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Abstract: Female chimpanzees (Pan troglodytes) are usually depicted as sexually submissive and bound by male coercion, because males are able to monopolize oestrous females, limiting a female's options for mate choice. We present behavioural data from a group of wild chimpanzees during a rare period in which up to 10 females cycled simultaneously, which prevented males from monopolizing oestrous females, thus changing the dynamic of male-female sexual interactions. Overall, we found that nulliparous and parous females employed different copulation calling strategies, reflecting their relative reproductive attractiveness and social standing within the community. Male partner rank, copulation duration, and dominant male audience further influenced calling behaviour, and there was a non-significant trend for females to increase calling as the number of cycling females increased. We conclude that female chimpanzees are capable of adjusting their copulation calling flexibly, by taking into account their own sexual attractiveness in order to incite male competition.

Female chimpanzees adjust copulation calls according to reproductive status and level of female competition

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***Highlights (for review)**

Highlights

- We examined 1,158 copulation calls from wild chimpanzee females.
- We found that calling strategies of nulliparous and parous females reflect their attractiveness.
- Females take into account their competitor's attractiveness as well as their own.
- Oestrus synchrony results in an increased likelihood of copulation calling for all females.
- Female calling differs according to copulation duration, partner rank, and audience of dominant male.

ABSTRACT

Female chimpanzees (*Pan troglodytes*) are usually depicted as sexually submissive and bound by male coercion, because males are able to monopolize oestrous females, limiting a female's options for mate choice. We present behavioural data from a group of wild chimpanzees during a rare period in which up to 10 females cycled simultaneously, which prevented males from monopolizing oestrous females, thus changing the dynamic of male-female sexual interactions. Overall, we found that nulliparous and parous females employed different copulation calling strategies, reflecting their relative reproductive attractiveness and social standing within the community. Male partner rank, copulation duration, and dominant male audience further influenced calling behaviour, and there was a non-significant trend for females to increase calling as the number of cycling females increased. We conclude that female chimpanzees are capable of adjusting their copulation calling flexibly, by taking into account their own sexual attractiveness in order to incite male competition.

Keywords: chimpanzee, parity, female competition, copulation call, sexual signal

INTRODUCTION

Sexual selection dictates a balance between mate competition and mate choice (Darwin, 1871; Trivers, 1972). Given that females are often the limiting sex, in systems where males are competitors and females are choosey, research on female mating strategies becomes essential for broadening our understanding of sexual selection theory. As a mating strategy, in many species female competition manifests in ways not necessarily directly associated with mating success: for example, through physical aggression, resource manipulation, infanticide, and reproductive suppression of others (Stockley and Bro-Jørgenson, 2011). In patrilocal primates, indirect female competition prevails (chimpanzees and bonobos: Pusey, Williams, and Goodall, 1997; Kano, 1992; humans: Benenson, 2013; Campbell, 2013). Human females in particular are noteworthy for indirect aggression toward female competitors, such as social exclusion (Benenson, Markovits, Thompson, and Wrangham, 2011) or punishing superiority (Winstead and Griffin, 2001).

In contrast to such subtle means of competition, overt tactics of male intra-sexual competition, such as coercion, are a pervasive strategy in many species, especially chimpanzees (Smuts, 1993; Clutton-Brock, 2007; Muller and Wrangham, 2009). Chimpanzee males prefer older, parous females and use selective aggression as a means of enacting this preference (Muller, Thompson, and Wrangham, 2006; Muller, Thompson, Kahlenberg, and Wrangham, 2011; Feldblum et al., 2014). As a counter-strategy to coercion, chimpanzee females sometimes tactically initiate sexual interactions with high-ranking males (Pieta, 2008), demonstrating that females modify their mating behaviour to reduce costs. In some chimpanzee populations, female choice appears to be the dominant mating strategy (Matsumoto-Oda, 1999; Stumpf and Boesch, 2005, 2006, 2010), a difference that may relate to the steepness of the male dominance hierarchy (Kaburu and Newton Fisher, 2015a). Prevalence of female choice has been argued to reflect communities where males differ little in competitive power: direct coercion may then be thwarted and males instead attempt to bias female choice, for example through grooming (Kaburu and Newton Fisher, 2015b). In contrast to the active debate and extensive data on male-male mating competition in chimpanzees, relatively few data are available on how female chimpanzees, or indeed any female primates, take female competitors into account during mating (Stumpf and Boesch, 2006; Townsend, Deschner, and Zuberbühler, 2008).

However, competition from other females may be especially important for nulliparous females in the face of males' preference for older, parous females.

Female chimpanzees are generally viewed as the more solitary and passive sex, yet resource competition between females is well-documented. For example, immigrant females compete in many day-to-day interactions with resident females over access to resources (Pusey and Schroepfer-Walker 2013), a level of competition that causes immigrants to avoid high-ranking females when ranging (Murray, Mane, and Pusey, 2007). While physical aggression between adult females is rare, there are multiple reports of selective aggression towards immigrant females, presumably because they pose a threat to resident females' resources (Boesch and Boesch-Ackermann, 2000, Pusey et al., 2008, Kahlenberg, Thompson, Muller, and Wrangham, 2008). Such aggression can be severe, preventing young females from immigrating (Pusey et al., 2008) and possibly involving female-led infanticidal behaviour towards immigrant mothers in at least one community (Townsend, Slocombe, Thompson, and Zuberbühler, 2007). Perhaps for this reason, immigrant females have been observed to rely on male protection and occasionally to ally with each other against resident females (chimpanzees: Nishida, 1979; Boesch and Boesch-Ackermann, 2000; Kahlenberg et al., 2008; gorillas: Watts, 1992).

In contrast, there are no comparable studies of female-female competition over sexual partners, apart from isolated anecdotes (e.g. Nishida, 1979). There is some evidence for indirect effects of intra-sexual competition, in that the stress of immigration appears to delay conception in immigrant females by several years despite the fact that they have regular sexual cycles (Nishida et al., 2003; Pusey and Schroepfer-Walker, 2013). Generally, female chimpanzees tend to avoid direct intra-sexual mating conflict by attracting male partners with signals of sexual receptivity: that is, visually salient sexual swellings, olfactory cues, and copulation calls (Deschner, Heistermann, Hodges, and Boesch, 2004; Townsend et al., 2008).

In many taxa, copulation calling is thought to incite competition between males while affording females protection from infanticide (O'Connell & Cowlishaw, 1994; Oda and Masataka, 1995; Semple, 1998; Pradhan, Engelhardt, van Schaik, and Maestripieri, 2006; Englehardt, Fischer, Neumann, Pfeifer, and Heistermann, 2012). Strategic call production is evidenced by reports of call repression and furtive behaviour in chimpanzees and geladas (*Theropithecus gelada*), for example during so-called 'furtive' copulations with low-ranking males, which allow females to promote paternity confusion while avoiding aggression from dominant males (Matsumoto-Oda & Tomonaga, 2005; Le Roux, Snyder-Mackler, Roberts, Beehner, and Bergman, 2013). Similarly, chimpanzee females can suppress copulation calls in the presence of equal or higher-ranking females (Townsend et al., 2008); having some measure of vocal control may mitigate infanticide risk (Townsend et al., 2007, 2008). Among bonobos (*Pan paniscus*), where high-ranking allies can lower the threat of female-female competition, females give copulation calls more frequently in the presence of the alpha female (Clay, Pika, Gruber, and Zuberbühler, 2011). Based on these findings, it is likely that female competition in the context of reproduction plays a role in the calling behaviour of *Pan*, the extent of which requires further investigation.

We reasoned that copulation calls allow females to compete indirectly with other cycling females by inciting competition amongst males. Chimpanzee copulation calls are individually distinct, but do not alter in acoustic structure across the ovarian cycle (Townsend, Deschner, and Zuberbühler, 2011). Competition is likely to be highest during periods when several females cycle simultaneously, which is then likely to lead to competition for sexual access to males. This may be particularly taxing on nulliparous females who are generally found less attractive than parous females (Muller and Mitani, 2005; Muller et al., 2006). We therefore predicted that copulation calls might be adjusted according to female attractiveness, i.e. parity. We tested the hypothesis that copulation calling strategy might differ for parous and nulliparous females against the null alternative that all females exhibit the same overall calling strategy. On the basis that attractiveness varies according to parity, we predicted nulliparous females would exhibit a more aggressive calling strategy, i.e. calling at higher rates, given their need to compete against more attractive parous females. (Indeed, preliminary data from the Kanyawara community suggested that nulliparous females give copulation calls more frequently than parous females: Thompson, Machanda, Muller, Kahlenberg, and Wrangham, 2013). We expected nulliparous females to be especially vulnerable when competition is high and many females are in oestrus.

METHODS

Study site and subjects

The study was conducted at the Budongo Conservation Field Station (BCFS), located in the Budongo Forest Reserve in Masindi, Uganda, a protected area totalling 794 km^2 of primarily semi-deciduous forest (Eggeling, 1974; Plumptre, 1996). Budongo Forest is home to an estimated population of 583 chimpanzees (Plumptre, Cox, and Mugume, 2003), including two habituated communities, Sonso and Waibira. Data were collected from the Sonso community, which included 66 total individuals (19 male, 47 female) at the time of the study. Fourteen adult and sub-adult males (9 adults, 5 sub-adults) were targeted for data collection as copulation partners. Of the females, 13 parous and 7 nulliparous females experienced an oestrous cycle during the study period and were targeted as focal individuals. Only one nulliparous female gave birth during the study; this female lost her first two infants in consecutive pregnancies (one to infanticide, one to unknown causes), and was thus excluded from analysis on the grounds that her parity status changed during the study period and her attractiveness as a fit mother was unclear.

Data collection

Data were collected in all-day focal follows of cycling females using all-occurrence sampling balanced across individuals (Altmann, 1974). Fieldwork was conducted between the periods of June 2011-August 2011, May 2012-April 2013, and September 2013-March 2014, totalling approximately 2,688 hours of observation time. We filmed 1,157 sexual interactions between males and oestrous females using a Panasonic HD V700 video camera, recording vocalizations with a Sennheiser MKE400 microphone. FileMaker Pro Advanced v. 11 was used to code filmed data for swelling stage, presence/absence of copulation call, partner identity and rank, audience, duration of copulation, and the number of females undergoing oestrus in the community at the time of copulation. We did not include female rank because we were unable to collect sufficient data on all focal females for reliable rank assessment.

Chimpanzee copulation calls are rhythmic, high frequency, acoustically distinct screams (Townsend et al., 2011). We limited our definition of copulation call to calls produced during a sexual act, although females occasionally produce calls during male inspection of their swellings. Swelling stage was estimated by the degree of wrinkling on a scale of 0-4, where 4 indicates a fully inflated swelling (Furuichi, 1987; Zuberbühler and Reynolds, 2005). Length of copulation was measured from the start of intromission to its cessation. Audience was defined as individuals within 50m of the focal female at the time of copulation. As copulation calls occur at a frequency of 700-1000 Hz (Townsend et al., 2008), we are confident that calls were audible to individuals within this range. Male dominance rank was assessed using pant grunt data, which is regularly used as a reliable indication of submission in male chimpanzees (Goodall, 1986).

Statistical analysis

We tested the factors that affected the probability of female copulation calling with a generalized linear mixed model (GLMM) with binomial error structure (Bolker et al., 2009). Age and parity were related in our sample and we therefore chose to include parity, given the prior evidence that parity is a measure of attractiveness in chimpanzees (Muller et al., 2006; Feldblum et al., 2014). We assessed the following predictor variables: partner rank (1-14, where 1 is high-ranking and 14 is low-ranking), copulation length (continuous, seconds), female parity (binary, parous/nulliparous), presence of a high-ranking male in the audience (binary, yes/no), presence of a parous female in the audience (binary, yes/no), number of nulliparous females in maximum oestrus (continuous), and number of parous females in maximum oestrus (continuous). Female identity and male identity were set as random effect variables. There were 16 instances in which multiple copulations occurred consecutively with identical audiences. We therefore fitted an additional random effect 'event' to account for repeated data points under identical conditions with reference to audience. However, the variance of this random effect was negligible (<0.0001) and we therefore decided to remove this term. We initially tested the interactions between parity and all other variables, to address whether factors affected mothers and non-mothers differently. We transformed numeric variables where necessary to achieve symmetric distributions and standardized them to mean=0 and SD=1 (Schielzeth, 2010). To confirm model validity, we used variance inflation factors (VIF, Fox and Weisberg, 2011), which verified that collinearity was not an issue (maximum VIF = 2.2). We checked for influential cases by calculating Cook’s distances (c.f.

Nieuwenhuis, Te Grotenhuis, and Pelzer, 2012): we identified one influential female and male, reflecting a total of 13 copulations. Removing these cases resulted in only minor changes of parameter estimates and did not affect our conclusions. Results are presented for the complete data set. We removed four interaction terms out of six tested because they did not improve model fit (likelihood ratio tests, LRT, all $\chi^2_1<2.6$, $P>0.1$, Quinn & Keough, 2002) and to be able to assess the importance of main effects comprised in interaction terms (Hector, von Felten, and Schmid, 2010). Using a likelihood ratio test, we tested the resulting full model against a null model comprised of the intercept and random effects. All statistical analyses were conducted using R (version 3.1.2; R Core Team, 2014) and the lme 4 package (version 1.0-7; Bates, Maechler, Bolker, and Walker, 2014).

Ethical Note

All methods received ethical approval from the University of St Andrews Animal Welfare and Ethics Committee, and met the International Primatological Society guidelines for the use of non-human primates in research. The Ugandan Wildlife Authority and Ugandan National Center for Science and Technology authorized fieldwork in Budongo under project no. NS372. The Sonso community is fully habituated to humans; nonetheless, researchers take precautions to remain seven meters’ distance from subjects at all times for the safety of both chimpanzees and humans. There were no invasive methods to this study, and all data collected were observational and posed neither harm or stress to the subjects.

RESULTS

Females produced copulation calls for 48.1% (557 calls) of 1,157 copulations, slightly more than has been reported previously (Hauser 1990, Townsend et al. 2011). The full model was significantly different from the null model (LRT: χ^2_9=43.29, $P < 0.001$; Table 1).

Duration and Partner Rank

Most intromissions were 5-10 seconds long, with an overall range between 2 and 15 seconds (mean = 8.33s). We found a significant interaction between parity and duration (LRT: χ^2_1=9.19, P=0.0024). For parous females, calling likelihood increased only marginally with longer intromission. For nulliparous females, this positive effect was much more pronounced. In general, nulliparous females were more likely to call than parous females, particularly during long copulations, for which nulliparous females were more than twice as likely to call compared to parous females (Figure 1).

Females, irrespective of their parity status, were more likely to give copulation calls when mating with high-ranking than low-ranking male partners (estimate=-0.37, SE=0.11, z = -3.50, P= 0.0005, Figure 2).

Audience

Male audience, but not female audience, predicted female calling behaviour. There was a significant interaction between parity and dominant male audience in the probability of call utterance (LRT: χ^2_1=5.84, P=0.0157; Figure 3). This interaction reflects the fact that, as the number of dominant males in the audience increased, nulliparous females were less likely to call, and parous females more likely to call. The number of parous females in the audience did not have a significant effect on female calling for either parous or nulliparous females (estimate=-0.05, SE=0.11, z=-0.44, P=0.6639).

Female competition

The minimum number of maximally swollen (stage 4) females on a given day was 0, and the maximum was 10, with an average of 3 fully swollen females per day. As the number of parous females in maximum oestrus increased, there was a non-significant trend for the probability of calling to rise (estimate=0.17, SE=0.09, z = 1.81, *P*=0.0701; we applied a logarithmic transformation to ‘number of parous females in oestrus’.). In contrast, the number of nulliparous females in full oestrus had no effect on either nulliparous or parous calling behaviour (estimate=-0.02, SE=0.08, z=-0.20, *P*=0.8399).

DISCUSSION

Our results indicate that female chimpanzees employ different calling strategies in specific circumstances, according to their reproductive attractiveness and social standing within the community. All females were more likely to call when mating with high-ranking male partners, and were more likely to call during longer copulations. Male partner rank predicted calling for all females, confirming previous findings that females are more likely to call when mating with males of high rank (Townsend et al., 2008). Nulliparous females were more likely to call than parous females regardless of duration or the number of dominant males in the audience. As the number of parous oestrous females increased, there was a non-significant trend for the likelihood of calling to increase for all females. However, dominant male audience affected parous and nulliparous females differently. While parous females were more likely to call as the number of dominant males in the audience increased, the probability of calling for nulliparous females decreased as the number of dominant males in the audience increased. Female calling strategies thus differed in four circumstances: female parity, copulation duration, dominant male audience, and (marginally) number of other cycling females.

Although all females were more likely to call during long copulations than short copulations, this effect was largely driven by nulliparous females; in contrast, parous females had only a marginal increase in the probability of a calling during long copulations. We suggest this difference may relate to nulliparous females' lack of experience, leading to higher levels of excitement or fear during longer copulations, which are inevitably more likely to be discovered by other individuals, including males of higher rank than their current partner. In support of the hypothesis that inexperienced individuals may be particularly frightened of discovery, nulliparous females called less when there were a high number of dominant males in the audience. As nulliparous females nonetheless maintained an overall higher calling rate than parous females, we regard an effect of fearful suppression to be the most likely explanation for this audience-driven reduction in calling, but other interpretations are possible. In Budongo, older females have a history of violence toward other females (Townsend et al., 2007; Townsend et al., 2008); although parous audience was not a significant predictor in our model, it is possible that dominant female audience plays a role in nulliparous call suppression, which we were unable to test for lack of female rank data. In contrast, parous females were more frequently the target of male coercion, yet they increased calling as the number of dominant males in the audience increased. Parous females therefore seem to increase advertisement strategically when high-ranking males were present, despite the risk of coercion. Indeed, one theory suggests that females call specifically in order to incite competition, as a means of ensuring the fittest mate (O'Connell & Cowlishaw, 1994).

Taken together, these results suggest that the high frequency of calling by nulliparous females may be driven by the need to attract attention to their reproductive status. Parous females are more attractive as partners for high-ranking males (Muller et al., 2006) and are more likely to be mate-guarded. Parous females may therefore produce copulation calls less overall than nulliparous females because they have less need to advertise their sexual status – either because male coercion prevents them from doing so, or because their desirable status means they don’t have to compete with other females. However, parous females seem to increase their calling strategically when the payoff is high, for example by inciting competition when multiple dominant males are present, therefore increasing paternal uncertainty among males and reducing females’ risk of infanticide.

A previous study with the same population found that low-ranking adult females suppressed copulation calls in the presence of equal- or higher-ranking females, and that this effect was stronger when they were mating with high-ranking males (Townsend et al., 2008). Because of the difficulty of establishing a reliable female dominance hierarchy due to sparse female interaction data, we instead used parous female audience as a proxy for dominant female audience; but we were unable to replicate the previous result using this measure, finding no effect of parous female audience on calling. However, social factors during the two studies were very different. During the first, few females were cycling simultaneously and female-led infanticide was a high risk (Townsend et al., 2007). In the second, many females were cycling and male-led infanticide was a high risk (Wilson et al., 2014). Given that females seem to modify their calling strategically, based on social factors, it is therefore likely that the previous threat from females may explain the difference in the sensitivity to female audience. In the same study, no effect of dominant male audience on female calls was found (Townsend et al., 2008); however, that study concentrated largely on older females, and we have shown that nulliparous females are more strongly influenced by dominant male audience than parous females.

We found a non-significant trend for females to produce more copulation calls when there were multiple females in oestrus, suggesting that females may call to distinguish themselves from the competition, in order to attract males in times of high female-female competition. This effect was only found when multiple parous females were in maximum oestrus, indicating that females might differentiate the threat level of potential competitors. It may therefore be that advertising becomes more relevant when female-female competition is high. One potential confound in our study is female age, which we were unable to include due to overlap with parity status. Future studies should attempt to distinguish between different categories of age and parity, as the combination of old age and parous status has proven important at other sites (Muller et al., 2006; Feldblum et al., 2014). Although we treated all copulation calls equally, females occasionally exhibit ‘deceptive’ swellings unaccompanied by ovulation (Goodall, 1986), and it is possible that we inadvertently included calls produced during anovulatory swellings. Since females do not adjust their calling during the peri-ovulatory period for cycles where they do ovulate (Townsend et al., 2011), we do not expect the possible inclusion of such calls to influence our results.

CONCLUSIONS

Our findings on the copulation calling of nulliparous females are consistent with their social standing: young, low ranking, and often new immigrants to the community. Female oestrus cycles have been described as a ‘social passport’ with which young females gain sexual partners and increase their social standing (Boesch and Boesch-Ackermann, 2000). Our data extend this metaphor to include copulation calling as a tool with which new females integrate by advertising their sexual status to males in the community. The differences between parous and nulliparous calling indicate a shift for reproductively successful females. We suggest that frequent calling may be the optimal strategy for nulliparous females, as a tactic to attract mates and increase their chance for reproductive success. With no offspring, and with little threat of male coercion, nulliparous females have more freedom to advertise their sexual receptivity. Nonetheless, we found that that suppression occurs where male coercion is a high risk because more dominant males are present.

In contrast, parous females call less overall, and only slightly increase calling with increasing copulation duration and dominant male audience. This marked departure from the nulliparous calling strategy might be due to several factors, including overall call suppression associated with an increased risk of male coercion and the need to protect offspring. Alternatively, the low likelihood of calling could merely reflect that parous females have less need to advertise. These two explanations are challenging to separate given that parous females are also more prone to coercion. Both parous and nulliparous females had a tendency to increase calling with the number of parous females in oestrus, suggesting that females might be able to assess the level of female competition and modify their calling strategy accordingly; this idea merits further testing.

Overall, our findings confirm the hypothesis that females of different reproductive status flexibly produce copulation calls using different strategies, which we argue reflect their attractiveness. This does not necessarily imply that females consciously assess their attractiveness: for instance, females might alter their calling behaviour in response to male interest, a reliable proxy of attractiveness. Strategic advertisement appears to be one way in which females indirectly compete with each other, echoing findings of indirect mate competition in human females.

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ABSTRACT

Female chimpanzees (*Pan troglodytes*) are usually depicted as sexually submissive and bound by male coercion, because males are able to monopolize oestrous females, limiting a female's options for mate choice. We present behavioural data from a group of wild chimpanzees during a rare period in which up to 10 females cycled simultaneously, which prevented males from monopolizing oestrous females, thus changing the dynamic of male-female sexual interactions. Overall, we found that nulliparous and parous females employed different copulation calling strategies, reflecting their relative reproductive attractiveness and social standing within the community. Male partner rank, copulation duration, and dominant male audience further influenced calling behaviour, and there was a non-significant trend for females to increase calling as the number of cycling females increased. We conclude that female chimpanzees are capable of adjusting their copulation calling flexibly, by taking into account their own sexual attractiveness in order to incite male competition.

Keywords: chimpanzee, parity, female competition, copulation call, sexual signal

INTRODUCTION

Sexual selection dictates a balance between mate competition and mate choice (Darwin, 1871; Trivers, 1972). Given that females are often the limiting sex, in systems where males are competitors and females are choosey, research on female mating strategies becomes essential for broadening our understanding of sexual selection theory. As a mating strategy, in many species female competition manifests in ways not necessarily directly associated with mating success: for example, through physical aggression, resource manipulation, infanticide, and reproductive suppression of others (Stockley and Bro-Jørgenson, 2011). In patrilocal primates, indirect female competition prevails (chimpanzees and bonobos: Pusey, Williams, and Goodall, 1997; Kano, 1992; humans: Benenson, 2013; Campbell, 2013). Human females in particular are noteworthy for indirect aggression toward female competitors, such as social exclusion (Benenson, Markovits, Thompson, and Wrangham, 2011) or punishing superiority (Winstead and Griffin, 2001).

In contrast to such subtle means of competition, overt tactics of male intra-sexual competition, such as coercion, are a pervasive strategy in many species, especially chimpanzees (Smuts, 1993; Clutton-Brock, 2007; Muller and Wrangham, 2009). Chimpanzee males prefer older, parous females and use selective aggression as a means of enacting this preference (Muller, Thompson, and Wrangham, 2006; Muller, Thompson, Kahlenberg, and Wrangham, 2011; Feldblum et al., 2014). As a counter-strategy to coercion, chimpanzee females sometimes tactically initiate sexual interactions with high-ranking males (Pieta, 2008), demonstrating that females modify their mating behaviour to reduce costs. In some chimpanzee populations, female choice appears to be the dominant mating strategy (Matsumoto-Oda, 1999; Stumpf and Boesch, 2005, 2006, 2010), a difference that may relate to the steepness of the male dominance hierarchy (Kaburu and Newton Fisher, 2015a). Prevalence of female choice has been argued to reflect communities where males differ little in competitive power: direct coercion may then be thwarted and males instead attempt to bias female choice, for example through grooming (Kaburu and Newton Fisher, 2015b). In contrast to the active debate and extensive data on male-male mating competition in chimpanzees, relatively few data are available on how female chimpanzees, or indeed any female primates, take female competitors into account during mating (Stumpf and Boesch, 2006; Townsend, Deschner, and Zuberbühler, 2008).

However, competition from other females may be especially important for nulliparous females in the face of males' preference for older, parous females.

Female chimpanzees are generally viewed as the more solitary and passive sex, yet resource competition between females is well-documented. For example, immigrant females compete in many day-to-day interactions with resident females over access to resources (Pusey and Schroepfer-Walker 2013), a level of competition that causes immigrants to avoid high-ranking females when ranging (Murray, Mane, and Pusey, 2007). While physical aggression between adult females is rare, there are multiple reports of selective aggression towards immigrant females, presumably because they pose a threat to resident females' resources (Boesch and Boesch-Ackermann, 2000, Pusey et al., 2008, Kahlenberg, Thompson, Muller, and Wrangham, 2008). Such aggression can be severe, preventing young females from immigrating (Pusey et al., 2008) and possibly involving female-led infanticidal behaviour towards immigrant mothers in at least one community (Townsend, Slocombe, Thompson, and Zuberbühler, 2007). Perhaps for this reason, immigrant females have been observed to rely on male protection and occasionally to ally with each other against resident females (chimpanzees: Nishida, 1979; Boesch and Boesch-Ackermann, 2000; Kahlenberg et al., 2008; gorillas: Watts, 1992).

In contrast, there are no comparable studies of female-female competition over sexual partners, apart from isolated anecdotes (e.g. Nishida, 1979). There is some evidence for indirect effects of intra-sexual competition, in that the stress of immigration appears to delay conception in immigrant females by several years despite the fact that they have regular sexual cycles (Nishida et al., 2003; Pusey and Schroepfer-Walker, 2013). Generally, female chimpanzees tend to avoid direct intra-sexual mating conflict by attracting male partners with signals of sexual receptivity: that is, visually salient sexual swellings, olfactory cues, and copulation calls (Deschner, Heistermann, Hodges, and Boesch, 2004; Townsend et al., 2008).

In many taxa, copulation calling is thought to incite competition between males while affording females protection from infanticide (O'Connell & Cowlishaw, 1994; Oda and Masataka, 1995; Semple, 1998; Pradhan, Engelhardt, van Schaik, and Maestripieri, 2006; Englehardt, Fischer, Neumann, Pfeifer, and Heistermann, 2012). Strategic call production is evidenced by reports of call repression and furtive behaviour in chimpanzees and geladas (*Theropithecus gelada*), for example during so-called 'furtive' copulations with low-ranking males, which allow females to promote paternity confusion while avoiding aggression from dominant males (Matsumoto-Oda & Tomonaga, 2005; Le Roux, Snyder-Mackler, Roberts, Beehner, and Bergman, 2013). Similarly, chimpanzee females can suppress copulation calls in the presence of equal or higher-ranking females (Townsend et al., 2008); having some measure of vocal control may mitigate infanticide risk (Townsend et al., 2007, 2008). Among bonobos (*Pan paniscus*), where high-ranking allies can lower the threat of female-female competition, females give copulation calls more frequently in the presence of the alpha female (Clay, Pika, Gruber, and Zuberbühler, 2011). Based on these findings, it is likely that female competition in the context of reproduction plays a role in the calling behaviour of *Pan*, the extent of which requires further investigation.

We reasoned that copulation calls allow females to compete indirectly with other cycling females by inciting competition amongst males. Chimpanzee copulation calls are individually distinct, but do not alter in acoustic structure across the ovarian cycle (Townsend, Deschner, and Zuberbühler, 2011). Competition is likely to be highest during periods when several females cycle simultaneously, which is then likely to lead to competition for sexual access to males. This may be particularly taxing on nulliparous females who are generally found less attractive than parous females (Muller and Mitani, 2005; Muller et al., 2006). We therefore predicted that copulation calls might be adjusted according to female attractiveness, i.e. parity. We tested the hypothesis that copulation calling strategy might differ for parous and nulliparous females against the null alternative that all females exhibit the same overall calling strategy. On the basis that attractiveness varies according to parity, we predicted nulliparous females would exhibit a more aggressive calling strategy, i.e. calling at higher rates, given their need to compete against more attractive parous females. (Indeed, preliminary data from the Kanyawara community suggested that nulliparous females give copulation calls more frequently than parous females: Thompson, Machanda, Muller, Kahlenberg, and Wrangham, 2013). We expected nulliparous females to be especially vulnerable when competition is high and many females are in oestrus.

METHODS

Study site and subjects

The study was conducted at the Budongo Conservation Field Station (BCFS), located in the Budongo Forest Reserve in Masindi, Uganda, a protected area totalling 794 km^2 of primarily semi-deciduous forest (Eggeling, 1974; Plumptre, 1996). Budongo Forest is home to an estimated population of 583 chimpanzees (Plumptre, Cox, and Mugume, 2003), including two habituated communities, Sonso and Waibira. Data were collected from the Sonso community, which included 66 total individuals (19 male, 47 female) at the time of the study. Fourteen adult and sub-adult males (9 adults, 5 sub-adults) were targeted for data collection as copulation partners. Of the females, 13 parous and 7 nulliparous females experienced an oestrous cycle during the study period and were targeted as focal individuals. Only one nulliparous female gave birth during the study; this female lost her first two infants in consecutive pregnancies (one to infanticide, one to unknown causes), and was thus excluded from analysis on the grounds that her parity status changed during the study period and her attractiveness as a fit mother was unclear.

Data collection

Data were collected in all-day focal follows of cycling females using all-occurrence sampling balanced across individuals (Altmann, 1974). Fieldwork was conducted between the periods of June 2011-August 2011, May 2012-April 2013, and September 2013-March 2014, totalling approximately 2,688 hours of observation time. We filmed 1,157 sexual interactions between males and oestrous females using a Panasonic HD V700 video camera, recording vocalizations with a Sennheiser MKE400 microphone. FileMaker Pro Advanced v. 11 was used to code filmed data for swelling stage, presence/absence of copulation call, partner identity and rank, audience, duration of copulation, and the number of females undergoing oestrus in the community at the time of copulation. We did not include female rank because we were unable to collect sufficient data on all focal females for reliable rank assessment.

Chimpanzee copulation calls are rhythmic, high frequency, acoustically distinct screams (Townsend et al., 2011). We limited our definition of copulation call to calls produced during a sexual act, although females occasionally produce calls during male inspection of their swellings. Swelling stage was estimated by the degree of wrinkling on a scale of 0-4, where 4 indicates a fully inflated swelling (Furuichi, 1987; Zuberbühler and Reynolds, 2005). Length of copulation was measured from the start of intromission to its cessation. Audience was defined as individuals within 50m of the focal female at the time of copulation. As copulation calls occur at a frequency of 700-1000 Hz (Townsend et al., 2008), we are confident that calls were audible to individuals within this range. Male dominance rank was assessed using pant grunt data, which is regularly used as a reliable indication of submission in male chimpanzees (Goodall, 1986).

Statistical analysis

We tested the factors that affected the probability of female copulation calling with a generalized linear mixed model (GLMM) with binomial error structure (Bolker et al., 2009). Age and parity were related in our sample and we therefore chose to include parity, given the prior evidence that parity is a measure of attractiveness in chimpanzees (Muller et al., 2006; Feldblum et al., 2014). We assessed the following predictor variables: partner rank (1-14, where 1 is high-ranking and 14 is low-ranking), copulation length (continuous, seconds), female parity (binary, parous/nulliparous), presence of a high-ranking male in the audience (binary, yes/no), presence of a parous female in the audience (binary, yes/no), number of nulliparous females in maximum oestrus (continuous), and number of parous females in maximum oestrus (continuous). Female identity and male identity were set as random effect variables. There were 16 instances in which multiple copulations occurred consecutively with identical audiences. We therefore fitted an additional random effect 'event' to account for repeated data points under identical conditions with reference to audience. However, the variance of this random effect was negligible (<0.0001) and we therefore decided to remove this term. We initially tested the interactions between parity and all other variables, to address whether factors affected mothers and non-mothers differently. We transformed numeric variables where necessary to achieve symmetric distributions and standardized them to mean=0 and SD=1 (Schielzeth, 2010). To confirm model validity, we used variance inflation factors (VIF, Fox and Weisberg, 2011), which verified that collinearity was not an issue (maximum VIF = 2.2). We checked for influential cases by calculating Cook’s distances (c.f.

Nieuwenhuis, Te Grotenhuis, and Pelzer, 2012): we identified one influential female and male, reflecting a total of 13 copulations. Removing these cases resulted in only minor changes of parameter estimates and did not affect our conclusions. Results are presented for the complete data set. We removed four interaction terms out of six tested because they did not improve model fit (likelihood ratio tests, LRT, all $\chi^2_1<2.6$, $P>0.1$, Quinn & Keough, 2002) and to be able to assess the importance of main effects comprised in interaction terms (Hector, von Felten, and Schmid, 2010). Using a likelihood ratio test, we tested the resulting full model against a null model comprised of the intercept and random effects. All statistical analyses were conducted using R (version 3.1.2; R Core Team, 2014) and the lme 4 package (version 1.0-7; Bates, Maechler, Bolker, and Walker, 2014).

Ethical Note

All methods received ethical approval from the University of St Andrews Animal Welfare and Ethics Committee, and met the International Primatological Society guidelines for the use of non-human primates in research. The Ugandan Wildlife Authority and Ugandan National Center for Science and Technology authorized fieldwork in Budongo under project no. NS372. The Sonso community is fully habituated to humans; nonetheless, researchers take precautions to remain seven meters' distance from subjects at all times for the safety of both chimpanzees and humans. There were no invasive methods to this study, and all data collected were observational and posed neither harm or stress to the subjects.

RESULTS

Females produced copulation calls for 48.1% (557 calls) of 1,157 copulations, slightly more than has been reported previously (Hauser 1990, Townsend et al. 2011). The full model was significantly different from the null model (LRT: χ^2_9=43.29, $P < 0.001$; Table 1).

Duration and Partner Rank

Most intromissions were 5-10 seconds long, with an overall range between 2 and 15 seconds (mean = 8.33s). We found a significant interaction between parity and duration (LRT: χ^2_1=9.19, P=0.0024). For parous females, calling likelihood increased only marginally with longer intromission. For nulliparous females, this positive effect was much more pronounced. In general, nulliparous females were more likely to call than parous females, particularly during long copulations, for which nulliparous females were more than twice as likely to call compared to parous females (Figure 1).

Females, irrespective of their parity status, were more likely to give copulation calls when mating with high-ranking than low-ranking male partners (estimate=-0.37, SE=0.11, z = -3.50, P= 0.0005, Figure 2).

Audience

Male audience, but not female audience, predicted female calling behaviour. There was a significant interaction between parity and dominant male audience in the probability of call utterance (LRT: χ^2_1=5.84, P=0.0157; Figure 3). This interaction reflects the fact that, as the number of dominant males in the audience increased, nulliparous females were less likely to call, and parous females more likely to call. The number of parous females in the audience did not have a significant effect on female calling for either parous or nulliparous females (estimate=-0.05, SE=0.11, z=-0.44, P=0.6639).

Female competition

The minimum number of maximally swollen (stage 4) females on a given day was 0, and the maximum was 10, with an average of 3 fully swollen females per day. As the number of parous females in maximum oestrus increased, there was a non-significant trend for the probability of calling to rise (estimate=0.17, SE=0.09, z = 1.81, *P*=0.0701; we applied a logarithmic transformation to ‘number of parous females in oestrus’.). In contrast, the number of nulliparous females in full oestrus had no effect on either nulliparous or parous calling behaviour (estimate=-0.02, SE=0.08, z=-0.20, *P*=0.8399).

DISCUSSION

Our results indicate that female chimpanzees employ different calling strategies in specific circumstances, according to their reproductive attractiveness and social standing within the community. All females were more likely to call when mating with high-ranking male partners, and were more likely to call during longer copulations. Male partner rank predicted calling for all females, confirming previous findings that females are more likely to call when mating with males of high rank (Townsend et al., 2008). Nulliparous females were more likely to call than parous females regardless of duration or the number of dominant males in the audience. As the number of parous oestrous females increased, there was a non-significant trend for the likelihood of calling to increase for all females. However, dominant male audience affected parous and nulliparous females differently. While parous females were more likely to call as the number of dominant males in the audience increased, the probability of calling for nulliparous females decreased as the number of dominant males in the audience increased. Female calling strategies thus differed in four circumstances: female parity, copulation duration, dominant male audience, and (marginally) number of other cycling females.

Although all females were more likely to call during long copulations than short copulations, this effect was largely driven by nulliparous females; in contrast, parous females had only a marginal increase in the probability of a calling during long copulations. We suggest this difference may relate to nulliparous females' lack of experience, leading to higher levels of excitement or fear during longer copulations, which are inevitably more likely to be discovered by other individuals, including males of higher rank than their current partner. In support of the hypothesis that inexperienced individuals may be particularly frightened of discovery, nulliparous females called less when there were a high number of dominant males in the audience. As nulliparous females nonetheless maintained an overall higher calling rate than parous females, we regard an effect of fearful suppression to be the most likely explanation for this audience-driven reduction in calling, but other interpretations are possible. In Budongo, older females have a history of violence toward other females (Townsend et al., 2007; Townsend et al., 2008); although parous audience was not a significant predictor in our model, it is possible that dominant female audience plays a role in nulliparous call suppression, which we were unable to test for lack of female rank data. In contrast, parous females were more frequently the target of male coercion, yet they increased calling as the number of dominant males in the audience increased. Parous females therefore seem to increase advertisement strategically when high-ranking males were present, despite the risk of coercion. Indeed, one theory suggests that females call specifically in order to incite competition, as a means of ensuring the fittest mate (O'Connell & Cowlishaw, 1994).

Taken together, these results suggest that the high frequency of calling by nulliparous females may be driven by the need to attract attention to their reproductive status. Parous females are more attractive as partners for high-ranking males (Muller et al., 2006) and are more likely to be mate-guarded. Parous females may therefore produce copulation calls less overall than nulliparous females because they have less need to advertise their sexual status – either because male coercion prevents them from doing so, or because their desirable status means they don’t have to compete with other females. However, parous females seem to increase their calling strategically when the payoff is high, for example by inciting competition when multiple dominant males are present, therefore increasing paternal uncertainty among males and reducing females’ risk of infanticide.

A previous study with the same population found that low-ranking adult females suppressed copulation calls in the presence of equal- or higher-ranking females, and that this effect was stronger when they were mating with high-ranking males (Townsend et al., 2008). Because of the difficulty of establishing a reliable female dominance hierarchy due to sparse female interaction data, we instead used parous female audience as a proxy for dominant female audience; but we were unable to replicate the previous result using this measure, finding no effect of parous female audience on calling. However, social factors during the two studies were very different. During the first, few females were cycling simultaneously and female-led infanticide was a high risk (Townsend et al., 2007). In the second, many females were cycling and male-led infanticide was a high risk (Wilson et al., 2014). Given that females seem to modify their calling strategically, based on social factors, it is therefore likely that the previous threat from females may explain the difference in the sensitivity to female audience. In the same study, no effect of dominant male audience on female calls was found (Townsend et al., 2008); however, that study concentrated largely on older females, and we have shown that nulliparous females are more strongly influenced by dominant male audience than parous females.

We found a non-significant trend for females to produce more copulation calls when there were multiple females in oestrus, suggesting that females may call to distinguish themselves from the competition, in order to attract males in times of high female-female competition. This effect was only found when multiple parous females were in maximum oestrus, indicating that females might differentiate the threat level of potential competitors. It may therefore be that advertising becomes more relevant when female-female competition is high. One potential confound in our study is female age, which we were unable to include due to overlap with parity status. Future studies should attempt to distinguish between different categories of age and parity, as the combination of old age and parous status has proven important at other sites (Muller et al., 2006; Feldblum et al., 2014). Although we treated all copulation calls equally, females occasionally exhibit ‘deceptive’ swellings unaccompanied by ovulation (Goodall, 1986), and it is possible that we inadvertently included calls produced during anovulatory swellings. Since females do not adjust their calling during the peri-ovulatory period for cycles where they do ovulate (Townsend et al., 2011), we do not expect the possible inclusion of such calls to influence our results.

CONCLUSIONS

Our findings on the copulation calling of nulliparous females are consistent with their social standing: young, low ranking, and often new immigrants to the community. Female oestrus cycles have been described as a ‘social passport’ with which young females gain sexual partners and increase their social standing (Boesch and Boesch-Ackermann, 2000). Our data extend this metaphor to include copulation calling as a tool with which new females integrate by advertising their sexual status to males in the community. The differences between parous and nulliparous calling indicate a shift for reproductively successful females. We suggest that frequent calling may be the optimal strategy for nulliparous females, as a tactic to attract mates and increase their chance for reproductive success. With no offspring, and with little threat of male coercion, nulliparous females have more freedom to advertise their sexual receptivity. Nonetheless, we found that that suppression occurs where male coercion is a high risk because more dominant males are present.

In contrast, parous females call less overall, and only slightly increase calling with increasing copulation duration and dominant male audience. This marked departure from the nulliparous calling strategy might be due to several factors, including overall call suppression associated with an increased risk of male coercion and the need to protect offspring. Alternatively, the low likelihood of calling could merely reflect that parous females have less need to advertise. These two explanations are challenging to separate given that parous females are also more prone to coercion. Both parous and nulliparous females had a tendency to increase calling with the number of parous females in oestrus, suggesting that females might be able to assess the level of female competition and modify their calling strategy accordingly; this idea merits further testing.

Overall, our findings confirm the hypothesis that females of different reproductive status flexibly produce copulation calls using different strategies, which we argue reflect their attractiveness. This does not necessarily imply that females consciously assess their attractiveness: for instance, females might alter their calling behaviour in response to male interest, a reliable proxy of attractiveness. Strategic advertisement appears to be one way in which females indirectly compete with each other, echoing findings of indirect mate competition in human females.

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Fig. 1: The interaction between parity and copulation duration in the probability of copulation call production. Parous females show a slight increase in likelihood of calling as duration increases. Nulliparous females show a larger increase in likelihood of calling as duration increases. Presented are model estimates based on centred and standardized data.

Fig. 2: **The effect of partner rank on the probability of copulation call production.** Females who mate with high-ranking males (left) are more likely to call than females who mate with low-ranking males (right). Presented are model estimates based on centred and standardized data.

Fig. 3: The interaction between parity and dominant male audience. As the number of dominant males increases, parous females show an increase in likelihood of calling, and nulliparous females show a decrease. We applied a logarithmic transformation to ‘male audience’. Data presented are centred.

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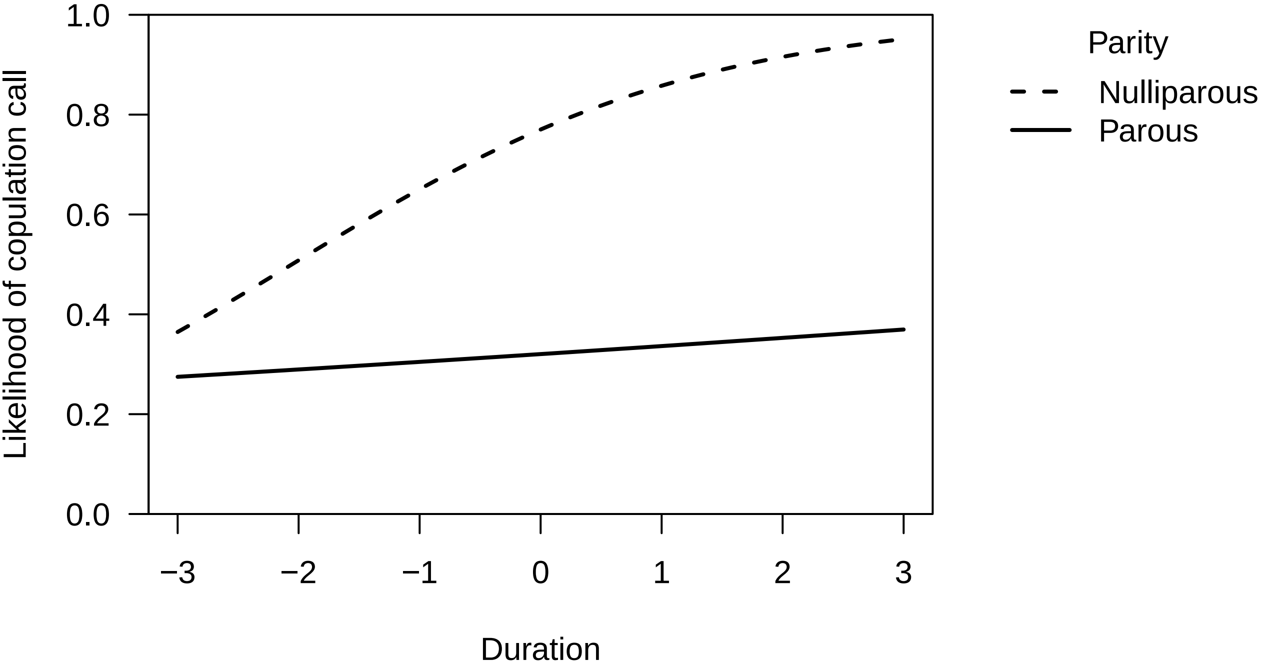
Figure 1



1.0
0.8
0.6
0.4
0.2
0.0
Likelihood of copulation call
−3
−2
−1
0
1
2
3
Duration
Parity
Nulliparous
Parous

Figure 2

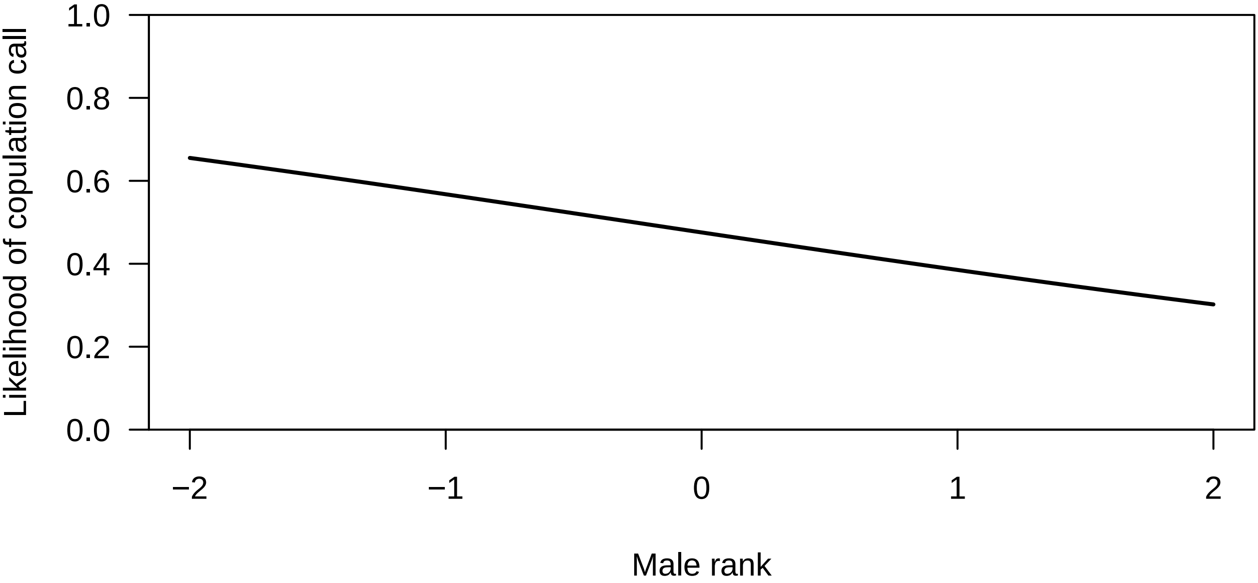

Likelihood of copulation call
1.0
0.8
0.6
0.4
0.2
0.0
−2
−1
0
1
2
Male rank

Figure 3

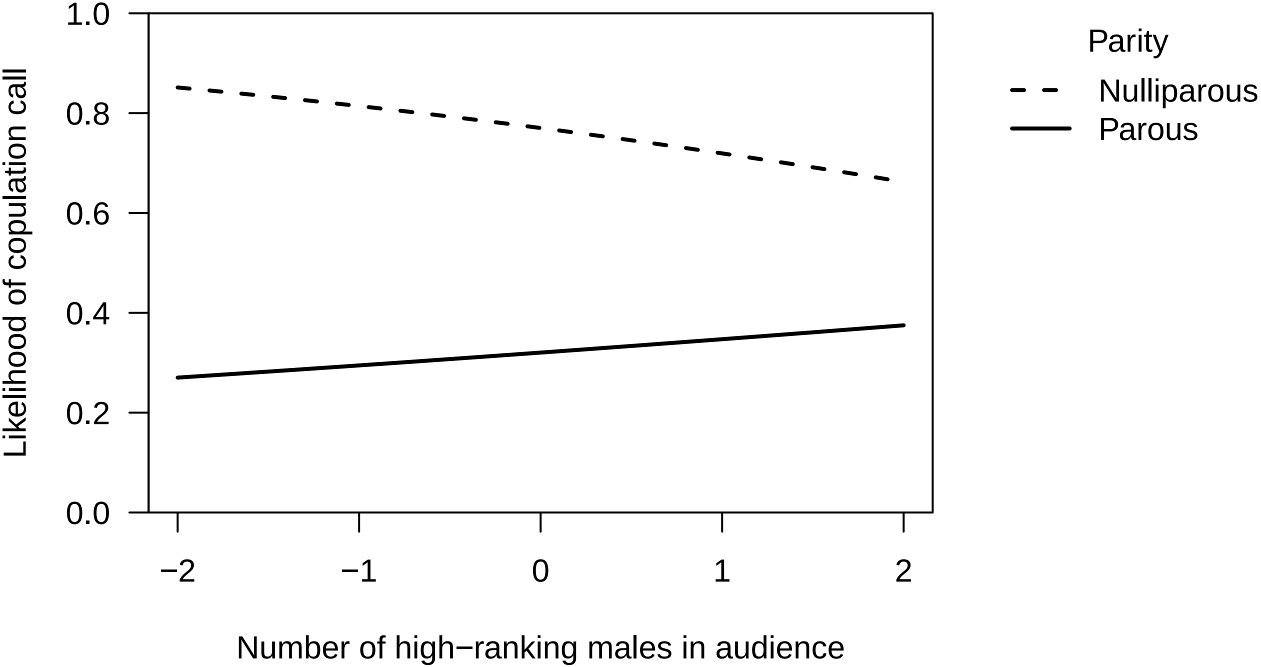

Likelihood of copulation call
1.0
0.8
0.6
0.4
0.2
0.0
−2
−1
0
1
2
Number of high−ranking males in audience
Parity
Nulliparous
Parous

Table 1

Table 1: Results of the GLMM testing factor affecting calling likelihood of female chimpanzees during copulation[1].

	Estimate	SE	*Z*	*CI*	*P*
Intercept	-0.752	0.341			
Parity (nulliparous)	1.962	0.619		0.749 – 3.174	
Parous in audience	-0.046	0.106	-0.435	-0.253 – 0.161	0.6639
Nulliparous in maximum oestrus	-0.017	0.084	-0.202	-0.181 – 0.147	0.8399
Parous in maximum oestrus	0.166	0.092	1.811	-0.014 – 0.346	0.0701
Number of high-ranking males in audience	0.121	0.116		-0.106 – 0.348	
Male partner dominance rank	-0.370	0.106	-3.501	-0.577 – -0.163	0.0005
Duration	0.073	0.084		-0.092 – 0.237	
IA parity : number of high-ranking males in audience	-0.389	0.161	-2.411	-0.705 – -0.073	0.0159
IA parity : duration	0.516	0.172	2.993	0.178 – 0.853	0.0028

[1] The reference level for parity is “parous” and is comprised in the intercept. *Z*, CI and *P* values are omitted for intercept and main effects comprised in interactions. IA = interaction. CI = 95% confidence interval.