

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±0.19
82 time per hour, i.e., once every 8h; non-swollen: 0.12±0.19, 1/9h] and directed much less
83 aggression towards non-cycling females [pregnant: 0.03±0.08, 1/32h; lactating: 0.03±0.08,
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±0.022 injuries per day, i.e., 1 injury every 73 days), followed by non-swollen
94 females (0.009±0.016, 1/115), lactating females (0.005±0.010, 1/191), and pregnant females
95 (0.005±0.009, 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 ± 0.09 times/h compared to 0.01 ± 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±sd:11.2±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	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

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

350 ^b Reference category: parous

351 ^c Reference category: J group

352 ^d 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	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]				

360 ^a Reference category: parous

361 ^b Reference category: J group

362 ^c 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 25th and 75th 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

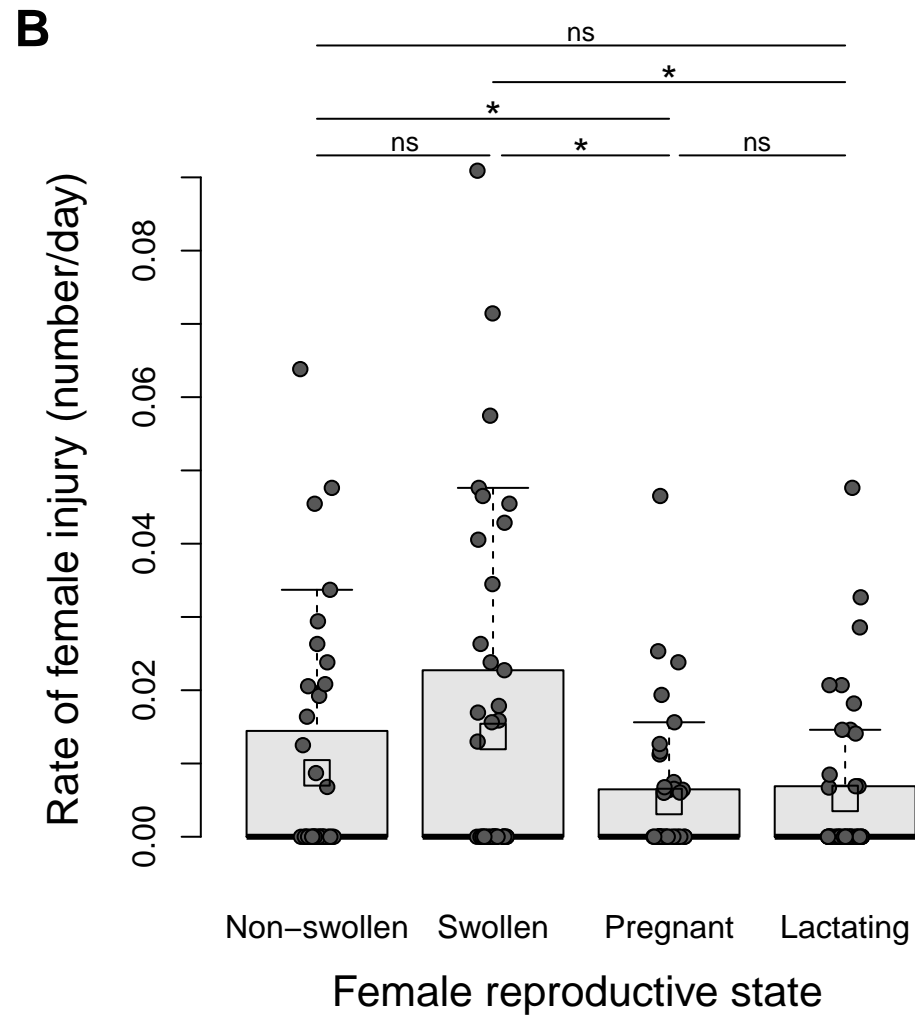
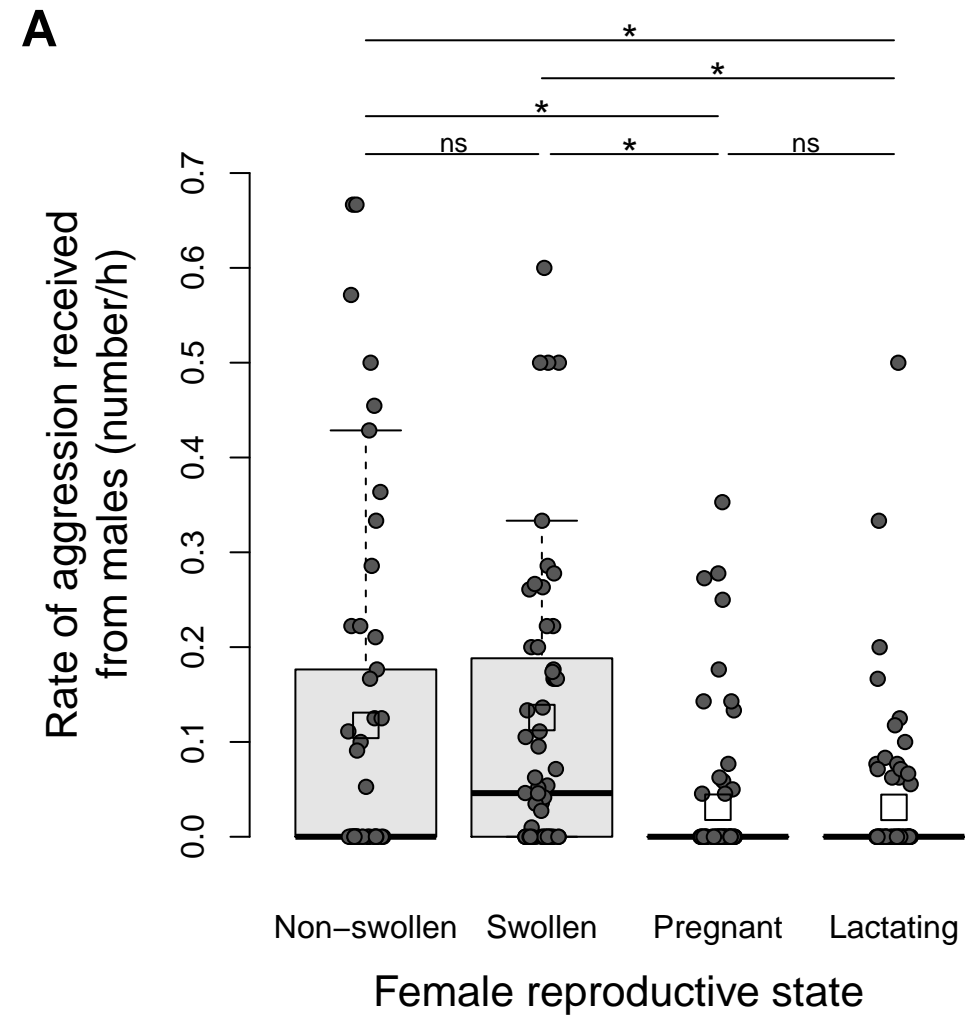
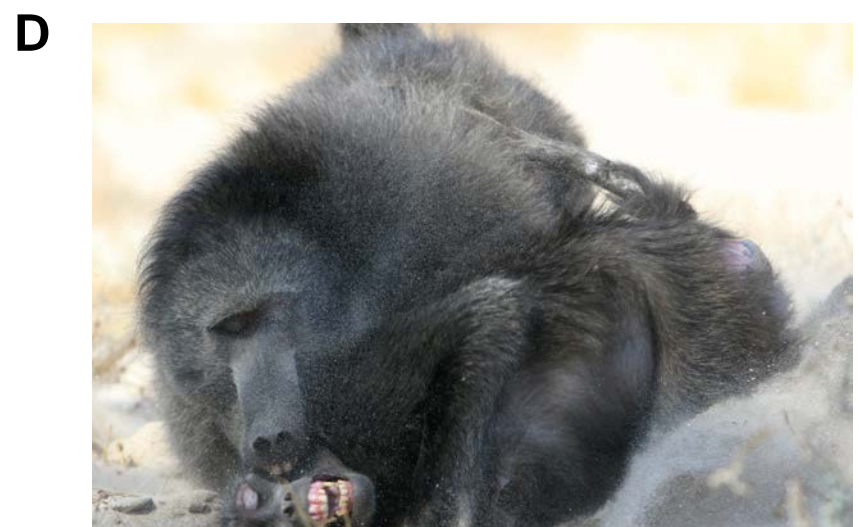
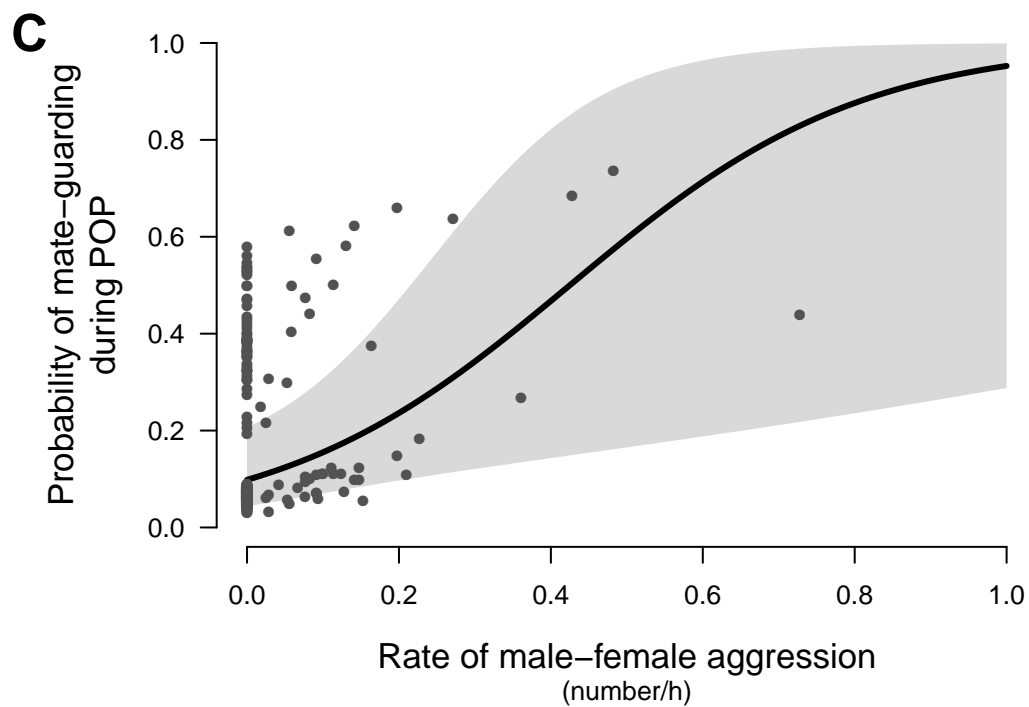
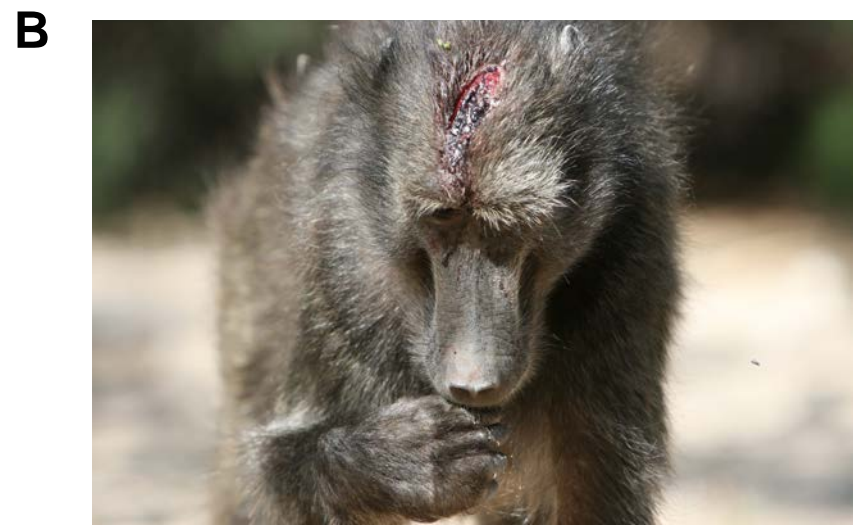
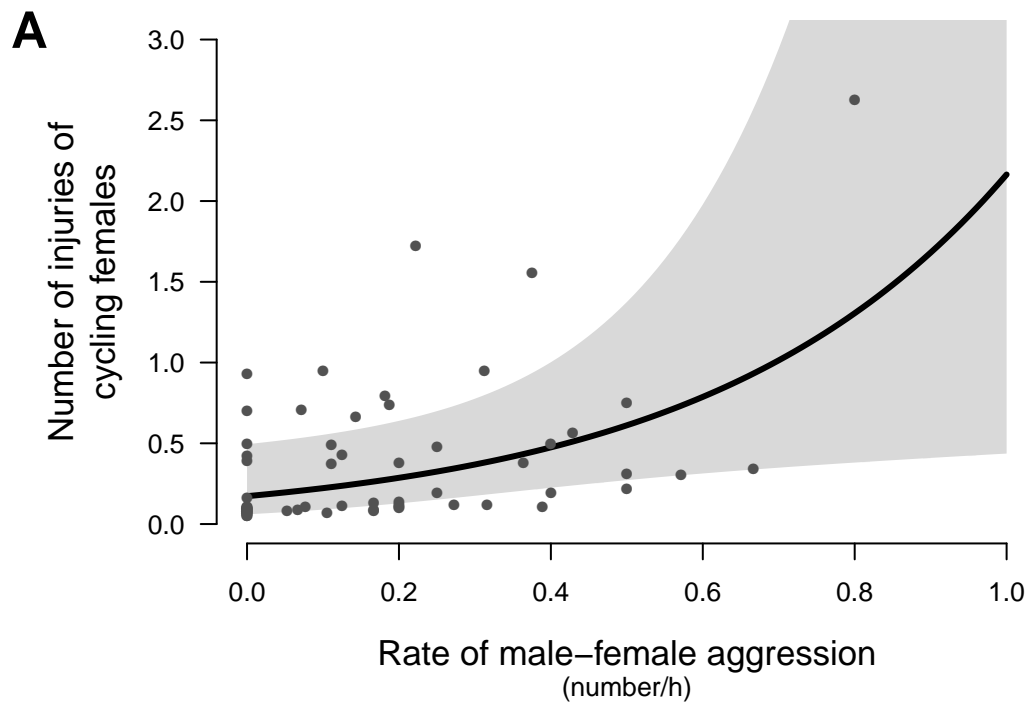


Figure 2



1 **STAR METHODS**

2

3 **CONTACT FOR REAGENT AND RESOURCE SHARING**

4 Further information and requests for protocols and datasets should be directed to and will be
5 fulfilled by the Lead Contact, Alice Baniel (alice.baniel@gmail.com).

6

7 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

8 *Study site and population*

9 We studied wild chacma baboons at Tsaobis Nature Park, a semi-arid environment in
10 Namibia [49]. We collected data from dawn to dusk on two habituated groups, called „J“ and
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
26 interactions (supplants, when one animal actively displaces another to take its place, and
27 displacements, when one animal passes close to another and makes it move away) and
28 agonistic interactions: attacks (any agonistic physical contacts including hits, bites, or
29 grabbing movements), chases (when one animal chases another for a distance of at least 3 m)
30 and threats (including staring, head bobbing, and ground sweeping while oriented toward the
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
33 changes, so a single hierarchy was calculated by pooling the aggression matrix across years.
34 In 2013-14 there were several demographic changes, so a separate hierarchy was calculated
35 for each year. We used Matman 1.1.4 (Noldus Information Technology 2003) in all cases.
36 The female dominance hierarchies were always linear (interactions in group L: $N_{05-06} = 1190$,
37 $N_{13} = 367$, $N_{14} = 1259$; interactions in group J: $N_{05-06} = 1173$, $N_{13} = 590$, $N_{14} = 978$; Landau's
38 linearity index h : $P < 0.05$ in all cases). All analyses presented here use the female's relative
39 rank (a standardization of absolute rank between 0 and 1), to control for differences in group
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
54 female gave birth within six months after the day of observation, lactating if she had a
55 dependant infant and had not yet resumed cycling, swollen if she was sexually receptive with
56 a perineal swelling, and non-swollen otherwise. For each cycle, we defined the POP as the 5-
57 day period preceding the day of swelling detumescence, during which ovulation generally
58 occurs [55,56]. Mate-guarding episodes were monitored *ad libitum*.

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
63 S7) during which we recorded 222 chases or attacks led by males. Supplants, displacements,
64 and threats were excluded because they are likely to be less stressful for females. We also
65 recorded 520 focal observations of 25 adult males, with 79 chases or attacks towards adult
66 females. In addition, we recorded *ad libitum* agonistic interactions, with 1579 chases or
67 attacks involving an identified adult male/female.

68

69 ***Observations of injuries***

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
77 described below. GLMMs were run using the glmer function of the lme4 package [57] in R
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-](https://github.com/AliceBaniel/Male-violence-and-sexual-intimidation-in-a-wild-primate-society)
210 [violence-and-sexual-intimidation-in-a-wild-primate-society](https://github.com/AliceBaniel/Male-violence-and-sexual-intimidation-in-a-wild-primate-society).

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290 test, LRT (assuming an asymptotic chi-square distribution of the test statistic), using the full
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292 computed the 95% confidence intervals of fixed factors (for multilevel categorical variables,
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294 checking that they did not cross zero). To test for pairwise differences between multiple
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296 sequentially [60]. To validate models, we checked the distribution of residuals (i.e., plotted
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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-](https://github.com/AliceBaniel/Male-violence-and-sexual-intimidation-in-a-wild-primate-society)
421 [violence-and-sexual-intimidation-in-a-wild-primate-society](https://github.com/AliceBaniel/Male-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 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>)

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)	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]				

^a Reference category: parous

^b Reference category: J group

^c 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]			
	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]				

^a Reference category: parous

^b Reference category: J group

^c 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	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	

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

^b Reference category: parous

^c Reference category: J group

^d 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 ^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

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

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

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

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

^e 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±sd:29.0±14.1, number of 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 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)	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]				

^a Reference category: parous

^b Reference category: J group

^c 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]