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(Article begins on next page)



2 Linguistic laws of brevity: conformity in *Indri indri*

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7 Abstract

8 Vocal and gestural sequences of several primates have been found to conform to two general principles of information
9 compression: the compensation between the duration of a construct and that of its components (Menzerath–Altmann law)
10 and an inverse relationship between signal duration and its occurrence (Zipf’s law of abbreviation). Even though Zipf’s
11 law of brevity has been proposed as a universal in animal communication, evidence on non-human primate vocal behavior
12 conformity to linguistic laws is still debated, and information on strepsirrhine primates is lacking. We analyzed the vocal
13 behavior of the unique singing lemur species (*Indri indri*) to assess whether the song of the species shows evidence for
14 compression. As roars have a chaotic structure that impedes the recognition of each individual utterance, and long notes are
15 usually given by males, we focused on the core part of the song (i.e., the *descending phrases*, composed of two–six units).
16 Our results indicate that indris’ songs conform to Zipf’s and Menzerath–Altmann linguistic laws. Indeed, shorter phrases
17 are more likely to be included in the song, and units’ duration decrease at the increase of the size of the phrases. We also
18 found that, despite a sexual dimorphism in the duration of both units and phrases, these laws characterize sequences of
19 both males and females. Overall, we provide the first evidence for a trade-off between signal duration and occurrence in the
20 vocal behavior of a strepsirrhine species, suggesting that selective pressures for vocal compression are more ancestral than
21 previously assumed within primates.

22 **Keywords** Vocal communication · Primates · Linguistic laws · Language evolution · Compression

23 Introduction

24 Investigating the statistical universals that underpin the
25 evolution of vocal complexity is essential to throw light on
26 the origins of linguistic abilities. Accordingly, comparative
27 studies are needed to assess whether the core features or
28 universals of human vocal communication are shared with
29 other species (Savage et al. 2015). Some of those are likely
30 to have evolved during primate evolution and be linked with
31 shared ancestry. Being non-human primates our closest living
32 relatives, their vocal communication systems have often
33 been regarded as the best model to understand which selec-
34 tive pressures lead to the uniqueness of human language

(Fedurek and Slocombe 2011). Indeed, different crucial
35 aspects underlying human vocal behavior shape the acous-
36 tic communication systems of other primates (Leroux and
37 Townsend 2020). For example, previous studies investigated
38 the ability to combine single components into larger struc-
39 tures and their referentiality (*Pan troglodytes*: Slocombe
40 and Zuberbühler 2005; *Pan paniscus*: Clay and Zuberbühler
41 2009; *Cercopithecus campbelli*: Ouattara et al. 2009; *Cal-
42 licebus nigrifrons*: Cäsar and Zuberbühler 2012), the turn-
43 taking among individuals (*Indri indri*: Gamba et al. 2016;
44 *Ateles geoffroyi*: Briseño-Jaramillo et al. 2018; *Macaca
45 fuscata*: Katsu et al. 2019), and the presence of rhythmic
46 patterns (*Indri indri*: Gamba et al. 2016; De Gregorio et al.
47 2019; *Tarsius spectrum gurskyae*: Clink et al. 2019).

To date, all the human languages tested have been found
49 to adhere to coding efficiency rules (Piantadosi et al. 2011).
50 In particular, they adhere to the Zipf’s Law of brevity (1936,
51 1945, 1949) and the Menzerath–Altmann Law (Altmann
52 1980): two postulates proposing that the informative ele-
53 ments are condensed as the result of selective pressures
54

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55 for (i) coding efficacy maximization and (ii) code length
56 minimization (Ferrer-i-Cancho et al. 2013). According to
57 Zipf's law, the element's length and frequency of use are
58 inversely related (Ferrer-i-Cancho et al. 2013), while Men-
59 zerath–Altmann law suggests that the longer the size of the
60 construction, the shorter that of its components (Altmann
61 1980). Compression has been hypothesized to represent
62 a universal principle in animal behavior (Ferrer-i-Cancho
63 et al. 2013). Indeed, evidence for conformity to compression
64 laws is widespread across *taxa*: from bottlenose dolphins'
65 whistle sequences (*Tursiops truncatus*: Ferrer-i-Cancho and
66 McCowan 2012) and surface behavioral patterns (Ferrer-i-
67 Cancho and Lusseau 2009) to avian species' vocal behavior,
68 as in Carolina chickadee (*Poecile carolinensis*: Freeberg and
69 Lucas 2012), and the African penguin (*Spheniscus demer-
70 sus*: Favaro et al. 2020) display songs. Zipf's law of brevity
71 also seems to define bats short-range communication (Luo
72 et al. 2013), and Demartsev and colleagues (2019) have
73 recently found that hyrax (*Procavia capensis*) vocal reper-
74 toire shows a sexually dimorphic signal optimization.

75 Studies of non-human primate vocal behavior showed
76 mixed evidence for conformity with the above-mentioned
77 laws. Indeed, besides humans (Zipf 1945; 1949; Strauss et al.
78 2007), vocalizations of the Formosan macaque (*Macaca
79 cyclopis*: Semple et al. 2010, 2013), geladas (*Theropithecus
80 gelada*: Gustison et al. 2016), eastern chimpanzees (*Pan
81 troglodytes schweinfurthii*: Fedurek et al. 2017), and moun-
82 tain gorillas (*Gorilla beringei beringei*: Watson et al. 2020),
83 as well as the gestural communication of western gorillas
84 (*Gorilla gorilla gorilla*: Genty and Byrne 2010) and chim-
85 panzees (Heesen et al. 2019), have shown evidence for
86 compression. Conversely, the vocal repertoires of at least
87 two new world primate species have been found to devi-
88 ate from the pattern predicted by compression principles
89 (*Callithrix jacchus*, *Cacajao melanocephalus*: Bezerra et al.
90 2011). However, a successive study found that the common
91 marmoset short-distance calls conform to Zipf's law (Ferrer-
92 i-Cancho and Hernández-Fernández 2013).

93 While the use of acoustic sequences is widespread across
94 species, within primates (Kershenbaum et al. 2016), a pecu-
95 liarity is represented by the so-called “singing primates”
96 (Geissmann 2000), which belong to four primate families
97 (i.e., Hylobatidae, Indriidae, Tarsiidae, Pitheciidae). A few
98 species from these families show the rare ability to commu-
99 nicate through songs (Haimoff 1986). Among those species,
100 adherence to Zipf's law of brevity has been recently found
101 in the songs of Müller's Bornean (*Hylobates muelleri*: Clink
102 et al. 2020a, b) and crested gibbons (*Nomascus nasutus*,
103 *Nomascus concolor*: Huang et al. 2020).

104 A further shared feature of speech prosody in human
105 communication is the lengthening of the last segment pre-
106 ceding the pause (final lengthening; Lindblom and Sundberg
107 2007). A parallel can be traced with recent findings on two

108 singing primates, the Cao-vit gibbon and the western black-
109 crested gibbon. Males of both species emit stereotyped vocal
110 sequences, where more extended units are more likely to be
111 given at the end rather than at the beginning of a sequence
112 (*Nomascus concolor*, *Nomascus nasutus*: Huang et al. 2020).

113 Semple et al. (2010) seminal work on the Formosan
114 macaque suggested the existence of common ground
115 between the communicative systems of both human and
116 non-human primates, particularly regarding the presence of
117 common rules governing signal duration and occurrence.
118 The authors also suggested that comparable evolutionary
119 forces may have led to increased coding efficiency in pri-
120 mate vocal behavior (Semple et al. 2010). Therefore, con-
121 sidering the ongoing debate about the presence of trade-
122 offs between signal duration and occurrence in non-human
123 primate sequences, research on previously ignored species
124 is necessary. Within the apes' superfamily, Hominoidea
125 diverged from the Hylobatidae family 13–33 million years
126 ago (Glazko and Nei 2003), while lemurs diverged more
127 than 70 million years ago (Herrera and Dávalos 2016).
128 Thus, the investigation of the only singing species among
129 lemurs significantly broadens our perspective on non-human
130 primate conformity to linguistic laws. Indri (*Indri indri*) is
131 the only singing lemur species (Haimoff 1986). Indris are
132 genetically monogamous (Bonadonna et al. 2014, 2019) and
133 live in small family groups made of the reproductive pair
134 and their offspring (Torti et al. 2017). Each group occu-
135 pies and defends an exclusive territory (Bonadonna et al.
136 2017) mainly using loud and complex vocal sequences (i.e.,
137 songs; Torti et al. 2013). Since territories are stable over
138 time (Bonadonna et al. 2020), songs also mediate intra- and
139 inter-group spatial dynamics across years (Bonadonna et al.
140 2020). Besides an introductory sequence (comprising roars
141 and long notes; Pollock 1986; Thalmann et al. 1993; Sor-
142 rentino et al. 2013) indris' songs are made of several dis-
143 crete vocal units (Gamba et al. 2011, 2016) organized in
144 phrases. Those sequences, also called descending phrases
145 because of a frequency pattern declining along with the
146 phrase (Thalmann et al. 1993; Sorrentino et al. 2013; Gamba
147 et al. 2016), constitute the core part of indris' song, can
148 include from two to six units (Thalmann et al. 1993; Gia-
149 coma et al. 2010; Gamba et al. 2016), and their organization
150 is sexually dimorphic (Zanoli et al. 2020). Songs can be
151 emitted as duets—when only the members of the reproduc-
152 tive pair sing together—or as choruses when one or more
153 non-reproductive members join the parents when singing.
154 All the individuals within a family group, aged one year or
155 above, can join the chorus (Torti et al. 2018; De Gregorio
156 et al. submitted R1).

157 By investigating the structure of phrases the indris gave
158 during the song, we aimed to understand whether the vocal
159 output of this species is subject to selective pressures for
160 information compression. Specifically, we measured (i)

161 whether indri phrases conform to the Zipf's law of brevity
 162 but, as evidence on other species is blended (Huang et al.
 163 2020; Clink et al. 2020a, b), we did not formulate a pre-
 164 cise prediction. Moreover, we investigated (ii) whether the
 165 structure of phrases conforms to the Menzerath–Altmann
 166 law, expecting that, in line with findings on most of the
 167 other primate species tested to date (geladas: Gustison et al.
 168 2016; chimpanzee: Fedurek et al. 2017; gibbons: Huang
 169 et al. 2020; Clink et al. 2020), the higher the number of
 170 units included in a phrase, the shorter the units' duration.
 171 Finally, we investigated (iii) the final lengthening, predicting
 172 that the last unit within a phrase would be longer than the
 173 previous ones, as demonstrated in humans (Lindblom and
 174 Sundberg 2007) and more recently in two singing primate
 175 species (Huang et al. 2020).

176 Methods

177 Data collection and analysis

178 We recorded spontaneous songs of ten indri groups populat-
 179 ing the Maromizaha Forest (18° 56' 49" S, 48° 27' 53" E)
 180 in Madagascar. Data were collected in the field from 2009
 181 to 2020, using solid-state recorders (Sound Devices 702,
 182 Olympus S100 and LS05, Tascam DR-100, DR-40, and
 183 DR-05, or Zoom H5) connected to a Sennheiser (ME 66 and
 184 ME 67) or AKG Acoustics (CK 98) shotgun microphones
 185 (sampling rate 44.1 kHz, 16-bit resolution). When recording
 186 the songs, thanks to the use of the focal animal sampling
 187 (Altmann 1974) and that of natural marks, we were able to
 188 attribute each vocalization to its actual emitter.

189 Indris' songs include the participation of at least two indi-
 190 viduals, we edited the songs using Praat 6.0.28 (Boersma
 191 and Weenink 2017) and manually selected and extracted the

fundamental frequency contour of each indri's contribution
 to the songs (all the emissions of a particular individual; De
 Gregorio et al. 2019). Following the methodology previ-
 ously described in Gamba et al. (2016) and De Gregorio
 et al. (2019), we then identified and labeled the *descending*
phrases based on the number of elements they included (a
 phrase can include from two to six units Thalmann et al.
 1993; Giacoma et al. 2010; Gamba et al. 2016); for instance,
 we labeled a phrase including four units as a DP₄ (Fig. 1).

We identified 8838 phrases (4127 DP₂, 3765 DP₃, 900
 DP₄, 46 DP₅), isolated from 683 songs and 1534 individ-
 ual contributions emitted by 53 individuals (28 males: 11
 dominant males and 17 non-dominant males; 25 females:
 11 dominant adult females, 14 non-dominant females). We
 annotated the number of units constituting each phrase
 (*phrase size*), the number of phrases included in each
 individual contribution to the song (*contribution size*),
 the duration of every single unit within the phrase, and
 the total duration of the phrase (Fig. 1). We then estimated
 the proportion of each phrase type in each individual con-
 tribution to the songs (*phrase proportion*, given by the
 ratio between the number of phrases of a certain type and
 the total number of phrases; Fig. 1) for all songs recorded
 between 2012 and 2020. Using the *lme4* package (Bates
 et al. 2015) in R (R Core Team 2019, version 3.6.1), we
 built a total of seven generalized linear mixed models
 (GLMMs): two models were used to investigate the phrase
 proportion, two to investigate the phrase duration, three
 to assess the unit duration variation (see Online Resource
 2). For all models, we verified the absence of collinear-
 ity among predictors by inspecting the variance inflation
 factors (*vif* package, Fox and Weisberg 2011). Through
 a likelihood ratio test (Dobson 2002), we then verified
 the significance of a full model (including both the fixed
 and random effects) against a null model (comprising the

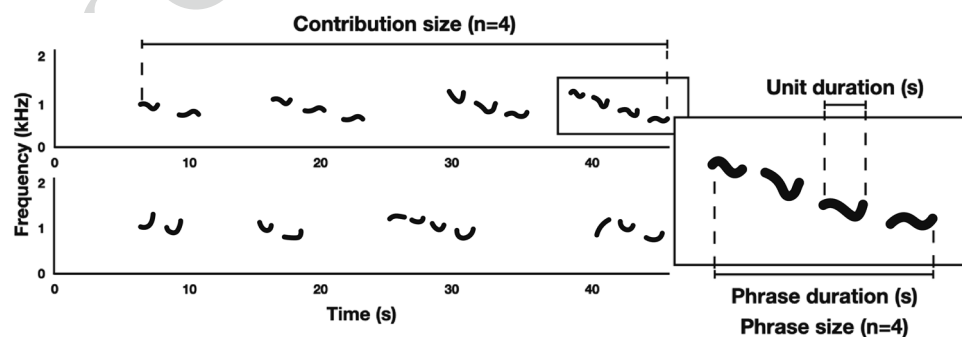


Fig. 1 Schematic representation of the spectrogram (time (s) on the x-axis, frequency (kHz) on the y-axis) of the isolated fundamental frequency of a male (upper) and a female (lower) indri. A descending phrase including four units (DP₄) is exemplified, to describe acoustic parameter collection of *contribution size* (in terms of the number of phrases included in an individual contribution), *phrase duration* (s)

and *size* (in terms of the number of units included in a phrase), *unit duration* (s). The ratio between the number of a phrase of a certain type and the total number of phrases represents the *phrase proportion* (i.e., the proportion of the two DP₃ in the male contribution represents the 50%). The spectrogram was generated in R, using the *See-wave* package (Seur and Aubin 2008)

227 random factors only) and measured the p value for each
 228 predictor using the R-function *drop1* (Barr et al. 2013).
 229 We first assessed whether the phrase type would influ-
 230 ence its occurrence, including phrase proportion as the
 231 response variable, and phrase type and sex as fixed factors.
 232 Moreover, to investigate whether the sex would influence
 233 the occurrence of different phrase types, we run a second
 234 model including phrase proportion as the response vari-
 235 able and an interaction between sex and phrase type as a
 236 fixed factor.

237 Consequently, to ensure whether the more common
 238 descending phrases would show a reduced duration, we
 239 run a model using the phrase duration as the response vari-
 240 able and phrase type and sex as fixed factors. To investi-
 241 gate the influence of both sex and phrase type, we run a
 242 fourth model, including phrase duration as the response
 243 variable and an interaction between sex and phrase type
 244 as a fixed factor.

245 The last three models investigated the unit duration varia-
 246 tion; we first assessed the relationship between the unit
 247 duration (response variable), its position in the phrase, the
 248 number of units constituting a phrase (phrase type), and
 249 the sex of the emitter (fixed factors). To assess both sex
 250 and phrase type's influence on the unit duration, we run
 251 a model including unit duration as the response variable
 252 and its position in the phrase and an interaction between
 253 sex and phrase type as fixed factors. Still, to consider the
 254 influence of the unit's position within the phrase, the last
 255 model included the unit duration as the response variable
 256 and an interaction between sex, phrase type, and position
 257 of the unit within the phrase as fixed factors. We included
 258 group, individual, and individual contributions (the last
 259 two nested) as random effects in all models. For those
 260 models containing an interaction between two or more fac-
 261 tors, we then performed all pairwise comparisons for each
 262 level of the interactions using a multiple contrast package
 263 (*multcomp* in R, Bretz et al. 2010) with a Tukey post hoc
 264 test and we reported estimate, z value, and p value. In each

case, data met the assumptions required (Anderson–Dar-
 ling normality test).

Results

Phrase proportion

267 Indris' songs included a similar proportion of phrases com-
 268 posed of two and three units (DP_2 : mean \pm sd = 0.471 ± 0.220 ;
 269 DP_3 : mean \pm sd = 0.485 ± 0.200), higher than that of
 270 longer phrases (DP_4 : mean \pm sd = 0.255 ± 0.164 ; DP_5 :
 271 mean \pm sd = 0.193 ± 0.191 ; Fig. 2a). This is supported by
 272 the results of the GLMMs, that indicated an effect of the
 273 phrase size on its occurrence, where the larger the phrases
 274 size, the smaller their proportion into the songs (full vs.
 275 null: $\chi^2 = 447.459$, $df = 4$, $p < 0.001$; Table 1). Conversely,
 276 we did not detect a difference in the frequency of occur-
 277 rence between phrases composed of two and three units nor
 278 between phrases including four and five units (Table 1).
 279 When considering the emitter's sex, we found that females
 280 and males showed only slightly differences in the propor-
 281 tion of phrases included in their songs (mean \pm sd; DP_2 ,
 282 males 0.488 ± 0.235 ; females: 0.453 ± 0.202 ; DP_3 , males:
 283 0.498 ± 0.205 ; females: 0.471 ± 0.193 ; DP_4 , males:
 284 0.295 ± 0.153 ; females: 0.233 ± 0.167 ; DP_5 , males:
 285 0.213 ± 0.208 ; females: 0.180 ± 0.181 ; Fig. 2a). As indi-
 286 cated by the model including the interaction between sex
 287 and phrase type, we did not detect a significant effect of the
 288 sex on the phrase occurrence for any of the phrase types (full
 289 versus null: $\chi^2 = 452.881$, $df = 7$, $p < 0.001$; males versus
 290 females: estimate = -0.005 , SE = 0.024 , t value = -0.224 ,
 291 $p = 0.824$; see Table 1; Fig. 2a).

Phrase duration

292 Our results also indicated that the larger the phrase size,
 293 the longer its duration (full versus null: $\chi^2 = 18,305.460$,
 294
 295
 296

Fig. 2 Density plot representing the proportion of the various phrase types included in the individual contributions to the song, for both sexes. **b** Density plot representing and the variation of the phrase duration in relation to the type of the phrase for both sexes. Plots were generated in R, using the *ggplot2* package (Wickham 2016)

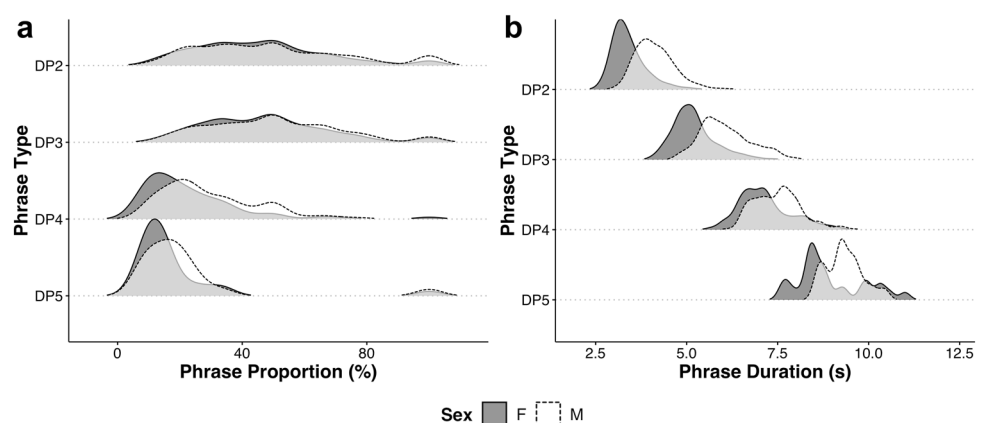


Table 1 Results of the Tukey test for the effect of the descending phrase type (left) and for the interaction including sex and phrase type (right) on the proportion of each phrase type (Anderson–Darling Normality test: $A = 32.669$, $p < 0.001$) included in a contribution

Phrase type	Proportion				Phrase type* sex	Proportion			
	Estimate	SE	<i>z</i> value	<i>p</i> value		Estimate	SE	<i>z</i> value	<i>p</i> value
DP3–DP2	0.014	0.008	1.818	0.238	DP2 (M vs F)	- 0.009	0.024	- 0.224	1.000
DP4–DP2	- 0.190	0.010	- 18.552	< 0.001	DP3 (M vs F)	- 0.009	0.024	- 0.379	1.000
DP5–DP2	- 0.245	0.031	- 7.956	< 0.001	DP4 (M vs F)	0.037	0.028	1.348	0.841
DP4–DP3	- 0.205	0.010	- 20.008	< 0.001	DP5 (M vs F)	0.026	0.065	0.405	1.000
DP5–DP3	- 0.260	0.031	- 8.428	< 0.001	-	-	-	-	-
DP5–DP4	- 0.054	0.031	- 1.755	0.267	-	-	-	-	-

Statistically significant values are indicated in bold

M males, *F* females, *DP2* Descending Phrase including two units, *DP3* Descending Phrase including three units, *DP4* Descending Phrase including four units, *DP5* Descending Phrase including five units

297 $df = 3$, $p < 0.001$). Indeed, with a mean duration of
 298 3.736 ± 0.630 s, DP_2 resulted significantly shorter than all
 299 other phrases (Fig. 2b; mean \pm SD: $DP_3 = 5.591 \pm 0.791$ s;
 300 $DP_4 = 7.277 \pm 0.743$ s; $DP_5 = 9.102 \pm 0.804$ s; DP_3 resulted
 301 significantly shorter than both DP_4 and DP_5 while DP_4
 302 were shorter than DP_5 (Table 2). We also found that phrase
 303 duration varies according to the sex of the emitter, where
 304 male phrases are longer than female ones (mean \pm sd; DP_2 ,
 305 males: 4.126 ± 0.550 s; females: 3.405 ± 0.489 s; DP_3 , males:
 306 6.073 ± 0.707 s; females: 5.201 ± 0.621 s; DP_4 , males:
 307 7.510 ± 0.691 s; females: 7.151 ± 0.740 s; DP_5 , males:
 308 9.329 ± 0.507 s; females: 8.945 ± 0.935 s; full versus null:
 309 $\chi^2 = 18,328.330$, $df = 4$, $p < 0.001$; males versus females:
 310 estimate = 0.145, SE = 0.023, *t* value = 74.922, $p < 0.001$;
 311 Fig. 2b). In particular, the model including an interaction
 312 between sex and phrase type showed that phrases duration
 313 varied with both sex of the emitter and type of the phrase,
 314 for phrases including up to four units. However, we did not
 315 find differences in the duration of DP_5 (full versus null:
 316 $\chi^2 = 18,448.360$, $df = 7$, $p < 0.001$; Table 2; Fig. 2b).

317 **Unit duration**

318 We found that unit duration was influenced by phrase
 319 size, position within the phrase, and the sex of the emitter

(full vs null: $\chi^2 = 11,315.51$, $df = 6$, $p < 0.001$). In par-
 320 ticular, we found that larger the phrase size, the shorter
 321 the units' duration (estimate = - 0.124, SE = 0.001, *t*
 322 value = - 99.570, $p < 0.001$) and that male units were
 323 longer than female ones (estimate = 0.184, SE = 0.020, *t*
 324 value = 8.994, $p < 0.001$). The model considering the inter-
 325 action between sex and phrase type (full vs null model:
 326 $\chi^2 = 11,677.690$, $df = 8$, $p < 0.001$) indicated that males
 327 emit longer units, regardless of the phrase size, in phrases
 328 including up to four units; we found no differences in the
 329 duration of units in phrases including five units (Fig. 3;
 330 Table 3). Our results also indicated that the units showed
 331 a progressive increase in duration along the phrase (see
 332 Table 3; Fig. 3). Indeed, all units but the second unit of
 333 phrases including four and five units were longer than all
 334 previous ones, for all phrase types (Table 4, Fig. 3).

335 Finally, we found that the unit duration was not only
 336 influenced by their position in the phrase, the type of
 337 phrase, and the sex, but also by an interaction among all
 338 these factors (full vs null model: $\chi^2 = 13,907.600$, $df = 33$,
 339 $p < 0.001$). Our results indeed indicated that the duration
 340 of all units differed between the sexes (with males giving
 341 longer units than females), and according to their position
 342 in the phrase, for phrases including up to four units (see
 343 Online Resource 1). Still, only the last unit of phrases
 344

Table 2 Results of the Tukey test for the effect of the descending phrase type (left) and for the interaction including sex and phrase type (right) on the phrase duration (Anderson–Darling Normality test: $A = 43.608$, $p < 0.001$)

Phrase type	Phrase duration				Phrase type* sex	Phrase duration			
	Estimate	SE	<i>z</i> value	<i>p</i> value		Estimate	SE	<i>z</i> value	<i>p</i> value
DP3–DP2	0.418	0.002	201.30	< 0.001	DP2 (M vs F)	0.160	0.017	9.086	< 0.001
DP4–DP2	0.706	0.003	202.81	< 0.001	DP3 (M vs F)	0.137	0.017	7.754	< 0.001
DP5–DP2	0.958	0.014	69.435	< 0.001	DP4 (M vs F)	0.087	0.01	4.709	< 0.001
DP4–DP3	0.288	0.003	83.49	< 0.001	DP5 (M vs F)	0.019	0.033	0.604	0.998
DP5–DP3	- 0.540	0.014	39.17	< 0.001	-	-	-	-	-
DP5–DP4	0.252	0.014	18.06	< 0.001	-	-	-	-	-

Statistically significant values are indicated in bold

M males, *F* females, *DP2* Descending Phrase including two units, *DP3* Descending Phrase including three units, *DP4* Descending Phrase including four units, *DP5* Descending Phrase including five units

Fig. 3 Density plots showing the duration of the different units included in a phrase, for the different phrase types, for males and females. **a** Descending phrase including two units; **b** Descending phrase including three units; **c** Descending phrase including four units; **d** Descending phrase including five units. Plots were generated in R, using the *ggplot2* package (Wickham 2016)

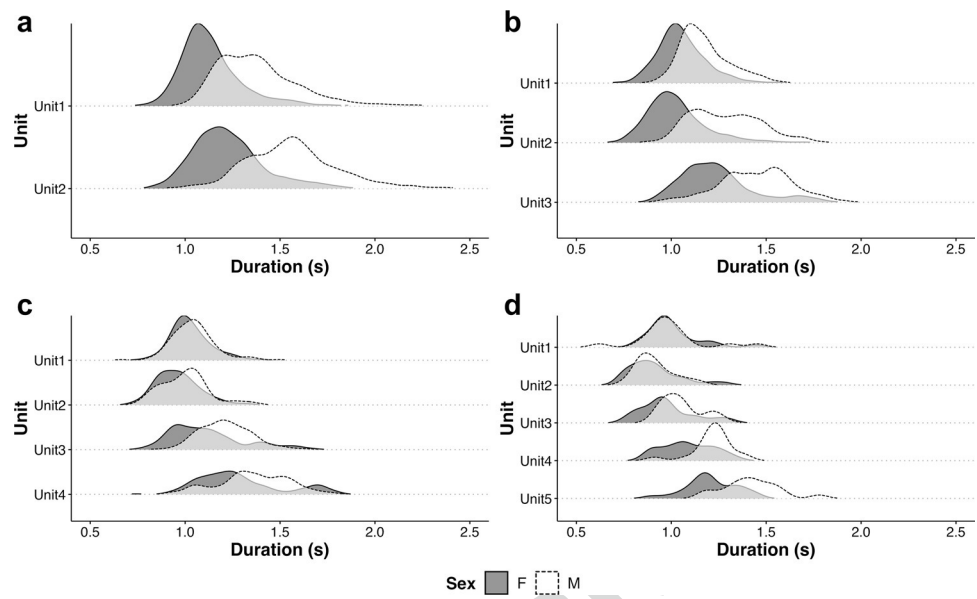


Table 3 Results of the Tukey test for the effect of the unit type (left) and for the interaction including sex and phrase type (right) on the unit duration (Anderson–Darling Normality test: $A = 273.7$, $p < 0.001$)

Unit type	Unit duration				Phrase type* sex	Unit duration			
	Estimate	SE	z	P		Estimate	SE	z	P
2nd–1st	0.048	0.001	29.841	< 0.001	DP2 (M vs F)	0.213	0.020	10.475	< 0.001
3rd–1st	0.017	0.002	86.766	< 0.001	DP3 (M vs F)	0.174	0.020	8.553	< 0.001
4th–1st	0.299	0.004	74.482	< 0.001	DP4 (M vs F)	0.126	0.021	6.099	< 0.001
5th–1st	0.434	0.017	26.014	< 0.001	DP5 (M vs F)	0.065	0.261	2.487	0.129
3rd–2nd	0.129	0.002	63.205	< 0.001					
4th–2nd	0.251	0.004	62.519	< 0.001					
5th–2nd	0.386	0.017	23.134	< 0.001					
4th–3rd	0.122	0.004	30.713	< 0.001					
5th–3rd	0.257	0.017	15.445	< 0.001					
5th–4th	0.135	0.017	8.006	< 0.001					

Statistically significant values are indicated in bold

M males, *F* females, *DP2* Descending Phrase including two units, *DP3* Descending Phrase including three units, *DP4* Descending Phrase including four units, *DP5* Descending Phrase including five units. Unit Type indicates the position of the unit within the phrase (i.e., 1st is the first unit within the phrase)

345 including five notes resulted sexually dimorphic (Table 4;
346 Fig. 3).

347 Discussion

348 Our findings provide the first compelling evidence that
349 the indris' songs follow both Zipf's law of brevity and the
350 Menzerath–Altmann law. This study is the first report for
351 adherence to linguistic laws in vocal sequences of a lemur
352 species. In conformity to Zipf's principle, we found that
353 an increase in the phrase size was negatively related to its
354 occurrence. Indeed, phrases composed of two and three units
355 tended to be included in the songs almost twice as often

356 as phrases comprising four or five units. When controlling
357 for the phrase duration, we also found that more common
358 phrase types (DP2 and DP3) were shorter than the infrequent
359 longer phrases. Our results are in line with previous findings
360 on other primate species vocal (Formosan macaque: Semple
361 et al. 2010, 2013) and gestural communication (western
362 gorilla: Genty and Byrne 2010; chimpanzee: Heesen
363 et al. 2019). This investigation, endorsing recent findings
364 on gibbons (Huang et al. 2020), also corroborates evidence
365 that primate songs conform to the Zipf's law of brevity
366 and broadens findings on the prevalence of this feature in
367 communication systems. We indeed demonstrated that,
368 unlike geladas (Gustison et al. 2016) and bats (Luo et al.
369 2013), where Zipf's law of brevity characterizes short-range

Table 4 Results of the Tukey post hoc test for the interaction including sex, phrase type, and unit position

	Phrase type	Unit type (mean duration \pm SD)	Estimate	SE	<i>z</i> value	<i>P</i> value
Males vs females	DP ₂	1st (1.249 \pm 0.210 s)	0.186	0.020	9.096	< 0.001
		2nd (1.385 \pm 0.284 s)	0.240	0.020	11.719	< 0.001
	DP ₃	1st (1.109 \pm 0.146 s)	0.118	0.020	5.747	< 0.001
		2nd (1.141 \pm 0.215 s)	0.233	0.020	11.377	< 0.001
		3rd (1.329 \pm 0.224 s)	0.170	0.020	8.289	< 0.001
	DP ₄	1st (1.033 \pm 0.110 s)	0.089	0.021	4.132	< 0.001
		2nd (0.975 \pm 0.123 s)	0.117	0.021	5.425	< 0.001
		3rd (1.148 \pm 0.185 s)	0.169	0.021	7.852	< 0.001
		4th (1.310 \pm 0.219 s)	0.131	0.021	6.072	< 0.001
	DP ₅	1st (1.000 \pm 0.152 s)	- 0.025	0.038	- 0.677	1.000
		2nd (0.910 \pm 0.121 s)	0.003	0.038	0.084	1.000
		3rd (1.008 \pm 0.133 s)	0.076	0.038	2.017	0.922
		4th (1.140 \pm 0.138 s)	0.114	0.038	3.011	0.213
		5th (1.294 \pm 0.174 s)	0.157	0.038	4.154	< 0.001

Statistically significant values are indicated in bold

M males, *F* females, *DP*₂ Descending Phrase including two units, *DP*₃ Descending Phrase including three units, *DP*₄ Descending Phrase including four units, *DP*₅ Descending Phrase including five units. Unit Type (for which we reported mean duration \pm standard deviation) indicates the position of the unit within the phrase (i.e., 1st is the first unit within the phrase)

vocalizations, this persists in long-distance communication as well, as found in two crested gibbon species whose loud morning call encompasses compression rules and follows Zipf's law of brevity (Huang et al. 2020). In line with Menznerath–Altmann law (1980), we found a negative relationship between the number of units included in a phrase and their duration, showing a trade-off between the duration of the construction and of its constituents. Such a kind of compensation is in line with a growing body of evidence regarding different species vocal behavior (banded penguins: Favaro et al. 2020; geladas: Gustison et al. 2016, chimpanzees: Fedurek et al. 2017; Bornean gibbon: Clink et al. 2020a, b; Cao-vit gibbon, western black-crested gibbon: Huang et al. 2020). The adherence to Menznerath–Altmann Law can be either the result of a selection for coding efficiency (Gustison et al. 2016) or it may depend on mechanical constraints on vocal production (Clink et al. 2020a, b), while compression (Bezerra et al. 2011) has been hypothesized to be the result of two pressures: accuracy (ambiguity avoidance) and efficiency (Ferrer-i-Cancho et al. 2020). In indris, (i) the emission of phrases with more units seems to only be possible as long as the duration of a phrase is balanced with that of its units and (ii) we demonstrated that indris reduce the length of their phonation (i.e., the portion of the song sang) at the increase of the song duration (De Gregorio et al. 2019). Finally, as reported in humans (Lindblom and Sundberg 2007) and two crested gibbon species (Huang et al. 2020), indris increased the duration of the units towards the very end of a phrase and, as recently suggested, the duration of a given unit may reflect breathing constraints related to the

emission of previous ones (Favaro et al. 2020). The shortening of units at the beginning of a sequence, therefore, may allow indris to avoid breathing constraints, as hypothesized for gibbons (Huang et al. 2020).

Furthermore, despite being focused on a subset of the vocal repertoire, our findings provide evidence that, at least at the phrase level, indris' songs sustain principles of vocal compression and, if on one hand physical constraints may impact signal duration, on the other hand, signal redundancy may allow indris to overcome loss of information due to signal compression. Indeed, redundancy maximization can represent a potential alternative to compression where the pressure for compression can cause a signal to be more sensitive to noise (Ferrer-i-Cancho et al. 2013). As gibbons' solo bouts, indri songs consist of a repetition of phrases and, as proposed for *Nomascus* gibbons, signal redundancy may compensate the loss of information generated by compression (Huang et al. 2020). The role of environmental features in forging the acoustic characteristics of signals and in influencing their perception has long been hypothesized (Marler 1967) and indeed natural selection favors signal structure and signaling strategies that maximize signals transmission while minimizing their degradation (Endler 1992). Indris use songs to mediate long-distance communication, in particular, to actively defend their territories (Torti et al. 2013; Bonadonna et al. 2017). We can conclude that song structure is likely to be adapted to the environment of emission. Different strategies have been proposed to cope with acoustic interference related to environmental features (Waser and Brown 1986). For example, noise-induced vocal adjustments

(common marmoset: Roy et al. 2011; cotton-top tamarin: Egnor and Hauser 2006), antiphonal calling, or redundant structures (Roy et al. 2011). Combining units into sequences may increase communication capacity (Plotkin and Nowak 2000): in indris, the combination of signal duration compression with phrases redundancy may represent a strategy to maximize signal transmission, and therefore, their long-distance communication is likely to be a balance between compression and efficacy. Moreover, indris' songs are loud calls given by multiple callers at the same time that can be used to convey information about sex (Gamba et al. 2016; De Gregorio et al. 2019), age (De Gregorio et al. in preparation), and individuality of the emitters (Torti et al. 2017). Songs can also vehiculate information about the individuals' reproductive status (Gamba et al. 2016), and are supposed to mediate mate attraction and pair formation at a distance (Torti et al. 2013).

On the one hand, as proposed for common marmosets, the persistent repetition of phrases guarantees the information redundancy (Roy et al. 2011). It allows avoiding the overlap with other individuals, which is crucial for non-reproductive indris to increase their chance to broadcast individuality and unpaired status (Gamba et al. 2016). On the other hand, the trade-off between units and phrases duration we found in males and females can represent the result of pressures acting on both sexes to ensure signal vehiculation (Favaro et al. 2020). Hence, we suggest that indris, as hypothesized for geladas (Gustison et al. 2016), chimpanzees (Fedurek et al. 2017) and gibbons (Clink et al. 2020a, b; Huang et al. 2020) cannot produce long phrases and long notes at the same time. Still, rather than being the sole product of selection for coding efficacy, their vocal production is the result of a compromise among the need to ensure signal transmission, the need to reduce energetic costs of producing an extended vocal sequence (i.e., marmoset vocal production; Ghazanfar et al. 2019), and limitations due to mechanical constraints on breathing control (MacLarnon and Hewitt 1999; Hewitt et al. 2002), as hypothesized for chimpanzees (Fedurek et al. 2017).

In conclusion, this study represents the first evidence of adherence to Zipf's law of brevity and Menzerath–Altmann law in the vocal behavior of a prosimian, a further dowel among those corroborating that selective pressures for compression are shared among different vocal communication systems (Ferrer-i-Cancho et al. 2013). Our results indicate that these features, previously demonstrated in humans, apes, and monkeys, characterize strepsirrhine vocal production as well. Therefore, selective pressures for vocal compression might be more ancestral than previously thought, within the order Primates.

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Author contributions DV and MG conceived the study design and the methodology; VT, DV, CDG, AZ, and TR collected the data; DV and MG conducted the formal analysis and investigation; DV wrote the manuscript, all authors edited the manuscript and approved its final version.

Data availability Data used in this study can be found at https://github.com/sciabola/ANCO2021_DATA

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval Research permits for this research have been granted from Direction des Eaux et Forêts and 'Madagascar National Parks' (formerly ANGAP). 2004: N190/MINENV.EF/SG/DGEF/DPB/SCBLF/RECH; 2005: N197/MINENV.EF/SG/DGEF/DPB/SCBLF/RECH; 2006: N172/06/MINENV.EF/SG/DGEF/DPB/SCBLF; 2007: N0220/07/MINENV.EF/SG/DGEF/DPSAP/SSE; 2008: N258/08/MEFT/SG/DGEF/DSAP/SSE; 2009: N243/09/MEF/SG/DGF/DCB.SAP/SLRSE; 2010: N118/10/MEF/SG/DGF/DCB.SAP/SCBSE and 293/10/MEF/SG/DGF/DCB.SAP/SCB; 2011: N274/11/MEF/SG/DGF/DCB.SAP/SCB; 2012: N245/12/MEF/SG/DGF/DCB.SAP/SCB; 2013: permit not required as data collection was performed by Malagasy citizens only. 2014: N066/14/MEF/SG/DGF/DCB.SAP/SCB; 2015: N180/15/MEEMF/SG/DGF/DAPT/SCBT; 2016: N98/16/MEEMF/SG/DGF/DAPT/SCB.Re and N217/16/MEEMF/SG/DGF/DSAP/SCB.Re; 2017: 73/17/MEEF/SG/DGF/DSAP/SCB.RE; 2018: 91/18/MEEF/SG/DGF/DSAP/SCB.Re; 2019: 118/19/MEDD/SG/DGEF/DSAP/DGRNE and 284/19/MEDD/SG/DGEF/DSAP/DGRNE; 2019/2020: 338/19/MEDD/SG/DGEF/DSAP/DGRNE. Approval for observational researches and for studies that do not involve animal handling are not required by our institutional committees.

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