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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.

## INTRODUCTION

Vocal repertoires provide essential information to the study of how communication systems evolve (Maynard Smith and Harper 2003). For example, studies of nonhuman primate vocal communication have provided valuable contributions to the debate about the basis for the evolution of language in humans (Dunbar 2009). Nonhuman primate vocal repertoire size correlates with time spent grooming and with group size (McComb and Semple 2005), providing support for the theory that the complexity of human language has gradually evolved with the increase of social complexity (Dunbar 2009). However, comparative studies of repertoire size are often undermined by two factors. First, vocal repertoire data are derived from studies using different methods (McComb and Semple 2005). Second, identification of the signal categories have traditionally relied on human observers' assessment of differences among vocalizations, and are thus subject to individual criteria. Although multivariate techniques have demonstrated that such categories may be appropriate (*e.g.* Range and Fischer 2004; Gamba and Giacoma 2007; Maretti *et al.* 2010; Fuller 2014), human assessment of vocalization types may reflect differences perceived by humans but not necessarily by the species (Green 1975; Hauser 1996; Fuller 2014).

New methodologies in the study of acoustic communication allow standardization across large datasets with limited assumptions (Clemins *et al.* 2006). These methods provide researchers with computer tools for exploring large databases without the disadvantages of subjective *a priori* classification, and are often referred to as 'unsupervised' (Stowell and Plumbley 2014; Kogan and Margoliash 1998; Stathopoulos *et al.* 2014). Among the many methods (Garcia and Reyes Garcia 2003; Koolagudi *et al.* 2012), some used for automatic speech recognition, such as dynamic

time warping, are increasingly used to investigate animal communication. Dynamic time warping has been useful for the classification of animal sounds in amphibians (Chen *et al.* 2012), birds (Anderson *et al.* 1996; Trawicki *et al.* 2005; Clemins and Johnson 2006; Ranjard and Ross 2008; Tao *et al.* 2008), marine mammals (Brown and Miller 2007), and primates (Riondato *et al.* 2013). These methods can be used to investigate the vocal repertoire across populations and species (Mercado III and Handel 2012; Ranjard *et al.* 2010) and improve our ability to make inferences about the evolution of human language (Fedurek and Slocombe 2011). Although unsupervised classification cannot guarantee to classify calls in a way that is meaningful to animals, it does ensure quantitative objective classification (Pozzi *et al.* 2010).

Due to their unique evolutionary history, lemurs are important subjects for comparative studies of vocal communication and may provide insights into the selective pressures that may have linked social and vocal complexity (Oda 2009). True lemurs (*Eulemur* spp.) are conspicuously vocal and that their vocal repertoire comprises low-pitched and high-pitched sounds (Petter and Charles-Dominique 1979, Macedonia and Stanger 1994; Gamba and Giacoma 2005). The presence of various call variants and combinations has also been demonstrated qualitatively (Macedonia and Stanger 1994). Previous studies showed that vocal repertoire may differ between species in *Eulemur fulvus* (Paillette and Petter 1978), *E. mongoz* (Curtis 1997), *E. macaco* (Gosset *et al.* 2001) and *E. coronatus* (Gamba and Giacoma 2007).

The aim of this study was to investigate objectively the vocal repertoire across *Eulemur* species to understand whether different species show different repertoire size

and vocalization types. We used an algorithm based on dynamic time warping to assess sound similarity (Ranjar *et al.* 2010). We then applied cluster analysis to identify groups of similar calls. To understand whether vocal repertoire size differs across *Eulemur* species we applied the same analytical process to datasets for different species, including the brown lemur (*E. fulvus*), the mongoose lemur (*E. mongoz*), the black lemur (*E. macaco*), and the crowned lemur (*E. coronatus*), whose repertoires were investigated in previous studies. We also analysed three species that were not included in previous quantitative vocal repertoire studies: the red-bellied lemur (*E. rubriventer*), the rufous brown lemur (*E. rufus*), and the blue-eyed black lemur (*E. flavifrons*). Qualitative studies of *Eulemur* species have shown a degree of similarity in the acoustic structure of the calls but shed little light on the quantitative evaluation of similarities and differences, and suffered from subjective identification of the call types (Macedonia and Stanger 1994; Gamba and Giacoma 2005). No previous study has combined, to our knowledge, the study of lemurs' vocal repertoire across different species using a quantitative unsupervised methodology.

We tested whether or not our unsupervised analyses identified the same vocalization types as previously described. Human sound recognition mechanisms are robust against noise changes and integrate many factors, resulting in accurate low-level acoustic classification. Humans can differentiate calls as discrete types when an unsupervised program, and possibly other species, would recognize a single type (Hauser 1996; Lippmann 1997). We, therefore, predicted that unsupervised clustering would find fewer vocalization types than previous studies. We also predicted that more variable vocalization types mask variation at a lower level, as in a clustering analysis of Guinea baboon calls (*Papio papio*, Maciej *et al.* 2013). Alternatively,

cluster analysis may highlight variants of vocal types showing a particular contextual occurrence and other types which overlap with the *a priori* classification.

## Methods

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

The recordings analysed for the purpose of this study were part of a large collection of lemur sounds at the Department of Life Sciences and Systems Biology, University of Torino. The recordings originate from various recording campaigns focused on lemur vocal behaviour that took place between 1999 and 2013. They were recorded in the wild and in captivity. The number of recording campaigns (hereafter corpora) and the number of calls within a corpus vary with species. We only considered calls emitted by adults. Detailed information about the corpora, sampling, data collection, and associated references is given in the Supporting Information (Appendix S1).

### *Clustering analyses*

To identify independent groupings and to visualize emerging vocal types (Nowicki and Nelson 1990), we clustered vocalizations of each species on the basis of their degree of dissimilarity, as measured by the pairwise comparison using dynamic time warping (Ranjard *et al.* 2010). Detailed information about the calculation of dissimilarity indices is given in the Supporting Information (Appendix S1). We used the affinity propagation tool (Frey and Dueck 2007) of the *apcluster* package in R (Bodenhofer *et al.* 2011; Hornik 2013). We labelled clusters with the 'representative' vocalization (the 'exemplar'), which was automatically chosen during the affinity propagation clustering process (see Supporting Information 1 (Appendix S2). The



cluster analysis used a squared negative Euclidean distance to measure dissimilarity and identify clusters. This clustering algorithm is based on similarities between pairs of data points. Affinity propagation clustering simultaneously considers all the data points as potential cluster centers (exemplars), then chooses the final centers through an iterative process, after which the corresponding clusters also emerge. Although we did not define the number of clusters or the number of exemplars (Bodenhofer et al. 2011), the preference (p) with which a data point is chosen as a cluster center influences the number of clusters in the final solution. Because affinity propagation clustering does not automatically converge to an optimal clustering solution, we used two external validation procedures. The first validation was based on the q-scanning process (where q corresponds to the sample quantile of p, modified from Wang *et al.* 2007; see also Bodenhofer *et al.* 2011). We evaluated the clusters obtained using different preferences using the Adjusted Rand Index (Hubert and Arabie 1985) to assess the stability of successive cluster solutions (Hennig 2007). The second cluster validation procedure was based on the Silhouette Index, which reflects the compactness and separation of clusters in the final solution (Maciej *et al.* 2013). When ranked and averaged between species both procedures indicated the median of all the similarities between data points to be the optimal value for the preference. We kept all the analysis settings the same across all datasets. We used the calls used as exemplars in the final clustering solution to label the respective clusters.

#### A posteriori *evaluation*

We evaluated the agreement between the clustering analyses and the *a priori* classification using the Adjusted Rand Index (Hubert and Arabie 1985; Table 1).

The terminology we use in the description of the polar dendrograms refers to Drout and Smith (2013). Each branch of the polar dendrogram is termed a 'branch' or a 'clade' while the terminal portion of each clade is called a 'leaf'. Two-leaved clades are called 'bifolious', but the number of leaves in a clade is not limited. While the horizontal orientation of dendrograms is irrelevant, its vertical arrangement is meaningful. The vertical position of the branch points indicates how similar or different they are from each other. Branches departing from the same branch point are most similar and belong to the same 'level'. In the polar dendrograms, levels are numbered from the center (root) to the outer ring.

We also ran a stepwise Discriminant Function Analysis (sDFA, IBM SPSS Statistics 21; Lehner 1996) using the acoustic parameters measured (Supporting Information 2, Appendix S3, see Gamba and Giacoma 2007 for details) using Praat (University of Amsterdam, Boersma and Weenink 2014). We used the sDFA to identify the weight of the different parameters contributing to the clustering process, although the acoustic analysis does not necessarily simulate feature extraction during the dynamic time warping. We ran the sDFA with the cluster information as the grouping variable to estimate how the acoustic parameters contributed to the classification of calls using leave-one-out cross-validation.

## **Results**

### *Vocal repertoire*

The cluster analysis showed variation in both the number of clusters and the distribution of calls across clusters with species (Table 1; see Supporting Information 3, Appendix S 5).

*E. fulvus* vocalizations were grouped into 11 clusters (Fig. 1; Table 1). sDFA showed an overall correct classification of 84.2% (cross-validated) when we used the clusters as the grouping variable. Signal duration (on the first discriminant function) and the first formant (F1, on the second discriminant function) had the highest loads in the model (Table 2).

[Table. 1 HERE]

[Fig. 1 HERE]

*E. rufus* vocalizations grouped into 10 clusters (Fig. 2; Table 1). sDFA showed an overall correct classification of 94.7% (cross-validated) when we used the clusters as the grouping variable. Signal duration (on the first discriminant function) and minimum Fundamental frequency (MinF0, on the second discriminant function) had the highest loads in the model (Table 2).

[Fig. 2 HERE]

*E. rubriventer* vocalizations grouped into 14 clusters (Fig. 3; Table 1). sDFA showed a correct classification of 73.5% (cross-validated) when we used the clusters as the grouping variable. Signal duration (on the first discriminant function) and the second formant (F2, on the second discriminant function) had the highest loads in the model (Table 2).

[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-

visual identification of vocal categories varied from a minimum of 7 vocalization types in *E. coronatus* to 14 types in *E. fulvus*, *E. rubriventer*, and *E. mongoz*. The overall range obtained by the unsupervised analysis was similar, ranging 9 - 14 clusters. Thus, audio-visual identification and unsupervised classification of vocalization types gave comparable estimates.

Our results support the prediction that average group size influences vocal repertoire size in part. Both audio-visual identification and unsupervised classification of vocalization types provide a repertoire size estimate of 14 calls for *E. rubriventer*, an estimate that is surprisingly larger than those observed for other species except *E. coronatus*, which have group sizes is 8.4 (Kappeler and Heymann 1996), while *E. rubriventer* has a mean group size of just 3 (Overdorff 1996) or 3.2 (Kappeler and Heymann 1996). *E. mongoz* have a similar average group size of 3.0-3.5 (Kappeler and Heymann 1996; Nadhurou et al. 2015) and show a repertoire size of 9 calls. Several authors have suggested a relationship between a species' social organization and its communication, proposing that an egalitarian social structure or stable social groups may favor diversity in communication signals (Mitani 1996). *E. rubriventer* is the only species we studied to have a stable, pair-bonded group structure (Tecot 2008). The other species live in one-male, multi-female groups or multi-male, multi-female groups (Fuentes 2002). The social organization in *E. mongoz* varies between populations, and includes both pair bonding and one-male, multi-female groups (Fuentes 2002). The larger distribution of *E. rubriventer* may also influence the diversity of vocal communication, as may the fact that we included only captive *E. rubriventer* in the analysis. However, vocal repertoire appears to be consistent across captive, wild-caught individuals (Colombo, unpublished data), suggesting that other

factors may have a stronger effect than the distribution range size. The strong relationships between repertoire size and stable social organization have been proposed for facial expressions (Preuschoft and van Hooff 1995) and the rate of vocal emissions (Mitani 1996), and further studies are needed to clarify whether pair-bonding also ‘places a selective premium’ (Mitani 1996, p. 246) on vocal repertoire size. In support of this proposal, pair-bonding is considered a key factor favoring the convergent evolution of complex singing displays (Geissmann 2000; Torti *et al.* 2013) in the ‘singing primates’ (*Indri indri*, *Tarsius* spp., *Presbytis* spp., and *Hylobates* spp., Haimoff 1986; *Indri indri*, Bonadonna *et al.* 2014).

We predicted that the unsupervised procedure would recognise a lower number of vocalization types. This was true for *Eulemur fulvus* (11 in the unsupervised analysis versus 14 in the audio-visual *a priori* assessment), *E. mongoz* (9 vs. 14), *E. rufus* (10 vs. 12) and *E. macaco* (10 vs. 11). The repertoire estimate derived from a previous study of *E. macaco* (N = 13; Gosset *et al.* 2001) exceeds both that observed during the reassessment process (N = 10) and the result of the cluster analysis (N = 10). Although the calls in our sample may be incomplete, we suspect that this discrepancy arose due to the different criteria used to assess vocalization types in these studies.

Our prediction that the unsupervised procedure would recognise a lower number of vocalization types was not supported in two cases: *Eulemur coronatus* (13 unsupervised versus seven audio-visual vocal types) and *E. mongoz* (14 vs. nine). In both cases, the unsupervised procedure recognized more than one type of alarm call. Previous studies of these species estimated a vocal repertoire size of 15 vocalizations

for *E. mongoz* (nine validated using sDFA; Nadhurou et al. 2015) and 10 vocalizations for *E. coronatus* (all validated using DFA, Gamba and Giacomini 2007). It is clear that different methods led to different estimates, but interesting that, in principle, dynamic time warping allows the identification of vocalization types using a smaller number of calls than sDFA. Whether these differences in vocal repertoire size reflect different arousal states or contexts is an interesting direction for future research.

#### *Cluster versus a priori classification*

Agreement between the clustering process and the *a priori* criteria was low, with values of the Adjusted Rand Index ranging between 0.18 (in *E. rubriventer*) and 0.32 (in *E. coronatus* and *E. macaco* and *E. rufus*). This supports the prediction that unsupervised clustering of the vocalizations would not find the vocalization types identified in previous studies. However, despite the differences with the *a priori* classification, the clusters obtained using dynamic time warping-generated dissimilarity indices revealed a remarkable potential for grouping calls on the basis of acoustic measurements of different parameters. Among the parameters, duration showed the heaviest loadings on the first discriminant function. Thus, the mismatching between the *a priori* classification and cluster analysis is in line with the suggestion that humans tend to recognize as discrete vocal types sounds that may be grouped into a single type when perceived by other species or classified by quantitative analyses (Hauser 1996).



Both duration and formants contributed to the identification of clusters in almost all the species considered. Formants are known to be crucial for the identification of vocalization types (Gamba 2014; Gamba and Giacoma 2007; Giacoma *et al.* 2011) and have the potential to provide listeners with individual and species-specific cues (Gamba *et al.* 2012a).

Snorts, clicks, and hoots were not selected as cluster representatives and were often grouped with different vocalization types to form fairly dishomogeneous clusters. This result is consistent across the species and is in line with previous data which suggest that low-pitched calls may be part of a graded system more than discrete emissions (Gamba and Giacoma 2007). Identifiable vocalization types are common, but calls with intermediate acoustic structure may also occur and may be either ‘oversplit’ by human listeners or not recognized as discrete by the unsupervised methodology we adopted. *Eulemur* low-pitched calls (grunts, clicks, grunted hoots, hoots, snorts, and possibly long grunts) are usually classified as contact calls (Rendall 2000; Gamba and Giacoma 2005; 2007; Gamba *et al.* 2012a; 2012b; Pflüger and Fichtel 2012). These low-pitched signals, especially grunts, are the most frequently emitted call type in *Eulemur* (Gamba and Giacoma 2005; Gamba *et al.* 2012a; Pflüger and Fichtel 2012). However, whether acoustic variation in low-pitched signals plays a role in encoding information other than emitter position is still unclear (Pflüger and Fichtel 2012).

The context of call emission is a powerful indicator of their social function and may provide crucial information to the investigation of acoustic structure (Rendall *et al.*

1999; Gros-Louis *et al.* 2008). Future studies are necessary to explore the contextual variation of the vocalization types, how the occurrence of vocal signals relates to their acoustic structure, and how this information can be integrated into unsupervised analyses.

Although there was low agreement between cluster analysis and *a priori* classification, distinct types of grunts and/or grunted hoots emerge in all species. In addition, grunts emitted by *E. coronatus* are identified as three different types. Long grunts, which are reported to denote contexts of disturbance and potential territorial predation, or are emitted during locomotion (Gamba and Giacoma, 2005; 2007; Pflüger and Fichtel 2012), occur in *Eulemur mongoz* and *E. fulvus*. Associations between low-pitched calls and tonal calls emerged as distinct clusters (grunt-tonal calls, long grunt-tonal calls) in all species except *E. rufus*, and have been reported for many species (Macedonia and Stanger 1994).

Our findings support the prediction that variation in particular vocal types may mask variation at a lower level, in agreement with a study of Guinea baboon calls (Maciej *et al.* 2013). In baboon calls, variation in screams was stronger than for other vocalization types. In five of six *Eulemur* species, we found that screams represented more than one (usually homogeneous) cluster (*Eulemur flavifrons* did not emit screams in the same situation in which other species emitted them). In *Eulemur fulvus* and *E. rufus*, we identified three clusters of territorial calls, while alarm calls formed three clusters in *E. coronatus* and five clusters in *E. flavifrons*. The fact that cluster analysis identified more than one cluster of alarm calls, screams, and territorial calls

indicates variability that has not been reported in previous studies (Macedonia and Stanger 1994; Gamba and Giacomini 2007). These results represent an operationally useful indication for future studies, which may link vocal variation with factors such as level of arousal, social interactions or audience composition (Fichtel and Hammerschmidt 2002; Stoeger *et al.* 2011; Slocombe and Zuberbühler 2007; Clay and Zuberbühler 2012).

In conclusion, dynamic time warping appears to be a promising method for deepening our knowledge of how lemurs encode information in their vocal signals, and allows the objective identification of vocalization types. We envisage the use of unsupervised classification in different circumstances, including field studies. For example, various researchers report that the classification of calls to be used in playback experiments is particularly challenging. Acoustic analysis may reveal that recorded calls may in fact be different signals (Rendall *et al.* 1999). Researchers can face the problem of classifying calls in different groups when in the field. In these situations, the unsupervised classification of a small number of calls can be very helpful to provide the investigator with an interpretable quantitative analysis, which may result in improved experimental design and aid in the evaluation of the results (Seiler *et al.* 2013).

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Supporting Information Online Resource 1 (Appendix S1 and S2), Online Resource 2 (Appendix S3), Online Resource 3 (Appendix S4 and S5), and Online Resource 4 (Appendix S6) are available online.

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## FIGURE LEGENDS

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

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

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

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

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

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

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

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

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

Vocalization	<i>E. fulvus</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
<b>Number of clusters</b>	<b>11</b>	<b>10</b>	<b>14</b>	<b>9</b>	<b>13</b>	<b>10</b>	<b>10</b>
<b>Adjusted Rand Index</b>	<b>0.27</b>	<b>0.32</b>	<b>0.18</b>	<b>0.24</b>	<b>0.32</b>	<b>0.32</b>	<b>0.25</b>

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 <sup>st</sup> D. f.	2 <sup>nd</sup> 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 (1<sup>st</sup> D. f.) and the second (2<sup>nd</sup> D. f.) discriminant functions. In brackets, we also reported the parameters showing the highest load on the discriminant functions.

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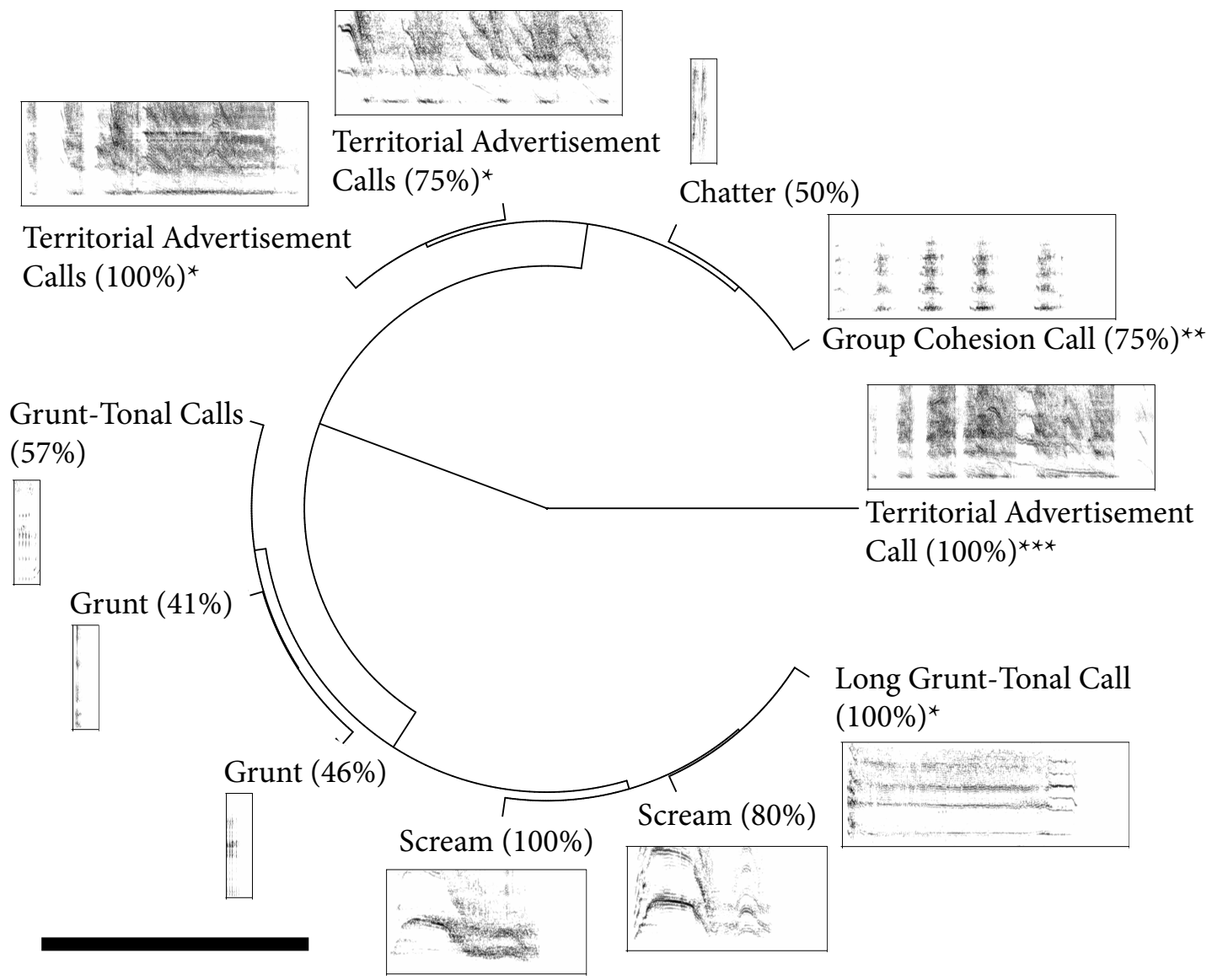


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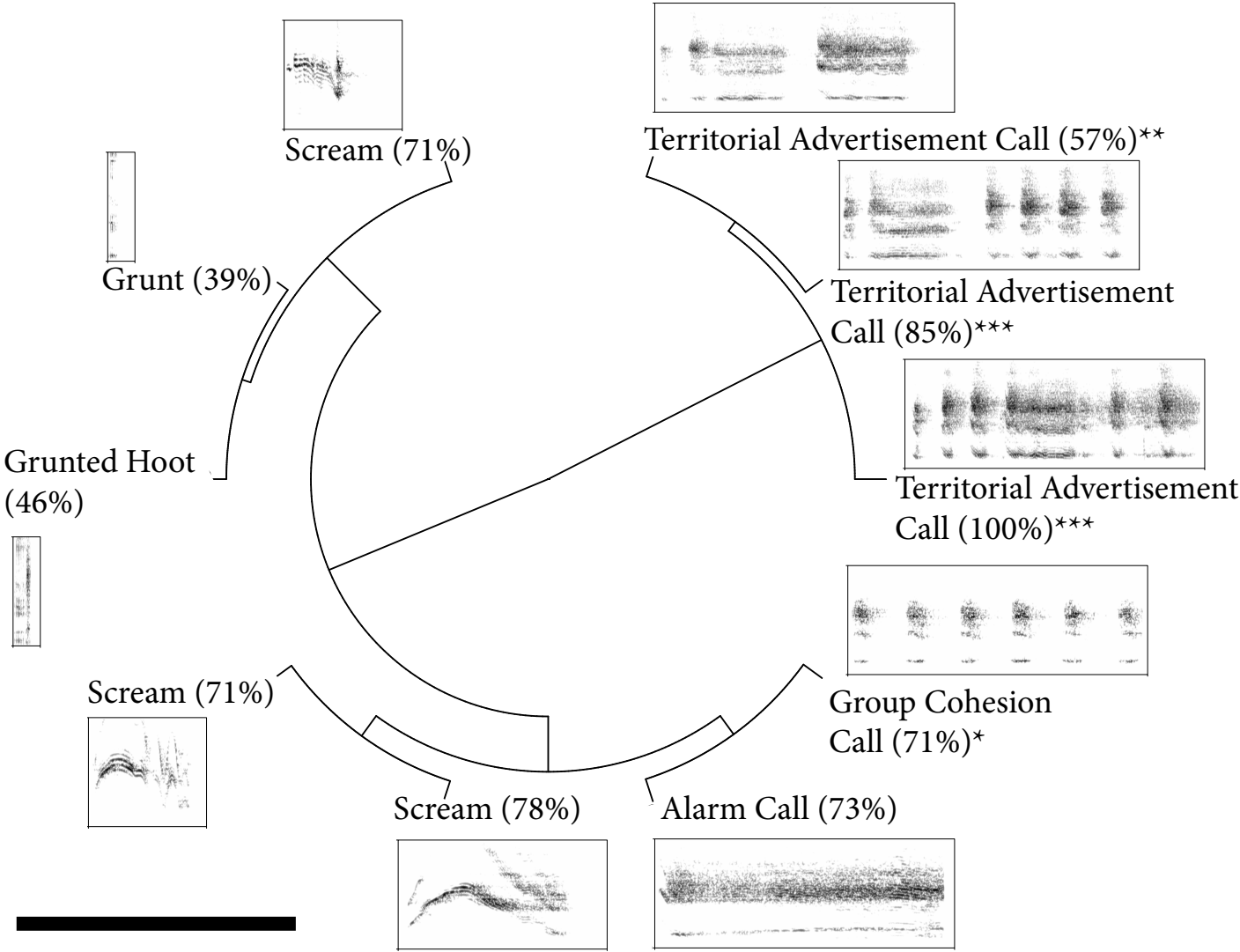




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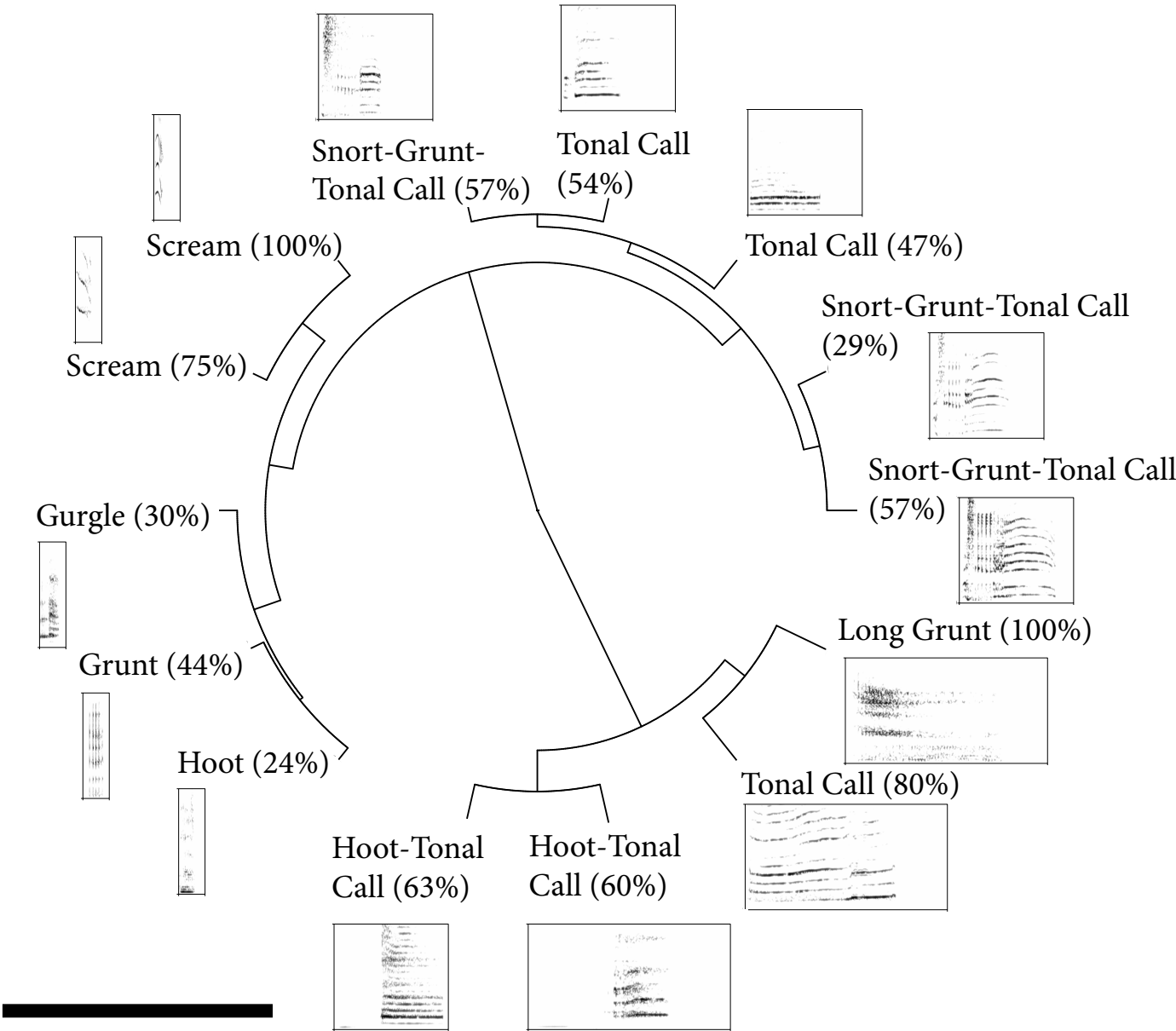


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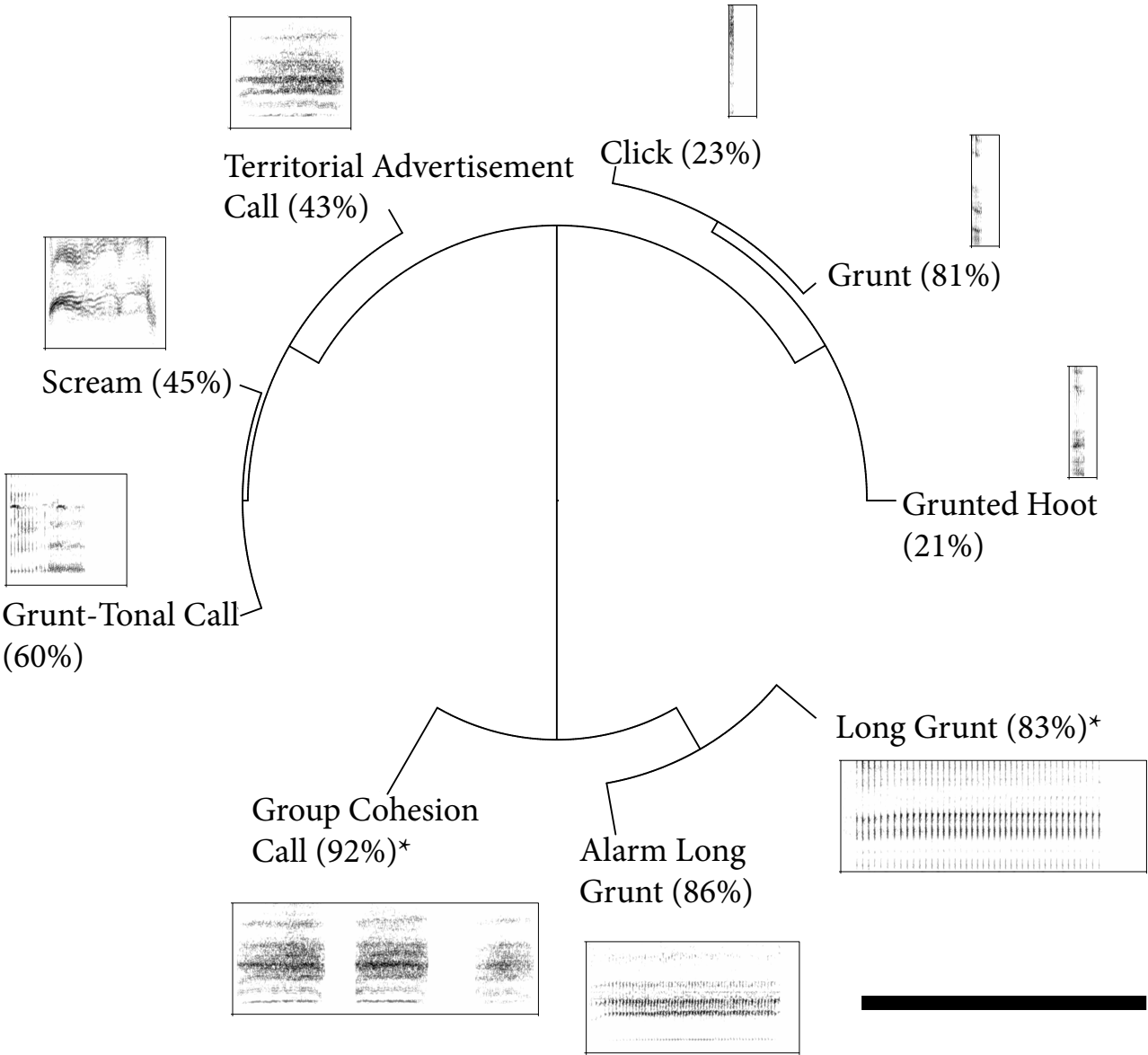


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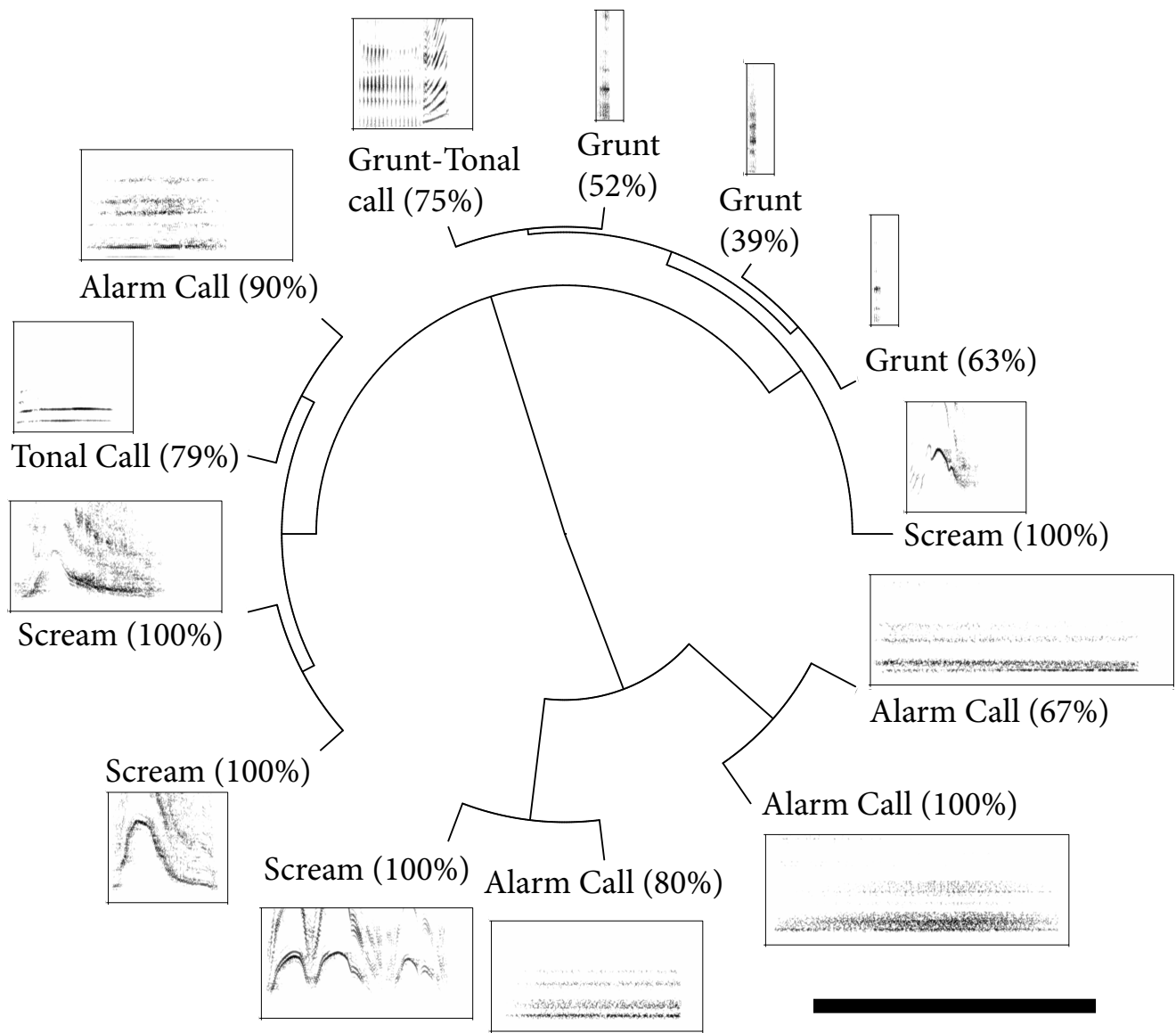


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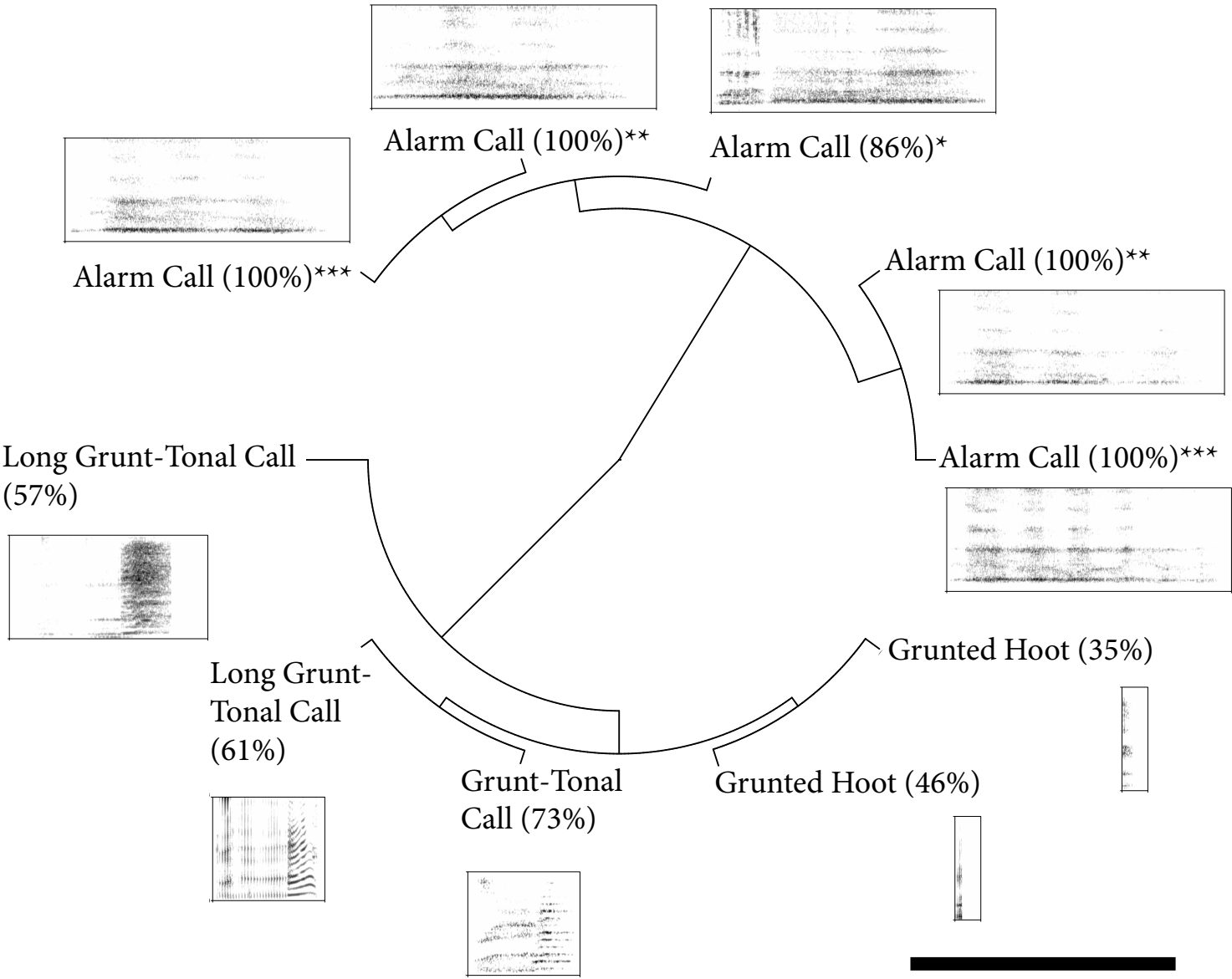


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