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1 Comparative analysis of the *Eulemur* vocal repertoire: a dynamic time warping

2 approach.

3

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20

21 **ABSTRACT**

22 The diversity of qualitative approaches and analytical methods has often undermined

23 comparative research on primate vocal repertoires. The purpose of the present work is

24 to introduce a quantitative method based on dynamic time warping to the study of

25 repertoire size in *Eulemur* spp. We obtained a large sample of calls of *E. coronatus*,

26 *E. flavifrons*, *E. fulvus*, *E. macaco*, *E. mongoz, E. rubriventer* and *E. rufus*, recorded

27 between 1999 and 2013 from captive and wild lemurs. We inspected recordings

28 visually using spectrograms, then cut and saved high-quality vocal emissions to single

29 files for further analysis. We extracted the acoustic features of all vocalizations of a

30 species using the Hidden Markov Model toolkit, an application of dynamic time

31 warping, then compared cepstral coefficients (a feature widely used in automatic

32 speaker recognition) pairwise. We analysed the results using Affinity Propagation

33 clustering. We found that *Eulemur* species share most of their vocal repertoire but

34 species-specific calls determine repertoire size differences. Repertoire size varied

35 from 9 and 14 vocalisation types among species, with a mean of 11. Group size is

36 thought to favour the evolution of vocal complexity at the species level but our results

37 suggest that this relationship should be reconsidered, as *Eulemur rubriventer* has the

38 largest vocal repertoire but shows a relatively small average group size when

39 compared to congeneric species.

40

41   **INTRODUCTION**
42

43   Vocal repertoires provide essential information to the study of how communication

44   systems evolve (Maynard Smith and Harper 2003). For example, studies of nonhuman

45   primate vocal communication have provided valuable contributions to the debate

46   about the basis for the evolution of language in humans (Dunbar 2009). Nonhuman

47   primate vocal repertoire size correlates with time spent grooming and with group size

48   (McComb and Semple 2005), providing support for the theory that the complexity of

49   human language has gradually evolved with the increase of social complexity

50   (Dunbar 2009). However, comparative studies of repertoire size are often undermined

51   by two factors. First, vocal repertoire data are derived from studies using different

52   methods (McComb and Semple 2005). Second, identification of the signal categories

53   have traditionally relied on human observers' assessment of differences among

54   vocalizations, and are thus subject to individual criteria. Although multivariate

55   techniques have demonstrated that such categories may be appropriate (*e.g.* Range

56   and Fischer 2004; Gamba and Giacoma 2007; Maretti *et al.* 2010; Fuller 2014),

57   human assessment of vocalization types may reflect differences perceived by humans

58   but not necessarily by the species (Green 1975; Hauser 1996; Fuller 2014).

59

60   New methodologies in the study of acoustic communication allow standardization

61   across large datasets with limited assumptions (Clemins *et al.* 2006). These methods

62   provide researchers with computer tools for exploring large databases without the

63   disadvantages of subjective *a priori* classification, and are often referred to as

64   'unsupervised' (Stowell and Plumbley 2014; Kogan and Margoliash 1998;

65   Stathopoulos *et al.* 2014). Among the many methods (Garcia and Reyes Garcia 2003;

66   Koolagudi *et al.* 2012), some used for automatic speech recognition, such as dynamic

67   time warping, are increasingly used to investigate animal communication. Dynamic

68   time warping has been useful for the classification of animal sounds in amphibians

69   (Chen *et al.* 2012), birds (Anderson *et al.* 1996; Trawicki *et al.* 2005; Clemins and

70   Johnson 2006; Ranjard and Ross 2008; Tao *et al.* 2008), marine mammals (Brown

71   and Miller 2007), and primates (Riondato *et al.* 2013). These methods can be used to

72   investigate the vocal repertoire across populations and species (Mercado III and

73   Handel 2012; Ranjard *et al.* 2010) and improve our ability to make inferences about

74   the evolution of human language (Fedurek and Slocombe 2011). Although

75   unsupervised classification cannot guarantee to classify calls in a way that is

76   meaningful to animals, it does ensure quantitative objective classification (Pozzi *et al.*

77   2010).

78

79   Due to their unique evolutionary history, lemurs are important subjects for

80   comparative studies of vocal communication and may provide insights into the

81   selective pressures that may have linked social and vocal complexity (Oda 2009).

82   True lemurs (*Eulemur* spp.) are conspicuously vocal and that their vocal repertoire

83   comprises low-pitched and high-pitched sounds (Petter and Charles-Dominique 1979,

84   Macedonia and Stanger 1994; Gamba and Giacoma 2005). The presence of various

85   call variants and combinations has also been demonstrated qualitatively (Macedonia

86   and Stanger 1994). Previous studies showed that vocal repertoire may differ between

87   species in *Eulemur fulvus* (Paillette and Petter 1978), *E. mongoz* (Curtis 1997), *E.*

88   *macaco* (Gosset *et al.* 2001) and *E. coronatus* (Gamba and Giacoma 2007).

89

90   The aim of this study was to investigate objectively the vocal repertoire across

91   *Eulemur* species to understand whether different species show different repertoire size

92   and vocalization types. We used an algorithm based on dynamic time warping to

93   assess sound similarity (Ranjard *et al.* 2010). We then applied cluster analysis to

94   identify groups of similar calls. To understand whether vocal repertoire size differs

95   across *Eulemur* species we applied the same analytical process to datasets for

96   different species, including the brown lemur (*E. fulvus*), the mongoose lemur (*E.

97   mongoz*), the black lemur (*E. macaco*), and the crowned lemur (*E. coronatus*), whose

98   repertoires were investigated in previous studies. We also analysed three species that

99   were not included in previous quantitative vocal repertoire studies: the red-bellied

100 lemur (*E. rubriventer*), the rufous brown lemur (*E. rufus*), and the blue-eyed black

101 lemur (*E. flavifrons*). Qualitative studies of *Eulemur* species have shown a degree of

102 similarity in the acoustic structure of the calls but shed little light on the quantitative

103 evaluation of similarities and differences, and suffered from subjective identification

104 of the call types (Macedonia and Stanger 1994; Gamba and Giacoma 2005). No

105 previous study has combined, to our knowledge, the study of lemurs' vocal repertoire

106 across different species using a quantitative unsupervised methodology.

107

108 We tested whether or not our unsupervised analyses identified the same vocalization

109 types as previously described. Human sound recognition mechanisms are robust

110 against noise changes and integrate many factors, resulting in accurate low-level

111 acoustic classification. Humans can differentiate calls as discrete types when an

112 unsupervised program, and possibly other species, would recognize a single type

113 (Hauser 1996; Lippmann 1997). We, therefore, predicted that unsupervised clustering

114 would find fewer vocalization types than previous studies. We also predicted that

115 more variable vocalization types mask variation at a lower level, as in a clustering

116 analysis of Guinea baboon calls (*Papio papio*, Maciej *et al.* 2013). Alternatively,

117   cluster analysis may highlight variants of vocal types showing a particular contextual

118   occurrence and other types which overlap with the *a priori* classification.

119

120   **Methods**

121

122   *Subjects, study sites, equipment, data collection and analysis.*

123   The recordings analysed for the purpose of this study were part of a large collection of

124   lemur sounds at the Department of Life Sciences and Systems Biology, University of

125   Torino. The recordings originate from various recording campaigns focused on lemur

126   vocal behaviour that took place between 1999 and 2013. They were recorded in the

127   wild and in captivity. The number of recording campaigns (hereafter corpora) and the

128   number of calls within a corpus vary with species. We only considered calls emitted

129   by adults. Detailed information about the corpora, sampling, data collection, and

130   associated references is given in the Supporting Information (Appendix S1).

131

132   *Clustering analyses*

133   To identify independent groupings and to visualize emerging vocal types (Nowicki

134   and Nelson 1990), we clustered vocalizations of each species on the basis of their

135   degree of dissimilarity, as measured by the pairwise comparison using dynamic time

136   warping (Ranjard *et al.* 2010). Detailed information about the calculation of

137   dissimilarity indices is given in the Supporting Information (Appendix S1). We used

138   the affinity propagation tool (Frey and Dueck 2007) of the *apcluster* package in R

139   (Bodenhofer *et al.* 2011; Hornik 2013). We labelled clusters with the 'representative'

140   vocalization (the 'exemplar'), which was automatically chosen during the affinity

141   propagation clustering process (see Supporting Information 1 (Appendix S2). The

142   cluster analysis used a squared negative Euclidean distance to measure dissimilarity

143   and identify clusters. This clustering algorithm is based on similarities between pairs

144   of data points. Affinity propagation clustering simultaneously considers all the data

145   points as potential cluster centers (exemplars), then chooses the final centers through

146   an iterative process, after which the corresponding clusters also emerge. Although we

147   did not define the number of clusters or the number of exemplars (Bodenhofer et al.

148   2011), the preference (p) with which a data point is chosen as a cluster center

149   influences the number of clusters in the final solution. Because affinity propagation

150   clustering does not automatically converge to an optimal clustering solution, we used

151   two external validation procedures. The first validation was based on the q-scanning

152   process (where q corresponds to the sample quantile of p, modified from Wang *et al.*

153   2007; see also Bodenhofer *et al.* 2011). We evaluated the clusters obtained using

154   different preferences using the Adjusted Rand Index (Hubert and Arabie 1985) to

155   assess the stability of successive cluster solutions (Hennig 2007). The second cluster

156   validation procedure was based on the Silhouette Index, which reflects the

157   compactness and separation of clusters in the final solution (Maciej *et al.* 2013).

158   When ranked and averaged between species both procedures indicated the median of

159   all the similarities between data points to be the optimal value for the preference. We

160   kept all the analysis settings the same across all datasets. We used the calls used as

161   exemplars in the final clustering solution to label the respective clusters.

162

163   A posteriori *evaluation*

164   We evaluated the agreement between the clustering analyses and the *a priori*

165   classification using the Adjusted Rand Index (Hubert and Arabie 1985; Table 1).

166

167 The terminology we use in the description of the polar dendrograms refers to Drout

168 and Smith (2013). Each branch of the polar dendrogram is termed a 'branch' or a

169 'clade' while the terminal portion of each clade is called a 'leaf'. Two-leaved clades are

170 called 'bifolious', but the number of leaves in a clade is not limited. While the

171 horizontal orientation of dendrograms is irrelevant, its vertical arrangement is

172 meaningful. The vertical position of the branch points indicates how similar or

173 different they are from each other. Branches departing from the same branch point are

174 most similar and belong to the same 'level'. In the polar dendrograms, levels are

175 numbered from the center (root) to the outer ring.

176

177 We also ran a stepwise Discriminant Function Analysis (sDFA, IBM SPSS Statistics

178 21; Lehner 1996) using the acoustic parameters measured (Supporting Information 2,

179 Appendix S3, see Gamba and Giacoma 2007 for details) using Praat (University of

180 Amsterdam, Boersma and Weenink 2014). We used the sDFA to identify the weight

181 of the different parameters contributing to the clustering process, although the

182 acoustic analysis does not necessarily simulate feature extraction during the dynamic

183 time warping. We ran the sDFA with the cluster information as the grouping variable

184 to estimate how the acoustic parameters contributed to the classification of calls using

185 leave-one-out cross-validation.

186

187 **Results**

188

189 *Vocal repertoire*

190 The cluster analysis showed variation in both the number of clusters and the

191 distribution of calls across clusters with species (Table 1; see Supporting Information

192 3, Appendix S 5).

193

194 *E. fulvus* vocalizations were grouped into 11 clusters (Fig. 1; Table 1). sDFA showed

195 an overall correct classification of 84.2% (cross-validated) when we used the clusters

196 as the grouping variable. Signal duration (on the first discriminant function) and the

197 first formant (F1, on the second discriminant function) had the highest loads in the

198 model (Table 2).

199 [Table. 1 HERE]

200 [Fig. 1 HERE]

201 *E. rufus* vocalizations grouped into 10 clusters (Fig. 2; Table 1). sDFA showed an

202 overall correct classification of 94.7% (cross-validated) when we used the clusters as

203 the grouping variable. Signal duration (on the first discriminant function) and

204 minimum Fundamental frequency (MinF0, on the second discriminant function) had

205 the highest loads in the model (Table 2).

206 [Fig. 2 HERE]

207 *E. rubriventer* vocalizations grouped into 14 clusters (Fig. 3; Table 1). sDFA showed

208 a correct classification of 73.5% (cross-validated) when we used the clusters as the

209 grouping variable. Signal duration (on the first discriminant function) and the second

210 formant (F2, on the second discriminant function) had the highest loads in the model

211 (Table 2).

212 [Fig. 3 HERE]

213 *E. mongoz* vocalizations grouped into nine clusters (Fig. 4; Table 1). sDFA showed a

214 correct classification of 69.2% (cross-validated) when we used the clusters as the

215 grouping variable. Signal duration and the third formant (F3) showed the highest

216 loading values on the first and the second discriminant functions respectively (Table

217 2).

218 [Fig. 4 HERE]

219 *E. coronatus* vocalizations grouped into 13 clusters (Fig. 5; Table 1). sDFA showed a

220 correct classification of 83.4% (cross-validated) when we used the clusters as the

221 grouping variable. Signal duration (on the first discriminant function) and the first

222 formant (F1, on the second discriminant function) had the highest loads in the model

223 (Table 2).

224 [Fig. 5 HERE]

225 *E. flavifrons* vocalizations grouped into 10 clusters (Fig. 6; Table 1). sDFA showed a

226 correct classification of 71.4% (cross-validated) when we used the clusters as the

227 grouping variable. Signal duration and the first formant had the highest loads on the

228 first two discriminant functions (Table 2).

229 [Fig. 6 HERE]

230 *E. macaco* vocalizations grouped into 10 clusters (Fig. 7; Table 1). sDFA showed a

231 correct classification of 82.0% when we used the clusters as the grouping variable.

232 Duration and F1 showed strongest correlation with the first two discriminant

233 functions, respectively (Table 2).

234 [Fig. 7 HERE]

235   [Table 2 HERE]

236   *External cluster evaluation*

237   The agreement between the *a priori* classification and the grouping identified by the

238   clustering analysis was relatively low across the species, ranging 0.18 - 0.32 (Table

239   1).

240

241   DISCUSSION

242   Our approach succeeded in categorizing vocalizations emitted by seven species using

243   dissimilarity indices. Dissimilarity indices have the advantage of being synthetic and

244   convenient but lack the detail of acoustic analysis (Maciej *et al.* 2013; Riondato *et al.*

245   2013). The discriminant model based on measures of temporal and frequency

246   parameters demonstrated that true lemurs calls can be assigned to independently

247   derived clusters identified on the basis of dissimilarity indices with a high rate of

248   correct classification. Furthermore, the accuracy achieved is in the range of that found

249   when the combination of pitch and filter features is classified *a priori* (Gamba and

250   Giacoma 2005; Gamba 2006).

251

252   *Diversity of the vocal repertoire*

253   True lemurs differ remarkably in their social organization and ecology (Tattersall and

254   Sussman 1998; Mittermeier *et al.* 2008). Thus we predicted differences in their vocal

255   communication signals, in line with previous studies (Macedonia and Stanger 1994;

256   McComb and Semple 2005). Our results support this prediction: we found that

257   different species show different repertoire size and vocalization types. The audio-

258   visual identification of vocal categories varied from a minimum of 7 vocalization

259   types in *E. coronatus* to 14 types in *E. fulvus*, *E. rubriventer*, and *E. mongoz*. The

260   overall range obtained by the unsupervised analysis was similar, ranging 9 - 14

261   clusters. Thus, audio-visual identification and unsupervised classification of

262   vocalization types gave comparable estimates.

263

264   Our results support the prediction that average group size influences vocal repertoire

265   size in part. Both audio-visual identification and unsupervised classification of

266   vocalization types provide a repertoire size estimate of 14 calls for *E. rubriventer*, an

267   estimate that is surprisingly larger than those observed for other species except *E.*

268   *coronatus*, which have group sizes is 8.4 (Kappeler and Heymann 1996), while *E.*

269   *rubriventer* has a mean group size of just 3 (Overdorff 1996) or 3.2 (Kappeler and

270   Heymann 1996). *E. mongoz* have a similar average group size of 3.0-3.5 (Kappeler

271   and Heymann 1996; Nadhurou et al. 2015) and show a repertoire size of 9 calls.

272   Several authors have suggested a relationship between a species' social organization

273   and its communication, proposing that an egalitarian social structure or stable social

274   groups may favor diversity in communication signals (Mitani 1996). *E. rubriventer* is

275   the only species we studied to have a stable, pair-bonded group structure (Tecot

276   2008). The other species live in one-male, multi-female groups or multi-male, multi-

277   female groups (Fuentes 2002). The social organization in *E. mongoz* varies between

278   populations, and includes both pair bonding and one-male, multi-female groups

279   (Fuentes 2002). The larger distribution of *E. rubriventer* may also influence the

280   diversity of vocal communication, as may the fact that we included only captive *E.*

281   *rubriventer* in the analysis. However, vocal repertoire appears to be consistent across

282   captive, wild-caught individuals (Colombo, unpublished data), suggesting that other

283 factors may have a stronger effect than the distribution range size. The strong

284 relationships between repertoire size and stable social organization have been

285 proposed for facial expressions (Preuschoft and van Hooff 1995) and the rate of vocal

286 emissions (Mitani 1996), and further studies are needed to clarify whether pair-

287 bonding also 'places a selective premium' (Mitani 1996, p. 246) on vocal repertoire

288 size. In support of this proposal, pair-bonding is considered a key factor favoring the

289 convergent evolution of complex singing displays (Geissmann 2000; Torti *et al.* 2013)

290 in the 'singing primates' (*Indri indri*, *Tarsius* spp., *Presbytis* spp., and Hylobates spp.,

291 Haimoff 1986; *Indri indri*, Bonadonna *et al.* 2014).

292

293 We predicted that the unsupervised procedure would recognise a lower number of

294 vocalization types. This was true for *Eulemur fulvus* (11 in the unsupervised analysis

295 versus 14 in the audio-visual *a priori* assessment), *E. mongoz* (9 vs. 14), *E. rufus* (10

296 vs. 12) and *E. macaco* (10 vs. 11). The repertoire estimate derived from a previous

297 study of *E. macaco* (N = 13; Gosset *et al.* 2001) exceeds both that observed during the

298 reassessment process (N = 10) and the result of the cluster analysis (N = 10).

299 Although the calls in our sample may be incomplete, we suspect that this discrepancy

300 arose due to the different criteria used to assess vocalization types in these studies.

301

302 Our prediction that the unsupervised procedure would recognise a lower number of

303 vocalization types was not supported in two cases: *Eulemur coronatus* (13

304 unsupervised versus seven audio-visual vocal types) and *E. mongoz* (14 vs. nine). In

305 both cases, the unsupervised procedure recognized more than one type of alarm call.

306 Previous studies of these species estimated a vocal repertoire size of 15 vocalizations

307   for *E. mongoz* (nine validated using sDFA; Nadhurou et al. 2015) and 10

308   vocalizations for *E. coronatus* (all validated using DFA, Gamba and Giacoma 2007).

309   It is clear that different methods led to different estimates, but interesting that, in

310   principle, dynamic time warping allows the identification of vocalization types using

311   a smaller number of calls than sDFA. Whether these differences in vocal repertoire

312   size reflect different arousal states or contexts is an interesting direction for future

313   research.

314

315   *Cluster versus* a priori *classification*

316   Agreement between the clustering process and the *a priori* criteria was low, with

317   values of the Adjusted Rand Index ranging between 0.18 (in *E. rubriventer*) and 0.32

318   (in *E. coronatus* and *E. macaco* and *E. rufus*). This supports the prediction that

319   unsupervised clustering of the vocalizations would not find the vocalization types

320   identified in previous studies. However, despite the differences with the *a priori*

321   classification, the clusters obtained using dynamic time warping-generated

322   dissimilarity indices revealed a remarkable potential for grouping calls on the basis of

323   acoustic measurements of different parameters. Among the parameters, duration

324   showed the heaviest loadings on the first discriminant function. Thus, the

325   mismatching between the *a priori* classification and cluster analysis is in line with the

326   suggestion that humans tend to recognize as discrete vocal types sounds that may be

327   grouped into a single type when perceived by other species or classified by

328   quantitative analyses (Hauser 1996).

329

330   Both duration and formants contributed to the identification of clusters in almost all

331   the species considered. Formants are known to be crucial for the identification of

332   vocalization types (Gamba 2014; Gamba and Giacoma 2007; Giacoma *et al.* 2011)

333   and have the potential to provide listeners with individual and species-specific cues

334   (Gamba *et al.* 2012a).

335

336   Snorts, clicks, and hoots were not selected as cluster representatives and were often

337   grouped with different vocalization types to form fairly dishomogeneous clusters.

338   This result is consistent across the species and is in line with previous data which

339   suggest that low-pitched calls may be part of a graded system more than discrete

340   emissions (Gamba and Giacoma 2007). Identifiable vocalization types are common,

341   but calls with intermediate acoustic structure may also occur and may be either

342   'oversplit' by human listeners or not recognized as discrete by the unsupervised

343   methodology we adopted. *Eulemur* low-pitched calls (grunts, clicks, grunted hoots,

344   hoots, snorts, and possibly long grunts) are usually classified as contact calls (Rendall

345   2000; Gamba and Giacoma 2005; 2007; Gamba *et al.* 2012a; 2012b; Pflüger and

346   Fichtel 2012). These low-pitched signals, especially grunts, are the most frequently

347   emitted call type in *Eulemur* (Gamba and Giacoma 2005; Gamba *et al.* 2012a; Pflüger

348   and Fichtel 2012). However, whether acoustic variation in low-pitched signals plays a

349   role in encoding information other than emitter position is still unclear (Pflüger and

350   Fichtel 2012).

351

352   The context of call emission is a powerful indicator of their social function and may

353   provide crucial information to the investigation of acoustic structure (Rendall *et al.*

354   1999; Gros-Louis *et al.* 2008). Future studies are necessary to explore the contextual

355   variation of the vocalization types, how the occurrence of vocal signals relates to their

356   acoustic structure, and how this information can be integrated into unsupervised

357   analyses.

358

359   Although there was low agreement between cluster analysis and *a priori*

360   classification, distinct types of grunts and/or grunted hoots emerge in all species. In

361   addition, grunts emitted by *E. coronatus* are identified as three different types. Long

362   grunts, which are reported to denote contexts of disturbance and potential territorial

363   predation, or are emitted during locomotion (Gamba and Giacoma, 2005; 2007;

364   Pflüger and Fichtel 2012), occur in *Eulemur mongoz* and *E. fulvus*. Associations

365   between low-pitched calls and tonal calls emerged as distinct clusters (grunt-tonal

366   calls, long grunt-tonal calls) in all species except *E. rufus*, and have been reported for

367   many species (Macedonia and Stanger 1994).

368

369   Our findings support the prediction that variation in particular vocal types may mask

370   variation at a lower level, in agreement with a study of Guinea baboon calls (Maciej et

371   al. 2013). In baboon calls, variation in screams was stronger than for other

372   vocalization types. In five of six *Eulemur* species, we found that screams represented

373   more than one (usually homogeneous) cluster (*Eulemur flavifrons* did not emit

374   screams in the same situation in which other species emitted them). In *Eulemur fulvus*

375   and *E. rufus*, we identified three clusters of territorial calls, while alarm calls formed

376   three clusters in *E. coronatus* and five clusters in *E. flavifrons*. The fact that cluster

377   analysis identified more than one cluster of alarm calls, screams, and territorial calls

378   indicates variability that has not been reported in previous studies (Macedonia and

379   Stanger 1994; Gamba and Giacoma 2007). These results represent an operationally

380   useful indication for future studies, which may link vocal variation with factors such

381   as level of arousal, social interactions or audience composition (Fichtel and

382   Hammerschmidt 2002; Stoeger *et al.* 2011; Slocombe and Zuberbühler 2007; Clay

383   and Zuberbühler 2012).

384

385   In conclusion, dynamic time warping appears to be a promising method for deepening

386   our knowledge of how lemurs encode information in their vocal signals, and allows

387   the objective identification of vocalization types. We envisage the use of unsupervised

388   classification in different circumstances, including field studies. For example, various

389   researchers report that the classification of calls to be used in playback experiments is

390   particularly challenging. Acoustic analysis may reveal that recorded calls may in fact

391   be different signals (Rendall *et al.* 1999). Researchers can face the problem of

392   classifying calls in different groups when in the field. In these situations, the

393   unsupervised classification of a small number of calls can be very helpful to provide

394   the investigator with an interpretable quantitative analysis, which may result in

395   improved experimental design and aid in the evaluation of the results (Seiler *et al.*

396   2013).

397

409

410   Supporting Information Online Resource 1 (Appendix S1 and S2), Online Resource 2

411   (Appendix S3), Online Resource 3 (Appendix S4 and S5), and Online Resource 4

412   (Appendix S6) are available online.

413

414
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707

FIGURE LEGENDS

709

710 **Fig. 1** Polar dendrogram (center) showing how vocalizations of *Eulemur fulvus* cluster
711 together (see Supporting Information 3, Appendix S4 for a detailed description of cluster
712 topology). For each cluster, we show a spectrogram (the horizontal axis represents time; the
713 vertical axis represents frequency) of the exemplar chosen during the affinity propagation
714 process. All spectrograms are generated in Praat with the following parameters: window
715 length: 0.025 sec, time range as shown (0.25-2.50 sec); frequency range: 0-10500 Hz;
716 dynamic range: 35-45 dB. The bar indicates 1 sec duration. Exceptions are indicated as
717 follows: * for 1.25 sec, ** for 1.50 sec, *** for 2.50 sec. Values in parentheses indicate the
718 percentage of the exemplar's vocalization type in a cluster. Additional information is given in
719 Supporting Information 3 (Appendix S4 and S5) and 4 (Appendix S6).

720 **Fig. 2** Polar dendrogram (center) showing how vocalizations of *Eulemur rufus* cluster
721 together (see Supporting Information 3, Appendix S4). For each cluster, we show a
722 spectrogram of the exemplar chosen during the affinity propagation process. All spectrograms
723 are generated in Praat with the following parameters: window length: 0.025 sec, time range as
724 shown (0.25-2.00 sec); frequency range: 0-10500 Hz; dynamic range: 35-45 dB. The bar
725 indicates 1 sec duration. Exceptions are indicated as follows: * for 1.25 sec, ** for 1.75 sec,
726 *** for 2.00 sec. Values in parentheses indicate the percentage of the exemplar's vocalization
727 type in a cluster. Additional information is given in Supporting Information 3 (Appendix S4
728 and S5) and 4 (Appendix S6).

729 **Fig. 3** Polar dendrogram (center) showing how vocalizations of *Eulemur rubriventer* cluster
730 together (see Supporting Information 3, Appendix S4). For each cluster, we show a
731 spectrogram of the exemplar chosen during the affinity propagation process. All spectrograms
732 are generated in Praat with the following parameters: window length: 0.025 sec, time range as
733 shown (0.25-0.75 sec); frequency range: 0-10500 Hz; dynamic range: 35-45 dB. The bar
734 indicates 1 sec duration. Values in parentheses indicate the percentage of the exemplar's
735 vocalization type in a cluster. Additional information is given in Supporting Information 3
736 (Appendix S4 and S5) and 4 (Appendix S6).

737

738 **Fig. 4** Polar dendrogram (center) showing how vocalizations of *Eulemur mongoz* cluster
739 together (see Supporting Information 3, Appendix S4). For each cluster, we show a
740 spectrogram of the exemplar chosen during the affinity propagation process. All spectrograms
741 are generated in Praat with the following parameters: window length: 0.025 sec, time range as
742 shown (0.25-1.25 sec); frequency range: 0-10500 Hz; dynamic range: 35-45 dB. The bar

743 indicates 1 sec duration. Exceptions are indicated as * for 1.25 sec. Values in parentheses
744 indicate the percentage of the exemplar's vocalization type in a cluster. Additional
745 information is given in Supporting Information 3 (Appendix S4 and S5) and 4 (Appendix S6).
746

747 **Fig. 5** Polar dendrogram (center) showing how vocalizations of *Eulemur coronatus* cluster
748 together (see Supporting Information 3, Appendix S4). For each cluster, we show a
749 spectrogram of the exemplar chosen during the affinity propagation process. All spectrograms
750 are generated in Praat with the following parameters: window length: 0.025 sec, time range as
751 shown (0.25-1.00 sec); frequency range: 0-10500 Hz; dynamic range: 35-45 dB. The bar
752 indicates 1 sec duration. Values in parentheses indicate the percentage of the exemplar's
753 vocalization type in a cluster. Additional information is given in Supporting Information 3
754 (Appendix S4 and S5) and 4 (Appendix S6).

755

756 **Fig. 6** Polar dendrogram (center) showing how vocalizations of *Eulemur flavifrons* cluster
757 together (see Supporting Information 3, Appendix S4). For each cluster, we show a
758 spectrogram of the exemplar chosen during the affinity propagation process. All spectrograms
759 are generated in Praat with the following parameters: window length: 0.025 sec, time range as
760 shown (0.25-2.50 sec); frequency range: 0-10500 Hz; dynamic range: 35-45 dB. The bar
761 indicates 1 sec duration. Exceptions are indicated as follows: * for 1.25 sec, ** for 1.75 sec,
762 *** for 2.00 sec. Values in parentheses indicate the percentage of the exemplar's vocalization
763 type in a cluster. Additional information is given in Supporting Information 3 (Appendix S4
764 and S5) and 4 (Appendix S6).

765

766 **Fig. 7** Polar dendrogram (center) showing how vocalizations of *Eulemur macaco* cluster
767 together (see Supporting Information 3, Appendix S4). For each cluster, we show a
768 spectrogram of the exemplar chosen during the affinity propagation process. All spectrograms
769 are generated in Praat with the following parameters: window length: 0.025 sec, time range as
770 shown (0.25-1.00 sec); frequency range: 0-10500 Hz; dynamic range: 35-45 dB. The bar
771 indicates 1 sec duration. Values in parentheses indicate the percentage of the exemplar's
772 vocalization type in a cluster. Additional information is given in Supporting Information 3
773 (Appendix S4 and S5) and 4 (Appendix S6).

774

Table 1. Distribution of the vocalizations indicated *a priori* and as they emerged from the cluster analysis.

Vocalization	*E. fulvus*	*E. rufus*	*E. rubriventer*	*E. mongoz*	*E. coronatus*	*E. flavifrons*	*E. macaco*
Alarm Call	0	1		0	4	5	1
Alarm Long Grunt		0		1			
Chatter	1		0	0		0	0
Click	0	0	0	1			0
Group Cohesion Call	1	1		1			
Grunted Hoot	0	1	0	1	0	2	0
Grunt	2	1	1	1	3	0	1
Grunt-Tonal Call	1	0	0	1	1	1	
Gurgle			1				
Hoot	0	0	1	0	0	0	0
Hoot-Tonal Call			2				
Long Grunt			1	1		0	1
Long Grunt-Tonal Call	1					2	1
Scream	2	3	2	1	4		5
Snort-Grunt			0				
Snort-Grunt-Tonal Call			3				
Snort	0	0	0	0			0
Territorial Advertisement Call	3	3		1			
Tonal Call-Grunt	0						
Tonal Call	0	0	3	0	1	0	1
Number of clusters	**11**	**10**	**14**	**9**	**13**	**10**	**10**
Adjusted Rand Index	**0.27**	**0.32**	**0.18**	**0.24**	**0.32**	**0.32**	**0.25**

Table 1. Distribution of the vocalizations indicated *a priori* and as they emerged from the cluster analysis. The numbers indicate the number of exemplars chosen during the clustering analysis for that particular vocalization. Grey-shaded cells show where a particular vocalization has not been assessed during the *a priori* classification. The number of clusters indicates the total number of clusters emerged during the Affinity Propagation process and the Adjusted Rand Index quantify the agreement between the *a priori* classification and the clustering analysis.

Table 2. Stepwise discriminant analysis results for the seven *Eulemur* species.

Species	Wilks' L.	P	CCR (%)	1st D. f.	2nd D. f.
E. fulvus	0.003	<0.001	84.2	88.9% (Duration)	11.1% (F1)
E. rufus	0.006	<0.001	94.7	98.2% (Duration)	1.0% (MinF0)
E. rubriventer	0.006	<0.001	73.5	91.7% (Duration)	7.2% (F2)
E. mongoz	0.037	<0.001	69.2	81.4% (Duration)	13.9% (F3)
E. coronatus	0.007	<0.001	83.4	96.6% (Duration)	2.8% (F1)
E. flavifrons	0.011	<0.001	71.4	84.6% (Duration)	14.1% (F1)
E. macaco	0.006	<0.001	82.0	78.2% (Duration)	16.1% (F1)

Table 2. The table shows the statistical results of the seven stepwise Discriminant Function Analyses (sDFA) using temporal parameters (Duration, Ptmin, Ptmax), fundamental frequency parameters (MeanF0, MinF0, MaxF0, RangeF0, StartF0, EndF0), and formants (F1, F2, F3). The grouping variable for each sDFA was the cluster membership resulted from the Affinity Propagation clustering analysis. We reported the Wilks' Lambda values (Wilks' L.), the p-values (P), the cross-validated correct classification rate (CCR) and the variance explained by the first (1st D. f.) and the second (2nd D. f.) discriminant functions. In brackets, we also reported the parameters showing the highest load on the discriminant functions.

Figure 1
Click here to download Figure: Gamba_et_al_Fig1R2.eps

Territorial Advertisement
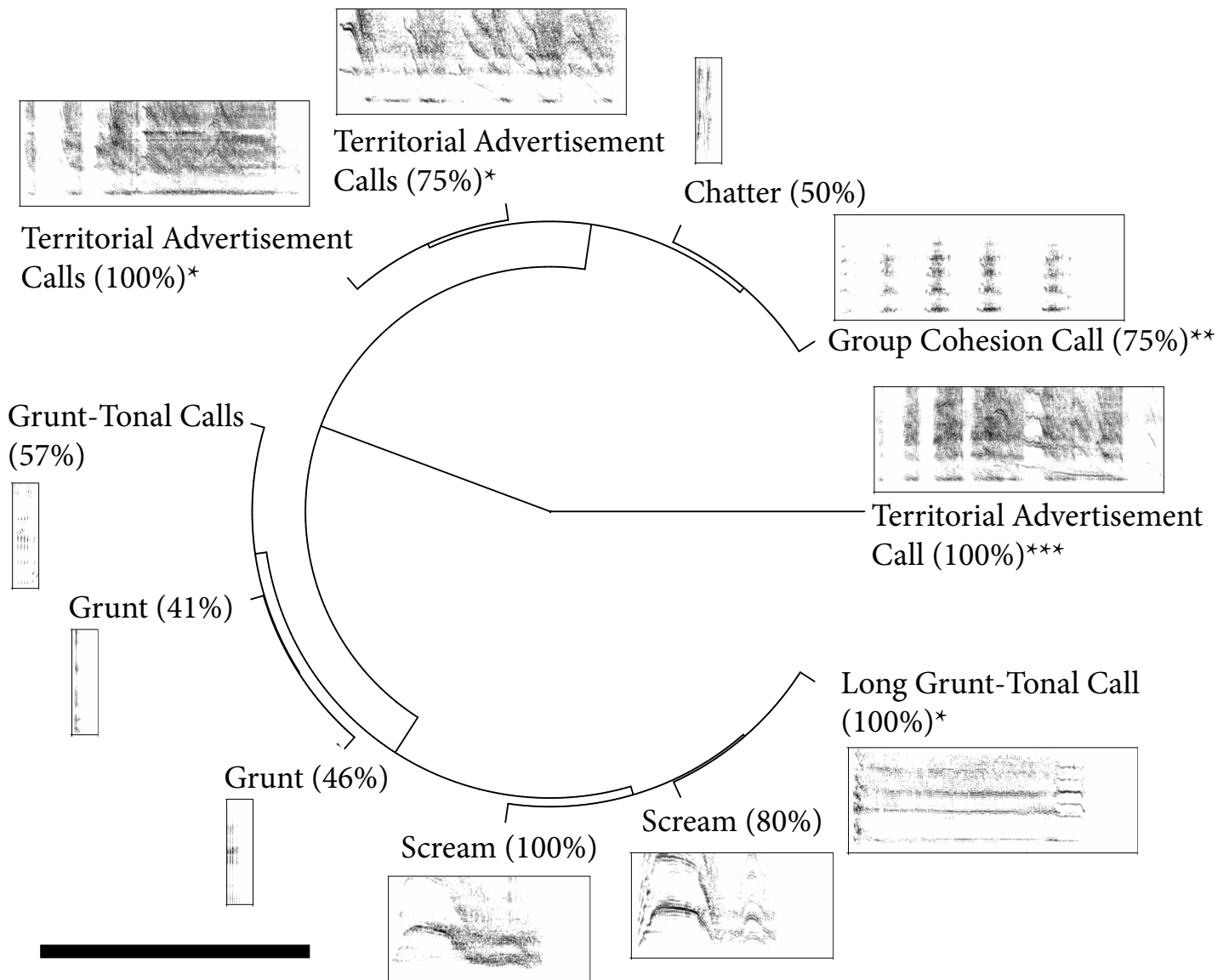Calls (75%)*

Chatter (50%)

Territorial Advertisement
Calls (100%)*

Group Cohesion Call (75%)**

Grunt-Tonal Calls
(57%)

Territorial Advertisement
Call (100%)***

Grunt (41%)

Long Grunt-Tonal Call
(100%)*

Grunt (46%)

Scream (100%)

Scream (80%)

Figure 2
Click here to download Figure: Gamba_et_al_Fig2R2.eps

Scream (71%)

Territorial Advertisement Call (57%)**

Grunt (39%)

Territorial Advertisement Call (85%)***

Grunted Hoot (46%)

Territorial Advertisement Call (100%)***

Scream (71%)

Group Cohesion Call (71%)*

Scream (78%)

Alarm Call (73%)
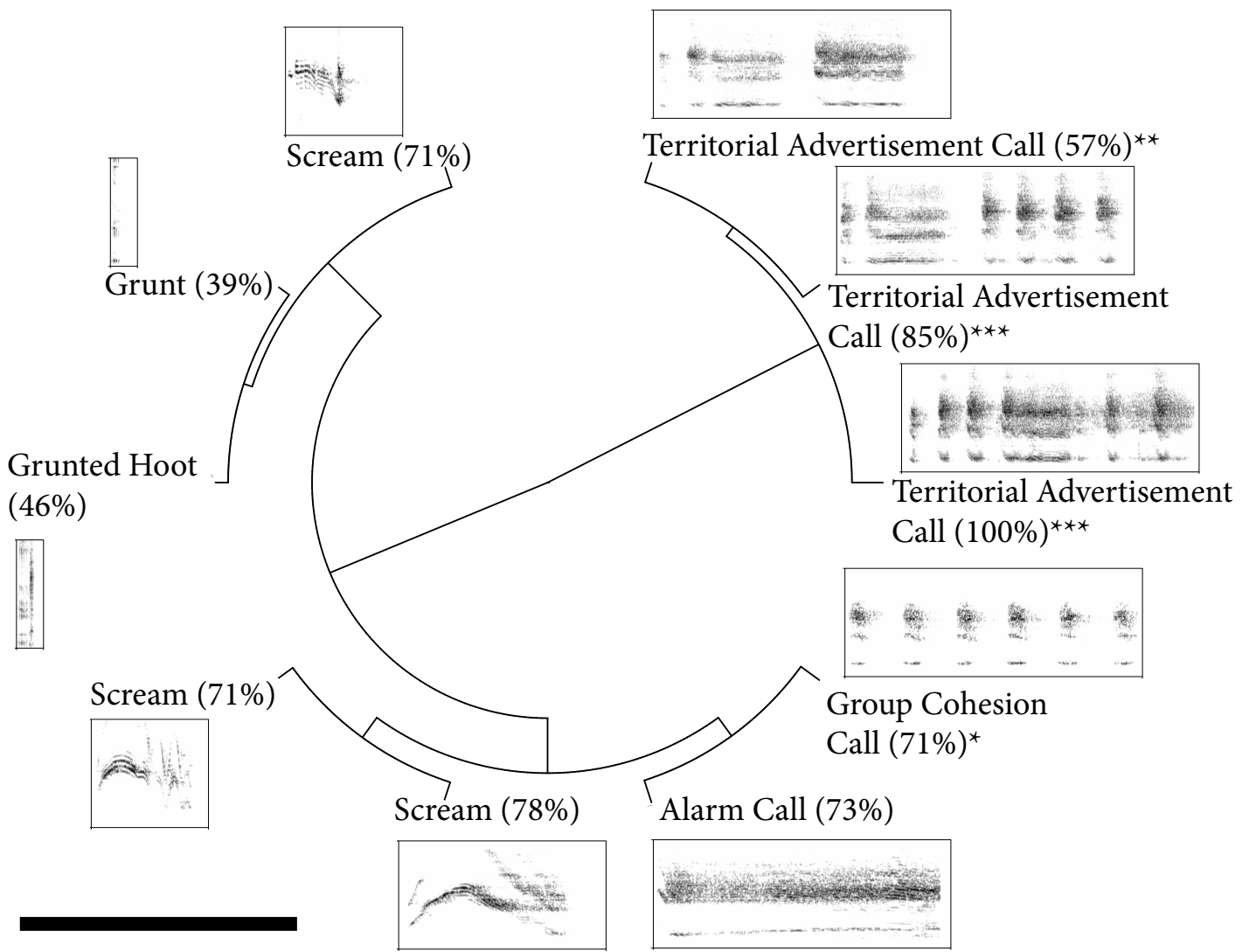
Figure 3
Click here to download Figure: Gamba_et_al_Fig3R2.eps

Snort-Grunt-Tonal Call (57%)

Tonal Call (54%)

Tonal Call (47%)

Snort-Grunt-Tonal Call (29%)

Scream (100%)

Snort-Grunt-Tonal Call (57%)

Scream (75%)

Long Grunt (100%)

Gurgle (30%)

Tonal Call (80%)

Grunt (44%)

Hoot (24%)

Hoot-Tonal Call (63%)

Hoot-Tonal Call (60%)

Territorial Advertisement Call (43%)

Click (23%)

Grunt (81%)

Scream (45%)

Grunted Hoot (21%)

Grunt-Tonal Call (60%)

Long Grunt (83%)*

Group Cohesion Call (92%)*

Alarm Long Grunt (86%)
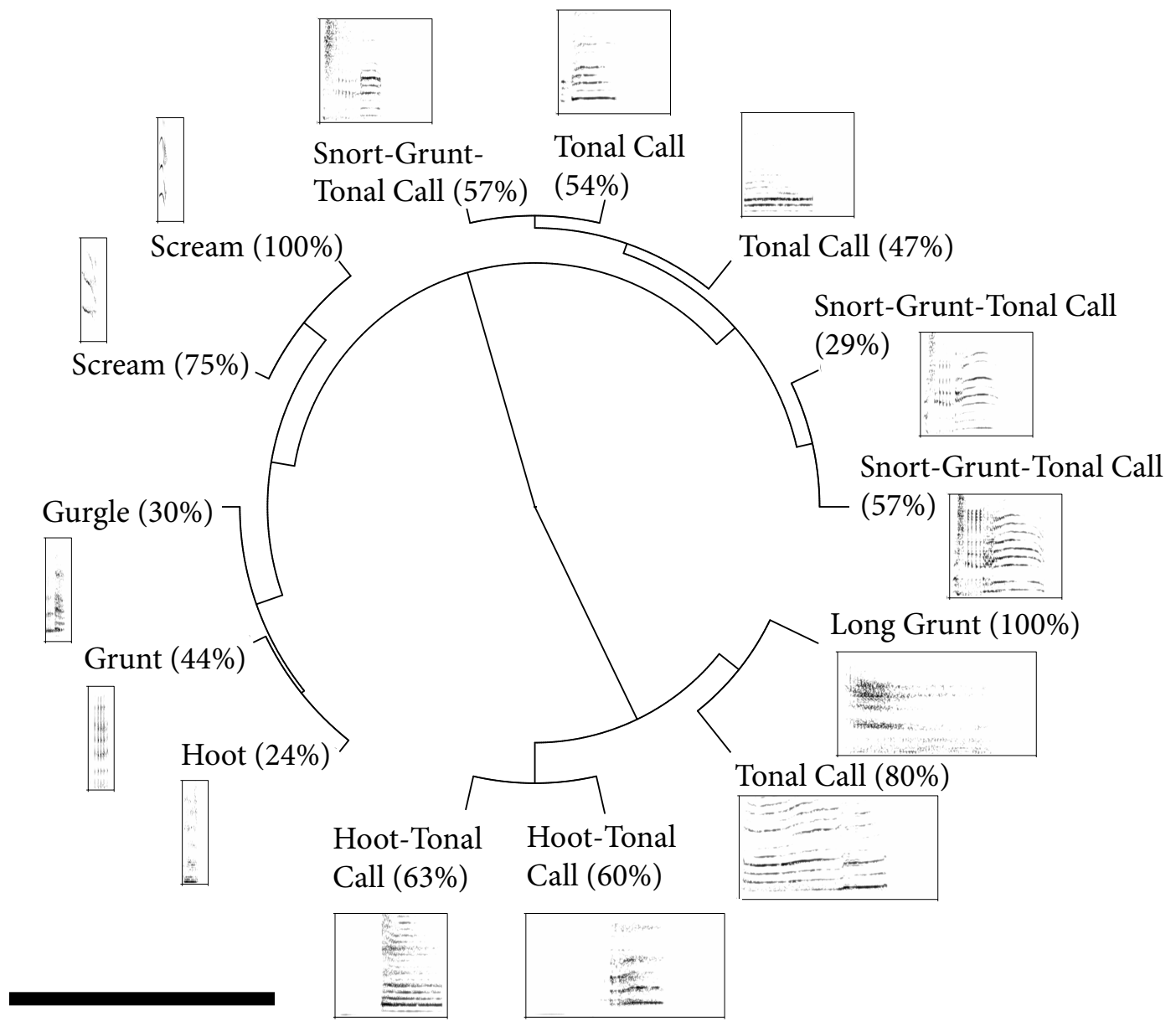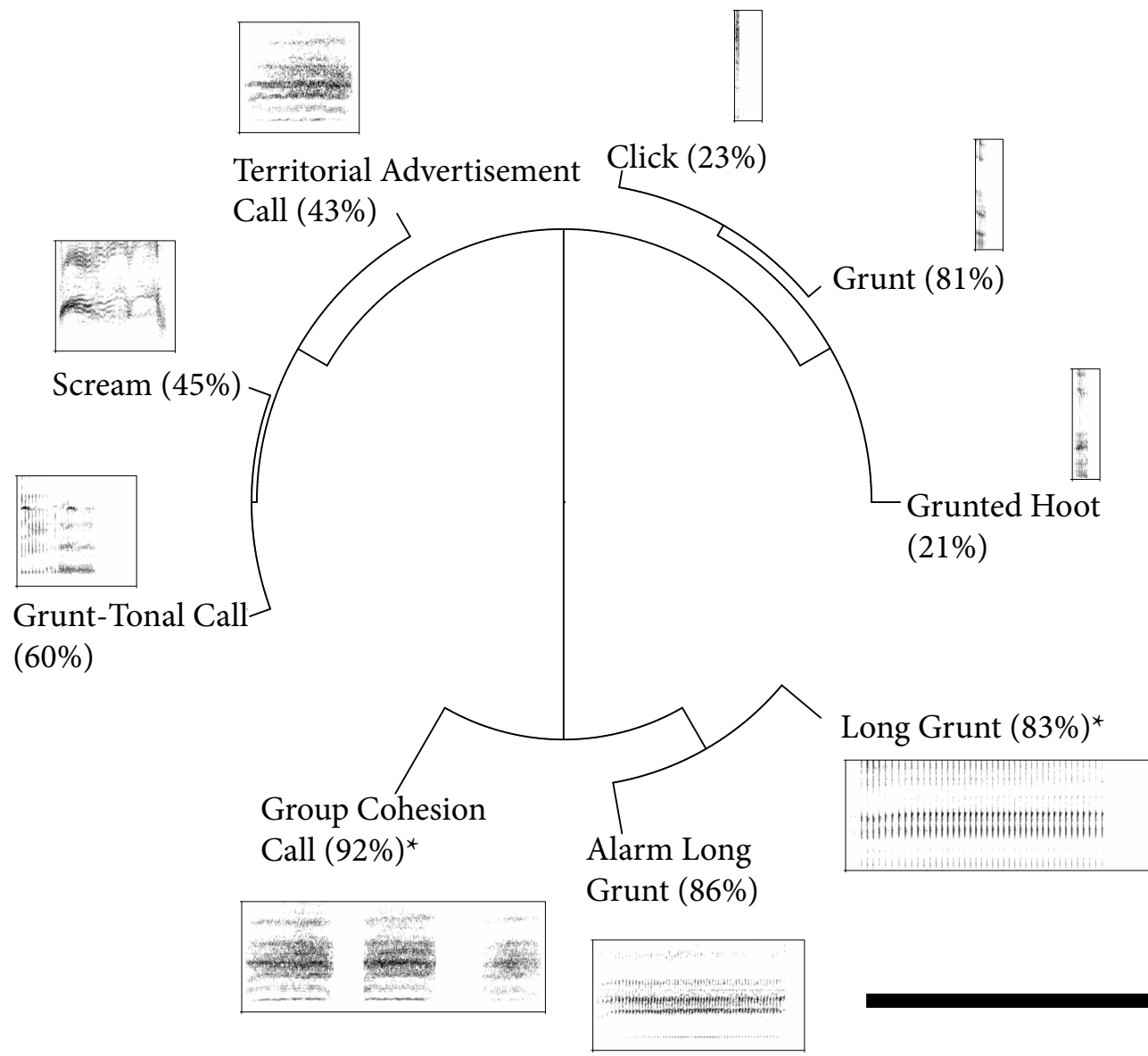
Figure 5
Click here to download Figure: Gamba_et_al_Fig5R2.eps

Grunt-Tonal call (75%)

Grunt (52%)

Grunt (39%)

Grunt (63%)

Alarm Call (90%)

Tonal Call (79%)

Scream (100%)

Scream (100%)

Scream (100%)

Scream (100%)

Alarm Call (80%)

Alarm Call (100%)

Alarm Call (67%)

Scream (100%)
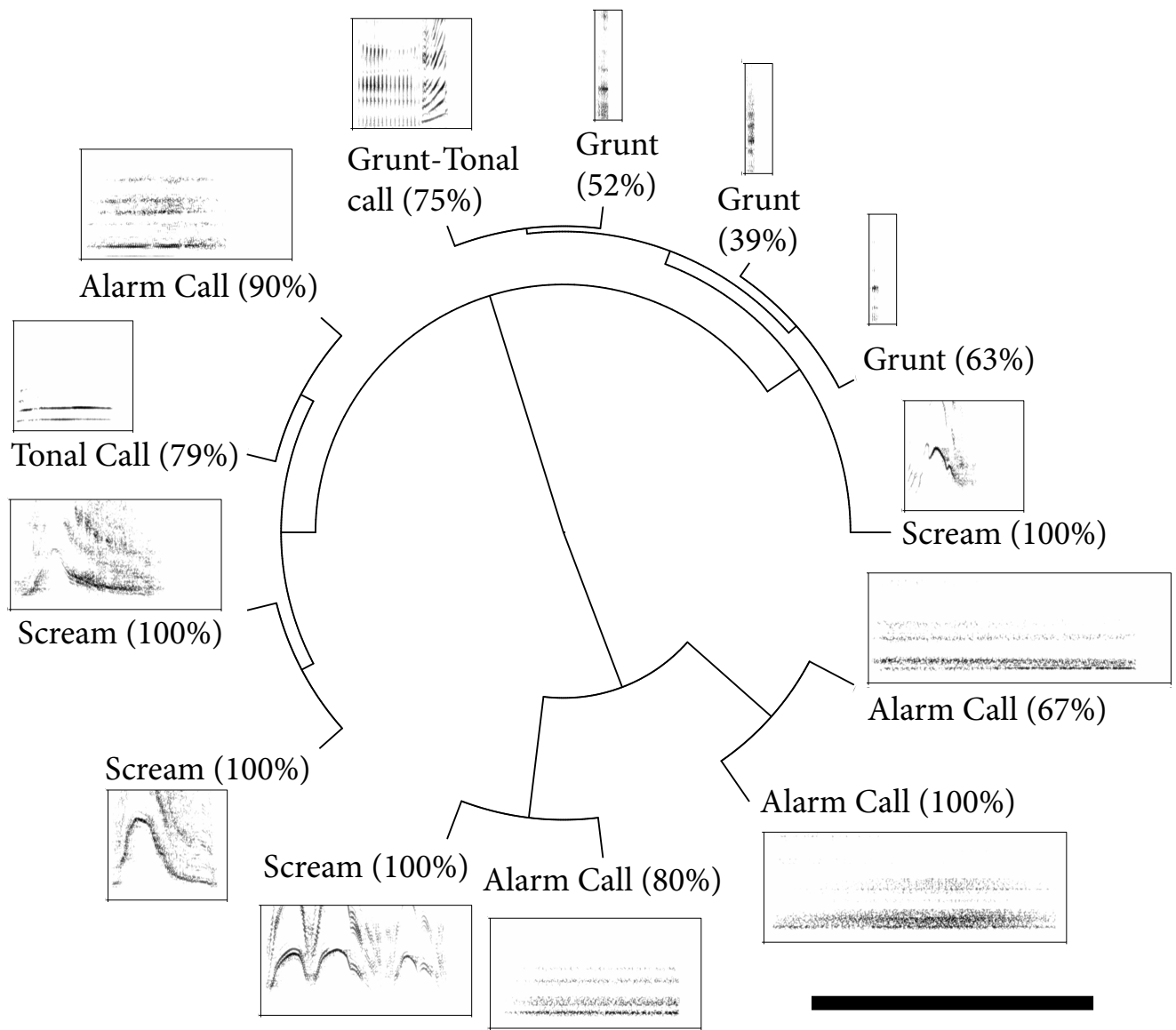
Figure 6
Click here to download Figure: Gamba_et_al_Fig6R2.eps

Alarm Call (100%)**

Alarm Call (86%)*

Alarm Call (100%)***

Alarm Call (100%)**

Alarm Call (100%)***

Long Grunt-Tonal Call (57%)

Grunted Hoot (35%)

Long Grunt-Tonal Call (61%)

Grunt-Tonal Call (73%)

Grunted Hoot (46%)

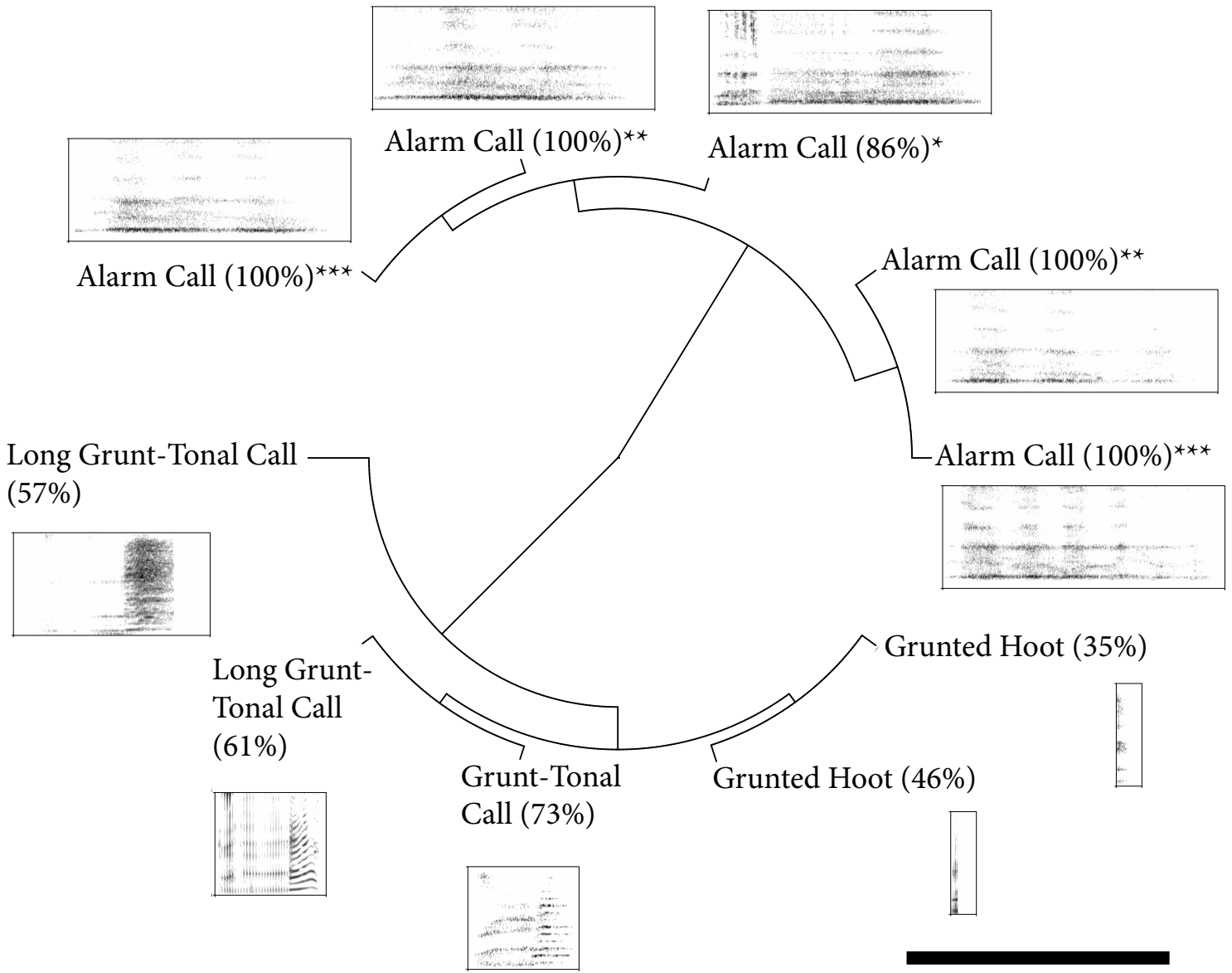Figure 7
Click here to download Figure: Gamba_et_al_Fig7R2.eps

Long Grunt (50%)

Scream (50%)

Long Grunt-Tonal Call (75%)

Alarm Call (100%)

Scream (88%)

Scream (50%)

Grunt (44%)

Scream (55%)

Tonal call (44%)

Scream (40%)