



Reluctant males: why blue monkey males reject female sexual advances

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Abstract

Classical sexual selection theory predicts that males should mate eagerly, yet blue monkey males often reject females' sexual invitations. We evaluated how males' responses to female solicitations related to female characteristics, number of males and conceptive females present, and the male's recent copulations. Using 12 years of data from a wild population, we found that males accepted only 20% of female solicitations. Odds of acceptance (copulation) increased for conceptive females, for females with whom the male copulated recently, and when fewer males were present. Odds of accepting nulliparous females decreased when more conceptive females were available, consistent with market models. Male responses did not relate to female rank or matings with other females the same day. When males responded negatively, nulliparous females were especially likely to receive aggression vs. mere refusal. Overall, males' decisions to mate with willing females depended both on female characteristics, especially fertility, and on social context.

Keywords

male mate choice, male rejections, female proceptivity, female attractivity, sexual behaviour, mating market.

1. Introduction

Classical sexual selection theory holds that when females invest more than males in the production of offspring, the primary factor limiting male reproductive success should be access to fertile females, and males should therefore copulate with as many females as possible (Bateman, 1948; Trivers, 1972). The stereotype of the 'eager male', an idea originally proposed by Darwin (1871), has been applied widely across the animal kingdom (Clutton-

Brock & Vincent, 1991; Kappeler & van Schaik, 2004; Dewsbury, 2005), and empirical evidence generally confirms that males with more mates have higher reproductive success (Janicke et al., 2016). Especially in mammals, where female parental investment much exceeds that of males and causes large sex differences in reproductive potential, males would be expected to copulate indiscriminately to maximize mating opportunities and ultimately reproductive success.

There is, however, growing evidence that males are choosy about their mates. In mammals, such choosiness is inferred from patterns of non-random pairing of reproductive males and females (in relation to phenotypic traits such as age, dominance rank or female reproductive potential, and/or based on a male's opportunity to choose), and also from direct observations of males allocating courtship, mate-guarding and mating behaviour differentially among potential mates (Berger, 1989; Szykman et al., 2001; Deschner et al., 2004; Preston et al., 2005; Parga, 2006; Mainguy et al., 2008; Setchell, 2016; Fitzpatrick & Servedio, 2018). Reports of males selectively rejecting the sexual advances of females appear to be rarer, although such behaviour does occur in some mammals (Saayman, 1970; Stumpf & Boesch, 2006), birds (Pinxten & Eens, 1997; Saether et al., 2001), and insects (Kvarnemo & Simmons, 1999; Gowaty et al., 2003). Here we expand our understanding of male mate choice, particularly in mammals, with a report of male sexual rejections in the blue monkey (*Cercopithecus mitis*). Such rejections are common in this species, allowing us to examine male reproductive decision making in a direct way, with the potentially confounding effects of male-male competition — at least that related to locating and accessing a mate — either absent or reduced.

The expectation that males should take advantage of every copulation opportunity assumes that mating is not costly for them. When a female approaches a male and invites copulation, costs might seem especially low, as the energetic burden of locating a mate and the risks associated with mate competition to gain access to her are much reduced. Nonetheless, males may face other costs that are greater than previously supposed (Tang-Martinez & Ryder, 2005): when mating, males expend energy (Higham et al., 2011), allocate resources to their ejaculate (Dewsbury, 1982; Wedell et al., 2002), and may become more vulnerable to predation and harassment from rivals (Alberts et al., 1996; Kappeler & van Schaik, 2004; Edward & Chapman, 2011). These particular costs may affect male primates (Emery Thompson

& Georgiev, 2014) and could potentially outweigh the benefit of possible fertilization, leading a male to reject a female's sexual invitation. For example, if a male is limited in how much ejaculate he can produce in a given period (Small, 1988; Wallen, 2001; Alfaro, 2005), or if he cannot sustain the energetic costs of both attracting mates and fighting off rival males (Alberts et al., 1996; Higham et al., 2011), rejecting a sexually interested female might be his best option at a given moment. In these circumstances, sperm supply or energetic demand limit his reproduction more than access to fertile females does, because he has more opportunities to mate than he has the resources to invest; this situation does not match the assumptions of classical sexual selection theory or the 'eager male' stereotype. Rejecting female sexual advances, then, is a way to express mate choice under the constraints imposed by high mating costs.

Male mate choice should reflect an assessment of female quality, and males should be most likely to reject females with lower chances of fertilization or lower probability of offspring survival (Bonduriansky, 2001; Alberts, 2012; Kappeler, 2012; Fitzpatrick & Servedio, 2018). Mammalian males should prefer females in the fertile part of their cycle (Edward & Chapman, 2011). In primate species with sexual swellings, which appear to advertise ovulation probabilistically (Street et al., 2016), males do modify their preferences based on changes in the swelling's appearance or size (Girolami & Bielert, 1987; Deschner et al., 2004; Alberts et al., 2006; Fitzpatrick et al., 2015), and generally reject proceptive but non-swollen females (Hall, 1962; Saayman, 1970; Seyfarth, 1978). Males are also known to choose females based on assessments of reproductive potential related to past reproductive history and condition (Berger, 1989; Jones et al., 2001; Fitzpatrick et al., 2015).

Other indicators of female quality in mammals, and primates in particular, might include dominance rank, age, and parity, as these factors affect female reproductive performance, such as age at first reproduction, interbirth interval, and infant survival rate (Setchell & Kappeler, 2003; Pusey, 2012). In some species, higher-ranking individuals have greater reproductive success, making dominance rank a good indicator of female quality (Majolo et al., 2012; Pusey, 2012). Males do copulate with and spend more time in proximity with higher-ranking females in several cercopithecine monkeys (Samuels et al., 1984; Keddy, 1986; Kuester & Paul, 1996; Zhang et al., 2010; Setchell, 2016) and other mammals (Szykman et al., 2000; Mainguy et al., 2008).

Additionally, in both primate (Bielert et al., 1986; Kuester & Paul, 1996; Muller et al., 2006; Setchell, 2016) and non-primate (Cant, 2000; Nichols et al., 2010; Cory & Schneider, 2016; Wang et al., 2016) species, males preferentially mate-guard and copulate with older or parous females vs. younger, nulliparous females.

In addition to female characteristics that influence male preferences, contextual factors might affect the expression of male choosiness, and thus influence how a male responds to a female's sexual invitation. The number of males in the group could influence male behaviour, because, as in other species with a modally one-male social organization, the proximity of rivals can stimulate sexual motivation and activity (Kummer et al., 1974; Anzenberger, 1993), thereby decreasing male choosiness and rejections of females. Scramble competition for females is also likely to be stronger in groups with more males, possibly making them more likely to accept female advances because of the risk of ending up with no mate at all (van Hooff, 2000; Dechaume-Moncharmont, et al., 2016). Finally, if males copy each other's mate preferences, a male may reduce his choosiness when other males are present to avoid high competition costs for his preferred female (Wronski et al., 2012; Ziege et al., 2012).

The presence of multiple females is another contextual factor that may influence male choosiness. A male might be more discriminating when there are more fertile females available because of a reduced monopolization potential (van Hooff, 2000); if he cannot copulate with all available females, he can better afford the cost of potential missed copulations related to choosiness (Edward & Chapman, 2011). Additionally, the absence or unavailability of a preferred female can increase the likelihood that a male will sexually interact with a less preferred female (Herbert, 1968). This scenario has 'market'-like elements, in that the supply of sexually receptive females, as well as their reproductive values, can, possibly together with the male's own 'bargaining power', affect mating behaviour that may vary accordingly on fine temporal or spatial scales (Noë, 2017). A male should reject a female solicitation if he can obtain a 'better deal' from a different partner, which will depend on his options (Hammerstein & Noë, 2016). The number of fertile females in the group thus has the potential to interact with other variables influencing male mate choice, whose effect on male responses may be strongest when many potential mates are available. For example, silverback

gorillas, who tend to reject the solicitations of pregnant (and therefore non-conceptive) females, are more likely to refuse females when there is more than one proceptive female in the group (Watts, 1991).

Finally, a male's recent sexual behaviour might affect the benefit of copulating (again) with a particular female, and thus his receptivity to her advances. If he mated with her recently and is unlikely to improve his chances of siring her offspring by re-mating, he might be more likely to reject her as a mate (Saether et al., 2001; Parga, 2006; Bro-Jørgensen, 2007). If copulations are costly, a male might reject a female if he has copulated with any female recently, because he is already receiving the benefits of a copulation and has already incurred the costs, and additional benefits might not outweigh additional costs.

In this study, we examined rejections by wild blue monkey males of a female's sexual advances. Blue monkeys generally live in one-male polygynous, female-philopatric groups, and adult females form linear matrilineal dominance hierarchies (Klass & Cords, 2015). Mating can occur at any point during the year, but most copulations and conceptions occur from June to August, and multiple females at once are sexually active and conceptive during the mating season (Cords et al., 1986; Cords, 2000). Multiple males may join the group during the mating season, and sometimes at other times of year, and they compete aggressively to join and stay in groups with sexually active females (Cords, 2000, 2002). Nevertheless, blue monkey females, rather than males, initiate most sexual interactions (95% during conceptive window, $N = 255$; Cords, data not shown) with approaches and proceptive signals. Such female sexual solicitations are often met by male indifference, and sometimes even aggression (Cords, data not shown). These male responses provide information about the female's attractivity (Saayman, 1970; Beach, 1976), and are thus relevant to the study of male mate choice.

Using data collected over 12 years from 10 groups, we examined how female characteristics, contextual factors, and a male's recent sexual behaviour predicted the male's response to female sexual invitations. We hypothesized that male rejections would relate to female quality and group composition at the time of the interaction, as these would influence the costs and benefits of copulating for the male. Specifically, we predicted that a male would be more likely to respond positively to a female that was likely to conceive, high-ranking, and reproductively experienced (i.e., parous). In addition, we predicted that males would be more likely to respond positively if they had

fewer options, i.e., if their groups contained a smaller number of fertile females on that day, and when their groups contained more rival males to stimulate sexual behaviour. Finally, we considered a male's recent copulations, predicting that males would be more likely to respond positively if they had had less sexual access to the soliciting female recently, and that copulations with a different female on the same day might also reduce the chance of a positive response if copulations are costly.

2. Material and methods

2.1. Study population

The study population inhabited the Kakamega Forest (0°19'N, 34°52'E, 1580 m asl), a rainforest in western Kenya (Mitchell et al., 2009). The study groups' home ranges occupied approximately 2 km² total, and monkeys occurred at a density of about 192 individuals/km² in this area (Fashing et al., 2012). The population had been under study since 1979, providing detailed long-term data on individual life histories, which allowed us to assess female characteristics such as age and parity (Cords, 2012). Our analysis included data from 12 calendar years (2006–2017) and from a total of 10 groups (4–7 at any one time, given three group fissions that occurred over the 12 years). During the study, female group sizes ranged from 3 to 28 adult females, and study groups averaged 1.0–1.6 males. We considered females to be adults if they were at least 4 years old (earliest known birth occurred at age 4.6 years for females included in this analysis, and gestation is ca. 176 days; Pazol et al., 2002), and males to be adult after emigration from their natal group (at median age of 7.1 years, Ekernas & Cords, 2007).

2.2. Data collection

During the study period, all study groups were monitored on a near daily basis by a team of trained observers (averaging 127 h per group per month; Cords, 2012). As part of long-term monitoring, and because females were both the predominant and only long-term adult members of social groups, observers prioritized focal follows of adult females, but also recorded all adult male–female social and sexual interactions that they observed at other times. Each interaction involved an approach (by either party) to within 2 m, and lasted until the male and female separated (> 2 m). Observers also identified which males were in the group on each day.

From these long-term records, we extracted for the present analysis all sexual interactions initiated by an identified female exhibiting proceptive behaviour (puckering the lips or presenting the hindquarters, behaviours unambiguously associated with sexual interactions; Pazol, 2003) to an identified male. We excluded rare cases of ‘exaggerated presenting’ (prolonged posturing with tail recurved over back) and rare cases of puckering or presenting while grooming, as these appear to be submissive nonsexual behaviours in blue monkeys. We also excluded interactions involving a female and resident male from different groups, or those that occurred during one 1.5-month period of gradual group fissioning, because male responses in these situations could have been influenced by contextual variables from both groups. Records in which observers did not explicitly note a male’s response to a female’s sexual solicitation, even if it was just to ignore her, were also dropped.

For each interaction in the data set, we classified the male’s response as positive (he copulated, i.e., mounted and thrust, with or without ejaculation) or negative (everything else, including ignoring the solicitation). These responses were not precisely timed but typically occurred within 5–15 s of the female’s solicitation. If a single interaction (without separation >2 m) included multiple solicitations and responses, we considered the overall response to be positive if the male mounted with thrusting after any solicitation therein. We conducted additional analyses in which we classified male responses differently. In one, we recoded the data into three ordinal categories of positive, intermediate and negative response (details in Results). In another, we focused only on negative responses, coded as either aggressive or non-aggressive.

We used the long-term records to extract information about the female and other contextual variables. Female-specific variables included fertility status, dominance rank and parity. Blue monkey females do not have sexual swellings or other external signs of fertility, so we assessed female fertility conservatively using Pazol et al.’s (2002) estimate of the 95% confidence interval for gestation length, and thus defined a female as ‘conceptive’ 162–190 days before any offspring’s birth (including stillbirths).

We assessed female dominance rank from annual compilations of dyadic asymmetric agonistic interactions among adult (parous) and large juvenile (≥ 5 years) females, as recorded by the field team whenever such interactions were observed. We analysed winner:loser matrices with the I&SI method as implemented in DomiCalc (Schmid & de Vries, 2013; Klass & Cords, 2015).

We expressed rank on a 0–1 (lowest to highest) scale for each group in each year.

Parity was also known from long-term study. We considered a female to be parous if she had given birth before, whether the infant lived or experienced peri-natal death. We chose parity over age as a measure of female reproductive experience because we assumed it would be easier for male monkeys to assess (parous females have visible nipples). Additionally, age at first birth is highly variable (range: 4.6–11 years; Cords & Chowdhury, 2010; Bronikowski et al., 2016), making age a less accurate indicator of reproductive experience.

We used the number of males seen in the group on the same day as the sexual interaction as a contextual variable reflecting the amount of male–male competition. We also used the number of other females in the group in their conceptive windows on that day as a contextual variable that indicated the male’s other options for fertile mates on a given day.

Finally, we considered a male’s recent sexual behaviour, determining (1) if the male had recent access to the same female, meaning that he copulated with her at any time that day or the previous day, and (2) if the male copulated with another female at any time on that same day. All of these data were available from daily observation records.

2.3. Data analysis

We used mixed-effects logistic and ordered logistic regressions (Stata 15, ‘melogit’ and ‘meologit’) to model male responses to the female’s solicitation (full data set: 8652 interactions involving 146 females and 83 males). Predictors included conceptive status (yes/no), rank (0–1 scale), female parity (parous/nulliparous), number of other females in the group that were conceptive on the day of the male–female interaction, number of males in the group on that same day, the male’s recent access to the female on the same or previous day (yes/no), and whether the male copulated with another female that day (yes/no). We initially included interaction effects of female characteristics (rank and parity) with the number of other conceptive females available that day, as males might be more choosy based on female characteristics when more conceptive females were available. We also included interactions between conceptive status and all other predictors, in case these predictors affected the outcome more when a female was conceptive vs. not conceptive. To facilitate interpretation of the main effects, however, we then

dropped interaction effects that were not significant. All models included individual IDs of male and female as random effects. We considered a predictor variable to have a significant influence on the response if the 95% confidence interval of its estimated odds ratio did not include one (Nakagawa & Cuthill, 2007). We report variance inflation factors (VIFs) to assess collinearity in the predictors.

3. Results

3.1. Male sexual responses

Males responded negatively to female sexual invitations most of the time: 80% of all interactions ($N = 8652$) involved a negative male response. Negative responses ($N = 6930$) included male aggression toward the female (4%), more neutral disinterest (ignore, 66%), and sociopositive but non-sexual interactions (headflag, follow, present for grooming, groom, sit-contact, sit-near (<1 m), 20%). A few additional negative responses suggested some level of sexual interest, but did not lead to full copulation (inspect a female's perineum, 3%; brief mount without thrusting, 7%).

About three quarters of female-initiated sexual interactions involved parous females, and most occurred when the female was not in her conceptive window (Table 1). In most cases the male had not been observed copulating with the same female on the same or previous day, nor was he known to have copulated with another female on the same day (Table 1). The number of conceptive females in the group (not including the female in the interaction, to reflect a male's other options) ranged from 0–8 (median = 0, IQR = 0–1; 60% were cases with no other conceptive females). Total number of males in group (including the male in the interaction) ranged from 1–11 (median = 1, IQR = 1–2; 28.4% occurred when there were 2 or more males present).

Table 1.

Characteristics of male–female interactions in the dataset ($N = 8652$).

Characteristic	%
Female parous	76.0
Female in conceptive window	11.0
Male copulated with this same female on same or previous day	19.0
Male copulated with another female on same day	22.6

Table 2.Mixed-effects logistic regression model of positive (vs. negative) male responses ($N = 8652$).

	Odds ratio	SE	Z	$p > Z $	95% CI
Female characteristics					
In conceptive window	1.39	0.12	3.76	<0.001	1.17–1.66
Dominance rank	1.26	0.16	1.80	0.073	0.98–1.61
Parous	1.01	0.09	0.08	0.936	0.85–1.20
Contextual predictors					
Total number of males in group	0.91	0.03	−2.77	0.006	0.85–0.97
Number of other conceptive females same day	0.87	0.05	−2.23	0.026	0.78–0.98
Male sexual behaviour					
Male copulated with this female on same or previous day	2.69	0.18	15.19	<0.001	2.37–3.06
Male copulated with another female same day	1.02	0.07	0.21	0.830	0.88–1.17
Interaction					
Parous × Number of other conceptive females today	1.15	0.08	2.15	0.031	1.01–1.31

Male and female ID were included as random effects: males: var ± SE = 0.41 ± 0.12 , 95% CI: 0.23–0.73; females: var ± SE = 0.08 ± 0.03 , 95% CI: 0.04–0.16.

3.2. Factors affecting male response

In the first model of male responses (positive vs. negative), the only significant interaction involved female parity and the number of other females in the group that were conceptive, and we retained this one interaction in our final model (Table 2). The final model was significant overall (i.e., fixed effects were not all simultaneously zero, Wald $\chi^2 = 276.72$, $p < 0.001$), and a likelihood ratio test comparing it to a model without random effects confirmed the importance of the mixed-effects approach ($\chi^2 = 336.58$, $p < 0.001$). All VIFs were < 1.11 .

Males were more likely to respond positively to females that were in their conceptive window (Table 2): the odds of a positive male response were 39% higher for conceptive vs. non-conceptive females. Males responded positively to 27% of interactions with a conceptive female ($N = 953$) and 19% of interactions with non-conceptive females ($N = 7699$; Figure 1).

Contrary to our prediction, female rank did not predict the odds of males responding positively, and showed no interaction with the number of other females in the group who were conceptive. In other words, there was no

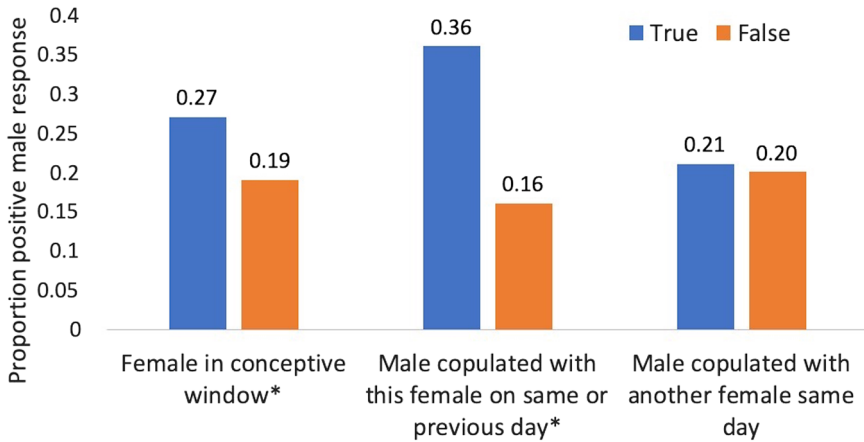


Figure 1. Relationship of male responses (% positive) to whether (true/false) female was conceptive, whether he had recent sexual access to the female, and whether he had copulated with a different female. * $p < 0.05$ (GLMM in Table 2).

evidence that males discriminated on the basis of female rank regardless of how many other conceptive females were available on the day of the interaction.

Also contrary to our prediction, a male was less likely to respond positively to female solicitation when more males were in the group. For each additional male in the group, the odds of a positive male response decreased by 10.3% (Table 2, Figure 2).

A male was much more likely to respond positively to a female if he had recently interacted with her sexually: the odds of a positive male response increased by 169% if he copulated with the same female on the same or previous day (Figure 1). Males responded positively to these females 36% of the time vs. 20% of the time otherwise. By contrast, whether the male copulated with a different female on the same day had no significant influence on his response. A male responded positively to a female about 20% of the time whether or not he had recently copulated with another female (Figure 1).

The significant interaction between female parity and number of other females in the group that were conceptive meant that when there were fewer conceptive females in the group, males responded similarly to parous and nulliparous females, but when the number of conceptive females in the group increased, the odds of a male responding positively to a nulliparous female decreased (Figure 3).

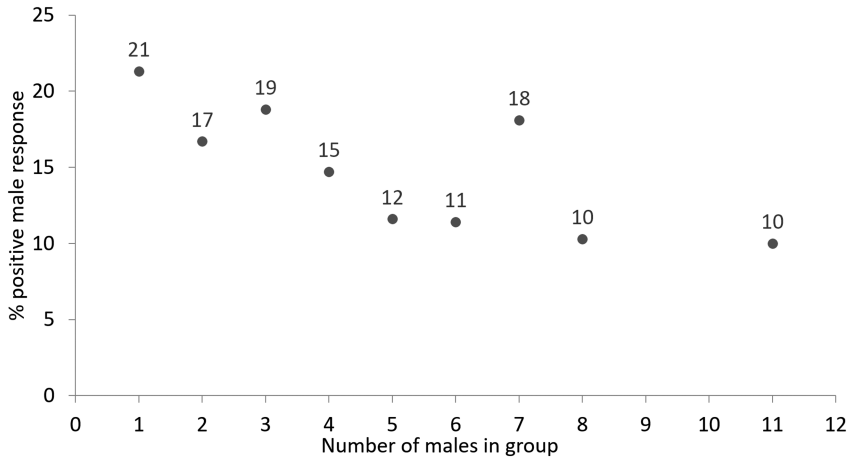


Figure 2. Relationship between male response type and number of males in the group. Sample sizes: 1 male, 6194; 2 males, 1218; 3 males, 656; 4 males, 279; 5 males, 138; 6 males, 105; 7 males, 22; 8 males, 29; 9 males, 0; 10 males, 1; 11 males, 10.

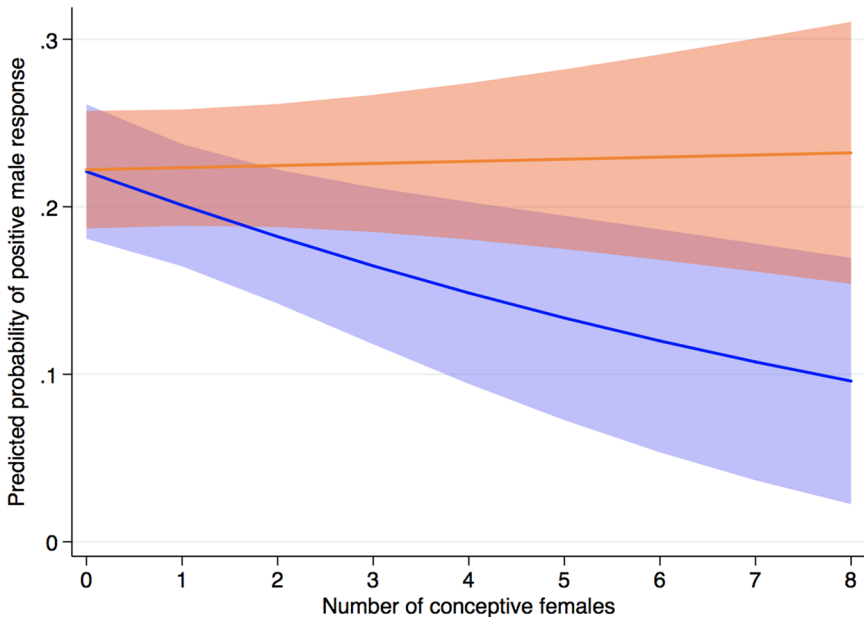


Figure 3. Interaction effect between female parity and number of other conceptive females, from Model 1. Males showed a weaker preference for nulliparous females (blue) vs. parous females (orange) when there were more conceptive females in the group. Shading shows 95% confidence intervals.

Some responses that we initially coded as negative could potentially be interpreted to suggest limited male sexual interest, even though they did not lead to copulation. To explore this idea, we ran an ordered mixed-effects logistic model with the same predictors, breaking male responses into three ordered categories: negative (aggression, ignore: 56%), intermediate (head-flag, follow, present for grooming, groom, sit-contact, sit-near, inspect female's perineum, mount (no thrust): 24%) and positive (mount-thrust, with or without ejaculation: 20%). Most predictors had an effect on male responses that was similar to the original model, but the interaction between parity and number of conceptive females was not significant (Table A1 in the Appendix).

3.3. Male aggressive responses

In 3% of all interactions, males responded not only negatively but even aggressively to females, chasing or threatening (with stares, open mouths, growls and/or lunges) females who had solicited them sexually. We investigated these aggressive responses by applying the same predictors as in Model 1 to the subset of interactions in which males responded negatively ($N = 6930$), thus modelling aggressive vs. non-aggressive (i.e., ignoring) negative responses. The final model (Model 2, Table 3), which did not include any interactions, was significant overall (i.e., fixed effects were not all simultaneously zero, Wald $\chi^2 = 15.94$, $p < 0.0256$), and a likelihood ratio test comparing it to a model without random effects confirmed the importance of the mixed-effects approach ($\chi^2 = 79.23$, $p < 0.00005$). All VIFs were < 1.11 . Only parity predicted the nature of a male's negative response, with the odds of an aggressive response 61% higher for nulliparous than for parous females. In this model of male rejections, parity predicted the male's response regardless of the number of other conceptive females in the group, contrasting with Model 1, which included both negative and positive responses and showed a significant interaction effect. Another difference between Models 1 and 2 was that number of other conceptive females was not a significant predictor of the intensity of a male's negative response (aggressive vs. not).

4. Discussion

Though a common assumption is that males will copulate whenever opportunity arises, our results show that male blue monkeys often refuse the sexual

Table 3.

Mixed effects logistic regression model of negative male responses ($N = 6930$), with non-aggressive responses as the reference class.

	Odds ratio	SE	Z	$p > Z $	95% CI
Female characteristics					
In conceptive window	0.65	0.16	-1.77	0.077	0.40–1.05
Dominance rank	1.16	0.25	0.72	0.471	0.77–1.76
Nulliparous	1.61	0.23	3.42	0.001	1.23–2.12
Contextual predictors					
Total number of males in group	1.02	0.07	0.40	0.689	0.91–1.16
Number of other conceptive females same day	0.97	0.06	-0.45	0.653	0.87–1.09
Male sexual behaviour					
Male copulated with this female on same or previous day	0.97	0.17	-0.20	0.840	0.68–1.36
Male copulated with another female same day	1.05	0.16	0.32	0.748	0.78–1.41

Male and female ID were included as random effects: males: var \pm SE = 0.46 ± 0.17 , 95% CI: 0.23–0.93; females: var \pm SE = 0.02 ± 0.06 , 95% CI: 0.00007–6.12.

advances of females, and that certain female characteristics and contextual variables predict male responses. Specifically, when invited by a female to copulate, a male was more likely to respond positively if the female was likely to conceive, when there were fewer males in the group, and when he had recently copulated with the same female. Males were less likely to respond positively to nulliparous females when the group contained more conceptive females. Although aggressive rejections of female invitations were rare, they were more likely to be directed to nulliparous females. This study appears to be one of few that documents male mating decisions directly, and considers both criteria related to the potential mate, as well as the context in which her invitation occurs.

The fact that blue monkey males were more likely to respond positively to the invitations of females in their conceptive windows is consistent with previous reports on baboons. After a female presented, male baboons did not copulate unless the female's sexual skin was swollen (Hall, 1962; Saayman, 1970). Unlike baboons, however, blue monkeys do not have sexual swellings, so males must be using other cues to detect when females are conceptive. Because we assessed conceptive status retroactively based on infant births, we may have missed windows during which a female was fertile but did not

actually conceive. If so, it is possible that female fertility has an even stronger effect on male response than our analyses suggest.

Males did not respond differently to females based on their dominance rank. In many primates, female rank affects reproductive success in terms of infant survival or maturation rates (Pusey, 2012), giving males incentives to copulate selectively with higher-ranking females (Kuester & Paul, 1996; Kappeler, 2012). In blue monkeys, however, dominance rank does not seem to predict female fertility (Roberts & Cords, 2013) or infant survival (Cords, 2018), perhaps minimizing the advantage to males of mate choice based on rank.

We found that males discriminated based on whether the female had previously given birth, but only when there were other conceptive females from which to choose. When multiple conceptive females were available, males preferentially copulated with parous females, whereas this preference was not evident when the supply of conceptive females was lower. Similar results have been reported in insects and fish (Shelley & Bailey, 1991; Berglund, 1995). Furthermore, in species where males exchange services for sex, males respond to higher supplies of conceptive females by performing these behaviours more frequently (Gumert, 2007; Norscia et al., 2009). These findings are consistent with a market-based view of male mate choice, in which male mating decisions reflect market parameters, specifically the supply of mates (Hammerstein & Noë, 2016). The findings also agree with the expectations of classical sexual selection theory, which predicts that males should not be choosy when access to mates limits their reproductive success (Andersson, 1994).

Female parity is often viewed as an indicator of fertility, as nulliparous females may experience low fecundity even though they mate, or as an indicator of experienced and presumably more successful mothering, which would contribute to infant survival (Anderson, 1986; Muller et al., 2006; Setchell, 2016). In the study population, it seems more likely that males preferred parous females for fertility reasons, as multiparous and primiparous females do not appear to differ in the likelihood that their infants will survive (Cords & Chowdhury, 2010). Parity was also a significant predictor when we modelled aggressive vs. non-aggressive male refusals, underscoring its importance in male mating decisions. Enomoto (1978), who briefly mentioned aggressive male responses to female sexual solicitations in Japanese

macaques, also noted that these responses were often given to young or nulliparous females. Nulliparous female blue monkeys are occasionally quite persistent in soliciting copulations from disinterested males, which may at least partly explain aggressive male responses; we note, however, that over half the aggressive responses were given to adult females.

Though we expected a larger number of males in the group to stimulate sexual activity, males were *less* likely to respond positively to female advances when groups contained more males. This finding might reflect the fact that rival males are distracting, and monitoring or interacting with them demands attention that interferes with mating. In addition, if mating itself attracts the attention of rival males, males may adjust their choosiness based on perceived risk, becoming more likely to reject females when a copulation creates a higher risk of aggression from rivals. In rhesus macaques, for instance, the presence of the alpha male inhibits copulations by other group members, most likely because alpha males sometimes aggressively interfere with copulations by subordinates (Overduin-de Vries et al., 2012). Although blue monkeys do not have copulation calls that could attract the attention of rival males (Lawes et al., 2013), males co-resident in a group are typically highly attentive to one another, and we have witnessed occasions when copulations seemed to stimulate aggression from rivals (Cords, 2000, 2002). Unfortunately, the data did not include more detailed information on the proximity of rival males at the time that females solicited males for sex, so the number of males in the group on the same day is our best proxy for potential male–male aggression. In any case, if mating decisions reflect the number of males in the group, it is clear that male mate choice is influenced not only by female quality, but also by social factors like the perceived risk of male–male competition.

A male was more likely to mate with a soliciting female if he copulated with her another time the same or previous day; however, the fact that a male copulated with a different female on the same day did not predict his response. A male was thus not influenced by his other copulations per se, only by copulations with his current partner, and then in a positive way. We were limited in that our data did not include timestamps of a male's copulations on a given day, so we could not specify that these effects were evident only for copulations that occurred before the interaction of interest. More generally, these findings do not support the idea that male rejections occur because males are reaching a limit in terms of the copulatory costs

(i.e., sperm supply or energetic demand) that they can bear. Indeed, blue monkey males can copulate multiple times on the same day (Cords et al., 1986). Instead, it seems that a male attempts to repeatedly inseminate a female that he has chosen or accepted as a mate. Multiple inseminations do not seem to result from sperm competition, given that males are not more likely to accept female invitations when other males are present in the group. Rather, multiple inseminations might be a way of maximizing the likelihood of conception when the female provides limited cues of her fertility.

Changing the way we coded responses, so that they included negative, intermediate, and positive categories, produced almost identical results. Males were more likely to respond positively to females in their conceptive window, when there were fewer males in group, and when they had recent sexual access to the same female. Only the interaction between female parity and number of conceptive females was no longer significant, and neither variable was significant on its own either. It appears that these variables did not influence male sexual interest in a more graded way, although they predicted actual copulation.

The variances for random effects also showed the importance of both partners' individual identities in influencing how a male responds to a female's mating solicitation. The random effect variances for males were higher than those for females in all models, suggesting that responses are especially variable among males, with less variance related to the identity of the soliciting female. Both field and laboratory studies have shown that male primates may have idiosyncratic sexual preferences for individual females without a clear relationship to conceptive status or hormone treatment (Hausfater, 1975; Dixson, 2012), which our study confirms.

4.1. Measuring male mate choice

Reports of male mate choice in mammals generally focus on male mating effort directed differentially to females, in terms of time spent in proximity, mate guarding behaviour, and proportion of copulations with preferred females (Berger, 1989; Szykman et al., 2000; Deschner et al., 2004; Preston et al., 2005; Heistermann et al., 2008; Mainguy et al., 2008; Higham et al., 2012; Setchell, 2016), rather than how males respond to sexual solicitations by potential mates. The latter represent informative decision points, however, allowing one to assess directly female attractivity to males (Saayman, 1970; Beach, 1976). Moreover, a male's decision at this moment is not constrained

by male–male competition to gain access to a female; by definition, she is both nearby and signalling eagerness to mate. By focusing on male responses to female invitations, we did not have to limit our analyses to the behaviour of the highest-ranking males, as other studies have done to avoid the confounding influence of male–male competition on a male’s sexual behaviour (Deschner et al., 2004; Fitzpatrick et al., 2015).

Clearly, however, measuring mate preferences in this way presupposes both that females regularly initiate sexual interactions by soliciting males for copulation, and that male responses are variable. The degree to which females initiate sexual encounters appears to vary widely across species: in primates, for instance, females initiated 24% of sexual interactions in chimpanzees (Stumpf & Boesch, 2006), 34% in baboons (Saayman, 1970), 63% in gorillas (Watts, 1991), 74% in howler monkeys (Jones, 1985), and almost all interactions in grey langurs (Sommer et al., 1992) as well as blue monkeys. The consistency of male responses to female invitations is also quite variable. Among primates alone, there are species in which males hardly ever refuse females, such as lemurs (Parga, 2006), and others like blue monkeys and baboons (Saayman, 1970; Seyfarth 1978) in which refusals are common. In mammals more broadly, consistency of male responses can also vary widely, ranging from males who sometimes reject proceptive females (Bro-Jørgensen, 2007) or respond differently to females based on female reproductive state (Ferkin & delBarco-Trillo, 2014), to males in species that uphold traditional sex roles (Janicke et al., 2016).

It is possible that, across species, female-biased sexual initiative and variable male responses are related. In species whose males receive many mating invitations, the males have many opportunities to mate. Relative to a male that must create his own mating opportunities by competing for and courting females, an invited male has less to lose in being choosy; moreover, in extreme situations of role reversal, a male may benefit from filtering out at least some repeat invitations by the same persistent female if mating with her repeatedly would not enhance his likelihood of impregnating her, and/or would reduce his chance of impregnating other females because of sperm depletion (Bro-Jørgensen, 2007). The different responses of alpha vs. subordinate male capuchins to proceptive females seem to illustrate how female sexual initiative and male reluctance are linked within a single species: alpha males, who receive frequent solicitations from females, initially respond

with disinterest, but subordinate males, who are solicited far less often, accept female advances much more readily (Alfaro, 2005; Carosi et al., 2005).

High rates of male refusals may also relate to how closely female sexual invitations align with fertility: specifically, if non-fertile females often solicit males for sex, male refusals may be relatively common. In baboons, for example, males refused over 95% of invitations from females without sexual swellings (Hall, 1962; Saayman, 1970). In our data, 89% of female invitations occurred outside the periods when conceptions occurred. This number may overestimate the proportion of invitations by non-fertile females, because our assessment of fertility probably overlooked ovulating females that failed to conceive. At the same time, and leading to an opposite bias, each conceptive period we identified by back-counting from births was 29 days long, but the female was likely fertile for only a small fraction of this interval (indeed, this fact may have contributed to males' refusing most (73%) of the invitations they received from females in their conceptive period). Generally, female catarrhine primates (Dixson, 2012), and blue monkeys in particular (Pazol, 2003) are known to mate when they are not ovulating, which may lead to relatively high numbers of sexual solicitations by non-fertile females. In blue monkeys, it remains unclear if this behaviour is part of an anti-infanticide strategy, or a by-product of other endocrine changes that characterize this species' reproductive biology (Pazol, 2003). The fact that males often refuse invitations from females who are not fertile suggests that females may not be able to fool potentially infanticidal males.

4.2. *Conclusion*

Long-standing stereotypes of the 'eager male' and the 'coy female' have dominated much of the literature on sexual selection, but these stereotypes do not always hold, even in mammals, whose strongly sex-biased patterns of parental investment create large sex differences in reproductive potential (Tang-Martinez, 2016). Male blue monkeys reject sexually motivated females more often than they respond positively. They appear to base their response to female sexual advances on variables that reflect female reproductive potential, as well as other social factors like the number of rival males. A preference for parous females was stronger when more conceptive females were present, as expected from the logic of supply and demand. Overall, this analysis illustrates that both characteristics of potential mates and the circumstances in which mating decisions are made can influence male mating decisions.

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Appendix**Table A1.**

Mixed-effects ordered logistic regression modelling male responses as positive, intermediate, or negative ($N = 8652$).

	Odds ratio	SE	Z	$p > Z $	95% CI
Female characteristics					
In conceptive window	1.32	0.10	3.54	<0.001	1.13–1.54
Dominance rank	1.20	0.12	0.87	0.384	0.89–1.36
Parous	0.96	0.06	−0.58	0.563	0.85–1.09
Contextual predictors					
Total number of males in group	0.91	0.03	−3.15	0.002	0.86–0.97
Number of other conceptive females same day	0.98	0.02	−0.70	0.482	0.94–1.03
Male sexual behaviour					
Male copulated with this female on same or previous day	2.35	0.14	14.48	<0.001	2.10–2.64
Male copulated with another female same day	0.10	0.06	−0.05	0.962	0.89–1.12

Male and female ID were included as random effects: males: var \pm SE = 0.39 ± 0.11 , 95% CI: 0.22–0.67; females: var \pm SE = 0.06 ± 0.02 , 95% CI: 0.031–0.12. All VIFs were <1.11. Non-significant interaction effects were dropped.