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ORIGINAL PAPER

Linguistic laws of brevity: conformity in *Indri indri*

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Abstract

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

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

Introduction

Investigating the statistical universals that underpin the evolution of vocal complexity is essential to throw light on the origins of linguistic abilities. Accordingly, comparative studies are needed to assess whether the core features or universals of human vocal communication are shared with other species (Savage et al. 2015). Some of those are likely to have evolved during primate evolution and be linked with shared ancestry. Being non-human primates our closest living relatives, their vocal communication systems have often been regarded as the best model to understand which selective pressures lead to the uniqueness of human language (Fedurek and Slocombe 2011). Indeed, different crucial aspects underlying human vocal behavior shape the acoustic communication systems of other primates (Leroux and Townsend 2020). For example, previous studies investigated the ability to combine single components into larger structures and their referentiality (*Pan troglodytes*: Slocombe and Zuberbühler 2005; *Pan paniscus*: Clay and Zuberbühler 2009; *Cercopithecus campbelli*: Ouattara et al. 2009; *Callicebus nigrifrons*: Cäsar and Zuberbühler 2012), the turn-taking among individuals (*Indri indri*: Gamba et al. 2016; *Ateles geoffroyi*: Briseño-Jaramillo et al. 2018; *Macaca fuscata*: Katsu et al. 2019), and the presence of rhythmic patterns (*Indri indri*: Gamba et al. 2016; De Gregorio et al. 2019; *Tarsius spectrum gurskyae*: Clink et al. 2019).

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

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

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

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

A further shared feature of speech prosody in human communication is the lengthening of the last segment preceding the pause (final lengthening; Lindblom and Sundberg 2007). A parallel can be traced with recent findings on two singing primates, the Cao-vit gibbon and the western black-crested gibbon. Males of both species emit stereotyped vocal sequences, where more extended units are more likely to be given at the end rather than at the beginning of a sequence (*Nomascus concolor*, *Nomascus nasutus:* Huang et al. 2020).

Semple et al. (2010) seminal work on the Formosan macaque suggested the existence of common ground between the communicative systems of both human and non-human primates, particularly regarding the presence of common rules governing signal duration and occurrence. The authors also suggested that comparable evolutionary forces may have led to increased coding efficiency in primate vocal behavior (Semple et al. 2010). Therefore, considering the ongoing debate about the presence of trade-offs between signal duration and occurrence in non-human primate sequences, research on previously ignored species is necessary. Within the apes' superfamily, Hominidae diverged from the Hylobatidae family 13–33 million years ago (Glazko and Nei 2003), while lemurs diverged more than 70 million years ago (Herrera and Dàvalos 2016). Thus, the investigation of the only singing species among lemurs significantly broadens our perspective on non-human primate conformity to linguistic laws. Indri (*Indri indri*) is the only singing lemur species (Haimoff 1986). Indris are genetically monogamous (Bonadonna et al. 2014, 2019) and live in small family groups made of the reproductive pair and their offspring (Torti et al. 2017). Each group occupies and defends an exclusive territory (Bonadonna et al. 2017) mainly using loud and complex vocal sequences (i.e., songs; Torti et al. 2013). Since territories are stable over time (Bonadonna et al. 2020), songs also mediate intra- and inter-group spatial dynamics across years (Bonadonna et al. 2020). Besides an introductory sequence (comprising roars and long notes; Pollock 1986; Thalmann et al. 1993; Sorrentino et al. 2013) indris' songs are made of several discrete vocal units (Gamba et al. 2011, 2016) organized in phrases. Those sequences, also called descending phrases because of a frequency pattern declining along with the phrase (Thalmann et al. 1993; Sorrentino et al. 2013; Gamba et al. 2016), constitute the core part of indris' song, can include from two to six units (Thalmann et al. 1993; Giacoma et al. 2010; Gamba et al. 2016), and their organization is sexually dimorphic (Zanoli et al. 2020). Songs can be emitted as duets—when only the members of the reproductive pair sing together—or as choruses when one or more non-reproductive members join the parents when singing. All the individuals within a family group, aged one year or above, can join the chorus (Torti et al. 2018; De Gregorio et al. submitted R1).

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

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

Methods

Data collection and analysis

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

Indris' songs include the participation of at least two individuals, we edited the songs using Praat 6.0.28 (Boersma 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 previously 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 DP_4 (Fig. 1).

We identified 8838 phrases (4127 DP_2, 3765 DP_3, 900 DP_4, 46 DP_5), isolated from 683 songs and 1534 individual 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 contribution 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 collinearity 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

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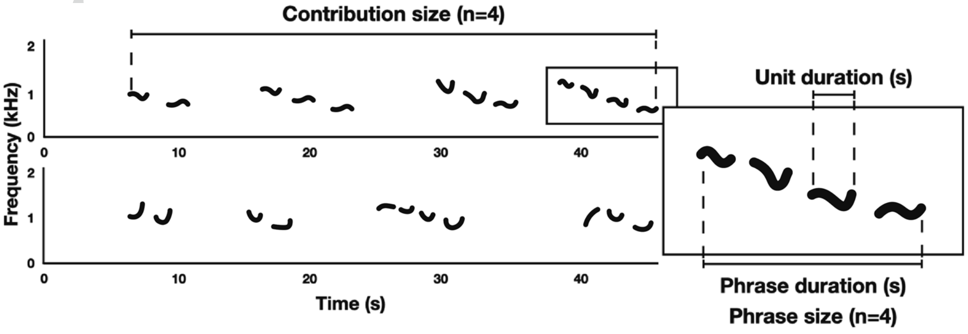

Fig. 1 Schematic representation of the spectrogram (time (s) on the x-axis, frequency (kHz) on the y-axis) of the isolated fundamental frequency of a male (upper) and a female (lower) indri. A descending phrase including four units (DP_4) is exemplified, to describe acoustic parameter collection of *contribution 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 DP_3 in the male contribution represents the 50%). The spectrogram was generated in R, using the *Seewave* package (Seur and Aubin 2008)

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

Consequently, to ensure whether the more common descending phrases would show a reduced duration, we run a model using the phrase duration as the response variable and phrase type and sex as fixed factors. To investigate the influence of both sex and phrase type, we run a fourth model, including phrase duration as the response variable and an interaction between sex and phrase type as a fixed factor.

The last three models investigated the unit duration variation; we first assessed the relationship between the unit duration (response variable), its position in the phrase, the number of units constituting a phrase (phrase type), and the sex of the emitter (fixed factors). To assess both sex and phrase type's influence on the unit duration, we run a model including unit duration as the response variable and its position in the phrase and an interaction between sex and phrase type as fixed factors. Still, to consider the influence of the unit's position within the phrase, the last model included the unit duration as the response variable and an interaction between sex, phrase type, and position of the unit within the phrase as fixed factors. We included group, individual, and individual contributions (the last two nested) as random effects in all models. For those models containing an interaction between two or more factors, we then performed all pairwise comparisons for each level of the interactions using a multiple contrast package (*multcomp* in R, Bretz et al. 2010) with a Tukey post hoc test and we reported estimate, *z* value, and *p* value. In each case, data met the assumptions required (Anderson–Darling normality test).

Results

Phrase proportion

Indris' songs included a similar proportion of phrases composed of two and three units (DP_2: mean ± sd = 0.471 ± 0.220; DP_3: mean ± sd = 0.485 ± 0.200), higher than that of longer phrases (DP_4: mean ± sd = 0.255 ± 0.164; DP_5: mean ± sd = 0.193 ± 0.191; Fig. 2a). This is supported by the results of the GLMMs, that indicated an effect of the phrase size on its occurrence, where the larger the phrases size, the smaller their proportion into the songs (full vs. null: $\chi2 = 447.459$, $df = 4$, $p < 0.001$; Table 1). Conversely, we did not detect a difference in the frequency of occurrence between phrases composed of two and three units nor between phrases including four and five units (Table 1). When considering the emitter's sex, we found that females and males showed only slightly differences in the proportion of phrases included in their songs (mean ± sd; DP_2, males 0.488 ± 0.235; females: 0.453 ± 0.202; DP_3, males: 0.498 ± 0.205; females: 0.471 ± 0.193; DP_4, males: 0.295 ± 0.153; females: 0.233 ± 0.167; DP_5, males: 0.213 ± 0.208; females: 0.180 ± 0.181; Fig. 2a). As indicated by the model including the interaction between sex and phrase type, we did not detect a significant effect of the sex on the phrase occurrence for any of the phrase types (full versus null: $\chi2 = 452.881$, $df = 7$, $p < 0.001$; males versus females: estimate = − 0.005, SE = 0.024, *t* value = − 0.224, $p = 0.824$; see Table 1; Fig. 2a).

Phrase duration

Our results also indicated that the larger the phrase size, the longer its duration (full versus null: $\chi2 = 18{,}305.460$,

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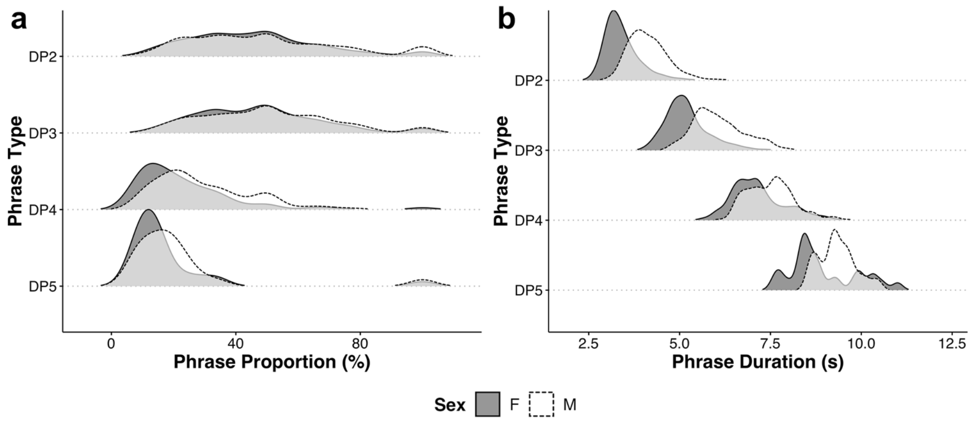

Fig. 2 Density plot representing the proportion of the various phrase types included in the individual contributions to the song, for both sexes. **b** Density plot representing and the variation of the phrase duration in relation to the type of the phrase for both sexes. Plots were generated in R, using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

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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	*z* value	*p* value		Estimate	SE	*z* value	*p* 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

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

Unit duration

We found that unit duration was influenced by phrase 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 particular, we found that larger the phrase size, the shorter the units' duration (estimate = – 0.124, SE = 0.001, t value = – 99.570, $p < 0.001$) and that male units were longer than female ones (estimate = 0.184, SE = 0.020, t value = 8.994, $p < 0.001$). The model considering the interaction between sex and phrase type (full vs null model: $\chi 2 = 11{,}677.690$, $df = 8$, $p < 0.001$) indicated that males emit longer units, regardless of the phrase size, in phrases including up to four units; we found no differences in the duration of units in phrases including five units (Fig. 3; Table3). Our results also indicated that the units showed a progressive increase in duration along the phrase (see Table 3; Fig. 3). Indeed, all units but the second unit of phrases including four and five units were longer than all previous ones, for all phrase types (Table 4, Fig. 3).

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

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	*z* value	*p* value		Estimate	SE	*z* value	*p* 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

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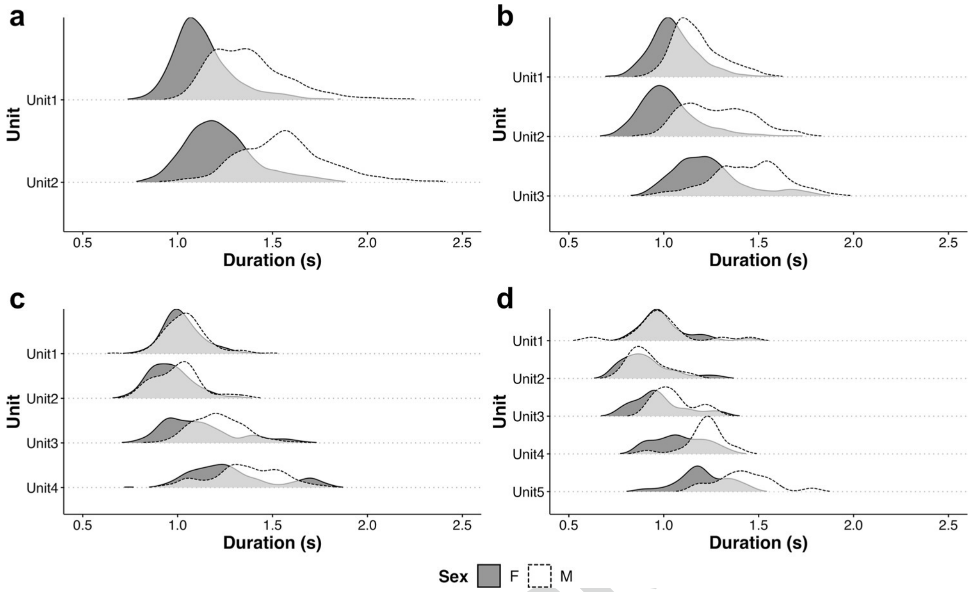

Fig. 3 Density plots showing the duration of the different units included in a phrase, for the different phrase types, for males and females. **a** Descending phrase including two units; **b** Descending phrase including three units; **c** Descending phrase including four units; **d** Descending phrase 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)

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

Discussion

Our findings provide the first compelling evidence that the indris' songs follow both Zipf's law of brevity and the Menzerath–Altmann law. This study is the first report for adherence to linguistic laws in vocal sequences of a lemur species. In conformity to Zipf's principle, we found that an increase in the phrase size was negatively related to its occurrence. Indeed, phrases composed of two and three units tended to be included in the songs almost twice as often as phrases comprising four or five units. When controlling for the phrase duration, we also found that more common phrase types (DP2 and DP3) were shorter than the infrequent longer phrases. Our results are in line with previous findings on other primate species vocal (Formosan macaque: Semple et al. 2010, 2013) and gestural communication (western gorilla: Genty and Byrne 2010; chimpanzee: Heesen et al. 2019). This investigation, endorsing recent findings on gibbons (Huang et al. 2020), also corroborates evidence that primate songs conform to the Zipf's law of brevity and broadens findings on the prevalence of this feature in communication systems. We indeed demonstrated that, unlike geladas (Gustison et al. 2016) and bats (Luo et al. 2013), where Zip's law of brevity characterizes short-range

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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 ± SD)	Estimate	SE	z value	P value
Males vs females	DP$_2$	1st (1.249 ± 0.210 s)	0.186	0.020	9.096	**< 0.001**
		2nd (1.385 ± 0.284 s)	0.240	0.020	11.719	**< 0.001**
	DP$_3$	1st (1.109 ± 0.146 s)	0.118	0.020	5.747	**< 0.001**
		2nd (1.141 ± 0.215 s)	0.233	0.020	11.377	**< 0.001**
		3rd (1.329 ± 0.224 s)	0.170	0.020	8.289	**< 0.001**
	DP$_4$	1st (1.033 ± 0.110 s)	0.089	0.021	4.132	**< 0.001**
		2nd (0.975 ± 0.123 s)	0.117	0.021	5.425	**< 0.001**
		3rd (1.148 ± 0.185 s)	0.169	0.021	7.852	**< 0.001**
		4th (1.310 ± 0.219 s)	0.131	0.021	6.072	**< 0.001**
	DP$_5$	1st (1.000 ± 0.152 s)	− 0.025	0.038	− 0.677	1.000
		2nd (0.910 ± 0.121 s)	0.003	0.038	0.084	1.000
		3rd (1.008 ± 0.133 s)	0.076	0.038	2.017	0.922
		4th (1.140 ± 0.138 s)	0.114	0.038	3.011	0.213
		5th (1.294 ± 0.174 s)	0.157	0.038	4.154	**< 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 (for which we reported mean duration ± 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 Menzerath–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 Menzerath–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

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(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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