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1 **Socially mediated overlap in vocal interactions between free-ranging black howler monkeys.**

2

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12

13 **Abstract:** “Conversation rules” such as overlap avoidance and coordinated overlap have been
14 reported in nonhuman animals, and seem to be adaptive responses to the requirements of social life.
15 Some species display both patterns in an apparently flexible way, but the social factors mediating
16 their respective usage remain poorly documented. We investigated potential social factors guiding
17 the usage of these temporal rules during collective howling in six free-ranging groups of black
18 howler monkeys (*Alouatta pigra*). First, we found that adult males’ vocalizations rarely overlap
19 those of other callers while most adult females’ calls overlap other members’ calls, especially that of
20 other females. Second, whereas some call types (notably affiliative calls) are typically emitted
21 without overlap, roars (agonistic loud calls) overlap more frequently. Third, coordinated overlap is
22 more frequent during inter-group competition. Our findings support the hypothesis that overlap
23 avoidance and coordinated overlap are two different (here sex-related) vocal alliance social
24 behaviors, at least for some nonhuman primates. More comparative investigations are now needed to
25 explore further their evolutionary trajectories in this lineage.

26 **INTRODUCTION**

27

28 Behavioural synchronization among individuals is crucial to group-living species (Engel &
29 Lamprecht, 1997), which is well illustrated by vocal interactions. In humans, conversations in both
30 modern and traditional cultures universally respect temporal rules, which facilitate mutual attention,
31 comprehensibility and responsiveness (France et al., 2001; Whittaker & O’Conaill, 1997). These
32 rules typically involve turn-taking, defined as an alternation of utterances between interlocutors and
33 speech overlap avoidance (Sacks et al., 1978; Stivers et al., 2009). The universality of conversational
34 temporal rules across human languages raised the question of their possible biological function and
35 phylogenetic origin (Pika et al., 2018). In the last decade, several studies have described vocal
36 interactions involving turn-taking rules and call overlap avoidance in a broad range of nonhuman
37 primate species (new-world monkeys Takahashi et al., 2015; old-world monkeys Lemasson et al.,
38 2010 and 2011, apes Levréro et al., 2019). These interactions mostly consist in (soft) contact call
39 exchanges typically involving two to four individuals vocalizing in alternation (“antiphony” pattern),
40 with an inter-call silence interval of up to five seconds ensuring overlap avoidance (review by
41 Pournault et al., 2020). These so-called “conversation-like” exchanges are used to strengthen social
42 bonds and maintain socio-spatial cohesion (Chow et al., 2015; Snowdon, 2001; Pika et al., 2018;
43 Pournault et al., 2020).

44 However, the conversation-like vocal exchange is just one category of vocal interaction
45 pattern found in the primate genera. Other patterns involve more or less occurrences of overlap
46 between callers (Henry et al., 2015; Pournault et al., 2020). In duets, for example, two individuals
47 synchronise long series of calls or songs using both coordinated overlaps and overlap avoidances in a
48 species-specific predictive way, mostly for mate attraction and guarding (Geissmann, 2002). Also,
49 choruses are vocal interactions comprising loud call types and involving several individuals who
50 overlap their calls in a less predictable temporal way (Greenfield 2016). Choruses are commonly

51 used in reproductive and agonistic contexts, such as territory defence or intergroup space regulation
52 (Chivers, 1969).

53 It thus remains unclear what selection pressures guided the evolution of call overlap vs
54 overlap-avoidance patterns. According to Yoshida & Okanoya (2005), the evolutionary pathway
55 suggests that overlap is more ancestral: overlap among several individuals (choruses) may have led
56 to the emergence of overlap between two individuals (duets) and then to antiphony, under the
57 influence of both natural and sexual selection pressures. However, a single species can regularly
58 exhibit different patterns: in some cases, individuals can flexibly switch between different temporal
59 organisations in a context-dependent way (Pougnault et al., 2020), suggesting that temporal patterns
60 are different strategies used to broadcast motivations and regulate social interactions. For example,
61 baboons emit within-group diurnal vocal antiphonies (Rendall et al., 2000) and choruses during
62 group encounters notably at dawn (Kitchen et al., 2003). The sex of callers can also influence the
63 temporal structure of the vocal interactions. In guenons, females call preferentially in antiphony,
64 while males either call alone or chorus with other conspecifics or heterospecific males (Gautier &
65 Gautier, 1977; Lemasson et al., 2010). This flexibility is also found in other taxa. For example,
66 bottlenose dolphins produce whistles in antiphony to coordinate social activities (Janik, 2000) and in
67 choruses during pre-sleep activities (Kremers et al., 2014), while caciques and nightingales use two
68 song types respectively associated with choruses and antiphonies (Thieltges et al., 2014; Naguib et
69 al., 2002).

70 One way of understanding how these calling patterns are socially modulated is to investigate
71 temporal patterns in a species presenting both overlap and overlap avoidance, like howler monkeys
72 (Baldwin & Baldwin, 1976; Whitehead 1995). Howler monkeys live in multi-male multi-female
73 groups (Kitchen, 2000), and are famous for their collective loud calls emitted a few times per day by
74 one or several group members (Sekulic, 1982). This howling behaviour has been proposed to fulfil
75 several functions, such as mate defence (da Cunha & Jalles-Filho, 2007), mate attraction (Bolt,

76 2013; Farmer et al., 2011; Whitehead, 1989), resource defence (Bolt et al., 2019, 2020; da Cunha &
77 Byrne, 2006; Van Belle et al., 2014a) and regulation of inter-group spacing (da Cunha & Byrne,
78 2006; Kitchen et al., 2015) by mutual avoidance or regular advertisement of occupancy (*A. pigra*,
79 Kitchen et al., 2015; Van Belle & Estrada, 2020) or active defence of borders (da Cunha & Jalles-
80 Filho, 2007).

81 Because they are composed of hundreds of calls emitted by several individuals for several
82 minutes in a row (Kitchen, 2004), howling bouts may at first sight appear a chorus with little to no
83 predictable temporal or social coordination. However, a growing body of evidence shows that they
84 are more rule-governed than expected and present a non-random organization. First, communal
85 participation is optional: the number of males and females joining a howling bout is context-
86 dependent. Overall, females call less than males (da Cunha et al., 2015; Briseño-Jaramillo et al.
87 2017), but join the chorus when the number of rival males exceeds the number of males in their
88 groups (Kitchen, 2006). Alpha males tend to participate more when vulnerable offspring are present
89 in the group (Kitchen et al., 2004), and subordinate males participate more when they have long-
90 term relationships with the alpha male (Kitchen et al., 2004). Second, howling bouts present a high
91 degree of call overlap but also short silence pauses (da Cunha et al., 2015). Third, the structure of
92 the howling bout can vary i) at the bout level, with the proportion of call types varying with the
93 context of emission and sex of the caller(s) (da Cunha et al., 2015; Kitchen et al., 2015; Briseño-
94 Jaramillo et al., 2017) and ii) at the call level, with variations of the acoustic structure of the calls
95 and the duration of vocal responses with the identity of the caller (Briseño-Jaramillo et al., 2015a;
96 Ceccarelli et al., 2021).

97 While females sometimes join the howling bouts, most studies have focused on male loud
98 calls. The justification of this bias is twofold. First, males are more involved than females in the
99 defence of their home range and the regulation of inter-group spacing (Sekulic, 1982; Kitchen,
100 2004). Second, howling bouts are composed of entwined vocal emissions of several individuals,

101 which make it hard to unravel each individual's utterance. Since males have a larger hyoid bone and
102 larynx than females, they have louder and deeper voices (Schön, 1971; Dunn et al., 2015), which
103 easily mask female calls (Bergman, 2010; Calegario-Marques & Bicca-Marques, 1995; da Cunha et
104 al., 2015; Oliveira, 2002). The lack of studies on female loud calls leads to a knowledge gap of the
105 precise sex-dependent social and temporal organization of the howling bouts.

106 In this study, we propose to fill this gap by investigating the factors influencing the flexible
107 use of temporally-ruled vocal patterns of howling bouts of black howler monkeys (*Alouatta pigra*).
108 This species lives in relatively small groups (1-3 adult males and 1-4 adult females, Kitchen 2000)
109 compared to other howler monkey species (Crockett & Eisenberg, 1987), which allowed us to
110 unravel each individual's participation in a given howling bout. Moreover, the complete vocal
111 repertoire of *A. pigra* has already been described elsewhere (Briseño-Jaramillo et al., 2017). We
112 conducted our work on six free-ranging groups of *A. pigra* in the Palenque National Park, Mexico.
113 We focussed on the social function of temporal rules, i.e., overlap avoidance and coordinated
114 overlap. We predicted that the use of specific temporal rules would vary with social factors, notably
115 the callers' characteristics (age and sex of the caller, sex of the caller's partner) and audience
116 context (presence and distance of neighbouring group, if any). Since males produce more
117 conspicuous vocalizations and are more involved in space regulation than females, we expected
118 them to display an antiphony pattern, in order to convey reliable and clear information about the
119 group's fighting capacity to neighbouring groups and to socially coordinate for a more efficient
120 within-group coalition. Females, on the contrary, emit softer vocalizations, occasionally participate
121 in howling bouts and bond more strongly (Pope, 2000). As such, we expected them to overlap in a
122 coordinated way with other females, in order to increase their chances of being heard and reinforce
123 intra-group cohesion. In line with the hypothesis that coordinated overlap serves a demonstrative
124 function (Pougnault, 2020), we also expected overlap to be associated with more agonistic call types
125 and with high arousal contexts such as inter-group encounters.

126 **METHODS**127 *Study sites and groups*

128 We observed six free-ranging social groups of black howler monkeys (*Alouatta pigra*). We collected
129 data from mature and immature individuals, i.e., respectively more and less than five years old
130 (Carpenter 1965; Balcells & Baró 2009; Benitez-Malvido et al., 2016). Infants, still depending on
131 their mothers for locomotion and feeding were not sampled here. Group compositions and sampling
132 efforts are given in Table 1. All individuals were well habituated to human presence and were
133 identified using physical features such as body size, genital pigmentation, permanent scars and botfly
134 marks (Briseño-Jaramillo et al., 2015a; Van Belle et al., 2009, 2014b).

135 Four groups (BA, MT, PK, MG) lived in the Palenque National Park (PNP, 17°27'51" N,
136 99°01'30" W), a Mayan archaeological site. The park is a 1771 ha area including 597 ha of primary
137 tropical rainforest (including 100-200 ha of buried Mayan city ruins), 300 ha of regenerating forest
138 and 874 ha of pasture land (Díaz Gallegos, 1996). The study groups have known adjacent home
139 ranges and are all surrounded by neighbouring groups (Briseño-Jaramillo et al., 2015a; Van Belle et
140 al., 2012; Estrada et al., 2002). The two other groups (CK, QL) lived in fragment forest patches,
141 including agricultural lands, urban areas with dispersed trees and secondary forest areas and located
142 10.3 ± 8.4 km from PNP. The groups living in fragment forest patches were isolated, i.e., they were
143 not surrounded by neighbouring groups.

144 Our research complied with protocols of the Animal Care Committee of Universidad
145 Nacional Autonoma de Mexico and adhered to the legal requirements of Mexico. Protocols were
146 approved by the Direccion General de Vida Silvestre (SEMARNAT), permit
147 SGPA/DGVS/00692/08.

148 *Acoustic recordings and observations*

149 Three groups (PK, MT, BA) were followed by MBJ with one or two assistants in Feb. - Jul.
150 2012, and the three other groups (MG, CK, QL) were followed by MB and one or two assistants in
151 Feb. - May. 2014. For logistic reasons, PK, MT and BA were followed from 06:00 to 18:00 while
152 QL and CK were followed from 05:30 to 9:00 and from 15:30 to 18:00, and MG was followed from
153 06:00 to 17:00.

154 All howling bouts emitted by the focal group were recorded. A directional microphone (SONY
155 ECM-672) and a tie microphone (EUROPSONIC ECM 104) connected to a digital audio recorder
156 (MARANTZ PMD661) were used for the recordings (Sample rate 44.1 kHz, resolution 16 bit, WAV
157 format). The first track was used to record monkeys' calls and the second track was used for
158 comments. All recordings were made at comparable distances (i.e. 20 to 30 meters). We considered a
159 bout as a period of synchronized loud roaring separated by more than one minute of silence from any
160 other loud roaring bout (Briseño-Jaramillo et al. 2017). During the howling bout, the two or three
161 observers spread around the group to reliably identify the identity of the provider for each call. This
162 was made possible because of the relatively limited group size, high spatial cohesion and low
163 vegetation density. The observers thus identified in the field each caller and commented on its
164 identity, simultaneously to each call emission.

165 The context of emission of the howling bout was also commented at the beginning of the
166 howling event: this comprised whether a neighbouring group was present, and if so, whether this
167 neighbouring group was close (directly visible by the observer, typically within 30m) or far (not
168 visible but auditorily spotted via branch cracking and/or vocalisations, typically between 30 and
169 100m). The times when each bout started and ended were also collected.

170 *Data processing*

171 Howling sequences involving a single caller were discarded as we focussed on social coordination.
172 Also, only howling bouts from focal group were considered in this study. Howling bouts are

173 composed of series of calls from different call categories. The vocal repertoire of howling bouts of
174 black howler monkeys *A. pigra* have been previously defined (Briseño-Jaramillo et al., 2017). It
175 comprises six acoustically and functionally call categories (Briseño-Jaramillo et al., 2017): “barks”
176 (typical bark and soft bark), “roars”, “roar variants” (frequency modulated roar and soft roar),
177 “agonistic calls” (metallic cackling notes and coo), “affiliative calls” (barked grunt, soft scream and
178 moo) and “grunts”, easily discriminable by stereotypic acoustic patterns. Using Avisoft-SASLab Pro
179 (Berlin, Germany) software, we built spectrograms with Fast Fourier transformation (FFT) and a
180 time window of 256 points. These spectrograms were used to score, for each call recorded: 1) the
181 call type name and 2) the presence / absence of overlap (i.e., whether the call started before the end
182 of a call from another group member) (see Fig. 1). We also reported from the comment track, for
183 each call: 3) the identity of the caller and 4) the context of emission. We coded a total of 112
184 howling bouts (see Table 1), comprising a total of 76,726 calls. Howling bouts lasted on average
185 11min 48s \pm 05min 49s and were composed of a mean of 541.9 \pm 521.7 SD calls per bout.

186 During a pilot phase, both observers (MB and MBJ) simultaneously but independently
187 recorded a howling bout (group QL, 5 min/calls) and separately coded callers’ identities and call
188 types. Although the precise threshold for a “substantial” inter-rater agreement is still debated
189 (Haligren, 2012), we found here a relatively strong agreement between our two observers given the
190 complexity of our data set (Cohen’s kappa test: $k=0.73$, Landis & Koch, 1977).

191 *Statistical analysis*

192 To address all our research questions and due to non-normal distribution of our data, we built
193 generalized linear mixed models (GLMMs). Since our dependent variable was the presence or
194 absence of overlap for each call occurrence, we fitted our mixed models with a Binomial error
195 structure (Zuur et al., 2009). We built a null model, which only included the random factors as
196 intercepts (i.e., group identity, caller identity and howling bout) and several full models, which

197 additionally included the fixed effects. We compared the null to each full model using a likelihood
198 ratio test (LRT) using an ANOVA (Zuur et al., 2009). If the LRT was significant ($P < 0.05$), we
199 performed Tukey post hoc comparisons with the multcomp package on the full model (function glht
200 in R, Hothorn et al., 2008).

201 - The first full model (GLMM1) assessed the influences on vocal overlap of callers'
202 characteristics and call type. Fixed factors for this GLMM were thus the age (mature and immature,
203 see Table 1), the sex (male or female) and the call type (i.e., six abovementioned call types). This
204 analysis was done with all studied groups (monkey groups $N=6$; howling bouts $N=112$; calls
205 $N=76,726$).

206 - The second full model (GLMM2) assessed the influence of contextual variations. We thus
207 included fixed factors: neighbouring groups absent, close or distant. Only four groups (PNP only)
208 could be included in this analysis as the two others had no neighbours (monkey groups $N=4$; howling
209 bouts $N=93$; calls $N=67,736$).

210 - The third full model (GLMM3) assessed whether the sex of the caller's partner influenced
211 the overlap behaviour of the caller, i.e., whether male and female preferred to overlap calls from
212 other males or females. To this end, we included sex of the partner as fixed factor. In this model, we
213 could only include two monkey groups (PN, BA), i.e., those where callers had the possibility to
214 overlap the same probability of females and males (PN: 3 mature females and 3 mature males / BA:
215 2 mature females and 2 mature males) (monkey groups $N=2$; howling bouts $N=64$; calls $N=43,546$).

216 Additionally, we tested for overdispersion (i.e., if the variance was larger than the mean in
217 our dependent variable) and result indicated no overdispersion for each of our models (values should
218 ideally be lower than 1.4): 0.58 (GLMM1), 0.74 (GLMM2) and 0.66 (GLMM3). We also tested the
219 stability of each model (for assessing overall influence over the model fit) by comparing the
220 estimates derived from a model based on all data with those obtained from models without identified

221 influential individuals (Nieuwenhuis et al., 2012). All the models remained significant after this
222 procedure. The fit of the models was evaluated as the proportion of variance explained by the
223 marginal coefficient of determination R^2_m , (i.e., the variance accounted for by fixed factors), and the
224 conditional coefficient of determination R^2_c (i.e., the variance accounted for by both fixed and
225 random factors) according to the method described in Nakagawa & Schielzeth (2013). All model
226 outputs are resumed in the Appendix 1, 2 and 3.

227 Statistical analyses were conducted using R version 3.5.2 (R Core Team 2016). GLMMs were
228 designed using the lme4 package (Bates et al., 2014), LRT tests were conducted with the ANOVA
229 function (Zuur et al., 2009), overdispersion was calculated using the blmecco package (function
230 dispersion.glmer in R, Korner-Nievergelt et al., 2015), stability of models was assessed using the
231 Cook's distance in the influence.ME package (Nieuwenhuis et al., 2012), fits of the models were
232 calculated with the "performance" package and we used the ggeffects package in R (Lüdecke et al.,
233 2020) to draw graphics.

234 A sample of the dataset and the full statistical code have been deposited in the Figshare data
235 repository at the following address:
236 [https://figshare.com/projects/Socially_mediated_overlap_in_vocal_interactions_between_free-](https://figshare.com/projects/Socially_mediated_overlap_in_vocal_interactions_between_free-ranging_black_howler_monkeys/115308)
237 [ranging_black_howler_monkeys/115308](https://figshare.com/projects/Socially_mediated_overlap_in_vocal_interactions_between_free-ranging_black_howler_monkeys/115308). The complete dataset is available upon reasonable request
238 to the corresponding author.

239

240 **RESULTS**

241

242 1) Influence of callers' identity and call type – bias on rates of vocal overlap

243 The full model ($R^2_m = 0.891$, $R^2_c = 0.429$) was significantly different from the null model
244 ($R^2_m = 0.886$, $R^2_c = 0.000$) (LRT: $\chi^2 = 19468$, $P < 0.0001$). The full model showed that caller's

245 identity (sexes: $\chi^2 = 119.064$, $P < 0.0001$; age: $\chi^2 = 17.984$, $P < 0.0001$) and call type ($\chi^2 = 6837.1$,
 246 $P < 0.0001$) significantly influenced vocal overlap.

247 Post hoc Tukey comparisons showed first that immature overlapped more than adult monkeys ($\beta =$
 248 1.15 , $SE = 0.27$, $Z = 4.24$, $P < 0.0001$) (Fig. 2) and females overlapped more often than males ($\beta = -$
 249 3.09 , $SE = 0.28$, $Z = -10.91$, $P < 0.0001$) (Fig. 2).

250 Second, roars overlapped more often than did affiliative calls ($\beta = 6.69$, $SE = 0.26$, $Z = 25.6$, $P <$
 251 0.0001), barks ($\beta = 5.96$, $SE = 0.08$, $Z = 78.09$, $P < 0.0001$), grunts ($\beta = 1.4$, $SE = 0.08$, $Z = 18.44$, $P <$
 252 0.0001) and roar variant calls ($\beta = -1.66$, $SE = 0.04$, $Z = -38.92$, $P < 0.0001$), but did not differ from
 253 agonistic calls ($\beta = 0.34$, $SE = 0.27$, $Z = 1.25$, $P = 0.77$). Agonistic calls overlapped more often than
 254 affiliative calls ($\beta = 6.34$, $SE = 0.36$, $Z = 17.6$, $P < 0.0001$), barks ($\beta = -5.62$, $SE = 0.27$, $Z = -20.38$,
 255 $P < 0.0001$), grunts ($\beta = -1.10$, $SE = 0.27$, $Z = -3.98$, $P < 0.0001$) and roar variants ($\beta = -1.32$, $SE =$
 256 0.27 , $Z = -4.88$, $P < 0.0001$). Roar variants overlapped more often than affiliative calls ($\beta = 5.02$, SE
 257 $= 0.26$, $Z = 19.49$, $P < 0.0001$) and barks ($\beta = 4.30$, $SE = 0.08$, $Z = 55.06$, $P < 0.0001$) but not than
 258 grunts ($\beta = -0.22$, $SE = 0.08$, $Z = 2.72$, $P = 0.05$). Grunts overlapped more often than barks ($\beta = 4.53$,
 259 $SE = 0.10$, $Z = 44.12$, $P < 0.001$) and affiliative calls ($\beta = 5.25$, $SE = 0.26$, $Z = 19.79$, $P < 0.001$).
 260 Affiliative calls overlapped more often than barks ($\beta = 0.72$, $SE = 0.26$, $Z = 2.78$, $P = 0.04$) (Fig. 3).

261

262 2) Influence of contextual variations of vocal overlap

263 The full model ($R^2_m = 0.889$, $R^2_c = 0.053$) was also significantly different from the null
 264 model ($R^2_m = 0.892$, $R^2_c = 0.000$), (LRT: $\chi^2 = 1518$, $P < 0.0001$). The model showed that neighbour
 265 context influenced the variations of vocal overlap ($\chi^2 = 1423.06$, $P < 0.0001$). Post hoc Tukey
 266 comparisons showed that overlap increased when a neighbouring group was present and close
 267 comparing to situations where neighbours were absent ($\beta = 2.66$, $SE = 0.09$, $Z = 30.21$, $P < 0.0001$)
 268 or distant ($\beta = -2.42$, $SE = 0.06$, $Z = -3751$, $P < 0.0001$). Moreover, overlap increased when a

269 neighbouring group was distant compared to when no neighbour was around ($\beta = 0.23$, $SE = 0.06$, Z
 270 $= 3.90$, $P = 0.0002$), (Fig. 4).

271 3) Influence of partners' sex on preferred targets of overlap:

272 The full model ($R^2_m = 0.894$, $R^2_c = 0.169$) was significantly different from the null model
 273 ($R^2_m = 0.889$, $R^2_c = 0.053$), (LRT: $\chi^2 = 915.55$, $P < 0.000$) and showed sex-differences in the overlap
 274 behaviours ($\chi^2 = 595.11$, $P < 0.0001$). Post hoc Tukey comparisons showed that female – female (i.e., a
 275 a female overlaps the previous call of another female) were more frequent than female – male (i.e., a
 276 female overlaps the previous call of another male) ($\beta = -4.07$, $SE = 0.21$, $Z = -19.0$, $P < 0.0001$), male
 277 – female ($\beta = -5.17$, $SE = 0.35$, $Z = -15.0$, $P < 0.0001$) and male – male ($\beta = -.5.9$, $SE = 0.35$, $Z = -$
 278 17.31 , $P < 0.0001$) overlaps (Fig. 5). Also, female – male overlaps were more frequent than male –
 279 female ($\beta = -1.06$, $SE = 0.32$, $Z = -3.41$, $P = 0.003$) and male – male ($\beta = -1.9$, $SE = 0.32$, $Z = -5.79$,
 280 $P < 0.0001$) overlaps. Finally, male – female overlaps were more frequent than male – male overlaps
 281 ($\beta = -0.75$, $SE = 0.06$, $Z = -12.27$, $P < 0.0001$) (Fig. 5).

282 **DISCUSSION**

283 Our study confirms that, far from being choruses with non-obvious temporal organizations,
 284 black howler monkeys' howling bouts are non-random coordinated vocal interactions. Both overlap
 285 avoidance and coordinated overlap are frequent but sex-dependent, suggesting, as predicted, a co-
 286 existence of two different strategies of vocal interaction and social synchronization: adult males
 287 avoid call overlap, while females and immature subjects typically overlap their calls (i.e., two or
 288 more individuals emit calls simultaneously). The sex of the overlapped partner also matters: females
 289 principally overlap other females' calls. Finally, overlap preferentially involves call types (such as
 290 roars and so-called agonistic calls) known to have an agonistic function (Baldwin & Baldwin, 1976;
 291 Whitehead, 1995) more frequently than more affiliative call types, and occurs more frequently
 292 during agonistic group encounters with close neighbour groups (Briseño-Jaramillo et al., 2017).

293 Overall, our findings suggest that temporal rules of howling bouts have social functions as discussed
294 below.

295 Overlap avoidance appears to be a “between-males” temporal rule, which could be used for
296 territory defence, inter-group spacing, as well as for intra-group socio-spatial coordination. Males
297 call more often and their call rates are higher than those of females and form the core of a howling
298 bout (Briseño-Jaramillo et al., 2017). Typically, the alpha male calls more frequently and sometimes
299 alone, but when the situation becomes particularly tense (e.g., when a neighbouring group is
300 present), other male group members join the howling bout (Kitchen, 2006) and form coalitions or
301 “vocal alliances.” Calling together could reinforce the coalition between resident males by
302 motivating one another and announce occupancy to the neighbours (Kitchen, 2000), which aims to
303 regulate inter-group spacing and to protect home range borders (Sekulic, 1982; Kitchen, 2000;
304 Garber & Kowalewski, 2011; Van Belle et al., 2014a). Male territorial neighbours can be
305 individually recognized by their voices, and neighbouring males who are not at their usual place are
306 particularly counterattacked (Briseño-Jaramillo et al. 2015a). Also, howler monkeys can discriminate
307 the number of opponent males based on neighbours’ howling bouts and adjust their behaviour
308 according to the risk (Kitchen, 2000). If male calls overlapped, it could be difficult for neighbouring
309 groups to recognize territorial neighbours and estimate the number of opponents. As a result, overlap
310 avoidance is probably a good strategy to facilitate group recognition and advertise the number of
311 males willing to defend the territory. Also, males from a given group can defend different parts of
312 the territory border (Stanford, 1998) but can lose sight of each other among the dense vegetation.
313 Overlap avoidance can thus help coordinate intra-group collective movements. This is in line with
314 the suggestion that males call in antiphony (Briseño-Jaramillo et al., 2015b), but turn-taking *per se*
315 (e.g., the number of successive turns) was not investigated in the present study and remains to be
316 more deeply studied.

317 Conversely, coordinated overlap appeared to be a “between-females” temporal rule. For
318 decades, the vocal role played by adult howler monkey females has attracted little to no attention.
319 We now know that females sometimes join howling bouts (Kitchen, 2006), and are able to produce
320 most of the supposedly male call types (Briseño-Jaramillo et al., 2017). However, females are more
321 discreet than males. They call less frequently than males, do not always join in males’ howling
322 displays (Kitchen, 2006) and never howl without male accompaniment (Kitchen, 2000). Moreover,
323 they call more during howling bouts in intergroup encounters compared to spontaneous howling
324 (Van Belle, 2015). Playback studies revealed that they are able to assess their group’s relative
325 fighting ability and reserve their participation for contests with less predictable outcomes (Kitchen,
326 2006). Moreover, female calls are much softer (Whitehead, 1987). The fact that females overlap their
327 calls almost exclusively with those of other females could be a way to produce louder sounds in
328 “unison.” The fact that immature individuals also do so is in line with the idea that this vocal strategy
329 is used to compensate for relatively non-loud voices. This vocal strategy could also function to
330 strengthen or to advertise female cohesion: indeed, females from the same group form strong bonds
331 (e.g., greater spatial proximities and less agonism among females than among males, Van Belle et
332 al., 2011) and are intolerant towards unfamiliar females (Pope, 2000). In conclusion, call overlap in
333 females may have extra-group and intra-group functions, such as reinforcement of intra-sex cohesion
334 and territory defence. Whether females joining the howling bouts has an influence on the outcome of
335 the communicative event remains, however, to be experimentally investigated.

336 Even if females overlap more often than males, males also do so on some occasions. Overall,
337 overlap was associated with more agonistic calls and more agonistic communicative contexts, which
338 is in line with our hypothesis that this power-demonstrating strategy plays a possible deterrent role.
339 Encounters with neighbours, particularly when the situation becomes critical, are associated with
340 very high arousal where males and females join forces (Neville et al., 1988), and individuals display
341 all sorts of arousal-related behaviours such as piloerection, breaking branches, and embracing

342 (Kitchen 2000). The fact that overlap is associated with strong agonism confirms that this temporal
343 rule fulfils a social function. More studies, notably playback experiments, are now needed to
344 evaluate whether temporal rules (coordinated overlap and overlap avoidance) affect the information
345 transfer among groups and impact the behavioural response of receivers.

346 Some authors previously classified howler monkeys' howling bouts as rather disorganized
347 choruses primarily functioning in inter-group communication (Chivers 1969; Baldwin & Baldwin
348 1976; Sekulic 1982). Here, we firstly show that howling bouts are non-randomly organised, which
349 fulfils both inter-group and intra-group functions. Indeed, call overlap and overlap avoidance seems
350 to play a role in competition regulation and group cohesion. Both coordinated overlap and overlap
351 avoidance could be found here serving sex-specific and context-dependent functions. Our results
352 thus confirm that *A. pigra* is an interesting species to investigate the evolution of temporal rules in
353 vocal communication. Investigating the organization of communication in species that use more
354 than one temporal rule is particularly interesting to highlight and understand the evolutionary
355 pressures acting on this trait and to which extent these rules are socially flexible (Yoshida &
356 Okanoya, 2005). Running more comparative studies can help to better picture how call use
357 flexibility, vocal interaction patterns and social needs co-evolved in primates, but also at a larger
358 phylogenetic scale. Our study confirms that overlap and overlap avoidance are two vocal strategies
359 that could have evolved in parallel to serve different social functions.

360

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362

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378

379 **Ethical standards**

380 Experiments comply with the current laws of Mexico.

381 **Conflict of interest**

382 The authors declare that they have no conflict of interest.

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609

610 **Data Availability Statement:** The data that support the findings of this study are available from the
611 corresponding author upon reasonable request.

612

Table 1. Characteristics of the six groups of black howler monkeys studied in two geographical locations.

Geographical location	Group Name	Group composition				Contact hours number	Observation periods	Sampled sequences number
		Mature males	Mature females	Immatures males	Immatures females			
Palenque National Park	PK	3	3	0	1	291 h	Feb. - Apr. 2012, Feb. 2014	35
	MT	2	1	3	2	297 h	Apr. - Jun. 2012, Feb. 2014	22
	BA	2	2	2	0	300 h	Jun. - May. 2012, Feb. 2014	29
Fragment forest patches	MG	1	2	1	1	92 h	Feb. - Mar. 2014	7
	QL	1	1	0	1	20 h	Feb. 2014	10
	CK	1	2	1	1	48 h	Feb. - Mar. 2014)	9

613

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615

616 **FIGURE LEGENDS**

617 **Figure 1. Female's overlap and male's overlap avoidance.** Spectrograms of extracts of howling
618 bouts involving two mature females (Fem 1 and 2) (a) and two mature males (Male 1 and 2) (b).
619 Spectrogram configuration: window type = Hann. window size =512 samples; overlap 50%.

620 **Figure 2. Rates of vocal overlap vary with caller identity.** Plots of predicted counts of the number
621 of overlapped calls on the (a) "Age of caller" (Immature vs Mature), and on the (b) "Sex of caller"
622 (Female vs Male) from six study groups of howler monkeys. Error bars represent the lower and
623 higher confidence interval estimate of the marginal effects (predicted counts) estimate.

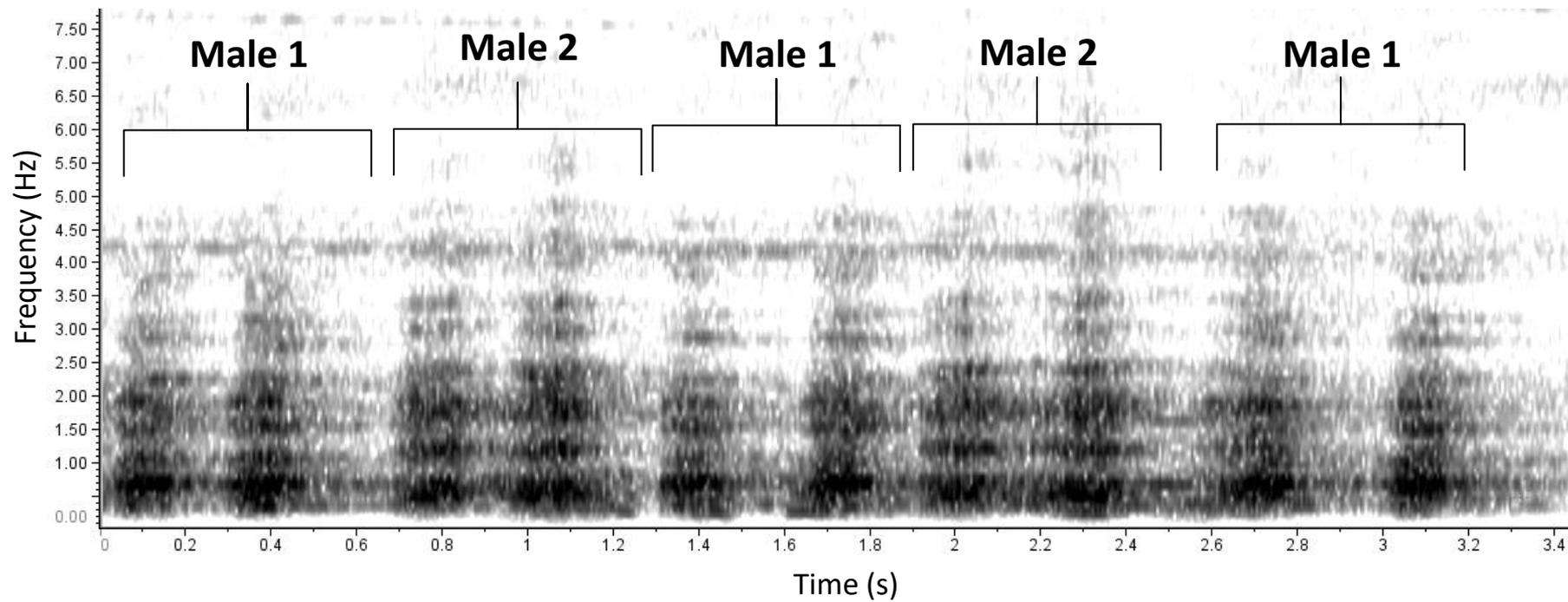
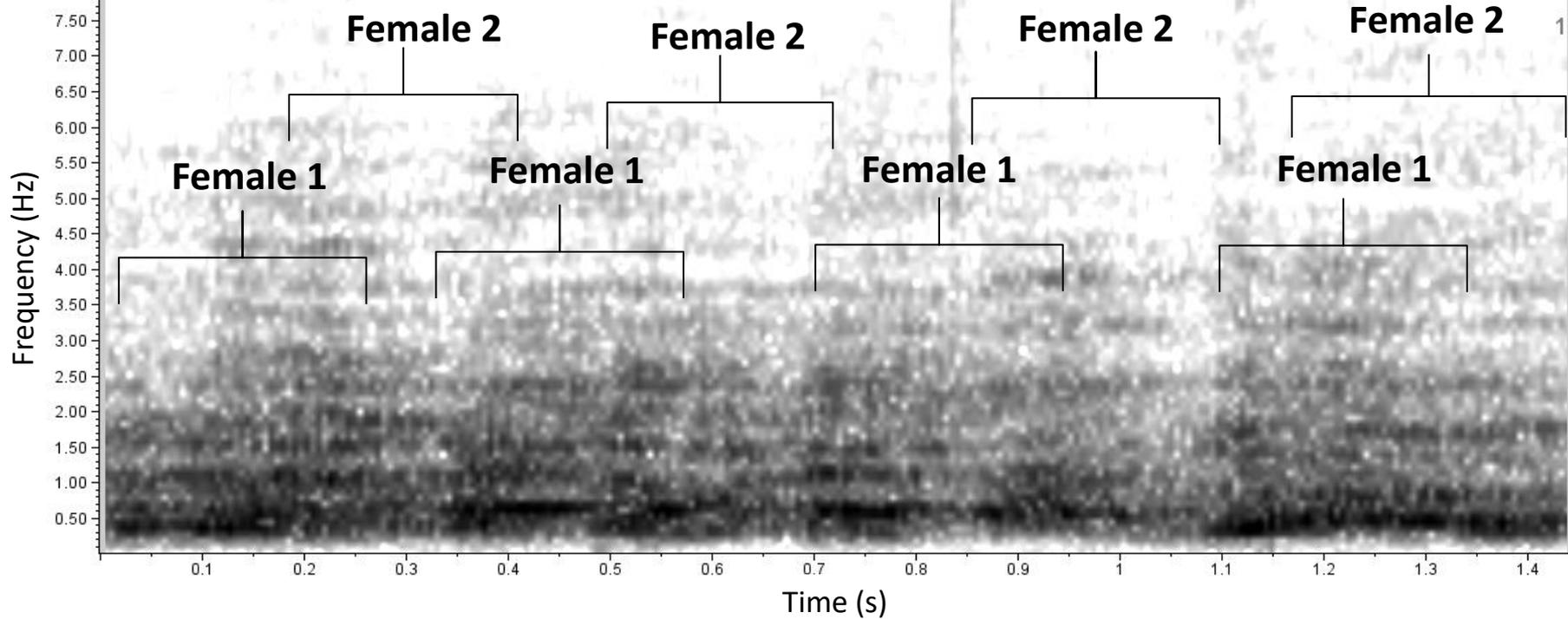
624 **Figure 3. Rates of vocal overlap vary with call types.** Plots of predicted counts the number of
625 overlapped calls on the estimated effect of overlapped calls on the "Call type" emitted by six study
626 groups of howler monkeys, Error bars represent the lower and higher confidence interval estimate of
627 the marginal effects (predicted counts) estimate.

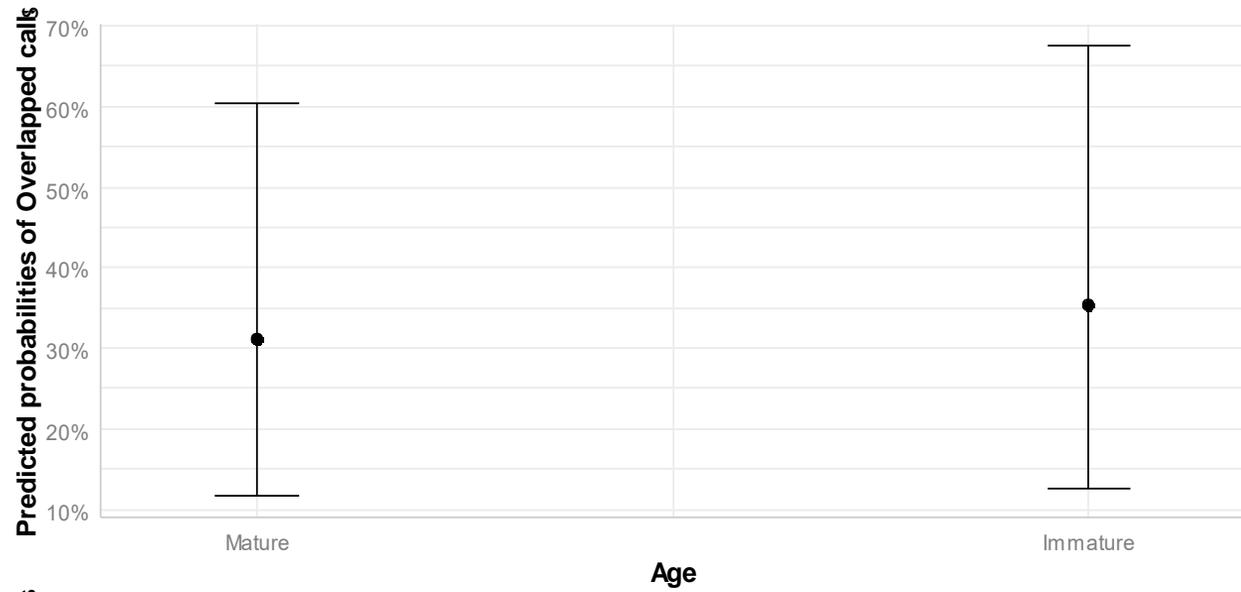
628 **Figure 4. Rates of vocal overlap vary with contexts.** Plots of predicted counts of the number of
629 overlapped calls on the "contexts" (Absent, distant and close neighbor) in four of our study groups of
630 howler monkeys. Error bars represent the lower and higher confidence interval estimate of the
631 marginal effects (predicted counts) estimate.

632 **Figure 5. Rates of vocal overlap vary with the targeted sex.** Plots of predicted counts of the
633 number of overlapped calls by males and females in relation with the sex of the preceding caller:
634 Female-Female (i.e., Female overlaps Female), Female-Male (i.e., Female overlaps Male), Male-
635 Female (i.e., Male overlaps Female), Male-Male (i.e., Male overlaps Male). Data come from two
636 study groups of howler monkeys. Error bars represent the lower and higher confidence interval
637 estimate of the marginal effects (predicted counts) estimate.

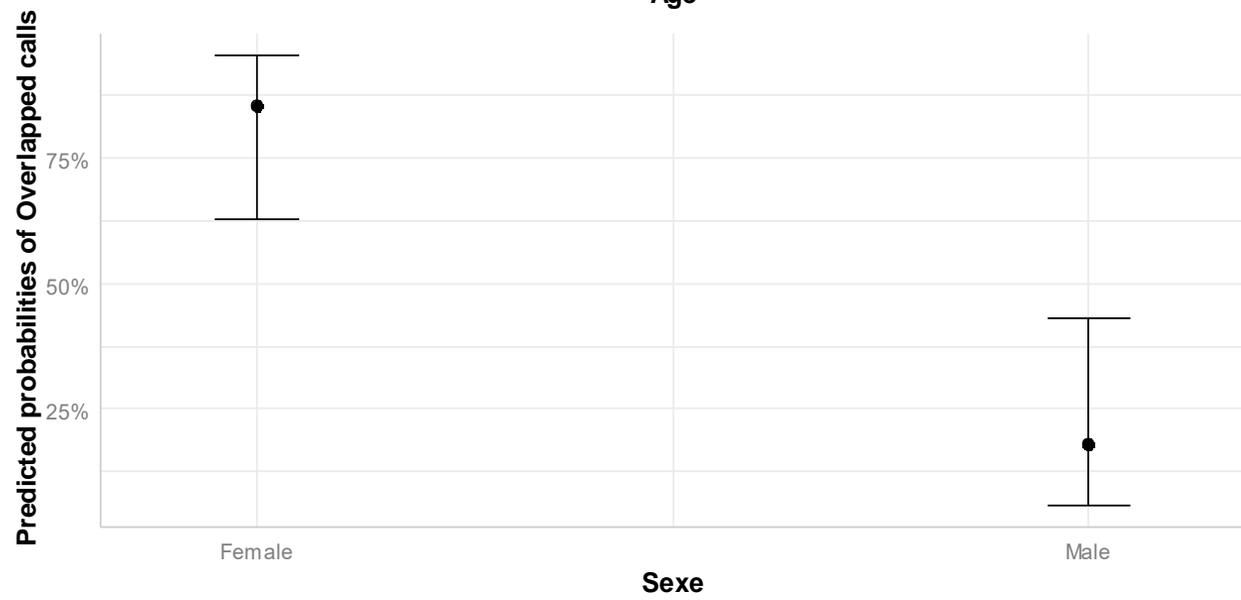
638 Graphical Abstract: Females overlapped most of their calls, while males took turns.

639

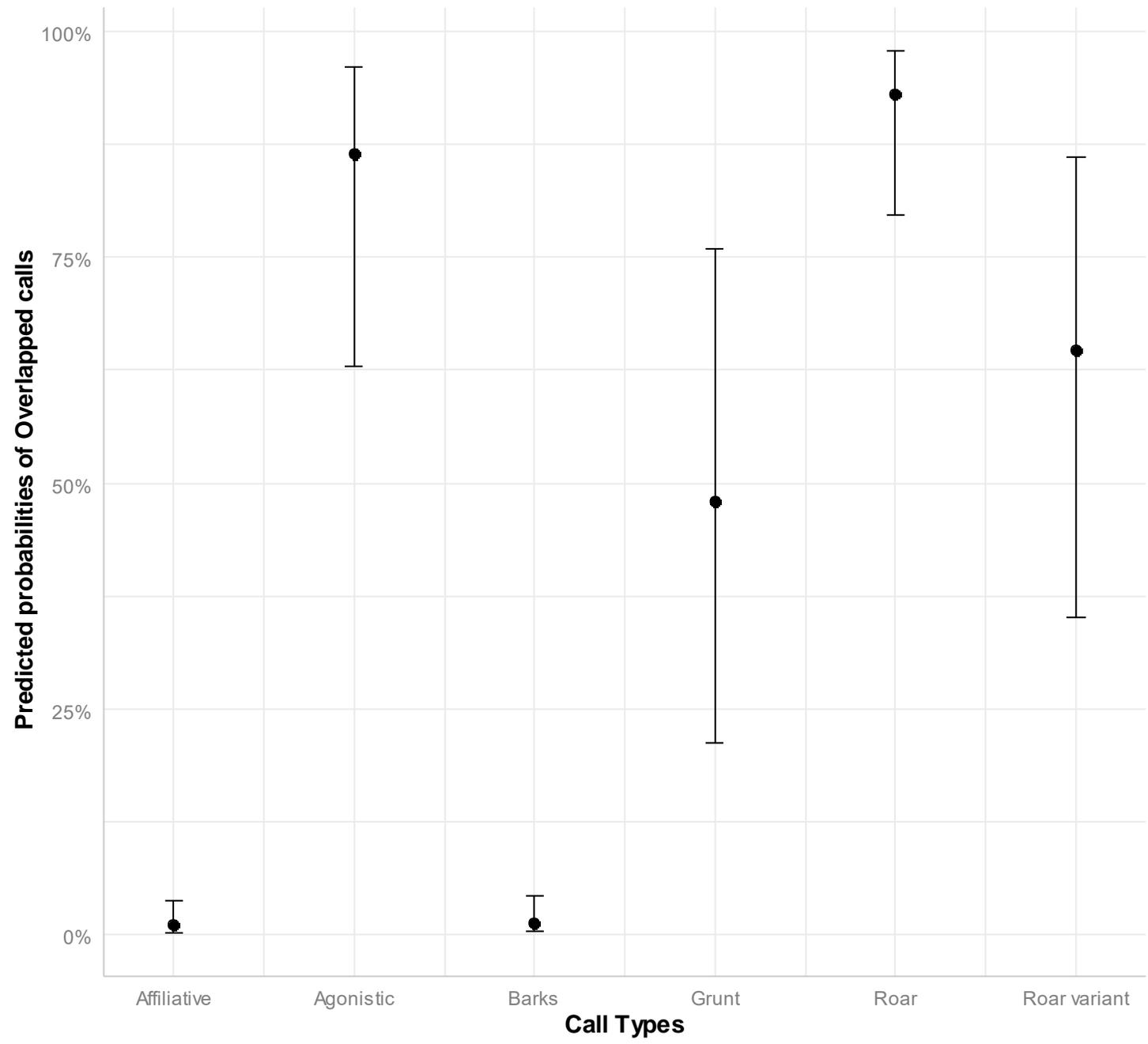


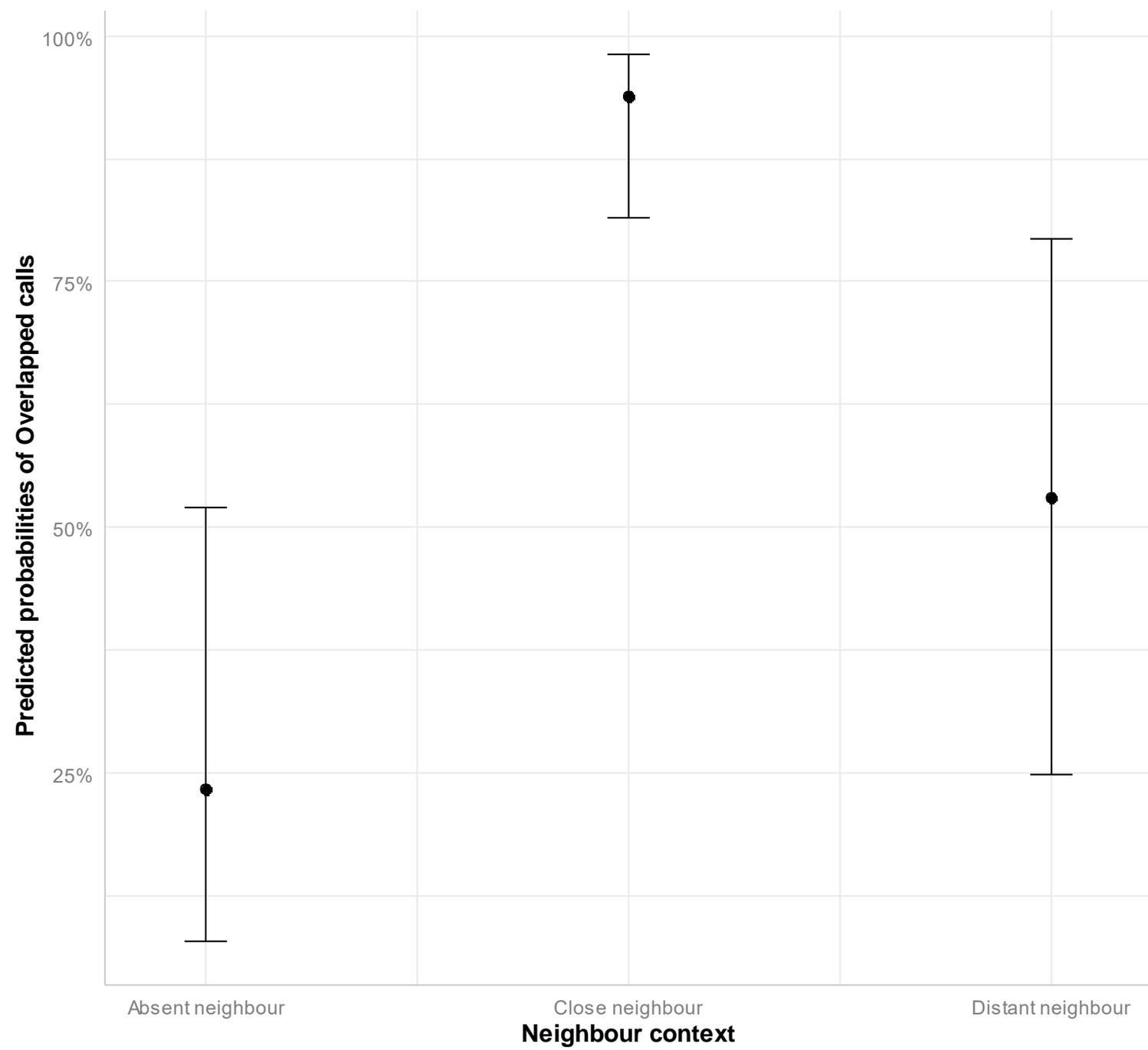


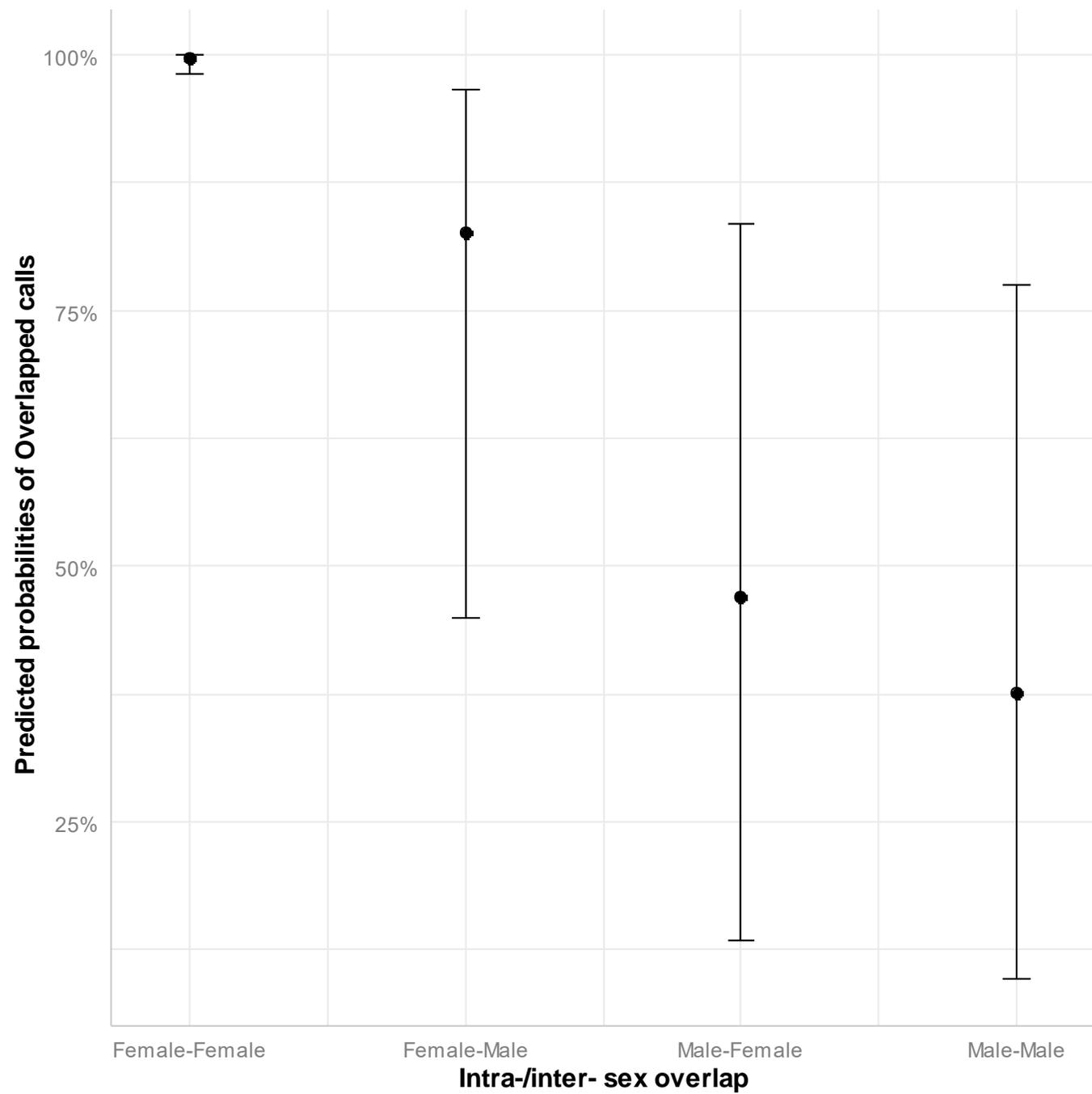
(a)



(b)







640 **APPENDIX 1**

641 Outputs of all GLMM models

642

643 **Results of the first full model (GLMM1) assessing the influences of callers' characteristics and**
644 **call types on vocal overlap**

Model 1= glmer(Calls overlapped ~ sex + age + call_type + (1 | group)+ (1 | sequence)+ (1 | identity))

Random factors	<i>Variance</i>	<i>SD</i>		
Identity (intercept)	9.599	3.098		
Sequence (intercept)	2.856	1.69		
Group (intercept)	1.49	1.22		
Fixed effects:				
	<i>Estimate</i>	<i>SD</i>	<i>Z value</i>	<i>Pr(> z)</i>
(Intercept)	-0.9353	0.656	-1.426	0.15394
sexM	-3.0965	0.2838	-10.912	<2.00E-16
ageIM	1.1531	0.2719	4.241	2.23E-05
Agonistic	6.3472	0.3603	17.615	<2.00E-16
Barks	0.7219	0.2594	2.783	0.00539
Grunt	5.2505	0.2653	19.791	<2.00E-16
Roar	6.6868	0.2579	25.923	<2.00E-16
RoarVariant	5.0251	0.2578	19.494	<2.00E-16
<i>AIC</i>	<i>BIC</i>	<i>LogLik</i>	<i>deviance</i>	<i>df.resid</i>
25516.1	25617.8	-12747	25494.1	76715

Factor 'Sex': 2 levels (M=Male, F=Female), Factor 'Age': 2 levels (M=Mature, IM=Immature), Factor 'Call type': 6 levels (barks, roars, roar variants, agonistic calls, affiliative calls, grunts)

645

APPENDIX 2

- Results of the second full model (GLMM2) assessing the influence of contextual variations on vocal overlap

Model 2 = glmer(Calls overlapped ~ neighbour_context + (1 | group)+ (1 | sequence)+ (1 | identity)

Random factors

	<i>Variance</i>	<i>SD</i>
Identity (intercept)	20.984	4.581
Sequence (intercept)	1.878	1.37
Group (intercept)	1.979	1.407

Fixed effects

	<i>Estimate</i>	<i>SD</i>	<i>Z Value</i>	<i>Pr(> z)</i>
(Intercept)	0.25153	0.84002	0.299	0.765
neighbour_Close	2.66069	0.08808	30.207	<2.00E-16
neighbour_Distant	0.23444	0.06012	3.899	9.65E-05

<i>AIC</i>	<i>BIC</i>	<i>logLik</i>	<i>deviance</i>	<i>df.resid</i>
37405.6	37460.4	-18696.8	37393.6	67730

Factor 'neighbour_context': 3 levels (neighbour Close, neighbour Distant, neighbour absent)

647 **APPENDIX 3**

648

649 **- Results of the third full model (GLMM3) assessing whether the sexes of the exchanging**
650 **partners influenced vocal overlap.**

651

Model 3 = glmer(Calls overlapped ~ suite + (1 | group)+(1 | sequence)+(1 | identity)

Random factors

	<i>Variance</i>	<i>SD</i>
Identity (intercept)	17.604	4.196
Sequence (intercept)	3.809	1.952
Group (intercept)	1.043	1.022

Fixed effects

	<i>Estimate</i>	<i>SD</i>	<i>Z Value</i>	<i>Pr(> z)</i>
(Intercept)	5.525	0.861	6.412	2.12E-09
FM	-4.066	0.215	-18.893	<2.00E-16
MF	-5.173	0.345	-14.979	<2.00E-16
MM	-5.927	0.342	-17.309	<2.00E-16

<i>AIC</i>	<i>BIC</i>	<i>logLik</i>	<i>deviance</i>	<i>df.resid</i>
20200.3	20261.1	-10093.2	20186.3	43539

Factor 'suite': 4 levels ('FF'= female overlaps female, 'FM'= female overlaps male, 'MM'= male overlaps male, 'MF'= male overlap female).

652