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1 **Call combinations in chimpanzees: a social tool?**

2  
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21

22 **Abstract**

23 A growing body of evidence suggests the capacity for animals to combine calls into larger  
24 communicative structures is more common than previously assumed. Despite its cross-taxa  
25 prevalence, little is known regarding the evolutionary pressures driving such combinatorial  
26 abilities. One dominant hypothesis posits that social complexity and vocal complexity are  
27 linked, with changes in social structuring (e.g. group size) driving the emergence of ever-more  
28 complex vocal abilities, such as call sequencing. In this paper, we tested this hypothesis through  
29 investigating combinatoriality in the vocal system of the highly social chimpanzee.  
30 Specifically, we predicted combinatoriality to be more common in socially-driven contexts and  
31 in females and lower-ranked males (socially challenging contexts and socially challenged  
32 individuals respectively). Firstly, through applying methods from computational linguistics  
33 (i.e. collocation analyses), we built an objective repertoire of combinatorial structures in this  
34 species. Second, we investigated what potential factors influenced call combination  
35 production. We show that combinatoriality is predominant in i) social contexts vs. non-social  
36 contexts, ii) females vs. males and iii) negatively correlates with male rank. Together, these  
37 results suggest one function of combinatoriality in chimpanzees may be to help individuals  
38 navigate their dynamic social world. More generally, we argue these findings provide support  
39 for the hypothesised link between social and vocal complexity and can provide insight into the  
40 evolution of our own highly combinatorial communication system, language.

41

42 **Keywords**

43 Social complexity hypothesis; *Pan troglodytes schweinfurthii*; evolution of language;  
44 combinatoriality; non-human primates

## 45 **Introduction**

46 Over the last two decades, a growing body of data has demonstrated animals can combine pre-  
47 existing calls from their repertoire into larger meaningful combinations. This important  
48 groundwork has helped further our understanding of animal vocal complexity (Arnold and  
49 Zuberbühler 2006; Coye et al. 2015; Coye et al. 2016; Engesser et al. 2016; Suzuki et al. 2016)  
50 and has attracted attention from language researchers given the potential parallels with  
51 language's combinatorial layers (Collier et al. 2014; Bolhuis et al. 2018a; Bolhuis et al. 2018b;  
52 Townsend et al. 2018; Engesser and Townsend 2019). Despite the upsurge in interest in animal  
53 call combinations, it is striking how little is known regarding the selective forces shaping their  
54 evolutionary emergence. In short, why animals combine calls remains little investigated, yet is  
55 crucial to gain insights into the evolution of combinatoriality, including that in language.

56

57 One potential hypothesis explaining the emergence of combinatoriality lies with  
58 communicative efficiency. Modelling work has, for example, posited that combining units not  
59 only allows for more efficient communication of new messages (in comparison to relying on  
60 creating new units altogether (Jackendoff 1999; Nowak et al. 2000)), but does so with a reduced  
61 risk for perceptual errors from receivers (Nowak et al. 1999; Nowak and Krakauer 1999).  
62 Emerging data in non-human animals partially support this hypothesis as species with small,  
63 limited repertoires transmit additional information through combining existing calls together  
64 in specific contexts (e.g. birds (Engesser et al. 2016), non-primate mammals (Collier et al.  
65 2020), non-human primates (Arnold and Zuberbühler 2006)).

66

67 Another prevailing, though non-mutually exclusive, hypothesis relates combinatoriality to the  
68 demands associated with social living (Freeberg et al. 2012). Specifically, this “social  
69 complexity hypothesis” stipulates more demanding social systems require increased

70 communicative competence (e.g. birds (Freeberg 2006; Krams et al. 2012), non-primate  
71 mammals (Pollard and Blumstein 2011; Manser et al. 2014), non-human primates (McComb  
72 and Semple 2005; Bouchet et al. 2013; Rebut et al. 2020; Pournault et al. 2021)), of which  
73 combinatoriality is arguably one form (Freeberg et al. 2012; Pollard and Blumstein 2012; Pika  
74 2017). This hypothesis has primarily been investigated across species, with findings suggesting  
75 more social species also display the most complex communication system (e.g. McComb and  
76 Semple 2005; Pournault et al. 2021). However, such approaches introduce potential  
77 confounding variables such as ecology or phylogeny that have not always been accounted for  
78 (Peckre et al. 2019). From this perspective, a within species investigation is complementary  
79 and valuable (e.g. Freeberg 2006; Collier et al. 2017) since it serves to control, to an extent, for  
80 such confounds. One prediction applicable to a within species design is that socially-driven  
81 contexts (e.g. agonism), in comparison to more ecologically driven contexts (e.g. feeding,  
82 travelling), will be particularly associated with call combination production. Previous empirical  
83 work in meerkats (*Suricata suricatta*) suggests social contexts are accompanied by call  
84 combinations, but here an objective quantification of the combinatorial repertoire was missing,  
85 and comparisons with non-social contexts were lacking (Collier et al. 2017). Furthermore,  
86 individuals subjected to socially more challenging contexts (e.g. being targeted more often or  
87 more severely in aggressive interactions), such as lower-ranked males and females, would  
88 arguably benefit from the more precise communicative potential afforded by combinations (e.g.  
89 avoiding any misinterpretation of a signal that could potentially lead to aggression from the  
90 receiver; Nowak et al. 1999; Nowak and Krakauer 1999). Thus, an additional prediction  
91 resulting from the social complexity hypothesis would be that these individuals are more likely  
92 to engage in call combination production.

93

94 Here, we tested these predictions pertaining to the social complexity hypothesis in the highly  
95 social and vocal chimpanzee: a model animal system to probe this evolutionary relationship.  
96 Chimpanzee social life is complex and multifaceted, characterised by fission-fusion dynamics,  
97 multi-male, multi-female societies, with a strict dominance hierarchy and frequent formation  
98 of enduring, prolonged relationships with both kin and non-kin, in many different contexts  
99 (Goodall 1986; Mitani et al. 2002; Reynolds 2005; Boesch et al. 2019). Vocally, chimpanzees  
100 have been shown to utilise an extensive repertoire of context-specific vocalisations (Goodall  
101 1986; Slocombe and Zuberbühler 2010) and have also been reported to flexibly recombine  
102 these calls into a number of combinations (e.g. 15 call types combined into 88 different type  
103 of combinations; Crockford and Boesch 2005). However, to date, little work has attempted to  
104 provide an objective overview of the chimpanzee combinatorial repertoire and almost nothing  
105 is known regarding the potential adaptive functions of such combinations (though see Leroux  
106 et al. 2021; demonstrating the “*pant-hoot + food call*” combination potentially serves an  
107 appeasement-like function).

108

109 In a previous study, methods from language sciences (specifically “collocation analyses”) were  
110 applied to identify non-random call combinations for follow-up targeted investigation, in this  
111 case the “*pant-hoot + food call*” combination (see Leroux et al. 2021). Here, we build on these  
112 findings using a more extensive data set to generate a holistic, detailed combinatorial repertoire  
113 in chimpanzees and subsequently probe the factors influencing non-random call combination  
114 production in this species, namely the influence of context, sex and rank. Specifically, we  
115 predicted higher rates of non-random call combinations in socially-driven contexts and in  
116 females and low-ranked males respectively (i.e. socially challenging situations and socially-  
117 challenged individuals).

118

## 119 **Methods**

### 120 *Study site and subjects*

121 The study was conducted with the Sonso community at the Budongo Conservation Field  
122 Station, Uganda. This community has been studied since 1990 and is well habituated to  
123 researchers (Reynolds 2005). The group consisted of 72 individuals, including 43 adults (12  
124 males, 31 females), however, 3 adult males died during the study period and were excluded  
125 from further data analyses (see ESM Table S1).

126

### 127 *Data collection*

128 Audio-recordings were conducted over 18-months using a Marantz PMD661 mk3 audio  
129 recorder (sample rate 44.1kHz, resolution 32bits, .wav format) connected to a Sennheiser  
130 ME66/K6 microphone. We collected 331h of focal data from 34 adults (9 males, 25 females)  
131 using 2h continuous focal follows. In line with previous work in great apes, a threshold of  $\leq 2$   
132 s between two distinct call types emitted by the same caller (up to six distinct call types could  
133 be sequentially produced, see ESM Figure S1) was used to initially identify a potential call  
134 combination (Crockford and Boesch 2005; Hedwig et al. 2014; Leroux et al. 2021). We  
135 excluded combinations for which it was not possible to verify this criterion spectrographically  
136 (e.g. chorusing). Furthermore, for each vocal utterance, we noted the call type(s) produced, the  
137 signaller's ID, its sex and the context of production. We excluded utterances for which the  
138 caller could not be unambiguously identified and to ensure calls were classified correctly, a  
139 second observer blind-coded a subset of the data (i.e. 10%) resulting in a high agreement  
140 between observers; Cohen's Kappa=0.85).

141

### 142 *Context definition*

143 We identified 10 contexts which we partitioned into two categories based on whether they  
 144 could be considered predominantly socially-driven or not (see Slocombe and Zuberbühler  
 145 2010; Hobaiter et al. 2017; and Table 1 for context definitions).

146

147 **Table 1.** Definition of the contexts identified to accompany vocal production of chimpanzees. + indicates socially-driven  
 148 contexts, - indicates non-social contexts.

Context	Social	Definition
Alarm	-	An individual is surprised or facing a potential threat (e.g. earth tremors, snake, bushpig...).
Affiliation	+	An individual seeks social support or positive physical contact from another (e.g. greeting).
Agonism	+	An individual seeks to display at, displace, chase away or physically attack another.
Copulation	-	An individual engages in, or solicits, copulation.
Feeding	-	An individual arrives at, prepares and ingests food. Includes nursing and drinking.
Grooming	+	An individual participates in grooming or requests grooming from another.
Mother-infant	+	Interactions between a mother and her offspring.
Playing	+	Two or more individuals engaged in play behavior (e.g. chasing-play, wrestling...).
Resting	-	An individual remains stationary without participating in any physical activity such as grooming or play.
Travelling	-	Locomotion from one area to another on the ground. Does not include brief locomotion (approx. 30m).

149 **social:** affiliation, agonism, grooming, mother-infant interaction, playing; **non-social:** alarm, copulation, feeding, resting,  
 150 travelling.

151

## 152 *Hierarchy*

153 Dominance status was calculated for adult males using Elo-ratings based on the production of  
 154 pant-grunts, vocalisations known to be a reliable indicator of dominance relationships in  
 155 chimpanzees (Goodall 1986; Neumann et al. 2011) (see ESM Table S2). Given the infrequent  
 156 nature of pant-grunt interactions between females, it was not possible to construct an equivalent  
 157 robust Elo-rating based hierarchy for females. Other potential proxies such as aggression



158 behavior between females also could not be invoked given their equally infrequent occurrence  
159 and unreliable nature (de Waal 1982; Goodall 1986).

160

### 161 *Collocation analyses*

162 Collocation analysis is a method traditionally used in computational linguistics to identify non-  
163 random word combinations within language corpora (hereon termed *collocates*, see Gries  
164 2013), i.e. it compares the co-occurrence of two given words with each other to their co-  
165 occurrence with other words. Concretely, collocation analysis is a measure of the relative  
166 attraction between two units – i.e. words – and how exclusively they associate with each other  
167 (e.g. in English: “*going*” collocates with “*to*”), and this method has been recently applied to  
168 animal data (Leroux et al. 2021; Bosshard et al. 2021). In line with previous work, we  
169 implemented two collocation analyses: a Multiple Distinctive and a Mutual Information  
170 Collocation Analysis (MDCA and MICA respectively). MDCA allows the investigation of  
171 whether one bigram (i.e. two-unit construction) occurs at frequencies higher than what would  
172 be expected by chance. Furthermore, it provides an estimation of ordering – i.e. whether A-B  
173 and B-A equally collocate or whether one specific order is dominant. MICA complements the  
174 MDCA analysis since it calculates the variability of co-occurring units through computing  
175 information values (Bosshard et al. 2021) and hence can, to some degree, correct for under-  
176 sampling issues. Specifically, even if a bigram occurs at very low frequency, if the association  
177 between the two units is exclusive, MICA will highlight this bigram as a significant collocation.  
178 This is particularly pertinent when working with smaller data sets and accounting for rare  
179 combinations as can be the case in animal communication.

180

181 In this study, we investigated the non-random nature of call type associations within call  
182 combinations composed of up to 6 distinct calls (see Figure S1 for distribution). However,

183 since, by definition, collocation analyses investigate the degree of association between two  
184 units, to avoid excluding >2 call combinations (which represent a substantial part of the data  
185 set (42%)) we decomposed call combinations comprising more than 2 calls into bigrams (e.g.  
186 a combination A-B-C was processed as two bigrams: A-B and B-C). To capture the dynamics  
187 of two-call combinations and larger structures, we conducted MDCA on both the entire data  
188 set (MDCA<sub>1</sub>) and on a data set including only two-call combinations (MDCA<sub>2</sub>). All collocation  
189 analyses were performed using an R script developed by S. Gries (Gries 2014).

190

### 191 *Demographic and contextual factors influencing call combination production*

192 To explore the potential factors influencing combinatoriality in chimpanzees, we probed the  
193 relative influence of demographic variables (sex and rank) and context on the production of  
194 call combinations. To ensure our analyses captured the influence of these factors specifically,  
195 we included in our analyses only non-random collocates highlighted by the collocation  
196 analyses. Furthermore, to ensure any factors highlighted to influence call combination  
197 production are not simply associated with vocal output more generally (e.g. males are known  
198 to be more vocal than females (Kalan, 2019; Crunchant et al. 2021)), we contrasted the  
199 influence of sex, context and rank on the production of single calls as well. As it was only  
200 feasible to calculate a dominance hierarchy for males, we conducted two distinct analyses  
201 investigating, on the one hand, the effect of sex and context, and on the other hand, the effect  
202 of rank on call combination production.

203

204 Firstly, to investigate the effects of sex and context, we performed a Generalized Linear Mixed  
205 Model (GLMM) with a Poisson family and a logit link function using the glmer function in R  
206 (lme4 package (Bates et al. 2015)). We fitted vocal output as the response variable –  
207 specifically the number of calls for single calls and number of non-random collocates for call

208 combinations. Modelling vocal output irrespective of the type of vocal production (single  
209 calls/collocates) allowed us to control for overall vocal production while maintaining a fully-  
210 factorial design. We fitted vocal production type, caller sex and context of production  
211 (social/non-social) as explanatory variables. Since we were interested specifically in call  
212 combination production, we implemented two-way interactions between vocal production type  
213 and i) sex and ii) context. Furthermore, to control for pseudo-replication, we included ID as a  
214 random factor and to control for variation in observation time, we set focal duration as an offset  
215 term which we log transformed to match the logit link function used (Zuur et al. 2009). Since  
216 initial analyses suggested the model was zero-inflated (DHARMA zero-inflation test,  
217 RatioObsSim=1.9,  $P<0.001$ ), we implemented a zero-inflated poisson (ZIP) GLMM in R  
218 (glmmTMB package (Brooks et al. 2017)). We checked model assumptions using the  
219 DHARMA package in R (Hartig 2020). The model was not over-dispersed ( $P=0.98$ ), no outliers  
220 were detected ( $P=0.72$ ), and visual inspection of the Q-Q plots confirmed the normality of the  
221 residuals (Kolmogorov-Smirnov test:  $P=0.69$ ).

222

223 Second, to investigate rank effects on call combination production in males and given our  
224 limited sample size ( $N=9$ ), we implemented non-parametric Spearman-rank correlation tests.  
225 Here, to control for observation time, we calculated a rate of calling by averaging the number  
226 of significant (above chance) collocates produced by each male over their respective focal  
227 duration and subsequently ran the test between rank and rate of production. Once more, to  
228 ensure any effect highlighted is not merely representative of the overall vocal production, we  
229 ran the same analysis on the rate of production of single calls.

230

231 Lastly, given that multiple collocates were extracted from >2 call combinations, we ran a  
232 reduced analysis controlling for non-independence of these collocates. Results with the reduced  
233 data set were identical to the original analyses (see ESM).

234

## 235 **Results**

236 We collected a total of 154 call combinations and 939 single calls produced by 22/34 and 34/34  
237 individuals respectively (10 females and 2 males never produced call combinations). More than  
238 half of combinations produced were composed of 2 calls (57%) with the remaining made up of  
239 3 calls (29%), 4 calls (10%), 5 calls (1%) and 6 calls (3%) (see ESM Figure S1). Overall, we  
240 detected 248 individual bigrams (see ESM Table S4).

241

### 242 *Collocation analyses*

243 An MDCA<sub>1</sub> implemented with all 248 bigrams highlighted 15 non-random constructions  
244 occurred more than expected by chance (Table 2) while MDCA<sub>2</sub> (only including two-call  
245 combinations,  $N=88$ ) demonstrated a significant relative attraction within 9 structures, all of  
246 which were also represented in MDCA<sub>1</sub> (Table 2).

247

248

249 **Table 2.** MDCA<sub>1</sub> on the 248 bigrams recorded. Columns and rows show the first and second call within a bigram respectively.  
 250 Values are pbins and can be translated to p-values (pbin  $>3 \Rightarrow P < 0.001$ ,  $>2 \Rightarrow P < 0.01$ ,  $>1.3 \Rightarrow P < 0.05$ ). Significant  
 251 results are colored in green. <sup>ε</sup> indicates non-random collocates highlighted by MDCA<sub>2</sub> (only on 2-call combinations) as well.  
 252 AH: Alarm hoo, B: Bark, C: Cough, H: Hoo, FC: Food call (termed rough grunts in Slocombe & Zuberbülher, 2010), P: Pant,  
 253 PB: Pant-bark, PG: Pant-grunt, PH: Pant-hoot, S: Scream, W: Whimper, WB: Waa-bark.  
 254

		First call										
		AH	B	C	FC	P	PB	PG	PH	S	W	WB
Second call	AH	0.0	0.0	0.0	0.0	0.0	-0.2	-0.4	-0.2	-0.1	0.0	2.4
	B	0.0	-0.2	3.1 <sup>ε</sup>	-0.2	0.0	-0.9	0.4	-1.2	0.9	-0.1	0.3
	FC	-0.1	-0.6	-0.2	-0.6	-0.1	-2.7	-6.5	24.0 <sup>ε</sup>	-1.7	-0.2	-0.9
	H	0.0	1.4 <sup>ε</sup>	0.0	0.0	0.0	-0.1	-0.2	-0.1	0.0	0.0	0.0
	P	0.0	-0.1	-0.1	-0.2	0.0	-0.7	4.1 <sup>ε</sup>	-0.9	-0.4	-0.1	-0.2
	PB	-0.1	-0.7	-0.3	-0.8	-0.2	-3.3	12.4 <sup>ε</sup>	-1.8	-0.8	-0.3	-1.2
	PG	-0.1	1.0	-0.2	-0.2	-0.1	3.2	-5.7	0.8	-0.4	-0.2	0.5
	PH	-0.1	-0.6	-0.2	5.1	1.5	-0.8	1.5 <sup>ε</sup>	-3.5	-1.0	-0.2	-0.2
	S	-0.1	1.0	-0.4	-0.9	-0.2	4.9	-0.9	-3.9	-2.4	2.1 <sup>ε</sup>	1.5
	W	0.0	0.0	0.0	-0.1	0.0	-0.2	-0.6	-0.3	2.9 <sup>ε</sup>	0.0	-0.1
	WB	1.0	0.2	0.4	-0.5	-0.1	-0.5	-2.3	-0.8	8.0 <sup>ε</sup>	-0.2	-0.7

255  
 256  
 257 To control for the relative infrequent occurrence of certain non-random constructions, we ran  
 258 a MICA. Irrespective of order, MICA highlighted 5 collocates for which the attraction between  
 259 the two calls exceeded chance level (ESM Table S5). Again, all five were previously  
 260 highlighted by the MDCA<sub>1</sub> (Table 2) and were rare and comparatively exclusive collocates (see  
 261 ESM Table S4).

262

### 263 *Demographic and contextual factors influencing call combination production:*

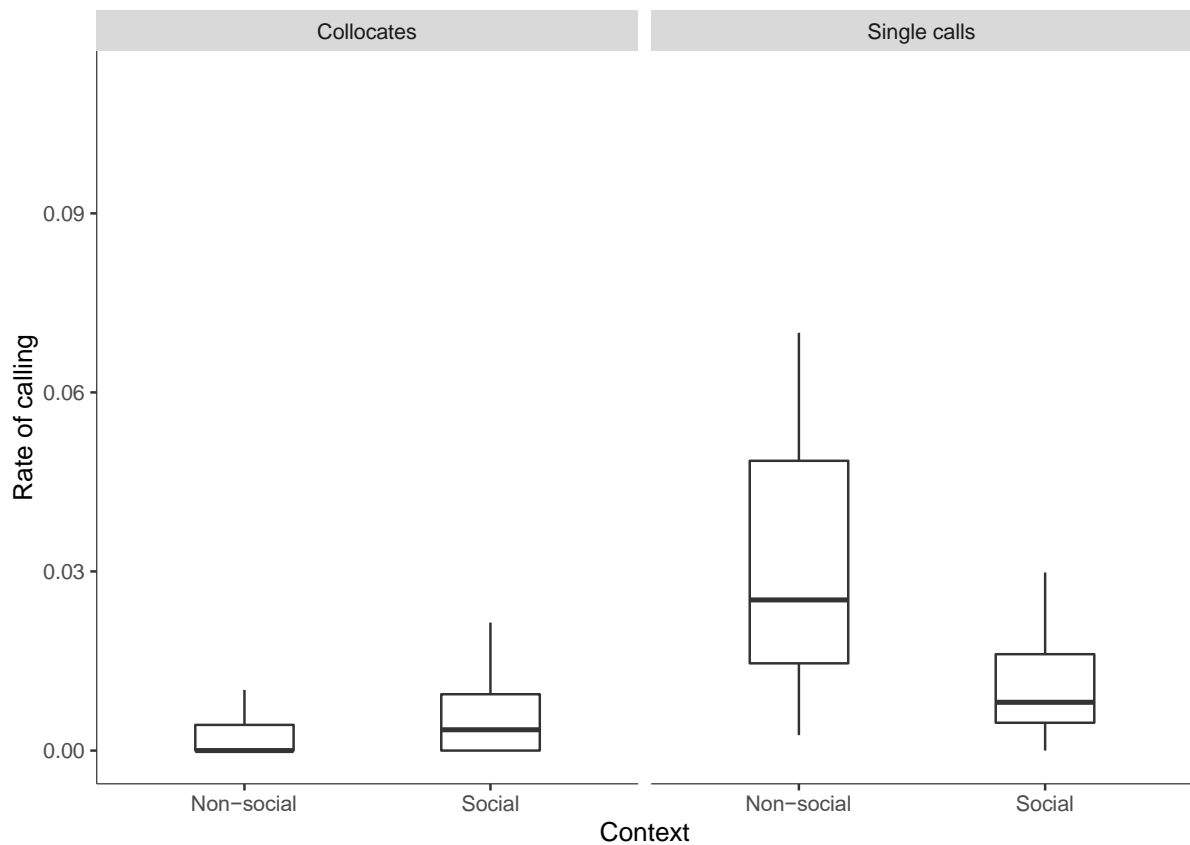
264 Of the 180 collocates highlighted as non-random by collocation analyses, 125 (69%) were  
 265 produced in social contexts whilst 55 (31%) were produced in non-social contexts. For single

266 calls, the reversed pattern was detected with 236 (25%) vs. 703 (75%) calls produced in a social  
267 vs. non-social contexts respectively.

268

269 A GLMM suggested that the interaction between the type of vocal utterance and context was  
270 significant ( $\chi^2=65.9$ ,  $df=1$ ,  $P<0.001$ , Table 3). Specifically, collocates were produced more in  
271 social contexts relative to non-social ones, in contrast to single calls for which the opposite  
272 pattern was observed (Figure 1).

273



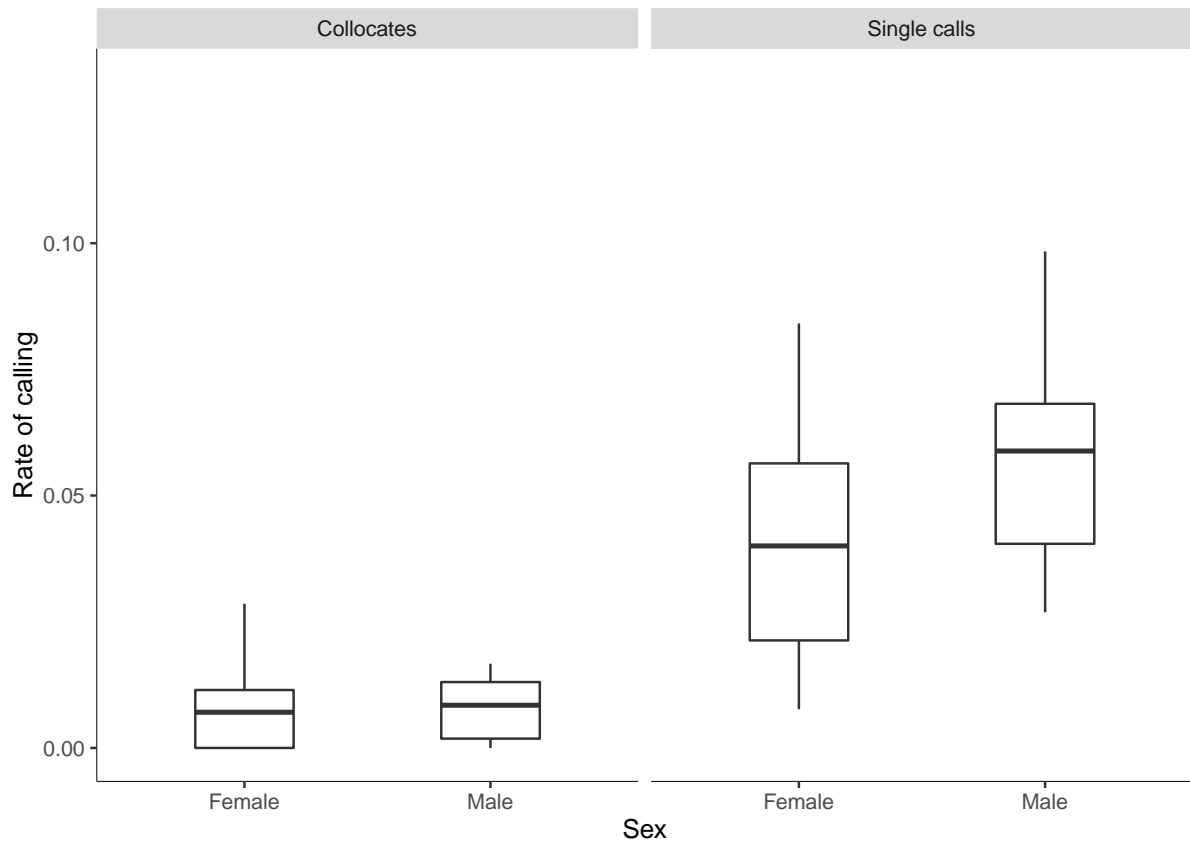
274 **Figure 1.** Production of significant collocates and single calls (per minute of observation) according to the context of  
275 production. Red dots show the raw data. Note: rate is used purely for visualisation purposes since model response variables  
276 were call number offset by focal time.

277

278 Similarly, an interaction between the type of vocal utterance and sex ( $\chi^2=14.4$ ,  $df=1$ ,  $P<0.001$ ,  
279 Table 3) existed indicating that while both sexes had generally equal vocal outputs, they

280 differed in the number of single vs. combinatorial structures they produced. Specifically, while  
281 males produced more single calls, this difference no longer persisted when considering the  
282 production of significant collocates (Figure 2).

283



284 **Figure 2.** Production of significant collocates and single calls (per minute of observation) according to the sex of the caller.  
285 Red dots show the raw data. Note: rate is used purely for visualisation purposes since model response variables were call  
286 number offset by focal time.

287

288 **Table 3.** GLMM testing the influence of the type of vocal production (single calls/collocates, 1/0), the sex of the caller  
 289 (male/female, 1/0) and the context of production (social/non-social, 1/0) on the number of vocal utterances produced.

	Estimate	Std. Error	Z value	<i>P</i>
(Intercept)	-5.642			
Type (single/collocates)	1.881	0.177	10.626	<0.001
Context	0.645	0.182	3.536	<0.001
Sex	-0.108	0.283	-0.382	0.703
Type:Sex	0.743	0.196	3.795	<0.001
Type:Context	-1.608	0.198	-8.119	<0.001

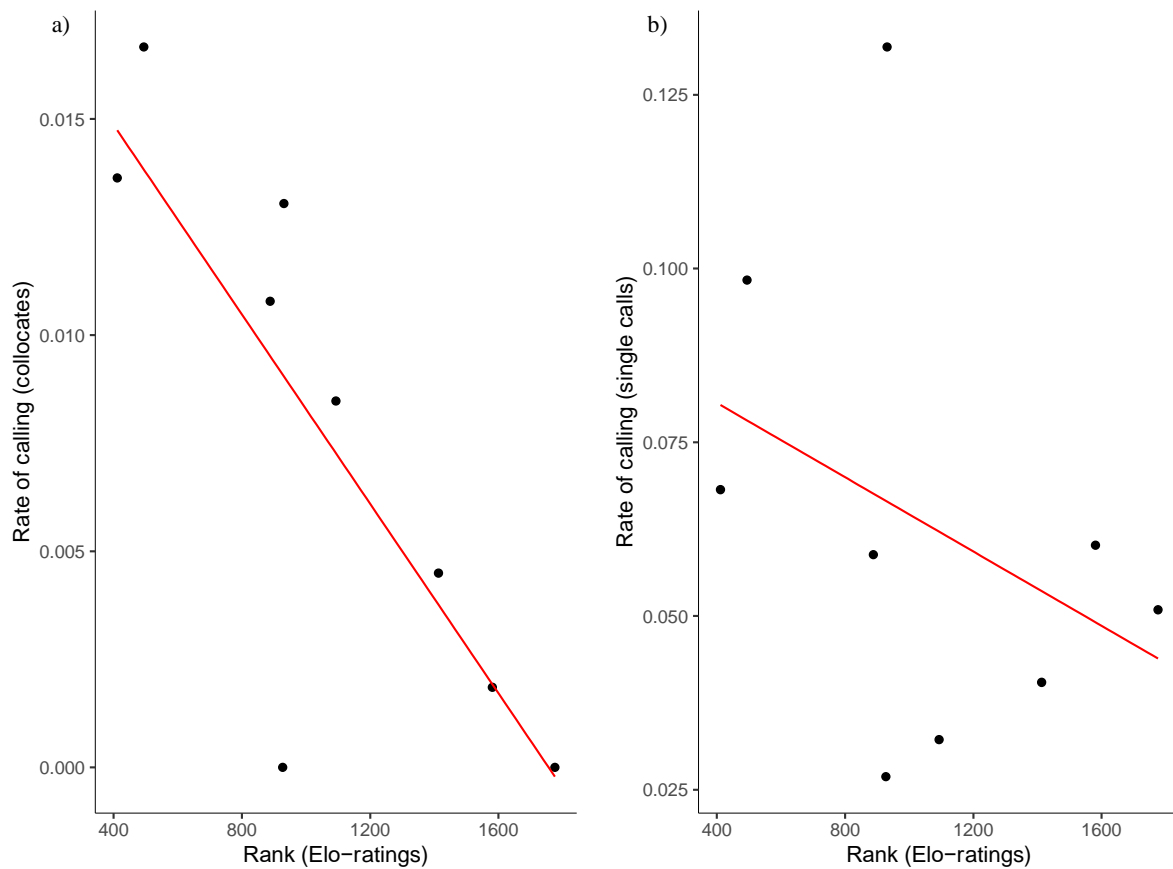
290  
291

292 To assess the significance of the model, we compared it to a reduced “null” model including  
 293 only the intercept and random factors using the anova function in R (Faraway 2015). Results  
 294 confirmed the full model fitted the data significantly better than the null model ( $AIC_{full}=780$ ;  
 295  $AIC_{null}=1696$ ;  $\chi^2=927.9$ ;  $P<0.001$ ).

296

297 Regarding the effect of rank on the production of significant collocates, a Spearman correlation  
 298 test revealed that the lower the rank, the more likely individuals were to produce collocates  
 299 ( $\rho=-0.74$ ,  $S=209.37$ ,  $P=0.02$ , Figure 3a), an effect that was not observed for single calls ( $\rho=-$   
 300  $0.35$ ,  $S=162$ ,  $P=0.35$ , Figure 3b).





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306

### 307 Discussion

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**Figure 3.** Production of significant collocates (a) and single calls (b) (per minute of observation) according to the rank of the individual. Black dots show the raw data. Red lines show the linear trend. Ranks based on Elo-ratings: the higher the value, the higher the rank.

Through utilising computational approaches implemented in language sciences, we built an objective call combination repertoire for chimpanzees. Specifically, we detected 15 non-random constructions that occurred above chance level, hence representing potential candidates for communicatively relevant call combinations. Interestingly, 6 out of these 15 collocates were detectable only when considering more than two-call combinations. This suggests these 6 specific constructions (FC-PH, P-PH, PB-PG, PB-S, WB-AH and WB-S, see Table 2) are likely involved in the construction of larger (>2 call) combinations (e.g. PG-PB-

315 S). Indeed, nearly half of the call combinations recorded during the study were comprised of  
316 more than two calls, a striking observation since existing data in non-human primates suggest  
317 call combinations in this clade are overwhelmingly restricted to two calls only (Miyagawa and  
318 Clarke 2019).

319

320 Furthermore, demographic and contextual data suggest the production of non-random  
321 collocates was driven by the accompanying context as well as the caller's sex and rank. Firstly,  
322 we found that whilst males produced more single calls than females, the production of non-  
323 random collocates did not differ between the sexes. This suggests, in females, the proportion  
324 of combinations in their total vocal production exceeds that in males. Secondly, we found that  
325 non-random collocates were produced more often in social contexts (e.g. agonism) in contrast  
326 to single calls which occurred more often in non-social contexts (e.g. travelling). Finally, in  
327 males, the rate of production of non-random collocates was negatively correlated with the  
328 individual's rank, an effect that did not hold for single calls. This suggests lower-ranking males  
329 produce more combinations compared with high-ranked males, independent of their overall  
330 vocal production.

331

332 Together, these results highlight a bias towards greater combinatoriality in i) socially  
333 challenging situations and ii) socially-challenged individuals – i.e. in more socially-driven  
334 contexts as well as in females and low-ranked males. This tentatively suggests that the social  
335 environment has played a key driving role in promoting combinatoriality in our closest-living  
336 relatives. Specifically, combining vocalisations together may facilitate the communication of  
337 not only a more precise message than single calls (Jackendoff 1999; Nowak et al. 2000) but  
338 one that is also more salient and less open to perceptual errors (Nowak et al. 1999; Nowak and  
339 Krakauer 1999). This in turn may help chimpanzees better navigate their intricate social world

340 and, for instance, reduce the risk of misinterpretation of signals that could potentially have  
341 severe consequences (e.g. aggression) (Goodall 1986). Related work in social carnivores has  
342 also highlighted the potential for social contexts to drive the production of call combinations  
343 (Collier et al. 2017). Through controlling for vocal behavior more generally (i.e. single calls  
344 and combinations), our data build on these findings, demonstrating in non-human primates,  
345 this is specific to combinations and not simply driven by increased vocal output in socially  
346 more demanding situations.

347

348 It is important to note that in chimpanzees, low-ranked individuals are not the only socially-  
349 challenged individuals. Indeed, high-ranked individuals have been shown to possess the  
350 highest cortisol levels (Muller et al. 2021) (though see Preis et al. 2019). However, it is well  
351 established that high-ranked males are responsible for initiating the majority of agonistic  
352 interactions they are involved in compared with lower-ranked males and (even more so)  
353 females (Muller 2002). This more overt physical negotiation (which simultaneously renders  
354 elaborate communication unnecessary) may therefore represent a behavioral strategy that is  
355 unavailable to lower-ranked individuals (males and females) who rely instead on more strategic  
356 communicative approaches. A similar reliance on vocal communication to navigate socially  
357 challenging situations has been reported at both the level of call production and more fine-  
358 grained acoustic structuring of vocalisations in primates (Kavanagh et al. 2021). For instance,  
359 females baboons (*Papio ursinus*) produce affiliative grunt vocalisations strategically to reduce  
360 the uncertainty of an impending interaction (Silk et al. 2016). Furthermore, low-ranked  
361 chimpanzees subjected to severe aggression also systematically exaggerate the acoustic  
362 properties of their screams when higher-ranked bystanders are present in the audience,  
363 potentially manipulating the audience to gain support (Slocombe and Zuberbühler 2007). Here,

364 we show such strategic vocal flexibility may also apply at the combinatorial layer of  
365 communication.

366

367 Furthermore, while non-random combinations may be more likely to represent  
368 communicatively relevant structures, detailed contextual data and behavioral responses to  
369 naturally occurring and experimentally presented combinations are key to clarifying function  
370 and meaning attribution (Engesser et al. 2016; Suzuki et al. 2016; Suzuki et al. 2017). Such  
371 evidence would not only support our findings but also further our understanding regarding the  
372 causal relationship underpinning social and vocal complexity, which remains, to date, unclear  
373 (McComb and Semple 2005). However, playback experiments are notoriously complicated to  
374 implement with wild apes and come with a whole host of logistical and ethical challenges (see  
375 Leroux and Townsend 2020). We argue the data presented here therefore represent a key first  
376 step towards a better understanding of the combinatorial nature of chimpanzee vocal  
377 communication and we hope it will help inform and guide future related research in the field.

378

379 Such comparative data linking vocal combinatoriality (or indeed other multi-modal  
380 combinations, see Fröhlich et al. 2019) and social complexity are central to disentangle the  
381 evolutionary roots of our own communication system. Human language is also highly  
382 combinatorial (Hurford 2008) and our social system is arguably the most complex in the animal  
383 kingdom, characterised by prosociality, hyper-cooperation and stable non-kin relationships  
384 (Kappeler and Silk 2010; Silk and House 2011; Burkart et al. 2014), yet little is still known  
385 regarding how and when language evolved. Insights into the combinatorial system of our  
386 closest living relatives, the great apes, and indeed other animals can help piece together i) the  
387 sorts of evolutionary forces that may have been at play during the emergence of our own  
388 communication system, ii) how this might have been influenced by existing cognitive biases

389 (Hayashi 2015) and iii) precisely when in our evolutionary history these abilities may have  
390 come online.

391

392 In conclusion, we provide promising evidence that call combination production in chimpanzees  
393 occurs disproportionately in socially-driven contexts as well as in females and low-ranked  
394 males, indicating combinatoriality in this species is driven by the social needs of an individual,  
395 providing support for the social complexity hypothesis for vocal combinatoriality.

396

397

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409

### 410 **Data availability**

411 Analyses reported in this article can be reproduced using the data provided by Leroux et al.  
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