Female chacma baboons modulate their sexual receptivity in response to male coercion

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Research in social mammals has revealed the complexity of female counter-strategies to reproductive competition and sexual conflict. For example, comparative research has shown that the length of female sexual receptivity varies with infanticide risk, but whether individuals can strategically adjust their period of receptivity from cycle to cycle remains unknown. This study addresses this gap by exploring whether wild female chacma baboons (*Papio ursinus*) modulate their receptivity in response to the social environment. Given that female chacma baboons (a) compete for paternal care and (b) that infanticide risk and coercion are high, we predicted that: females could (a) shorten their receptive period to reduce intrasexual aggression and (b) male coercion, or (c) increase their conceptive period to access multiple or their preferred male. We quantified 158 receptivity cycles from 47 females recorded over 15 years. Females' swelling duration, but not maximal-swelling, had low repeatability between females, but most variation in both phases stemmed from within females. We found evidence that females decrease their oestrous duration in response to an increasing number of in-group males, possibly to decrease their exposure to sexual coercion. We thus present preliminary evidence for an unexplored mechanism under sexual selection: female cycle length manipulation.

Keywords: cycle length manipulation, sexual selection, sexual coercion, social environment, female competition

Introduction

Recent advances in sexual selection theory underline the importance of both mate choice and intrasexual female competition in generating variance in female reproductive success [1–4]. In the first case, it may be advantageous for females to concentrate paternity into a single male who can provide benefits in the form of good genes or of paternal services such as protection to her or her offspring. However, in group-living species, a number of social pressures may decrease the possibility for females to express their mating preference. For example, recent studies highlight the role of sexual conflict [5], which frequently manifests via infanticide in mammals. Indeed, infanticide risk may push females to mate with multiple rather than single partners, in order to dilute paternity among multiple males who subsequently restrain from attacking an offspring that they could have sired [6,7]. Female choice may be further constrained by sexual coercion, when males direct aggression to females [3,5,8], either to increase the probability that they will mate with them or to decrease the probability that they will mate promiscuously [9]. In such cases, females will mate with their aggressors if resisting is more costly than giving in (i.e., convenience polyandry) [5]. In groups of water striders (*Aquarius remigis*), aggressive males acquire more matings than less aggressive ones [10]. In primates, male baboons (*Papio ursinus*) that attack pre-ovulatory females are more likely to monopolize them when receptive [11] and females do not copulate close to adult males to avoid bystanders' aggression [11,12]. Also, female chimpanzees (*Pan troglodytes*) initiate copulations most frequently with those males that were most aggressive towards them throughout their cycle [13,14] and male lemurs (*Lemur catta*) that are not preferred can force copulations [15]. However, male coercion can lead to female counterstrategies and antagonistic co-evolution between the sexes [5] since it is associated to multiple costs for females: for example when they are forced to mate with subordinate or incompatible males, when coercion manifested as direct aggression/harassment increases stress hormone secretion [14], when it leads caring males to reduce parental care [8] or when it impairs female choice [16].

Females also face intrasexual competition over access to males and reproductive resources [17–20]. This competition for access to males increases when there is synchrony of females' fertility (i.e., ovarian synchrony), which creates a female-biased operational sex ratio (OSR) and increases aggression received by receptive females [21,22]. In general, females compete with consexuals for (a) their preferred mates (e.g., chacma baboons: [21]; red-fronted lemurs: [23]), for (b) paternal services for their offspring (e.g., chacma baboons: [24,25]) and (c) other reproductive resources [26], such as breeding territories (e.g., lek center [27]) or food

resources [28]. Those benefits are achieved either through monopolisation of resources directly from females (i.e., contest competition for food) [29] or indirectly (e.g., nutrient-rich spermatophores in insects:[30]; low predation risk in lek centers [27]). Antagonism for (a), (b) and (c) can manifest through non-aggressive interactions (e.g., signals: [30]) and escalate up to physical aggression, which can be detrimental to the receiver's short- or long-term fitness [31].

When facing coercion and intrasexual competition, females may use cycle manipulation by adjusting the length of the receptive period of the menstrual cycle (cycle length manipulation, hereafter CLM) as one counterstrategy. Such a mechanism could be under selection as it can potentially decrease the rate of aggression females receive from (1) intrasexual competition and (2) sexual coercion, or (3) alternatively it might increase females' probability of mating with their preferred or multiple males (increase female mate choice). Theoretical and experimental evidence for cycle manipulation exists [32,33], with studies detecting physiological changes in female cycling patterns (e.g., changes to cycle length, resumption of cycling) in response to the social environment. Socially-stressed primate females, for example by being harassed near menstruation, have longer menstrual cycles [34]. Cycling female yellow baboons that receive aggression from consexuals tend to have more cycles to conception and longer interbirth intervals [31], while pregnant females that are systematically harassed experience reduced fitness (through non-normal gestation length, spontaneous abortion, and premature delivery) [31]. Psychosocial stress stemming from social instability, in the form of male take-overs, induces female physiological responses too: the presence of unfamiliar males can mediate early sexual maturation [35,36] or abortion [37] in female mammals, in a likely effort to limit infanticide risk. Novel males in geladas prompt females of any state (immature, cycling, lactating, or pregnant) to start or resume cycling [36,38], while female hamadryas with young infants develop swellings to advertise a reduced postpartum amenorrhea that results in copulations with novel males during take-overs [33]. However, these swellings are deceptive signals that ultimately decrease infanticide risk (four out of five infants survived in [33]) since females did not conceive during the first cycles after the take-over, their reproduction was not accelerated and the interbirth intervals were not shorter compared to times with no male take-overs. Despite the above results though, no study to date has specifically proposed CLM, or tested for it, as a further potential mechanism under selection.

In this study, we explored whether females adjust the duration of their oestrus in response to the social environment to either reduce aggression from (1) coercive males or (2) other females or to increase their access to (3) their preferred or (4) multiple males. We focused

on female chacma baboons because they exhibit elevated female-female competition, compared to other primates [25,39,40], live in multimale-multifemale groups, mate promiscuously [11,41], and have exaggerated swellings that reliably indicate females' stage of the follicular phase of the oestrus cycle [32]. Female chacma baboons are an ideal model to study female intra- and intersexual competition, as well as sexual coercion, since they target the dominant male as a sexual partner [25,40], but also mate promiscuously [21], outside their peak swelling, to establish more males with a nonzero paternity probability or to initiate male-male competition (e.g., sperm competition) [12,32]. In addition, male's monopolisation of only one receptive female at a time (i.e., mate-guarding: [19,24]) results in female-female competition over sexual access to particular males [21,25], who might be better able to protect them from aggressive consexuals or provide future postpartum care for the offspring [42].

To address our overarching aim, we proceeded in two steps. First, we explored the variation within and among females in the durations of swelling and maximal-swelling stages of the cycle. We aimed to quantify the repeatability of females' receptivity phases to determine their flexibility, predicting large variation within females. Second, we tested whether intersexual or intrasexual selection, or sexual conflict in the form of male coercion, could explain the remaining variation in the duration of specific cycle phases (summarised in Table 1). First, considering female intrasexual selection, we tested whether female competition for paternal care explains variation in the duration of receptivity (the avoidance of female aggression hypothesis [H1]). Pregnant and lactating females aggressively target swollen ones to decrease competition for paternal care of their own offspring, or to induce reproductive suppression so that their own infants are not born at the same time as many others [43]. For this reason, we predicted that more in-group pregnant and lactating females result in higher stress levels in cycling females, which in turn leads receptive females to deflate quickly. This response should, ultimately, decrease their exposure to consexual aggression. Our second hypothesis deals with intersexual selection and sexual conflict (H2): we hypothesized that females would manipulate their swelling and maximal-swelling duration to access the dominant mate (the paternity concentration hypothesis, H2a). We predicted that, when competition for access to the alpha male was likely because there were simultaneously-swollen individuals, females would delay ovulation by elongating their swelling or maximal-swelling duration to increase the probability of mating with this male. By doing so females may benefit from (a) good genes [25,32] and from (b) concentrating paternity certainty in their preferred male, usually the dominant, who is also the most likely to pose a future risk of infanticide if they fail to mate with him [25,44]. We also tested whether the risk of infanticide from multiple

males explains patterns of variation in female baboons' cycle-phases (the paternity confusion hypothesis, H2b). We predicted that females would increase their swelling or maximal-swelling length as the operational sex ratio (OSR) becomes female-skewed—and female-female mating competition increases accordingly—so they still manage to mate with many males and reduce infanticide risk. Finally, we tested whether the effect of social instability in the form of high numbers of in-group males (i.e., strong male-male competition) explains patterns of variation in a female's receptivity phases. We predicted that a male-skewed OSR or a high number of in-group males induces high male-male competition, which translates into an increased risk of sexual coercion for receptive females [11,24]. Females may thus shorten their oestrous period to escape or minimize the aggression received from coercive males (the avoidance of male coercion hypothesis, H2c).

Table 1

Hypotheses, predictions and support for the hypotheses proposed to affect the duration of female cycle-specific phases

Hypotheses		**Predictions**	**Support?**[1]	
Hypothesis	Explanation		SD[2]	MSD[3]
H1: Intrasexual selection	*H1. Avoidance of female aggression hypothesis* = Females shorten their sexual receptivity to decrease their exposure to aggression from pregnant and lactating females who compete for access to paternal care .	↑ PL[4] -> ↓ (M)SD to ↓ consexual aggression.	—	—
H2: Intersexual selection & Sexual conflict	H2a: *Paternity concentration hypothesis* = Females lengthen their sexual receptivity to increase their chances of mating with the alpha male when several other females are simultaneously swollen.	↑ simultaneously receptive females -> ↑ (M)SD to ↑ access to preferred (dominant) male.	—	—
	H2b: *Paternity confusion hypothesis* = Females lengthen their sexual receptivity to mate with multiple males and decrease infanticide risk when the operational sex-ratio is female-biased.	Female-biased OSR -> ↑ (M)SD to mate with many males and confuse paternity.	—	—
	H2c: *Avoidance of male coercion hypothesis* = Females shorten their sexual receptivity to decrease their exposure to sexual coercion when there is strong male-male competition and social instability because of high numbers of in-group males.	Male-biased OSR or ↑ in-group males -> ↓ (M)SD to avoid coercive behaviour.	+	—

[1] + = support models, — = no support; [2]SD= swelling duration, [3]MSD= maximal-swelling duration; [4]PL = the sum of in-group pregnant and lactating females.

Materials and Methods

Study site and animals

Data were collected from identifiable females within two habituated groups, J and L, of a wild chacma baboon population at Tsaobis Leopard Park (22º22´S, 15º 44´E) in central Namibia. Studies on this population, which have been ongoing since 2000 [45], have revealed that the naturally-foraging baboons [45] exhibit low predation risk [46] and high female-female aggression rates [21,25] that can result in reproductive suppression [25]. Over the course of the study, troop numbers fluctuated around a median of 55 (44–69) in J troop and 52 (21–71) in L troop.

The data used in this study were collected periodically over 15 years, from 2005 to 2019, during field seasons lasting between 2 and 8 months *per annum*, usually during the austral winter. During field seasons, troops were visited daily, when possible, with some interruptions for other tasks or unforeseen circumstances. During troop visits, we collected data on troop composition (see below) and individual behaviour *ad libitum*.

Individuals' ages were known from observing births or from patterns of dentition wear following capture. Individuals' relative ranks were calculated annually from *ad libitum* recorded dominance interactions in the package Matman 1.1.4 (Noldus Information Technology, 2013). Absolute ranks were converted to a relative scale ranging from 0 (lowest rank) to 1 (highest rank), to control for group size, using the formula $1-((1-r)/(1-n))$, with r being individual's absolute rank ranging from 1 to the total group size n.

Troop composition and reproductive state data

Each day that the troop was contacted, a census was completed that recorded the identities of the individuals present and the reproductive states of each adult female. Females' reproductive states were recorded as: (1) pregnant (determined *post hoc* based on lack of resumption of swelling, reddening of the paracallosal skin and subsequent birth); (2) lactating (i.e., period following the birth of an infant until cycle resumption); (3) oestrous/swollen (i.e., exhibiting periovulatory swelling of the anogenital region); (4) non-swollen (i.e., deturgescent but not pregnant). For females in oestrus, we also recorded swelling size on a scale from 0.5 (smallest)-4 (largest), on an absolute (*cf.* the population) rather than relative (*cf.* for that particular female) scale [47]. As mentioned above, baboon troops were not followed daily, and as such there were some missing data during some females' cycles. We discarded any

observations where the start or end of the swelling duration was missing and thus could introduce inaccuracy.

For females in oestrus, swelling duration was calculated as the number of continuous days that a female was recorded with a swelling of any size. Because different mechanisms could act on the different parts of the cycle, in addition to swelling durations, we calculated the maximal-swelling duration as the number of days the focal female exhibited the largest swelling size during that respective cycle. We excluded from the initial data 8 observations of maximal-swelling duration which were calculated as 0, i.e., observations that showed that females were only swollen, and this resulted in 158 swellings and 158 maximal-swellings from 47 females (median number of swellings / female = 5, range = 1-14).

We calculated five variables describing aspects of the social environment relevant to our hypotheses: for H1 we calculated (1) the sum of pregnant and lactating females ("PL") during the time a focal female was either swollen or maximally-swollen. For hypothesis H2a, we measured the number of other females that were (2) not maximally-swollen and (3) maximally-swollen, both when the focal female started swelling. To test hypothesis H2b and part of H2c, we calculated the (4) operational sex ratio ("OSR") as the ratio of sexually active females (i.e., swollen at any level) to adult males. For H2c, we also calculated the (5) the number of in-group adult males.

Statistical analyses

All statistical analyses were performed using R (version 4.0.3, 2020-10-10).

Question 1: Repeatability of receptivity

To determine how much variation in females' receptivity part of the cycle was due to differences between individuals, we calculated the repeatability (R) of the swelling and maximal-swelling durations. R is calculated as $\frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$, where σ_α^2 represents the between-group variance, σ_ε^2 the within-group variance ($\sigma_\alpha^2 + \sigma_\varepsilon^2 =$ the total phenotypic variance, V_p [48]). A relatively high R estimate would indicate that the dependent variable exhibits high between- and low within-female variance; low values of R indicate traits with high within-female or low between-female variation [48].

We calculated R using the `rpt` function (`rptR` package), which can calculate repeatability for Poisson-distributed data, such as we had, while controlling for the following confounding fixed effects [49]: relative rank and age. Female identity and troop were included

as random effects. The permutations and bootstrapping were set to 1000 and confidence intervals at 95%.

Question 2: Social determinants of swelling duration

To determine whether the social environment affected swelling durations, we used generalized linear mixed models (GLMMs; `glmer` function, lme4 package [50]) to control for repeated measures on individuals and the Poisson distribution of the duration counts. All models followed the same basic structure and were specified to use "bobyqa" as an optimizer: they included as fixed effects female age and relative rank, female identity and troop as random effects, and specific predictor variables that targeted each hypothesis. To test for H1, H2a, H2b and part of H2c—the effect of a male-skewed OSR—we ran two models (Table 2, models 1 and 2) with the following predictors: to test for H1 we included the number of pregnant and lactating females specified with a rank interaction because higher-ranking females primarily harass lower-ranking ones. To test for H2a, we used the number of not maximally-swollen females when a focal female started swelling when the response was swelling duration; and the number of maximally-swollen females when a focal female started swelling when the response was maximal-swelling duration. Thirdly, to test for H2b and part of H2c—the effect of a male-skewed OSR—we included the operational sex ratio (OSR, i.e., no. of receptive females/no. of adult males) as a predictor. Finally, to test for H2c we ran two more models (Table 2, models 3 and 4, one for swelling and one for maximal-swelling duration) with the same predictors as models 1 and 2, but with the number of in-group males instead of OSR, since the former is a proxy of social instability in the sense that male ranks are more volatile when there is more competition (i.e., more males) (A. Carter, E. Huchard, pers. Obs.).

Results

Females were swollen for an average (median) of 22 days (mean = 22.29, range 8-44) and maximally-swollen for 6 days (median, mean = 6.6, range 1-24). There were no differences between troops (Mann-Whitney U test: swelling duration: W = 3458.5, p = 0.233; maximal-swelling duration: W = 3097, p = 0.949).

Question 1: Repeatability of receptivity

Swelling duration was repeatable at the individual level (R = 0.148, SE = 0.083, CI = [0, 0.284], p = 0.012) (Table A1; Figure A1a), but most variation stemmed from within females

(Figure A2). Maximal-swelling duration was not repeatable (R = 0, SE = 0.03, CI = [0, 0.113], p = 1; Table A1; Figure A1b) and all variation was detected within females (Figure A2).

Question 2: Social determinants of swelling duration

Age was the only fixed effect predictor that consistently predicted swelling (model 1: $\beta = -0.009$, SE = 0.004, $p = 0.030$; model 3: $\beta = -0.008$, SE = 0.004, $p = 0.064$) and maximal-swelling duration (model 2: $\beta = -0.038$, SE = 0.011, $p < 0.001$; model 4: $\beta = -0.035$, SE = 0.011, $p = 0.001$) in three models. Rank was not significant in any model.

H1: Intrasexual selection

Avoidance of female aggression hypothesis

Neither swelling nor maximal-swelling duration responded to an increase in the number of pregnant and lactating individuals (swelling: $\beta = -0.008$, SE = 0.023, $p > 0.05$; maximal-swelling: $\beta = -0.051$, SE = 0.043, $p > 0.05$; Table 2; Figure 1).

H2: Intersexual selection

H2a Paternity concentration hypothesis

We tested whether female-female competition for the dominant mate contributed to variation in swelling or maximal-swelling duration. However, we found no support for this: greater numbers of simultaneously (non-maximally and maximally) swollen females did not induce an increase in either duration ($\beta = -0.015$, SE = 0.017, $p > 0.05$; $\beta = 0.12$, SE = 0.078, $p > 0.05$, respectively; Table 2; Figure 1).

H2b Paternity confusion hypothesis

We predicted that females should elongate their swelling or maximal-swelling phase in response to a female-biased OSR to be able to mate with many males and reduce infanticide risk. However, neither the length of swelling nor of maximal-swelling duration was significantly impacted by this predictor (GLMMs, swelling: $\beta = 0.053$, SE = 0.066, $p > 0.05$; maximal-swelling: $\beta = -0.179$, SE = 0.107, $p > 0.05$; Table 2; Figure 1).

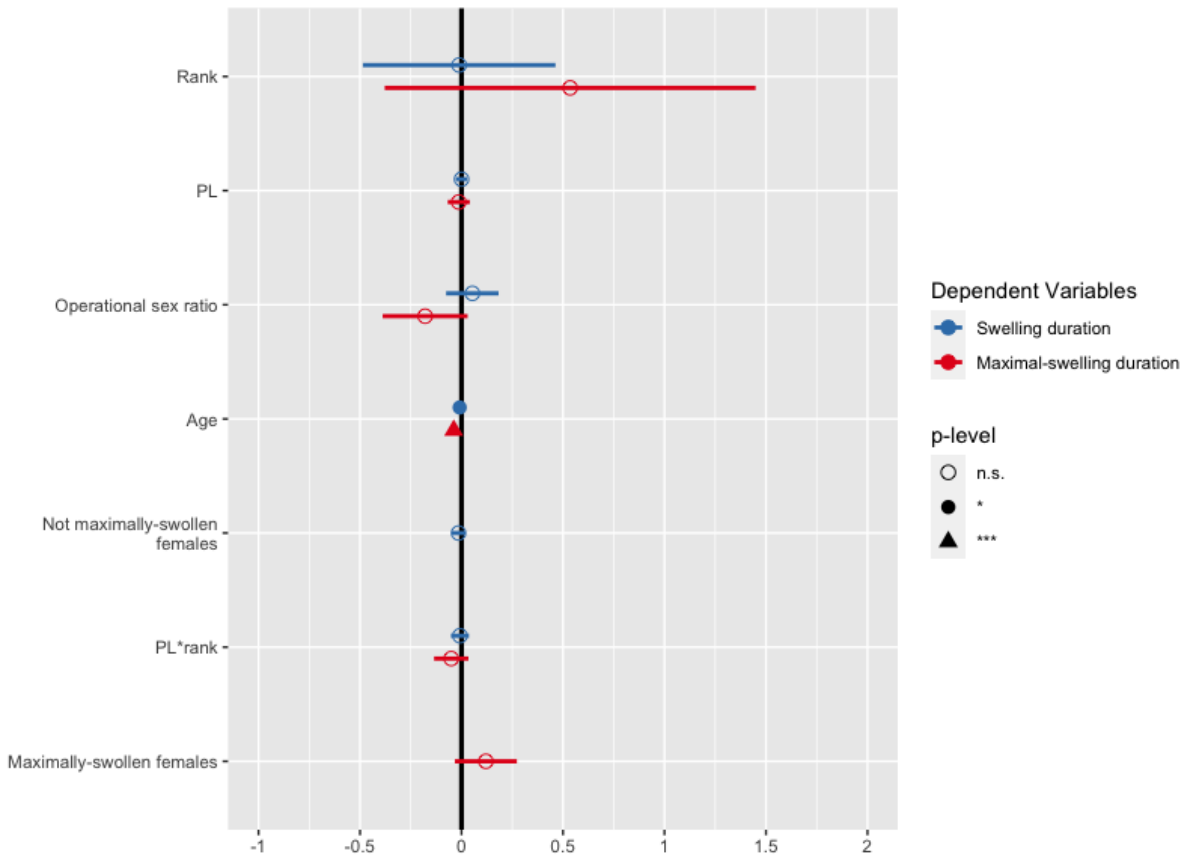

Figure 1**:** Standardised forest plot estimates of models 1 and 2 with swelling (blue) and maximal-swelling duration (red) as response variables. Only age shows a significant effect.

H2c Avoidance of male coercion hypothesis

When testing our last 'avoidance of sexual coercion' hypothesis, we found that swelling duration followed the predicted decrease with an increasing number of males (Figure 2; Table 2). While the OSR did not affect swelling duration, the number of males did: each additional male decreased swelling duration by 1.021 days (β = -0.021, SE = 0.009, p = 0.013; Figure 2). The length of maximal-swelling period, however, was unaffected by the number of males (β = -0.025, SE = 0.017, p = 0.134; Table 2).

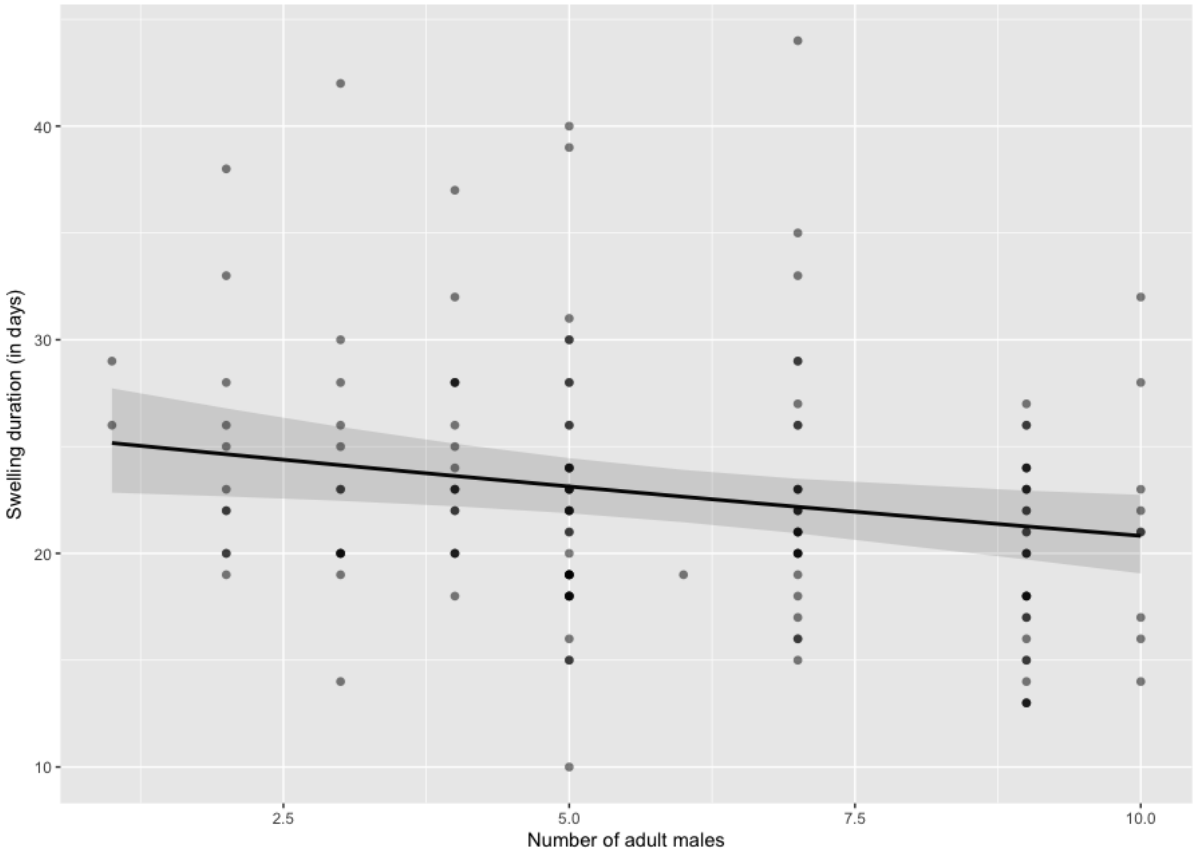

Figure 2**:** Effect of the number of males on female swelling duration. The line indicates the predicted effect on swelling duration by varying the focal variable, number of males. The shaded area represents the 95% CI, the dots show the predicted values, with grey dots being single observations and black dots multiple overlapping observations.

Table 2

Results of GLMMs with swelling or maximal-swelling duration as response variables. Age and rank were fixed effects, and troop and female identity were random effects in all models. Estimate measures the effect of the predictor on the response variable and is given in log-scale.

Models	***Hypothesis tested***	***Response[1]***	***Predictor for specific hypothesis***	***Estimate***	***SE***	***z-value***	***p-value***
Model 1→ SD[1]: PL[2]*rank + OSR[3] + not-mxm ♀[4]	H1	SD	PL*rank	-0.008	0.023	-0.334	0.738
	H2a	SD	not-mxm ♀	-0.015	0.017	-0.841	0.400
	H2b & H2c	SD	OSR(♀/♂)	0.053	0.066	0.809	0.419
Model 3→ SD: PL*rank + males[5] + not-mxm	H2c	SD	males	-0.021	0.009	-2.473	**0.013**
Model 2→ MSD[1]: PL*rank + OSR + mxm-sw ♀[6]	H1	MSD	PL*rank	-0.051	0.043	-1.173	0.241
	H2a	MSD	mxm-sw ♀	0.12	0.078	1.539\	0.124
	H2b & H2c	MSD	OSR(♀/♂)	-0.179	0.107	-1.678	0.093

Model 4→ MSD: PL*rank + males + mxm-sw ♀	H2c	MSD	males	-0.025	0.017	-1.499	0.134

[1]Swelling duration (SD), maximal-swelling duration (MSD), [2]sum of pregnant (P) and lactating females (L), [3]operational sex ratio, [4]the number of not-maximally-swollen females when a focal female started swelling, [5]the number of adult males, [6]the number of maximally-swollen females when a focal female started swelling.

Discussion

The present study investigated the variation in the length of receptivity within versus across females. We tested whether females could manipulate receptivity to decrease aggression from competitors or coercive males or increase their mating opportunities. First, we detected high within-female variation in the length of sexual receptivity. Second, we found support for the 'avoidance of male coercion hypothesis', suggesting that females may be able to strategically adjust the length of their sexual receptivity to their social environment.

Our results support CLM as a sexually-selected mechanism that reduces the costs of male coercion. Our results show that the duration of the swollen part of the cycle is reduced, but not of the maximally-swollen phase; the number of non-swollen days between two cycles seems unaffected (data not shown). Overall, this suggests that females may start swelling at the same time of their oestrus cycle, but may reach maximal-swelling size slightly earlier when they are more males in the group, and then show the same duration of maximal-swelling. Chacma baboon males start to coerce females even before they start to swell [11], which may explain why swelling duration, but not maximal-swelling duration, changed in response to the number of adult males in the group. Shorter swelling durations when male-male competition and risk of coercion is high could lead to shorter periods of aggression and a lower risk of injury [11], an adaptive response from females to male coercion. Perhaps surprisingly, a male-biased OSR did not elicit a similar response. This may be because it does not capture social instability and male-male competition as accurately as the number of in-group males: a male-skewed OSR can be either due to a low number of swollen females or to a high number of in-group males, but only the latter was expected to affect females' cycles.

We propose two possible mechanisms that may produce the effect of CLM. First, previous studies in baboons have shown that socially-induced stress may result in a decrease of the swollen period [34,43], which is probably mediated by increased female cortisol levels [51]. The social dynamics involving male immigration events, high male-male competition and unstable male hierarchies are stressful for females because they typically increase the intensity of coercion [16,25,52] and harassment [34,43,53]. It is possible that the same mechanism is

responsible for the shortening of the cycle we observe in this population. Indeed, higher circulating cortisol could compromise the timing of the expression of follicle stimulating hormone, a mechanism seen in ewes [54]. However, glucocorticoids in cycling chacma baboon females did not rise during male take-over events [52], suggesting that cortisol may not be the mechanism. A second possible mechanism is that females might arrive faster at maximal-swelling—thus showing the reported decrease in the swelling period—via a male-mediated increase in estrogen levels, similar to the Vandenbergh effect, i.e., the earlier than normal female maturation in the presence of an unrelated adult male [35]. Estrogen is positively correlated with swelling size in baboons [55], and estrogen has been implicated in earlier sexual maturation in geladas following the arrival of a novel male [36].

Our results also suggest that the costs of coercion may, in this population, be comparatively higher than the risk of infanticide for females. At a comparative level, increased infanticide risk is associated with elongated receptivity periods across Cercopithecine primates [32]. It would thus seem adaptive for females to elongate, rather than shorten, their receptivity in response to a high number of males which increases infanticide risk [25]. At Tsaobis, the costs of coercion for females may be high [11] and the risk of infanticide relatively low compared to some other chacma baboon populations such as Moremi, with a much lower frequency of dominance take-overs, possibly due to the lower predation risk [56]. In addition, mate-guarding episodes are long in chacma baboons, and as a consequence paternity certainty towards the alpha-male is high, suggesting that females either fail to dilute paternity certainty due to indirect coercion [57], or alternatively chose to concentrate paternity in order to gain paternal services [44]. This may also explain the lack of evidence for H2b: paternity dilution is costly or not a necessary strategy for Tsaobis females.

We predicted that higher numbers of receptive females would prompt an elongation of oestrous duration so that females can concentrate paternity in the alpha male but found no support for such prediction. At least two explanations may account for this absence of evidence. First, because female chacma baboons are non-seasonal breeders [25], oestrous synchrony in this population is low, with a median of two concurrently swollen females. Consequently, mating with the preferred male is possible for most cycling females and females may not need to elongate their fertile period. Second, the substantial aggression among cycling females in Tsaobis [21,25] may limit females' propensity to extend their receptivity period. This is predominantly true for lower-ranking oestrous females and females who are not mate-guarded, which tend to be the usual target of aggression from higher-ranking females.

One reason why the number of pregnant and lactating females did not affect receptivity duration could be that female reproductive suppression in the form of aggression was given by the female friends of a particular male [24]. Specifically, aggression was initiated by pregnant and lactating females who were friends of the male that was mate-guarding the receptive female. A more targeted approach that considers as a predictor the number of female friends a swollen female's mate-guarding male has might therefore provide evidence for CLM. Alternatively, as for the other explanations, sexual coercion from males might have larger consequences on female fitness and be under stronger selection.

Lastly, we found that maximal-swelling duration was not repeatable, whereas almost 15% of the variance in the swelling phase was repeatable. Our results do not mean that there are no between-individual differences in maximal-swelling duration, but rather that those differences are not large relative to within-individual differences and are not consistent between females. The failure to detect significant repeatability in maximal-swelling duration could also reflect individual variation in the physiological responses to aggression and stress stemming from changes in the social environment. Our findings show that cycle phases are labile traits that females are potentially manipulating. At a comparative level, high variation in oestrous duration has been detected in animals (e.g., captive jaguars, with a mean duration of 10.42 and a range of 7 to 15 days [58]). Women, in contrast, show repeatable cycle length, even though there is some variation within [59] and across women [60], as well as extensive variation in average cycle length across human populations [61]. Here, it may be that baboons' low repeatability of swelling duration reflects a greater selective pressure on females' ability to manipulate cycle length than women, who conceal ovulation [62].

In summary, this study correlated variation in the length of female sexual receptivity with aspects of the social environment that may influence the intensity of female reproductive competition and of intersexual conflict. We reported empirical evidence for cycle length manipulation as a possible female counter-strategy to male coercion. Specifically, we found that receptive females respond to an increment in the number of in-group males by decreasing their swelling duration, presumably to reduce male coercion. In contrast, we failed to find any evidence that female-female competition, or female counter-strategies to infanticide, may influence the length of sexual receptivity, while we confirmed previous research that suggested the OSR is not an accurate predictor of rates of female-female aggression [25,63]. Following these results, future investigations and cross-population studies of the scale and sources of variation of sexual receptivity within and among females, and of the underlying physiological mechanisms responsible for the lengthening of swelling duration, will further confirm the

extent to which females can modulate it in response to changes in their social environment. In any case, it seems that CLM will favor an extension of receptivity in cases of increased infanticide and low coercion risk, and the opposite when infant survival is more or less secure.

Ethics

Our research procedures were evaluated and approved by the Ethics Committee of the Zoological Society of London and the Ministry of Environment and Tourism, Namibia (MET Research/ Collecting Permits 886/2005, 1039/2006, 1186/2007, 1302/2008, 1379/2009, 1486/2010, 1486/2011, 1696/2012, 1786/2013, 1892/ 2014, 2009/2015, 2147/2016, 2303/2017, RPIV00392018/2019) and adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

Data accessibility

Authors' contributions

AJC, EH and FD contributed to the conceptualization. AJC and EH designed the study. GC established the study system and oversaw data collection, with assistance from AJC and EH. FD performed the statistical analyses. All authors contributed to draft the manuscript. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests

We declare we have no competing interests.

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