

1    **TITLE**

2    Male violence and sexual intimidation in a wild  
3    primate society

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27 **SUMMARY**

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

47

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

50

51 **RESULTS**

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

77       First, we investigated whether the reproductive state of females, defined as swollen  
78 (sexually receptive), non-swollen (non-sexually receptive, the non-fertile phase of the cycle),  
79 pregnant, or lactating, influenced their chances of receiving aggression from males using a  
80 generalized linear mixed model („GLMM“, see STAR Methods and Table S1). We found that  
81 males preferentially targeted cycling females [swollen: mean±standard deviation:  $0.13\pm0.19$   
82 time per hour, i.e., once every 8h; non-swollen:  $0.12\pm0.19$ , 1/9h] and directed much less  
83 aggression towards non-cycling females [pregnant:  $0.03\pm0.08$ , 1/32h; lactating:  $0.03\pm0.08$ ,  
84 1/32h] (Table S2, Figure 1a). Cycling females could also attract male aggression if they  
85 generate frequent conflicts because males regularly intervene in conflicts (the male policing  
86 hypothesis) [5,28]. However, cycling females do not initiate more aggression towards other  
87 group members than non-cycling females (see STAR Methods and Table S3).

88       Second, we tested whether male aggression is costly for cycling females. Of the few  
89 female injuries with an observed cause, 78% were inflicted by adult males ( $N=17/22$ ). We  
90 tested whether the risk of injury is higher in cycling than non-cycling females using a GLMM  
91 (see STAR Methods and Table S1). Daily rates of female injury varied across the  
92 reproductive cycle, and mirrored the rate of male aggression: swollen females received most  
93 injuries ( $0.014\pm0.022$  injuries per day, i.e., 1 injury every 73 days), followed by non-swollen  
94 females ( $0.009\pm0.016$ , 1/115), lactating females ( $0.005\pm0.010$ , 1/191), and pregnant females  
95 ( $0.005\pm0.009$ , 1/208) (Table S4, Figure 1b). We also found that, within a given cycle, females  
96 that faced higher rates of aggression from males suffered more injuries (Table 1, Fig. 2a,b).

97       Third, we tested whether male aggression increases male mating success immediately  
98 (sexual harassment and punishment) and/or in the future (sexual intimidation). To test  
99 whether a male was more likely to copulate with a female within 5, 10, 15 or 20 minutes of  
100 assaulting her, we used a matched-control analysis [29]. We tested the difference in the  
101 proportion of observations containing copulations with the aggressor in the post-aggression

102 („PA“) and matched-control („MC“) (no aggressive event) observations, using McNemar's  
103 Chi-squared tests (see STAR Methods). We found no support for short-term sexual  
104 harassment: the probability of copulation did not increase in the 5-20 minutes following male  
105 aggression, for either unguarded (Table S5a) or mate-guarded females (Table S5b).

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

112 We tested whether a male's probability of mate-guarding a female at her peak fertility  
113 (i.e., during her peri-ovulatory period, called „POP“) increased as a function of the mean  
114 hourly rate of aggression received by the female from this male *prior* to her POP, during the  
115 same oestrus cycle (calculated using focal observation data) (see STAR Methods and Table  
116 S1). We found that a female who received more aggression from a male throughout her cycle  
117 was more likely to be mate-guarded by him during her ovulatory window at the end of that  
118 cycle (Table 2, Fig. 2c,d). Overall, females received aggression through their cycle from their  
119 future male consort at a rate of  $0.04 \pm 0.09$  times/h compared to  $0.01 \pm 0.05$  times/h from other  
120 males. Similar results were found when estimating the rate of male-female aggression using  
121 *ad libitum* data (Table S6).

122 This last set of results could possibly result from a female preference for aggressive  
123 males, rather than from sexual coercion [8,9]. Under this scenario, we would expect some  
124 males to express aggressive phenotypes, and females to express a preference for these  
125 aggressive phenotypes. To test this alternative hypothesis, we included an additional fixed  
126 effect in the GLMM described above, a proxy of male general propensity to aggression,

127 estimated as the *ad libitum* daily rate of male aggression initiated toward any individual of the  
128 group per year. In contrast to the dyadic rate of aggression received by a female from a male  
129 during an oestrus cycle, a male's general rate of aggression was not found to influence his  
130 probability of mate-guarding that female (Table 2, Table S6) .

131

## 132 **DISCUSSION**

133 Our study extends previous work on sexual coercion in mammals in three ways. First, our  
134 results present new evidence supporting the use of sexual intimidation by wild chacma  
135 baboons. Such behaviour, previously reported only in chimpanzees [17–20], may therefore  
136 occur in a wider range of primates and strengthens the case for an evolutionary origin of  
137 human sexual intimidation [2,3]. Earlier work in baboons has underlined the importance of  
138 conditioning aggression by male hamadryas baboons, typically expressed when females leave  
139 their spatial proximity [30–32], and has also reported higher rates of male aggression against  
140 cycling (versus non-cycling) females in chacma baboons [33–36]. Our results further link  
141 male-female aggression to mating rates, in support of a core prediction of the sexual coercion  
142 hypothesis. By attacking females repeatedly in the weeks preceding ovulation, males appear  
143 to increase their chances of monopolizing sexual access to females around ovulation, which  
144 in turn increases their probability of successful reproduction [26,27]. Although we cannot  
145 demonstrate the causality of this link using correlative data, our analyses rule out several  
146 alternative hypotheses, including the proposal that cycling females receive more male  
147 aggression than non-cycling females because they are more aggressive, and the proposal that  
148 females prefer to mate with aggressive males.

149 Second, we conducted a detailed characterization of the mechanisms of sexual  
150 coercion through an analysis of behavioural sequences that reveals the temporal decoupling  
151 between aggression and matings. Our results suggest that direct coercion is more important

152 than indirect coercion (i.e., males attempt to increase their own mating rates rather than to  
153 decrease those of others), by showing that males rarely punish females who mate with rivals,  
154 although it may not be possible to fully disentangle these effects because one aggressive act  
155 may simultaneously encourage a female to mate and discourage her to leave.

156 Third, our study points to important fitness costs of sexual intimidation for females.  
157 Previous evidence has been limited to the finding that fertile female chimpanzees experience  
158 higher stress levels than non-fertile females [17]. Here we show that sexual violence is an  
159 important source of injuries for fertile females, which can compromise their survival (Fig 2b).  
160 Our study may therefore offer an evolutionary explanation for the co-variation between  
161 female injury rates and fertility cycles that has been reported from a range of mammals [37–  
162 42], including baboons [43,44].

163 Several factors may favour the use of sexual intimidation in baboons and  
164 chimpanzees, including the coexistence of males and females in large groups for long periods  
165 of time, their sexual dimorphism in body size and armaments, and long-term memory of  
166 previous interactions [45,46]. Sexual intimidation may occur in other mammals sharing these  
167 traits, but could have easily gone undocumented due to the temporal decoupling between  
168 aggression and matings [6]. Recognizing the importance of discreet forms of sexual coercion,  
169 by examining their taxonomic distribution and fitness consequences, should become an  
170 important focus for future research. The widespread use of sexual intimidation by males may  
171 help to explain core aspects of reproductive strategies with consequences for the evolution of  
172 mate choice, social structure and sexual dimorphism [47,48].

173

#### 174 **AUTHOR CONTRIBUTIONS**

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

177

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344 **Table 1. Male aggression represents the main risk of injury for cycling females. Related to Figure 2a.**

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

Response variable	Fixed factors	Levels	95% confidence interval			LRT	df	P-value
			Estimate	SE				
Number of injuries received in a given cycle <sup>a</sup>	<b>Rate of male aggression during cycle</b>		2.53	1.11	[0.36 ; 4.70]	4.74	1	<b>0.029</b>
	Female rank		1.04	0.57	[-0.08 ; 2.17]	3.51	1	0.061
	Female parity <sup>b</sup>	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 <sup>c</sup>	L	-0.64	0.57	[-1.76 ; 0.48]	1.31	1	0.253
	Year <sup>d</sup>	2014	-0.38	0.53	[-1.43 ; 0.66]	0.52	1	0.470

349 <sup>a</sup>The number of days of the cycle observed fitted as an offset fixed factor, which modelize a daily rate of injury

350 <sup>b</sup>Reference category: parous

351 <sup>c</sup>Reference category: J group

352 <sup>d</sup>Reference category: 2013. Injuries were only collected in 2013 and 2014.

353 **Table 2. Male-female aggression predicts future mating success for males. Related to Figure 2c.**

354 Influence of the mean hourly rate of aggression received from a male by an unguarded female throughout her oestrus cycle but prior to peri-  
 355 ovulatory period (POP) (calculated from focal observations) on the same male's probability of mate-guarding her during her subsequent POP.  
 356 Parameters and tests are based on 58 cycles and 74 male-female aggressive acts, distributed among 30 females (number of focal observations per  
 357 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 using a GLMM.  
 358 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  
 359 for the significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables.

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

360 <sup>a</sup> Reference category: parous361 <sup>b</sup> Reference category: J group362 <sup>c</sup> Reference category: 2005. LRT tests are used to test for significance of the whole variable "Year", while the confidence intervals are used  
 363 to test for significance of each level of the variable.

364 **FIGURES LEGENDS**

365

366 **Figure 1. Cycling females receive more aggression from males and more injuries than non-cycling females. A: related to Table S2, B:**  
367 **related to Table S4.**

368 Distribution of the **(a)** mean rate of male aggression against females and **(b)** mean rate of female injuries across female reproductive states.  
369 Boxplots are drawn from the raw individual means per year (represented by black dots). The bottom and top of the box respectively represent the  
370 25th and 75th quartiles, and the bold horizontal line the median. Whiskers include the interquartile range. Open squares represent the mean of the  
371 distribution. Note that the boxes representing the rate of aggression received by pregnant and lactating females are not visible because the  
372 median, the 25<sup>th</sup> and 75<sup>th</sup> quartiles are equal to zero. Comparisons are denoted by “\*\*” if significant and by “ns” otherwise.

373

374

375 **Figure 2. Male-female aggression predicts future mating success for males and risk of injury for females. A: related to Table 1, C:**  
376 **related to Table 2.**

377 **(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  
378 received during the same cycle (calculated from focal observations). Black dots represent partial residuals of the GLMM, the black line is the  
379 model prediction, and the grey area the confidence intervals. The prediction line is drawn holding all other fixed effects constant, using the  
380 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,  
381 when there were 9 adult males present, in 2014). **(b)** A female injured three times by her mate-guarding male on the head, who died for unknown  
382 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  
383 relation to the mean rate of aggression received from him throughout the cycle (calculated from focal observations). The prediction line is drawn  
384 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. **(d)** A male  
385 directs aggression towards a female. Photo credit: Alecia Carter.

Figure 1

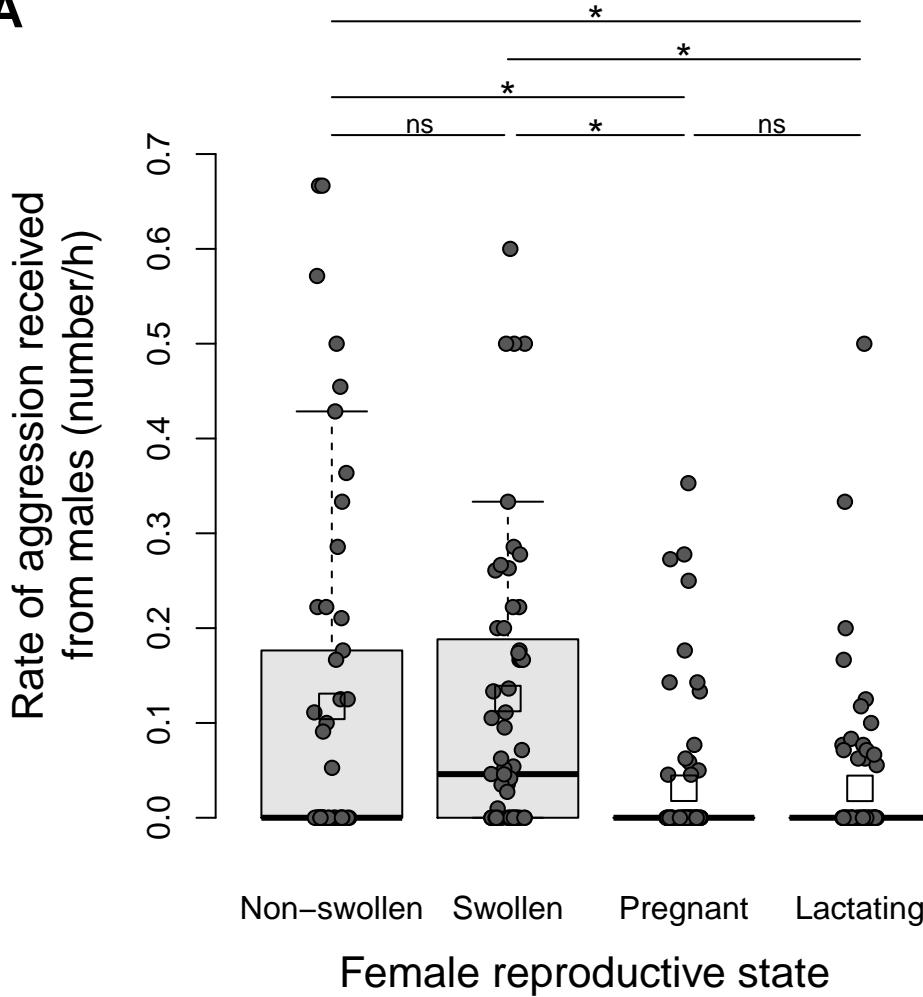
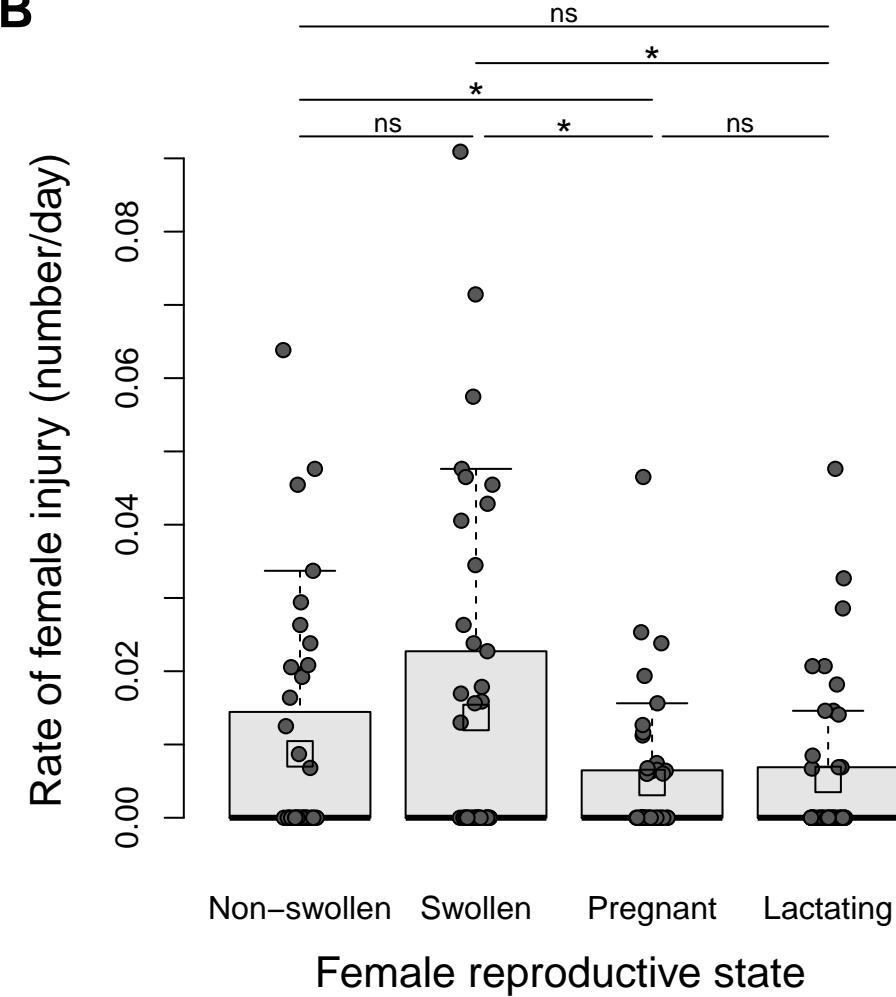
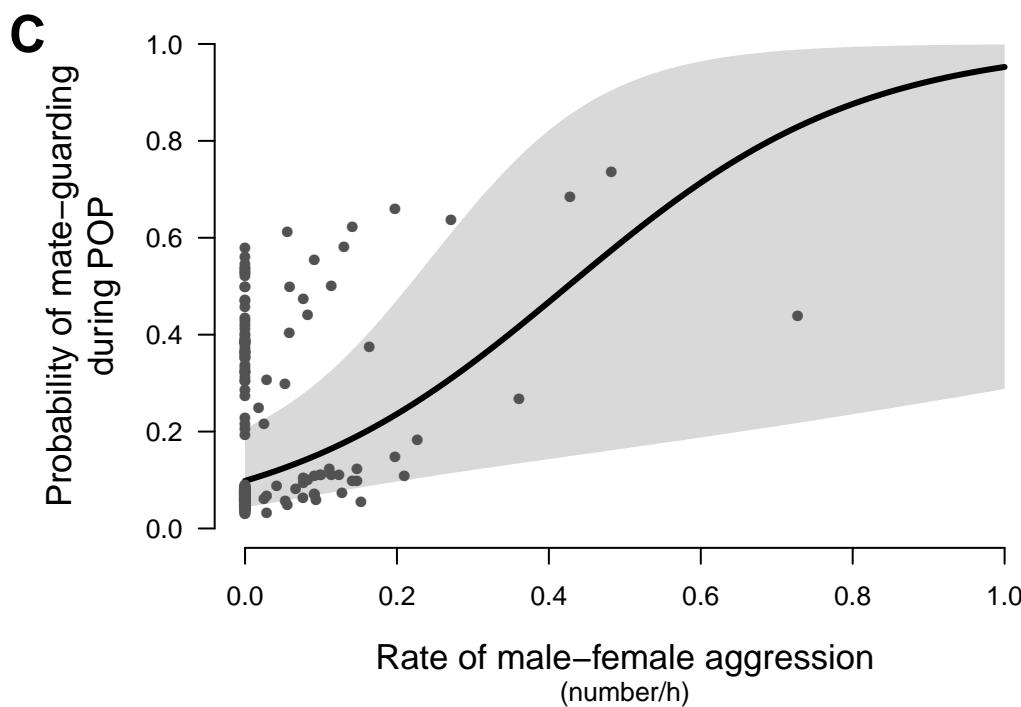
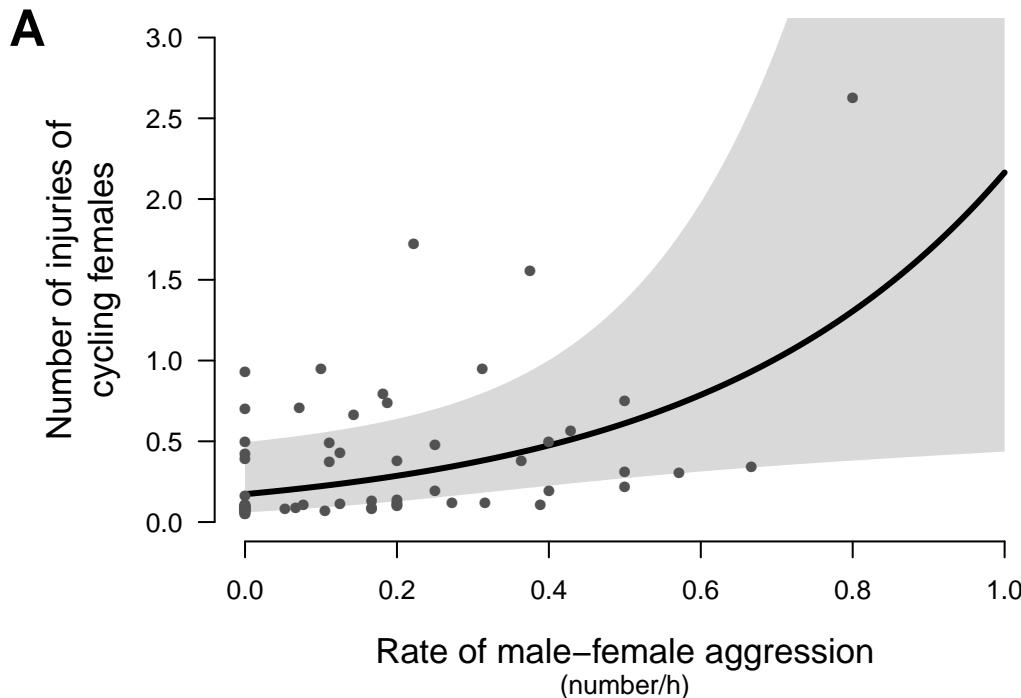
**A****B**

Figure 2



1    **STAR METHODS**

2

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5    fulfilled by the Lead Contact, Alice Baniel (alice.baniel@gmail.com).

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7    **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

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11   „L“, over four different periods: June-December 2005, Mai 2006-January 2007, June-October  
12   2013 and May-November 2014. Number of adults in J group ranged from 6-9 males and 17  
13   females in 2005; 4-5 males and 17 females in 2006; 7-10 males and 17 females in 2013; 7-8  
14   males and 18 females in 2014. L group comprised 3 males and 9 females in 2005; 4-5 males  
15   and 9-11 females in 2006; 9-11 males and 18-19 females in 2013; 9 males and 17-19 females  
16   in 2014. All adults were individually recognizable and observable at close range. Age (in  
17   years) was estimated from a combination of known birth dates and dental patterns of tooth  
18   eruption and wear, examined during prior captures [24]. Only adults were included in the  
19   study. Males were considered adult when they reached eight years of age [50] and females  
20   when they reached menarche [51]. Female parity (nulliparous or parous) was determined  
21   based on long-term life-history data.

22

23   **METHOD DETAILS**

24   *Establishment of dominance ranks of males and females*

25 Individual ranks were assessed through focal and *ad libitum* observations of approach-avoid  
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29 grabbing movements), chases (when one animal chases another for a distance of at least 3 m)  
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31 targeted individual). Our approach to the female dominance hierarchy was contingent upon  
32 the demographic stability of the study period. In 2005-2006 there were few demographic  
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36 The female dominance hierarchies were always linear (interactions in group L: N<sub>05-06</sub> = 1190,  
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38 linearity index h: P<0.05 in all cases). All analyses presented here use the female's relative  
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40 size. This was calculated using the formula: 1-((1-r)/(1-n)), where r is the absolute rank of an  
41 individual (ranging from 1 to the group size, n). In contrast to the female hierarchy, the male  
42 hierarchy was much less stable [52]. Thus, male ranks were established for each study period  
43 using an Elo-rating procedure implemented in the R package EloRating (version 0.43) [53]  
44 which gives a score for each individual on each day of observation. Compared to dyadic  
45 interaction matrices where ranks are calculated over a given time period, an Elo-rating  
46 procedure allows the continuous updating of ranks according to the temporal sequence of  
47 interactions [53,54]. To obtain comparable ratings across the entire study period, we derived a  
48 daily standardized rank by scaling the Elo-rating score of each individual proportionally

49 between 0 (corresponding to the minimal score and thus the lowest ranking male) and 1  
50 (corresponding to the maximal score and the highest ranking male).

51

52 ***Female reproductive state & mate-guarding patterns***

53 Female reproductive state was recorded daily as pregnant (determined *a posteriori*) if a  
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55 dependant infant and had not yet resumed cycling, swollen if she was sexually receptive with  
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57 day period preceding the day of swelling detumescence, during which ovulation generally  
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59

60 ***Behavioural data***

61 We conducted one-hour focal animal samples on all adults. We conducted 3439 focal  
62 observations on 53 females distributed across reproductive states (see sample size in Table  
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68

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

74

## 75 QUANTIFICATION AND STATISTICAL ANALYSIS

76 We ran a combination of GLMMs (summarized in Table S1) and matched-control analyses  
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78 version 3.3.1 [58]. The significance of the fixed factors was tested using a likelihood ratio  
79 test, LRT (assuming an asymptotic chi-square distribution of the test statistic), using the full  
80 model (to avoid problems arising from stepwise model selection procedures: [59]. We further  
81 computed the 95% confidence intervals of fixed factors (for multilevel categorical variables,  
82 confidence intervals were used to test the significance of each level of the variable by  
83 checking that they did not cross zero). To test for pairwise differences between multiple  
84 levels of a categorical variable (e.g., “reproductive state”) we changed the reference category  
85 sequentially [60]. To validate models, we checked the distribution of residuals (i.e., plotted  
86 the residuals against the continuous predictors and checked that the residuals were normally  
87 distributed).

88

### 89 *Male aggression and female reproductive state*

90 A binomial GLMM with a logit link function was run, using the probability that a female  
91 receives male aggression during a one-hour focal observation (yes/no) as the response  
92 variable. Reproductive state was fitted as a fixed factor together with the following control  
93 variables: female dominance rank, female parity (nulliparous or parous), group sex ratio (the  
94 number of adult females divided by the number of adult males, in case females receive more  
95 male aggression when the sex ratio is more male-biased), year, and group identity. Random  
96 factors comprised female identity and the date of focal sampling. Results are in Table S2.

97 To test the male policing hypothesis, we investigated whether the reproductive state of  
98 females influenced their propensity to initiate aggression toward group members. A binomial

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

107

108 ***Male aggression and female injuries***

109 The number of injuries received by a female in a given reproductive state was modelled as a  
110 GLMM with a Poisson error structure. The number of days spent in each reproductive state  
111 was log-transformed and included as an offset variable. Fixed effects comprised: female  
112 reproductive state, dominance rank, parity, group sex ratio, year, and group identity. Female  
113 identity was included as a random effect. Results are in Table S4.

114 To test whether females who experience more male aggression during their oestrus  
115 cycle suffer more injuries, we ran a second GLMM with a Poisson error structure using the  
116 number of injuries received in a given cycle as the response variable. The log-transformed  
117 number of days spent in each cycle was fitted as an offset variable. The mean rate (number  
118 per hour) of aggressive acts received from any adult male by the female throughout her cycle  
119 (calculated using female focal observations) was fitted as a fixed effect. Other fixed and  
120 random effects were similar to the previous model, except that the operational sex ratio (the  
121 number of cycling females divided by the number of adult males) was fitted instead of the  
122 group sex ratio. We included a cycle only if we had >5 focal observations for a female in that  
123 cycle. Results are in Table 1.

124

125 ***Sexual harassment and male mating success***

126 Using both male and female focal observations, we tested whether an adult male was more  
127 likely to copulate with a female after he attacked her across 4 different time intervals (x=5,  
128 10, 15 and 20 minutes). We did not have enough matched-control observations to investigate  
129 longer time intervals. After each incidence of male-female aggression during a focal follow,  
130 we selected the x following minutes of observation, hereafter the post-aggression (PA)  
131 observation, and assessed whether a copulation occurred with the male aggressor (no: 0; yes:  
132 1). To each PA observation, we matched an observation of the same length of time for the  
133 same female, where no male aggression occurred during the previous x minutes, hereafter the  
134 matched-control (MC) observation, and assessed whether she copulated with the male  
135 aggressor of the PA observation. We compared the difference in the proportions of  
136 observations including copulations between the post-aggression (PA) and matched-control  
137 (MC) observations using McNemar's Chi-squared tests.

138       Matched control (MC) observations corresponding to a particular post-aggression  
139 (PA) observation were chosen from 60-minutes focal observations of (1) the same female,  
140 who was (2) in the same consortship status as in the PA observation (unguarded, or guarded  
141 by the same male), and (3) in the same cycle and located less than 7 days apart from the PA  
142 observation. For PA observations that had several possible MC observations, we paired MC  
143 and PA observations in a way that minimized the number of times each MC observation was  
144 reused. For models investigating periods of x minutes post-aggression (x taking a range of  
145 values from 5 to 20, with increments of 5), the first x minutes of each MC observation were  
146 discarded in case an event of male-female aggression occurred immediately before the start of  
147 the focal. Within suitable 60-minutes MC observations, the time period selected as an MC  
148 sample (which was less than the duration of the entire focal observation) was chosen

149 randomly. Some focal observations were used to draw more than one MC sample (for  
150 example, minutes 15-20 and then minutes 45-50 of a 60-minutes focal observation). In such  
151 cases, we attempted to sample non-overlapping time periods within the 60-minutes  
152 observation. When this was not possible (e.g. the same 60-minutes observation was used to  
153 draw three MC samples for the dataset looking at intervals of 20 minutes), we randomly  
154 deleted some PA observations relying on this 60-minutes observation in order to keep only  
155 independent PA/MC pairs. In the PA samples, when the x minutes were incomplete (e.g.  
156 when a second incidence of male-female aggression occurred within the same time interval or  
157 when the focal observation finished before the end of the time interval), we reduced the time  
158 interval of the matched MC sample accordingly so that the matched PA and MC samples are  
159 of similar duration. However, we only kept aggressive acts that were followed by at least 1  
160 minute of observation (see Table S4 for the median observation time after aggressive acts for  
161 each analysis). Note that across the 4 different datasets (i.e. 5, 10, 15, 20 min), the same PA-  
162 MC pairs were kept but the random sampling of MC samples within 60-minutes observations  
163 was rerun for each dataset (in order to optimize the sample size in each dataset).

164 We ran these analyses separately for unguarded and mate-guarded females, since we  
165 may expect different coercion strategies from males not involved in mate-guarding or from  
166 male consorts (who already have sexual access to females and may not benefit from  
167 harassment). Results are in Table S5.

168

#### 169 ***Punishment and male mating success***

170 We tested whether an adult male was more likely to attack a female after she has copulated  
171 with a rival using a similar matched-control analysis across 3 different time intervals (x=5, 10,  
172 15 minutes). We did not have enough matched-control observations to investigate longer time  
173 intervals. After each copulation, we determined whether the female received aggression from

174 a male who was not involved in the copulation, within a given time interval. For these post-  
175 copulation (PC) observations, we selected MC observations, without a copulation event, as  
176 described above. Although this analysis focuses on adult male aggression, we included  
177 copulations with juvenile males because adult males may punish females who mate with  
178 juveniles.

179 We similarly ran these analyses separately for unguarded and mate-guarded females,  
180 to test for punishment both from any male for unguarded females and from the male consort  
181 for mate-guarded females. Extra-pair copulations during mate-guarding are rare in chacma  
182 baboons, but still occur in 4% of cases in our dataset (31 out of 726 copulations). Results are  
183 in Table S5.

184

185 ***Sexual intimidation and male mating success***

186 We ran a binomial GLMM using the probability that each resident male mate-guards the  
187 female during her POP (yes/no) as the response variable. Fixed factors comprised the mean  
188 rate of aggression received by the female from the male during the entire cycle, but *prior to*  
189 her POP, calculated as the total number of aggressive acts received during focal observations  
190 divided by the number of observation hours, prior to her POP; female dominance rank and  
191 parity; male dominance rank (to control for increased access of dominant males to receptive  
192 females); operational sex ratio; year; and group identity. To test the alternative hypothesis of  
193 female preference for aggressive male phenotypes, we included an additional fixed effect: the  
194 rate of male aggression toward any individual of the group (total number of *ad libitum*  
195 aggressive acts initiated by a male per year divided by the time spent in the group that year  
196 and by the number of individuals in the group to control for differences in group size).  
197 Random effects comprised the female and male identities, and cycle identity. Only cycles for  
198 which we had >5 focal observations of a given female were included. Results are in Tale 2.

199 This analysis was replicated using *ad libitum* records of male-female aggression to  
200 ensure our estimated rates of aggression reliably captured variation across dyads. We ran the  
201 same model as above but calculating the mean daily rate of aggression received by the female  
202 from the male during her entire cycle, but *prior to* her POP, as the total number of *ad libitum*  
203 aggressive acts received divided by the number of days observed in the cycle. We only  
204 included cycles for which >10 days of group observations were available. Results are in  
205 Table S6.

206

## 207 **DATA AND SOFTWARE AVAILABILITY**

208 The datasets necessary to run the analyses included in this paper and the associated legends  
209 have been deposited in the public depository GitHub at: <https://github.com/AliceBaniel/Male->  
210 violence-and-sexual-intimidation-in-a-wild-primate-society.

211

## 212 **STAR METHODS**

213

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294 checking that they did not cross zero). To test for pairwise differences between multiple  
295 levels of a categorical variable (e.g., “reproductive state”) we changed the reference category  
296 sequentially [60]. To validate models, we checked the distribution of residuals (i.e., plotted  
297 the residuals against the continuous predictors and checked that the residuals were normally  
298 distributed).

299

300    ***Male aggression and female reproductive state***

301    A binomial GLMM with a logit link function was run, using the probability that a female  
302    receives male aggression during a one-hour focal observation (yes/no) as the response  
303    variable. Reproductive state was fitted as a fixed factor together with the following control  
304    variables: female dominance rank, female parity (nulliparous or parous), group sex ratio (the  
305    number of adult females divided by the number of adult males, in case females receive more  
306    male aggression when the sex ratio is more male-biased), year, and group identity. Random  
307    factors comprised female identity and the date of focal sampling. Results are in Table S2.

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

318

319    ***Male aggression and female injuries***

320    The number of injuries received by a female in a given reproductive state was modelled as a  
321    GLMM with a Poisson error structure. The number of days spent in each reproductive state  
322    was log-transformed and included as an offset variable. Fixed effects comprised: female  
323    reproductive state, dominance rank, parity, group sex ratio, year, and group identity. Female  
324    identity was included as a random effect. Results are in Table S4.

325 To test whether females who experience more male aggression during their oestrus  
326 cycle suffer more injuries, we ran a second GLMM with a Poisson error structure using the  
327 number of injuries received in a given cycle as the response variable. The log-transformed  
328 number of days spent in each cycle was fitted as an offset variable. The mean rate (number  
329 per hour) of aggressive acts received from any adult male by the female throughout her cycle  
330 (calculated using female focal observations) was fitted as a fixed effect. Other fixed and  
331 random effects were similar to the previous model, except that the operational sex ratio (the  
332 number of cycling females divided by the number of adult males) was fitted instead of the  
333 group sex ratio. We included a cycle only if we had >5 focal observations for a female in that  
334 cycle. Results are in Table 1.

335

336 ***Sexual harassment and male mating success***

337 Using both male and female focal observations, we tested whether an adult male was more  
338 likely to copulate with a female after he attacked her across 4 different time intervals (x=5,  
339 10, 15 and 20 minutes). We did not have enough matched-control observations to investigate  
340 longer time intervals. After each incidence of male-female aggression during a focal follow,  
341 we selected the x following minutes of observation, hereafter the post-aggression (PA)  
342 observation, and assessed whether a copulation occurred with the male aggressor (no: 0; yes:  
343 1). To each PA observation, we matched an observation of the same length of time for the  
344 same female, where no male aggression occurred during the previous x minutes, hereafter the  
345 matched-control (MC) observation, and assessed whether she copulated with the male  
346 aggressor of the PA observation. We compared the difference in the proportions of  
347 observations including copulations between the post-aggression (PA) and matched-control  
348 (MC) observations using McNemar's Chi-squared tests.

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

373 MC pairs were kept but the random sampling of MC samples within 60-minutes observations  
374 was rerun for each dataset (in order to optimize the sample size in each dataset).

375 We ran these analyses separately for unguarded and mate-guarded females, since we  
376 may expect different coercion strategies from males not involved in mate-guarding or from  
377 male consorts (who already have sexual access to females and may not benefit from  
378 harassment). Results are in Table S5.

379

380 ***Punishment and male mating success***

381 We tested whether an adult male was more likely to attack a female after she has copulated  
382 with a rival using a similar matched-control analysis across 3 different time intervals ( $x=5, 10,$   
383 15 minutes). We did not have enough matched-control observations to investigate longer time  
384 intervals. After each copulation, we determined whether the female received aggression from  
385 a male who was not involved in the copulation, within a given time interval. For these post-  
386 copulation (PC) observations, we selected MC observations, without a copulation event, as  
387 described above. Although this analysis focuses on adult male aggression, we included  
388 copulations with juvenile males because adult males may punish females who mate with  
389 juveniles.

390 We similarly ran these analyses separately for unguarded and mate-guarded females,  
391 to test for punishment both from any male for unguarded females and from the male consort  
392 for mate-guarded females. Extra-pair copulations during mate-guarding are rare in chacma  
393 baboons, but still occur in 4% of cases in our dataset (31 out of 726 copulations). Results are  
394 in Table S5.

395

396 ***Sexual intimidation and male mating success***

397 We ran a binomial GLMM using the probability that each resident male mate-guards the  
398 female during her POP (yes/no) as the response variable. Fixed factors comprised the mean  
399 rate of aggression received by the female from the male during the entire cycle, but *prior to*  
400 her POP, calculated as the total number of aggressive acts received during focal observations  
401 divided by the number of observation hours, prior to her POP; female dominance rank and  
402 parity; male dominance rank (to control for increased access of dominant males to receptive  
403 females); operational sex ratio; year; and group identity. To test the alternative hypothesis of  
404 female preference for aggressive male phenotypes, we included an additional fixed effect: the  
405 rate of male aggression toward any individual of the group (total number of *ad libitum*  
406 aggressive acts initiated by a male per year divided by the time spent in the group that year  
407 and by the number of individuals in the group to control for differences in group size).  
408 Random effects comprised the female and male identities, and cycle identity. Only cycles for  
409 which we had >5 focal observations of a given female were included. Results are in Tale 2.

410 This analysis was replicated using *ad libitum* records of male-female aggression to  
411 ensure our estimated rates of aggression reliably captured variation across dyads. We ran the  
412 same model as above but calculating the mean daily rate of aggression received by the female  
413 from the male during her entire cycle, but *prior to* her POP, as the total number of *ad libitum*  
414 aggressive acts received divided by the number of days observed in the cycle. We only  
415 included cycles for which >10 days of group observations were available. Results are in  
416 Table S6.

417

## 418 DATA AND SOFTWARE AVAILABILITY

419 The datasets necessary to run the analyses included in this paper and the associated legends  
420 have been deposited in the public depository GitHub at: <https://github.com/AliceBaniel/Male->  
421 violence-and-sexual-intimidation-in-a-wild-primate-society.

422



**Table S1. Summary of the statistical analyses explained in the STAR Methods. Related to STAR Methods.**

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 <b>or ad lib</b> 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> )

**Table S2. Male-female aggression varies according to female reproductive state. Related to Figure 1a.**

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 3439 focal observations (including 172 observations with aggression) distributed among 53 females. 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 variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables.

Response variable	Fixed factors	Levels	Estimate	SE	95% confidence interval	LRT	df	P-value
Probability of receiving aggression from males (0/1)	<b>Reproductive state</b>	Swollen (ref: non-swollen)	-0.14	0.21	[-0.55 ; 0.28]	32.53	3	<b>&lt;0.001</b>
		Pregnant (ref: non-swollen)	-1.02	0.27	<b>[-1.56 ; -0.48]</b>			
		Lactating (ref: non-swollen)	-1.26	0.31	<b>[-1.86 ; -0.65]</b>			
		Swollen (ref: pregnant)	0.89	0.25	<b>[0.41 ; 1.37]</b>			
		Swollen (ref: lactating)	1.12	0.28	<b>[0.57 ; 1.67]</b>			
		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 <sup>a</sup>	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 <sup>b</sup>	L	-0.13	0.21	[-0.55 ; 0.29]	0.36	1	0.551
	<b>Year<sup>c</sup></b>	2006	-0.42	0.35	[-1.10 ; 0.26]	74.41	3	<b>&lt;0.001</b>
		2013	-1.00	0.45	<b>[-1.88 ; -0.12]</b>			
		2014	1.14	0.29	<b>[0.57 ; 1.71]</b>			

<sup>a</sup> Reference category: parous<sup>b</sup> Reference category: J group<sup>c</sup> Reference category: 2005

**Table S3. Aggression emitted by females does not vary according to their reproductive state. Related to STAR Methods.**

Influence of female reproductive state on the probability of initiating aggression toward any individual of the group during a one-hour focal observation. Parameters and tests are based on 3439 focal observations (including 843 observations with aggression) distributed among 53 females. 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 variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables.

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 ]				
<b>Female rank</b>			2.30	0.18	<b>[1.95 ; 2.64]</b>	70.10	1	<b>&lt;0.001</b>	
Female parity <sup>a</sup>		nulliparous	0.19	0.13	[ -0.06 ; 0.44 ]	2.13	1	0.145	
<b>No of individuals in group</b>			-0.02	0.01	<b>[ -0.04 ; -0.01 ]</b>	9.05	1	<b>0.003</b>	
Group <sup>b</sup>		L	-0.15	0.13	[ -0.40 ; 0.10 ]	1.31	1	0.252	
<b>Year<sup>c</sup></b>		2006	0.46	0.18	<b>[0.11 ; 0.81]</b>	101.47	3	<b>&lt;0.001</b>	
		2013	1.12	0.26	<b>[0.61 ; 1.63]</b>				
		2014	2.19	0.27	<b>[1.67 ; 2.71]</b>				

<sup>a</sup> Reference category: parous<sup>b</sup> Reference category: J group<sup>c</sup> Reference category: 2005

**Table S4. Females' risk of injury varies according to their reproductive state. Related to Figure 1b.**

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. 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 variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables.

Response variable	Fixed factors	Levels	95% confidence interval			LRT	df	P-value	
			Estimate	SE					
Number of female injuries <sup>a</sup>	<b>Reproductive state</b>	Swollen (ref: non-swollen)	0.46	0.29	[-0.11 ; 1.03]	15.85	3	<b>0.001</b>	
		Pregnant (ref: non-swollen)	-0.73	0.34	<b>[-1.39 ; -0.07]</b>				
		Lactating (ref: non-swollen)	-0.37	0.33	[-1.01 ; 0.27]				
		Swollen (ref: pregnant)	1.19	0.31	<b>[0.59 ; 1.79]</b>				
		Swollen (ref: lactating)	0.83	0.3	<b>[0.24 ; 1.42]</b>				
		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 <sup>b</sup>	nulliparous	0.04	0.40	[-0.74 ; 0.82]			
		Sex ratio		-0.26	0.67	[-1.57 ; 1.06]			
Group <sup>c</sup>		L		0.43	0.32	[-0.20 ; 1.06]	1.75	1	0.186
			2014	0.40	0.28	[-0.15 ; 0.95]			

<sup>a</sup>The number of days spent in the reproductive state was fitted as an offset fixed factor, which modelize a daily rate of injury

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

<sup>c</sup> Reference category: J group

<sup>d</sup> Reference category: 2013. Injuries were only collected in 2013 and 2014.

**Table S5. Males do not use sexual harassment nor punishment against females. Related to STAR Methods.**

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-guarded females. For sexual harassment, we tested the difference between the proportion of copulations during post-aggression (PA) and matched-control (MC) observations 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 (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.

	(a) Unguarded females							(b) Mate-guarded females							
	N. cop in PA <sup>a</sup> / agg in PC <sup>b</sup>	N. cop/agg in MC <sup>c</sup>	Sample size <sup>d</sup>	X <sup>2</sup>	df	P- value <sup>e</sup>	Median time of observation	N. cop in PA <sup>a</sup> / agg in PC <sup>b</sup>	N. cop/agg in MC <sup>c</sup>	Sample size <sup>d</sup>	X <sup>2</sup>	df	P- value <sup>e</sup>	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

<sup>a</sup> Number of PA observations including a copulation with the male aggressor (for harassment)

<sup>b</sup> Number of PC observations where aggression was received from a non-copulating male after a copulation (for punishment).

<sup>c</sup> Number of MC observations with a copulation (for harassment) or with an aggressive act (for punishment).

<sup>d</sup> Number of PA-MC or PC-MC pairs available for the test.

<sup>e</sup> McNemar's Chi-squared test.

**Table S6. Male-female aggression (calculated using *ad libitum* data) predicts future mating success for males. Related to STAR Methods.**

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 (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 male-female aggressive acts, 2240 total aggressive acts from males, distributed among 34 females (number of days of observation per cycle: mean $\pm$ sd:29.0 $\pm$ 14.1, number of mate-guarding males per cycle: 1.10 $\pm$ 0.69, range: [0-4]), and 39 males, and performed using a GLMM controlling for female identity, male identity and cycle identity (fitted 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 significance of each variable, while the confidence intervals are used to test for the significance of each level of the qualitative variables.

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)	<b>Rate of male-female aggression during cycle</b>		10.65	2.39	<b>[5.96 ; 15.34]</b>	27.02	1	<b>&lt;0.001</b>
	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
	<b>Female parity<sup>a</sup></b>	nulliparous	-0.88	0.36	<b>[-1.58 ; -0.18]</b>	6.77	1	<b>0.009</b>
	<b>Male rank</b>		2.34	0.60	[1.17 ; 3.52]	13.75	1	<b>&lt;0.001</b>
	Operational sex ratio		0.40	0.73	[-1.03 ; 1.83]	0.30	1	0.583
	Group <sup>b</sup>	L	0.34	0.36	[-0.36 ; 1.05]	0.91	1	0.34
	<b>Year<sup>c</sup></b>	2006	0.81	0.64	<b>[-0.43 ; 2.06]</b>	11.69	3	<b>0.009</b>
		2013	-1.10	0.69	[-2.46 ; 0.26]			
		2014	-0.49	0.71	[-1.88 ; 0.90]			

<sup>a</sup> Reference category: parous

<sup>b</sup> Reference category: J group

<sup>c</sup> Reference category: 2005

**Table S7. Sample size of behavioural focal observations. Related to STAR Methods.**

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]