

17 **Abstract**

18 Recordings of sooty mangabeys (*Cercocebus torquatus atys*) in their natural environment were used
19 to compile the vocal repertoire of this species. All calls are described according to their acoustic
20 features and the behavioural context in which they occurred. Descriptions are supplemented by
21 quantitative measurements of call occurrence of all age-sex classes. This study was designed to
22 increase our understanding of the influence of phylogeny and habitat constraints on the acoustic
23 features of vocalizations by filling the gap of our knowledge about vocalizations of terrestrial old
24 world primates that live in dense rainforests.

25

26 **Introduction**

27 One important aspect in the study of the evolution of nonhuman primate vocal behaviour is to
28 uncover the selective pressures that shape the structure of vocalizations and determine the repertoire
29 morphology. Traditionally, repertoires have either been described as ‘graded’ or ‘discrete’, or a
30 mixture of the two (Marler 1967, 1976). A graded signal system is characterized by continuous
31 acoustic variation between and/or within signal types, with no obvious distinct boundaries that allow a
32 listener to discriminate easily between one signal type and another. Discrete repertoires, on the other
33 hand, contain signals with no intermediates between call types. Marler hypothesized that graded vocal
34 repertoires should evolve when individuals inhabit relatively open habitat and interact at high rates and
35 at close range with conspecifics. In contrast, discrete vocal repertoires should be favoured when
36 auditory signals must operate without accompanying visual or other contextual cues; for example, in
37 forest habitats or when being broadcast over long distances (Marler 1976). Marler also hypothesized
38 that long-distance calls should be acoustically distinct because other cues may be lacking.

39 Most information about the structure of vocal repertoires has been collected either on savannah-
40 dwelling old-world monkeys or arboreal new world monkeys or lemurs (e.g. Macedonia 1993; Schott
41 1975; Fischer & Hammerschmidt 2002; Cleveland & Snowdon 1982; Struhsaker 1967). However, to
42 obtain a comprehensive understanding of the effects of phylogenetic descent and habitat on the
43 acoustic structure of vocalizations, it is essential to accumulate information about related species living
44 in habitats with different demands on the acoustical features of vocalizations. For example, compared
45 to savannah dwelling monkeys, primates that live in forest habitats face the problem of sound
46 transmission through dense vegetation. Several studies have shown that vocalizations used for
47 defending territories or enhancing inter-group spacing have acoustical features that improve long-
48 distance transmission through rain forest environments (e.g. cottontop and Geoffroy's tamarins
49 (Cleveland & Snowdon 1982); langurs (Horwich 1976); gibbons (Deputte 1982); mangabeys (Waser
50 1982). The dominant energy of these calls usually falls between 500 and 2500 Hz, frequencies that
51 travel farther than higher frequency sounds (Marten & Marler 1977; Waser & Waser 1977)). In
52 contrast to calls that are used for long-distance communication, calls used in within group
53 communication typically are produced at higher frequencies and lower source levels.

54 Sooty Mangabeys (*Cercocebus torquatus atys*) are Old World monkeys that belong to the family
55 cercopithecidae. Traditionally, all mangabeys have been combined into the single genus *Cercocebus*
56 (Napier & Napier 1967) that was commonly divided into two species groups: the terrestrial torquatus-
57 group and the arboreal albigena-group. However, recent studies suggest that these species-groups are
58 paraphyletic (Barnicott & Hewett-Emmett 1972; Cronin & Sarich 1976; Disotell 1996; Fleagle &
59 McGraw 1999) and should be placed in two separate genera. Accordingly, the torquatus-group,
60 including sooty mangabeys, is assigned to the genus *Cercocebus*, which is most closely related with

61 mandrills and drills (*Mandrillus*), whereas the albigena-group belongs to the genus *Lophocebus*, which
62 is most closely related to baboons (*Papio*) and geladas (*Theropithecus*).

63 Sooty mangabeys are terrestrial, forest-dwelling monkeys that live in large multi-male-multi-female
64 groups. Considering their phylogenetic descent as well as the general features of sooty mangabey
65 social organization and the dense vegetation in the Taï forest, where visibility ranges between 5-20
66 meters, sooty mangabeys constitute an interesting species to fill the gap of our knowledge about the
67 acoustical structure of vocalizations of terrestrial Old World monkeys living in rainforests. We
68 describe the acoustic features of the most frequent vocalizations given by different sex-age classes and
69 examine the behavioural context in which specific call types are produced.

70

71 **Methods**

72 *Study site and subjects*

73 The study was carried out over a 16-month period (April 2000 – December 2001) on free-ranging
74 sooty mangabeys in the Taï National Park in Ivory Coast (6° 20 'N to 5°10'N and 4°20'W to 6°50'W).
75 The park is the last remaining major block of primary forest in West Africa and covers approximately
76 454,000 ha. Visibility ranges from 5 to 20 meters throughout the home range of our study group.

77 During the study period, group size ranged between 98 and 122 animals. All animals were well
78 habituated to human observers and recognized individually. The group has been under study since
79 1997.

80

81 *Data collection*

82 Behavioural data were collected by focal animal sampling (Altmann 1974). Focal samples were 15
83 minutes long with at least 60 minutes between consecutive samples of the same individual. During
84 observations, we used instantaneous sampling (Altmann 1974) to record the activity (foraging,

85 travelling, social interaction or resting) and the position of the focal animal relative to others. Spatial
86 positions were designated by the presence of other individuals in a circular area with a radius of 10
87 meters surrounding the focal animal. If there were other individuals on all sides, the focal was in the
88 centre position (c), if other individuals were on only one side, the focal was considered to be in a
89 border position (b), whereas if no other group member was within 10 meters, the focal was scored to
90 be in the periphery (p). Social interactions and vocalizations were recorded continuously (for details of
91 the ethogram see Range & Noe 2002).

92 Behavioural data were recorded by F. Range on adult females during the first study period (April –
93 August 00) and on juveniles during the second study period (May – December 01). Y. Meystre
94 collected behavioural data on adult males (October 00 – April 01).

95

96 All vocalizations were recorded opportunistically during the second study period (May – December
97 2001) using a Sony-DAT PCM-M1 recorder and a Sennheiser directional microphone (ME 68).
98 Whenever a call was recorded, information regarding the caller's identity, the behavioural context, and
99 the identity of the neighbours within 5 meters was determined. Behavioural context was described as
100 accurately as possible.

101

102 *Data analysis*

103 **1. Behavioural analysis**

104 Grunting time for each female was defined as the percentage of minutes during focal animal
105 sampling when the focal individual grunted at least once. We used the Wilcoxon matched pair test to
106 determine whether or not grunting was dependent on the spatial position of the focal animal within the
107 group (center vs. periphery or border).

108 We calculated hourly rates of vocalizations for different sex and age classes by dividing the total
109 number of calls heard during focal samples by the sum of the total observation time. Correlations
110 between dominance rank and rate of vocalizations were calculated using the Spearman rank
111 coefficient.

112

113 **2. Acoustic analysis**

114 To document the acoustic features of the sooty mangabey vocal repertoire we used only
115 vocalizations tape-recorded from adult individuals. A total of 737 calls were analysed. All statistical
116 analyses were performed on individual means.

117 Tape-recorded vocalizations of sooty mangabeys were categorized by ear. For those call types for
118 which only a small number of examples were recorded, the spectrographic analysis was performed
119 using Cool Edit (Syntrillium, Phoenix, AZ). We measured call duration, dominant frequency and the
120 number of syllables for these calls.

121 Vocalization types for which sample size were large were submitted to the SIGNAL sound analysis
122 system (Beeman, 1996) and a fast Fourier transform was conducted (grunts: 1024-pt FFT, time step: 3
123 ms, frequency resolution: 11 Hz; twitter: 1024-pt FFT, time step: 3 ms, frequency resolution: 46 Hz;
124 alarm calls: 1024-pt FFT, time step: 5 ms, frequency resolution: 46 Hz). The resulting frequency time
125 spectra were analysed with a custom software program, LMA 8.4 (Hammerschmidt 1990). The
126 program extracts different call parameters that describe the acoustic structure of each call. For the
127 present analysis we used the following two parameters:

128

129 1. Duration (ms): Time between the onset and end of a call.

130 2. Median of the first dominant frequency band (Hz): i.e. the median of the lowest dominant
131 frequency band calculated across all time segments of a call.

132

133 We used Mann-Whitney-U tests to compare acoustic features in different contexts. The presented
134 spectrograms were generated with Avisoft-SASLab.

135

136 **Results**

137 **Grunts.** Grunts are short vocalizations given in a variety of contexts (Figure 1). They were the most
138 frequent vocalizations given by all members of the group. The mean (\pm SD) duration of female grunts
139 was 119.67 ± 16.86 ms ($N = 34$). The median of the first dominant frequency band of grunts given by
140 females had a mean (\pm SD) of 263.52 ± 59.34 Hz ($N = 34$).

141

142 Figure 1

143

144 *Temporal structure*

145 A clear variation in temporal structure of call bouts was observed between adult males and adult
146 females. Adult males usually grunted several times in a row with regular intervals of about 186.58 ms
147 between grunts ($n = 5$)(Figure 2), whereas inter-call intervals in female grunts ranged from a few
148 seconds to a few minutes and varied between contexts.

149 In contrast to females, the overall rate that adult males grunted was negatively correlated with rank
150 (Spearman rank correlation $r_s = -0.745$; $n = 11$; $p = 0.0084$) (Meystre 2002).

151

152 Figure 2

153

154 *Behavioural context*

155 **Adult females:**

156 1. Foraging: Adult females often grunted when they were feeding or searching for food. Usually,
157 individuals gave several grunts with varying inter-call intervals from a few seconds up to several
158 minutes. Focal females grunted significantly more often when they were in a border or peripheral
159 position compared to situations when they were surrounded by other group members (Wilcoxon
160 matched pairs test, $n = 24$ females, $z = -4.143$, $p < 0.001$).

161 2. Social grunts not involving infants: Adult females and juveniles often grunted when they
162 approached or groomed another group member or when they were approached or groomed by
163 another individual.

164 3. Social grunts involving infants: Females and juveniles often approached, grunted and embraced
165 adult females with infants. In contrast to other grunts, individuals in this context always grunted
166 several times with a short, regular inter-call interval and usually incorporated another vocalization,
167 the twitter, into the sequence in this context.

168 4. Other: Grunts were also recorded when animals were travelling or sitting. However, small
169 sample sizes limited testing if these grunts differed from grunts given during foraging or social
170 interactions.

171

172 Grunts tape-recorded during social interactions (Figure 2B and 2C) such as approaching, embracing,
173 grooming and infant handling differed significantly in the median dominant frequency band from
174 grunts recorded during foraging (Figure 2A) but not in the mean grunt duration (Table 1).

175

176 Table 1

177

178 **Adult males:**

179 1. Dominance interactions: Adult males often grunted after they approached or threatened a
180 lower-ranking male and that male had reacted with submissive behaviour.

181 2. Male-female interaction: Adult females with sexual swellings often approached and presented
182 their swellings to adult males, who inspected the swellings but then turned away. When the female
183 left, the males usually grunted.

184 3. Foraging: Adult males occasionally grunted during foraging.

185

186 Due to small sample sizes no statistical analysis is available on the acoustic structure of grunts
187 given by adult males.

188

189 **Twitter.** A mangabey twitter could sound soft and melodic or sometimes a bit harder, almost harsh
190 (Figure 3). We currently don't know if these acoustic differences are due to individuality or context.
191 Twitters given by adult females during foraging and social interactions were always given as trains
192 with up to 23 syllable (median = 5.6, n = 33). Mean duration (\pm SD) of syllables was 50.26 ± 6.60 ms
193 (n = 33). Each syllable consisted of several, irregular modulated frequency bands ranging between 1
194 and 20 kHz. The mean (\pm SD) of the fundamental frequency band was 2026.68 ± 72.17 Hz (n = 33).

195

196 Figure 3

197

198 Twitters were only heard from adult females and juveniles of both sexes and usually given in
199 similar behavioural contexts as grunts:

200 1. Foraging: Adult females as well as juveniles of both sexes frequently twittered when they were
201 searching for food. Calls were often answered by other nearby animals either by emitting the same
202 call type or by grunting (Figure 3A).

203 2. Handling infant: As described above, individuals often twittered in combination with grunts
204 when they touched or handled an infant (Figure 3B).

205 3. Sitting between subgroups: During low-food availability, groups of sooty mangabeys are
206 usually widely dispersed when foraging and distances between small groups of individuals can
207 reach up to 100 meters. In these circumstances, adult females were often observed producing a
208 certain type of twitter (Figure 3C+D). Typically, this vocalization was accompanied by the
209 signaller looking towards the direction of another subgroup. As soon as a subgroup would
210 approach the other, the vocalizing female would stop calling and join the other animals.

211 No significant difference was found between the acoustical structure of twitters given during
212 foraging and twitters given when handling an infant regarding the number of syllables per call or the
213 median of the first frequency band (Table 2). However, the duration of syllables was significantly
214 longer during foraging compared to the duration of syllables given in social interactions (Table 2).

215

216 **Agonistic Vocalizations**

217 **Screams.** Screams are noisy vocalizations produced only in agonistic interactions. The duration of
218 screams emitted by adult females ranged in length from 0.22 to 3.121 seconds (mean = 1.35 s; n = 25).

219 They were comprised of both tonal and harsh elements. The tonal structure – fundamental with several
220 accompanying overtones – was often overlaid with wide-band noise up to 15 kHz. The intensity of this

221 noise differed between calls so that in some calls the harmonic structure was not visible at all (Figure
222 4A). In other calls, harmonic structure became visible in the beginning of a scream (Figure 4B) or
223 appeared occasionally throughout the call (Figure 4C).

224

225 Figure 4

226

227 Most screams were recorded from juvenile animals and adult females. Even though conflicts
228 between adult males were frequent, adult males rarely screamed. Screaming of adult and juvenile
229 animals occurred in two sub-categories of aggressive interactions.

230 1. Screams occurred during contact aggression when, after a conflict, the aggressor took the tail of
231 the loser into its mouth. During the tail bite, the loser crouched to the ground, screamed and often
232 defecated (Figure 4A). Screaming in this context was observed in all sex-age classes but rarely in
233 adult males. Overall rates were rather low for adult females (0.04 h⁻¹) and slightly higher for
234 juveniles (0.09 h⁻¹).

235 2. Individuals frequently screamed when they themselves were attacked but redirected the
236 aggression towards the aggressor. Most frequently, this behaviour was observed of juveniles
237 challenging either other juveniles or adult females (0.34 h⁻¹). Adult females often screamed when
238 they directed aggression towards adult or sub-adult males (Figure 4B und C), but also when
239 attacking other females or juveniles (0.03 h⁻¹). Only once we tape-recorded an adult male
240 screaming at another group member - an adult male (Figure 4D). The screaming of individuals in
241 this behavioural category often resulted in agonistic support from nearby animals.

242

243 Due to small sample size, we could not test whether the amount of bandwidth (noise) in a scream
244 was correlated with different patterns of agonistic interactions.

245 In contrast to older animals, infants screamed in a wide variety of behavioural contexts. They were
246 also observed to give screams that occurred in combination with harsh twitters when the mother
247 neglected or rejected their attempts to drink or to be carried as well as when alarm calls occurred
248 (Figure 4E).

249
250 **Growl.** All tape-recorded growls were comprised of several acoustically similar syllables that were
251 sometimes combined with other call types (see below). Each growl syllable consisted of a low
252 fundamental frequency band with several accompanying overtones (Figure 5A+B). The fundamental
253 frequency for adult female growls was 236.36 ± 171.89 Hz (mean \pm SD; $n = 11$). The upper limit of
254 the total energy of these calls ranged from 1000 to 11500 Hz for individual females (mean \pm SD =
255 4436.36 ± 2917.28 Hz; $n = 11$).

256
257 Figure 5

258
259 Individuals of all sex/age classes used this vocalization in agonistic interactions with other group
260 members. Typically, the higher-ranking individual in a conflict raised its eyebrows, stared and growled
261 at the opponent. Often, the aggressor would alternate this behavioural sequence with rapid turns of its
262 head towards other high-ranking individuals, which often resulted in agonistic support.

263

264

265 **Other threat vocalizations**

266 Four other vocalizations were recorded during agonistic interactions of group members. Three
267 different calls were heard in combination with growls during the same type of agonistic interaction as
268 described above. The “grumble” lasted between 266 to 482 ms and had a fundamental frequency
269 between 100 and 200 Hz (n = 3) Figure 6A). Two other calls (Figure 6B and C) were recorded only a
270 few times during agonistic encounters. The first, a “hoo” call, occurred between growl syllables and
271 had a rich harmonic structure. The latter call was very similar to the twitter given by adult females
272 sitting between subgroups and alarm calls and occurred mainly in intense conflicts.

273 The last call type, “wau” was heard five times during the entire study and was recorded only once
274 (Figure 6D). Adult males that watched an intense fight between other adult male members of the group
275 emitted the call.

276

277 Figure 6

278

279 **Copulation call.** Only females emitted these calls, and only when they had a sexual swelling. The
280 mean duration (\pm SD) of copulation calls was 7.47 ± 2.24 seconds (n = 21). Copulation calls were
281 given as phrases with up to 31 syllables (median = 15; n = 21). Usually, calls of individual females
282 were compromised of two tonal syllable types with different acoustical structures (Figure 7).

283

284 Figure 7

285

286 In Tai, sooty mangabeys exhibited a distinct mating season. Females emitted these calls mainly
287 during copulations. Males usually did not vocalize during copulation, but sometimes grumbled after
288 ejaculation.

289

290 **Long call (Whoop Gobble).** All long calls started with an introductory note, which could be
291 separated from the rest of the call by up to 4.45 seconds (Figure 8). After that, the call was comprised
292 of one or two types of tonal syllables. The first type was a long, frequency modulated syllable with a
293 frequency bandwidth of about 1200 Hz. The second type was much shorter, showed less frequency
294 modulation and had several harmonics reaching frequencies up to 5200 Hz ($n = 5$). While the first
295 syllable type was present in all analysed calls the second type was only present in two calls from two
296 different males. All long calls ended with a frequency-modulated call that had several harmonics. The
297 endnote was again separated from the main part of the call by several hundred milliseconds.

298

299 Figure 8

300

301 Long calls were given exclusively by adult males. The males would usually call several times and
302 often alternate long calls with alarm calls (see below). Long calls were often heard in the morning or
303 when another mangabey group was nearby. The call was also sometimes heard in combination with
304 sightings or actual attacks of predators.

305

306 **Alarm calls.** Alarm calls of adult females had a median duration of 383.33 ms and were
307 significantly shorter than alarm calls emitted by adult males, which had a median duration of 641.05
308 ms (Mann-Whitney $U = 19.50$; $n_1 = 21$; $n_2 = 7$; $p < 0.01$). Moreover, the median of the first dominant

309 frequency band was significantly higher in alarm calls given by adult females (2189 Hz) than in alarm
310 calls given by adult males (1573.67 Hz)(Mann-Whitney U = 5.00; $n_1 = 21$; $n_2 = 7$; $p < 0.001$).

311

312 Sooty mangabeys gave alarm calls mainly towards three different predators: snakes, eagles and
313 leopards.

314 1. Snakes: Sooty mangabeys have only been observed to react towards Gabon vipers (*Bitis*
315 *gabonica*). These snakes were found regularly (2-3 times per week) by group members and always
316 elicited alarm calls. Upon hearing the alarm calls, other mangabeys approached the vocalizing
317 animal, climbed 1 or 2 meters up into a tree and scanned the forest floor for the viper.

318 2. Eagles: One of the main predators of sooty mangabeys in Taï is the crowned eagle (Shultz &
319 Noë, 2000; Shultz, 2001) Although actual predation attempts were observed infrequently (3 times
320 in 6 months), the eagle was detected at least 4 or 5 times per week perching up in a tree or flying
321 over the canopy close to the group eliciting alarm calls by mangabeys.

322 3. Leopard: Leopards have been observed to attack members of our observation group several
323 times. Typically, sooty mangabeys jumped up into a tree upon hearing or seeing a leopard and
324 gave alarm calls.

325

326 We found no significant difference in duration or median of the first dominant frequency band
327 between male alarm calls given in three different contexts: eagle, group encounter and leopard
328 (Kruskal-Wallis Test; $H = 2.424$; $df = 2$; $p > 0.05$ and Kruskal-Wallis Test; $H = 0.157$; $df = 2$; $p >$
329 0.05). Alarm calls given by adult females in different contexts – eagle, viper and leopard – differed
330 significantly in duration (Kruskal-Wallis Test; $H = 8.272$; $df = 2$; $p < 0.05$) but not in the median of the
331 first dominant frequency band (Kruskal-Wallis Test; $H = 3.047$; $df = 2$; $p > 0.05$).

332

333 **Discussion**

334 The sooty mangabey vocal repertoire consists of nineteen vocalizations that differed from each
335 other either in their acoustical structure or in the behavioural context with which they were associated.
336 The number of audibly distinct calls given by sooty mangabeys is similar to the number of audibly
337 distinct call types given by other primate species (e.g. baboons (*Papio spec.*): 15 (Rowell & Hinde
338 1962); *Macaca fuscata*: 37 (Itani 1963); *Cercopithecus aethiops*: 36 (Struhsaker 1967); *Pan*
339 *troglodytes*: 25 (Goodall 1965)). However, it is likely that we missed some rare vocalizations due to
340 the limited scope of this study, and that the vocal repertoire of sooty mangabeys will have to be revised
341 over time.

342 With respect to acoustic features that improve sound transmission through dense vegetation, all long
343 distance vocalizations were compatible with our expectations and had their strongest energy within the
344 frequency range of 500 to 2500 Hz.

345 Sooty mangabeys use close-range vocalizations that seem very similar to vocalizations used by
346 savannah dwelling species (e.g. vervets and baboons). Acoustic analyses of grunts that were tape-
347 recorded in a variety of behavioural contexts showed differences in the acoustical structure of grunts

348 given in foraging and social contexts as has been demonstrated for other primate species (e.g. savannah
349 baboons (Cheney & Seyfarth 1982; Rendall et al. 1999). A more detailed acoustical analysis of
350 mangabey grunts will test whether these differences persist if we control for individuality and whether
351 more specific behavioural contexts can be distinguished. In contrast to grunts, twitters given by adult
352 mangabey females and juveniles are remarkably different from vocalizations emitted by savannah-
353 dwelling old-world monkeys, but are similar to vocalizations given by arboreal new-world monkeys
354 (e.g. *Samiri sciureus* (Winter et al. 1969)).

355 The comparison of the acoustical structure of vocalizations between species is particularly
356 interesting in regard to the factors that underlie repertoire morphology (Fischer & Hammerschmidt,
357 2002). It has been theorized that the acoustic structure of vocalizations is determined by the call's
358 functions (Marler 1965; Marler 1967). If vocalizations are used over long distances, they should be
359 discrete to reduce ambiguity between call types, whereas vocalizations that are emitted during face-to
360 face interactions can be more graded since other cues – visual and olfactory - are available to help the
361 receiver determine the signal's meaning. However, some recent studies also showed that these
362 predictions are not always met. The Barbary macaques' alarm calls, for instance, form an acoustic
363 continuum despite significant variation in relation to the stimulus that elicited the calling (Fischer et al.
364 1995). Even more puzzling, baboon alarm calls grade into their contact and contest calls (Fischer et al.
365 2001; 2002).

366 Several playback experiments have demonstrated, however, that although human observers describe
367 certain close-range calls as graded signals, monkeys perceive these calls in a more discrete manner and
368 react differently according to small differences in the acoustic structure (e.g. Cheney & Seyfarth 1982;
369 Rendall et al. 1999; Fischer 1998; Fischer et al. 2001b). Moreover, although alarm calls can be
370 acoustically discrete from each other, they also can grade into other, close range vocalizations that are

371 used in social contexts. For example, vervet snake alarm calls can easily be discriminated from vervet
372 eagle or leopard alarm calls, but they grade into chutters that are used in vervet close-range vocal
373 communication (Struhsaker 1967; Cheney 1984).

374 Sooty mangabeys are terrestrial, and most social interactions occur when individuals face each
375 other. According to the theory (Marler 1965; 1967), we expected that calls given in these situations
376 would be acoustically graded. Grunts, twitters, growls and screams seem to be acoustically discrete,
377 but gradations occur within call types.

378 In contrast to these close-range vocalizations, we would have expected alarm calls and calls that are
379 used to communicate between subgroups or neighbouring groups to be more discrete. Considering the
380 spectrograms of twitters, intermediate forms of twitters given in different contexts seem likely.
381 Moreover, twitters seem to grade acoustically into snake and possibly leopard alarm calls.
382 Furthermore, male alarm calls given in response to different predators did not differ in acoustical
383 structure from each other. This last result was probably due in part to high within-male variation in the
384 acoustical structures of alarm calls, and in part to the ambiguity of situations in the field. For example,
385 even though we heard a neighbouring group nearby, the tape-recorded alarm call might have been
386 given in response to an eagle that was not detected by the observer. However, if only contextual
387 ambiguity were responsible for this effect, no variation in acoustical features of alarm calls by adult
388 females would have been expected. We did, however, find that at least duration differed significantly
389 between alarm calls given towards different predators. A larger sample size of alarm calls from known
390 adult males and carefully designed playback experiments will help to elucidate this question.

391 In accordance with other studies on vocalizations of non-human primates, it seems that several
392 factors such as body size, phylogenetic descent, social structure and probably habitat may be important
393 in shaping a species' repertoire (Hohmann & Herzog 1985; Hauser 1993; Hammerschmidt & Fischer

394 1998; Fischer & Hammerschmidt 2002). Our study shows that sooty mangabeys use both vocalizations
395 reported for savannah dwelling old world species and vocalizations used by arboreal new world
396 species. Moreover, acoustic gradations seem to occur between and within call types, a result, puzzling
397 especially in regard to long-range vocalizations and the functional hypothesis about the evolution of
398 graded versus discrete vocalizations. However, play back experiments have yet to be conducted to
399 examine whether mangabeys recode the graded variation in vocalizations into discrete meaningful
400 units.

401

402

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411

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487 **Legends**

488

489 **Figure 1:** Representative grunts from one female sooty mangabey in three different contexts. A)
490 Foraging; B) Social, not involving an infant; C) Social, involving an infant.

491 **Figure 2:** A) Male grunting bout. B) One grunt from the same male.

492 **Figure 3:** A) Twitter of a foraging adult female. B) Twitter of an adult female handling an infant. C) and D)
493 Twitters from two adult females sitting between two subgroups.

494 **Figure 4:** A) Adult female screaming after tail bite from another, higher ranking female. B) Adult
495 female screaming at a sub-adult male C) Adult female screaming at an adult male D) Adult male
496 screaming at another adult male. E) Infant chattering and then screaming at its mother who resists the
497 attempts of her infant to nurse.

498 **Figure 5:** A) Adult female growling. B) Third syllable of the first call.

499 **Figure 6:** A) Adult female grumbling. B) Call element recorded during growling of a 5 year old male.
500 C) Call elements recorded during growling of juvenile female. D) “Wau” call of adult male.

501 **Figure 7:** Copulation call of an adult female with maximum sexual swelling.

502 **Figure 8:** Loud call (Whoop gobble) of the alpha male. I-Note = Introductory Note. E – Note =
503 Endnote.

504 **Figure 9:** A) Snake (Adult females). B) Snake (Adult male). C) Eagle (Adult female). D) Eagle (Adult
505 male). E) Leopard (Adult female). F) Leopard (Adult male). E) Group encounter (Adult male)

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507 **Table 1:** Parameters that were analysed to detect differences in the acoustic structure of grunts and
508 twitters between contexts. Contextual differences were tested with the Mann-Whitney U test.

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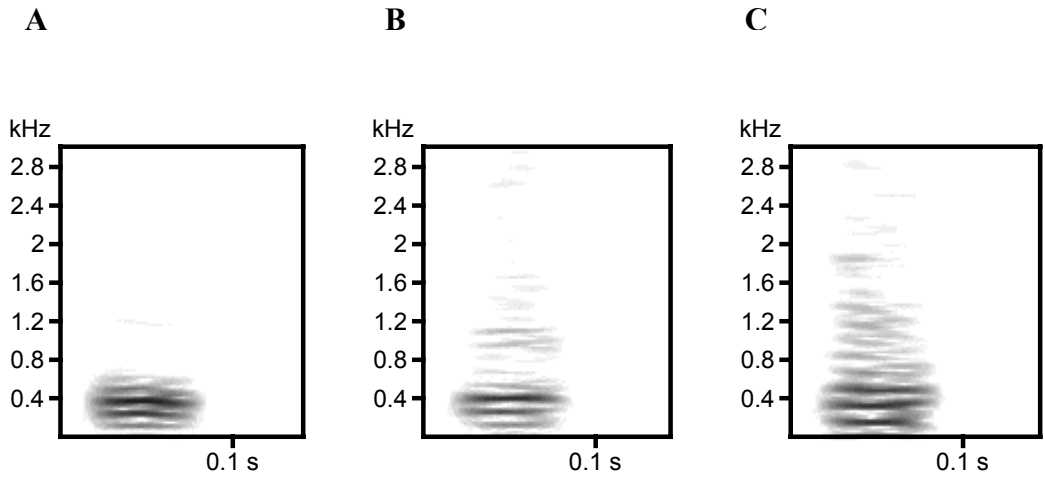
510 **Figures and Tables**

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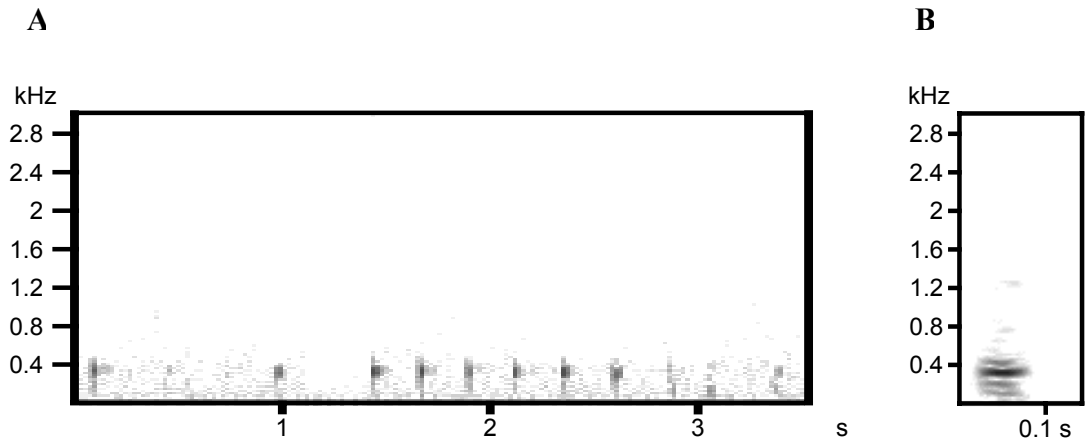


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516 **Figure 1**

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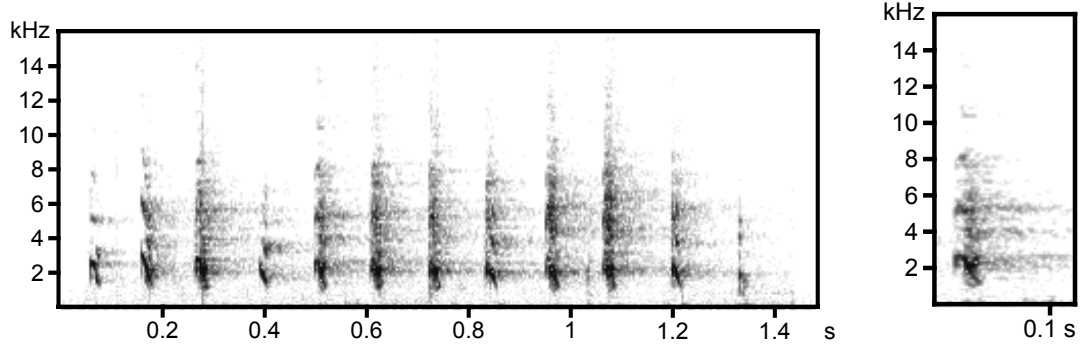


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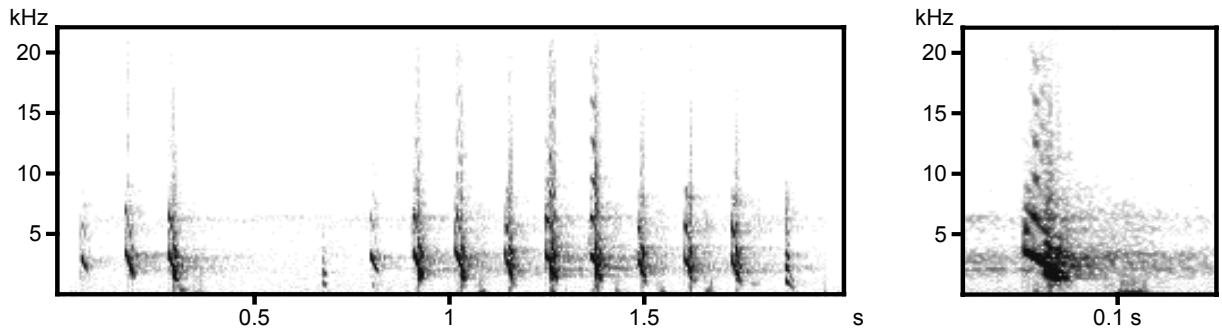
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A



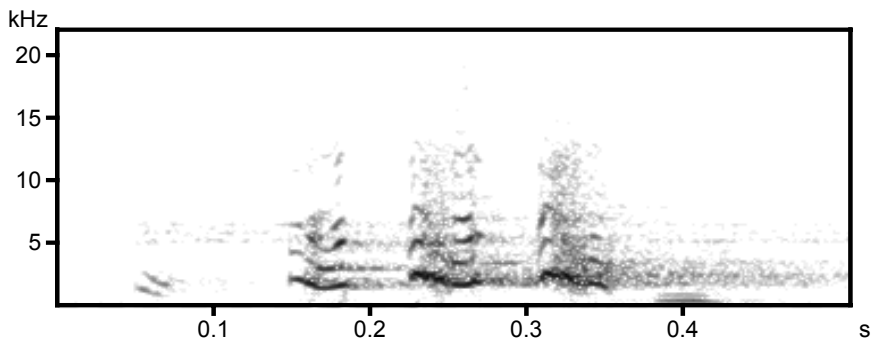
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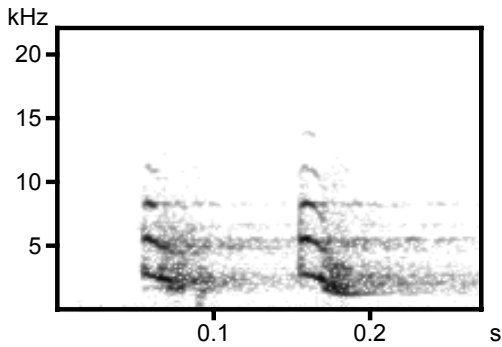
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C



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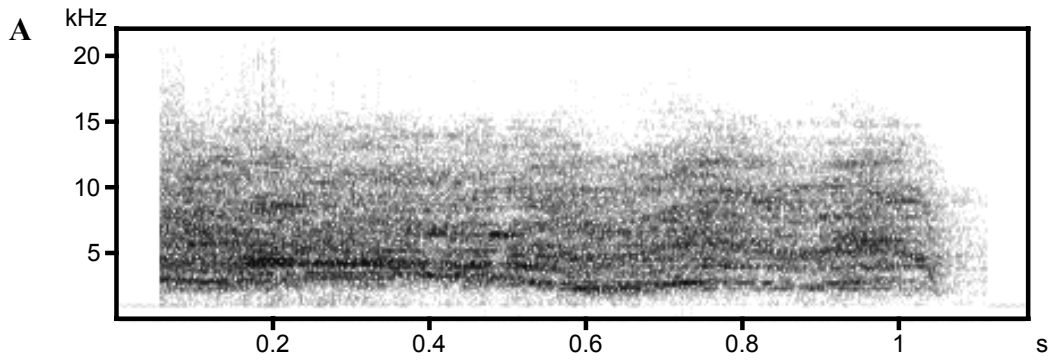
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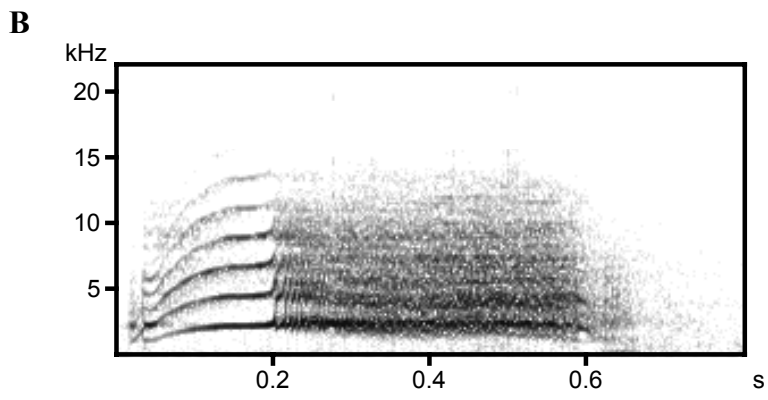
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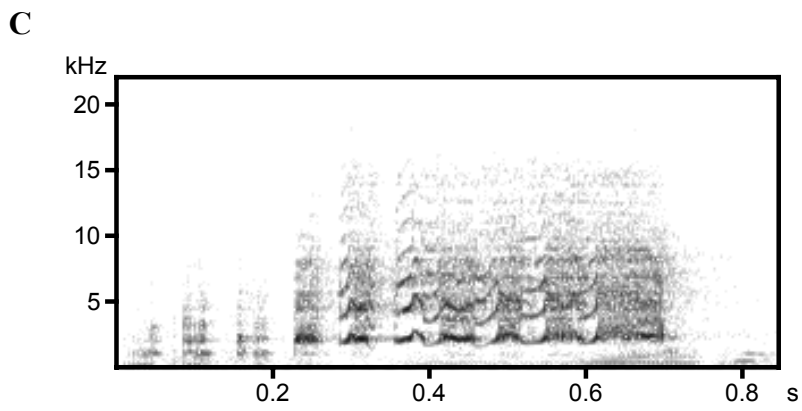
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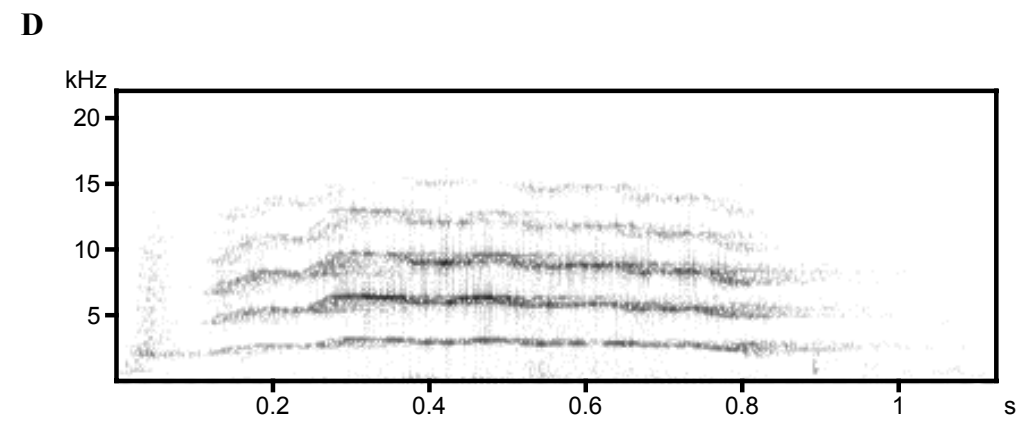
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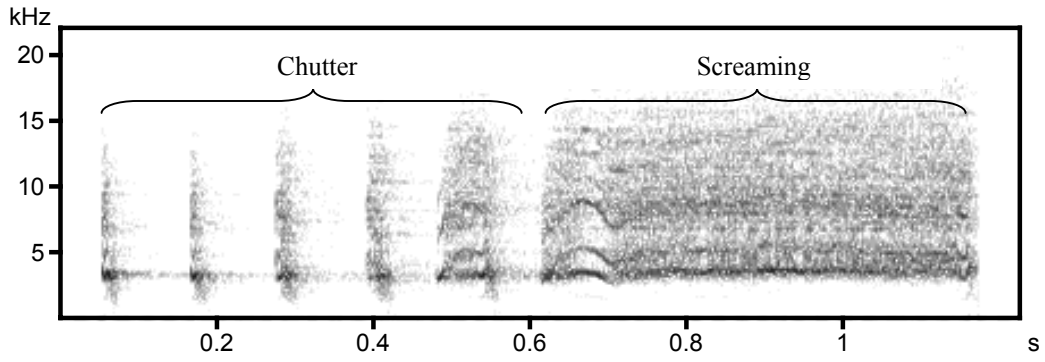


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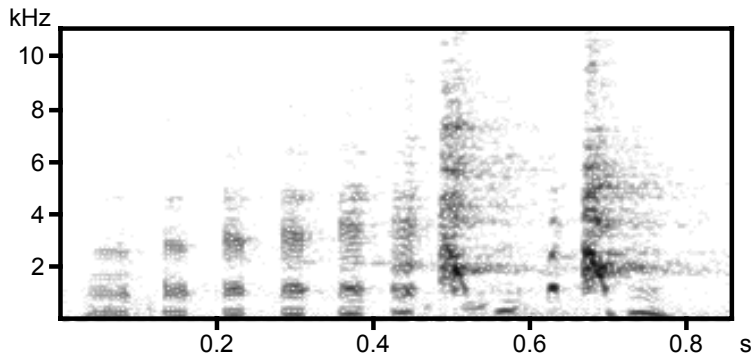
536 **Figure 4**

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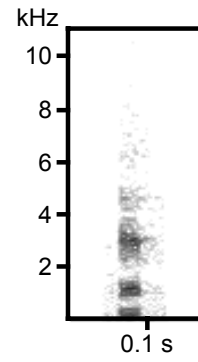
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541 **Figure 5**

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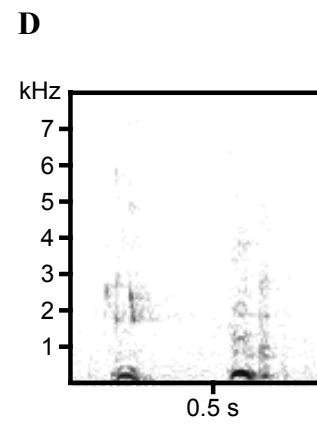
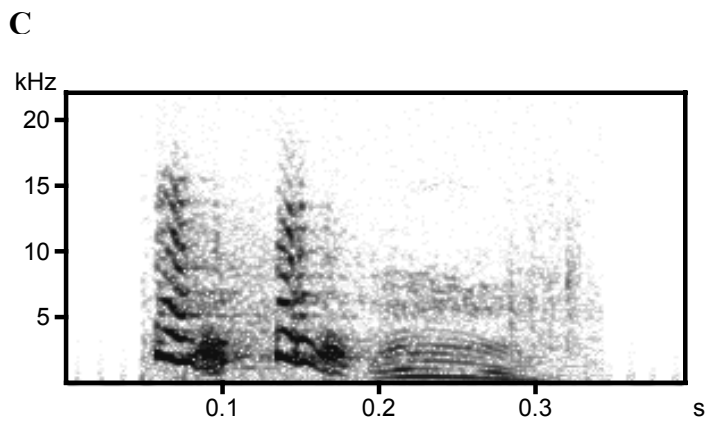
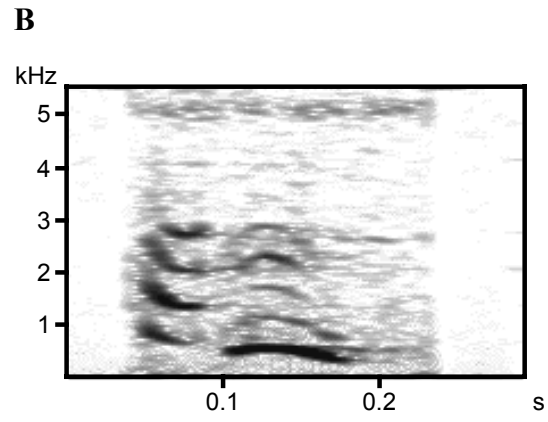
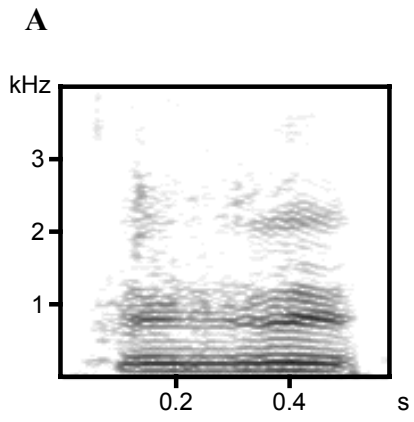
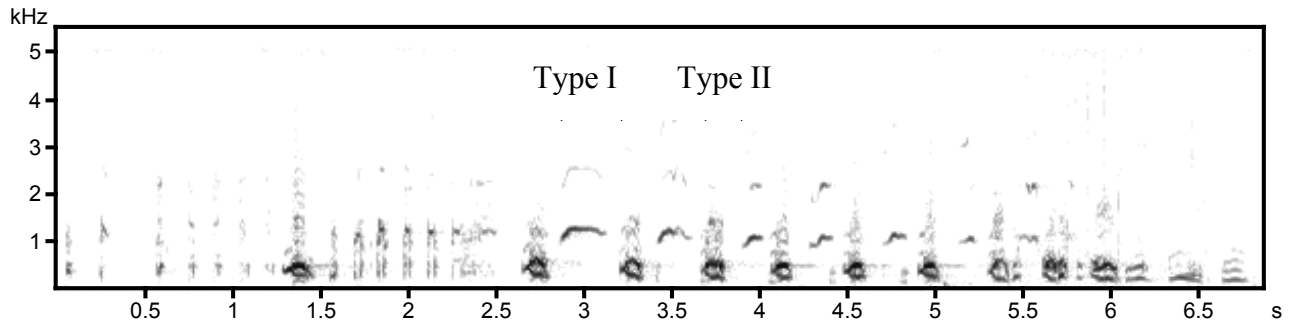


Figure 6

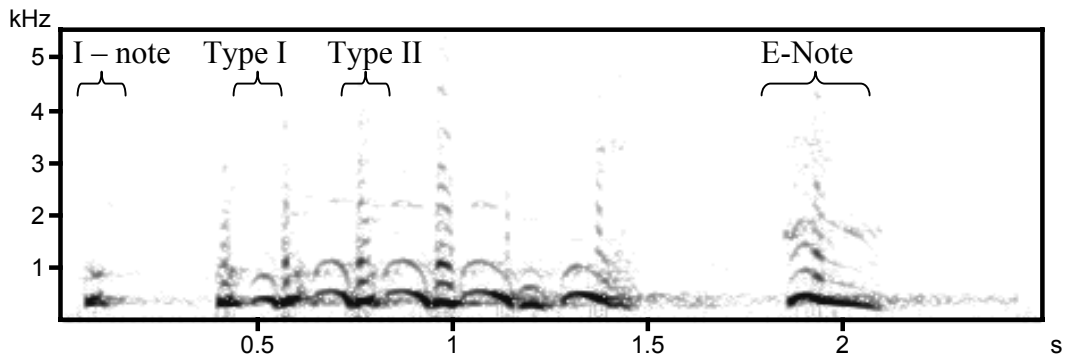
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552 **Figure 7**

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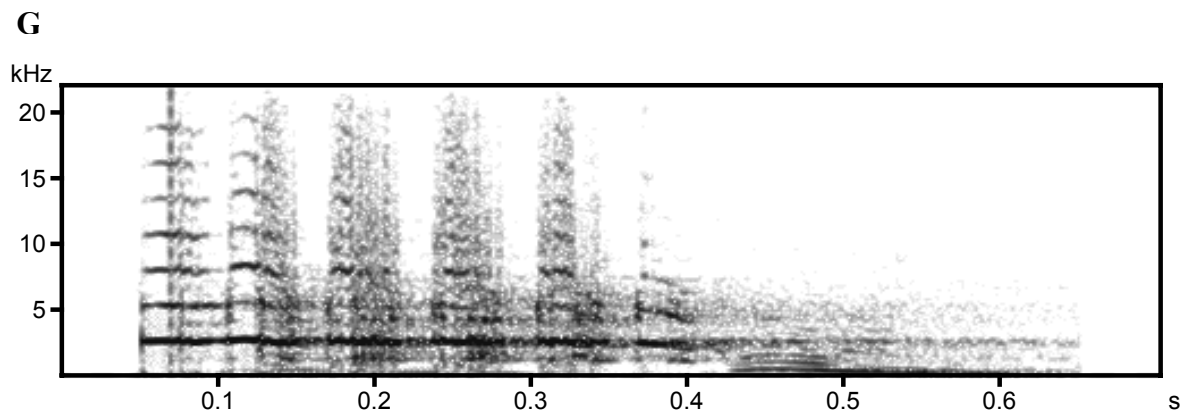
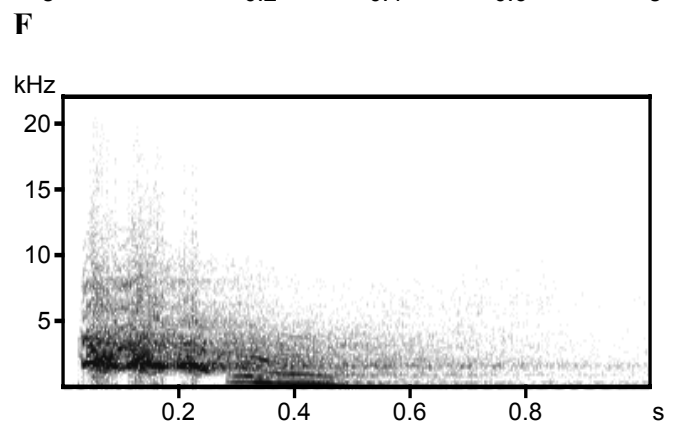
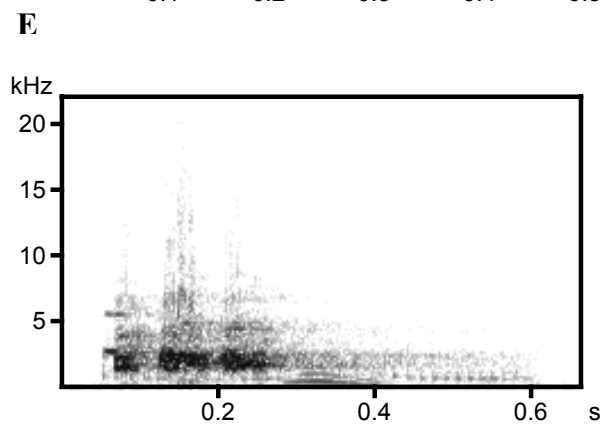
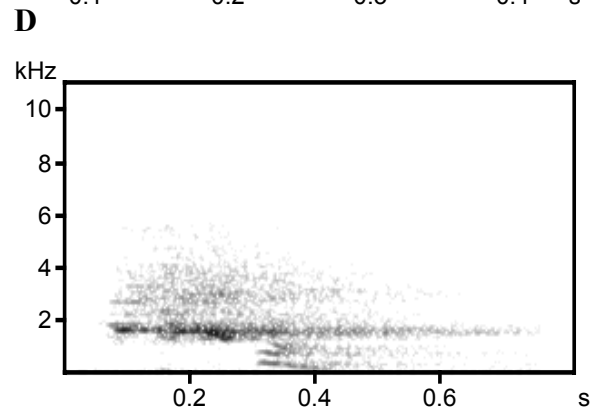
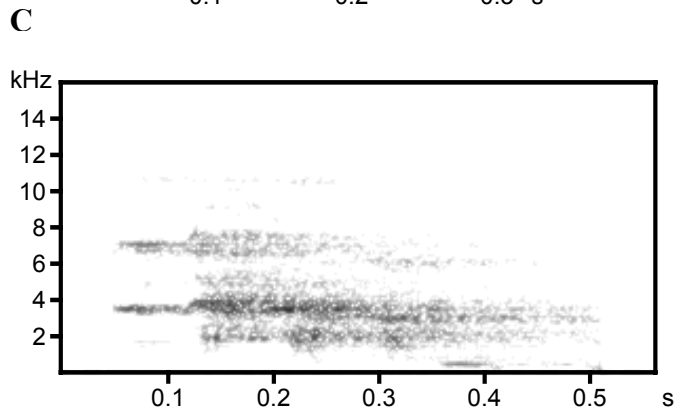
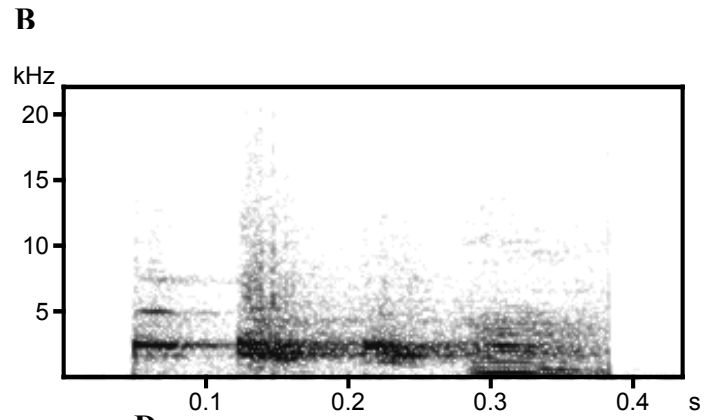
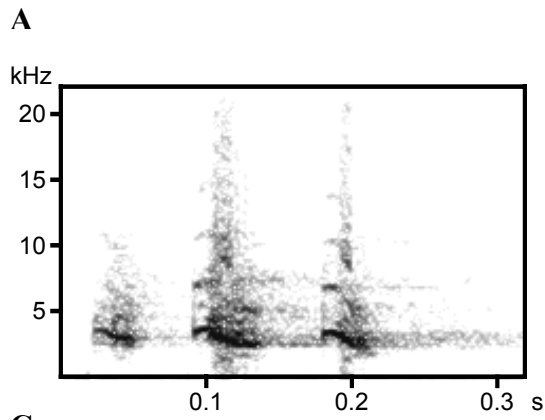


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555 **Figure 8**

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Figure 9

562 **Table 1**

Vocalization	Context	Social		Foraging		U	p
		Mean	n	Mean	n		
Grunts (Adult females)							
Median dominant frequency [Hz]		282.92	26	226.16	31	240.00	**
Duration [Ms]		114.9	26	116.5	31	383.50	Ns
Twitters (Adult females)							
Syllables per call		7.51	24	5.27	22	193.5	Ns
Median dominant frequency of syllables [Hz]		1997.31	24	2053.34	22	218.00	Ns
Duration of syllables [Ms]		35.38	24	60.8313	22	123.00	*

563 *p < 0.05, **p < 0.01