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## Flexible use of contact calls in a species with high fission-fusion dynamics

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### ABSTRACT

The 'social complexity hypothesis' posits that complex social systems (that entail high uncertainty) require complex communicative systems (with high vocal flexibility). In species with fission-fusion dynamics, where the fluid composition of temporary subgroups increases the uncertainty with which group members must manage their social relationships, vocal communication must be particularly flexible. This study assessed whether contact call rates vary with caller and audience characteristics in free-living spider monkeys, as well as with fission and fusion events. Adult females and immature

1  
2 35 individuals called more when in small audience settings, while audience size did not influence adult  
3  
4 36 males. Adults called more when in the presence of the opposite sex, whereas immatures vocalized  
5  
6 37 more in subgroups composed only by females. Females also called more when with their mature  
7  
8 38 sons. We found higher call rates in periods during which fission and fusion events took place than in  
9  
10 39 periods with more stable compositions and when the composition after a fission or fusion event  
11  
12 40 changed from one sex to two sexes. A flexible use of contact calls allows individuals to identify  
13  
14 41 themselves when they join others, particularly if they are members of the opposite sex. This socio-  
15  
16 42 spatial cohesion function reduces the uncertainty about subgroup composition.  
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20 43

21  
22 44 **Key words:** Vocal flexibility, contact calls, social uncertainty, audience effect, New World monkeys  
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## 26 27 46 28 47 **INTRODUCTION** 29 30 48

31  
32  
33 49 According to the “social complexity hypothesis for communicative complexity”, patterns of  
34  
35 50 communication and patterns of social organization are functionally related [1,2]. Animals living in  
36  
37 51 complex social groups should thus use complex communication systems. Several studies have shown  
38  
39 52 support for this hypothesis in the case of vocal signals from a broad range of taxa, including  
40  
41 53 primates, with an impact of social complexity on vocal repertoire composition [3–5], acoustic  
42  
43 54 diversity and plasticity [6–8], vocal exchange rules [9] and context-dependent call rate flexibility  
44  
45 55 [10,11]. However, given that the motor control that non-human primates have over their vocal tracts  
46  
47 56 is limited [12] and that their vocal repertoires are composed by a limited number of call types  
48  
49 57 [13,14], an effective way to deal with this problem, in the context of a complex social environment,  
50  
51 58 is to use the same type of vocalization in a flexible way to transmit different messages or to fulfill  
52  
53 59 different social functions. Evidence of vocal flexibility under social influences (see also “pragmatic  
54  
55 60 flexibility” in [15]) has been provided in several nonhuman primate species [16,17].  
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1  
2 62 While there is no consensus about the definition of social complexity [18], it is widely  
3  
4 63 accepted that uncertainty is a prominent characteristic of complex systems [11]. Fission-fusion  
5  
6 64 dynamics, a property of animal groups that split in temporary aggregations (subgroups from here on;  
7  
8 65 [19], can lead to a high variability in subgroup composition. This variability implies a highly variable  
9  
10 66 social context in which any group member may find itself. In an effort to quantify this variability in  
11  
12 67 subgroup composition, Ramos-Fernandez et al. [20] used information theoretic measures of the  
13  
14 68 amount of uncertainty found in the composition of subgroups formed by different species. This  
15  
16 69 uncertainty is higher in species with high degrees of fission-fusion dynamics, like spider monkeys  
17  
18 70 (*Ateles geoffroyi*) and chimpanzees (*Pan troglodytes*), than in multi-level species that form variable  
19  
20 71 subgroups but with a more predictable composition, like geladas (*Theropitecus gelada*). In spider  
21  
22 72 monkeys and chimpanzees, individuals experience a high level of uncertainty about the particular set  
23  
24 73 of associates they have at any given time. Thus, it is expected that these species will have developed  
25  
26 74 behavioral mechanisms to reduce this uncertainty [20,21].  
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34 76 The vocal repertoire of nonhuman primates is typically composed of several acoustically and  
35  
36 77 functionally distinctive types of calls. Some of these call types have a clearly identifiable function,  
37  
38 78 such as alarm calls (associated with the presence of danger) [22], threat or distress calls (associated  
39  
40 79 with social conflicts) [23], or food calls (associated with foraging and feeding) [24,25]. Other call  
41  
42 80 types, are emitted at any time of day in a wide variety of contexts [26]. Within this category is the  
43  
44 81 so-called “contact call”, the signal type with the highest individual acoustic variability within the  
45  
46 82 repertoire [27]. In most nonhuman primates, these call types may function for regulating spatial  
47  
48 83 cohesion facilitating the location of group members by auditory signals, an essential requirement for  
49  
50 84 species living in visually dense habitats [26,28] and that experience high uncertainty in the  
51  
52 85 composition of their subgroups, as mentioned above. But these calls may also function, in a non-  
53  
54 86 mutually exclusive way, in regulating social cohesion by facilitating and maintaining social bonds  
55  
56 87 [29]. In fluid societies, identifying callers at a distance could play an important role in maintaining  
57  
58 88 social relationships by reducing the uncertainty about the presence/absence of important partners.  
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1  
2 89           There is evidence that shows that spider monkeys use contact calls for both spatial and social  
3  
4 90 cohesion. It is known that one of these calls, the whinny call, contains information about caller  
5  
6 91 identity and they have been shown to allow individuals to obtain information about subgroup  
7  
8 92 members' locations[30,31]. They can serve a spacing function by which callers regulate their  
9  
10 93 positions relative to each other through an evaluation of potential consequences based on their  
11  
12 94 relationships [32]. Whinnies could thus help to mediate interindividual spacing during contexts  
13  
14 95 where too much proximity increases feeding competition, and this seems particularly true for  
15  
16 96 females who experience a lot of competition and call more than males during foraging [32]. In line  
17  
18 97 with that, there is evidence that contact call rates, more so again for females, are positively correlated  
19  
20 98 with the number of individuals joining or leaving their subgroup [32]. In addition, playback  
21  
22 99 experiments showed that whinnies can promote the approach of close associates of a caller compared  
23  
24 100 to other, less closely related, individuals [30,31]. Whinnies are loud enough to be audible by any  
25  
26 101 member of a given subgroup and beyond [30]. Ordóñez-Gómez et al. [33] showed that individuals  
27  
28 102 even lower the fundamental frequency of whinnies to facilitate communication and to maintain  
29  
30 103 contact with distant individuals (those traveling outside their subgroup). Social cohesion is also  
31  
32 104 supported by Briseño-Jaramillo et al. [34] showing that call-matching between two individuals is  
33  
34 105 higher between preferred grooming partners, in line with the Dunbar's "grooming-at-distance"  
35  
36 106 hypothesis [35].  
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43 107           The evidence points at the whinny's main function being related to regulating subgroup  
44  
45 108 composition, by promoting the cohesion between callers and their closely associated recipients, and  
46  
47 109 at the same time the repulsion of other recipients of the same call who are not closely associated with  
48  
49 110 the caller. It is not yet clear, however, how individuals use their calls in contexts that vary in the  
50  
51 111 uncertainty levels (e.g. during fusion, fission or stable periods). During these changing periods, could  
52  
53 112 the whinnies function in maintaining sex-segregation and regulating sex-encounters? During stable  
54  
55 113 periods, could whinnies function in the coordination of interindividual distances to different audience  
56  
57 114 compositions? If so, will it be reflected in call rates at the individual and subgroup level? And  
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1  
2 115 finally, it is not known whether the presence of a specific individual in the audience modifies  
3  
4 116 individual vocal behavior.  
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9 118 In this study, we take advantage of the large variability in subgroup composition shown by  
10  
11 119 the species to evaluate how vocal behavior at the individual and subgroup levels varies between  
12  
13 120 different social contexts. We evaluate whether different age-sex classes flexibly use contact calls in  
14  
15 121 diverse social contexts and whether fission and fusion events, when subgroup composition changes,  
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17  
18 122 are also associated with differences in calling behavior. Spider monkeys occupy large areas of dense  
19  
20 123 forest habitats with patches of fruit trees that change seasonally [36]. They live in groups with a high  
21  
22 124 degree of fission–fusion dynamics, where the size and spatial cohesion of subgroups is dynamically  
23  
24  
25 125 adjusted depending on the availability and distribution of food [37,38]. Sex is clearly a structuring  
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27 126 factor of these subgroups, as its more common to observe single- than mixed-sex subgroups [39].  
28  
29 127 Adult males are philopatric and more socially active than adult females [40], developing strong,  
30  
31  
32 128 long-lasting relationships with one another and cooperating to compete with neighboring groups’  
33  
34 129 males [41]. Conversely, adult females disperse from their natal group and do not establish strong  
35  
36 130 bonds with kin group members [42]. Thus, males are keen to maintain social bonds, while females  
37  
38  
39 131 are less gregarious [43]. Hence, the value of adult female relationships is assumed to be low [44], as  
40  
41 132 they spend less time with other group members than adult males and form smaller subgroups or  
42  
43 133 forage alone with dependent offspring [45,46], interacting affiliatively less than males do amongst  
44  
45 134 them [39]. Mixed-sex relationships involve high rates of aggression from males to females, including  
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47  
48 135 coalitionary behaviors between males when they are in mixed-sex subgroups [39]. However, male-  
49  
50 136 female relationships can vary in different circumstances (e.g. the reproductive status of females) [43]  
51  
52 137 or kinship (e.g. long-term associations between mothers and mature males offspring) [47].  
53

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55 138  
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57 139 Specifically, we studied how individuals of different age/sex classes flexibly modify their  
58  
59 140 vocal behavior according to the social context by testing how contact call rates vary according to  
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141 three factors: subgroup size and composition, and presence of specific individuals in the subgroup.

1  
2 142 We also studied how fission and fusion events affect the calling rate at the level of the subgroup, by  
3  
4 143 comparing their calling rate during periods when subgroups come together and they split in two,  
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6 144 compared to other periods when no fission or fusion event occurs.  
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8  
9 145 We hypothesized that 1) if contact calls are used to regulate inter-individual distances (notably via  
10  
11 146 the attraction and repulsion of conspecifics, depending on their social relationships), then subgroup  
12  
13 147 size should differentially affect male and female calling behavior. Because competition (notably for  
14  
15 148 food) affects females more than males [48] and because they are less invested than males in the  
16  
17  
18 149 regulation of social relationships in general [44], we predicted that large subgroups would inhibit  
19  
20 150 female calling but stimulate male calling. Due to strong maternal influence, we expected that  
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22 151 immature individuals would present the same pattern as mature females. Second, whinnies could  
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24  
25 152 help in the regulation of subgroup composition and notably the presence of the same or opposite sex,  
26  
27 153 as callers are approached by close associates and potentially avoided by others [32]. We  
28  
29 154 hypothesized that, 2) if whinnies function in coordinating sex-segregation and regulating sex-  
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31  
32 155 encounters, contact call rates would depend on the sexual composition of the audience. We expected  
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34 156 call rates in adult females and males to be affected by the presence of the opposite sex in the  
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36 157 audience, especially in the case of males, who have been shown to engage in higher coalition rates  
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38  
39 158 with other males when in the presence of females. Due to the lack of sexual maturity, we also did not  
40  
41 159 expect immatures to be affected by the presence of the opposite sex in the same way than mature sex  
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43 160 subgroups, compared to other times when fusions led to the same sex-based composition or when  
44  
45 161 there were no fusion events.  
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## 50 163 **METHODS**

### 53 164 **Study site and subjects**

56 165 Field work was conducted during 98 days in total from September 2016 to April 2017. The  
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58 166 study site is located within the *Otoch Ma'ax Yetel Kooh* reserve, close to the Punta Laguna village in  
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60 167 the Yucatan Peninsula, Mexico (20 ° 38' N, 87 ° 38' W). Further details about the study site can be

1  
2 168 found in Ramos-Fernandez et al. [20]. One observer (MBJ) collected all the data on a single and  
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4 169 habituated group of free-ranging black-handed spider monkeys (*Ateles geoffroyi*), composed of 40  
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6 170 individuals (see Table S1 in Supplementary material). Individuals were identified based on facial and  
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8  
9 171 genitalia markings and on pelage coloration. In this study we considered individuals as adults if they  
10  
11 172 were at least five years old [49,50].  
12

### 13 **Behavioural observations**

14  
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16  
17 174 Spider monkeys live in groups that constantly vary in size, cohesion and composition [37]. We  
18  
19 175 considered all individuals within 30 m from one another at a given time as members of the same  
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21  
22 176 subgroup [30]. Observations were conducted on all individuals, older than one year old, which  
23  
24 177 included 20 matures (6 males, 14 females) and 16 immatures (7 males, 9 females). Immatures were on  
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26 178 average  $3.0 \pm 1.3$  years old throughout the study period. Individuals less than one year old were not  
27  
28 179 included in the analysis since they were never recorded emitting the contact call types included in this  
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30  
31 180 study. Different subgroups were followed during consecutive days for periods of 4 to 8 hrs. per day  
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33 181 (i.e., 32 hours per week) for a total of 548 hours. Because the size and the composition of these  
34  
35 182 subgroups can be widely variable (subgroup size  $8.1 \pm 5.0$  individuals), the observed subgroup was  
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37  
38 183 semi-randomly selected, trying to equalize the total number of observation hours per individual  
39  
40 184 ( $83.7 \pm 15$  hours per individual, see supplementary material). To do so, the observer followed different  
41  
42 185 subgroups on consecutive days and switched subgroups whose composition did not change after three  
43  
44  
45 186 hours in a given day. Therefore, the time spent with a given subgroup varied ( $3\text{hrs } 16\text{min} \pm 1\text{hr } 38\text{min}$ ).  
46

47 187 All contact call emissions were recorded using the *all occurrence sampling* method, collecting  
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49  
50 188 all utterances given by any individual in the subgroup during a given time period [51]. Spider monkeys'  
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52 189 whinnies (including the two subtypes: low- and high-pitched whinnies [52] are easily recognizable by  
53  
54 190 ear as they show a stereotyped acoustic structure composed of a series of repeated frequency modulated  
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56  
57 191 elements [34,53]. The identities and time of all individuals joining (fusion) and leaving (fission) the  
58  
59 192 sampled subgroup were monitored continuously, allowing for the calculation of the time that each  
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193 individual spent in the same subgroup with each other. To ensure the reliability of the identification of



1  
 2 194 all sampled individuals, the observer (MBJ, systematically positioned in the center of the area occupied  
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 4 195 by the subgroup) was assisted by one to three experienced research assistants who were distributed all  
 5  
 6 196 around in order to have visual access to all subgroup members and helped with the tracking and the  
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 8  
 9 197 identification of the individuals and their whinnies. We thus recorded a total of 3340 of whinnies from  
 10  
 11 198 mature individuals and 743 whinnies from immature individuals, failing to identify callers in our  
 12  
 13 199 observed subgroup on 157 occasions.  
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 15

## 16 200 **Data processing**

17  
 18  
 19 201 To evaluate if the changes in audience size and composition affected individual call rates, all  
 20  
 21 202 observations were distributed into different time periods during which the composition of the studied  
 22  
 23  
 24 203 subgroup remained stable. For example, if during an observation lasting 3 hours in total, a subgroup  
 25  
 26 204 member left after 1 hour, two stable periods of time (one lasting 1 hour and a second one lasting 2  
 27  
 28 205 hours) were distinguished. For each such period of time, we counted the number of contact calls (per  
 29  
 30  
 31 206 unit of observation time) emitted by each individual and listed the following associated characteristics  
 32  
 33 207 of the audience:

- 34  
 35  
 36 208 - Subgroup size: The total number of individuals present in the audience, that is the subgroup  
 37  
 38 209 size of the caller minus 1;  
 39  
 40
- 41 210 - Subgroup composition: "*Alone*" (i.e. single adult subject or mother with immature offspring;  
 42  
 43 211 this was named "*only-mother*" when the study subject was an immature offspring knowing  
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 45  
 46 212 that immature individuals were never observed alone and never observed alone with mature  
 47  
 48 213 males), "*same-sex*" (i.e. only mature individuals of the same sex as the caller are present),  
 49  
 50 214 "*opposite-sex*" (i.e. only mature individuals of the opposite sex as the caller are present),  
 51  
 52  
 53 215 "*both- sexes*" (i.e. mixed-sex audience).  
 54
- 55  
 56 216 - Presence or absence of mature male offspring "*with and without son*" (for mothers only).  
 57

58  
 59 217 To evaluate if the fission and fusion events affected the occurrence of contact call rates, we used the  
 60  
 218 subgroup call rate as opposed to the individual call rate in order to have a sufficient time of observation

1  
2 219 under different conditions. We counted the number of calls emitted by all subgroup members 45 min  
3  
4 220 before and 45min after a fission-fusion event (only fusion, only fission or both fission and fusion). We  
5  
6 221 noted the “composition of the audience” (only females, only males, both sexes, alone) before and after  
7  
8  
9 222 this fission-fusion event, and we noted if the social composition remained in the same “audience sex  
10  
11 223 composition” (one sex-one sex, both sexes-both sexes) or if it changed (one sex-both sexes, both sexes-  
12  
13 224 one sex). For comparative purposes, we considered 90 min as an optimal period of time to see the  
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15  
16 225 impact of an audience change, since that is the average time that a subgroup remains stable (i.e. without  
17  
18 226 fissions or fusions; [54]). All calls collected outside of these periods with fission-fusion events were  
19  
20 227 considered to occur during stable periods. We included periods shorter than 90 min when for any  
21  
22 228 reason we could not follow the subgroup. Consequently, when during the 45 min after the social  
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24  
25 229 change there was any other social change, the time of the fission-fusion event was prolonged, we noted  
26  
27 230 the total duration.

### 30 231 **Statistical analysis**

31  
32  
33 232 To test the effects of size and sex composition of audience on individual contact call rate, we built a  
34  
35 233 generalized linear mixed model (GLMM) per age-sex category, conducting a total of four analyses for  
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37  
38 234 different individual categories: mature females, mature males, immature females and immature males.  
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40 235 For each model, fixed effects were the subgroup composition categories and the number of individuals.  
41  
42 236 To assess the effects of presence (1) or absence (0) of a mature son, we ran an additional GLMM.  
43  
44  
45 237 Caller identities and the date of observation were included as random factors for all models. Since our  
46  
47 238 dependent variable was a rate, we ran GLMMs using a Poisson distribution with a log-link function  
48  
49 239 [55]. For all the GLMM models, we compared a null model including only the random factors with a  
50  
51 240 full model including all fixed effects and their interactions. We compared the null and full models  
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53  
54 241 using a likelihood ratio test (LRT) with the ANOVA function [56]. We selected the full model as the  
55  
56 242 final if the LRT was significant and only then performed Tukey post hoc comparisons. We used the  
57  
58 243 *lme4*, *visreg* and *multcomp* packages[57,58] in R (R Core Team 2016).  
59  
60

1  
2 244 To test whether call rate varied with fission-fusion events (where periods were categorized into  
3  
4 245 fusion only, fission only, both fission and fusion and stable) and whether call rate varied with changes  
5  
6 246 in “audience sex composition” (one sex-one sex, one sex-both sexes, both sexes-one sexe, both sexes-  
7  
8  
9 247 both sexes), we conducted two general linear models (GLM) tests. In addition, we explored whether  
10  
11 248 call rate varied before and after fission-fusion events or changes in “audience sex composition”. We  
12  
13 249 ran a linear mixed model (LMM) with fission-fusion event, changes in audience sex composition and  
14  
15 250 time (before and after social events or changes in audience sex composition) as fixed effects, call rate  
16  
17  
18 251 as dependent variable, and identity of the event as random effect. We included in the model all main  
19  
20 252 effects and the interactions between “fission-fusion event” and the “before or after the event” (45min  
21  
22 253 before and after change) and “changes in audience sex composition” and “before or after the event”.  
23  
24  
25 254 Because call rate residuals did not meet the assumptions of no significant outliers and normal  
26  
27 255 distribution, we log-transformed call rate to meet both assumptions. The variances were homogeneous  
28  
29 256 (Levene's test:  $p = 0.1$  and  $0.9$ , respectively). We report partial eta squared ( $\eta^2$ ) and Tukey post hoc  
30  
31  
32 257 tests for ANOVA tests. We used IBM SPSS Statistics (v.25) to run the ANOVAs and LMM.  
33

34  
35 258 The complete data set and the full statistical code have been deposited in the Figshare data  
36  
37 259 repository at the following address: <https://figshare.com/s/e97dc3930ce827dd103c>.  
38

39  
40 260 All field observations were in accordance with the ethical standards and legal requirements of  
41  
42 261 the National Commission for Protected Areas in Mexico. Protocols were approved by the “Dirección  
43  
44 262 General de Vida Silvestre” (SEMARNAT, permit #SGPA/DGVS/1405/15).  
45  
46

## 47 263 48 49 50 264 **RESULTS**

### 51 52 53 265 *1. 1. Effects of size and composition of audience on individual call rate*

54  
55  
56 266 Audience size and audience composition influenced signalers differently depending on their sex and  
57  
58  
59 267 age (Table S2, Figures 1 and 2).  
60

1  
2 269 - *Mature females*  
3

4 270 Concerning mature females, the full model was significantly different from the null model (LRT:  
5  
6 271  $\chi^2=1071.4$ ;  $P<0.0001$ ), showing that mature females' calling rate was affected negatively by the  
7  
8  
9 272 number of individuals in the audience: the smaller the audience, the higher their call rate ( $\chi^2=-7.62$ ;  
10  
11 273  $P=0.005$ ). Their calling rate was also affected by the sexual composition of the audience ( $\chi^2=1128.1$ ;  
12  
13 274  $P<0.0001$ ), regardless of the audience size ( $\chi^2=6.04$ ;  $P=0.109$ ). Post-hoc Tukey comparisons showed  
14  
15  
16 275 that mature females emitted calls at higher rates when only males were present in the audience, than  
17  
18 276 when both males and females were present, and still lower call rates when they were with other  
19  
20 277 females, their offspring or alone.  
21

22 278  
23  
24  
25 279 - *Mature males*  
26

27 280 Concerning mature males, the full model was also significantly different from the null model (LRT:  
28  
29 281  $\chi^2=122.81$ ;  $P<0.0001$ ). But conversely to mature females, mature males' contact call rates were not  
30  
31  
32 282 affected by the size of the audience ( $\chi^2=1.85$ ;  $P=0.17$ ). Similarly, to mature females, the mature males'  
33  
34 283 call rates were affected by the sexual composition of the audience: they called at higher rates when the  
35  
36 284 opposite sex was present ( $\chi^2=60.38$ ;  $P<0.0001$ ), regardless of the audience size ( $\chi^2=5.25$ ;  $P=0.07$ ).  
37  
38  
39 285 Post-hoc Tukey comparisons showed that mature males called at higher rates when mature females  
40  
41 286 were present (with or without other males) than when being in an uni-sex subgroup.  
42

43 287  
44  
45 288 - *Immature females*  
46

47  
48 289 Contrary to mature females and males, a sex difference was not found in immature signalers. The full  
49  
50 290 models were significantly different from the null models (LRT:  $\chi^2=49.91$ ;  $P<0.0001$ ) showing that  
51  
52 291 immature females' ( $\chi^2=-11.89$ ;  $P=0.0006$ ) similarly to mature females, were affected negatively by  
53  
54  
55 292 the size of the audience: the smaller the audience, the higher the call rates. Additionally, immature  
56  
57 293 female call rates were affected by the sexual composition of the audience but in a direction opposite  
58  
59 294 to adults ( $\chi^2=19.88$ ;  $P=0.0002$ ) with a significant interaction between social composition of the  
60

audience and audience size ( $\chi^2=49.91$ ;  $P=0.04$ ). Immature females presented higher call rates when they were with their mother or with other members of the same sex than when in the presence of males.

### - *Immature males*

In the same way as immature females, the full model was significantly different from the null models (LRT:  $\chi^2=302.22$ ;  $P<0.0001$ ), showing that immature males' call rates ( $\chi^2=15.42$ ;  $P<0.0001$ ) were affected negatively by the size of the audience: the smaller the audience, the higher the call rates. Similar to immature females call rates were affected by the sexual composition of the audience in a direction opposite to adults ( $\chi^2=166.79$ ;  $P<0.0001$ ) regardless of the audience size ( $\chi^2=4.05$ ;  $P=0.26$ ). In the same way, immature male call rates called more when they were with their mother or with other members of the same sex than when being in presence of other females.

## 2. *The effects of a specific individual's presence on contact call rates*

The presence of a specific individual within the audience also influences mature females' contact call rates. The full model was significantly different from the null model (LRT:  $\chi^2=105.11$ ;  $P<0.0001$ ), showing that mature females' call rates were significantly affected by the presence of their mature son in the audience ( $\chi^2=10.59$ ;  $P<0.0001$ ), calling at higher rates when their mature male offspring were present in the subgroup than when they were not (Table S2, Fig. 2).

## 3. *Effects of fission-fusion events on subgroup call rate*

### - *Call rate during fission-fusion, fission, fusion or no events*

At the subgroup level, call rates are higher than at the individual level (Fig. 3) as they represent the sum of individual calling rates, which range as in Fig. 1 and Fig. 2. These rates varied significantly depending on the occurrence of fission-fusion events ( $F_{3, 165} = 33.6$ ,  $p < 0.0001$ ,  $\eta^2 = 0.38$ ). The post hoc test showed that subgroup call rate was significantly higher during periods when both fissions and fusions occurred than during periods when only fusion or fissions occurred. We observed the lowest

1  
2 320 call rates during fission events, which were not statistically different from periods with no fissions or  
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4 321 fusions (Table S3, Fig. 3).

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6  
7 322 ***- Call rate depending on the change of subgroup composition***

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9  
10 323 We also found that call rate varied significantly with changes in audience composition during fission  
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12 324 and fusion events ( $F_{4,164} = 22.3$ ,  $p < 0.0001$ ,  $\eta^2 = 0.88$ ). The post hoc test showed that call rate was  
13  
14 325 higher when there was a change from one sex to two sexes and when both sexes remained in the group,  
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16  
17 326 intermediate when there were no changes in sex audience and for changes from two sexes to one sex,  
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19 327 and lower when there were no audience changes in the group (Table S4, Fig. 3).

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21  
22 328 The LMM showed that call rate varied with fission-fusion events and changes in audience sex  
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24 329 composition ( $F_{2,135} = 32.4$ ,  $p < 0.0001$ ; and  $F_{3,135} = 6.6$ ,  $p < 0.0001$ , respectively), the effect of the  
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26  
27 330 before or after the event variable and its interactions with other factors were not significant (Time:  
28  
29 331  $F_{1,135} = 1.1$ ,  $p = 0.07$ ; fission-fusion event\*before or after the event:  $F_{2,135} = 1.5$ ,  $p = 0.2$ ; and changes  
30  
31 332 in audience sex composition\* before or after the event:  $F_{3,135} = 1.4$ ,  $p = 0.2$ ), suggesting that call rate  
32  
33  
34 333 did not vary before and after fission-fusion events and that the effects of type of fission-fusion event  
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36 334 and changes in audience sex composition are similar regardless of whether one looks at the 45 minutes  
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38 335 before or after the event.

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44 337 **DISCUSSION**

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47 338 We studied functional and mechanistic aspects of vocal flexibility in spider monkeys, a species with  
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49 339 high levels of social complexity according to several metrics [20,43,59]. We evaluated whether  
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52 340 individual spider monkeys vary their emission of contact calls with the size and composition of the  
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54 341 subgroup they are in, and whether calling at the subgroup level increases during periods where fission  
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56 342 and fusion events occur. We found that audience of subgroup size and composition significantly  
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59 343 affected the contact call rates of all age-sex classes but, as predicted, in an age- and sex-dependent  
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344 way. Our first hypothesis was partially validated: call rates of mature females and immature

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2 345 individuals of both sexes decreased when the subgroup size increased. This was not the case for the  
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4 346 mature males' call rate. In support of our second hypothesis, we found that mature females and males  
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6 347 increased their call rates when there was at least one individual of the opposite sex in the subgroup.  
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8  
9 348 Immature individuals were also affected by the sexual composition of the audience, but the pattern  
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11 349 was the opposite as the adults', with more calls when they were with their mother or with other  
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13 350 members of the same sex. In support of our third hypothesis, we found that mature females called more  
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15 351 when their mature sons were present in the audience. Finally, in concordance with our fourth  
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18 352 hypothesis, contact call rates were higher during periods with higher social instability (during fission-  
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20 353 fusion events) than during more stable periods, especially when there was a change in sex composition.  
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23 354 We predicted that large audiences would inhibit females from calling but stimulate males,  
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25 355 mainly because females are affected more than males for food competition, and they are less invested  
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28 356 in managing their social relationships [48] . Adult females indeed showed lower call rates when the  
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30 357 number of individuals in the audience increased. Adult females seem to be more involved than males  
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32 358 in repelling potential competitors and avoiding aggressive interactions [60]. Given that the intensity  
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35 359 of competition is impacted by group size and that large groups go through more tense situations [61],  
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37 360 a possible interpretation is that females are actually using whinnies to regulate subgroup size  
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39 361 depending on food availability. This was actually one of the first suggested functions of the whinny  
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42 362 [62] but the evidence so far has been equivocal [30,52]. A simpler explanation, based on the cohesion  
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44 363 function of whinnies, is that females are less prone to losing touch with the rest of the subgroup when  
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46 364 in larger subgroups, simply because more individuals are easier to keep track of by the noise they make  
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48 365 while moving or by their own whinnies. Smaller subgroups may require higher rates of calling by  
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51 366 individuals simply to stay in touch with the rest of the subgroup.  
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53  
54 367 As expected, contact call rates of immature individuals presented the same pattern as their  
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56 368 mothers. This goes in line with previous findings showing that immature spider monkeys' associations  
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58 369 with other group members are primarily determined by their mother's [47]. However, it is also possible  
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60 370 that immatures call more in small groups for different reasons than their mother; for example, that the

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2 371 mother's calls motivated their offspring to vocalize. Because adult males are known to be more socially  
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4 372 active than adult females [45,50], we predicted that larger subgroups would trigger more calling from  
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6 373 them. But we did not find this. It is possible that adult males are less sensitive than adult females and  
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9 374 immatures to the size composition of the audience because their social interactions with other group  
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11 375 members are generally relaxed and face lower levels of feeding competition. Further studies should  
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13 376 investigate whether the presence of individuals with more or less preferred social bonds or kinship  
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16 377 influence male calling.

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19 378 We also found that contact call rates were influenced by the sexual composition of the  
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21 379 audience. Interestingly, while adult males and females called more in the presence of the opposite sex,  
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23 380 immatures called more in the presence of a same-sex partner. This supports a function of contact calls  
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25 381 in the regulation of encounters and spacing mediation between the sexes. Our results are different to  
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27  
28 382 those obtained by Dubreuil et al [32], who showed that adult female spider monkeys called more in  
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30 383 larger subgroups. However, they also found that mature females (the study had insufficient calls for  
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32 384 male analysis) were more likely to vocalize in the first place when the number of males increased, then  
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35 385 when the number of females increased, and lastly when the number of males decreased or fissioned  
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37 386 her subgroup, but not when the number of females decreased. Spider monkeys tend to form sex-  
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39 387 segregated subgroups [40,45] and encounters between sexes (during subgroup fusions) can be tense,  
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42 388 with both sexes prone to receiving aggression from other adults within their group [63]. Increasing the  
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44 389 rates of whinnies in presence of the opposite sex may reduce the risk of aggressive interactions by  
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46 390 facilitating the location of others and spacing out appropriately [32]. In chimpanzees, the presence of  
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49 391 certain males was the most important parameter in the regulation of female call rates [64]. Intra-sex  
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51 392 competition could be another factor responsible for the tension observed during inter-sexes reunions,  
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53 393 and individuals could call to attract allies or identify themselves to avoid aggression. Competition  
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55 394 between males for access to females is attested by high rates of appeasing embracing behaviors among  
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58 395 males during sex encounters [39]. Competition between females is also observed with new immigrant  
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60 396 females being more vulnerable to attack from resident females [46].



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2 397 The fact that the immatures' pattern differs from that of mature individuals could be due to the  
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4 398 different social interest from males and females but also the interest they may have in individuals of  
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6 399 the same sex as a reference to socialize. For example, immature males presented more affiliative  
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9 400 interactions to adult males than do immature females [47]. Vocal usage certainly follows social  
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11 401 development, as immatures typically show same-sex preferential bonding before developing  
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13 402 heterosexual relationships [65]. In spider monkeys, strong male–male bonds begin early in life [80].  
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16 403 As predicted, mature females presented higher contact call rates when mature sons were  
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19 404 present in the audience. The presence of an important social partner is a strong influence on an  
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21 405 individual's decision to produce calls [66]. More calls in the presence of kin partners are frequently  
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23 406 found in primates [67,68]. Our findings support the idea that, in spider monkeys, female-male close  
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25 407 relationships in adulthood are kin-biased [47]. Cases where females provide care and protect mature  
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28 408 sons, and vice versa, can be found in the spider monkeys' literature [47,69,70]. The presence of a  
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30 409 mature son may also help dissuade aggression directed toward the mother herself or toward younger  
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32 410 offspring and therefore, be a factor in promoting a mother's overall reproductive success [47]. Also  
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35 411 supporting these results, adult females may be more prone to respond to the whinnies of their  
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37 412 juvenile offspring than any other juveniles [71]. This suggests that contact calls in spider monkeys  
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39 413 also play a role in mother-offspring spatial coordination.  
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42 414 We have analyzed contact calling rates at the individual and subgroup levels. Individual  
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45 415 calling rates differed between contexts, albeit by small amounts. These small differences could  
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47 416 certainly have a functional impact if every recipient has a certain probability of behaving in a certain  
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49 417 way in response (approaching, retreating, calling in response) to every vocalization it hears. In the  
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52 418 long term, and over all individuals that could be recipients, there would be an effect in terms of the  
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54 419 fission-fusion dynamics and the maintenance of social relationships between callers and recipients.  
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56 420 The fact that females call more when in smaller subgroups, and those males call equally regardless of  
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59 421 subgroup size, could imply that subgroups of all sizes would maintain an approximately constant call  
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422 rate. However, when we analyzed the effect of fission and fusion events on this subgroup calling

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2 423 rate, we identified sources of variation that may be related to cohesion and spacing functions of  
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4 424 whinnies, in the context of a dynamic subgroup composition. Indeed, social instability affected  
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6 425 contact call rates at this subgroup level. We registered more calling in subgroups during periods with  
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9 426 fission and fusion events, when social instability was higher, than during events when subgroups  
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11 427 only fissioned or during periods without changes. This result is consistent with previous studies  
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13 428 suggesting that contact calls allow individuals to obtain information about subgroup members'  
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16 429 locations [30], and can serve a spacing function [32] regulating fission-fusion events. During periods  
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18 430 with high uncertainty, a flexible use of whinnies, which contain information about individual  
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20 431 identity, might be helping to identify and locate individuals who, depending on their social  
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22 432 relationship with the caller, might approach or retreat from it. In our study, subgroups called at  
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24  
25 433 higher rates when individuals may have been trying to obtain information from the other individuals  
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27 434 that were joining the subgroup (e.g. identity or location), that is during a fusion. Additionally, more  
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29 435 calls were registered when subgroups changed their sex composition (from one to two sexes, or vice  
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31  
32 436 versa) than when sex composition remain stable. It seems, then, that there is a more evident  
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34 437 "negotiation" based on whinnies during periods of greater tension and/or uncertainty, such as the  
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36 438 arrival of individuals of the opposite sex.

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39 439 We did not find significant differences between subgroup call rates emitted 45 min before  
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42 440 and 45 min after fission- fusions, probably due to the fact that the change in subgroup composition is  
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44 441 a continuous process, rather than an instantaneous event. Therefore, we cannot conclude that the  
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46 442 emission of calls before or after fusion or fission could influence the individuals to join or leave from  
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49 443 the subgroup. Complementary studies would be necessary, taking into account the position of two  
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51 444 subgroups before they fuse and the exact time and distance between all individuals.

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54 445 In terms of the possible mechanisms underlying vocal flexibility, our results on audience  
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56 446 effects support the idea of voluntary use of vocalizations in non-human primates. The decision of an  
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59 447 individual to vocalize or remain silent could be shaped across learned contingencies and depends on  
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448 the constant evaluation of current circumstances, comprising the relationship quality between caller

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2 449 and receivers, the caller's present motivational state, and their particular socio-ecological interests  
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4 450 [2]. Individuals could decide which of many contextual cues are relevant, and that may require  
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6 451 elaborate cognitive processes. For example, female calling behavior in chimpanzees, who also have  
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9 452 high degrees of fission-fusion dynamics and a marked difference in the social status of males and  
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11 453 females [72], was moderated by social inhibition, which increased with the number of bystanders  
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13 454 [64]. Inhibitory skills are associated with social complexity as they prevent inappropriate responses  
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16 455 in dynamic social environments[59,73]. Vocal inhibition is also found in chimpanzees when females  
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18 456 do not produce copulation calls while other females are nearby [74], and in capuchins who do not  
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20 457 emit food calls when the risk of competition is high [25].  
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23 458 Spider monkeys have been shown to perform at comparable levels to chimpanzees in  
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26 459 inhibitory control laboratory tasks [59], leading to the suggestion that comparable degrees of fission-  
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28 460 fusion dynamics in both taxa require similar inhibitory control of behaviors that might be  
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30 461 inappropriate in particular social settings within a widely varying social environment [59]. Here we  
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33 462 have found that, despite their limited vocal repertoire, spider monkeys appear to be skilled at  
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35 463 modifying call usage in different social contexts. They could also be varying other aspects of their  
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37 464 calls depending on the social context. For example, there is evidence that they are able to modify  
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39 465 their calls as a function of the distance between callers and recipients, as individuals emitted and  
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42 466 respond with low frequency whinnies when callers are outside a subgroup (separated by long  
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44 467 distances) to facilitate vocal contact [33].  
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47 468 From a functional perspective, our findings suggest that: (1) contact call usage in monkeys is  
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49 469 flexible and context-dependent, (2) contact calls are signals that may serve several non-mutually  
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52 470 exclusive functions and the composition of subgroups could largely be regulated by whinnies during  
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54 471 fission and fusion events in the context of sex-segregated groups. Individuals are able to adapt to the  
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56 472 nuances of the immediate and changing social scene characteristic of a society with a high degree of  
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59 473 fission–fusion dynamics [75] and (3) contact calls are used to reduce the uncertainty about subgroup  
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474 composition and serve a socio-spatial cohesion function. From a mechanistic perspective, our results

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2 475 add to the growing number of empirical demonstrations of audience effects in animals [76]. Further  
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4 476 research is needed to determine whether the presence of specific individuals (other kin individuals,  
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6 477 or close affiliates) can also influence call rates [77,78]. Our results support the idea that studying the  
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9 478 potential effects of audience in species with complex social systems could allow us to predict which  
10  
11 479 specific social variables may be responsible for selection on new or more complex signals and their  
12  
13 480 adaptive functions [2].  
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40  
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42  
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45 495 data curation.  
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49 497  
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51 498  
52  
53 499 REFERENCES

- 54  
55 500  
56  
57 501 1. Freeberg TM, Dunbar RI, Ord TJ. 2012 Social complexity as a proximate and ultimate factor  
58  
59 502 in communicative complexity. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 1785–1801.  
60  
503 (doi:doi.org/10.1098/rstb.2011.0213).

- 1  
2 504 2. Peckre L, Kappeler PM, Fichtel C. 2019 Clarifying and expanding the social complexity  
3  
4 505 hypothesis for communicative complexity. *Behav. Ecol. Sociobiol.* **73**, 11. (doi:10.1007/s00265-018-  
5  
6 506 2605-4).
- 7  
8  
9 507 3. McComb K, Semple S. 2005 Coevolution of vocal communication and sociality in primates.  
10  
11 508 *Biol. Lett.* **1**, 381–385. (doi:10.1098/rsbl.2005.0366).
- 12  
13 509 4. Manser MB, Jansen DA, Graw B, Hollén LI, Bousquet CA, Furrer RD, Le Roux A. 2014  
14  
15 510 Vocal complexity in meerkats and other mongoose species. In *Advances in the Study of Behavior*  
16  
17 (Vol. 46, pp. 281-310). Academic Press. (doi.org/10.1016/B978-0-12-800286-5.00006-7).
- 18 511  
19  
20 512  
21 513 5. Kavanagh E *et al.* 2021 Dominance style is a key predictor of vocal use and evolution across  
22  
23 514 nonhuman primates. *R. Soc. Open Sci.* **8**, 210873. (doi.org/10.1098/rsos.210873).
- 24  
25  
26 515 6. May-Collado LJ, Wartzok D. 2007 The freshwater dolphin *Inia geoffrensis geoffrensis*  
27  
28 516 produces high frequency whistles. *J. Acoust. Soc. Am.* **121**, 1203–1212.
- 29  
30 517 7. Pollard KA, Blumstein DT. 2012 Evolving communicative complexity: insights from rodents  
31  
32 and beyond. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 1869–1878. (doi.org/10.1098/rstb.2011.0221).
- 33 518  
34  
35 519 8. Rebout N *et al.* 2020 Tolerant and intolerant macaques show different levels of structural  
36  
37 520 complexity in their vocal communication. *Proc. R. Soc. B* **287**, 20200439.  
38  
39 doi.org/10.1098/rspb.2020.0439).
- 40 521  
41  
42 522 9. Pougnault L, Levréro F, Leroux M, Paulet J, Bombani P, Dentressangle F, Deruti L, Mulot B,  
43  
44 523 Lemasson A. 2022 Social pressure drives “conversational rules” in great apes. *Biol. Rev.* **97**, 749–  
45  
46 524 765. (doi.org/10.1111/brv.12821)
- 47  
48  
49 525 10. Coye, C., Zuberbühler, K., Lemasson, A. (2022). The evolution of vocal communication:  
50  
51 526 inertia and divergence in two closely related primates. *Int. J. Primatol.* *In press*
- 52  
53 527 11. Rebout, N., De Marco, A., Sanna, A., Micheletta, J., Lone, J-C., van Den Berg, R.F., Sterck,  
54  
55 E.H.M., Langermans, J.A.M., Thierry, B., Lemasson, A. (2022). Tolerant and intolerant macaques  
56 528 differ in the context specificity of their calls and how they ‘comment’ on the interactions of others.  
57  
58 529 *Behav Ecol Sociobiol*, in press.
- 59  
60 530

- 1  
2 531 12. Lameira AR, Maddieson I, Zuberbühler K. 2014 Primate feedstock for the evolution of  
3  
4 532 consonants. *Trends Cogn. Sci.* **18**, 60–62. (doi:10.1016/j.tics.2013.10.013)  
5
- 6 533 13. Hammerschmidt K, Fischer J. 2008 Constraints in primate vocal production. In *The evolution*  
7  
8 534 *of communicative creativity: from fixed signals to contextual flexibility* (eds U Griebel, KD Oller),  
9  
10 pp. 93–119. Cambridge, MA.  
11535
- 12  
13536 14. Owren MJ, Amoss RT, Rendall D. 2011 Two organizing principles of vocal production:  
14  
15537 Implications for nonhuman and human primates. *Am. J. Primatol.* **73**, 530–544.  
16  
17 (doi:10.1002/ajp.20913).  
18538
- 19  
20539 15. Cheney DL, Seyfarth RM. 2018 Flexible usage and social function in primate vocalizations.  
21  
22540 *Proc. Natl. Acad. Sci.* , 201717572. (doi.org/10.1073/pnas.1717572115).  
23  
24
- 25541 16. Lemasson A, Ouattara K, Zuberbühler K. 2013 Exploring the gaps between primate calls  
26  
27542 and human language. In *The evolutionary emergence of language: evidence and inference* . (eds R  
28  
29543 Botha, M Everaert), pp. 181–203. Oxford University Press.  
30  
31
- 32544 17. Zuberbühler K. 2012 Cooperative breeding and the evolution of vocal flexibility. In *The*  
33  
34545 *Oxford handbook of language evolution*. The Oxford Handbook of Language Evolution (eds  
35  
36546 R K Gibson and M Tallerman). Oxford University Press.  
37  
38547 (doi:10.1093/oxfordhb/9780199541119.013.0005).  
39
- 40  
41548 18. Fischer J. 2017 Primate vocal production and the riddle of language evolution. *Psychon. Bull.*  
42  
43549 *Rev.* **24**, 72–78. (doi.org/10.3758/s13423-016-1076-8).  
44
- 45550 19. Aureli F *et al.* 2008 Fission-fusion dynamics: new research frameworks. *Curr. Anthropol.* **49**,  
46  
47 627–654. (doi:10.1016/j.cub.2008.08.020).  
48551
- 49  
50552 20. Ramos-Fernandez G *et al.* 2018 Quantifying uncertainty due to fission–fusion dynamics as a  
51  
52553 component of social complexity. *Proc. R. Soc. B Biol. Sci.* **285**, 20180532.  
53  
54554 (doi:10.1098/rspb.2018.0532).  
55
- 56  
57555 21. Aureli F, Schino G. 2019 Social complexity from within: how individuals experience the  
58  
59556 structure and organization of their groups. *Behav. Ecol. Sociobiol.* **73**, 1–13.  
60  
557 (doi.org/10.1007/s00265-018-2604-5).

- 1  
2 558 22. Zuberbühler K, Jenny D, Bshary R. 1999 The predator deterrence function of primate alarm  
3  
4 559 calls. *Ethology* **105**, 477–490. (doi.org/10.1046/j.1439-0310.1999.00396.x).  
5
- 6 560 23. Slocombe KE, Zuberbühler K. 2005 Functionally referential communication in a  
7  
8 561 chimpanzee. *Curr. Biol.* **15**, 1779–1784. (doi.org/10.1016/j.cub.2005.08.068).  
9  
10  
11 562 24. Caine NG, Addington RL, Windfelder TL. 1995 Factors affecting the rates of food calls  
12  
13 563 given by red-bellied tamarins. *Anim. Behav.* **50**, 53–60. (doi:10.1006/anbe.1995.0220).  
14  
15  
16 564 25. Di Bitetti M. 2005 Food-associated calls and audience effects in tufted capuchin monkeys,  
17  
18 565 *Anim. Behav.* **69**, 911–919. (doi:10.1016/j.anbehav.2004.05.021)  
19  
20 566 26. Candiotti A, Zuberbühler K, Lemasson A. 2012 Convergence and divergence in Diana  
21  
22 567 monkey vocalizations. *Biol. Lett.* **8**, 382–385. (doi:10.1098/rsbl.2011.1182)  
23  
24  
25 568 27. Bouchet H, Blois-Heulin C, Lemasson A. 2013 Social complexity parallels vocal complexity:  
26  
27 569 a comparison of three non-human primate species. *Front. Psychol.* **4**.  
28  
29 570 (doi:10.3389/fpsyg.2013.00390)  
30  
31  
32 571 28. Kondo N, Izawa E-I, Watanabe S. 2012 Crows cross-modally recognize group members but  
33  
34 572 not non-group members. *Proc. R. Soc. B Biol. Sci.* **279**, 1937–1942. (doi:10.1098/rspb.2011.2419)  
35  
36 573 29. Arlet M, Jubin R, Masataka N, Lemasson A. 2015 Grooming-at-a-distance by exchanging  
37  
38 574 calls in non-human primates. *Biol. Lett.* **11**, 20150711. (doi.org/10.1098/rsbl.2015.0711).  
39  
40  
41 575 30. Ramos-Fernández G. 2005 Vocal Communication in a Fission-Fusion Society: Do Spider  
42  
43 576 Monkeys Stay in Touch With Close Associates? *Int. J. Primatol.* **26**, 1077–1092.  
44  
45 577 (doi:10.1007/s10764-005-6459-z)  
46  
47  
48 578 31. Teixidor P, Byrne RW. 1999 The 'whinny' of spider monkeys: individual recognition before  
49  
50 579 situational meaning. *Behaviour* **136**, 279–308. (doi:10.1163/156853999501333).  
51  
52 580 32. Dubreuil C, Notman H, Pavelka MS. 2015 Sex Differences in the Use of Whinny  
53  
54 581 Vocalizations in Spider Monkeys (*Ateles geoffroyi*). *Int. J. Primatol.* **36**, 412–428. (doi:  
55  
56 582 10.1007/s10764-015-9832-6).  
57  
58  
59  
60

- 1  
2 583 33. Ordóñez-Gómez JD, Santillan-Doherty AM, Hammerschmidt K. 2019 Acoustic variation of  
3  
4 584 spider monkey (*Ateles geoffroyi*) contact calls is related to caller isolation and affects listeners'  
5  
6 585 responses. *Plos One* **14**, e0213914. (doi.org/10.1371/journal.pone.0213914).  
7
- 8  
9 586 34. Briseno-Jaramillo M, Ramos-Fernández G, Palacios-Romo TM, Sosa-López JR, Lemasson  
10  
11 587 A. 2018 Age and social affinity effects on contact call interactions in free-ranging spider monkeys.  
12  
13 588 *Behav. Ecol. Sociobiol.* **72**, 192. (doi.org/10.1007/s00265-018-2615-2).  
14
- 15  
16 589 35. Dunbar RI. 1993 Coevolution of neocortical size, group size and language in humans. *Behav.*  
17  
18 590 *Brain Sci.* **16**, 681–694. (https://doi.org/10.1017/S0140525X00032325).  
19
- 20 591 36. Milton K. 2000 Quo vadis? Tactics of food search and group movement in primates and other  
21  
22 592 animals. *Move Why Anim. Travel Groups* , 375–417. (doi:10.1007/s10071-007-0080-9).  
23
- 24  
25 593 37. Pinacho-Guendulain B, Ramos-Fernández G. 2017 Influence of fruit availability on the  
26  
27 594 fission–fusion dynamics of spider monkeys (*Ateles geoffroyi*). *Int. J. Primatol.* **38**, 466–484. (doi:  
28  
29 595 10.1007/s10764-017-9955-z).  
30
- 31  
32 596 38. Asensio N, Korstjens AH, Aureli F. 2009 Fissioning minimizes ranging costs in spider  
33  
34 597 monkeys: a multiple-level approach. *Behav. Ecol. Sociobiol.* **63**, 649–659. (doi:10.1007/s00265-008-  
35  
36 598 0699-9).  
37
- 38  
39 599 39. Slater KY, Schaffner CM, Aureli F. 2009 Sex differences in the social behavior of wild  
40  
41 600 spider monkeys (*Ateles geoffroyi yucatanensis*). *Am. J. Primatol.* **71**, 21–29.  
42  
43 601 (doi:doi.org/10.1002/ajp.20618).  
44
- 45  
46 602 40. Ramos-Fernandez G, Boyer D, Aureli F, Vick LG. 2009 Association networks in spider  
47  
48 603 monkeys (*Ateles geoffroyi*). *Behav. Ecol. Sociobiol.* , 999–1013. (doi:10.1007/s00265-009-0719-4).  
49
- 50 604 41. Watts DP. 1998 Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National  
51  
52 605 Park, Uganda. *Behav. Ecol. Sociobiol.* **44**, 43–55. (doi:doi.org/10.1007/s002650050513).  
53
- 54  
55 606 42. Wrangham RW. 1980 An ecological model of female-bonded primate groups. *Behaviour* ,  
56  
57 607 262–300. (www.jstor.org/stable/4534085).  
58  
59  
60



- 1  
2 608 43. Aureli F, Schaffner CM. 2008 Social interactions, social relationships and the social system  
3  
4 609 of spider monkeys. *Spider Monkeys Behav. Ecol. Evol. Genus Ateles* (ed Campbell CJ), pp. 236–265.  
5  
6 610 Cambridge, MA  
7  
8  
9 611 44. Van Schaik CP, Aureli F. 2000 The natural history of valuable relationships. *In Natural*  
10  
11 612 *conflict resolution*. (eds F Aureli F, FBM de Waal) University of California Press; pp. 307–333,  
12  
13 613 Berkeley, CA.  
14  
15  
16 614 45. Fedigan LM, Baxter MJ. 1984 Sex differences and social organization in free-ranging spider  
17  
18 615 monkeys (*Ateles geoffroyi*). *Primates* **25**, 279–294. (doi:10.1007/BF02382267).  
19  
20 616 46. Shimooka Y. 2003 Seasonal variation in association patterns of wild spider monkeys (*Ateles*  
21  
22 617 *belzebuth belzebuth*) at La Macarena, Colombia. *Primates* **44**, 83–90. (doi:10.1007/s10329-002-  
23  
24 618 0028-2).  
25  
26  
27 619 47. Vick LG. 2008 11 Immaturity in spider monkeys: a risky business. In: Spider monkeys:  
28  
29 620 behavior, ecology, and evolution of the genus *Ateles* (ed Campbell CJ). Cambridge University  
30  
31 621 Press, pp 255–288, New York.  
32  
33  
34 622 48. Koenig A. 2002 Competition for resources and its behavioral consequences among female  
35  
36 623 primates. *Int. J. Primatol.* **23**, 759–783. (doi:10.1023/A:1015524931226).  
37  
38  
39 624 49. Symington MM. 1987 Sex ratio and maternal rank in wild spider monkeys: when daughters  
40  
41 625 disperse. *Behav. Ecol. Sociobiol.* **20**, 421–425. (doi:0.1007/BF00302985).  
42  
43 626 50. Shimooka Y, Cambell CJ, Di Fiore A, Felton AM, Izawa K, Link A, Nishimura A,  
44  
45 627 Ramos-Fernandez G, Wallace RB. 2008 Demography and group composition of *Ateles*. In: Spider  
46  
47 628 monkeys: behavior, ecology, and evolution of the genus *Ateles* (ed Campbell CJ). Cambridge  
48  
49 629 University Press, pp 329–348, New York.  
50  
51  
52 630 51. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour*, 227–267.  
53  
54 631 (doi:10.1163/156853974X00534).  
55  
56  
57 632 52. Ramos-Fernández G. 2008 Communication in spider monkeys: the function and mechanisms  
58  
59 633 underlying the use of the whinny. In: Spider monkeys: behavior, ecology, and evolution of the genus  
60  
634 *Ateles* (ed Campbell CJ). Cambridge University Press, pp 220–235, New York.

- 1  
2 635 53. Eisenberg JF. 1976 Communication mechanisms and social integration in the black spider  
3  
4 636 monkey, *Ateles fusciceps robustus*, and related species.  
5
- 6 637 54. Ramos-Fernandez G. 2001 Patterns of association, feeding competition and vocal  
7  
8 638 communication in spider monkeys, *Ateles geoffroyi*. Ph.D. dissertation, University of Pennsylvania.  
9  
10
- 11 639 55. Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS.  
12  
13 640 2009 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol.*  
14  
15 641 *Evol.* **24**, 127–135. (doi:10.1016/j.tree.2008.10.008).  
16  
17
- 18 642 56. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009 Zero-truncated and zero-  
19  
20 643 inflated models for count data. In *Mixed effects models and extensions in ecology with R*, pp. 261–  
21  
22 644 293. Springer. (doi:10.1007/978-0-387-87458-6\_11).  
23  
24
- 25 645 57. Bates D, Maechler M, Bolker B, Walker S. 2014 lme4: Linear mixed-effects models using  
26  
27 646 Eigen and S4. *R Package Version 1*, 1–23.  
28
- 29 647 58. Hothorn T, Bretz F, Westfall P. 2008 Simultaneous inference in general parametric models.  
30  
31 648 *Biom. J.* **50**, 346–363. (doi:10.1002/bimj.200810425).  
32  
33
- 34 649 59. Amici F, Aureli F, Call J. 2008 Fission-fusion dynamics, behavioral flexibility, and inhibitory  
35  
36 650 control in primates. *Curr. Biol.* **18**, 1415–1419. (doi:10.1016/j.cub.2008.08.020).  
37  
38
- 39 651 60. Asensio N, Korstjens AH, Schaffner CM, Aureli F. 2008 Intragroup aggression, fission–  
40  
41 652 fusion dynamics and feeding competition in spider monkeys. *Behaviour* **145**, 983–1001.  
42  
43 653 (www.jstor.org/stable/40295874)  
44
- 45 654 61. Janson CH, Goldsmith ML. 1995 Predicting group size in primates: foraging costs and  
46  
47 655 predation risks. *Behav. Ecol.* **6**, 326–336. (doi:10.1093/beheco/6.3.326).  
48  
49
- 50 656 62. Chapman CA, Lefebvre L. 1990 Manipulating foraging group size: spider monkey food calls  
51  
52 657 at fruiting trees. *Anim. Behav.* **39**, 891–896. (doi.org/10.1016/S0003-3472(05)80953-4).  
53  
54
- 55 658 63. Rebecchini L, Schaffner CM, Aureli F. 2011 Risk is a component of social relationships in  
56  
57 659 spider monkeys. *Ethology* **117**, 691–699. (doi:10.1111/j.1439-0310.2011.01923.x).  
58
- 59 660 64. Laporte MN, Zuberbühler K. 2010 Vocal greeting behaviour in wild chimpanzee females.  
60  
661 *Anim. Behav.* **80**, 467–473. (doi:10.1016/j.anbehav.2010.06.005).

- 1  
2 662 65. Harlow HF. 1958 The nature of love. *Am. Psychol.* **13**, 673.  
3
- 4 663 66. Slocombe KE, Kaller T, Turman L, Townsend SW, Papworth S, Squibbs P, Zuberbühler K.  
5  
6 664 2010 Production of food-associated calls in wild male chimpanzees is dependent on the composition  
7  
8  
9 665 of the audience. *Behav. Ecol. Sociobiol.* **64**, 1959–1966. (doi:10.1007/s00265-010-1006-0).  
10
- 11 666 67. Hauser MD, Marler P. 1993 Food-associated calls in rhesus macaques (*Macaca mulatta*): I.  
12  
13 667 Socioecological factors. *Behav. Ecol.* **4**, 194–205. (doi:10.1093/beheco/4.3.194).  
14
- 15  
16 668 68. Pollick AS, Gouzoules H, de Waal FBM. 2005 Audience effects on food calls in captive  
17  
18 669 brown capuchin monkeys, *Cebus apella*. *Anim. Behav.* **70**, 1273–1281.  
19  
20 670 (doi:10.1016/j.anbehav.2005.03.007)  
21
- 22 671 69. Chapman CA. 1990 Association patterns of spider monkeys: the influence of ecology and sex  
23  
24  
25 672 on social organization. *Behav. Ecol. Sociobiol.* **26**, 409–414. (doi: 10.1007/BF00170898).  
26
- 27 673 70. Valero A, Schaffner CM, Vick LG, Aureli F, Ramos-Fernandez G. 2006 Intragroup lethal  
28  
29 674 aggression in wild spider monkeys. *Am. J. Primatol. Off. J. Am. Soc. Primatol.* **68**, 732–737.  
30  
31  
32 675 (doi:10.1002/ajp.20263).  
33
- 34 676 71. Byrne R, Teixidor P. 1999 The 'whinny' of spider monkeys: Individual recognition before  
35  
36 677 situational meaning. *Behaviour* **136**, 279–308. (doi.org/10.1163/156853999501333).  
37
- 38  
39 678 72. Wrangham RW. 1986 16. Ecology and Social Relationships in Two Species of Chimpanzee.  
40  
41 679 *Ecol. Asp. Soc. Evol.*, 352. (doi.org/10.1515/9781400858149).  
42
- 43 680 73. Santos LR, Ericson BN, Hauser MD. 1999 Constraints on problem solving and inhibition:  
44  
45 681 Object retrieval in cotton-top tamarins (*Saguinus oedipus oedipus*). *J. Comp. Psychol.* **113**, 186.  
46  
47  
48 682 (doi:10.1037/0735-7036.113.2.186).  
49
- 50 683 74. Townsend SW, Deschner T, Zuberbühler K. 2008 Female chimpanzees use copulation calls  
51  
52 684 flexibly to prevent social competition. *PLoS One* **3**, e2431. (doi:10.1371/journal.pone.0002431).  
53
- 54  
55 685 75. Di Fiore A, Campbell CJ. 2007 The atelines: variation in ecology, behavior, and social  
56  
57 686 organization. In: *Primates in Perspective*, (eds Campbell C, Fuentes A, MacKinnon KC, Panger M,  
58  
59 687 *Bearder SK*), Oxford University Press, 155–185, New York.  
60

- 1  
2 688 76. Coppinger B, Cannistraci RA, Karaman F, Kyle SC, Hobson EA, Freeberg TM, Hay JF. 2017  
3  
4 689 Studying audience effects in animals: What we can learn from human language research. *Anim.*  
5  
6 690 *Behav.* **124**, 161–165.  
7  
8  
9 691 77. Schel AM, Machanda Z, Townsend SW, Zuberbühler K, Slocombe KE. 2013 Chimpanzee  
10  
11 692 food calls are directed at specific individuals. *Anim. Behav.* **86**, 955–965.  
12  
13 693 (doi:10.1016/j.anbehav.2013.08.013).  
14  
15  
16 694 78. Slocombe KE, Zuberbühler K. 2007 Chimpanzees modify recruitment screams as a function  
17  
18 695 of audience composition. *Proc. Natl. Acad. Sci.* **104**, 17228–17233. (doi:10.1073/pnas.0706741104).  
19  
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## 23 697 **FIGURE LEGENDS**

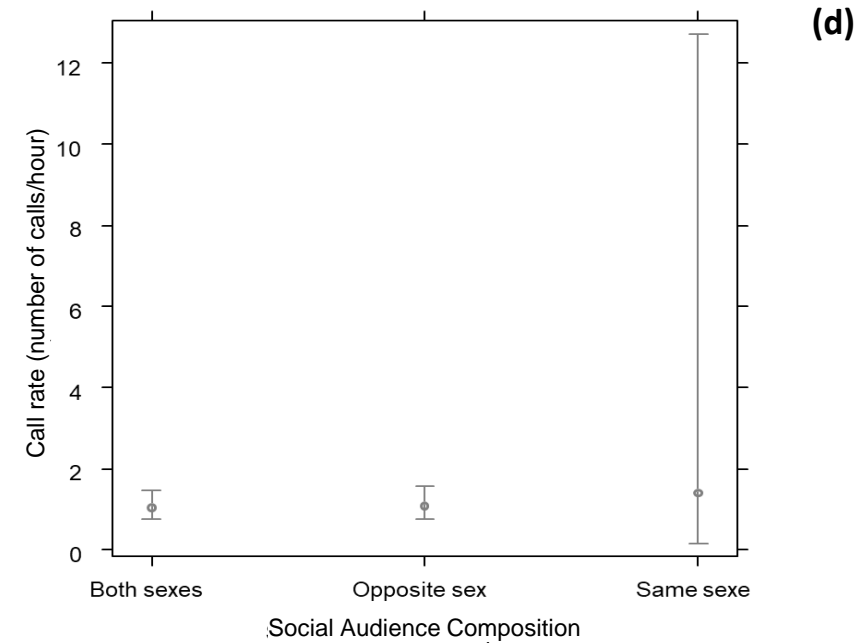
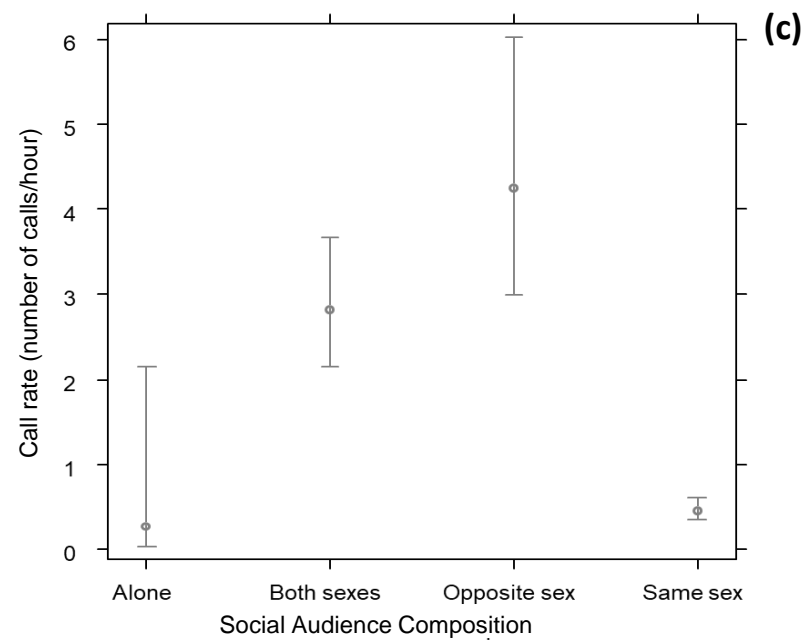
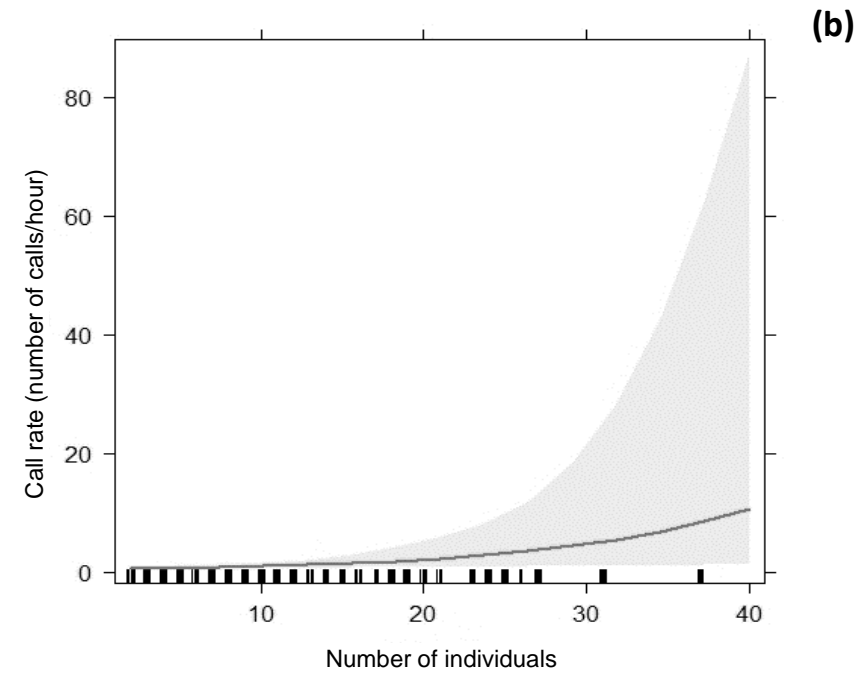
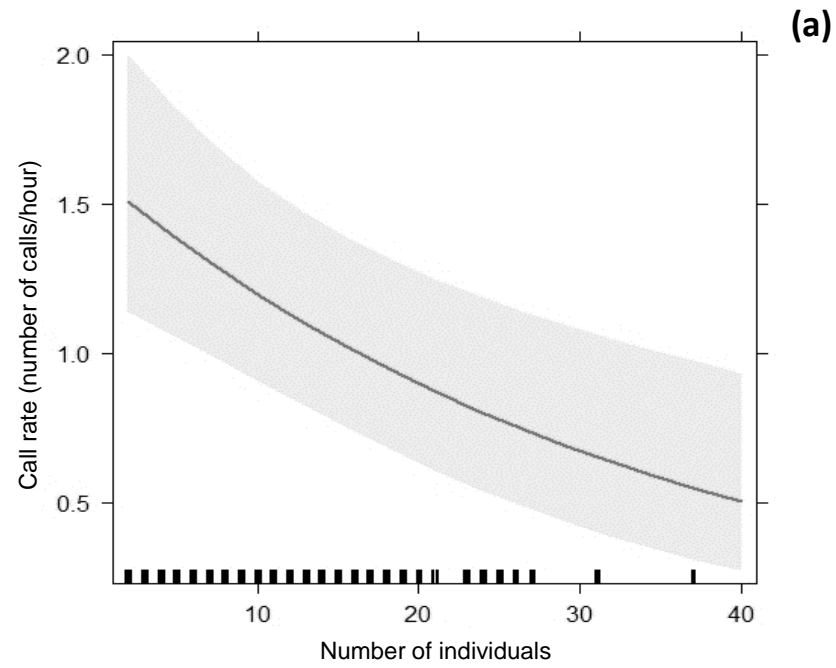
25 698 Figure 1. At the top of the figure, we find the effects plot that shows the expected influence of audience  
26 699 size on the individual call rates of (a) mature females and (b) males. The lines represent predicted  
27 700 means derived from the generalized linear mixed model. The gray area represents the 95% confidence  
28 701 interval and the rug plot at the bottom of the graphs shows the location of the audience size values. At  
29 702 the bottom of the figure, we find the effects plot that shows the expected influence of social audience  
30 703 individual call rates of (c) mature females and (d) males calling. The points are the fitted values of  
31 704 each category of social audience and their standard errors which are based on the covariance matrix of  
32 705 the estimated regression coefficients.  
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35 706 Figure 2. Effects plot shows the expected influence of mature son presence or absence on the call rate  
36 707 by mature female spider monkeys. The points are the fitted values of each category (presence or  
37 708 absence) and their standard errors which are based on the covariance matrix of the estimated regression  
38 709 coefficients.  
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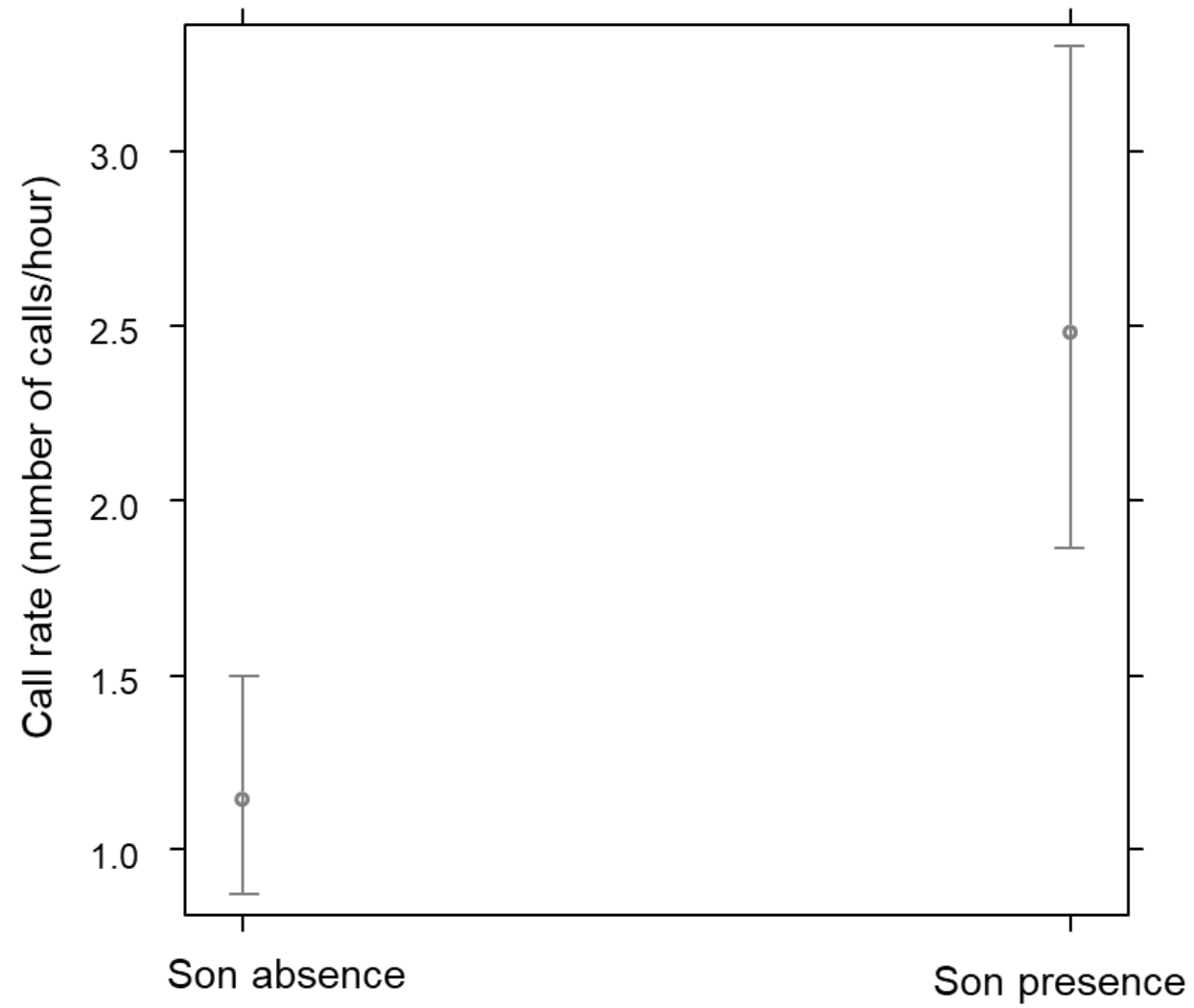
40 710 Figure 3. Plots showing the effects of social events and changes in audience composition on call rate.  
41 711 Error bars show the standard error. Letters indicate the results of the post hoc test, where groups with  
42 712 the same letters indicate nonsignificant differences.  
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**Mature females**

**Mature males**



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