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Sexually dimorphic phrase organization in the song of the indris (*Indri indri*)

Running title: Phrase organization in the indris

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Abstract

Animal acoustic communication often takes the form of complex sequences, composed of multiple distinct acoustic units, which can vary in their degree of stereotypy. Studies of sequence variation may contribute to our understanding of the structural flexibility of primates' songs, which can provide essential ecological and behavioral information about variability at the individual, population, and specific level and provide insights into the mechanisms and drivers responsible for the evolutionary change of communicative traits. We studied intra and inter-individual variation in the song structuring of a singing primate, the indri (*Indri indri*). Indri groups emit duets and choruses in which they combine long notes, short single units, and phrases consisting of a variable number of units (from two to six) with slightly descending frequency. Males' and females' contributions to the song differ in the temporal and frequency structure of song units and repertoire size. We calculated the similarity of phrase organization across different individual contributions using the Levenshtein distance, a logic distance that expressed the minimum cost to convert a sequence into another and can measure differences between two sequences of data. We then analyzed the degree of similarity within and between individuals and found that: i) the phrase structure of songs varied between reproductive males and females: female structuring of the song showed a higher number of phrases if compared to males; ii) Male contributions to the song were overall more similar to those of other males than were female contributions to the song of other females; iii) male contributions were more stereotyped than female contributions, which showed greater individual flexibility. The picture emerging from phrase combinatorics in the indris is in agreement with previous findings of rhythmic features and song repertoire size of the indris, which also suggested that female songs are potentially less stereotyped than those of males.

Keywords: syntax, language evolution, primates, singing, Levenshtein distance

Research Highlights

- This study demonstrated that male and female adult indris differed in the phrase organization of their songs.
- Male contributions to the song were overall more similar to those of other males and more stereotyped than females' ones.

Graphical Abstract

Figure 2 works as graphical abstract for this manuscript.

Introduction

Communication between conspecifics often involves the use of vocalizations because acoustic signals allow encoding a considerable amount of information in a short time (Bradbury & Vehrencamp, 2011). Animal vocal signals can be emitted in the form of short vocalizations or given in sequences of variable length (Catchpole & Slater, 2008). In addition to the well-known example of birdsong, other animals such as insects, amphibians, and mammals (including bats, rodents, primates, and cetaceans) also emit complex acoustic sequences (Kershenbaum et al., 2016). Although animals showed a limited ability to concatenate vocal emissions in phrases when compared to humans (Berwick, Okanoya, Beckers & Bolhuis, 2011), their vocal sequences may contain information on species and individual identity (e.g., starlings (*Sturnus vulgaris*), wolves (*Canis lupus*), dolphins (*Tursiops truncatus*), and rock hyraxes (*Procavia capensis*)). Animal vocal sequences may also encode information about external cues such as resource availability, e.g., food calls in chimpanzees (*Pan troglodytes*), or predator threats in marmots (*Marmota* spp.; Kershenbaum et al., 2016).

The understanding of the role played by the acoustic sequences in a particular species' repertoire often involves the comparison of sequences within and between individuals, as well as within and between groups, so that it is possible to quantify the nature of the variation and potentially correlate it to ecological and behavioral factors (Kershenbaum et al., 2014).

So far, the studies of primate call organization focused on contact calls or alarm calls (Clarke, Reichard & Zuberbühler, 2006) with scarce investigations of song structure variation within contexts (Torti, Gamba, Rabemananjara & Giacoma, 2013). There is a lack of information about whether primate males and females combine units in songs using different phrase combinations. It is essential to examine the sex-dimorphic traits of primate songs because knowledge of sex differences in song organization may be critical in our understanding of what is biologically informative, especially in sexually monomorphic species. Moreover, information available on the variability within a species is very little (Honda & Okanoya, 1999; Takahasi, Yamada & Okanoya, 2010). Few investigations on primate vocal sequences are currently available and none of them are evaluating the stereotypy of song structure between sexes using a string metric (Gustison, Semple, Ferrer-i-Cancho & Bergman, 2016). While traditional methods may not apply to a wide array of questions, string metrics can be used to investigate different organizational levels, are entirely objective, and their results are verifiable (Heeringa, 2004).

Indris (*Indri indri*, Gmelin, 1788) represent a distinctive species for studying vocal communication because of their rich repertoire (Maretti, Sorrentino, Finomana, Gamba & Giacoma, 2010; Valente et al., 2019) and the impressive loud songs, unique among lemurs (Gamba et al., 2016; Torti et al., 2017), which can be heard at a distance up to 2 km (Pollock, 1986). Data on sound pressure levels revealed that the sound levels of the indri's song reached 110 dB (estimated at 0.50 m; Torti, *pers. obs.*). This level can be compared to ring-tailed lemurs (*Lemur catta*), which showed a call amplitude ranging between 85 and 89 dB (at 1 m, Macedonia, 1993). The song of the indris, which lasts 40-250 s, consists of a long series of modulated units, organized in phrases (Gamba, Favaro, Torti, Sorrentino & Giacoma, 2011), uttered simultaneously by males and females, including juveniles, of the same group (Maretti et al., 2010). These types of units are emitted exclusively during the song (Valente et al., 2019).

Previous research showed that the indris can emit songs in different contexts and that the song can elicit different behaviors depending on its acoustic structure. Songs given in different contexts showed differences in their temporal structure that are distinguishable by visual inspection of the spectrograms and by ear (Torti et al. 2013). Cohesion songs were emitted when the individuals of a group were dispersed in their territory, while advertisement songs were usually given when the animals of the same group were in visual contact at the boundary of their territory (Torti et al., 2013). Cohesion songs were followed by emitters traveling significantly further than following the advertisement song, confirming the different functions of the song uttered in different contexts (i.e., cohesion songs bring together the members of a group, and advertisement songs inform neighbors about the sex, age, and status of singing individuals). Other studies have shown that male and female contributions to the song differ, both quantitatively and qualitatively, in the temporal structure of the units emitted (Giacoma, Sorrentino, Rabarivola & Gamba, 2010; Sorrentino, Gamba & Giacoma, 2012). Vocal sexual dimorphism is also present in the modulation of the frequency of vocal utterances, in the duration of unit types and the rhythmic structure of a contribution (Gamba et al., 2016; De Gregorio et al., 2018).

Since the indris' songs can be interpreted as a string of easily identifiable phrases (Gamba et al., 2016), they represent an ideal case for the study of the variability of phrase concatenation in primate songs. Among the methods for investigating different levels of structural variation in acoustic displays, we chose the Levenshtein distance, which is a quantitative method for measuring the similarity of sequences (hereafter LD; Margoliash, Staicer & Inoue, 1991). The LD is a logical distance commonly used to quantify the difference between two strings of data (e.g., human words, sequences of visual movements or sequences of song themes; Gooskens & Heeringa, 2004). This technique has often been used to measure similarity in human dialects (Wieling, Montemagni, Nerbonne & Baayen, 2014), and it has been applied to animal vocal sequences, but for a very limited number of species (Indigo bunting, *Passerina cyanea*, Margoliash et al., 1991; Willow warbler, *Phylloscopus trochilus*, Gil & Slater, 2000; Humpback whale, *Megaptera novaeangliae*: Helweg, Cato, Jenkins, Garrigue & McCauley, 1998; Tougaard & Eriksen, 2006; Garland et al., 2012).

Although songs are often referred to as a male's prerogative, we have particular insights showing that monogamous females may also use the song overlapping male song functions (e.g., Eastern whip bird (*Psophodes olivaceus*), Rogers, Langmore, & Mulder, 2007; Levin, 1996a; 1996b). Females may use songs for mate attraction (Rogers et al., 2007), and they may even show a more elaborated song repertoire (Australian magpies (*Gymnorhina tibice* Brown & Farabaugh, 1991). Like Eastern whip birds and Australian magpies, indris are monogamous (Torti et al., 2017; Bonadonna et al., 2019), form groups that occupy non-overlapping areas in the forest (Bonadonna et al., 2017), and use the songs to inform neighboring groups about the occupation of a territory and to actively defend resources during group encounters (Torti et al., 2013). Thus, we hypothesized that the female contribution to the song would be structurally different from that of males.

Studies of song structure in bird duets also suggested that females' songs would be more acoustically variable than that of males (Logue & Gammon, 2004), in line with the territorial model of bird duet evolution (Farabaugh, 1982). In birds, duetting occurs most commonly where birds hold year-round territories, and it is associated with sexually monomorphic species that form long-term monogamous pair bonds (Riebel, Odom, Langmore & Hall, 2019). Indri females showed significantly higher variation in the rhythm of their contributions to the song and a higher potential to synchronize with males (De Gregorio et al., 2018). Thus, we hypothesized that the adjustment in the rhythmic structure of their contribution would also be reflected in a sexually dimorphic phrases combination, where one should expect males to produce songs with a more stereotyped structure. Similarly to pair living bird species (Rogers et al., 2007), indri females may use songs for mate guarding and attraction, and song structural variability and complexity may have evolved to provide conspecifics with information on females' fitness and survival.

Methods

Observations and recordings

We studied 8 groups (N= 36 individuals) living in the Maromizaha Forest (18°56'49"S, 48°27'53"E). We recorded the animals between 2011 and 2017. We observed one social group per week, from Monday to Friday approximately from 6 AM to 1 PM, when the animals usually start resting and sleeping until the day after (Pollock, 1975). All recordings were carried out without the use of playback stimuli, and nothing was done to modify the behavior of the indris. We recorded 142 songs, consisting of duets and choruses with a maximum of five individuals singing in the same song. For the analysis, we only considered the contribution of the reproductive individuals, for a total of 17 focal animals from eight social groups: nine reproductive adult males, and eight reproductive adult females. An example of an indri song and the singers' contributions is shown in Figure 1. The different number of males and females is motivated by the fact that, during the study period, the reproductive male of a group changed. All the songs were recorded using solid-state recorders (Olympus LS05, Tascam DR-100, Tascam DR-05) with a sampling rate of 44.1 kHz (16-bit depth) during all the recording sessions. When recording the songs, we were always at a distance between 2 and 20 m from the animals, with the microphone oriented toward the focal singing individuals. We always kept visual contact with the vocalizing animals and maximized our efforts to face the focal animals during the emission of the song. Since indri songs emitted in different contexts have different acoustic structure, in order to avoid any bias due to these differences, we considered, from multiple years, only those songs that were labeled as advertisement songs and were recorded in the same context (Torti et al., 2013). Using the focal animal sampling technique (Altmann, 1974), we were able to attribute each vocalization to its signaler. We will refer to every individual uttered portion within a song or a chorus as an 'individual contribution'.

During this study, we did not have any physical contact with the animals, and we recorded only spontaneously emitted songs. We have received permits for this research, each year, from "Direction des Eaux et Forêts" and "Madagascar National Parks": 2011 - N° 274/11/MEF/SG/D GF/DCB.SAP/SCB, 2012 N°245/12/MEF/SG/DGF/DCB.SAP/SCB, 2014 - N°066/14/MEF/SG/DGF/DCB.SAP/SCB, 2015 - N° 180/ 15/ MEEMF/ SG/ DGF/ DAPT/ SCBT; 2016 - N° 98/ 16/ MEEMF/ SG/ DGF/ DAPT/ SCB.Re and N° 217/ 16/MEEMF/ SG/ DGF/ DSAP/ SCB.Re, 2017 - 73/17/MEEF/SG/DGF/DSAP/SCB.RE. The data collection in 2013 did not require a permit because performed by our Malagasy collaborators only.

We adhered to applicable international, national, and/or institutional guidelines for the study on animals and nonhuman primates, including the American Society of Primatologist (ASP) Principle for the Ethical Treatment of nonhuman Primates, and the

European Union directive guidelines for the study on animals and nonhuman primates (Directive 2010/63/EU). The study did not require IACUC approval.

Acoustic and statistical analyses

We edited segments containing indri songs using Praat 6.0.30 (Boersma & Weenink 2008) and BORIS 5.1 (Friard & Gamba 2016). For each recorded song, we created a spectrogram with a view range between 0 and 5000 Hz, a window length of 0.09 s, and a dynamic range of 65.0 dB. We saved each song in a single audio file in WAV format (Waveform audio file format). We saved the information related to the identity of each singer in a Praat textgrid. We then labeled all the vocal units (each single sound constituting the modulated part of the song; Thalmann, Geissmann, Simona & Mutschler, 1993) according to their belonging to a song portion (long notes or descending phrases, see Torti et al., 2013 for details) and to a descending phrase (hereafter, DP; see Torti et al., 2017 for details). Songs given in different contexts showed differences in their temporal structure that are distinguishable by visual inspection of the spectrograms and by ear (Torti et al. 2013). We considered phrases consisting of two (DP2), three (DP3), four (DP4), five (DP5), and six (DP6) units. This information was saved in Praat and exported to a Microsoft© Excel spreadsheet (Gamba, Friard & Giacoma, 2012). Since all the steps of the labeling process have been done by a single operator (A.Z.), we avoided the possibility of encountering errors due to observer differences. To understand whether there were differences in song structure between sexes, we investigated the DPs similarity in each contribution. We transformed each contribution in a string of labels separated by a break symbol (e.g., DP2|DP3|DP4|DP3). The resulting string represents the concatenation of the phrases uttered within a contribution (and it is a measure of phrase organization). From the 142 songs, we obtained 142 strings for females (with an average of 17.88 songs per individual, SD = 5.44), and 119 strings for males (with an average of 13.22 songs per individual, SD = 5.91). Using R (R Core Team, 2015; version 3.3.3), we calculated the Levenshtein distance (LD) for each pair of strings (package *stringdist* 0.9.4.2 in R; van der Loo, 2014) because this methodology provides a robust quantitative approach for the study of animal acoustic sequences (Kershenbaum & Garland, 2015). The distance calculates the minimum number of necessary changes (insertions, deletions, and substitutions) to transform one string into another (Kohonen, 1985). We obtained a squared matrix consisting of the distances between each pair of strings, then averaged LDs and calculated within- and between-individual means (Fig. 2), to investigate whether females and males differed in their degree of variation. For this purpose, we ran Mantel tests (9999 randomizations) using a matrix featuring the average individual means against a model matrix consisting of 0 when the corresponding individuals were of the same sex (Krull et al., 2012), and 1 when they were opposite sexes (package *vegan* in R; Oksanen et al., 2013). When investigating differences at the group level or within-sex, we used the non-parametric paired samples Wilcoxon test to compare the average individual LDs of each member of a pair or the within- versus between-individual LDs because, with such a small sample size, the Mantel test is not recommended (Legendre & Fortin, 1989). Only for the Wilcoxon test, the group in which the male changed was entered twice, considering the two pairs as different groups. We obtained a lower number of male contributions because the reproductive females also engaged in duets with immature male offspring (N = 23).

Results

We analyzed 261 individual contributions consisting of a total of 2018 phrases. We obtained 77 ± 21 (mean + standard deviation) phrases per male and 78 ± 23 phrases per female. We found that average phrase duration was 1.285 s (range: 0.380 - 3.000 s). The number of phrases in the individual song ranged between 2 and 27.

We found a significant difference between the LDs calculated for males and females, where females showed higher average individual means than males (Mantel test: r = 0.167, P = 0.002; Fig. 2). In all groups, the females had higher LDs (LD = 6.497 + 1.674) than males (LD = 3.946 + 0.814), showing that female contribution to the song was less stereotyped (Fig. 3, Wilcoxon paired test: V = 0, df = 7; P = 0.008). It is noticeable that the individuals Eva, which sang with three different males and had a high number of recordings (N=39), showed remarkable differences compared to other females. Both females and males showed a higher variability at between-individuals ($LD_{females}$ = 7.386 + 0.709, LD_{males} = 4.885 + 0.325) than within-individual level (Fig. 3), except for the females of groups 4 and 8. Overall, we found a significant difference between within- and between-individual LDs (Wilcoxon paired test: V = 0, df = 7; P = 0.008).

Discussion

We examined differences in the order of phrases emitted during the songs by reproductive male and female indris living in the same population. We hypothesized that female contributions to the song may function differently in phrase concatenation from those of males. We found support for our predictions. The phrase structure of songs indeed differed between males and females, and female contributions were less stereotyped than those of males. The LDs showed that the between-individual stereotypy of male contributions was higher than females' one. Males, therefore, appeared to produce songs that are overall more similar to those of other males. In agreement with previous studies that reported sexual dimorphism in the overall timing and repertoire size (Giacoma et al., 2010), and in the frequency modulation, duration and rhythm (Gamba et al., 2016; Torti et al., 2017, De Gregorio et al., 2018), we found that male and female indris also differed in the phrase organization of their songs. Female structuring of the song showed a higher number of phrases if compared to males, independently of the phrases being of the same or different type. This result is in line with previous studies on family-living and pair-bonded primate and bird species (Deputte, 1982; Savage, Snowdon, Giraldo & Soto, 1996; Snowdon, 2017; Riebel et al., 2019; Levin, 1996a; 1996b), endorsing that in a socially monogamous, monomorphic species which holds year-round territories, sex differences in vocal output are frequent (Marshall & Marshall, 1976). Furthermore, despite the fact that songs are considered to be males' peculiar features (Cowlishaw, 1996), our results confirm that also monogamous females use songs and that female song can be more elaborate than those of males. Female song phrase concatenation is more complex than males' because even if males are playing the primary role in territorial defense, females' role in territorial disputes can be essential. Female songs may be critical for advertising their identity as well as resources holding potential. For instance, vocal fights, in which females and males are singing together, are often sufficient to resolve group encounters, reducing the occurrence of physical fights (Bonadonna et al., 2020). Future studies may investigate whether female dispersal distance and territorial changes over the years may contribute to a deeper understanding of this sex-dimorphic variation. Expanding previous findings that showed how indri female contribution to the song was more varied in the rhythm (De Gregorio et al., 2018), we showed that the combination and repertoire of the phrases are also more extensive than those shown by males. Females not only have a broader repertoire of units, but they also emit descending phrases that we did not observe in males (e.g., descending phrases of six units). Considering those previous findings, our results may suggest that the differences in song structuring could be used to convey information about the sex and the status of the singers that can be assessed at a distance by conspecifics.

In agreement with previous findings on the different role of males and females during the song (Giacoma et al., 2010), we found that female song is potentially more distinctive than the male one. These results are in agreement with previous findings on birds (Brown & Farabaugh, 1991), confirming that in those species in which females are involved in territorial defense, their repertoires are as large or larger than those of males, on the level of both units and phrases. Territorial defense is crucial for survival and reproduction in pair-bonding species that occupy stable territories, and even if female involvement in territorial defense is different from that of the reproductive male, they participate in joining with their partner. An increasing body of literature (e.g., Hall, Rittenbach, & Vehrencamp, 2015) supported the view that same-sex competition is the primary driver of female song elaboration. It can be the case of the indris, where females may benefit from multiple mating partners to increase tolerance by neighboring males (Bonadonna et al., 2014). As mentioned above, females can advertise the occupancy of an area as well as their quality and resource-holding potential. In support of the higher variability in female song structure, there is also the recent evidence that genetic relatedness may play a critical role in determining the characteristics of DPs in males, whereas it may have a lesser impact on female songs (Torti et al., 2017). A more variable song structure may add up to a more flexible structuring of the phrase notes, but further investigations are needed.

This work also expands on and complements previous studies on humpback whales (Helweg et al., 1998; Tougaard & Eriksen, 2006; Garland et al., 2012), showing that the Levenshtein distance is simple, efficiently computable and highly applicable to any behavioral data that are produced in a sequence. Our results confirmed that the Levenshtein distance method is a simple but powerful technique that can be applied to assess stereotypy or divergence between sexes.

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Figure legend:

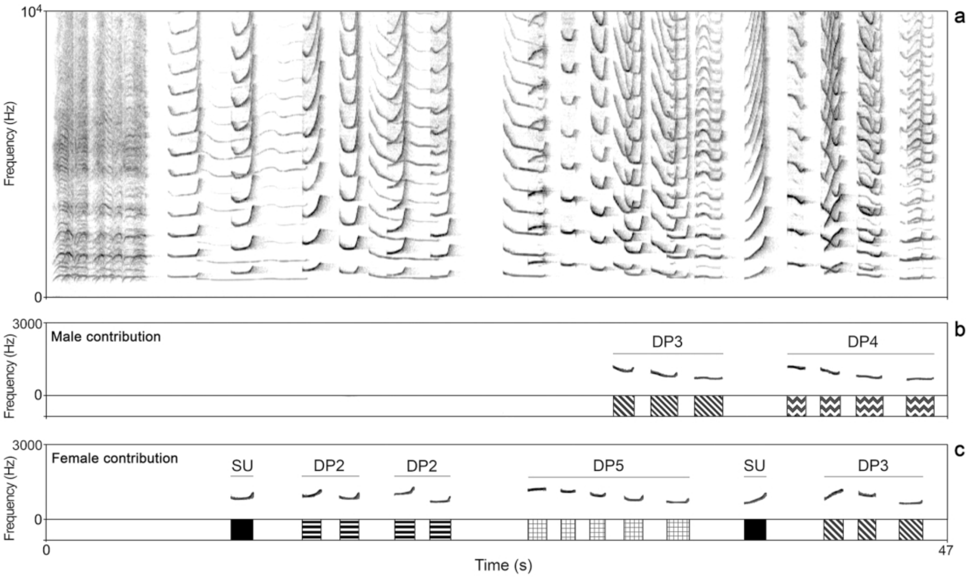
Figure 1: *Spectrographic and schematic representation of an indri song.* Spectrograms of an indri song (a) showing a typical sequence of units given by one male and one female. Schematic representation of the fundamental frequency of the descending phrase units given by one male (b) and one female (c). Box fill patterns denote the phrase type: black boxes mark single units (SU), horizontal lines boxes mark DP2, diagonal lines boxes mark DP3, wavy lines boxes mark DP4, and checkered boxes mark DP5. The spectrograms were generated in Praat with the following parameters: window length: 0.05 s; dynamic range: 50 dB; frequency range: 0 to 10.000 Hz (a), 0 to 3.000 Hz (b,c).

Figure 2: The Levenshtein Distances showing song structuring in male and female indris of the studied groups. Individuals are shown on the vertical axis; sexes are shown on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker and bigger the dots, the higher are the distances between the individual contributions to the song. This plot was generated using the R package *corrplot* (vers. 0.84; Wei & Simko, 2017).

Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight studied groups. Bar plot describing the individual and overall degree of stereotypy and variability expressed by the average Levenshtein Distances (LDs). Within-individual LDs are reported for females (white bars) and males (black bars), as well as between-individual LDs (grey bars for females, striped bars for males). Group 3 is reported twice because the male of the reproductive pairs changed in 2014. Capped lines represent Standard Deviation.

Research Highlights

- This study demonstrated that male and female adult indris differed in the phrase organization of their songs.
- Male contributions to the song were overall more similar to those of other males and more stereotyped than females' ones.



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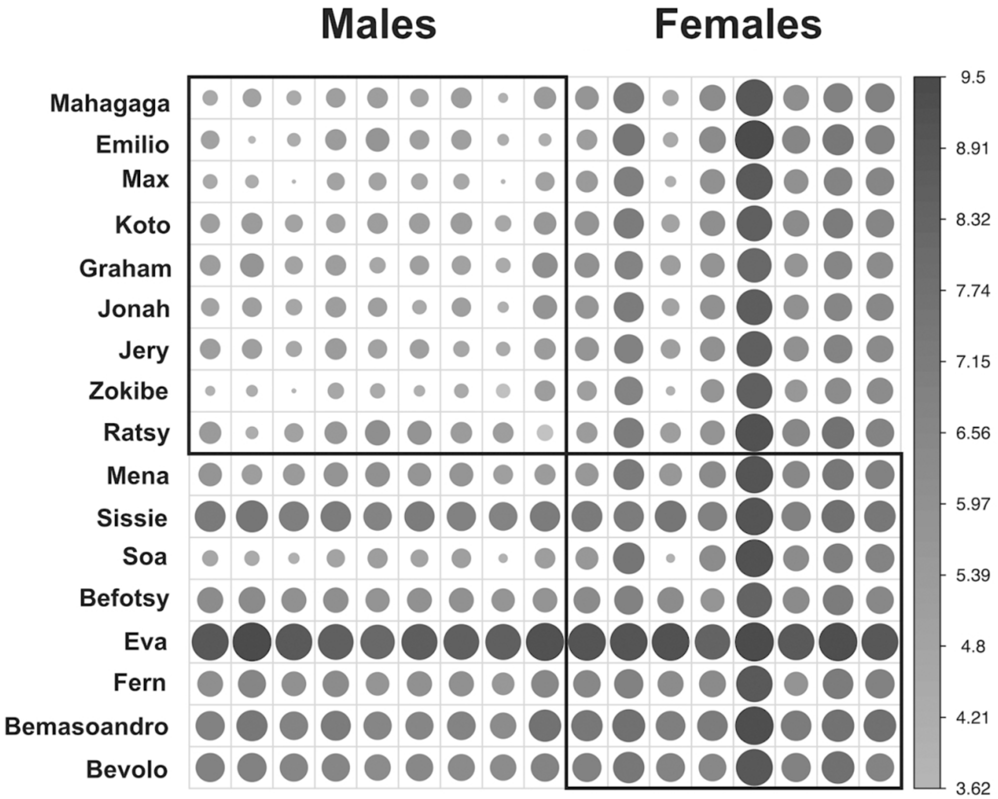

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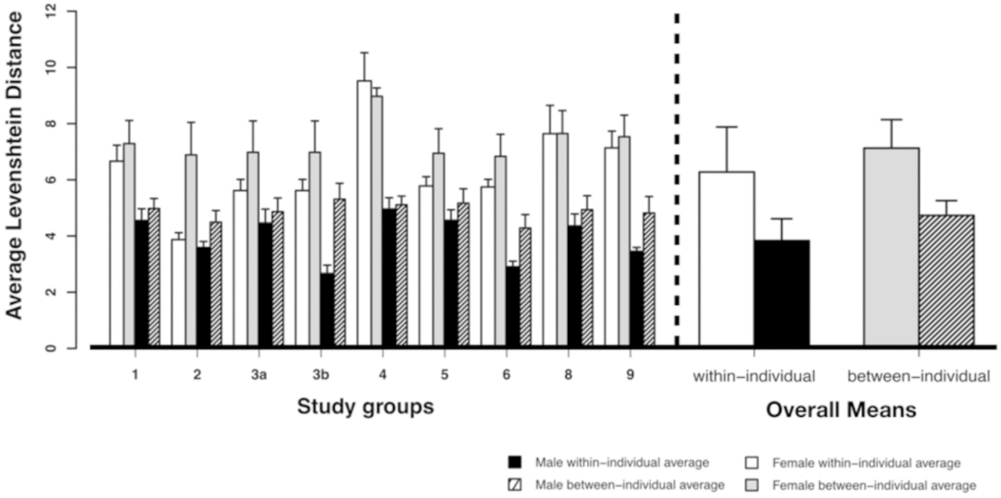

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Sexually dimorphic phrase organization in the song of the indris (*Indri indri*)

Running title: Phrase organization in the indris

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Abstract

Animal acoustic communication often takes the form of complex sequences, composed of multiple distinct acoustic units, which can vary in their degree of stereotypy. Studies of sequence variation may contribute to our understanding of the structural flexibility of primates' songs, which can provide essential ecological and behavioral information about variability at the individual, population, and specific level and provide insights into the mechanisms and drivers responsible for the evolutionary change of communicative traits. ~~Several methods have been used for investigating different levels of structural information and sequence similarity in acoustic displays.~~ We studied intra and inter-individual variation in the song structuring of a singing primate, the indri (*Indri indri*)~~,~~ ~~which inhabits the montane rain forests of Madagascar~~. Indri groups emit duets and choruses in which they combine long notes, short single units, and phrases consisting of a variable number of units (from two to six) with slightly descending frequency. Males' and females' contributions to the song differ in the temporal and frequency structure of song units and repertoire size. We calculated the similarity of phrase organization across different individual contributions using the Levenshtein distance, a logic distance that expressed the minimum cost to convert a sequence into another and can measure differences between two sequences of data. We then analyzed the degree of similarity within and between individuals and found that: i) the phrase structure of songs varied between reproductive males and females: female structuring of the song showed a higher number of phrases if compared to males; ii) Male contributions to the song were overall more similar to those of other males than were female contributions to the song of other females; iii) male contributions were more stereotyped than female contributions, which showed greater individual flexibility. The picture emerging from phrase combinatorics in the indris is in agreement with previous findings of rhythmic features and song repertoire size of the indris, which also suggested that female songs are potentially less stereotyped than those of males.

Keywords: syntax, language evolution, primates, singing, Levenshtein distance

Research Highlights

- This study demonstrated that male and female adult indris differed in the phrase organization of their songs.
- Male contributions to the song were overall more similar to those of other males and more stereotyped than females' ones.

Graphical Abstract

Figure 2 works as graphical abstract for this manuscript.

Introduction

Communication between conspecifics often involves the use of vocalizations because acoustic signals allow encoding a considerable amount of information in a short time (Bradbury & Vehrencamp, 2011). Animal vocal signals can be emitted in the form of short vocalizations or given in sequences of variable length (Catchpole & Slater, 2008). In addition to the well-known example of birdsong, other animals such as insects, amphibians, and mammals (including bats, rodents, primates, and cetaceans) also emit complex acoustic sequences (Kershenbaum et al., 2016). Although animals showed a limited ability to concatenate vocal emissions in phrases when compared to humans (Berwick, Okanoya, Beckers & Bolhuis, 2011), their vocal sequences may contain information on species and individual identity (e.g., starlings (*Sturnus vulgaris*), wolves (*Canis lupus*), dolphins (*Tursiops truncatus*), and rock hyraxes (*Procavia capensis*)). Animal vocal sequences may also encode information about external cues such as resource availability, e.g., food calls in chimpanzees (*Pan troglodytes*), or predator threats in marmots (*Marmota* spp.; Kershenbaum et al., 2016).

The understanding of the role played by the acoustic sequences in a particular species' repertoire often involves the comparison of sequences within and between individuals, as well as within and between groups, so that it is possible to quantify the nature of the variation and potentially correlate it to ecological and behavioral factors (Kershenbaum et al., 2014).

So far, the studies of primate call organization focused on contact calls or alarm calls (Clarke, Reichard & Zuberbühler, 2006) with scarce investigations of song structure variation within contexts (Torti, Gamba, Rabemananjara & Giacoma, 2013). There is a lack of information about whether primate males and females combine units in songs using different phrase combinations. It is essential to examine the sex-dimorphic traits of primate songs because knowledge of sex differences in song organization may be critical in our understanding of what is biologically informative, especially in sexually monomorphic species. Moreover, information available on the variability within a species is very little (Honda & Okanoya, 1999; Takahasi, Yamada & Okanoya, 2010). Few investigations on primate vocal sequences are currently available and none of them are evaluating the stereotypy of song structure between sexes using a string metric (Gustison, Semple, Ferrer-i-Cancho & Bergman, 2016). While traditional methods may not apply to a wide array of questions, string metrics can be used to investigate different organizational levels, are entirely objective, and their results are verifiable (Heeringa, 2004).

Indris (*Indri indri*, Gmelin, 1788) represent a distinctive species for studying vocal communication because of their rich repertoire (Maretti, Sorrentino, Finomana, Gamba & Giacoma, 2010; Valente et al., 2019) and the impressive loud songs, unique among lemurs (Gamba et al., 2016; Torti et al., 2017), which can be heard at a distance up to 2 km (Pollock, 1986). Data on sound pressure levels revealed that the sound levels of the indri's song reached 110 dB (estimated at 0.50 m; Torti, *pers. obs.*). This level can be compared to ring-tailed lemurs (*Lemur catta*), which showed a call amplitude ranging between 85 and 89 dB (at 1 m, Macedonia, 1993). The song of the indris, which lasts 40-250 s, consists of a long series of modulated units, organized in phrases (Gamba, Favaro, Torti, Sorrentino & Giacoma, 2011), uttered simultaneously by males and females, including juveniles, of the same group (Maretti et al., 2010). These types of units are emitted exclusively during the song (Valente et al., 2019).

Previous research showed that the indris can emit songs in different contexts and that the song can elicit different behaviors depending on its acoustic structure. Songs given in different contexts showed differences in their temporal structure that are distinguishable by visual inspection of the spectrograms and by ear (Torti et al. 2013). Cohesion songs were emitted when the individuals of a group were dispersed in their territory, while advertisement songs were usually given when the animals of the same group were in visual contact at the boundary of their territory (Torti et al., 2013). Cohesion songs were followed by emitters traveling significantly further than following the advertisement song, confirming the different functions of the song uttered in different contexts (i.e., cohesion songs bring together the members of a group, and advertisement songs inform neighbors about the sex, age, and status of singing individuals). Other studies have shown that male and female contributions to the song differ, both quantitatively and qualitatively, in the temporal structure of the units emitted (Giacoma, Sorrentino, Rabarivola & Gamba, 2010; Sorrentino, Gamba & Giacoma, 2012). Vocal sexual dimorphism is also present in the modulation of the frequency of vocal utterances, in the duration of unit types and the rhythmic structure of a contribution (Gamba et al., 2016; De Gregorio et al., 2018).

Since the indris' songs can be interpreted as a string of easily identifiable phrases (Gamba et al., 2016), they represent an ideal case for the study of the variability of phrase concatenation in primate songs. Among the methods for investigating different levels of structural variation in acoustic displays, we chose the Levenshtein distance, which is a quantitative method for measuring the similarity of sequences (hereafter LD; Margoliash, Staicer & Inoue, 1991). The LD is a logical distance commonly used to quantify the difference between two strings of data (e.g., human words, sequences of visual movements or sequences of song themes; Gooskens & Heeringa, 2004). This technique has often been used to measure similarity in human dialects (Wieling, Montemagni, Nerbonne & Baayen, 2014), and it has been applied to animal vocal sequences, but for a very limited number of species (Indigo bunting, *Passerina cyanea*, Margoliash et al., 1991; Willow warbler, *Phylloscopus trochilus*, Gil & Slater, 2000; Humpback whale, *Megaptera novaeangliae*: Helweg, Cato, Jenkins, Garrigue & McCauley, 1998; Tougaard & Eriksen, 2006; Garland et al., 2012).

Although songs are often referred to as a male's prerogative, we have particular insights showing that monogamous females may also use the song overlapping male song functions (e.g., Eastern whip bird (*Psophodes olivaceus*), Rogers, Langmore, & Mulder, 2007; Levin, 1996a; 1996b). Females may use songs for mate attraction (Rogers et al., 2007), and they may even show a more elaborated song repertoire (Australian magpies (*Gymnorhina tibice* Brown & Farabaugh, 1991). Like Eastern whip birds and Australian magpies, indris are monogamous (Torti et al., 2017; Bonadonna et al., 2019), form groups that occupy non-overlapping areas in the forest (Bonadonna et al., 2017), and use the songs to inform neighboring groups about the occupation of a territory and to actively defend resources during group encounters (Torti et al., 2013). Thus, we hypothesized that the female contribution to the song would be structurally different from that of males.

Studies of song structure in bird duets also suggested that females' songs would be more acoustically variable than that of males (Logue & Gammon, 2004), in line with the territorial model of bird duet evolution (Farabaugh, 1982). In birds, duetting occurs most commonly where birds hold year-round territories, and it is associated with sexually monomorphic species that form long-term monogamous pair bonds (Riebel, Odom, Langmore & Hall, 2019). Indri females showed significantly higher variation in the rhythm of their contributions to the song and a higher potential to synchronize with males (De Gregorio et al., 2018). Thus, we hypothesized that the adjustment in the rhythmic structure of their contribution would also be reflected in a sexually dimorphic phrases combination, where one should expect males to produce songs with a more stereotyped structure. Similarly to pair living bird species (Rogers et al., 2007), indri females may use songs for mate guarding and attraction, and song structural variability and complexity may have evolved to provide conspecifics with information on females' fitness and survival.

Methods

Observations and recordings

We studied 8 groups (N= 36 individuals) living in the Maromizaha Forest (18°56'49"S, 48°27'53"E). We recorded the animals between 2011 and 2017. We observed one social group per week, from Monday to Friday approximately from 6 AM to 1 PM, when the animals usually start resting and sleeping until the day after (Pollock, 1975). All recordings were carried out without the use of playback stimuli, and nothing was done to modify the behavior of the indris. We recorded 142 songs, consisting of duets and choruses with a maximum of five individuals singing in the same song. For the analysis, we only considered the contribution of the reproductive individuals, for a total of 17 focal animals from eight social groups: nine reproductive adult males, and eight reproductive adult females. An example of an indri song and the singers' contributions is shown in Figure 1. The different number of males and females is motivated by the fact that, during the study period, the reproductive male of a group changed. All the songs were recorded using solid-state recorders (Olympus LS05, Tascam DR-100, Tascam DR-05) with a sampling rate of 44.1 kHz (16-bit depth) during all the recording sessions. When recording the songs, we were always at a distance between 2 and 20 m from the animals, with the microphone oriented toward the focal singing individuals. We always kept visual contact with the vocalizing animals and maximized our efforts to face the focal animals during the emission of the song. Since indri songs emitted in different contexts have different acoustic structure, in order to avoid any bias due to these differences, we considered, from multiple years, only those songs that were labeled as advertisement songs and were recorded in the same context (Torti et al., 2013). Using the focal animal sampling technique (Altmann, 1974), we were able to attribute each vocalization to its signaler. We will refer to every individual uttered portion within a song or a chorus as an 'individual contribution'.

During this study, we did not have any physical contact with the animals, and we recorded only spontaneously emitted songs. We have received permits for this research, each year, from "Direction des Eaux et Forêts" and "Madagascar National Parks": 2011 - N° 274/11/MEF/SG/D GF/DCB.SAP/SCB, 2012 N°245/12/MEF/SG/DGF/DCB.SAP/SCB, 2014 - N°066/14/MEF/SG/DGF/DCB.SAP/SCB, 2015 - N° 180/ 15/ MEEMF/ SG/ DGF/ DAPT/ SCBT; 2016 - N° 98/ 16/ MEEMF/ SG/ DGF/ DAPT/ SCB.Re and N° 217/ 16/MEEMF/ SG/ DGF/ DSAP/ SCB.Re, 2017 - 73/17/MEEF/SG/DGF/DSAP/SCB.RE. The data collection in 2013 did not require a permit because performed by our Malagasy collaborators only.

We adhered to applicable international, national, and/or institutional guidelines for the study on animals and nonhuman primates, including the American Society of Primatologist (ASP) Principle for the Ethical Treatment of nonhuman Primates, and the

European Union directive guidelines for the study on animals and nonhuman primates (Directive 2010/63/EU). The study did not require IACUC approval.

Acoustic and statistical analyses

We edited segments containing indri songs using Praat 6.0.30 (Boersma & Weenink 2008) and BORIS 5.1 (Friard & Gamba 2016). For each recorded song, we created a spectrogram with a view range between 0 and 5000 Hz, a window length of 0.09 s, and a dynamic range of 65.0 dB. We saved each song in a single audio file in WAV format (Waveform audio file format). We saved the information related to the identity of each singer in a Praat textgrid. We then labeled all the vocal units (each single sound constituting the modulated part of the song; Thalmann, Geissmann, Simona & Mutschler, 1993) according to their belonging to a song portion (long notes or descending phrases, see Torti et al., 2013 for details) and to a descending phrase (hereafter, DP; see Torti et al., 2017 for details). Songs given in different contexts showed differences in their temporal structure that are distinguishable by visual inspection of the spectrograms and by ear (Torti et al. 2013). We considered phrases consisting of two (DP2), three (DP3), four (DP4), five (DP5), and six (DP6) units. This information was saved in Praat and exported to a Microsoft© Excel spreadsheet (Gamba, Friard & Giacoma, 2012). Since all the steps of the labeling process have been done by a single operator (A.Z.), we avoided the possibility of encountering errors due to observer differences. To understand whether there were differences in song structure between sexes, we investigated the DPs similarity in each contribution. We transformed each contribution in a string of labels separated by a break symbol (e.g., DP2|DP3|DP4|DP3). The resulting string represents the concatenation of the phrases uttered within a contribution (and it is a measure of phrase organization). From the 142 songs, we obtained 142 strings for females (with an average of 17.88 songs per individual, SD = 5.44), and 119 strings for males (with an average of 13.22 songs per individual, SD = 5.91). Using R (R Core Team, 2015; version 3.3.3), we calculated the Levenshtein distance (LD) for each pair of strings (package *stringdist* 0.9.4.2 in R; van der Loo, 2014) because this methodology provides a robust quantitative approach for the study of animal acoustic sequences (Kershenbaum & Garland, 2015). The distance calculates the minimum number of necessary changes (insertions, deletions, and substitutions) to transform one string into another (Kohonen, 1985). We obtained a squared matrix consisting of the distances between each pair of strings, then averaged LDs and calculated within- and between-individual means (Fig. 2), to investigate whether females and males differed in their degree of variation. For this purpose, we ran Mantel tests (9999 randomizations) using a matrix featuring the average individual means against a model matrix consisting of 0 when the corresponding individuals were of the same sex (Krull et al., 2012), and 1 when they were opposite sexes (package *vegan* in R; Oksanen et al., 2013). When investigating differences at the group level or within-sex, we used the non-parametric paired samples Wilcoxon test to compare the average individual LDs of each member of a pair or the within- versus between-individual LDs because, with such a small sample size, the Mantel test is not recommended (Legendre & Fortin, 1989). Only for the Wilcoxon test, the group in which the male changed was entered twice, considering the two pairs as different groups. We obtained a lower number of male contributions because the reproductive females also engaged in duets with immature male offspring (N = 23).

Results

We analyzed 261 individual contributions consisting of a total of 2018 phrases. We obtained 77 ± 21 (mean ± standard deviation) phrases per male and 78 ± 23 phrases per female. We found that average phrase duration was 1.285 s (range: 0.380 - 3.000 s). The number of phrases in the individual song ranged between 2 and 27.

We found a significant difference between the LDs calculated for males and females, where females showed higher average individual means than males (Mantel test: r = 0.167, P = 0.002; Fig. 2). In all groups, the females had higher LDs (LD = 6.497 + 1.674) than males (LD = 3.946 + 0.814), showing that female contribution to the song was less stereotyped (Fig. 3, Wilcoxon paired test: V = 0, df = 7; P = 0.008). It is noticeable that the individuals Eva, which sang with three different males and had a high number of recordings (N=39), showed remarkable differences compared to other females. Both females and males showed a higher variability at between-individuals ($LD_{females}$ = 7.386 + 0.709, LD_{males} = 4.885 + 0.325) than within-individual level (Fig. 3), except for the females of groups 4 and 8. Overall, we found a significant difference between within- and between-individual LDs (Wilcoxon paired test: V = 0, df = 7; P = 0.008).

Discussion

We examined differences in the order of phrases emitted during the songs by reproductive male and female indris living in the same population. We hypothesized that female contributions to the song may function differently in phrase concatenation from those of males. We found support for our predictions. The phrase structure of songs indeed differed between males and females, and female contributions were less stereotyped than those of males. The LDs showed that the between-individual stereotypy of male contributions was higher than females' one. Males, therefore, appeared to produce songs that are overall more similar to those of other males. In agreement with previous studies that reported sexual dimorphism in the overall timing and repertoire size (Giacoma et al., 2010), and in the frequency modulation, duration and rhythm (Gamba et al., 2016; Torti et al., 2017, De Gregorio et al., 2018), we found that male and female indris also differed in the phrase organization of their songs. Female structuring of the song showed a higher number of phrases if compared to males, independently of the phrases being of the same or different type. This result is in line with previous studies on family-living and pair-bonded primate and bird species (Deputte, 1982; Savage, Snowdon, Giraldo & Soto, 1996; Snowdon, 2017; Riebel et al., 2019; Levin, 1996a; 1996b), endorsing that in a socially monogamous, monomorphic species which holds year-round territories, sex differences in vocal output are frequent (Marshall & Marshall, 1976). Furthermore, despite the fact that songs are considered to be males' peculiar features (Cowlishaw, 1996), our results confirm that also monogamous females use songs and that female song can be more elaborate than those of males. Female song phrase concatenation is more complex than males' because even if males are playing the primary role in territorial defense, females' role in territorial disputes can be essential. Female songs may be critical for advertising their identity as well as resources holding potential. For instance, vocal fights, in which females and males are singing together, are often sufficient to resolve group encounters, reducing the occurrence of physical fights (Bonadonna et al., 2020). Future studies may investigate whether female dispersal distance and territorial changes over the years may contribute to a deeper understanding of this sex-dimorphic variation. Expanding previous findings that showed how indri female contribution to the song was more varied in the rhythm (De Gregorio et al., 2018), we showed that the combination and repertoire of the phrases are also more extensive than those shown by males. Females not only have a broader repertoire of units, but they also emit descending phrases that we did not observe in males (e.g., descending phrases of six units). Considering those previous findings, our results may suggest that the differences in song structuring could be used to convey information about the sex and the status of the singers that can be assessed at a distance by conspecifics.

In agreement with previous findings on the different role of males and females during the song (Giacoma et al., 2010), we found that female song is potentially more distinctive than the male one. These results are in agreement with previous findings on birds (Brown & Farabaugh, 1991), confirming that in those species in which females are involved in territorial defense, their repertoires are as large or larger than those of males, on the level of both units and phrases. Territorial defense is crucial for survival and reproduction in pair-bonding species that occupy stable territories, and even if female involvement in territorial defense is different from that of the reproductive male, they participate in joining with their partner. An increasing body of literature (e.g., Hall, Rittenbach, & Vehrencamp, 2015) supported the view that same-sex competition is the primary driver of female song elaboration. It can be the case of the indris, where females may benefit from multiple mating partners to increase tolerance by neighboring males (Bonadonna et al., 2014). As mentioned above, females can advertise the occupancy of an area as well as their quality and resource-holding potential. In support of the higher variability in female song structure, there is also the recent evidence that genetic relatedness may play a critical role in determining the characteristics of DPs in males, whereas it may have a lesser impact on female songs (Torti et al., 2017). A more variable song structure may add up to a more flexible structuring of the phrase notes, but further investigations are needed.

This work also expands on and complements previous studies on humpback whales (Helweg et al., 1998; Tougaard & Eriksen, 2006; Garland et al., 2012), showing that the Levenshtein distance is simple, efficiently computable and highly applicable to any behavioral data that are produced in a sequence. Our results confirmed that the Levenshtein distance method is a simple but powerful technique that can be applied to assess stereotypy or divergence between sexes.

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Figure legend:

Figure 1: *Spectrographic and schematic representation of an indri song.* Spectrograms of an indri song (a) showing a typical sequence of units given by one male and one female. Schematic representation of the fundamental frequency of the descending phrase units given by one male (b) and one female (c). Box fill patterns denote the phrase type: black boxes mark single units (SU), horizontal lines boxes mark DP2, diagonal lines boxes mark DP3, wavy lines boxes mark DP4, and checkered boxes mark DP5. The spectrograms were generated in Praat with the following parameters: window length: 0.05 s; dynamic range: 50 dB; frequency range: 0 to 10.000 Hz (a), 0 to 3.000 Hz (b,c).

Figure 2: The Levenshtein Distances showing song structuring in male and female indris of the studied groups. Individuals are shown on the vertical axis; sexes are shown on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker and bigger the dots, the higher are the distances between the individual contributions to the song. This plot was generated using the R package *corrplot* (vers. 0.84; Wei & Simko, 2017).

Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight studied groups. Bar plot describing the individual and overall degree of stereotypy and variability expressed by the average Levenshtein Distances (LDs). Within-individual LDs are reported for females (white bars) and males (black bars), as well as between-individual LDs (grey bars for females, striped bars for males). Group 3 is reported twice because the male of the reproductive pairs changed in 2014. Capped lines represent Standard Deviation.