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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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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

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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
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56 87 [29]. In fluid societies, identifying callers at a distance could play an important role in maintaining
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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
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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"
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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
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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
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55 113 periods, could whinnies function in the coordination of interindividual distances to different audience
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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
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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
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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
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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
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24
25 125 adjusted depending on the availability and distribution of food [37,38]. Sex is clearly a structuring
26
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,
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31
32 128 long-lasting relationships with one another and cooperating to compete with neighboring groups’
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34 129 males [41]. Conversely, adult females disperse from their natal group and do not establish strong
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36 130 bonds with kin group members [42]. Thus, males are keen to maintain social bonds, while females
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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
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43 133 forage alone with dependent offspring [45,46], interacting affiliatively less than males do amongst
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45 134 them [39]. Mixed-sex relationships involve high rates of aggression from males to females, including
46
47
48 135 coalitionary behaviors between males when they are in mixed-sex subgroups [39]. However, male-
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50 136 female relationships can vary in different circumstances (e.g. the reproductive status of females) [43]
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52 137 or kinship (e.g. long-term associations between mothers and mature males offspring) [47].
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57 139 Specifically, we studied how individuals of different age/sex classes flexibly modify their
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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
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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
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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
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17
18 149 regulation of social relationships in general [44], we predicted that large subgroups would inhibit
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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,
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27 153 as callers are approached by close associates and potentially avoided by others [32]. We
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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
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41 159 expect immatures to be affected by the presence of the opposite sex in the same way than mature sex
42
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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48 162

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
3
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**

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17 174 Spider monkeys live in groups that constantly vary in size, cohesion and composition [37]. We
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19 175 considered all individuals within 30 m from one another at a given time as members of the same
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22 176 subgroup [30]. Observations were conducted on all individuals, older than one year old, which
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24 177 included 20 matures (6 males, 14 females) and 16 immatures (7 males, 9 females). Immatures were on
25
26 178 average 3.0 ± 1.3 years old throughout the study period. Individuals less than one year old were not
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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
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35 182 subgroups can be widely variable (subgroup size 8.1 ± 5.0 individuals), the observed subgroup was
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38 183 semi-randomly selected, trying to equalize the total number of observation hours per individual
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40 184 (83.7 ± 15 hours per individual, see supplementary material). To do so, the observer followed different
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42 185 subgroups on consecutive days and switched subgroups whose composition did not change after three
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44
45 186 hours in a given day. Therefore, the time spent with a given subgroup varied ($3\text{hrs}16\text{min} \pm 1\text{hr}38\text{min}$).
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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
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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**

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 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
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 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
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 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;
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 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),
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 52
 53 215 "*both- sexes*" (i.e. mixed-sex audience).
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- 55
 56 216 - Presence or absence of mature male offspring "*with and without son*" (for mothers only).
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58
 59 217 To evaluate if the fission and fusion events affected the occurrence of contact call rates, we used the
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 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
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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
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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
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20 227 considered to occur during stable periods. We included periods shorter than 90 min when for any
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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
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27 230 the total duration.

30 231 **Statistical analysis**

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32
33 232 To test the effects of size and sex composition of audience on individual contact call rate, we built a
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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.
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42 236 To assess the effects of presence (1) or absence (0) of a mature son, we ran an additional GLMM.
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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
52
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-
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8
9 247 both sexes), we conducted two general linear models (GLM) tests. In addition, we explored whether
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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
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15 250 time (before and after social events or changes in audience sex composition) as fixed effects, call rate
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18 251 as dependent variable, and identity of the event as random effect. We included in the model all main
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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 (η^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.
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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*

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55
56 266 Audience size and audience composition influenced signalers differently depending on their sex and
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58
59 267 age (Table S2, Figures 1 and 2).
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1
2 269 - *Mature females*
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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
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8
9 272 number of individuals in the audience: the smaller the audience, the higher their call rate ($\chi^2=-7.62$;
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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
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15
16 275 that mature females emitted calls at higher rates when only males were present in the audience, than
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18 276 when both males and females were present, and still lower call rates when they were with other
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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:
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29 281 $\chi^2=122.81$; $P<0.0001$). But conversely to mature females, mature males' contact call rates were not
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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.
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43 287
44
45 288 - *Immature females*
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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
3
4 321 fusions (Table S3, Fig. 3).

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
11
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
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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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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:
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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
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31 332 in audience sex composition* before or after the event: $F_{3,135} = 1.4$, $p = 0.2$), suggesting that call rate
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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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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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27
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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34
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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41
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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15
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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34
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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41
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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48
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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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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48
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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22

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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32
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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51
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
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11 479 specific social variables may be responsible for selection on new or more complex signals and their
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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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18 695 of audience composition. *Proc. Natl. Acad. Sci.* **104**, 17228–17233. (doi:10.1073/pnas.0706741104).
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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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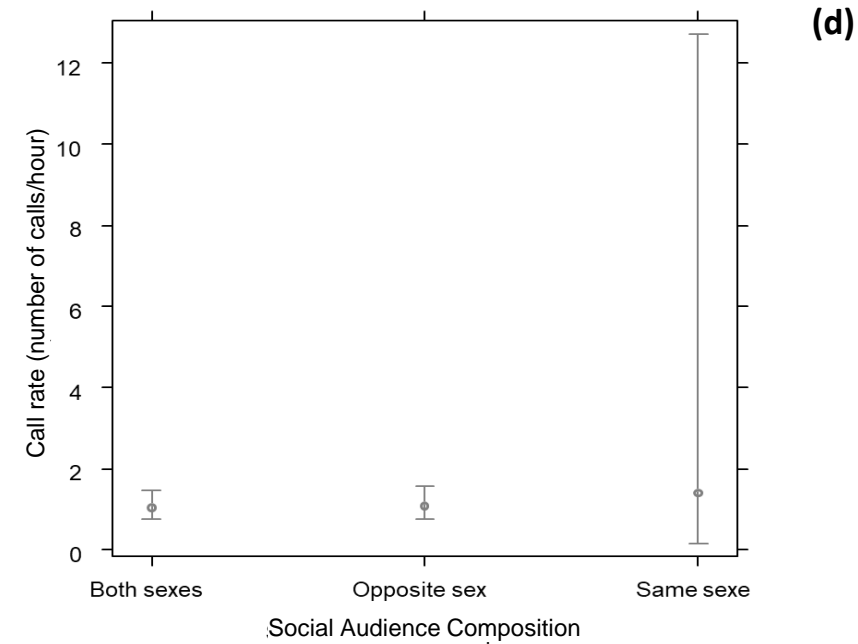
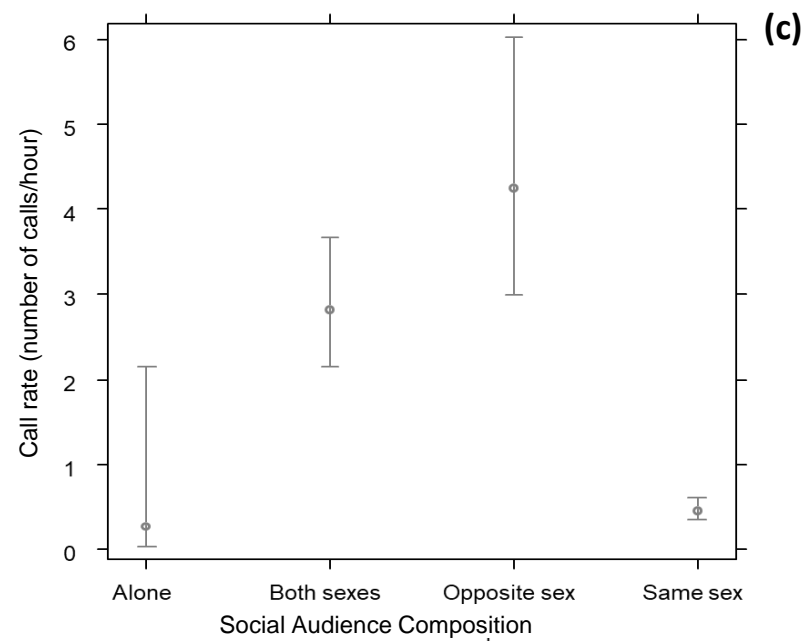
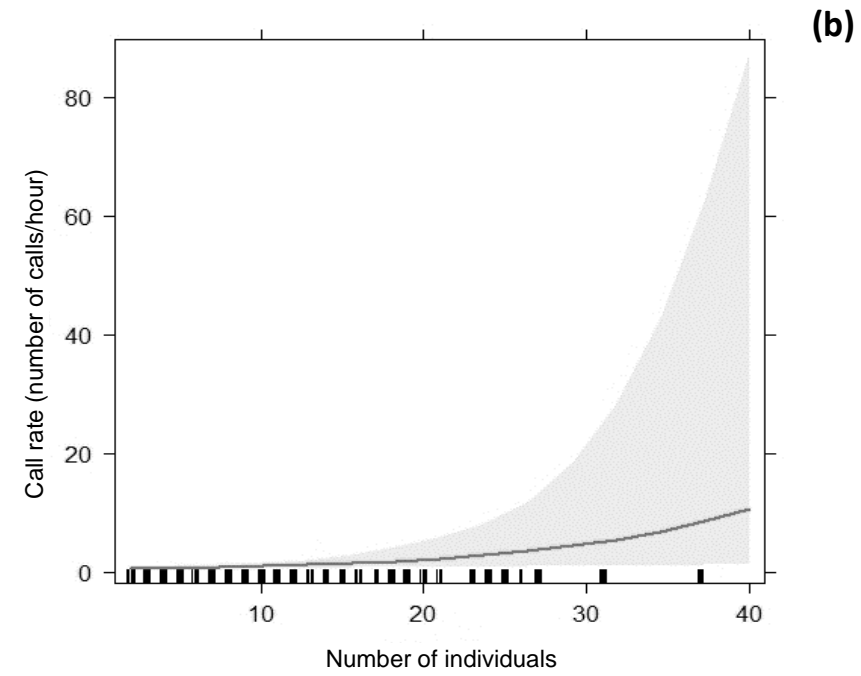
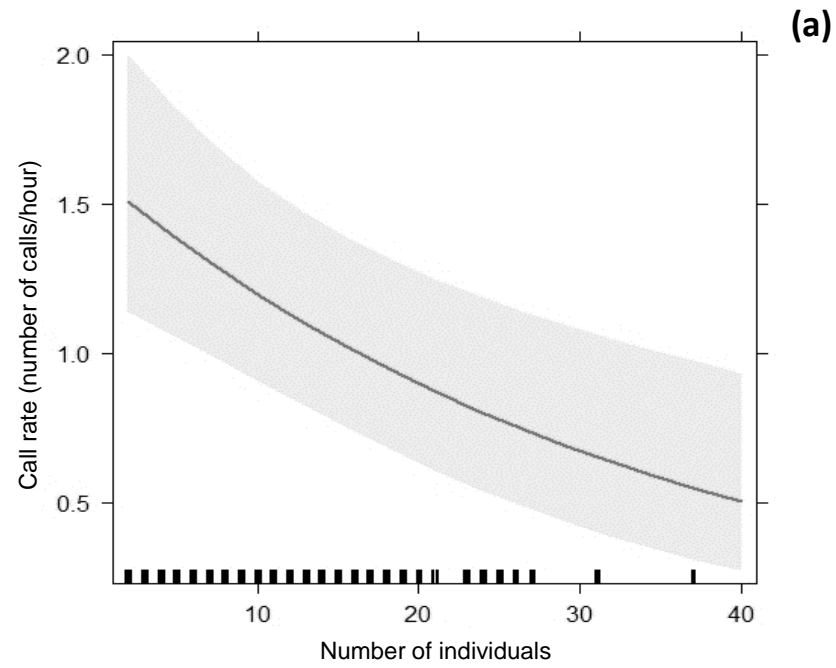
35 706 Figure 2. Effects plot shows the expected influence of mature son presence or absence on the call rate
36 707 by mature female spider monkeys. The points are the fitted values of each category (presence or
37 708 absence) and their standard errors which are based on the covariance matrix of the estimated regression
38 709 coefficients.
39 709

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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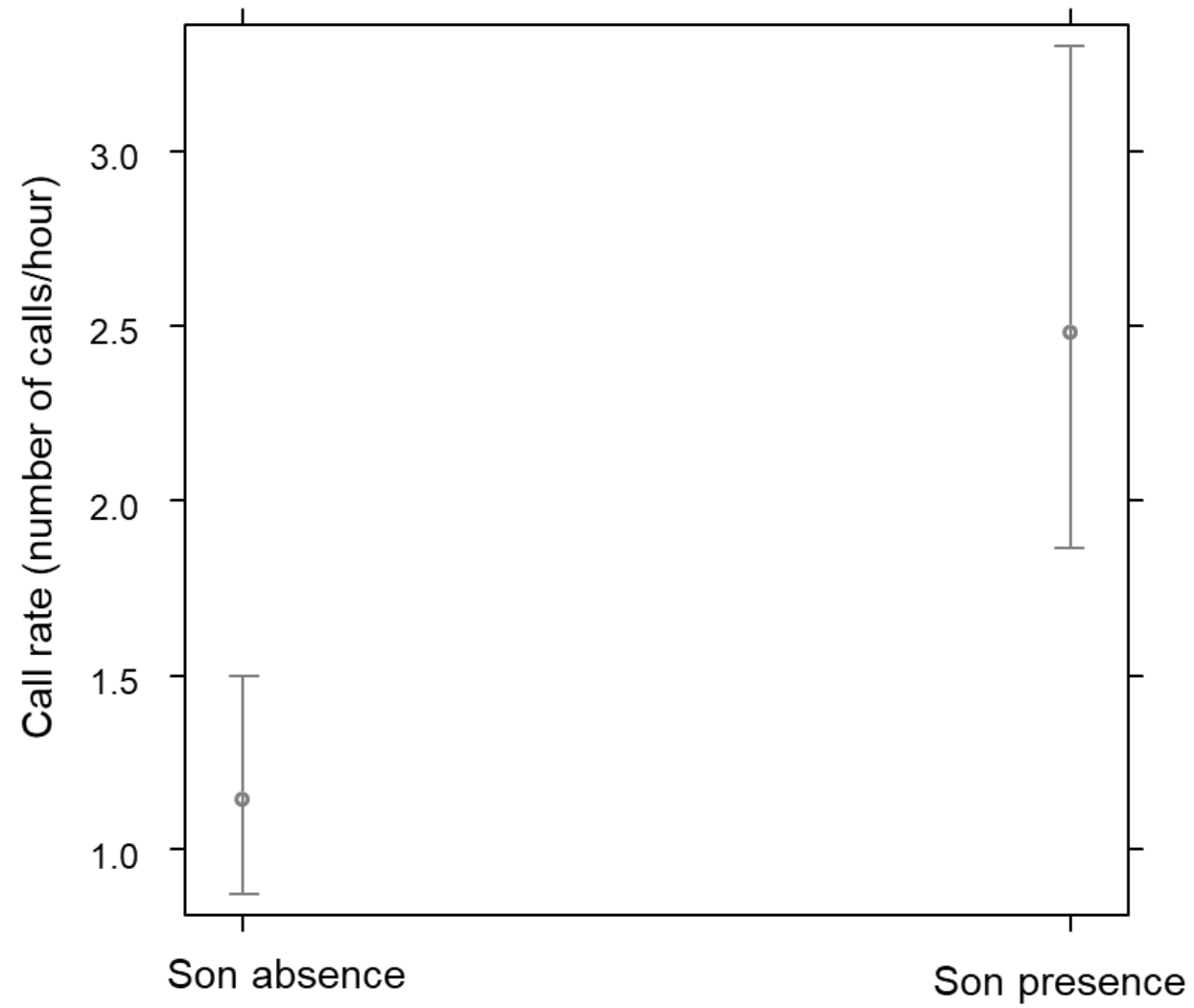
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Mature females

Mature males



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