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Comparative Analysis of the Vocal Repertoire of Eulemur: A Dynamic Time Warping Approach

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

3

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19 analysis, unsupervised classification, cluster analysis.

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 Giacomini 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 Giacomini 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

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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

708 **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	<i>E. fulvius</i>	<i>E. rufus</i>	<i>E. rubriventer</i>	<i>E. mongoz</i>	<i>E. coronatus</i>	<i>E. flavifrons</i>	<i>E. macaco</i>
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 (%)	1 st D. f.	2 nd D. f.
<i>E. fulvus</i>	0.003	<0.001	84.2	88.9% (Duration)	11.1% (F1)
<i>E. rufus</i>	0.006	<0.001	94.7	98.2% (Duration)	1.0% (MinF0)
<i>E. rubriventer</i>	0.006	<0.001	73.5	91.7% (Duration)	7.2% (F2)
<i>E. mongoz</i>	0.037	<0.001	69.2	81.4% (Duration)	13.9% (F3)
<i>E. coronatus</i>	0.007	<0.001	83.4	96.6% (Duration)	2.8% (F1)
<i>E. flavifrons</i>	0.011	<0.001	71.4	84.6% (Duration)	14.1% (F1)
<i>E. macaco</i>	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

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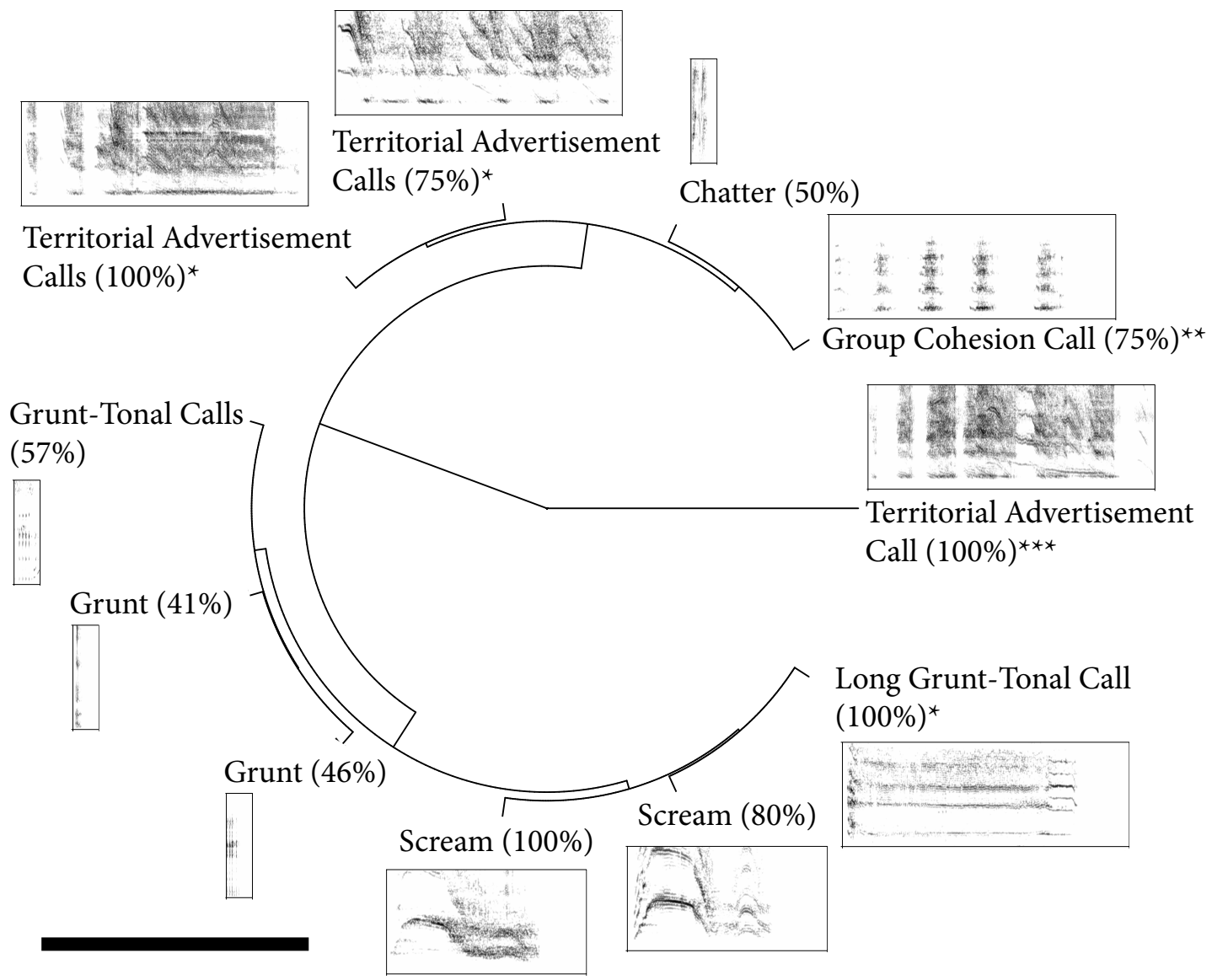


Figure 2

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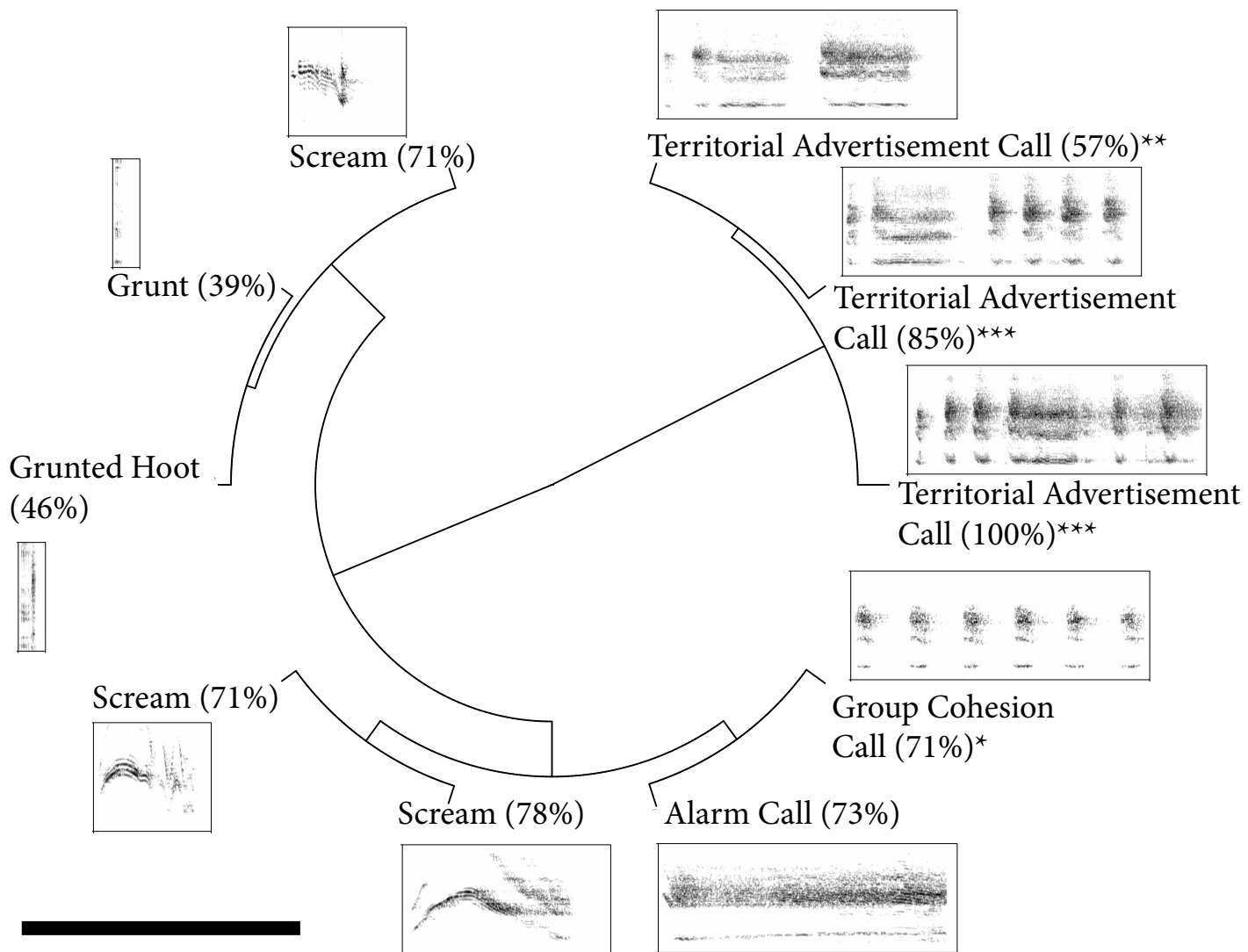


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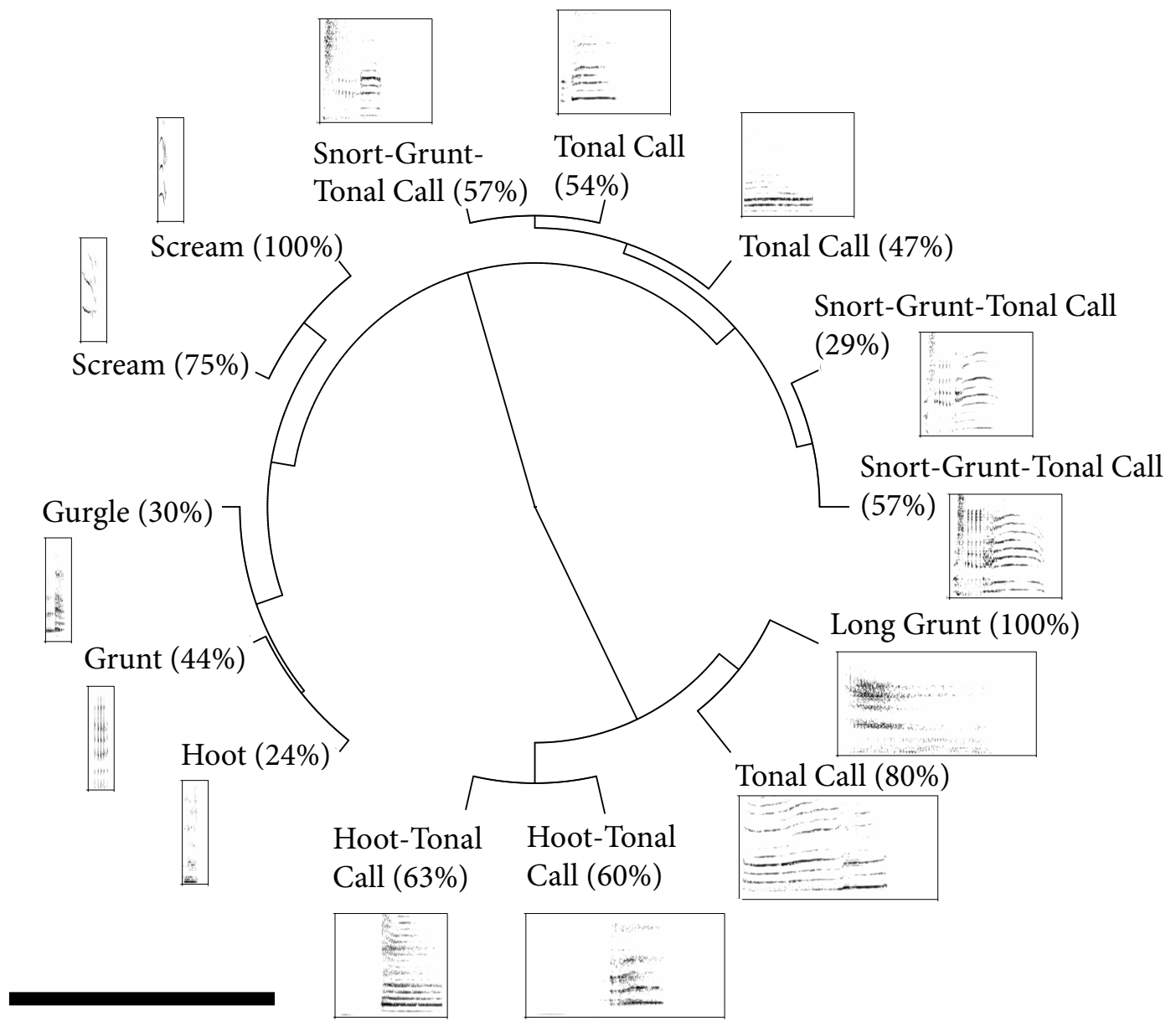


Figure 4

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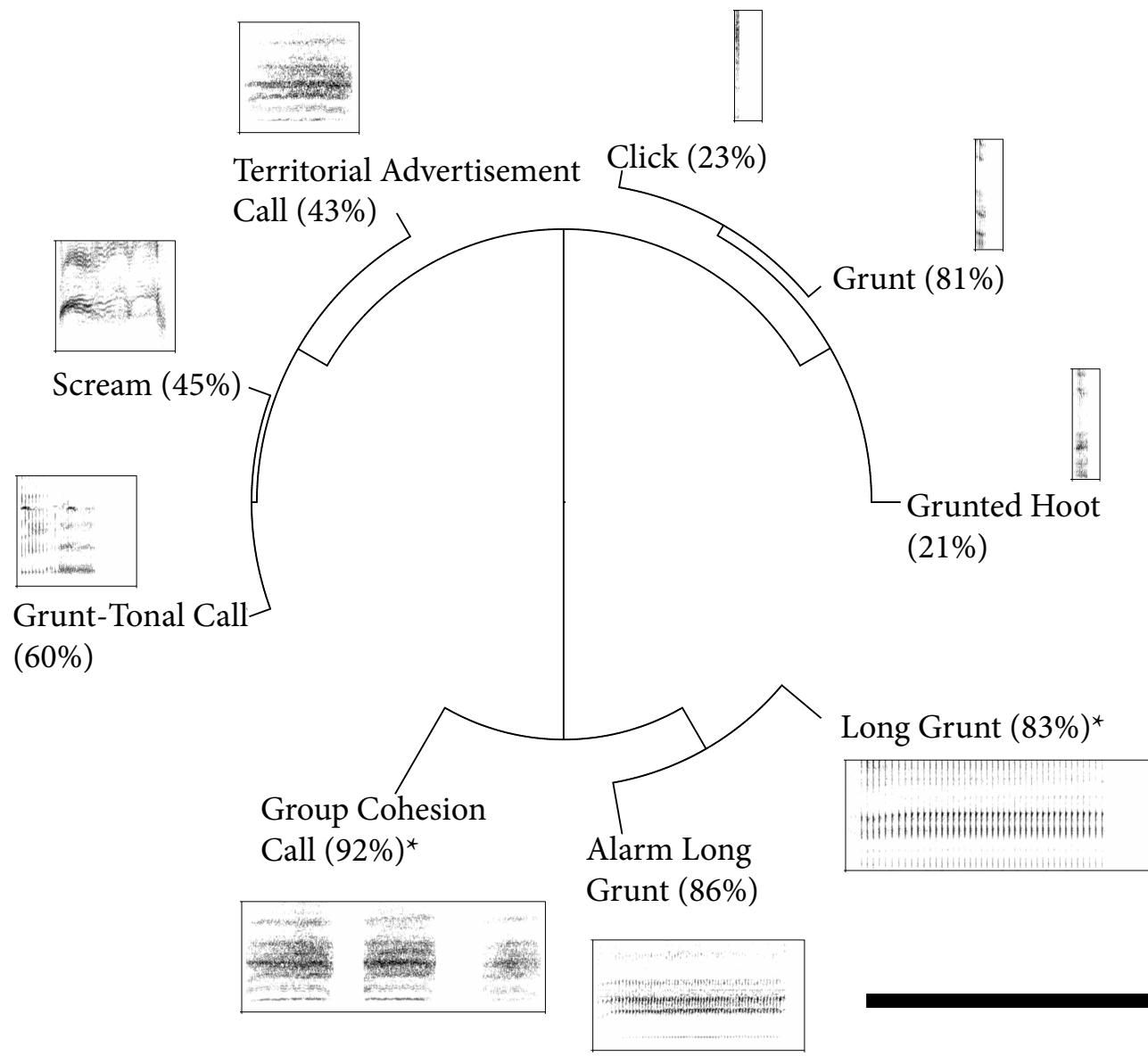


Figure 5

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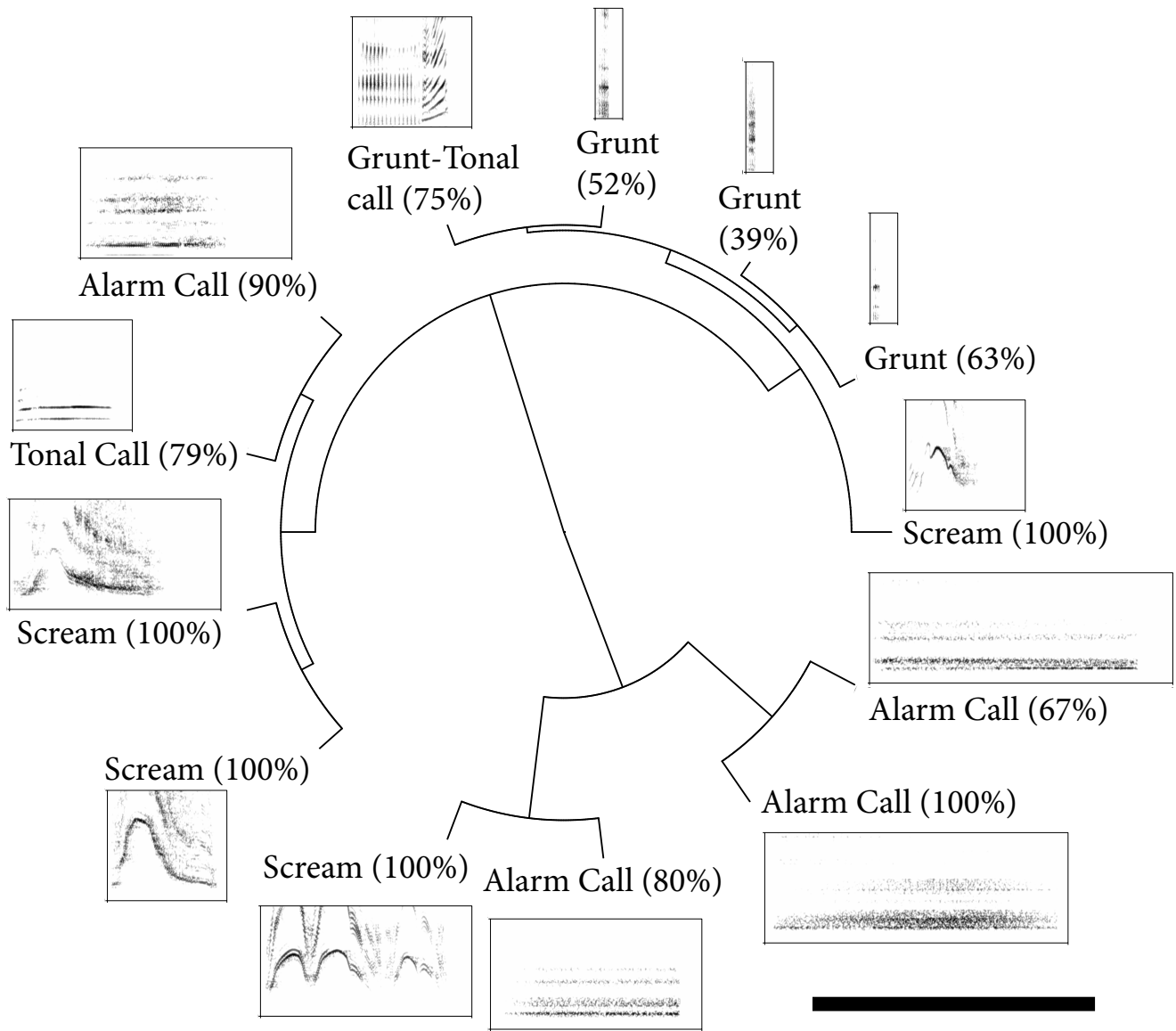


Figure 6

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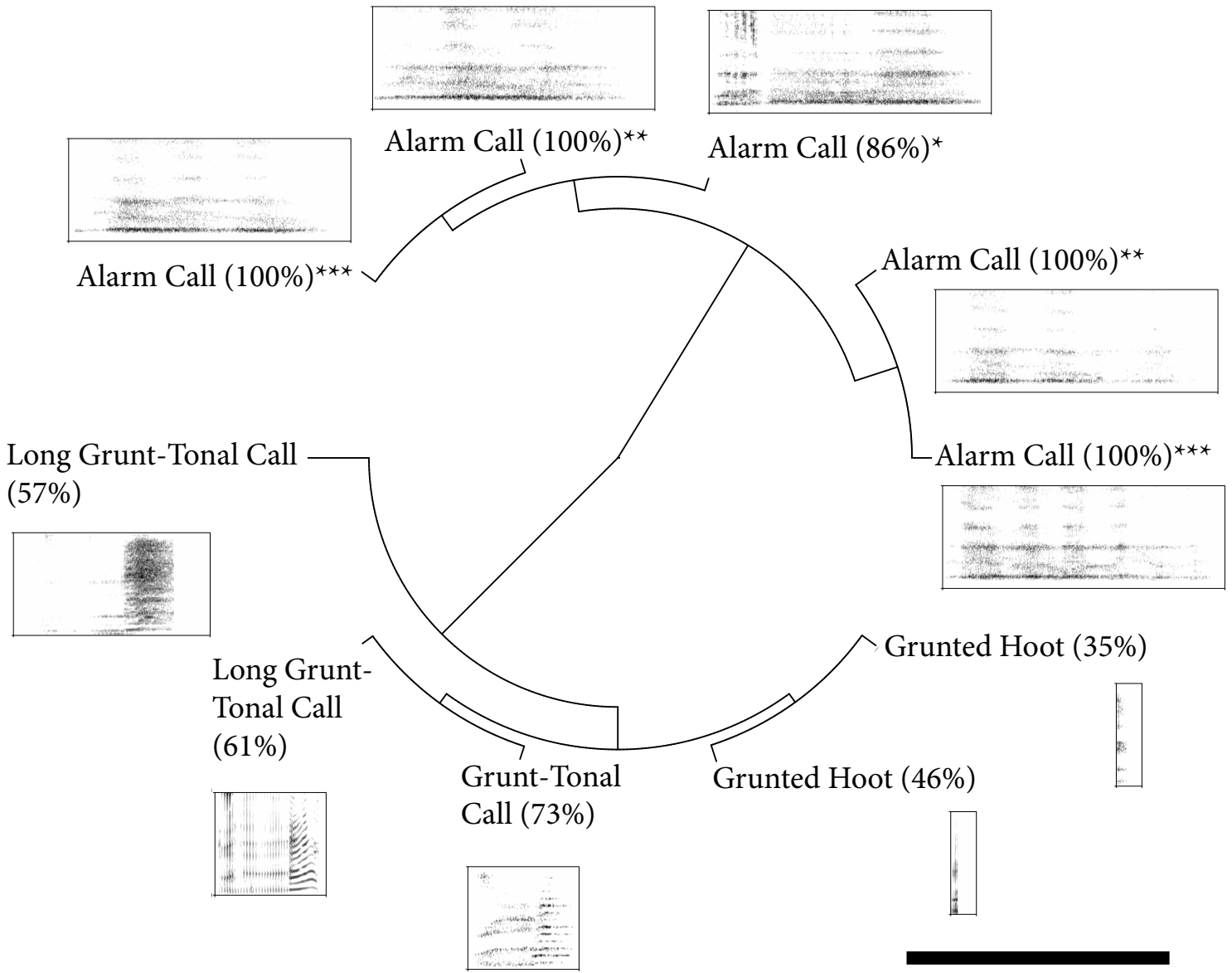


Figure 7

[Click here to download Figure: Gamba_et_al_Fig7R2.eps](#)

