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

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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**

- 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.

## 1 ABSTRACT

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

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

16

## 17 INTRODUCTION

18 Sexual selection dictates a balance between mate competition and mate choice (Darwin,  
19 1871; Trivers, 1972). Given that females are often the limiting sex, in systems where  
20 males are competitors and females are choosy, research on female mating strategies  
21 becomes essential for broadening our understanding of sexual selection theory. As a  
22 mating strategy, in many species female competition manifests in ways not necessarily  
23 directly associated with mating success: for example, through physical aggression,  
24 resource manipulation, infanticide, and reproductive suppression of others (Stockley and  
25 Bro-Jørgenson, 2011). In patrilocal primates, indirect female competition prevails

26 (chimpanzees and bonobos: Pusey, Williams, and Goodall, 1997; Kano, 1992; humans:  
27 Benenson, 2013; Campbell, 2013). Human females in particular are noteworthy for  
28 indirect aggression toward female competitors, such as social exclusion (Benenson,  
29 Markovits, Thompson, and Wrangham, 2011) or punishing superiority (Winstead and  
30 Griffin, 2001).

31

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

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

52

53 Female chimpanzees are generally viewed as the more solitary and passive sex, yet  
54 resource competition between females is well-documented. For example, immigrant  
55 females compete in many day-to-day interactions with resident females over access to  
56 resources (Pusey and Schroepfer-Walker 2013), a level of competition that causes  
57 immigrants to avoid high-ranking females when ranging (Murray, Mane, and Pusey,  
58 2007). While physical aggression between adult females is rare, there are multiple reports  
59 of selective aggression towards immigrant females, presumably because they pose a threat  
60 to resident females' resources (Boesch and Boesch-Ackermann, 2000, Pusey et al., 2008,  
61 Kahlenberg, Thompson, Muller, and Wrangham, 2008). Such aggression can be severe,  
62 preventing young females from immigrating (Pusey et al., 2008) and possibly involving  
63 female-led infanticidal behaviour towards immigrant mothers in at least one community  
64 (Townsend, Slocombe, Thompson, and Zuberbühler, 2007). Perhaps for this reason,  
65 immigrant females have been observed to rely on male protection and occasionally to ally  
66 with each other against resident females (chimpanzees: Nishida, 1979; Boesch and  
67 Boesch-Ackermann, 2000; Kahlenberg et al., 2008; gorillas: Watts, 1992).

68

69 In contrast, there are no comparable studies of female-female competition over sexual  
70 partners, apart from isolated anecdotes (e.g. Nishida, 1979). There is some evidence for  
71 indirect effects of intra-sexual competition, in that the stress of immigration appears to  
72 delay conception in immigrant females by several years despite the fact that they have  
73 regular sexual cycles (Nishida et al., 2003; Pusey and Schroepfer-Walker, 2013).

74 Generally, female chimpanzees tend to avoid direct intra-sexual mating conflict by

75 attracting male partners with signals of sexual receptivity: that is, visually salient sexual  
76 swellings, olfactory cues, and copulation calls (Deschner, Heistermann, Hodges, and  
77 Boesch, 2004; Townsend et al., 2008).

78

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

95

96 We reasoned that copulation calls allow females to compete indirectly with other cycling  
97 females by inciting competition amongst males. Chimpanzee copulation calls are  
98 individually distinct, but do not alter in acoustic structure across the ovarian cycle  
99 (Townsend, Deschner, and Zuberbühler, 2011). Competition is likely to be highest during

100 periods when several females cycle simultaneously, which is then likely to lead to  
101 competition for sexual access to males. This may be particularly taxing on nulliparous  
102 females who are generally found less attractive than parous females (Muller and Mitani,  
103 2005; Muller et al., 2006). We therefore predicted that copulation calls might be adjusted  
104 according to female attractiveness, i.e. parity. We tested the hypothesis that copulation  
105 calling strategy might differ for parous and nulliparous females against the null alternative  
106 that all females exhibit the same overall calling strategy. On the basis that attractiveness  
107 varies according to parity, we predicted nulliparous females would exhibit a more  
108 aggressive calling strategy, i.e. calling at higher rates, given their need to compete against  
109 more attractive parous females. (Indeed, preliminary data from the Kanyawara community  
110 suggested that nulliparous females give copulation calls more frequently than parous  
111 females: Thompson, Machanda, Muller, Kahlenberg, and Wrangham, 2013). We expected  
112 nulliparous females to be especially vulnerable when competition is high and many  
113 females are in oestrus.

114

## 115 **METHODS**

### 116 *Study site and subjects*

117 The study was conducted at the Budongo Conservation Field Station (BCFS), located in the  
118 Budongo Forest Reserve in Masindi, Uganda, a protected area totalling 794 km<sup>2</sup> of primarily  
119 semi-deciduous forest (Eggeling, 1974; Plumptre, 1996). Budongo Forest is home to an  
120 estimated population of 583 chimpanzees (Plumptre, Cox, and Mugume, 2003), including  
121 two habituated communities, Sonso and Waibira. Data were collected from the Sonso  
122 community, which included 66 total individuals (19 male, 47 female) at the time of the study.  
123 Fourteen adult and sub-adult males (9 adults, 5 sub-adults) were targeted for data collection  
124 as copulation partners. Of the females, 13 parous and 7 nulliparous females experienced an

125 oestrous cycle during the study period and were targeted as focal individuals. Only one  
126 nulliparous female gave birth during the study; this female lost her first two infants in  
127 consecutive pregnancies (one to infanticide, one to unknown causes), and was thus excluded  
128 from analysis on the grounds that her parity status changed during the study period and her  
129 attractiveness as a fit mother was unclear.

### 130 *Data collection*

131 Data were collected in all-day focal follows of cycling females using all-occurrence  
132 sampling balanced across individuals (Altmann, 1974). Fieldwork was conducted between  
133 the periods of June 2011-August 2011, May 2012-April 2013, and September 2013-March  
134 2014, totalling approximately 2,688 hours of observation time. We filmed 1,157 sexual  
135 interactions between males and oestrous females using a Panasonic HD V700 video  
136 camera, recording vocalizations with a Sennheiser MKE400 microphone. FileMaker Pro  
137 Advanced v. 11 was used to code filmed data for swelling stage, presence/absence of  
138 copulation call, partner identity and rank, audience, duration of copulation, and the  
139 number of females undergoing oestrus in the community at the time of copulation. We did  
140 not include female rank because we were unable to collect sufficient data on all focal  
141 females for reliable rank assessment.

142

143 Chimpanzee copulation calls are rhythmic, high frequency, acoustically distinct screams  
144 (Townsend et al., 2011). We limited our definition of copulation call to calls produced during  
145 a sexual act, although females occasionally produce calls during male inspection of their  
146 swellings. Swelling stage was estimated by the degree of wrinkling on a scale of 0-4, where 4  
147 indicates a fully inflated swelling (Furuichi, 1987; Zuberbühler and Reynolds, 2005). Length  
148 of copulation was measured from the start of intromission to its cessation. Audience was  
149 defined as individuals within 50m of the focal female at the time of copulation. As copulation

150 calls occur at a frequency of 700-1000 Hz (Townsend et al., 2008), we are confident that calls  
151 were audible to individuals within this range. Male dominance rank was assessed using pant  
152 grunt data, which is regularly used as a reliable indication of submission in male chimpanzees  
153 (Goodall, 1986).

#### 154 *Statistical analysis*

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

175 Nieuwenhuis, Te Grotenhuis, and Pelzer, 2012): we identified one influential female and  
176 male, reflecting a total of 13 copulations. Removing these cases resulted in only minor  
177 changes of parameter estimates and did not affect our conclusions. Results are presented for  
178 the complete data set. We removed four interaction terms out of six tested because they did  
179 not improve model fit (likelihood ratio tests, LRT, all  $\chi^2_1 < 2.6$ ,  $P > 0.1$ , Quinn & Keough,  
180 2002) and to be able to assess the importance of main effects comprised in interaction terms  
181 (Hector, von Felten, and Schmid, 2010). Using a likelihood ratio test, we tested the resulting  
182 full model against a null model comprised of the intercept and random effects. All statistical  
183 analyses were conducted using R (version 3.1.2; R Core Team, 2014) and the lme4 package  
184 (version 1.0-7; Bates, Maechler, Bolker, and Walker, 2014).

#### 185 *Ethical Note*

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

194

## 195 **RESULTS**

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

### 199 *Duration and Partner Rank*

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

207 Females, irrespective of their parity status, were more likely to give copulation calls when  
208 mating with high-ranking than low-ranking male partners (estimate=-0.37, SE=0.11,  $z = -$   
209 3.50,  $P= 0.0005$ , Figure 2).

### 210 *Audience*

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

### 218 *Female competition*

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

226

## 227 DISCUSSION

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

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

263 Taken together, these results suggest that the high frequency of calling by nulliparous females  
264 may be driven by the need to attract attention to their reproductive status. Parous females are  
265 more attractive as partners for high-ranking males (Muller et al., 2006) and are more likely to  
266 be mate-guarded. Parous females may therefore produce copulation calls less overall than  
267 nulliparous females because they have less need to advertise their sexual status – either

268 because male coercion prevents them from doing so, or because their desirable status means  
269 they don't have to compete with other females. However, parous females seem to increase  
270 their calling strategically when the payoff is high, for example by inciting competition when  
271 multiple dominant males are present, therefore increasing paternal uncertainty among males  
272 and reducing females' risk of infanticide.

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

289 We found a non-significant trend for females to produce more copulation calls when there  
290 were multiple females in oestrus, suggesting that females may call to distinguish themselves  
291 from the competition, in order to attract males in times of high female-female competition.  
292 This effect was only found when multiple parous females were in maximum oestrus,

293 indicating that females might differentiate the threat level of potential competitors. It may  
294 therefore be that advertising becomes more relevant when female-female competition is high.  
295 One potential confound in our study is female age, which we were unable to include due to  
296 overlap with parity status. Future studies should attempt to distinguish between different  
297 categories of age and parity, as the combination of old age and parous status has proven  
298 important at other sites (Muller et al., 2006; Feldblum et al., 2014). Although we treated all  
299 copulation calls equally, females occasionally exhibit ‘deceptive’ swellings unaccompanied  
300 by ovulation (Goodall, 1986), and it is possible that we inadvertently included calls produced  
301 during anovulatory swellings. Since females do not adjust their calling during the peri-  
302 ovulatory period for cycles where they do ovulate (Townsend et al., 2011), we do not expect  
303 the possible inclusion of such calls to influence our results.

304

## 305 **CONCLUSIONS**

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

317 risk because more dominant males are present.

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

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

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1 **ABSTRACT**

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

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

16

17 **INTRODUCTION**

18 Sexual selection dictates a balance between mate competition and mate choice (Darwin,  
19 1871; Trivers, 1972). Given that females are often the limiting sex, in systems where  
20 males are competitors and females are choosy, research on female mating strategies  
21 becomes essential for broadening our understanding of sexual selection theory. As a  
22 mating strategy, in many species female competition manifests in ways not necessarily  
23 directly associated with mating success: for example, through physical aggression,  
24 resource manipulation, infanticide, and reproductive suppression of others (Stockley and  
25 Bro-Jørgenson, 2011). In patrilocal primates, indirect female competition prevails

26 (chimpanzees and bonobos: Pusey, Williams, and Goodall, 1997; Kano, 1992; humans:  
27 Benenson, 2013; Campbell, 2013). Human females in particular are noteworthy for  
28 indirect aggression toward female competitors, such as social exclusion (Benenson,  
29 Markovits, Thompson, and Wrangham, 2011) or punishing superiority (Winstead and  
30 Griffin, 2001).

31

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

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

52

53 Female chimpanzees are generally viewed as the more solitary and passive sex, yet  
54 resource competition between females is well-documented. For example, immigrant  
55 females compete in many day-to-day interactions with resident females over access to  
56 resources (Pusey and Schroepfer-Walker 2013), a level of competition that causes  
57 immigrants to avoid high-ranking females when ranging (Murray, Mane, and Pusey,  
58 2007). While physical aggression between adult females is rare, there are multiple reports  
59 of selective aggression towards immigrant females, presumably because they pose a threat  
60 to resident females' resources (Boesch and Boesch-Ackermann, 2000, Pusey et al., 2008,  
61 Kahlenberg, Thompson, Muller, and Wrangham, 2008). Such aggression can be severe,  
62 preventing young females from immigrating (Pusey et al., 2008) and possibly involving  
63 female-led infanticidal behaviour towards immigrant mothers in at least one community  
64 (Townsend, Slocombe, Thompson, and Zuberbühler, 2007). Perhaps for this reason,  
65 immigrant females have been observed to rely on male protection and occasionally to ally  
66 with each other against resident females (chimpanzees: Nishida, 1979; Boesch and  
67 Boesch-Ackermann, 2000; Kahlenberg et al., 2008; gorillas: Watts, 1992).

68

69 In contrast, there are no comparable studies of female-female competition over sexual  
70 partners, apart from isolated anecdotes (e.g. Nishida, 1979). There is some evidence for  
71 indirect effects of intra-sexual competition, in that the stress of immigration appears to  
72 delay conception in immigrant females by several years despite the fact that they have  
73 regular sexual cycles (Nishida et al., 2003; Pusey and Schroepfer-Walker, 2013).

74 Generally, female chimpanzees tend to avoid direct intra-sexual mating conflict by

75 attracting male partners with signals of sexual receptivity: that is, visually salient sexual  
76 swellings, olfactory cues, and copulation calls (Deschner, Heistermann, Hodges, and  
77 Boesch, 2004; Townsend et al., 2008).

78

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

95

96 We reasoned that copulation calls allow females to compete indirectly with other cycling  
97 females by inciting competition amongst males. Chimpanzee copulation calls are  
98 individually distinct, but do not alter in acoustic structure across the ovarian cycle  
99 (Townsend, Deschner, and Zuberbühler, 2011). Competition is likely to be highest during

100 periods when several females cycle simultaneously, which is then likely to lead to  
101 competition for sexual access to males. This may be particularly taxing on nulliparous  
102 females who are generally found less attractive than parous females (Muller and Mitani,  
103 2005; Muller et al., 2006). We therefore predicted that copulation calls might be adjusted  
104 according to female attractiveness, i.e. parity. We tested the hypothesis that copulation  
105 calling strategy might differ for parous and nulliparous females against the null alternative  
106 that all females exhibit the same overall calling strategy. On the basis that attractiveness  
107 varies according to parity, we predicted nulliparous females would exhibit a more  
108 aggressive calling strategy, i.e. calling at higher rates, given their need to compete against  
109 more attractive parous females. (Indeed, preliminary data from the Kanyawara community  
110 suggested that nulliparous females give copulation calls more frequently than parous  
111 females: Thompson, Machanda, Muller, Kahlenberg, and Wrangham, 2013). We expected  
112 nulliparous females to be especially vulnerable when competition is high and many  
113 females are in oestrus.

114

## 115 **METHODS**

### 116 *Study site and subjects*

117 The study was conducted at the Budongo Conservation Field Station (BCFS), located in the  
118 Budongo Forest Reserve in Masindi, Uganda, a protected area totalling 794 km<sup>2</sup> of primarily  
119 semi-deciduous forest (Eggeling, 1974; Plumptre, 1996). Budongo Forest is home to an  
120 estimated population of 583 chimpanzees (Plumptre, Cox, and Mugume, 2003), including  
121 two habituated communities, Sonso and Waibira. Data were collected from the Sonso  
122 community, which included 66 total individuals (19 male, 47 female) at the time of the study.  
123 Fourteen adult and sub-adult males (9 adults, 5 sub-adults) were targeted for data collection  
124 as copulation partners. Of the females, 13 parous and 7 nulliparous females experienced an

125 oestrous cycle during the study period and were targeted as focal individuals. Only one  
126 nulliparous female gave birth during the study; this female lost her first two infants in  
127 consecutive pregnancies (one to infanticide, one to unknown causes), and was thus excluded  
128 from analysis on the grounds that her parity status changed during the study period and her  
129 attractiveness as a fit mother was unclear.

### 130 *Data collection*

131 Data were collected in all-day focal follows of cycling females using all-occurrence  
132 sampling balanced across individuals (Altmann, 1974). Fieldwork was conducted between  
133 the periods of June 2011-August 2011, May 2012-April 2013, and September 2013-March  
134 2014, totalling approximately 2,688 hours of observation time. We filmed 1,157 sexual  
135 interactions between males and oestrous females using a Panasonic HD V700 video  
136 camera, recording vocalizations with a Sennheiser MKE400 microphone. FileMaker Pro  
137 Advanced v. 11 was used to code filmed data for swelling stage, presence/absence of  
138 copulation call, partner identity and rank, audience, duration of copulation, and the  
139 number of females undergoing oestrus in the community at the time of copulation. We did  
140 not include female rank because we were unable to collect sufficient data on all focal  
141 females for reliable rank assessment.

142

143 Chimpanzee copulation calls are rhythmic, high frequency, acoustically distinct screams  
144 (Townsend et al., 2011). We limited our definition of copulation call to calls produced during  
145 a sexual act, although females occasionally produce calls during male inspection of their  
146 swellings. Swelling stage was estimated by the degree of wrinkling on a scale of 0-4, where 4  
147 indicates a fully inflated swelling (Furuichi, 1987; Zuberbühler and Reynolds, 2005). Length  
148 of copulation was measured from the start of intromission to its cessation. Audience was  
149 defined as individuals within 50m of the focal female at the time of copulation. As copulation

150 calls occur at a frequency of 700-1000 Hz (Townsend et al., 2008), we are confident that calls  
151 were audible to individuals within this range. Male dominance rank was assessed using pant  
152 grunt data, which is regularly used as a reliable indication of submission in male chimpanzees  
153 (Goodall, 1986).

#### 154 *Statistical analysis*

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

175 Nieuwenhuis, Te Grotenhuis, and Pelzer, 2012): we identified one influential female and  
176 male, reflecting a total of 13 copulations. Removing these cases resulted in only minor  
177 changes of parameter estimates and did not affect our conclusions. Results are presented for  
178 the complete data set. We removed four interaction terms out of six tested because they did  
179 not improve model fit (likelihood ratio tests, LRT, all  $\chi^2_1 < 2.6$ ,  $P > 0.1$ , Quinn & Keough,  
180 2002) and to be able to assess the importance of main effects comprised in interaction terms  
181 (Hector, von Felten, and Schmid, 2010). Using a likelihood ratio test, we tested the resulting  
182 full model against a null model comprised of the intercept and random effects. All statistical  
183 analyses were conducted using R (version 3.1.2; R Core Team, 2014) and the lme4 package  
184 (version 1.0-7; Bates, Maechler, Bolker, and Walker, 2014).

#### 185 *Ethical Note*

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

194

## 195 **RESULTS**

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

### 199 *Duration and Partner Rank*

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

207 Females, irrespective of their parity status, were more likely to give copulation calls when  
208 mating with high-ranking than low-ranking male partners (estimate=-0.37, SE=0.11,  $z = -$   
209 3.50,  $P= 0.0005$ , Figure 2).

### 210 *Audience*

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

### 218 *Female competition*

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

226

## 227 **DISCUSSION**

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

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

263 Taken together, these results suggest that the high frequency of calling by nulliparous females  
264 may be driven by the need to attract attention to their reproductive status. Parous females are  
265 more attractive as partners for high-ranking males (Muller et al., 2006) and are more likely to  
266 be mate-guarded. Parous females may therefore produce copulation calls less overall than  
267 nulliparous females because they have less need to advertise their sexual status – either

268 because male coercion prevents them from doing so, or because their desirable status means  
269 they don't have to compete with other females. However, parous females seem to increase  
270 their calling strategically when the payoff is high, for example by inciting competition when  
271 multiple dominant males are present, therefore increasing paternal uncertainty among males  
272 and reducing females' risk of infanticide.

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

289 We found a non-significant trend for females to produce more copulation calls when there  
290 were multiple females in oestrus, suggesting that females may call to distinguish themselves  
291 from the competition, in order to attract males in times of high female-female competition.  
292 This effect was only found when multiple parous females were in maximum oestrus,

293 indicating that females might differentiate the threat level of potential competitors. It may  
294 therefore be that advertising becomes more relevant when female-female competition is high.  
295 One potential confound in our study is female age, which we were unable to include due to  
296 overlap with parity status. Future studies should attempt to distinguish between different  
297 categories of age and parity, as the combination of old age and parous status has proven  
298 important at other sites (Muller et al., 2006; Feldblum et al., 2014). Although we treated all  
299 copulation calls equally, females occasionally exhibit ‘deceptive’ swellings unaccompanied  
300 by ovulation (Goodall, 1986), and it is possible that we inadvertently included calls produced  
301 during anovulatory swellings. Since females do not adjust their calling during the peri-  
302 ovulatory period for cycles where they do ovulate (Townsend et al., 2011), we do not expect  
303 the possible inclusion of such calls to influence our results.

304

## 305 **CONCLUSIONS**

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

317 risk because more dominant males are present.

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

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

335

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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

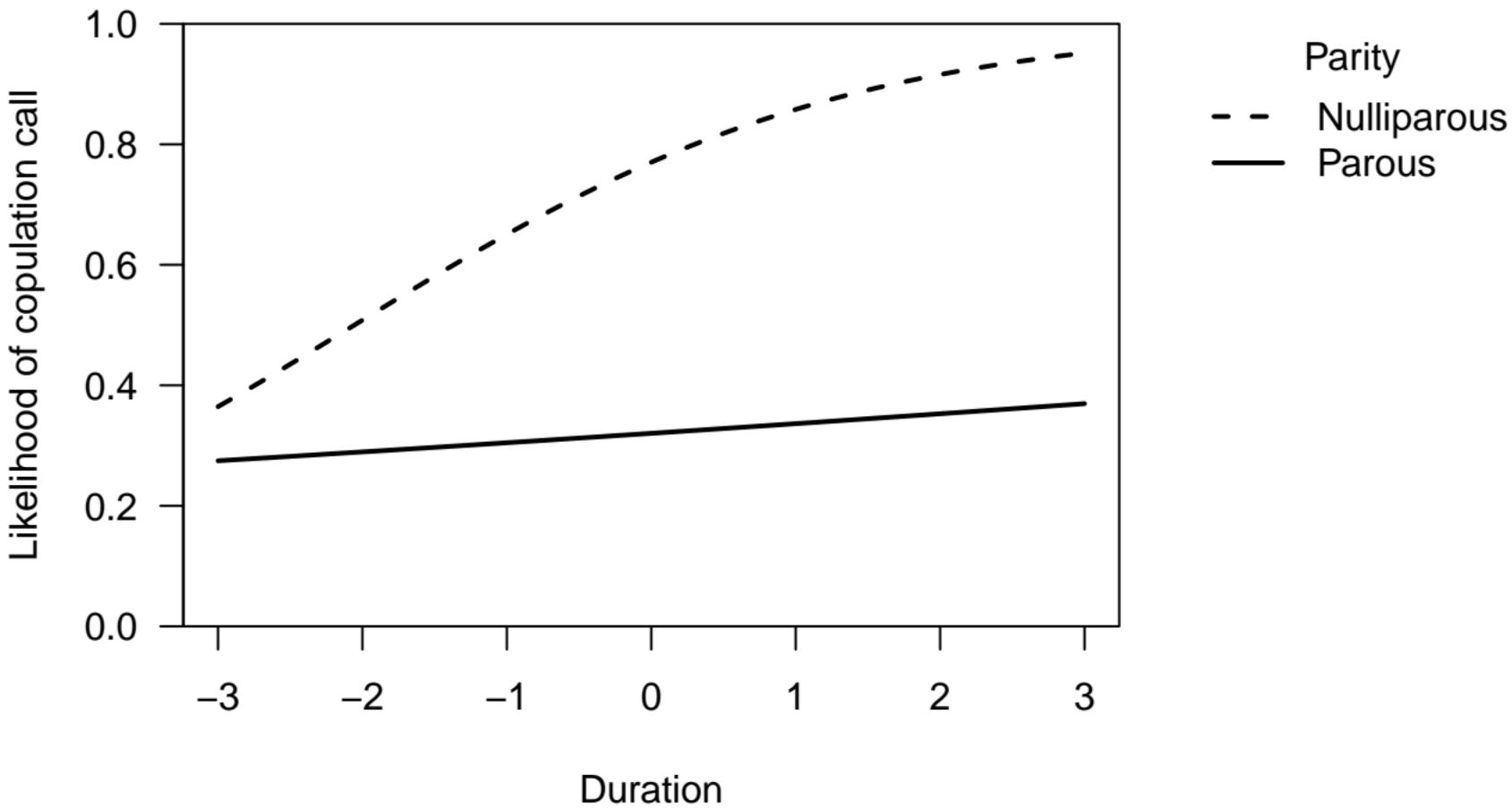
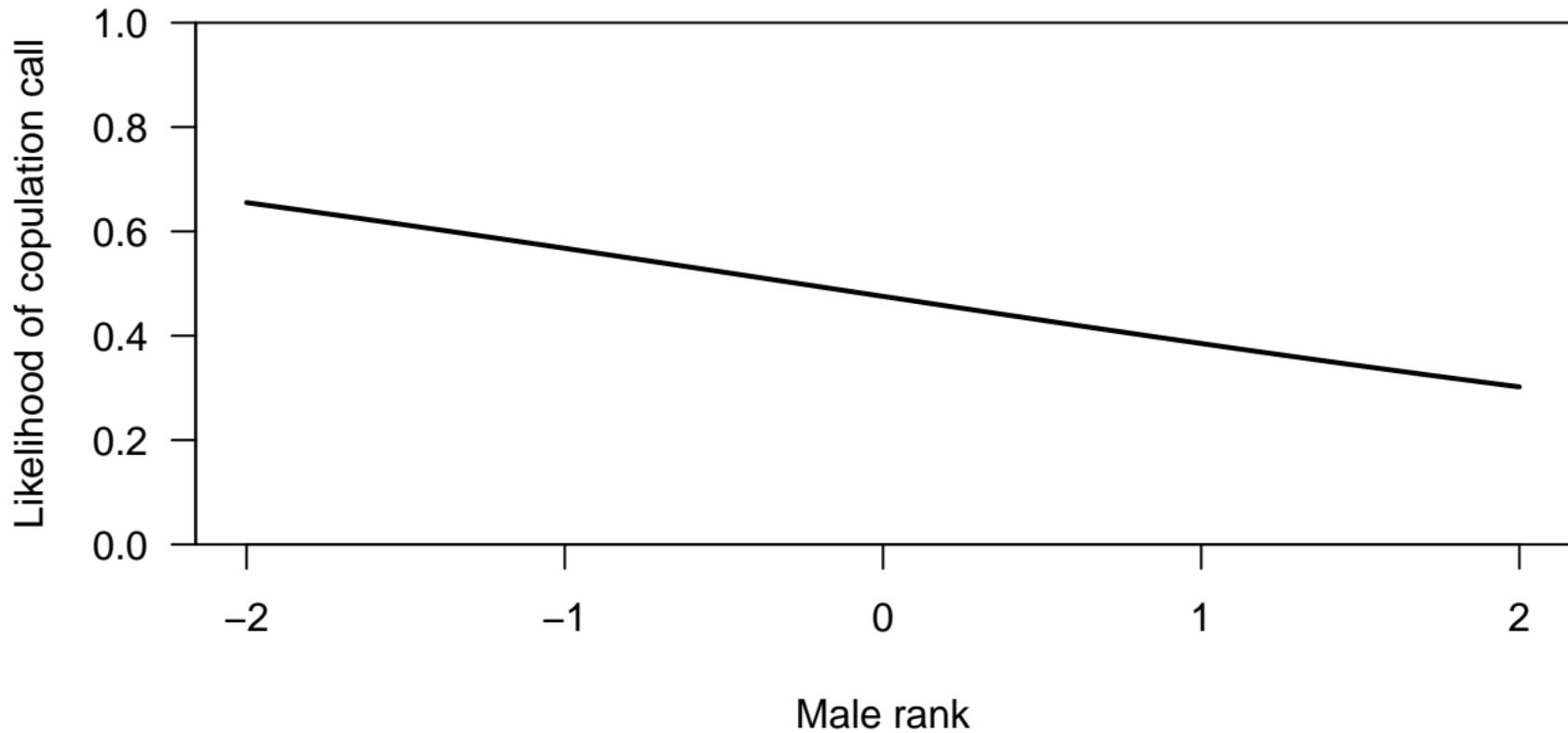
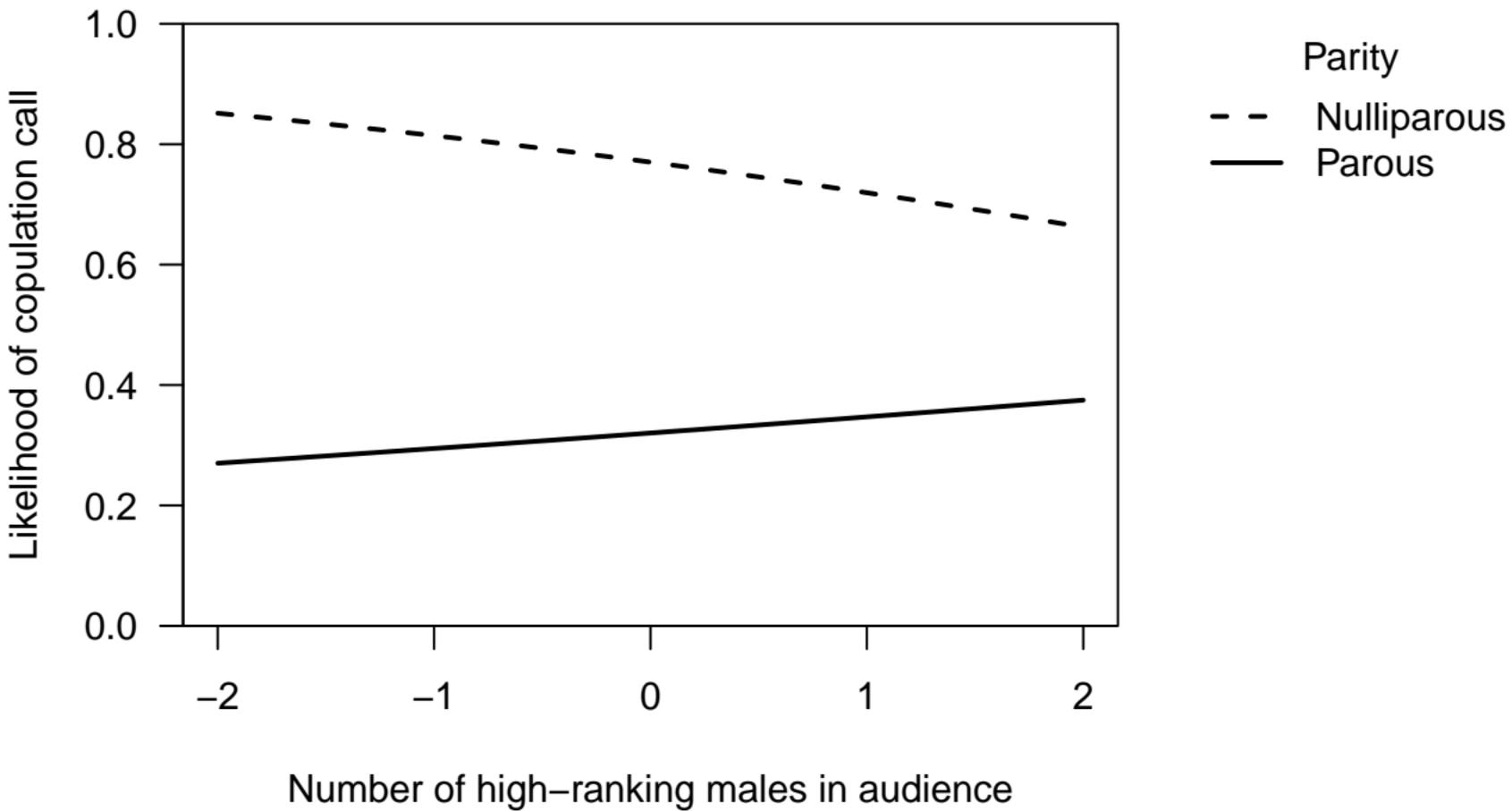


Figure 2



**Figure 3**



**Table 1:** Results of the GLMM testing factor affecting calling likelihood of female chimpanzees during copulation<sup>1</sup>.

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

<sup>1</sup>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.