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Comparative Analysis of the Vocal Repertoires of the Indri (*Indri indri*) and the Diademed Sifaka (*Propithecus diadema*)

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Corresponding Author:	Teresa Raimondi Università degli Studi di Torino: Università degli Studi di Torino Torino, Torino ITALY	
Corresponding Author Secondary Information:		
Corresponding Author's Institution:	Università degli Studi di Torino: Università degli Studi di Torino	
Corresponding Author's Secondary Institution:		
First Author:	Daria Valente	
First Author Secondary Information:		
Order of Authors:	Daria Valente	
	Longondraza Miaretsoa	
	Alessio Anania	
	Francesco Costa	
	Alessandra Mascaro	
	Teresa Raimondi	
	Chiara De Gregorio	
	Valeria Torti	
	Olivier Friard	
	Jonah Ratsimbazafy	
	Cristina Giacoma	
	Marco Gamba	
Order of Authors Secondary Information:		
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	Parco Natura Viva	Dr Daria Valente
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relying on frequency bins, t-SNE data reduction, and a hard-clustering analysis. We first quantified the vocal repertoire of *P. diadema*, finding consistent results for the 9 putatively identified call types. When comparing this repertoire with a previously published repertoire of *I. indri*, we found highly species-specific repertoires, with only 2% of the calls misclassified by species identity. The loud calls of the two species were very distinct, while the low-frequency calls were more similar. Our results pinpoint the role of phylogenetic history, social and environmental features on the evolution of communicative systems and contribute to a deeper understanding of the evolutionary roots of primate vocal differentiation. We conclude by arguing that standardized and reproducible techniques, like the one we employed, allow robust comparisons and should be prioritized in the future.

Comparative analysis of the vocal repertoires of the indri (*Indri indri*) and the diademed sifaka (*Propithecus diadema*)

Daria Valente^{1,2+@}, Longondraza Miaretsoa^{1,3+}, Alessio Anania¹⁺, Francesco Costa¹, Alessandra Mascaro¹, Teresa Raimondi^{1@}, Chiara De Gregorio¹, Valeria Torti¹, Olivier Friard¹, Jonah Ratsimbazafy³, Cristina Giacoma^{1#}, Marco Gamba^{1#}

@corresponding author

+Shared first authorship

#Shared senior authorship

¹ *Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy*

² *Equipe de Neuro-Ethologie Sensorielle (ENES), Centre de Recherche en Neurosciences de Lyon (CRNL), CNRS, INSERM, University of Lyon/Saint-Étienne, Saint-Étienne, France*

³ *Groupe d'Etude et de Recherche sur les Primates de Madagascar (GERP), Antananarivo, Madagascar.*

Corresponding authors:

Teresa Raimondi

Dipartimento di Scienze della Vita e Biologia dei Sistemi – Università degli Studi di Torino
Via Accademia Albertina, 13 – 10123 – Torino (TO) – Italy

+39 0116704559

teresa.raimondi@unito.it

Daria Valente

Equipe de Neuro-Ethologie Sensorielle (ENES)

21, rue du Dr. Paul Michelon 42100 Saint-Etienne, France

Dipartimento di Scienze della Vita e Biologia dei Sistemi – Università degli Studi di Torino
Via Accademia Albertina, 13 – 10123 – Torino (TO) – Italy

daria.valente@unito.it

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Supporting information

Information on group size and composition, sampling days, overall observation time (ESM Table SI) and a comparison between the vocal types identified in our study and the alleged homologous call types in congeneric species (ESM Table SII) are available online.

Conflict of Interest

The authors declare that they have no conflict of interest.

Author Contributions

MG formulated the idea; DV, CDG, VT, AA, FC, AM, LM collected the data; OF, MG, DV, AA, FC conducted acoustic analyses; DV and MG performed statistical analyses; DV and TR implemented data visualization; MG, DV, AA, CDG wrote the manuscript; all authors provided editorial advice.

1 **Comparative analysis of the vocal repertoires of the indri (*Indri indri*) and the**
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5 **Abstract**

6 Strepsirrhine vocalisations are extraordinarily diverse and cross-species comparisons are needed to
7 explore how this variability evolved. We contributed to the investigation of primate acoustic diversity
8 by comparing the vocal repertoire of two sympatric lemur species, *Propithecus diadema* and *Indri indri*.
9 These diurnal species belong to the same taxonomic family and have similar activity patterns but
10 different social structures. These features make them excellent candidates for an investigation of the
11 phylogenetic, environmental, and social influence on primate vocal behaviour. We recorded 3 *P. diadema*
12 groups in 2014 and 2016. From 1872 recordings we selected and assigned 3814 calls to 9 *a priori* call
13 types, on the basis of their acoustic structure. We implemented a reproducible technique performing an
14 acoustic feature extraction relying on frequency bins, t-SNE data reduction, and a hard-clustering
15 analysis. We first quantified the vocal repertoire of *P. diadema*, finding consistent results for the 9
16 putatively identified call types. When comparing this repertoire with a previously published repertoire
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19 more similar. Our results pinpoint the role of phylogenetic history, social and environmental features on
20 the evolution of communicative systems and contribute to a deeper understanding of the evolutionary
21 roots of primate vocal differentiation. We conclude by arguing that standardized and reproducible
22 techniques, like the one we employed, allow robust comparisons and should be prioritized in the future.

23
24 **Keywords** vocal repertoire - primates - clustering - phylogeny - sensory drive - social complexity

25 **Introduction**

26 Acoustic signals play various roles in mate choice, resource defence, and species recognition in a
27 broad range of taxa (Wilkins et al. 2013), including lemurs (Rakotonirina et al. 2016). Divergence in acoustic
28 traits mediates discrimination within and between species, and has been proposed to play a role in speciation
29 and evolution (Wilkins et al. 2013; Zimmermann 2016). This is particularly true for sympatric cryptic species,
30 in which species-specific vocal signals and recognition systems are involved in driving reproductive isolation.
31 For instance, recent research showed this mechanism in species of the genera *Microcebus* (Braune et al. 2008)
32 and *Phaner* (Forbanka 2020). The complexity of mammalian vocal communication has been studied to
33 understand possible factors determining convergent evolutionary patterns (Charlton and Reby 2016) and
34 species-specific differences (Gamba et al. 2015) and three main evolutionary frameworks have been proposed
35 for the diversification of communication systems and vocal flexibility (Schuster et al. 2012).

36 First, the Phylogenetic Hypothesis suggests that phylogeny determines the vocal repertoire of a species
37 (Ord and Garcia-Porta 2012), implying that closely-related members of a taxonomic group will have very
38 similar signals (Zimmermann 2017). This hypothesis is supported by studies indicating concordance between
39 vocal and genetic diversity across *Nomascus* species (Thinh et al. 2011). However, there is no evidence
40 indicating a relationship between vocal behaviour and phylogeny across lemurs (Zimmermann 2017; Hending
41 et al. 2020), including the Indriidae family (Ramanankirahina et al. 2016).

42 Second, the Social Complexity Hypothesis posits that the evolution of vocal communication and that
43 of social life are related (Pollard and Blumstein 2012; Bouchet et al. 2013), such that a more complex social
44 system requires more subtle communicative abilities to mediate interactions among group members (Freeberg
45 et al. 2012). Under this hypothesis, the diversity in the communicative signals of a species is related either to
46 a stable and egalitarian social structure (Mitani 1996) or to group size (McComb and Semple 2005, Kappeler
47 2019, Peckre et al. 2019). For instance, social structure and social organisation reflect the vocal repertoire
48 complexity in *Cercopithecus neglectus*, *Cercopithecus campbelli*, and *Cercocebus torquatus* (Bouchet et al.
49 2013).

50 Third, and finally, the Sensory Drive Hypothesis (Endler 1992) suggests that signals, sensory systems,
51 and microhabitat choice coevolve, with signal evolution being driven by environmental conditions, including
52 predation (Zimmermann 2017). This hypothesis is supported by the acoustic windows occupied by *Microcebus*

53 spp., *Mirza* spp., and *Cheirogaleus* spp. (Zimmermann 2018) which use high frequency and ultrasonic
54 components. The latter are rare among primates and appear to have evolved to cope with the social and
55 ecological needs of a dispersed social network (Zimmermann 2018). The acoustic frequency window is likely
56 a balance between being conspicuous to conspecifics while remaining cryptic for predators (Zimmermann
57 2018).

58 Although many lemurs live in smaller groups than other primates (Kappeler and Heymann 1996) some
59 lemur species live in large groups. Such groups may require sophisticated intelligence (social intelligence;
60 Dunbar 1996) and signals to modulate the relationships among group members (Oda 2008, Matsuzawa 2008).
61 For instance, the gregarious *Lemur catta* has a repertoire of 22 call types (Macedonia 1993) while other species,
62 like *Eulemur rufifrons* and *Propithecus verreauxi*, show referential-like calling (Fichtel and Kappeler 2002).
63 Call types and use also differ with sex in *Eulemur coronatus* (Gamba and Giacoma 200), *Mirza zaza* (Seiler
64 et al. 2019), and *Lepilemur edwardsi* (Rasoloharijaona et al. 2006). Hence, lemur vocal diversity may provide
65 useful information on the selective pressures that may have played a role in the evolution of vocal
66 communication (Oda 2008).

67 Among lemurs, *Indri indri* is the only species that sings (Giacoma et al. 2010; Baker-Médard et al.
68 2013; Torti et al. 2013, 2017; De Gregorio et al. 2019). Recent studies showed that indri's song possesses a
69 rhythmic structure (Gamba et al. 2016; De Gregorio et al. 2019, De Gregorio et al. 2021a), conforms to the
70 linguistic laws of brevity (Valente et al. 2021), shows an ontogenetic development (De Gregorio et al. 2021b),
71 and a sex-dimorphic phrase organization (Zanoli et al. 2020). This species shows a rich vocal repertoire,
72 including distinct alarm calls for terrestrial and aerial predators (Maretti et al. 2010) and several call types
73 mediating intra-group dynamics (Valente et al. 2019). In contrast, information on the vocal communication of
74 *Propithecus diadema* is limited to qualitative accounts examining the role of vocal behaviour in contact
75 seeking (Petter and Charles-Dominique 1979), and anti-predatory behaviour (Petter and Charles-Dominique
76 1979; Macedonia and Stanger 1994; Oda and Masataka 1996; Wright 1998; Fichtel and Kappeler 2002, 2011;
77 Patel and Owren 2012; Fichtel 2014). All *Propithecus* species have call types with comparable structures and
78 functions (Petter and Charles-Dominique 1979; Macedonia and Stanger 1994; Oda and Masataka 1996; Wright
79 1998; Fichtel and Kappeler 2002, 2011; Patel and Owren 2012; Fichtel 2014; Online Resource 2). An
80 exception is the zzuss, a call type only occurring in the repertoire of *P. diadema*, *P. candidus*, *P. perrieri*, and

81 *P. edwardsi* (Patel and Owren 2012; Anania et al. 2018; Wright 1998; Macedonia and Stanger 1994). The four
82 western *Propithecus* species (*P. verreauxi*, *P. coquereli*, *P. coronatus*, *P. deckenii*) and *P. tattersalli* do have
83 a call type serving similar functions to the zzuss (terrestrial predator alarming and group coordination, Patel
84 and Owren 2012) but with a different acoustic structure (Petter and Charles-Dominique 1979; Macedonia and
85 Stanger 1994; Oda and Masataka 1996; Fichtel 2014). Within the genus, the most investigated call types are
86 the alarm calls of *P. verreauxi* and *P. coquereli* (Fichtel and Kappeler 2014), and the zzuss of *P. candidus*
87 (Patel and Owren 2012). The latter represents the only quantitative description of a call type of eastern
88 *Propithecus* species.

89 To understand the extent to which the vocal systems of two strepsirrhine species differ, we compared
90 the calls of two sympatric and similar-sized lemur species, *Indri indri* and *Propithecus diadema*, belonging to
91 the same taxonomic family (Indriidae), both inhabiting the same rainforest environment and having diurnal
92 habits (Geissmann and Mutschler 2006). These species are the largest extant lemurs, and their estimated
93 pairwise divergence time ranges between 18 (Kistler et al. 2015; Masters et al. 2013; Federman et al. 2016)
94 and 29-36 MYA (Roos et al. 2004; Fritz et al. 2009; Antonelli et al. 2017; Fabre et al. 2009). *Propithecus*
95 *diadema* lives in multimale/multifemale groups of 2 to 8 individuals (Powzyk 1997; Irwin 2008; Weir 2014),
96 while *I. indri* groups range from 2 to 5 individuals (Glessner and Britt 2005; Torti et al. 2017; Torti et al. 2018;
97 Bonadonna et al. 2020), usually comprising a monogamous reproductive pair and their offspring (Bonadonna
98 et al. 2019). Thanks to these features, they are suitable subjects to investigate the effect of the phylogenetic,
99 environmental, and social influence on their vocal behaviour. Moreover, *Indri indri* and *P. diadema* emit calls
100 in similar contexts. Both species vocalise in the presence of terrestrial disturbance (disturbance call in *P.*
101 *diadema*, wheezing grunt and kiss-wheeze in *I. indri*; Macedonia and Stanger 1994) or aerial predators (roaring
102 vocalisations: Macedonia and Stanger 1994; Powzyk 1997). Calls are also used to coordinate group
103 movements during foraging or displacing activities (Petter and Charles-Dominique 1979; Macedonia and
104 Stanger 1994).

105 We compared the number of distinct call types and their spectro-temporal structure, in the light of the
106 Phylogenetic Hypothesis, Sensory Drive Hypothesis, and Social Complexity Hypothesis. *Indri indri* and *P.*
107 *diadema* belong to the same taxonomic family, so the Phylogenetic Hypothesis predicts that their repertoires
108 should be more similar to one another than to those of more distantly-related species. We also predict the vocal

109 repertoires of the two species will be similar to one another, based on the Sensory Drive Hypothesis. Lastly,
110 we tested two versions of the Social Complexity Hypothesis. First, if vocal repertoire size is positively related
111 to group size (McComb and Semple 2005), we predict that *P. diadema*, which lives in larger groups, will have
112 a larger repertoire than *I. indri*, which lives in smaller groups. Conversely, if vocal diversification is driven by
113 a stable and egalitarian social structure (Mitani 1996) we predict a larger repertoire in pair-living, monogamous
114 *I. indri*, than in the more despotic *P. diadema*, with its multimale/multifemale groups.

115

116 **Methods**

117 *Data collection*

118 We conducted the study in four forest sites: Analamazaotra Special Reserve (Madagascar National Parks, 18°
119 56' S - 48° 25' E), Andasibe-Mantadia National Park (Madagascar National Parks, 18° 28' S - 48° 28' E),
120 Mitsinjo Forest Station (Association Mitsinjo, 18° 56' S - 48° 24' E), and Maromizaha Protected Area (Groupe
121 d'Étude et de Recherche sur les Primates de Madagascar, 18° 56' 49" S – 48° 27' 33" E).

122 We collected vocalisations of *I. indri* by sampling 18 habituated groups between 2005 and 2018.
123 Group size ranged from two to six individuals (mean \pm SD = 4.2 \pm 1.2). We collected vocalisations of *P.*
124 *diadema* by sampling three habituated groups in 2014 and 2016. Group size ranged from eight to ten
125 individuals (mean \pm SD = 8.8 \pm 0.8). Further information on data collection (groups size and composition,
126 sampling days, and overall observation time) can be found in Online Resource 1. For both species, we followed
127 a focal group for one to five consecutive days, observing animals at a distance ranging from 0.5 to 20 m. We
128 identified individuals using morphological criteria such as fur patterns and other natural marks. Both species
129 are diurnal and their activity pattern is concentrated during the first half of the day (Pollock 1975; Petter and
130 Charles-Dominique 1979). *Indri indri* vocal emissions are concentrated in the early morning (Geissmann and
131 Mutschler 2006). *Propithecus diadema* calls can be emitted anytime throughout the day but are more common
132 early in the morning and at the beginning of the afternoon (Petter and Charles-Dominique 1979). We, therefore,
133 monitored the groups daily, from 06:00 h until their activities started to decrease (usually around 14:00 h),
134 using focal animal sampling to collect data (Altmann 1974). Occasionally, we also collected audio and video
135 recordings of individuals' utterances using *ad libitum* sampling (Altmann 1974). We recorded spontaneous
136 vocalisations using a Sennheiser ME66 or a Sennheiser ME67 shotgun directional microphone (frequency

137 response range of both microphones: 40-20000 Hz \pm 2.5 dB) connected to a solid-state digital audio recorder,
138 a Sound Devices 702 (frequency response range: 10-40000 Hz +0.1/-0.5 dB), or a Tascam DR- 100 MKII
139 (frequency response range: 20-20000 Hz +1/-3 dB). We set the recorders at a sampling rate of 44.1 kHz and
140 an amplitude resolution of 16 or 24 bit. We recorded signals emitted from individuals at 15 to 20 m depending
141 on signal intensity, weather conditions, and canopy thickness. We made recordings with the microphone facing
142 the caller or in the direction of the whole group. We did not deliberately manipulate or modify the animals'
143 behaviour and recorded only spontaneous vocal emissions.

144

145 *Acoustical and statistical analyses*

146 We visually inspected all recordings using Praat 6.0.28 (Boersma and Weenink, University of Amsterdam).
147 For *P. diadema*, we acquired 8946 calls from 1872 initial recordings, of which we chose 3814 calls for acoustic
148 analyses. We selected high-quality vocal emissions (higher intensity and lower background noise) and
149 discarded noisy and overlapping calls (multiple individuals and different species) and vocalisations uttered by
150 infants. We discarded calls where the signal to noise ratio was lower than 12 dB, that were acoustically
151 distorted, or that overlapped with other sounds (Gamba et al. 2015).

152 Vocal emissions can include sequences of repeated temporally close calls. We considered two
153 emissions as distinct calls when they were separated by at least 0.025 s. This threshold is recognized in humans
154 and non-human animals, including primates, as a natural psychophysical boundary representing the minimum
155 time interval needed by the auditory system to differentiate between two distinct acoustic signals (Kuhl and
156 Padden 1983; Liberman 1991). In the field, we noticed that different call types can be emitted sequentially
157 (e.g., the mmm is often uttered after a roar chorus; AA *pers. obs.*). Within the recordings, we found that the
158 most conspicuous association concerned zzuss and tsk. We, therefore, measured the mean duration of the silent
159 interval between these two call types across 145 recorded sequences. We normalized each sound file using a
160 scale to peak function in Praat (Comazzi et al. 2016) and assigned it to nine a priori classes based on audio-
161 visual evaluation (Lemasson et al. 2014). Some call types are described in studies of rainforest *Propithecus*
162 (Petter and Charles-Dominique 1979; Macedonia and Stanger 1994; Wright 1998; Powzyk 1997; Patel and
163 Owren 2012). We chose the names zzuss (n = 400), roar (n = 176), and grunt (n = 145) to ensure consistency
164 with the literature (Macedonia and Stanger 1994; Wright 1998; Patel and Owren 2012). We labelled new call

165 types according to the sound quality (chatter-squeal, n = 317; soft grunt, n = 221), the hypothesized function
166 (lost call, n = 193), or with onomatopoeic terms (hum, n = 1927; mmm, n = 246; tsk, n = 189). For each call
167 type, we measured duration, mean, minimum, and maximum fundamental frequency. We also considered the
168 range of emission and phonatory mechanisms.

169 We employed the methodology shown in Valente et al. (2019) and used a custom-made script in Praat
170 to extract spectral coefficients for each call: we measured the total duration of a sound and divided it into ten
171 equal portions. Then, considering a frequency range from 50 to 22000 Hz, representing the frequency spectrum
172 covered by the calls in our sample, we split each portion into frequency bands (or bins) of 500 Hz each (e.g.,
173 50–500 Hz, 501–1000 Hz), then extracted the energy value of each bin (through the function ‘Get band energy’
174 in Praat). The resultant dataset included the duration and 220 frequency parameters for each call. We used the
175 Rtsne package (Krijthe 2015) in R (R Core Team 2021) to embed the dataset into a bi-dimensional plan through
176 a t-distributed stochastic neighbour embedding (Van der Maaten and Hinton 2008) with a Barnes-Hut
177 implementation, initializing the algorithm with perplexity = 40 and theta = 0.5. We then submitted the reduced
178 dataset, containing two features, to a clustering procedure, using a k-means algorithm (MacQueen 1967).

179 Lastly, we investigated whether the two species shared some call types and assessed the difference
180 among the two vocal repertoires. For the comparison, we used a dataset of 3360 calls used to quantify *I. indri*'s
181 repertoire (Valente et al. 2019), containing 10 call types: clacson, hum, grunt, kiss, long tonal call, roar, short
182 tonal call, songbit, wheeze, and wheezing grunt. Valente and colleagues used the same acoustic approach
183 (extraction of duration and spectral coefficients of the calls, Valente et al. 2019), which allowed us to combine
184 the features of all calls of both species into a single dataset. We first reduced the combined data through a t-
185 SNE based compression, then submitted the compressed dataset to a k-means clustering algorithm (MacQueen
186 1967). We used t-SNE to visualize data.

187

188 ***Ethical note***

189 We conducted observational research without manipulating animals, with permission of the Malagasy
190 Ministry of Environment and Forests, Research permits: 2005 [N°197/MINENV.EF/SG/DGEF/DPB/SCBLF/
191 RECH], 2006 [N°172/06/MINE NV.EF/SG/DGEF/DPB/SCBLF], 2007 [N°0220/07/MINENV.EF/SG/
192 DGEF/DPSAP/SSE], 2008 [N°258/08/MEFT/SG/DGEF/DSAP/SSE], 2009[N°243/09/MEF/SG/DGF/

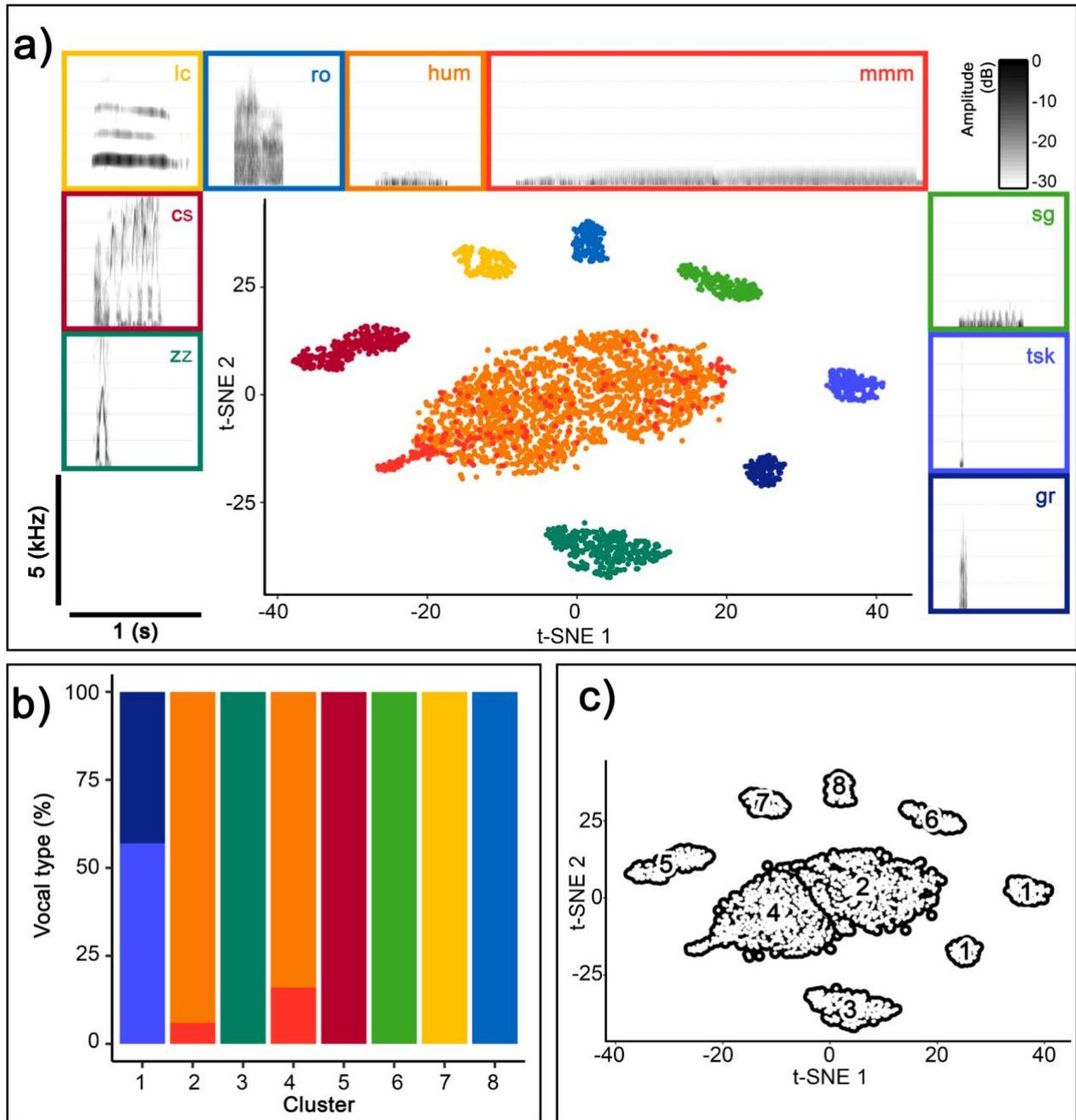
193 DCB.SAP/SLRSE], 2010 [N°118/10/MEF/SG/DGF/DCB.SAP/SCBSE, N°293/10/MEF/SG/DGF/DCB.
194 SAP/SCB], 2011 [N° 274/11/MEF/SG/ DGF/DCB.SAP/SCB], 2012 [N°245/12/MEF/SG/DGF/DCB.SAP/
195 SCB], 2014 [N°066/14/MEF/SG/DGF/DCB.SAP/SCB], 2015 [N°180/15/MEEMF/SG/DGF/DAPT/SCBT],
196 2016 [N°98/16/MEEMF/SG/DGF/DAPT/SCB.Re, N°217/16/MEEMF/SG/DGF/DSAP/SCB.Re], 2017
197 [N°73/17/MEEF/SG/DGF/DSAP/SCB.RE], 2018 [N°91/18/MEEF/SG/DGF/DSAP/SCB.Re]. We declare
198 the data collection procedure conforming to the national legislation and international regulation concerning
199 animal welfare.

200

201 **Results**

202 *t-SNE mapping: Propithecus diadema calls*

203 The algorithm identified eight clouds of points, where each point represents a call and each cloud might
204 represent a cluster (Van der Maaten and Hinton 2008), so we imposed $k = 8$ for k-means clustering (Fig. 1c).
205 The eight different clusters were mostly consistent with the putative identification of calls and with their
206 acoustic structure (Table 1). Clusters 3, 5, 6, 7, and 8 included one vocal type each: zzuss, chatter-squeal, soft
207 grunt, lost call, and roar, respectively (Fig. 1a, 1c). Conversely, both Clusters 2 and 4 mainly included hum
208 (94% and 84%) and mmm (6% and 16%, Fig. 1b). Grunt and tsk were grouped in Cluster 1 (Fig. 1b, 1c).
209 Analysis of a subsample of 145 zzuss-tsk sequences showed that when these two calls are uttered sequentially,
210 the mean duration of the pause between them is $0.62 \pm SD 0.11$ s.



211

212 **Fig. 1** Representation of *P. diadema* calls (recorded in Maromizaha Protected Area in 2014 and 2016) on a bi-
 213 dimensional plan obtained by initializing a t-SNE algorithm with perplexity = 40 and theta = 0.5. a)
 214 Visualization of t-SNE mapping combined with a priori identification of call types (cs = chatter-squeal, gr =
 215 grunt, hum = hum, lc = lost call, mmm = mmm, ro = roar, sg = soft grunt, tsk = tsk, zz = zzuss). We generated
 216 spectrograms (Hanning window, 512 samples, overlap = 64, zero-padding = 16) using the R package *Seewave*
 217 (Sueur et al. 2008). b) The distribution of vocal types within the clusters. Colours follow those in panel a. c)

218 Results of k-means clustering on the bi-dimensional vector produced using t-SNE. Numbers indicate clusters
219 (i.e., 1 = Cluster 1).

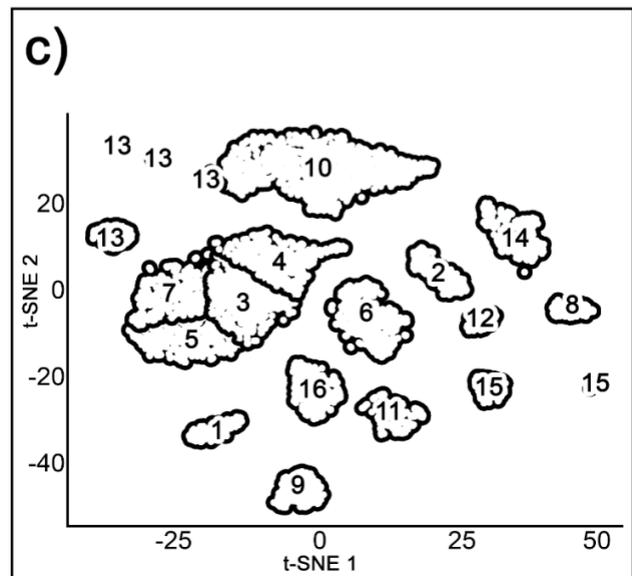
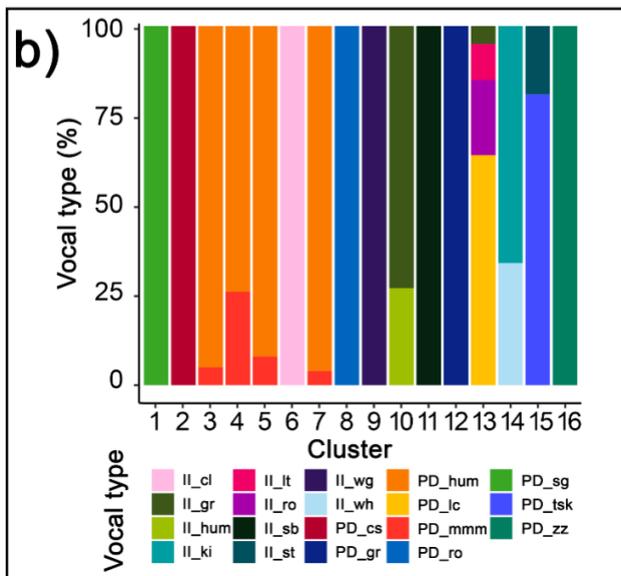
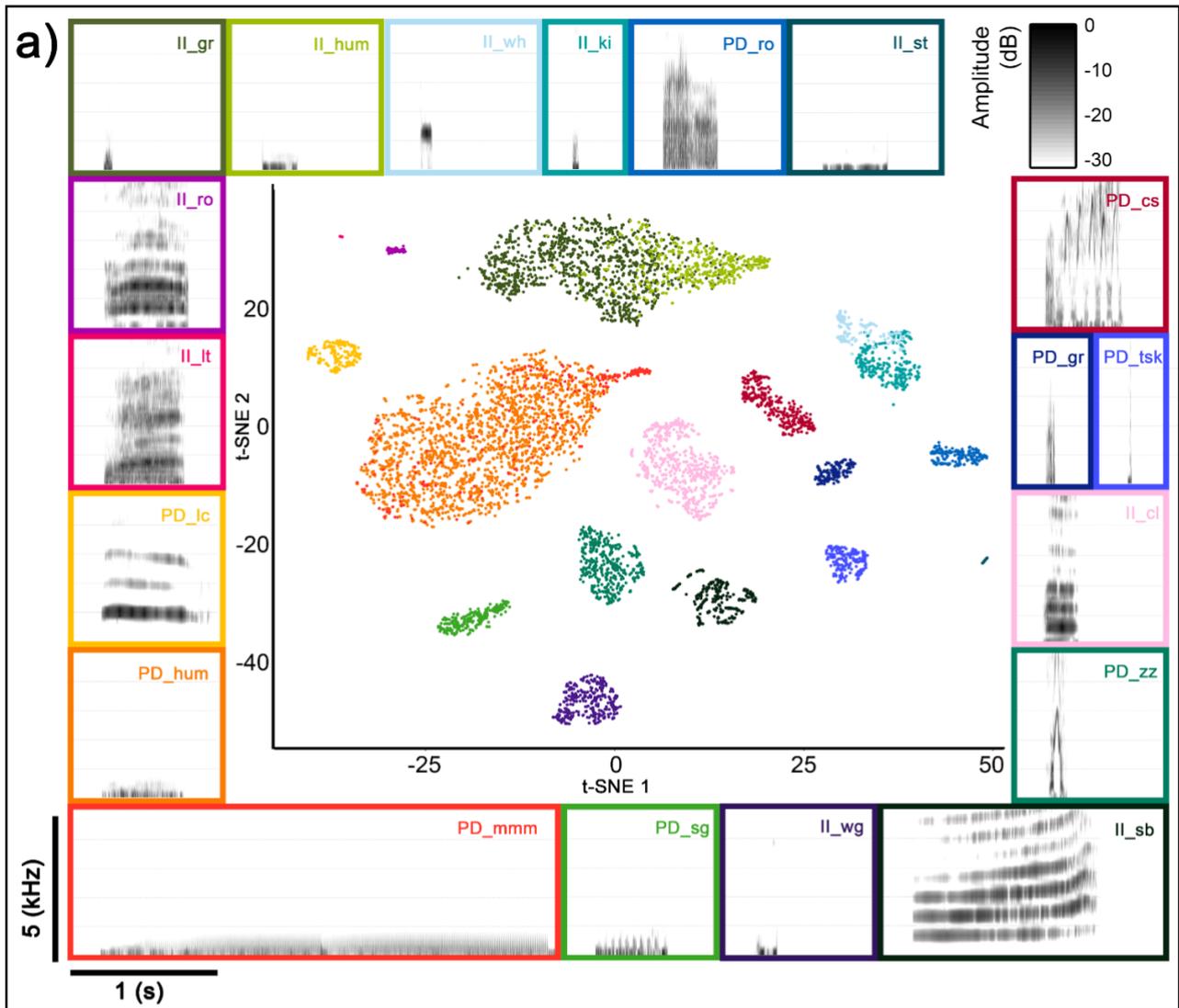
220 **Table 1** Definition of call types emitted by *Propithecus diadema* recorded in Maromizaha Protected Area in 2014 and 2016.

<i>Call Type</i>	<i>Description</i>	<i>Duration (s)</i>	<i>Mean f0 (Hz)</i>	<i>Max f0 (Hz)</i>	<i>Min f0 (Hz)</i>	<i>Range</i>	<i>Phonatory mechanism</i>
Chatter-squeal	High-amplitude, high-pitched tonal call. Usually uttered in sequences of short signals.	0.38 ± 0.375	2098.61 ± 530.71	2849.51 ± 1466.29	1287.75 ± 1069.53	Long	Semi-open mouth
Grunt	Medium-pitched short pulses. Usually emitted in sequences.	0.06 ± 0.02	1408.98 ± 61.16	1506.98 ± 567.83	1341.28 ± 518.09	Short	Open mouth
Hum	Low-pitched tonal call.	0.40 ± 0.09	281.80 ± 152.08	562.85 ± 771.06	150.15 ± 197.47	Short	Closed mouth
Lost Call	Medium-pitched, medium-amplitude tonal call.	0.71 ± 0.30	927.80 ± 58.65	1014.80 ± 264.00	800.73 ± 148.42	Long	Slightly-open mouth
Mmm	Low-pitched tonal call, normally with low modulation. Often emitted in sequence or in overlap between individuals. Frequently emitted after a roar call.	2.55 ± 0.94	392.91 ± 329.20	1704.57 ± 1603.97	115.73 ± 128.69	Short	Closed mouth, often emitted with the head turning on a transverse plane
Roar	Medium-pitched broadband calls, emitted in choral sequences of short utterances.	0.15 ± 0.08	1058.12 ± 66.23	1141.69 ± 654.49	992.02 ± 639.07	Long	Open mouth
Soft grunt	Low-pitched, low-amplitude short pulses of broadband noise.	0.31 ± 0.15	457.47 ± 172.48	848.21 ± 990.91	313.51 ± 185.10	Short	Closed mouth
Tsk	Low amplitude short clicks. It follows a zzuss or a zzuss-tsk sequence.	0.03 ± 0.02				Short	Semi-open mouth
Zzuss	High-amplitude, high-pitched, harmonic short call. It can be followed by tsk within 1s (mean = 0.62 ± SD 0.11 s).	0.18 ± 0.21	2054.39 ± 474.34	2623.31 ± 969.57	1430.15 ± 948.57	Long	Closed mouth

221 Acoustic parameters (duration, mean, maximum, and minimum fundamental frequency are expressed as mean ± standard deviation). We evaluated the range of
 222 emission (short vs. long) based on the call amplitude and the possible occurrence of counter-calling within or between groups.

223 ***t-SNE mapping: calls of Propithecus diadema and Indri indri***

224 The algorithm identified 16 clouds of points, so we chose $k = 16$ for k-means clustering. The 16 clusters were
225 partially consistent with the putative identification of calls. Clusters 1, 2, 8, 12, and 16 each included a single
226 call type: soft grunt, chatter-squeal, roar, grunt, zzuss, respectively (all belonging to *P. diadema*'s vocal
227 repertoire, Fig. 2a, 2c). Clusters 6, 9, and 11 included *I. indri*'s clacson, wheezing grunt, and songbit,
228 respectively. Clusters 3, 4, 5, and 7 included mostly hum (95%, 74%, 92%, 96%) and a smaller percentage of
229 mmm, both emitted by *P. diadema* (5%, 26%, 8%, 4% respectively, Fig. 2b). Cluster 10 grouped *I. indri*'s
230 grunt and hum (73% and 27%, Fig. 2b) while Cluster 14 grouped indri's kiss and wheeze (66% and 34%, Fig.
231 2b). Cluster 13 grouped *P. diadema*'s lost call (64%) with *I. indri*'s roar, long tonal call, and grunt (21, 10%,
232 and 5%, respectively). Cluster 15 included mainly *P. diadema*'s tsk (81%) (Fig. 2b).



233

234 **Fig. 2** Representation of *P. diadema* and *I. indri* calls on a bi-dimensional plan obtained by initializing a t-

235 SNE algorithm with perplexity = 40 and theta = 0.5. a) Visualization of the t-SNE mapping combined with

236 the a priori identification of call types (II = *I. indri*; cl = clacson, gr = grunt, hum = hum, lt = long tonal call,
237 ki =kiss, ro = roar, sb = songbit, st = short tonal call, wg = wheezing grunt, wh = wheeze, PD = *P. diadema*;
238 cs = chatter-squeal, gr = grunt, hum = hum, lc = lost call, mmm = mmm, ro = roar, sg = soft grunt, tsk = tsk,
239 zz = zzuss). We recorded calls of *I. indri* in four forest sites (Analamazaotra Special Reserve, Andasibe-
240 Mantadia National Park, Mitsinjo Forest Station, and Maromizaha Protected Area) from 2005 to 2018, and
241 calls of *P. diadema* in Maromizaha Protected Area in 2014 and 2016. We generated spectrograms (Hanning
242 window, 512 samples, overlap = 64, zero-padding = 16) using the R package *Seewave* (Sueur et al. 2008). b)
243 The distribution of the call types within the clusters. Colours follow those in the panel a. c) Results of the k-
244 means clustering performed on the bi-dimensional vector produced using the t-SNE. Numbers indicate the
245 relative clusters (i.e., 1 = Cluster 1).

246

247 **Discussion**

248 Our cluster analysis of the vocal repertoire of *P. diadema* highlighted the presence of eight clusters,
249 mostly consistent with the a priori identification of the calls, with only a few call types grouping together.
250 Based on acoustic and spectrographic analysis, we identified nine distinct call types. Five clusters showed
251 homogenous grouping of as many call types: lost call, chatter-squeal, soft grunt, zzuss, and roar. Two of the
252 remaining clusters showed a mixture of hum and mmm (94% and 6% in one case, 84% and 16% in the other),
253 possibly indicating some gradation between the two (Wadewitz et al. 2015). The last cluster also grouped two
254 call types: tsk and grunt. Given the results, we estimated the vocal repertoire of *P. diadema* to consist of nine
255 call types, with some showing a graded structure (tsk and grunt, and mmm and hum, in particular). We used
256 this estimate in our comparisons.

257 Comparison between the vocal repertoire of *P. diadema* and that of *I. indri* showed that loud calls of
258 both species possess distinctive features, while some low-frequency calls resulted grouped together, meaning
259 that these call types are characterized by similar spectro-temporal features. We identified eight homogeneous
260 groups. Five (chatter squeal, both grunt and soft grunt, roar, and zzuss) were *P. diadema*'s most distinctive
261 calls. Three (clacson, wheezing grunt, and songbit) were *I. indri* calls. This analysis suggested four clusters
262 mainly consisting of *P. diadema*'s low-pitched calls, like hum and mmm (the latter in smaller percentages). It
263 also confirmed the gradedness between these two call types found in the singles-species analyses. Two other

264 clusters (10 and 14) grouped mostly *I. indri*'s low- (grunt and hum; 61%) and medium-pitched calls (wheeze
265 and kiss; 66%). This result is in line with previous analyses of lemur low-pitched calls, in which the grunt,
266 click, grunted hoot, hoot, snort, and long grunt of *Eulemur* ssp. (Gamba and Giacoma 2005, 2007; Gamba et
267 al. 2012; Pflüger and Fichtel 2012; Nadhurou et al. 2015) showed little differentiation compared to alarm calls
268 or high-pitched calls. Interestingly, two other clusters included *P. diadema*'s tsk (81%) and *I. indri*'s short tonal
269 call (19%) as well as *P. diadema*'s lost call (64%) and *I. indri*'s roar and long tonal call (21%; 10%). These
270 clusters grouped voiceless calls (e.g., tsk) and calls with a more broadband structure (e.g., roar, both long and
271 short tonal call). This finding shows how feature extraction can be useful to characterize resonance frequencies
272 of lemur calls, agreeing with earlier evidence (Gamba et al. 2015).

273 *P. diadema*'s roar and *I. indri*'s clacson were among the most distinctive call types. *P. diadema*'s roar
274 is emitted in presence of raptors across congeneric species (Petter and Charles-Dominique 1979; Macedonia
275 and Stanger 1994; Wright 1998; Fichtel and Kappeler 2002), and *I. indri*'s clacson also mediates anti-predatory
276 behaviour and is given in presence of terrestrial predators (Macedonia and Stanger 1994; Maretti et al. 2010).
277 We also found both species' loud calls to be unambiguous (for instance, *I. indri*'s songbit and *P. diadema*'s
278 chatter-squeal and zzuss). Two studies have addressed the role of species-specific signalling in lemurs (Braune
279 et al. 2008, Rakotonirina et al. 2016), with conflicting results. Support for species recognition driven by
280 advertisement calls has been found in *Microcebus* spp. (Braune et al. 2008) while acoustic signalling seems
281 not to be involved in species recognition across *Eulemur* species (Rakotonirina et al. 2016). A mechanism
282 similar to that demonstrated in *Microcebus* spp. (Braune et al. 2008) could allow *I. indri* and *P. diadema* to
283 distinguish among hetero- and conspecifics at distance, in an environment where the acoustic channel is more
284 effective than the visual one (Waser and Brown 1986). The stereotypy we found in the loud calls of our subject
285 species is partly in line with the Sensory Drive (Endler 1992) and the Acoustic Adaptation Hypotheses, both
286 of which state that vocal signals are adapted to the environment in which they are emitted (Morton 1975;
287 Endler 1992). The acoustic structure of vocal signals, and in particular that of those used for long-distance
288 communication, is expected to be optimized to ensure sound propagation. This is especially true in closed
289 habitats, where higher vegetation density represents a greater surface for reverberation and absorption than in
290 open habitats (Waser and Brown 1986). However, our results do not fully support the Sensory Drive
291 Hypothesis, since only a small portion of *P. diadema*'s vocal repertoire (tsk and lost call) clustered with *I.*

292 *indri* calls. A study of *Microcebus murinus*, *M. ravelobensis*, *M. berthae*, and *M. lehilahytsara* also did not
293 support the Sensory Drive Hypothesis, suggesting that predatory pressures may be more relevant in shaping
294 vocal communication than differences in habitat structure (Zimmermann 2016).
295 Our findings only partially supported our predictions based on the Social Complexity Hypothesis (McComb
296 and Semple 2005; Bouchet et al. 2013). The hypothesis predicts that the species living in a larger group -
297 namely *P. diadema* - would have a bigger repertoire size; (McComb and Semple 2005). We found no support
298 this prediction and *P. diadema*'s repertoire consisted of a smaller number of different call types than that of *I.*
299 *indri* (10, Valente et al. 2019). Moreover, a repertoire including nine call types, with an average group size of
300 five individuals (Irwin 2008), conflicts with the group size - vocal repertoire size paradigm. At least two other
301 primate species with comparable group size (*Saguinus fuscicollis*: 5.9 individuals, *Leontopithecus rosalia*: 5.8
302 individuals) have a vocal repertoire of 16 call types (McComb and Semple 2005). However, the Social
303 Complexity Hypothesis also predicts that the species living in an egalitarian social structure - like *I. indri* -
304 require a more sophisticated communicative system, in terms of the number of different call types in their
305 repertoire, i.e. the repertoire size; Mitani 1996). Our results, indicating a smaller repertoire in *P. diadema*, are
306 in line with this second prediction and with studies on other lemur species. For example, the same deviation
307 from the paradigm group size - vocal repertoire size has been shown in *E. rubriventer* (with an average group
308 size of three individuals and a repertoire of 14 call types; Gamba et al. 2015) and *I. indri* (with a group size
309 ranging from four to six individuals and a repertoire of ten call types; Pollock et al. 1975; Valente et al. 2019).

310 In terms of vocal repertoire size, *P. diadema* is more similar to *I. indri* than to other more
311 phylogenetically distant species, such as *L. catta* (22 call types; Macedonia 1993) and the sympatric *Varecia*
312 *variegata* (16 call types; Pereira et al. 1988; Gamba et al. 2003). Furthermore, the repertoire size in *P. diadema*
313 is in line with the variation displayed within the Indriidae family (three to ten, Zimmermann 2017) and in
314 particular with that of two other *Propithecus* species, with a repertoire of six (*P. verreauxi*, Zimmermann 2017)
315 and 10 call types (*P. candidus*, Patel and Owren 2012). Nonetheless, in contrast with the Phylogenetic
316 Hypothesis, besides their size, the vocal repertoires of *I. indri* and *P. diadema* differed from each other. This
317 is not surprising, given that the last common ancestor of the two species lived at least 18 MYA (Kistler et al.
318 2015; Masters et al. 2013; Federman et al. 2016) and that closely-related Indriidae species show acoustic
319 differences (*P. deckenii* and *P. coronatus*: Fichtel 2014). Moreover, across lemurs, there is no pattern of vocal

320 similarity based on phylogenetic proximity (Bergey and Patel 2008; Gamba et al. 2015; Zimmermann 2017;
321 Hending et al. 2020). This lack of correlation also applies to the Indriidae family (Ramanankirahina et al.
322 2016). Despite the phylogenetic relatedness, closely-related species exhibiting the same social pattern but
323 different activity mode (diurnal vs nocturnal, respectively), also differ in the complexity of vocal signalling (*I.*
324 *indri* and *Avahi occidentalis*, Ramanankirahina et al. 2016).

325 Interestingly, *P. diadema* had the same vocal repertoire size as *Daubentonia madagascariensis*
326 (studied in captivity; Stanger and Macedonia 1994), which is a solitary nocturnal species (Sterling and
327 McCreless 2006). According to some authors, *D. madagascariensis* descended from the most basal divergence
328 from all other lemur taxa (Delpero et al. 2006), while recent evidence suggests it descended from independent
329 colonization of Madagascar (Gunnell et al. 2018). Thus, considering the phylogenetic history, common
330 ancestry of the vocal behaviour of these species is unlikely.

331 Some of the comparisons we make rely on studies employing analogous methods (i.e., *Eulemur* spp.,
332 Gamba et al. 2015). However, other vocal repertoire estimates rely on different approaches (i.e., Stanger and
333 Macedonia 1994; McComb and Semple 2005). Thus our comparisons should be taken with caution: different
334 methodologies used to measure repertoires lead to very different results and the lack of common acoustic and
335 statistical approaches undermines cross-taxa comparisons (Peckre et al. 2019).

336 The use of computationally accessible and powerful methods opens new perspectives in the study of
337 acoustic signals (Sainburg et al. 2020). The t-SNE embedding allowed efficient analysis of the vocal repertoire
338 of *P. diadema*, in line with findings on other animal species (mammals: *Mus musculus*, *Megaptera*
339 *novaeangliae*, *Pteronura brasiliensis*, *Macaca mulatta*; birds: *Taeniopygia guttata*; Sainburg et al. 2020). The
340 t-SNE also allowed us to compare the calls of *P. diadema* with those of another diurnal species in the Indriidae
341 family, *I. indri* (Valente et al. 2019). In line with studies using unsupervised clustering in the quantitative
342 analysis of animal vocalisations (Gamba et al. 2015; Riondato et al. 2017), we found that the extraction of
343 linear frequency bins revealed a remarkable potential for grouping calls based on their spectrographic
344 similarity, comparable to clusters obtained using dynamic time warping-generated dissimilarity indices.

345 The standardized technique we employed in this study allowed us to reduce the need for a priori human
346 input and to overcome potential limitations due to human perceptual bias (Sainburg et al. 2020). We do not
347 neglect the importance of previous work, but argue that standardized and reproducible techniques (for

348 alternatives see Gamba et al. 2015, where the authors employed a combination of Dynamic Time Warping and
349 clustering algorithms, or Sainburg et al. 2020, where the authors compared the efficiency of data reduction
350 algorithms across multiple datasets) should be prioritized in the future.

351

352 **Conclusions**

353 Our study supports previous findings on lemurs: it is likely that Indriidae vocal diversity has been
354 shaped by a combination of social and environmental characteristics, and phylogenetic history
355 (Ramanankirahina et al. 2016). Further research could investigate synapomorphies and autapomorphies in the
356 vocal repertoires of the Indriidae family. For instance, some call types, such as the roar and the lost call (the
357 first emitted in the anti-aerial predator context, the other used to regulate the group cohesion are comparable
358 in structure and functions across *Propithecus* species (Online Resource 2). On the other hand, the main
359 terrestrial disturbance call differs structurally between two groups of *Propithecus* species, one consisting of
360 the species producing the zzuss (*P. diadema*, *P. candidus*, *P. perrieri*, and *P. edwardsi*; Patel and Owren 2012;
361 Anania et al. 2018; Wright 1998; Macedonia and Stanger 1994) and the other including the species emitting
362 the tchi-fak (*P. verreauxi*, *P. coquereli*, *P. coronatus*, *P. deckenii*, and *P. tattersalli*- representing the so-called
363 western species, evolutionarily split from eastern species; Pastorini et al. 2001; Mayor et al. 2004; Rumpler et
364 al. 2004 but see Herrera and Davalos 2016). The acoustic divergence between zzuss and tchi-fak does not
365 completely follow the current spatial proximity of these species' distributions, or the type of environment (dry
366 forest, rainforest, transitional forest). Furthermore, acoustic differences in the loud calls of closely-related
367 species living in the same environment have been demonstrated (*P. deckenii* and *P. coronatus*; Fichtel 2014).
368 A comparison among *Propithecus* species could highlight which factors (genetic, anatomical, social,
369 ecological, or biogeographical) have been important in the evolution of vocal signals and provide us with clues
370 about why some acoustic structures have been conserved and others have changed in the divergence of species.

371

372 **Data availability**

373 The dataset is available from the corresponding author on reasonable request.

374

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