elo-rating procedure implemented in the R package EloRating
163 (version 0.43) [5] which gives a score for each individual on each day of observation. Compared to dyadic
164 interaction matrices where ranks are calculated over a given time period, an Elo-rating procedure allows the
165 continuous updating of ranks according to the temporal sequence of interactions [5,6]. To obtain comparable
166 ratings across the entire study period, we derived a daily standardized rank by scaling the Elo-rating score of
167 each individual proportionally between 0 (corresponding to the minimal score and thus the lowest ranking male)
168 and 1 (corresponding to the maximal score and the highest ranking male).

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171 **Appendix 5. General details on GLMMs procedures**

172 GLMMs were run using the `glmer` function of the `lme4` package [7] in R version 3.3.1 [8]. The significance of
173 the fixed factors was tested using a likelihood ratio test, LRT (assuming an asymptotic chi-square distribution of
174 the test statistic), using the full model (to avoid problems arising from stepwise model selection procedures: [9]).
175 We further computed the 95% confidence intervals of fixed factors (for multilevel categorical variables,
176 confidence intervals were used to test the significance of each level of the variable by checking that they did not
177 cross zero). To test for pairwise differences between multiple levels of a categorical variable (e.g., "reproductive
178 state") we changed the reference category sequentially [10]. To validate models, we checked the distribution of
179 residuals (i.e., plotted the residuals against the continuous predictors and checked that the residuals were
180 normally distributed).

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