

Current Biology

Male Violence and Sexual Intimidation in a Wild Primate Society

Highlights

- Male aggression preferentially targets fertile females in chacma baboons
- Male aggression represents a major source of injuries for fertile females
- Male aggressors have higher mating success in the long term, but not immediately
- These results provide evidence for sexual intimidation in a wild non-human primate

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In Brief

Sexual intimidation is frequent in humans, but its evolutionary origins remain speculative because few animal studies have investigated comparable long-term forms of sexual violence. Baniel et al. study chacma baboons and show that males intimidate females to mate with them, and that sexual violence is the main source of injuries to females.

Male Violence and Sexual Intimidation in a Wild Primate Society

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SUMMARY

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

RESULTS

Animal studies of sexual conflict have focused on its more conspicuous forms, including infanticide [10, 11], forced

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

First, we investigated whether the reproductive state of females, defined as swollen (sexually receptive), non-swollen (non-sexually receptive, the non-fertile phase of the cycle), pregnant, or lactating, influenced their chances of receiving aggression from males using a generalized linear mixed model (GLMM; see STAR Methods and Table S1). We found that males preferentially targeted cycling females (swollen: mean \pm SD: 0.13 \pm 0.19 times per hr, i.e., once every 8 hr;

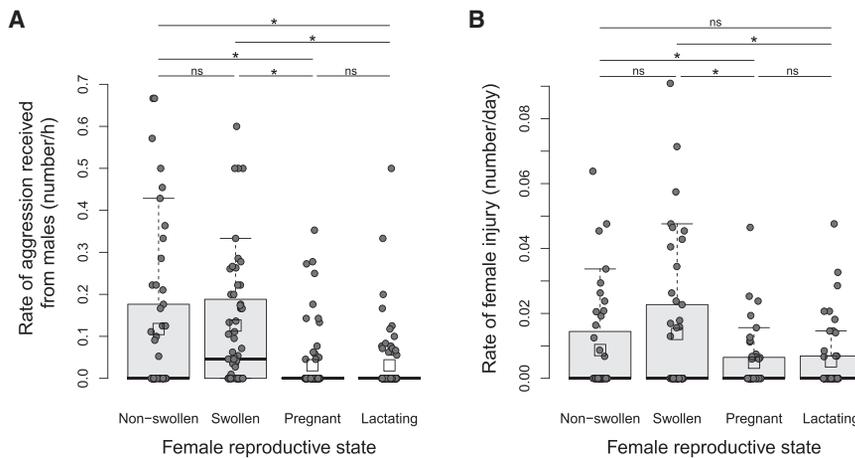


Figure 1. Cycling Females Receive More Aggression from Males and More Injuries Than Non-Cycling Females

Distribution of the mean rate of male aggression against females (A) and mean rate of female injuries across female reproductive states (B). Boxplots are drawn from the raw individual means per year (represented by black dots). The bottom and top of the box respectively represent the 25th and 75th quartiles, and the bold horizontal line the median. Whiskers include the interquartile range. Open squares represent the mean of the distribution. Note that the boxes representing the rate of aggression received by pregnant and lactating females are not visible because the median and the 25th and 75th quartiles are equal to zero. * $p \leq 0.05$; ns, not significant. See also [Tables S2 and S4](#).

non-swollen: 0.12 ± 0.19 , 1 per 9 hr) and directed much less aggression toward non-cycling females (pregnant: 0.03 ± 0.08 , 1 per 32 hr; lactating: 0.03 ± 0.08 , 1 per 32 hr) ([Table S2](#); [Figure 1A](#)). Cycling females could also attract male aggression if they participate in frequent conflicts because males regularly intervene in conflicts (the “male policing” hypothesis) [5, 28]. However, cycling females do not initiate more aggression toward other group members than non-cycling females (see [STAR Methods](#) and [Table S3](#)).

Second, we tested whether male aggression is costly for cycling females. Of the few female injuries with an observed cause, 78% were inflicted by adult males ($n = 17/22$). We tested whether the risk of injury is higher in cycling than non-cycling females using a GLMM (see [STAR Methods](#) and [Table S1](#)). Daily rates of female injury varied across the reproductive cycle and mirrored the rate of male aggression: swollen females received the most injuries (0.014 ± 0.022 injuries per day, i.e., 1 injury every 73 days), followed by non-swollen females (0.009 ± 0.016 , 1 per 115 days), lactating females (0.005 ± 0.010 , 1 per 191 days), and pregnant females (0.005 ± 0.009 , 1 per 208 days) ([Table S4](#); [Figure 1B](#)). We also found that, within a given cycle, females that faced higher

rates of aggression from males suffered more injuries ([Table 1](#); [Figures 2A and 2B](#)).

Third, we tested whether male aggression increases male mating success immediately (sexual harassment and punishment) and/or in the future (sexual intimidation). To test whether a male was more likely to copulate with a female within 5, 10, 15, or 20 min of assaulting her, we used a matched-control analysis [29]. We tested the difference in the proportion of observations containing copulations with the aggressor in the post-aggression (PA) versus matched-control (MC) (no aggressive event) observations, using McNemar’s chi-square tests (see [STAR Methods](#)). We found no support for short-term sexual harassment: the probability of copulation did not increase in the 5–20 min following male aggression for either unguarded ([Table S5A](#)) or mate-guarded females ([Table S5B](#)).

We used a similar approach to investigate whether the probability of females receiving male aggression increased within 5, 10, or 15 min after copulating with a rival male. We tested the difference in the proportion of aggression received from males who had not mated with the focal female in the post-copulation (PC) versus MC (no copulation) observations (see [STAR Methods](#)). We found no evidence for punishment either by non-mated

Table 1. Male Aggression Represents a Major Risk of Injury for Cycling Females

Response Variable	Fixed Factors	Levels	Estimate	SE	95% Confidence		LRT	df	p Value
					Interval				
Number of injuries received in a given cycle ^a	<i>Rate of male aggression during cycle</i>		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

Influence of the mean hourly rate of male aggression received by cycling females (calculated from focal observations) on daily rate of female injury. Parameters and tests are based on the observation of 30 injuries and 119 aggressive acts, distributed among 64 cycles of 30 different females (number of focals per cycle: 11.2 ± 5.0 [mean \pm SD]). Significant variables ($p \leq 0.05$) are shown in italics. SE: standard error; LRT, statistic of a likelihood ratio test, df, degrees of freedom. See also [Figure 2A](#).

^aThe number of days of the cycle observed was fitted as an offset fixed factor, to model a daily rate of injury.

^bReference category: parous.

^cReference category: J group.

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

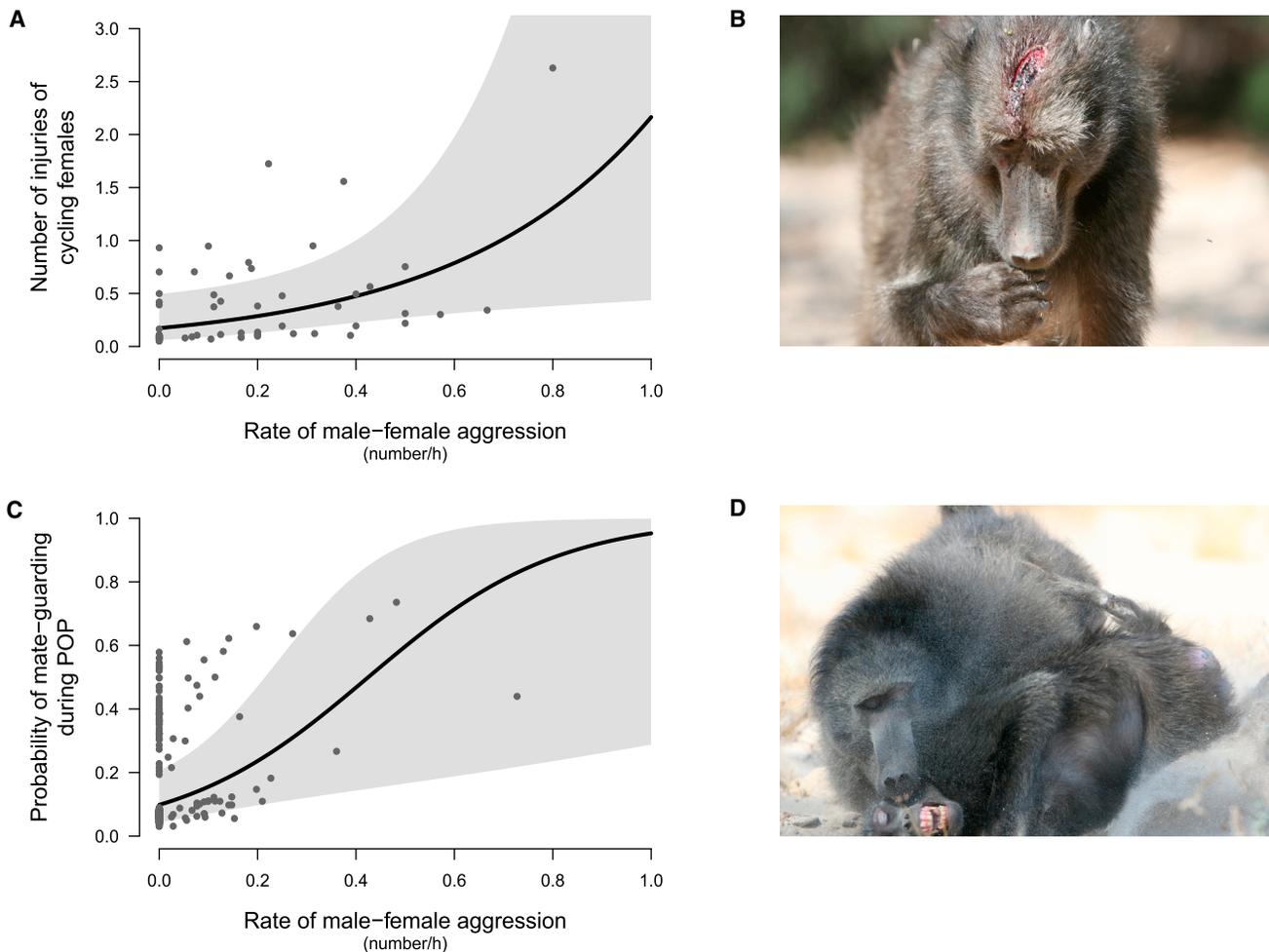


Figure 2. Male-Female Aggression Predicts Risk of Injury for Females and Future Mating Success for Males

(A) Partial residual plot of the number of injuries incurred by cycling females during a cycle in relation to the mean rate of male aggression received during the same cycle (calculated from focal observations). Black dots represent partial residuals of the GLMM, the black line is the model prediction, and the gray area represents the confidence interval. The prediction line is drawn holding all other fixed effects constant, using the median for numeric variables and most common category for factors (i.e., for a multiparous female of rank 0.6, cycling over 38 days, in L group, when there were 9 adult males present, in 2014).

(B) A female injured three times on the head by her mate-guarding male. This female died of unknown causes six months later.

(C) Partial residual plot of the probability of establishing a mate-guarding episode with a male in the peri-ovulatory period of a cycle in relation to the mean rate of aggression received from him throughout the cycle (calculated from focal observations). The prediction line is drawn for a multiparous female of rank 0.5, a male of rank 0.5, and an overall aggression rate of 0.005 times per day, in L group, in 2014.

(D) A male directs aggression toward a female. Photo credit: Alecia Carter.

See also [Tables 1 and 2](#).

males for unguarded females ([Table S5A](#)) or by the consort male for guarded females ([Table S5B](#)).

We tested whether a male's probability of mate-guarding a female at her peak fertility (i.e., during her peri-ovulatory period; POP) increased as a function of the mean hourly rate of aggression received by the female from this male prior to her POP, during the same estrous cycle (calculated using focal observation data) (see [STAR Methods](#) and [Table S1](#)). We found that a female who received more aggression from a male throughout her cycle was more likely to be mate-guarded by him during her ovulatory window at the end of that cycle ([Table 2](#); [Figures 2C and 2D](#)). Overall, females received aggression throughout their cycle from their future male con-

sort at a rate of 0.04 ± 0.09 times per hr compared to 0.01 ± 0.05 times per hr from other males. Similar results were found when estimating the rate of male-female aggression using *ad libitum* data ([Table S6](#)).

This last set of results could possibly reflect a female preference for aggressive males, rather than sexual coercion [[8](#), [9](#)]. Under this scenario, we would expect some males to express aggressive phenotypes, and females to express a preference for these aggressive phenotypes. To test this alternative hypothesis, we included an additional fixed effect in the GLMM described above, a proxy of male general propensity to aggression, estimated as the *ad libitum* daily rate of male aggression initiated toward any individual of the group per year. In contrast

Table 2. Male-Female Aggression Predicts Future Mating Success for Males

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)	<i>Rate of male-female aggression during cycle</i>		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
	<i>Female parity^a</i>	<i>nulliparous</i>	-0.96	0.43	[-1.80; -0.12]	5.82	1	0.016
	<i>Male rank</i>		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
	<i>Year^c</i>	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]			

Influence of the mean hourly rate of aggression received from a male by an unguarded female throughout her estrous cycle but prior to peri-ovulatory period (POP) (calculated from focal observations) on the same male's probability of mate-guarding her during her subsequent POP. Parameters and tests are based on 58 cycles and 74 male-female aggressive acts, distributed among 30 females (number of focal observations per cycle: 16.07 ± 12.00 [mean \pm SD]; number of mate-guarding males per cycle: 1.20 ± 0.72 , range: [0–4]) and 39 males, analyzed using a GLMM. Significant variables ($p \leq 0.05$) are shown in italics. Likelihood ratio tests (LRTs) were used to test the significance of each variable, while confidence intervals were used to test the significance of each level of the qualitative variables. See also [Figure 2C](#).

^aReference category: parous.

^bReference category: J group.

^cReference category: 2005.

to the dyadic rate of aggression received by a female from a male during an estrous cycle, a male's general rate of aggression was not found to influence his probability of mate-guarding that female ([Table 2](#); [Table S6](#)).

DISCUSSION

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

Second, we conducted a detailed characterization of the mechanisms of sexual coercion through an analysis of behavioral

sequences that reveals the temporal decoupling between aggression and matings. Our results suggest that direct coercion is more important than indirect coercion (i.e., males attempt to increase their own mating rates rather than to decrease those of others), by showing that males rarely punish females who mate with rivals, although it may not be possible to fully disentangle these effects because one aggressive act may simultaneously encourage a female to mate and discourage her to leave.

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

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

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information includes seven tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.06.013>.

AUTHOR CONTRIBUTIONS

A.B. and E.H. designed the study and collected the data. A.B. ran the analyses. All authors contributed to the drafting of the manuscript.

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REFERENCES

1. WHO (2013). Global and Regional Estimates of Violence against Women: Prevalence and Health Effects of Intimate Partner Violence and Non-Partner Sexual Violence (World Health Organization). http://apps.who.int/iris/bitstream/10665/85239/1/9789241564625_eng.pdf.
2. Smuts, B. (1992). Male aggression against women: An evolutionary perspective. *Hum. Nat.* 3, 1–44.
3. Wilson, M., and Daly, M. (2009). Coercive violence by human males against their female partners. In *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females*, M.N. Muller, and R.W. Wrangham, eds. (Harvard University Press), pp. 271–291.
4. Wrangham, R.W., and Muller, M.N. (2009). Sexual coercion in humans and other primates: the road ahead. In *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females*, M.N. Muller, and R.W. Wrangham, eds. (Harvard University Press), pp. 451–468.
5. Muller, M.N., Kahlenberg, S.M., and Wrangham, R.W. (2009). Male aggression and sexual coercion of females in primates. In *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females*, M.N. Muller, and R.W. Wrangham, eds. (Harvard University Press), pp. 3–22.
6. Clutton-Brock, T.H., and Parker, G.A. (1995). Sexual coercion in animal societies. *Anim. Behav.* 49, 1345–1365.
7. Smuts, B.B., and Smuts, R.W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv. Study Behav.* 22, 1–63.
8. Cordero, C., and Eberhard, W.G. (2003). Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* 16, 1–6.
9. Pizzari, T., and Snook, R.R. (2003). Perspective: sexual conflict and sexual selection: chasing away paradigm shifts. *Evolution* 57, 1223–1236.
10. van Schaik, C.P., Pradhan, G.R., and van Noordwijk, M.A. (2004). Mating conflict in primates: infanticide, sexual harassment and female sexuality. In *Sexual Selection in Primates: New and Comparative Perspectives*, P.M. Kappeler, and C.P. van Schaik, eds. (Cambridge University Press), pp. 131–150.
11. Lukas, D., and Huchard, E. (2014). Sexual conflict. The evolution of infanticide by males in mammalian societies. *Science* 346, 841–844.
12. Emlen, S.T., and Wrege, P.H. (1986). Forced copulations and intra-specific parasitism: two costs of living in the white fronted bee-eater. *Ethology* 71, 2–29.
13. Knott, C.D., and Kahlenberg, S. (2007). Orangutans in perspective: forced copulations and female mating resistance. In *Primates in Perspective*, S. Bearder, C.J. Campbell, A. Fuentes, K.C. MacKinnon, and M. Panger, eds. (Oxford University Press), pp. 290–305.
14. Clutton-Brock, T.H., Price, O., and MacColl, A. (1992). Mate retention, harassment and the evolution of ungulate leks. *Behav. Ecol.* 3, 234–242.
15. Connor, R.C., Richards, A.F., Smolker, R.A., and Mann, J. (1996). Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour* 133, 37–69.
16. Cappelzozzo, H.L., Túnez, J.I., and Cassini, M.H. (2008). Sexual harassment and female gregariousness in the South American sea lion, *Otaria flavescens*. *Naturwissenschaften* 95, 625–630.
17. Muller, M.N., Kahlenberg, S.M., Emery Thompson, M., and Wrangham, R.W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proc. Biol. Sci.* 274, 1009–1014.
18. Muller, M.N., Emery Thompson, M., Kahlenberg, S., and Wrangham, R. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behav. Ecol. Sociobiol.* 65, 921–933.
19. Feldblum, J.T., Wroblewski, E.E., Rudicell, R.S., Hahn, B.H., Paiva, T., Cetinkaya-Rundel, M., Pusey, A.E., and Gilby, I.C. (2014). Sexually coercive male chimpanzees sire more offspring. *Curr. Biol.* 24, 2855–2860.
20. Kaburu, S.S.K., and Newton-Fisher, N.E. (2015). Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. *Behav. Ecol. Sociobiol.* (Print) 69, 1039–1052.
21. Enomoto, T. (1981). Male aggression and the sexual behavior of Japanese monkeys. *Primates* 22, 15–23.
22. Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behaviour* (Harvard University Press).
23. Bulger, J.B. (1993). Dominance rank and access to estrous females in male savanna baboons. *Behaviour* 127, 67–103.

24. Huchard, E., Courtiol, A., Benavides, J.A., Knapp, L.A., Raymond, M., and Cowlshaw, G. (2009). Can fertility signals lead to quality signals? Insights from the evolution of primate sexual swellings. *Proc. Biol. Sci.* *276*, 1889–1897.
25. Weingrill, T., Lycett, J.E., Barrett, L., Hill, R.A., and Henzi, S.P. (2003). Male consortship behaviour in chacma baboons: the role of demographic factors and female conceptive probabilities. *Behaviour* *140*, 405–427.
26. Alberts, S.C., Watts, H.E., and Altmann, J. (2003). Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim. Behav.* *65*, 821–840.
27. Alberts, S.C., Buchan, J.C., and Altmann, J. (2006). Sexual selection in wild baboons: from mating opportunities to paternity success. *Anim. Behav.* *72*, 1177–1196.
28. Smuts, B.B. (1985). *Sex and Friendship in Baboons* (Aldine).
29. De Waal, F., and Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus monkeys. *Behaviour* *85*, 224–241.
30. Kummer, H. (1968). *Social Organization of Hamadryas Baboons: A Field Study* (Chicago University Press).
31. Swedell, L., and Schreier, A. (2009). Male aggression toward females in hamadryas baboons: conditioning, coercion, and control. In *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females*, M.N. Muller, and R.W. Wrangham, eds. (Harvard University Press), pp. 244–268.
32. Polo, P., and Colmenares, F. (2012). Behavioural processes in social context: female abductions, male herding and female grooming in hamadryas baboons. *Behav. Processes* *90*, 238–245.
33. Cheney, D.L., and Seyfarth, R.M. (1977). Behavior of adult and immature male baboons during intergroup encounters. *Nature* *269*, 404–406.
34. Cowlshaw, G. (1995). Behavioural patterns in baboon group encounters: the role of resource competition and male reproductive strategies. *Behaviour* *132*, 75–86.
35. Kitchen, D.M., Cheney, D.L., and Seyfarth, R.M. (2005). Contextual factors mediating contests between male chacma baboons in Botswana: effects of food, friends and females. *Int. J. Primatol.* *26*, 105–125.
36. Kitchen, D.M., Beehner, J.C., Bergman, T.J., Cheney, D.L., Crockford, C., Engh, A.L., Fischer, J., Seyfarth, R.M., and Wittig, R.M. (2009). The causes and consequences of male aggression directed at female chacma baboons. In *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females*, M.N. Muller, and R.W. Wrangham, eds. (Harvard University Press), pp. 128–156.
37. Le Boeuf, B.J., and Mesnick, S. (1991). Sexual behaviour of male northern elephant seals: I. Lethal injuries to adult females. *Behaviour* *116*, 143–162.
38. Szykman, M., Engh, A.L., Van Horn, R.C., Boydston, E.E., Scribner, K.T., and Holekamp, K.E. (2003). Rare male aggression directed toward females in a female-dominated society: baiting behavior in the spotted hyena. *Aggress. Behav.* *29*, 457–474.
39. Linklater, W.L., Cameron, E.Z., Minot, E.O., and Stafford, K.J. (1999). Stallion harassment and the mating system of horses. *Anim. Behav.* *58*, 295–306.
40. Hohmann, G., and Fruth, B. (2003). Intra- and inter-sexual aggression by bonobos in the context of mating. *Behaviour* *140*, 1389–1413.
41. Manson, J.H. (1994). Male aggression: a cost of female mate choice in Cayo Santiago rhesus macaques. *Anim. Behav.* *48*, 473–475.
42. Réale, D., Boussès, P., and Chapuis, J.-L. (1996). Female-biased mortality induced by male sexual harassment in a feral sheep population. *Can. J. Zool.* *74*, 1812–1818.
43. Archie, E.A., Altmann, J., and Alberts, S.C. (2014). Costs of reproduction in a long-lived female primate: injury risk and wound healing. *Behav. Ecol. Sociobiol. (Print)* *68*, 1183–1193.
44. MacCormick, H.A., MacNulty, D.R., Bosacker, A.L., Lehman, C., Bailey, A., Anthony Collins, D., and Packer, C. (2012). Male and female aggression: lessons from sex, rank, age, and injury in olive baboons. *Behav. Ecol.* *23*, 684–691.
45. Cheney, D.L., and Seyfarth, R.M. (2007). *Baboon Metaphysics: The Evolution of a Social Mind* (University of Chicago Press).
46. Stumpf, R.M., Martinez-Mota, R., Milich, K.M., Righini, N., and Shattuck, M.R. (2011). Sexual conflict in primates. *Evol. Anthropol.* *20*, 62–75.
47. Caizergues, A., and Lambrechts, M.M. (1999). Male “macho” mammals exploiting females versus male “Don Juan” birds exploited by females: the opposite-sex exploitation (OSEX) theory. *Ecol. Lett.* *2*, 204–206.
48. Pradhan, G.R., and van Schaik, C.P. (2009). Why do females find ornaments attractive? The coercion-avoidance hypothesis. *Biol. J. Linn. Soc. Lond.* *96*, 372–382.
49. R Core Team (2015). *R: A language and environment for statistical computing* (R Foundation for Statistical Computing). <http://www.r-project.org/>.
50. Bates, D., Maechler, M., Bolker, B., and Walker, S. (2014). lme4: linear mixed-effects models using ‘Eigen’ and S4. R package version 1.1-7. <https://cran.r-project.org/web/packages/lme4/index.html>.
51. Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., and Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Anim. Behav.* *82*, 911–921.
52. Cowlshaw, G. (1997). Refuge use and predation risk in a desert baboon population. *Anim. Behav.* *54*, 241–253.
53. Alberts, S.C., and Altmann, J. (1995). Balancing costs and opportunities: dispersal in male baboons. *Am. Nat.* *145*, 279–306.
54. Altmann, J., and Alberts, S.C. (2003). Variability in reproductive success viewed from a life-history perspective in baboons. *Am. J. Hum. Biol.* *15*, 401–409.
55. Baniel, A., Cowlshaw, G., and Huchard, E. (2016). Stability and strength of male-female associations in a promiscuous primate society. *Behav. Ecol. Sociobiol.* *70*, 761–775.
56. Albers, P.C.H., and de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Anim. Behav.* *61*, 489–495.
57. Higham, J.P., Heistermann, M., Ross, C., Semple, S., and Maclarnon, A. (2008). The timing of ovulation with respect to sexual swelling detumescence in wild olive baboons. *Primates* *49*, 295–299.
58. Daspre, A., Heistermann, M., Hodges, J.K., Lee, P.C., and Rosetta, L. (2009). Signals of female reproductive quality and fertility in colony-living baboons (*Papio h. anubis*) in relation to ensuring paternal investment. *Am. J. Primatol.* *71*, 529–538.
59. Mundry, R., and Nunn, C.L. (2009). Stepwise model fitting and statistical inference: turning noise into signal pollution. *Am. Nat.* *173*, 119–123.
60. Pinheiro, J.C., and Bates, D.M. (2000). *Mixed-Effects Models in S and S-PLUS* (Springer).

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
chacma baboon (<i>Papio ursinus</i>)	N/A	N/A
Software and Algorithms		
R version 3.3.1	[49]	http://www.r-project.org/
Package lme4	[50]	https://cran.r-project.org/web/packages/lme4/index.html
Package Elo-rating	[51]	https://cran.r-project.org/web/packages/EloRating/EloRating.pdf
MatMan 1.1.4	N/A	http://www.noldus.com/knowledge-base/matman

CONTACT FOR REAGENT AND RESOURCE SHARING

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

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study site and population

We studied wild chacma baboons at Tsaobis Nature Park, a semi-arid environment in Namibia [52]. The study was approved by the Ethics Committee of the Zoological Society of London (BPE/671). We collected data from dawn to dusk on two habituated groups, called 'J' and 'L', over four different periods: June–December 2005, Mai 2006–January 2007, June–October 2013 and May–November 2014. Number of adults in J group ranged from 6–9 males and 17 females in 2005; 4–5 males and 17 females in 2006; 7–10 males and 17 females in 2013; 7–8 males and 18 females in 2014. L group comprised 3 males and 9 females in 2005; 4–5 males and 9–11 females in 2006; 9–11 males and 18–19 females in 2013; 9 males and 17–19 females in 2014. All adults were individually recognizable and observable at close range. Age (in years) was estimated from a combination of known birth dates and dental patterns of tooth eruption and wear, examined during prior captures [24]. Only adults were included in the study. Males were considered adult when they reached eight years of age [53] and females when they reached menarche [54]. Female parity (nulliparous or parous) was determined based on long-term life-history data.

METHOD DETAILS

Establishment of dominance ranks of males and females

Individual ranks were assessed through focal and *ad libitum* observations of approach-avoid interactions (supplants, when one animal actively displaces another to take its place, and displacements, when one animal passes close to another and makes it move away) and agonistic interactions: attacks (any agonistic physical contacts including hits, bites, or grabbing movements), chases (when one animal chases another for a distance of at least 3 m) and threats (including staring, head bobbing, and ground sweeping while oriented toward the targeted individual). Our approach to the female dominance hierarchy was contingent upon the demographic stability of the study period. In 2005–2006 there were few demographic changes, so a single hierarchy was calculated by pooling the aggression matrix across years. In 2013–14 there were several demographic changes, so a separate hierarchy was calculated for each year. We used Matman 1.1.4 (Noldus Information Technology 2003) in all cases. The female dominance hierarchies were always linear (interactions in group L: $N_{05-06} = 1190$, $N_{13} = 367$, $N_{14} = 1259$; interactions in group J: $N_{05-06} = 1173$, $N_{13} = 590$, $N_{14} = 978$; Landau's linearity index h : $p < 0.05$ in all cases). All analyses presented here use the female's relative rank (a standardization of absolute rank between 0 and 1), to control for differences in group size. This was calculated using the formula: $1 - ((1-r)/(1-n))$, where r is the absolute rank of an individual (ranging from 1 to the group size, n). In contrast to the female hierarchy, the male hierarchy was much less stable [55]. Thus, male ranks were established for each study period using an Elo-rating procedure implemented in the R package EloRating (version 0.43) [51] which gives a score for each individual on each day of observation. Compared to dyadic interaction matrices where ranks are calculated over a given time period, an Elo-rating procedure allows the continuous updating of ranks according to the temporal sequence of interactions [51, 56]. To obtain comparable ratings across the entire study period, we derived a daily standardized rank by scaling the Elo-rating score of each individual proportionally between 0 (corresponding to the minimal score and thus the lowest ranking male) and 1 (corresponding to the maximal score and the highest ranking male).

Female reproductive state and mate-guarding patterns

Female reproductive state was recorded daily as pregnant (determined *a posteriori*) if a female gave birth within six months after the day of observation, lactating if she had a dependant infant and had not yet resumed cycling, swollen if she was sexually receptive with a perineal swelling, and non-swollen otherwise. For each cycle, we defined the POP as the 5-day period preceding the day of swelling detumescence, during which ovulation generally occurs [57, 58]. Mate-guarding episodes were monitored *ad libitum*.

Behavioral data

We conducted one-hour focal animal samples on all adults. We conducted 3439 focal observations on 53 females distributed across reproductive states (see sample size in Table S7) during which we recorded 222 chases or attacks led by males. Supplants, displacements, and threats were excluded because they are likely to be less stressful for females. We also recorded 520 focal observations of 25 adult males, with 79 chases or attacks toward adult females. In addition, we recorded *ad libitum* agonistic interactions, with 1579 chases or attacks involving an identified adult male/female.

Observations of injuries

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

QUANTIFICATION AND STATISTICAL ANALYSIS

We ran a combination of GLMMs (summarized in Table S1) and matched-control analyses described below. GLMMs were run using the `glmer` function of the `lme4` package [50] in R version 3.3.1 [49]. The significance of the fixed factors was tested using a likelihood ratio test, LRT (assuming an asymptotic chi-square distribution of the test statistic), using the full model (to avoid problems arising from stepwise model selection procedures [59]). We further computed the 95% confidence intervals of fixed factors (for multilevel categorical variables, confidence intervals were used to test the significance of each level of the variable by checking that they did not cross zero). To test for pairwise differences between multiple levels of a categorical variable (e.g., “reproductive state”) we changed the reference category sequentially [60]. To validate models, we checked the distribution of residuals (i.e., plotted the residuals against the continuous predictors and checked that the residuals were normally distributed).

Male aggression and female reproductive state

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

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

Male aggression and female injuries

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

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

Sexual harassment and male mating success

Using both male and female focal observations, we tested whether an adult male was more likely to copulate with a female after he attacked her across 4 different time intervals ($x = 5, 10, 15$ and 20 min). We did not have enough matched-control observations to

investigate longer time intervals. After each incidence of male-female aggression during a focal follow, we selected the x following minutes of observation, hereafter the post-aggression (PA) observation, and assessed whether a copulation occurred with the male aggressor (no: 0; yes: 1). To each PA observation, we matched an observation of the same length of time for the same female, where no male aggression occurred during the previous x minutes, hereafter the matched-control (MC) observation, and assessed whether she copulated with the male aggressor of the PA observation. We compared the difference in the proportions of observations including copulations between the post-aggression (PA) and matched-control (MC) observations using McNemar's Chi-square tests.

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

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

Punishment and male mating success

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

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

Sexual intimidation and male mating success

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

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

DATA AND SOFTWARE AVAILABILITY

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