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Song structure and sex specific features in the indris

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In the dense tropical rainforests of Madagascar, visual communication is impeded by obstacles. Lemurs use scent marking to communicate at a short distance and loud calls to communicate at a long range. The Indri (*Indri indri*) is a diurnal primate that emits choruses of three distinct types. The song types are essential in advertising position within the group territory, in deciding the sorts of aggressive group encounters, and in maintaining cohesion between animals dispersed during feeding. A detailed examination of the advertisement songs showed that three main parts constitute them. The last, most consistent of these parts, showed phrases consisting of units emitted with a descending frequency. The rhythm of these units changed significantly between phrases of different durations and the sexes. We also found that the unit structure may provide conspecifics with information on the individual identity of the emitter and that male songs, but not female's, are more similar to those of their parent of the same sex than to other indris. The song of the indris is an effective way to transfer information at a long distance and may transmit sex and individual identity information.

1. INTRODUCTION

The relationship between sexual selection and vocal communication in primates has been thoroughly investigated (Delgado 2006). Sexual dimorphism in primate vocal production may emerge as various forms (Bouchet et al. 2010); divergences between sexes may indeed include differences in terms of call types (*Cercocebus torquatus*, Bouchet et al. 2010; *Pongo pygmaeus* and *Pongo abelii*, Askew and Morrogh-Bernard 2016), a differential contextual variation in the usage of calls (e.g. male loud calls mediating intergroup spacing: *Macaca silenus*, *Trachypithecus johnii*, Herzog and Hohmann 1984; female copulation calls: *Pan paniscus*, Clay and Zuberbuhler 2011; *Macaca sylvanus*, Pfefferle et al. 2008; *Papio cynocephalus*, Semple 2001). Still, discrepancies may be found in terms of call rates (Hohmann, 1991), rhythmic capacities (Babiszewska et al. 2015; Gamba et al. 2016), frequency modulation (*Papio ursinus*, Ey et al. 2007), duration (Delgado 2006; *Papio ursinus*, Ey et al. 2007), or combination of calls (*Cercocebus torquatus*, Bouchet et al. 2010; *Theropithecus gelada*, Gustison et al. 2016). Differences in call structure and usage may implicate a different social role of males and females (Gautier & Gautier-Hion 1977) and may also encode cues enabling listeners to recognize emitter's sex (Bouchet et al. 2010) or even individuality, a crucial function in forest-dwelling, arboreal primates, where callers may often be out of sight (Dunn et al. 2015).

Recently, a link between sexual dimorphism in calls frequency and social system has been proposed (Puts et al. 2016). In several species of anthropoid primates, indeed, polygynous species show more pronounced sexual dimorphism in fundamental frequency, when compared to monogamous ones. In particular, several studies highlighted the presence of a marked dimorphism in the size of the vocal sac in polygynous species (*Gorilla gorilla*, *Pongo pygmaeus*), which also produce sex-specific calls (Harcourt et al. 1993; Delgado and Van Schaik 2000). On the other side, species with a less evident dimorphism do not emit sex-specific calls either, as in the group cohesion pant hoots of the chimpanzees, given by both sexes (Mitani and Nishida 1993). Although most species communicate through relatively simple vocal emissions, few taxa use complex sequences of units, known as songs (Clarke et al. 2006). Songs consist of a series of notes emitted in succession, generating a precise sequence in time (Brenowitz et al. 2010) that can be organized in phrases (Geismann 2000). According to Haimoff (1983; 1986), mammalian song production is indeed restricted to a limited number of taxa, and only 10% of the primate species show singing behavior, that seems to be related to a socially monogamous and territorial lifestyle (Snowdon 2017). The so-called 'singing primates' include Asian Gibbons (Geissmann 1993), some species of the genera *Tarsius* (MacKinnon and MacKinnon 1980; Niemitz et al. 1991; Nietsch and Kopp 1998) and *Callicebus* (Robinson, 1979) and the lemur *Indri indri* (Pollock 1986).

Most primate species exhibiting singing behavior also show sexual monomorphism in body size and social monogamy (Dixson 2013). Moreover, despite most of these species having animals of both sexes participating in the duets, the singing pattern and note types are stiffly sex-specific (Giacoma et al. 2010). The structures of the songs and duets show great variations at both interspecific and intraspecific levels: gibbons, for example, not only exhibit species-specific singing patterns and note types; indeed, they also are sex-specific (Cowlshaw, 1992) and even individual-specific (*Hylobates moloch*, Dallmann and Geismann 2001; *Hylobates albibarbis*, Wanelik et al. 2013; *Nomascus concolor*, Sun et al. 2010). The variability among primates' song structure has also been supported by different studies on Titi Monkeys (Gen. *Callicebus*). Robinson (1979) found that in *Callicebus cupreus* duets are achieved by females and males alternating the different parts (Robinson 1979), but also that females exhibit lower-pitched bellows than males. Tarsiers also show sexually dimorphic calls, further characterized by individual variation (Řeháková-Petrů et al. 2012).

In the present study, we aimed to investigate differences in the acoustics of units given by male and female indris (*Indri indri*) during their song. The indris inhabit the dense rainforest of eastern Madagascar, where they live in small family groups (Bonadonna et al. 2019). These lemurs produce long and modulated songs, usually introduced by a series of roars, comprising three main groups of elements: long notes, single notes, and descending phrases. The descending phrases consist of a series of notes with a descending frequency pattern and represent most of the vocal output. Previous studies found marked sexual dimorphism in the overall output of the indris' song (Giacoma et al. 2010), and both in the rhythmic structure of phrases (Gamba et al. 2016) and songs (De Gregorio et al. 2019). We wanted to investigate sex dimorphism at a finer scale, by considering the note repertoire of this species. Therefore, we used the number of units in a phrase to indicate the phrase type and the position a unit occupied within a phrase to label each unit. Despite the lack of dimorphism in body size, given the previous results on indri vocal behavior sexual dimorphism (Giacoma et al. 2010; Gamba et al. 2016; De Gregorio et al. 2019) we expected to find males showing a longer unit duration. Following the findings by Haimoff and Tilson (1985), we also expected to find small differences in the frequency parameters, which are critical to retaining the communicative process.

2. MATERIALS AND METHODS

A. DATA COLLECTION

We recorded spontaneous songs from nine *Indri indri* groups inhabiting the Maromizaha forest (18° 56' 49'' S, 48° 27' 53'' E), from 2011 to 2018. We assessed individual identity by direct observation of the singers using focal animal sampling (Altmann 1974), which were recognized using natural marks. We used solid-state recorders (Sound Devices 702, Olympus S100 and LS05, and Tascam DR-100, DR-40, and DR-05) with a sampling rate of 44.1 kHz and 16 bit. Recorders were equipped with Sennheiser (ME 66 and ME 67) or AKG Acoustics (CK 98) shotgun microphones. When recording the songs, we were always at a distance comprised between two and 20m from the indris, with the microphone orientated toward the focal singing individual. We focused our analyses on 273 songs uttered by 11 reproductive pairs consisting of 20 individuals, ten females and ten males (in two groups, the reproductive pair changed; Table 1).

Sampling Years	Group	Individual	Sex
2011-2018	1MZ	Bevolo	F
		Jery	M
2011-2018	2MZ	Soa	F
		Max	M
2011-2014	3MZ*	Mena	F
		Ratsy	M
2015-2018	3MZ*	Mena	F
		Mahagaga	M
2014-2018	4MZ	Eva	F
		Koto	M
2014-2017	5MZ*	Fern	F
		Graham	M
2018	5MZ*	Graham	M
		Takona	F
2014-2018	6MZ	Befotsy	F
		Zokibe	M
2014-2018	8MZ	Bemasoandro	F
		Jonah	M
2014-2018	9MZ	Sissie	F
		Emilio	M
2014	10MZ	Joeline	F
		Tia	M

Table 1. Group composition of the *Indri indri* groups involved in the study.

* indicates the groups in which the reproductive pair changed

B. ACOUSTIC ANALYSIS

We transferred the information related to individual singing in a Praat textgrid and then edited the song using Praat 6.0.28 (Boersma and Weenink 2017). We then manually extracted the fundamental frequency of all units given by a particular indri and stored the file as a .wav file. We then split each unit in a separate file and measured the following variables: total duration of the unit (duration, s), minimum (*minf0*, Hz), maximum (*maxf0*, Hz), range (*rangef0*, Hz), and Mean Absolute Slope (*maslope*, Hz) of the fundamental frequency. The script also saved into a file the frequency value of 50 pitch points across the duration of each unit. These pitch points were used to illustrate the frequency modulation of each type of unit which is presented in Fig. 1. As we were interested in investigating sex dimorphism across the different units occurring during the song and that we could recognize the units and phrases indicated by previous studies (Thalman et al. 1993; Giacoma et al. 2010; Gamba et al. 2016) we labelled each unit as a long note (LN), a single unit (SN), or as being part of a phrase. As descending phrases (hereafter DP, Gamba et al. 2016) could consist of two to six units (e.g. DP2, DP3, DP5), their units were labelled following their order in the phrase (e.g. the first unit of a DP4 as DP4-1, the third as DP4-3). We considered phrases comprising two, three, and four units for the present study and discarded those particular units that showed a low recording quality (e.g. did not have a continuous fundamental frequency). We obtained a total of 9417 song units, of which: 691 long notes, 794 single notes, 1375 DP2-1; 1358 DP2-2; 1355 DP3-1, 1355 DP3-2, 1331 DP3-3; 289 DP4-1, 289 DP4-2, 290 DP4-3, 290 DP4-4.

C. STATISTICAL ANALYSIS

We ran five Generalized Linear Mixed Models (lme4 package, Bates et al. 2015) in R (R Core Team 2018; version 3.5.1), to understand whether the song units showed sexually dimorphic features, both at a temporal and spectral level. All variables were log-transformed. We used four models to investigate frequency variation, using *minf0*, *maxf0*, *rangef0*, and *maslope* as response variables. A fifth model included duration (s) as the response variable. In all models, we used sex and unit type (dp_unit) as fixed factors and singer identity (ID_ind), song (ID_song) and descending phrase (dp_code) as random factors. Since we predicted that the sex of the emitter and position of the unit in the song or within a phrase would influence the features of a particular unit, we included in the model an interaction between the sex of the emitter and the type of unit. For each model, we rejected the incidence of predictors collinearity by inspecting the variance inflation factors (vif package; Fox and Weisberg 2011) and then verified the significance of the full model (Forstmeier and Schielzeth 2011) against its relative null model (including the random factors exclusively), by using a likelihood ratio test (detailed procedure in Gamba et al. 2016). Using the R-function “drop1” (Barr et al. 2013), we calculated the P values for the individual predictors. We then performed pairwise comparisons for each level of the factors with the Tukey test (multcomp in R, Bretz et al. 2010), adjusting the P-values using the Bonferroni correction. We reported estimate, standard error (SE), z- and P-values for each test.

3. RESULTS

We investigated whether sex and unit type influenced the units' duration and frequency. The models built to examine the frequency variation significantly differed from the null model (*maxf0*: $\chi^2 = 11533.130$, $df = 21$, $P < 0.001$; *minf0*: $\chi^2 = 4209.39$, $df = 21$, $P < 0.001$; *rangef0*: $\chi^2 = 4858.67$, $df = 21$, $P < 0.001$; *maslope*: $\chi^2 = 11089.44$, $df = 21$, $P < 0.001$) as well as the model investigating the units' *duration* ($\chi^2 = 8943.068$, $df = 21$, $P < 0.001$).

We found that unit's duration significantly differed between the two sexes for three unit types. Males indeed produced longer DP2-2s, DP3-2s, and LNs than females (Table 2, Figure 1C). The maximum fundamental frequency (*maxf0*) differed between the sexes for most unit types (Table 1, Figure 1A, 1B): males showed higher maximum frequency values than females in DP2-2s while females showed higher maximum frequency values than males in the first two notes of DP3s, in the last two notes of the DP4s, in long notes, and single notes. The minimum fundamental frequency (*minf0*) value resulted significantly different between sexes in the long notes only, with female units showing a higher frequency than male ones. Conversely, the fundamental frequency range (*rangef0*) appeared to be sexually dimorphic only in the units organized in phrases. In particular, we detected a difference in DP2-2s, and in the last two units of the phrases comprising three (DP3-2s and DP3-3s) and four units (DP4-3s, DP4-4s), with females exhibiting higher values than males in all cases (see Table 1).

We also found a gender related difference also in the units' Mean Absolute Slope (*maslope*). Males showed higher values than females in DP3-1s and DP4-1s. By contrast, female units showed higher values than male ones in Long Notes, in the second unit of DP2s and DP3s (DP2-2 and DP3-2, respectively), and in DP4-3s (see Table 1). The differences reflected in Mean Absolute Slope are also apparent in Fig. 1, where modulation of the notes produced by males and females differed markedly.

Sex (M-F): Unit Type	DP2-1	DP2-2	DP3-1	DP3-2	DP3-3	DP4-1	DP4-2	DP4-3	DP4-4	LN	SN	
Duration	E	0.104	0.153	0.017	0.138	0.084	-0.041	0.028	0.086	0.054	0.469	0.102
	SE	0.031	0.031	0.031	0.031	0.031	0.035	0.035	0.035	0.035	0.033	0.031
	z	3.335	4.893	0.550	4.424	2.718	-1.180	0.817	2.493	1.548	14.294	3.226
	P	0.064	<0.001	1.000	<0.001	0.334	0.998	1.000	0.509	0.991	<0.001	0.089
Min F0	E	0.013	-0.024	-0.104	-0.021	-0.009	0.002	0.009	0.001	0.004	-0.066	-0.029
	SE	0.012	0.012	0.012	0.012	0.012	0.017	0.017	0.017	0.017	0.014	0.013
	z	1.096	-2.016	-0.877	-1.729	-0.768	1.439	0.547	0.048	0.239	-4.804	-2.181
	P	1.000	0.886	1.000	0.973	1.000	0.997	1.000	1.000	1.000	<0.001	0.791
Max F0	E	0.001	0.098	0.019	-0.075	-0.066	0.028	0.000	-0.074	-0.084	-0.085	-0.072
	SE	0.015	0.015	0.015	0.015	0.015	0.018	0.018	0.018	0.018	0.016	0.016
	z	0.532	-6.475	1.270	-4.975	-4.384	1.598	0.017	-4.141	-4.669	-5.183	-4.630
	P	1.000	<0.001	0.999	<0.001	<0.001	0.987	1.000	<0.001	<0.001	<0.001	<0.001
Range F0	E	-0.031	-0.435	0.010	-0.320	-0.376	0.039	-0.037	-0.419	-0.522	-0.182	-0.201
	SE	0.060	0.061	0.060	0.060	0.060	0.074	0.074	0.074	0.075	0.065	0.063
	z	-0.523	-7.216	1.730	-5.334	-6.248	0.539	-0.507	-5.664	-7.038	-2.795	-3.195
	P	1.000	<0.001	0.971	<0.001	<0.001	1.000	1.000	<0.001	<0.001	0.302	0.109
MA Slope	E	0.151	-0.429	0.284	-0.573	-0.241	0.349	0.089	-0.041	-0.238	-0.482	-0.221
	SE	0.073	0.073	0.073	0.073	0.073	0.092	0.092	0.092	0.092	0.081	0.078
	z	2.060	-5.840	3.877	-7.828	-3.286	3.794	0.973	-4.465	-2.593	-5.915	-2.862
	P	0.852	<0.001	0.011	<0.001	0.083	0.015	1.000	<0.001	0.452	<0.001	0.260

Table 2. Results of the pairwise comparisons using the interaction between Sex and Unit Type.

For each response variable (e.g. Duration), we reported Estimate (E), Standard Error (SE), z value (z), and p value (P) of the respective GLMM. We used the interaction between Sex and Unit Type as fixed factor and singer identity, song, and descending phrase as random factors. Males showed longer duration and higher frequency values than females in all the statistically significant tests (indicated in bold). M: males; F: females; DP2-1 and DP2-2: first and second unit of the phrase comprising two notes; DP3-1, DP3-2, DP3-3: first, second, and third unit of the phrase comprising three notes; DP4-1, DP4-2, DP4-3, DP4-4: first, second, third, and fourth of the phrase comprising four notes; LN: long notes; SN: single notes.

Temporal and frequency variation of the unit types

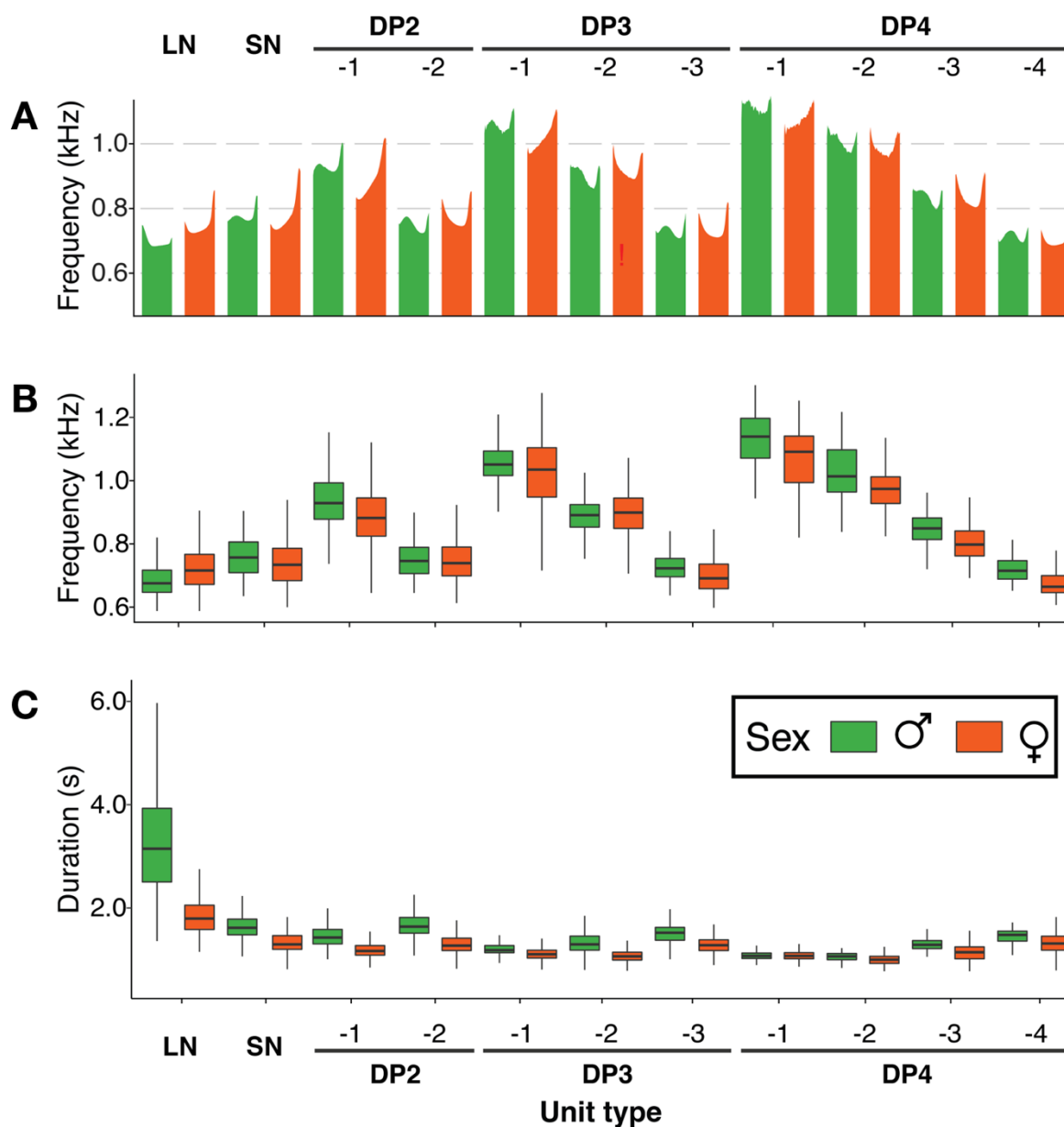


Figure 1. Frequency and duration variation among unit types and between sexes.

Barplot of the average frequency (A) among unit types in the two sexes. Boxplot of the average frequency (B) and duration (C) among unit types in the two sexes (males in green, females in light red); solid lines indicate the standard deviation.

4. DISCUSSION

In the indris, songs are part of a larger set of species-specific vocalizations (Valente et al. 2019). Calls are shorter than songs and play a role in short distance communication or alarm, whereas songs usually play a critical role in territorial defense and can be heard at long distance (Giacoma et al. 2010; Gamba et al. 2011). In agreement with the previous finding of Giacoma and colleagues (2010), we found that the indris are capable of emitting vocal units with or without concatenating them into phrases. The phrases and the other units, namely long notes and single notes, constitute the individual song, which is given simultaneously with other members of the family group. Although previous studies have shown that the overall contribution and the average duration of the units differ remarkably between males and females (Giacoma et al. 2010; Gamba et al. 2016), our analysis shows only limited support for the presence of sexually dimorphic traits at the unit level when we consider their position within a phrase or their occurrence in the song.

Only two of the elements concatenated in descending phrases showed significant differences in duration. The second units of DP2 and DP3 given by males were significantly longer than those by females. Also, long notes were significantly longer in males, showing duration almost doubled when compared to female's ones. This finding can be explained by the fact that long notes are elements which are not strictly related to other units. Indeed, the structure of the descending phrases is more constrained, with units whose duration is rigidly related to phrase length (Gamba et al. 2016).

We also found that the difference in *maxf0* is consistent in five out of 9 unit types given during the descending phrases and for both long and single notes. For the above five unit types these differences are also reflected in differences in *rangef0*, as *minf0* did not change between the sexes (except for long notes). It seems that females were usually giving units showing a higher F0, contradicting the finding of Gamba and colleagues (2016). The finding of Gamba and colleagues (2016) may have presented a cumulative effect deriving from the number of units of particular type that males may emit. When considered by unit types, females frequency values are higher especially because of the upsweep at the end of most DP units (see Figure 1).

Frequency modulation of each unit appeared to have the potential for advertising the sex of the emitter, as shown by *maslope*, which was significant for 6 out of 11 unit types. Even if it is unclear the extent to which fundamental frequency variation can provide cues to potential mates or competitors, we cannot rule out the fact that it may advertise for critical features of the emitter that can be assessed at a distance by conspecifics (Leitner et al. 2001). It is also interesting to notice that males or females may showed different trends in Mean Absolute Slope, suggesting that modulation of particular units by be highly informative for the sex of the emitter.

Sexual selection has been proposed as the primary evolutionary mechanism for the evolution of gibbon song: males and females produce sexually dimorphic song bouts, and songs are used in mate and home range defense, and in mate attraction (Cowlshaw 1996). Puts and colleagues (2016) proposed a link between sexual dimorphism in fundamental frequency and social system. In several species of anthropoid primates, polygynous species (where the sexual selection is stronger) show greater sexual dimorphism in fundamental frequency, when compared to monogamous ones. However, the case of indri is peculiar. Their song is very sophisticated (Thalmann et al. 1993) and differences in the frequency and durational variables may be both critical to encode information (Wanelik et al. 2013).

Such a complicated series of units showed only partial evidence of sexual dimorphism in terms of each note and its position in the repertoire, but a broad picture in which both duration and fundamental frequency are considered may demonstrate how indris' units encode information about the sex (and possibly other features) of the emitter.

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