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Manuscripts

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

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3   **Running title: Phrase organization in the indris**

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35 **Abstract**

37 Animal acoustic communication often takes the form of complex sequences, composed

38 of multiple distinct acoustic units, which can vary in their degree of stereotypy. Studies

39 of sequence variation may contribute to our understanding of the structural flexibility of

40 primates' songs, which can provide essential ecological and behavioral information about

41 variability at the individual, population, and specific level and provide insights into the

42 mechanisms and drivers responsible for the evolutionary change of communicative traits.

43 We studied intra and inter-individual variation in the song structuring of a singing

44 primate, the indri (*Indri indri*). Indri groups emit duets and choruses in which they

45 combine long notes, short single units, and phrases consisting of a variable number of

46 units (from two to six) with slightly descending frequency. Males' and females'

47 contributions to the song differ in the temporal and frequency structure of song units and

48 repertoire size. We calculated the similarity of phrase organization across different

49 individual contributions using the Levenshtein distance, a logic distance that expressed

50 the minimum cost to convert a sequence into another and can measure differences

51 between two sequences of data. We then analyzed the degree of similarity within and

52 between individuals and found that: i) the phrase structure of songs varied between

53 reproductive males and females: female structuring of the song showed a higher number

54 of phrases if compared to males; ii) Male contributions to the song were overall more

55 similar to those of other males than were female contributions to the song of other

56 females; iii) male contributions were more stereotyped than female contributions, which

57 showed greater individual flexibility. The picture emerging from phrase combinatorics in

58 the indris is in agreement with previous findings of rhythmic features and song repertoire

59 size of the indris, which also suggested that female songs are potentially less stereotyped

60 than those of males.

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65 **Research Highlights**

66 ● This study demonstrated that male and female adult indris differed in the phrase

67 organization of their songs.

68 ● Male contributions to the song were overall more similar to those of other males

69 and more stereotyped than females' ones.

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71 **Graphical Abstract**

72 Figure 2 works as graphical abstract for this manuscript.

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78 **Introduction**

79   Communication between conspecifics often involves the use of vocalizations because

80   acoustic signals allow encoding a considerable amount of information in a short time

81   (Bradbury & Vehrencamp, 2011). Animal vocal signals can be emitted in the form of

82   short vocalizations or given in sequences of variable length (Catchpole & Slater, 2008).

83   In addition to the well-known example of birdsong, other animals such as insects,

84   amphibians, and mammals (including bats, rodents, primates, and cetaceans) also emit

85   complex acoustic sequences (Kershenbaum et al., 2016). Although animals showed a

86   limited ability to concatenate vocal emissions in phrases when compared to humans

87   (Berwick, Okanoya, Beckers & Bolhuis, 2011), their vocal sequences may contain

88   information on species and individual identity (e.g., starlings (*Sturnus vulgaris*), wolves

89   (*Canis lupus*), dolphins (*Tursiops truncatus*), and rock hyraxes (*Procavia capensis*)).

90   Animal vocal sequences may also encode information about external cues such as

91   resource availability, e.g., food calls in chimpanzees (*Pan troglodytes*), or predator threats

92   in marmots (*Marmota* spp.; Kershenbaum et al., 2016).

93   The understanding of the role played by the acoustic sequences in a particular species'

94   repertoire often involves the comparison of sequences within and between individuals, as

95   well as within and between groups, so that it is possible to quantify the nature of the

96   variation and potentially correlate it to ecological and behavioral factors (Kershenbaum

97   et al., 2014).

98   So far, the studies of primate call organization focused on contact calls or alarm calls

99   (Clarke, Reichard & Zuberbühler, 2006) with scarce investigations of song structure

100 variation within contexts (Torti, Gamba, Rabemananjara & Giacoma, 2013). There is a

101 lack of information about whether primate males and females combine units in songs

102 using different phrase combinations. It is essential to examine the sex-dimorphic traits of

103   primate songs because knowledge of sex differences in song organization may be critical

104   in our understanding of what is biologically informative, especially in sexually

105   monomorphic species. Moreover, information available on the variability within a species

106   is very little (Honda & Okanoya, 1999; Takahasi, Yamada & Okanoya, 2010). Few

107   investigations on primate vocal sequences are currently available and none of them are

108   evaluating the stereotypy of song structure between sexes using a string metric (Gustison,

109   Semple, Ferrer-i-Cancho & Bergman, 2016). While traditional methods may not apply to

110   a wide array of questions, string metrics can be used to investigate different organizational

111   levels, are entirely objective, and their results are verifiable (Heeringa, 2004).

112   Indris (*Indri indri*, Gmelin, 1788) represent a distinctive species for studying vocal

113   communication because of their rich repertoire (Maretti, Sorrentino, Finomana, Gamba

114   & Giacoma, 2010; Valente et al., 2019) and the impressive loud songs, unique among

115   lemurs (Gamba et al., 2016; Torti et al., 2017), which can be heard at a distance up to 2

116   km (Pollock, 1986). Data on sound pressure levels revealed that the sound levels of the

117   indri's song reached 110 dB (estimated at 0.50 m; Torti, *pers. obs.*). This level can be

118   compared to ring-tailed lemurs (*Lemur catta*), which showed a call amplitude ranging

119   between 85 and 89 dB (at 1 m, Macedonia, 1993). The song of the indris, which lasts 40-

120   250 s, consists of a long series of modulated units, organized in phrases (Gamba, Favaro,

121   Torti, Sorrentino & Giacoma, 2011), uttered simultaneously by males and females,

122   including juveniles, of the same group (Maretti et al., 2010). These types of units are

123   emitted exclusively during the song (Valente et al., 2019).

124   Previous research showed that the indris can emit songs in different contexts and that the

125   song can elicit different behaviors depending on its acoustic structure. Songs given in

126   different contexts showed differences in their temporal structure that are distinguishable

127   by visual inspection of the spectrograms and by ear (Torti et al. 2013). Cohesion songs

128   were emitted when the individuals of a group were dispersed in their territory, while

129   advertisement songs were usually given when the animals of the same group were in

130   visual contact at the boundary of their territory (Torti et al., 2013). Cohesion songs were

131   followed by emitters traveling significantly further than following the advertisement

132   song, confirming the different functions of the song uttered in different contexts (i.e.,

133   cohesion songs bring together the members of a group, and advertisement songs inform

134   neighbors about the sex, age, and status of singing individuals). Other studies have shown

135   that male and female contributions to the song differ, both quantitatively and

136   qualitatively, in the temporal structure of the units emitted (Giacoma, Sorrentino,

137   Rabarivola & Gamba, 2010; Sorrentino, Gamba & Giacoma, 2012). Vocal sexual

138   dimorphism is also present in the modulation of the frequency of vocal utterances, in the

139   duration of unit types and the rhythmic structure of a contribution (Gamba et al., 2016;

140   De Gregorio et al., 2018).

141   Since the indris' songs can be interpreted as a string of easily identifiable phrases (Gamba

142   et al., 2016), they represent an ideal case for the study of the variability of phrase

143   concatenation in primate songs. Among the methods for investigating different levels of

144   structural variation in acoustic displays, we chose the Levenshtein distance, which is a

145   quantitative method for measuring the similarity of sequences (hereafter LD; Margoliash,

146   Staicer & Inoue, 1991). The LD is a logical distance commonly used to quantify the

147   difference between two strings of data (e.g., human words, sequences of visual

148   movements or sequences of song themes; Gooskens & Heeringa, 2004). This technique

149   has often been used to measure similarity in human dialects (Wieling, Montemagni,

150   Nerbonne & Baayen, 2014), and it has been applied to animal vocal sequences, but for a

151   very limited number of species (Indigo bunting, *Passerina cyanea*, Margoliash et al.,

152   1991; Willow warbler, *Phylloscopus trochilus*, Gil & Slater, 2000; Humpback whale,

153   *Megaptera novaeangliae*: Helweg, Cato, Jenkins, Garrigue & McCauley, 1998; Tougaard

154   & Eriksen, 2006; Garland et al., 2012).

155   Although songs are often referred to as a male's prerogative, we have particular insights

156   showing that monogamous females may also use the song overlapping male song

157   functions (e.g., Eastern whip bird (*Psophodes olivaceus*), Rogers, Langmore, & Mulder,

158   2007; Levin, 1996a; 1996b). Females may use songs for mate attraction (Rogers et al.,

159   2007), and they may even show a more elaborated song repertoire (Australian magpies

160   (*Gymnorhina tibice* Brown & Farabaugh, 1991). Like Eastern whip birds and Australian

161   magpies, indris are monogamous (Torti et al., 2017; Bonadonna et al., 2019), form groups

162   that occupy non-overlapping areas in the forest (Bonadonna et al., 2017), and use the

163   songs to inform neighboring groups about the occupation of a territory and to actively

164   defend resources during group encounters (Torti et al., 2013). Thus, we hypothesized that

165   the female contribution to the song would be structurally different from that of males.

166   Studies of song structure in bird duets also suggested that females' songs would be more

167   acoustically variable than that of males (Logue & Gammon, 2004), in line with the

168   territorial model of bird duet evolution (Farabaugh, 1982). In birds, duetting occurs most

169   commonly where birds hold year-round territories, and it is associated with sexually

170   monomorphic species that form long-term monogamous pair bonds (Riebel, Odom,

171   Langmore & Hall, 2019). Indri females showed significantly higher variation in the

172   rhythm of their contributions to the song and a higher potential to synchronize with males

173   (De Gregorio et al., 2018). Thus, we hypothesized that the adjustment in the rhythmic

174   structure of their contribution would also be reflected in a sexually dimorphic phrases

175   combination, where one should expect males to produce songs with a more stereotyped

176   structure. Similarly to pair living bird species (Rogers et al., 2007), indri females may use

177   songs for mate guarding and attraction, and song structural variability and complexity

178   may have evolved to provide conspecifics with information on females' fitness and

179   survival.

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183   **Methods**

184   **Observations and recordings**

185   We studied 8 groups (N= 36 individuals) living in the Maromizaha Forest (18°56'49"S,

186   48°27'53"E). We recorded the animals between 2011 and 2017. We observed one social

187   group per week, from Monday to Friday approximately from 6 AM to 1 PM, when the

188   animals usually start resting and sleeping until the day after (Pollock, 1975). All

189   recordings were carried out without the use of playback stimuli, and nothing was done to

190   modify the behavior of the indris. We recorded 142 songs, consisting of duets and

191   choruses with a maximum of five individuals singing in the same song. For the analysis,

192   we only considered the contribution of the reproductive individuals, for a total of 17 focal

193   animals from eight social groups: nine reproductive adult males, and eight reproductive

194   adult females. An example of an indri song and the singers' contributions is shown in

195   Figure 1. The different number of males and females is motivated by the fact that, during

196   the study period, the reproductive male of a group changed. All the songs were recorded

197   using solid-state recorders (Olympus LS05, Tascam DR-100, Tascam DR-05) with a

198   sampling rate of 44.1 kHz (16-bit depth) during all the recording sessions. When

199   recording the songs, we were always at a distance between 2 and 20 m from the animals,

200   with the microphone oriented toward the focal singing individuals. We always kept visual

201   contact with the vocalizing animals and maximized our efforts to face the focal animals

202   during the emission of the song. Since indri songs emitted in different contexts have

203   different acoustic structure, in order to avoid any bias due to these differences, we

204   considered, from multiple years, only those songs that were labeled as advertisement

205   songs and were recorded in the same context (Torti et al., 2013). Using the focal animal

206   sampling technique (Altmann, 1974), we were able to attribute each vocalization to its

207   signaler. We will refer to every individual uttered portion within a song or a chorus as an

208   'individual contribution'.

209   During this study, we did not have any physical contact with the animals, and we recorded

210   only spontaneously emitted songs. We have received permits for this research, each year,

211   from "Direction des Eaux et Forêts" and "Madagascar National Parks": 2011 - N°

212   274/11/MEF/SG/D GF/DCB.SAP/SCB, 2012 N°245/12/MEF/SG/DGF/DCB.SAP/SCB,

213   2014 - N°066/14/MEF/SG/DGF/DCB.SAP/SCB, 2015 - N° 180/ 15/ MEEMF/ SG/ DGF/

214   DAPT/ SCBT; 2016 - N° 98/ 16/ MEEMF/ SG/ DGF/ DAPT/ SCB.Re and N° 217/

215   16/MEEMF/ SG/ DGF/ DSAP/ SCB.Re, 2017 - 73/17/MEEF/SG/DGF/DSAP/SCB.RE.

216   The data collection in 2013 did not require a permit because performed by our Malagasy

217   collaborators only.

218   We adhered to applicable international, national, and/or institutional guidelines for the

219   study on animals and nonhuman primates, including the American Society of

220   Primatologist (ASP) Principle for the Ethical Treatment of nonhuman Primates, and the

221   European Union directive guidelines for the study on animals and nonhuman primates

222   (Directive 2010/63/EU). The study did not require IACUC approval.

223   **Acoustic and statistical analyses**

224   We edited segments containing indri songs using Praat 6.0.30 (Boersma & Weenink

225   2008) and BORIS 5.1 (Friard & Gamba 2016). For each recorded song, we created a

226   spectrogram with a view range between 0 and 5000 Hz, a window length of 0.09 s, and a

227   dynamic range of 65.0 dB. We saved each song in a single audio file in WAV format

228   (Waveform audio file format). We saved the information related to the identity of each

229   singer in a Praat textgrid. We then labeled all the vocal units (each single sound

230   constituting the modulated part of the song; Thalmann, Geissmann, Simona & Mutschler,

231   1993) according to their belonging to a song portion (long notes or descending phrases,

232   see Torti et al., 2013 for details) and to a descending phrase (hereafter, DP; see Torti et

233   al., 2017 for details). Songs given in different contexts showed differences in their

234   temporal structure that are distinguishable by visual inspection of the spectrograms and

235   by ear (Torti et al. 2013). We considered phrases consisting of two (DP2), three (DP3),

236   four (DP4), five (DP5), and six (DP6) units. This information was saved in Praat and

237   exported to a Microsoft© Excel spreadsheet (Gamba, Friard & Giacoma, 2012). Since all

238   the steps of the labeling process have been done by a single operator (A.Z.), we avoided

239   the possibility of encountering errors due to observer differences. To understand whether

240   there were differences in song structure between sexes, we investigated the DPs similarity

241   in each contribution. We transformed each contribution in a string of labels separated by

242   a break symbol (e.g., DP2|DP3|DP4|DP3). The resulting string represents the

243   concatenation of the phrases uttered within a contribution (and it is a measure of phrase

244   organization). From the 142 songs, we obtained 142 strings for females (with an average

245   of 17.88 songs per individual, SD = 5.44), and 119 strings for males (with an average of

246   13.22 songs per individual, SD = 5.91). Using R (R Core Team, 2015; version 3.3.3), we

247   calculated   the   Levenshtein   distance   (LD)   for   each   pair   of   strings

248   (package *stringdist* 0.9.4.2 in R; van der Loo, 2014) because this methodology provides

249   a robust quantitative approach for the study of animal acoustic sequences (Kershenbaum

250   & Garland, 2015). The distance calculates the minimum number of necessary changes

251   (insertions, deletions, and substitutions) to transform one string into another (Kohonen,

252   1985). We obtained a squared matrix consisting of the distances between each pair of

253   strings, then averaged LDs and calculated within- and between-individual means (Fig. 2),

254   to investigate whether females and males differed in their degree of variation. For this

255   purpose, we ran Mantel tests (9999 randomizations) using a matrix featuring the average

256   individual means against a model matrix consisting of 0 when the corresponding

257   individuals were of the same sex (Krull et al., 2012), and 1 when they were opposite sexes

258   (package *vegan* in R; Oksanen et al., 2013). When investigating differences at the group

259   level or within-sex, we used the non-parametric paired samples Wilcoxon test to compare

260   the average individual LDs of each member of a pair or the within- versus between-

261   individual LDs because, with such a small sample size, the Mantel test is not

262   recommended (Legendre & Fortin, 1989). Only for the Wilcoxon test, the group in which

263   the male changed was entered twice, considering the two pairs as different groups. We

264   obtained a lower number of male contributions because the reproductive females also

265   engaged in duets with immature male offspring (N = 23).

266

267 **Results**

268 We analyzed 261 individual contributions consisting of a total of 2018 phrases. We

269 obtained 77 ± 21 (mean $\pm$ standard deviation) phrases per male and 78 ± 23 phrases per

270 female. We found that average phrase duration was 1.285 s (range: 0.380 - 3.000 s). The

271 number of phrases in the individual song ranged between 2 and 27.

272 We found a significant difference between the LDs calculated for males and females,

273 where females showed higher average individual means than males (Mantel test: r =

274 0.167, P = 0.002; Fig. 2). In all groups, the females had higher LDs (LD = 6.497 + 1.674)

275 than males (LD = 3.946 + 0.814), showing that female contribution to the song was less

276 stereotyped (Fig. 3, Wilcoxon paired test: V = 0, df = 7; P = 0.008). It is noticeable that

277 the individuals Eva, which sang with three different males and had a high number of

278 recordings (N=39), showed remarkable differences compared to other females. Both

279 females and males showed a higher variability at between-individuals ($LD_{females}$ = 7.386

280 + 0.709, LD_{males} = 4.885 + 0.325) than within-individual level (Fig. 3), except for the

281 females of groups 4 and 8. Overall, we found a significant difference between within- and

282 between-individual LDs (Wilcoxon paired test: V = 0, df = 7; P = 0.008).

283 **Discussion**

284 We examined differences in the order of phrases emitted during the songs by reproductive

285 male and female indris living in the same population. We hypothesized that female

286 contributions to the song may function differently in phrase concatenation from those of

287 males. We found support for our predictions. The phrase structure of songs indeed

288 differed between males and females, and female contributions were less stereotyped than

289   those of males. The LDs showed that the between-individual stereotypy of male

290   contributions was higher than females' one. Males, therefore, appeared to produce songs

291   that are overall more similar to those of other males. In agreement with previous studies

292   that reported sexual dimorphism in the overall timing and repertoire size (Giacoma et al.,

293   2010), and in the frequency modulation, duration and rhythm (Gamba et al., 2016; Torti

294   et al., 2017, De Gregorio et al., 2018), we found that male and female indris also differed

295   in the phrase organization of their songs. Female structuring of the song showed a higher

296   number of phrases if compared to males, independently of the phrases being of the same

297   or different type. This result is in line with previous studies on family-living and pair-

298   bonded primate and bird species (Deputte, 1982; Savage, Snowdon, Giraldo & Soto,

299   1996; Snowdon, 2017; Riebel et al., 2019; Levin, 1996a; 1996b), endorsing that in a

300   socially monogamous, monomorphic species which holds year-round territories, sex

301   differences in vocal output are frequent (Marshall & Marshall, 1976). Furthermore,

302   despite the fact that songs are considered to be males' peculiar features (Cowlishaw,

303   1996), our results confirm that also monogamous females use songs and that female song

304   can be more elaborate than those of males. Female song phrase concatenation is more

305   complex than males' because even if males are playing the primary role in territorial

306   defense, females' role in territorial disputes can be essential. Female songs may be critical

307   for advertising their identity as well as resources holding potential. For instance, vocal

308   fights, in which females and males are singing together, are often sufficient to resolve

309   group encounters, reducing the occurrence of physical fights (Bonadonna et al., 2020).

310   Future studies may investigate whether female dispersal distance and territorial changes

311   over the years may contribute to a deeper understanding of this sex-dimorphic variation.

312   Expanding previous findings that showed how indri female contribution to the song was

313   more varied in the rhythm (De Gregorio et al., 2018), we showed that the combination

314   and repertoire of the phrases are also more extensive than those shown by males. Females

315   not only have a broader repertoire of units, but they also emit descending phrases that we

316   did not observe in males (e.g., descending phrases of six units). Considering those

317   previous findings, our results may suggest that the differences in song structuring could

318   be used to convey information about the sex and the status of the singers that can be

319   assessed at a distance by conspecifics.

320   In agreement with previous findings on the different role of males and females during the

321   song (Giacoma et al., 2010), we found that female song is potentially more distinctive

322   than the male one. These results are in agreement with previous findings on birds (Brown

323   & Farabaugh, 1991), confirming that in those species in which females are involved in

324   territorial defense, their repertoires are as large or larger than those of males, on the level

325   of both units and phrases. Territorial defense is crucial for survival and reproduction in

326   pair-bonding species that occupy stable territories, and even if female involvement in

327   territorial defense is different from that of the reproductive male, they participate in

328   joining with their partner. An increasing body of literature (e.g., Hall, Rittenbach, &

329   Vehrencamp, 2015) supported the view that same-sex competition is the primary driver

330   of female song elaboration. It can be the case of the indris, where females may benefit

331   from multiple mating partners to increase tolerance by neighboring males (Bonadonna et

332   al., 2014). As mentioned above, females can advertise the occupancy of an area as well

333   as their quality and resource-holding potential. In support of the higher variability in

334   female song structure, there is also the recent evidence that genetic relatedness may play

335   a critical role in determining the characteristics of DPs in males, whereas it may have a

336   lesser impact on female songs (Torti et al., 2017). A more variable song structure may

337 add up to a more flexible structuring of the phrase notes, but further investigations are

338 needed.

339 This work also expands on and complements previous studies on humpback whales

340 (Helweg et al., 1998; Tougaard & Eriksen, 2006; Garland et al., 2012), showing that the

341 Levenshtein distance is simple, efficiently computable and highly applicable to any

342 behavioral data that are produced in a sequence. Our results confirmed that the

343 Levenshtein distance method is a simple but powerful technique that can be applied to

344 assess stereotypy or divergence between sexes.

345

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541   **Figure legend:**

542   *Figure 1*: *Spectrographic and schematic representation of an indri song.* Spectrograms

543   of an indri song (a) showing a typical sequence of units given by one male and one

544   female. Schematic representation of the fundamental frequency of the descending

545   phrase units given by one male (b) and one female (c). Box fill patterns denote the

546   phrase type: black boxes mark single units (SU), horizontal lines boxes mark DP2,

547   diagonal lines boxes mark DP3, wavy lines boxes mark DP4, and checkered boxes mark

548   DP5. The spectrograms were generated in Praat with the following parameters: window

549   length: 0.05 s; dynamic range: 50 dB; frequency range: 0 to 10.000 Hz (a), 0 to 3.000

550   Hz (b,c).

551   *Figure 2: The Levenshtein Distances showing song structuring in male and female*

552   *indris of the studied groups.* Individuals are shown on the vertical axis; sexes are shown

553   on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker

554   and bigger the dots, the higher are the distances between the individual contributions to

555   the song. This plot was generated using the R package *corrplot* (vers. 0.84; Wei &

556   Simko, 2017).

557   *Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight*

558   *studied groups.* Bar plot describing the individual and overall degree of stereotypy and

559   variability expressed by the average Levenshtein Distances (LDs). Within-individual

560   LDs are reported for females (white bars) and males (black bars), as well as between-

561   individual LDs (grey bars for females, striped bars for males). Group 3 is reported twice

562   because the male of the reproductive pairs changed in 2014. Capped lines represent

563   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

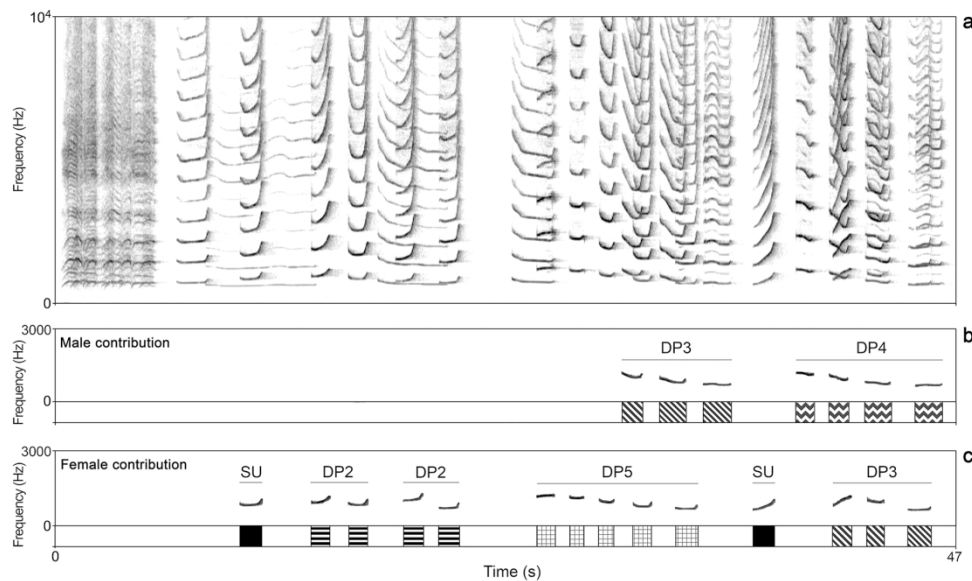males and more stereotyped than females' ones.

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).
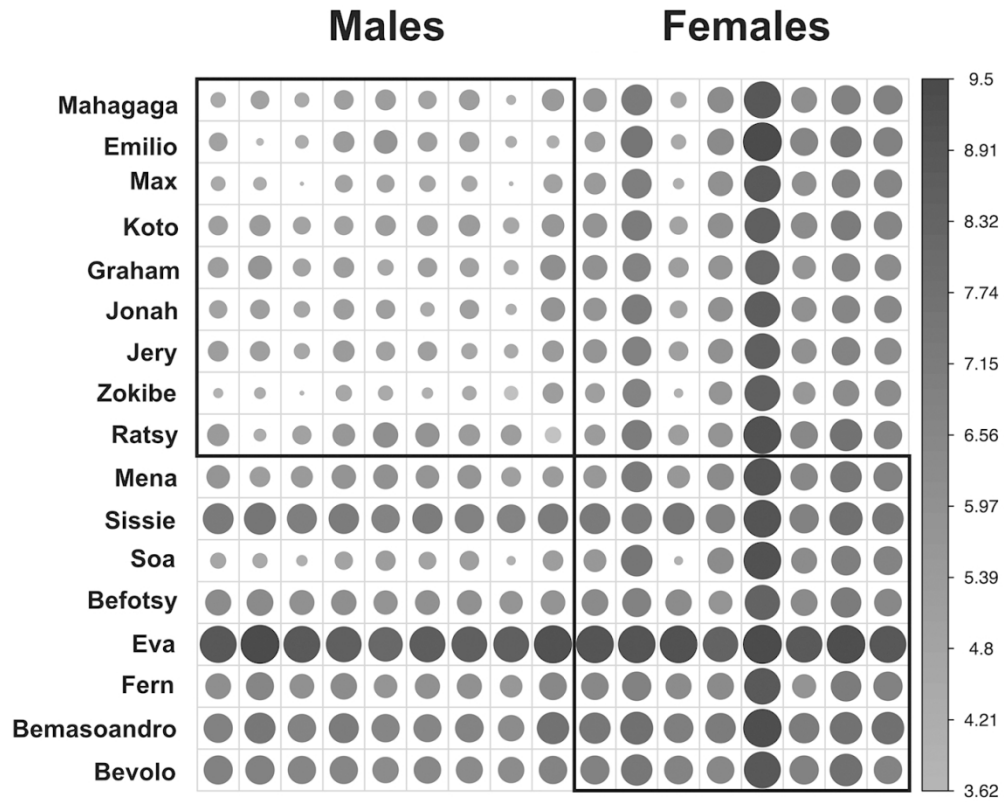
Figure 2: The Levenshtein Distances showing song structuring in male and female indris of the studied groups. Individuals are shown on the vertical axis; sexes are shown on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker and bigger the dots, the higher are the distances between the individual contributions to the song. This plot was generated using the R package corrplot (vers. 0.84; Wei & Simko, 2017).
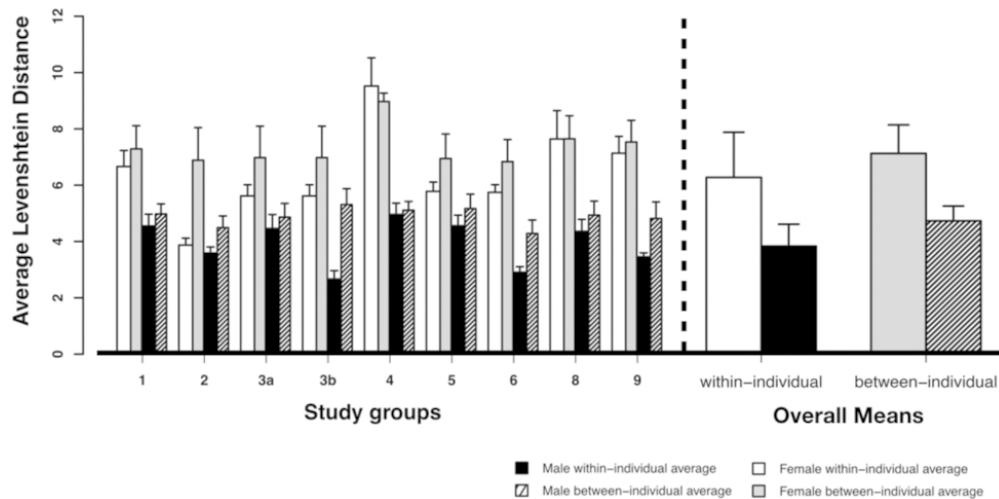
Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight studied groups. Bar plot describing the individual and overall degree of stereotypy and variability expressed by the average Levenshtein Distances (LDs). Within-individual LDs are reported for females (white bars) and 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.

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

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3 **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

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60 the indris is in agreement with previous findings of rhythmic features and song repertoire

61 size <mark>of the indris</mark>, which also suggested that female songs are potentially <mark>less stereotyped</mark>

62 than those of males.

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

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Research Highlights

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67 ● This study demonstrated that male and female adult indris differed in the phrase

68 organization of their songs.

69 ● Male contributions to the song were overall more similar to those of other males

70 and more stereotyped than females' ones.

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72 **Graphical Abstract**

73 Figure 2 works as graphical abstract for this manuscript.

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80   **Introduction**

81   Communication between conspecifics often involves the use of vocalizations because

82   acoustic signals allow encoding a considerable amount of information in a short time

83   (Bradbury & Vehrencamp, 2011). Animal vocal signals can be emitted in the form of

84   short vocalizations or given in sequences of variable length (Catchpole & Slater, 2008).

85   In addition to the well-known example of birdsong, other animals such as insects,

86   amphibians, and mammals (including bats, rodents, primates, and cetaceans) also emit

87   complex acoustic sequences (Kershenbaum et al., 2016). Although animals showed a

88   limited ability to concatenate vocal emissions in phrases when compared to humans

89   (Berwick, Okanoya, Beckers & Bolhuis, 2011), their vocal sequences may contain

90   information on species and individual identity (e.g., starlings (*Sturnus vulgaris*), wolves

91   (*Canis lupus*), dolphins (*Tursiops truncatus*), and rock hyraxes (*Procavia capensis*)).

92   Animal vocal sequences may also encode information about external cues such as

93   resource availability, e.g., food calls in chimpanzees (*Pan troglodytes*), or predator threats

94   in marmots (*Marmota* spp.; Kershenbaum et al., 2016).

95   The understanding of the role played by the acoustic sequences in a particular species'

96   repertoire often involves the comparison of sequences within and between individuals, as

97   well as within and between groups, so that it is possible to quantify the nature of the

98   variation and potentially correlate it to ecological and behavioral factors (Kershenbaum

99   et al., 2014).

100 So far, the studies of primate call organization focused on contact calls or alarm calls

101 (Clarke, Reichard & Zuberbühler, 2006) with scarce investigations of song structure

102 variation within contexts (Torti, Gamba, Rabemananjara & Giacoma, 2013). There is a

103 lack of information about whether primate males and females combine units in songs

104   using different phrase combinations. It is essential to examine the sex-dimorphic traits of

105   primate songs because knowledge of sex differences in song organization may be critical

106   in our understanding of what is biologically informative, especially in sexually

107   monomorphic species. Moreover, information available on the variability within a species

108   is very little (Honda & Okanoya, 1999; Takahasi, Yamada & Okanoya, 2010). Few

109   investigations on primate vocal sequences are currently available and none of them are

110   evaluating the stereotypy of song structure between sexes using a string metric (Gustison,

111   Semple, Ferrer-i-Cancho & Bergman, 2016). While traditional methods may not apply to

112   a wide array of questions, string metrics can be used to investigate different organizational

113   levels, are entirely objective, and their results are verifiable (Heeringa, 2004).

114   Indris (*Indri indri*, Gmelin, 1788) represent a distinctive species for studying vocal

115   communication because of their rich repertoire (Maretti, Sorrentino, Finomana, Gamba

116   & Giacoma, 2010; Valente et al., 2019) and the impressive loud songs, unique among

117   lemurs (Gamba et al., 2016; Torti et al., 2017), which can be heard at a distance up to 2

118   km (Pollock, 1986). Data on sound pressure levels revealed that the sound levels of the

119   indri's song reached 110 dB (estimated at 0.50 m; Torti, *pers. obs.*). This level can be

120   compared to ring-tailed lemurs (*Lemur catta*), which showed a call amplitude ranging

121   between 85 and 89 dB (at 1 m, Macedonia, 1993). The song of the indris, which lasts 40-

122   250 s, consists of a long series of modulated units, organized in phrases (Gamba, Favaro,

123   Torti, Sorrentino & Giacoma, 2011), uttered simultaneously by males and females,

124   including juveniles, of the same group (Maretti et al., 2010). These types of units are

125   emitted exclusively during the song (Valente et al., 2019).

126   Previous research showed that the indris can emit songs in different contexts and that the

127   song can elicit different behaviors depending on its acoustic structure. Songs given in

128   <mark>different contexts showed differences in their temporal structure that are distinguishable</mark>

129   <mark>by visual inspection of the spectrograms and by ear (Torti et al. 2013).</mark> Cohesion songs

130   were emitted when the individuals of a group were dispersed in their territory, while

131   advertisement songs were usually given when the animals of the same group were in

132   visual contact at the boundary of their territory (Torti et al., 2013). Cohesion songs were

133   followed by emitters traveling significantly further than following the advertisement

134   song, confirming the different functions of the song uttered in different contexts (i.e.,

135   cohesion songs bring together the members of a group, and advertisement songs inform

136   neighbors about the sex, age, and status of singing individuals). Other studies have shown

137   that male and female contributions to the song differ, both quantitatively and

138   qualitatively, in the temporal structure of the units emitted (Giacoma, Sorrentino,

139   Rabarivola & Gamba, 2010; Sorrentino, Gamba & Giacoma, 2012). <mark>Vocal sexual</mark>

140   <mark>dimorphism</mark> is also present in the modulation of the frequency of vocal utterances, in the

141   duration of unit types and the rhythmic structure of a contribution (Gamba et al., 2016;

142   De Gregorio et al., 2018).

143   Since the indris' songs can be interpreted as a string of easily identifiable phrases (Gamba

144   et al., 2016), they represent an ideal case for the study of the variability of phrase

145   concatenation in primate songs. Among the methods for investigating different levels of

146   <mark>structural variation</mark> in acoustic displays, we chose the Levenshtein distance, which is a

147   quantitative method for measuring the similarity of sequences (hereafter LD; Margoliash,

148   Staicer & Inoue, 1991). The LD is a logical distance commonly used to quantify the

149   difference between two strings of data (e.g., human words, sequences of visual

150   movements or sequences of song themes; Gooskens & Heeringa, 2004). This technique

151   has often been used to measure similarity in human dialects (Wieling, Montemagni,

152   Nerbonne & Baayen, 2014), and it has been applied to animal vocal sequences, but for a

153   very limited number of species (Indigo bunting, *Passerina cyanea*, Margoliash et al.,

154   1991; Willow warbler, *Phylloscopus trochilus*, Gil & Slater, 2000; Humpback whale,

155   *Megaptera novaeangliae*: Helweg, Cato, Jenkins, Garrigue & McCauley, 1998; Tougaard

156   & Eriksen, 2006; Garland et al., 2012).

157   Although songs are often referred to as a male's prerogative, we have particular insights

158   showing that monogamous females may also use the song overlapping male song

159   functions (e.g., Eastern whip bird (*Psophodes olivaceus*), Rogers, Langmore, & Mulder,

160   2007; Levin, 1996a; 1996b). Females may use songs for mate attraction (Rogers et al.,

161   2007), and they may even show a more elaborated song repertoire (Australian magpies

162   (*Gymnorhina tibice* Brown & Farabaugh, 1991). Like Eastern whip birds and Australian

163   magpies, indris are monogamous (Torti et al., 2017; Bonadonna et al., 2019), form groups

164   that occupy non-overlapping areas in the forest (Bonadonna et al., 2017), and use the

165   songs to inform neighboring groups about the occupation of a territory and to actively

166   defend resources during group encounters (Torti et al., 2013). Thus, we hypothesized that

167   the female contribution to the song would be structurally different from that of males.

168   Studies of song structure in bird duets also suggested that females' songs would be more

169   acoustically variable than that of males (Logue & Gammon, 2004), in line with the

170   territorial model of bird duet evolution (Farabaugh, 1982). In birds, duetting occurs most

171   commonly where birds hold year-round territories, and it is associated with sexually

172   monomorphic species that form long-term monogamous pair bonds (Riebel, Odom,

173   Langmore & Hall, 2019). Indri females showed significantly higher variation in the

174   rhythm of their contributions to the song and a higher potential to synchronize with males

175   (De Gregorio et al., 2018). Thus, we hypothesized that the adjustment in the rhythmic

176   structure of their contribution would also <mark>be reflected</mark> in a sexually dimorphic phrases

177   combination, where one should expect males to produce songs with a more stereotyped

178   structure. <mark>Similarly to pair living bird species (Rogers et al., 2007), indri females may use</mark>

179   <mark>songs for mate guarding and attraction, and song structural variability and complexity</mark>

180   <mark>may have evolved to provide conspecifics with information on females' fitness and</mark>

181   <mark>survival.</mark>

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185   **Methods**

186   **Observations and recordings**

187   We studied 8 groups (N= 36 individuals) living in the Maromizaha Forest (18°56'49"S,

188   48°27'53"E). We recorded the animals between 2011 and 2017. We observed one social

189   group per week, from Monday to Friday approximately from 6 AM to 1 PM, when the

190   animals usually start resting and sleeping until the day after (Pollock, 1975). All

191   recordings were carried out without the use of playback stimuli, and nothing was done to

192   modify the behavior of the indris. We recorded 142 songs, consisting of duets and

193   choruses with a maximum of five individuals singing in the same song. For the analysis,

194   we only considered the contribution of the reproductive individuals, for a total of 17 focal

195   animals from eight social groups: nine reproductive adult males, and eight reproductive

196   adult females. An example of an indri song and the singers' contributions is shown in

197   Figure 1. The different number of males and females is motivated by the fact that, during

198   the study period, the reproductive male of a group changed. All the songs were recorded

199   using solid-state recorders (Olympus LS05, Tascam DR-100, Tascam DR-05) with a

200   sampling rate of 44.1 kHz (16-bit depth) during all the recording sessions. When

201   recording the songs, we were always at a distance between 2 and 20 m from the animals,

202   with the microphone oriented toward the focal singing individuals. We always kept visual

203   contact with the vocalizing animals and maximized our efforts to face the focal animals

204   during the emission of the song. Since indri songs emitted in different contexts have

205   different acoustic structure, in order to avoid any bias due to these differences, we

206   considered, from multiple years, only those songs that were labeled as advertisement

207   songs and were recorded in the same context (Torti et al., 2013). Using the focal animal

208   sampling technique (Altmann, 1974), we were able to attribute each vocalization to its

209   signaler. We will refer to every individual uttered portion within a song or a chorus as an

210   'individual contribution'.

211   During this study, we did not have any physical contact with the animals, and we recorded

212   only spontaneously emitted songs. We have received permits for this research, each year,

213   from "Direction des Eaux et Forêts" and "Madagascar National Parks": 2011 - N°

214   274/11/MEF/SG/D GF/DCB.SAP/SCB, 2012 N°245/12/MEF/SG/DGF/DCB.SAP/SCB,

215   2014 - N°066/14/MEF/SG/DGF/DCB.SAP/SCB, 2015 - N° 180/ 15/ MEEMF/ SG/ DGF/

216   DAPT/ SCBT; 2016 - N° 98/ 16/ MEEMF/ SG/ DGF/ DAPT/ SCB.Re and N° 217/

217   16/MEEMF/ SG/ DGF/ DSAP/ SCB.Re, 2017 - 73/17/MEEF/SG/DGF/DSAP/SCB.RE.

218   The data collection in 2013 did not require a permit because performed by our Malagasy

219   collaborators only.

220   We adhered to applicable international, national, and/or institutional guidelines for the

221   study on animals and nonhuman primates, including the American Society of

222   Primatologist (ASP) Principle for the Ethical Treatment of nonhuman Primates, and the

223   European Union directive guidelines for the study on animals and nonhuman primates

224   (Directive 2010/63/EU). The study did not require IACUC approval.

225   **Acoustic and statistical analyses**

226   We edited segments containing indri songs using Praat 6.0.30 (Boersma & Weenink

227   2008) and BORIS 5.1 (Friard & Gamba 2016). For each recorded song, we created a

228   spectrogram with a view range between 0 and 5000 Hz, a window length of 0.09 s, and a

229   dynamic range of 65.0 dB. We saved each song in a single audio file in WAV format

230   (Waveform audio file format). We saved the information related to the identity of each

231   singer in a Praat textgrid. We then labeled all the vocal units (each single sound

232   constituting the modulated part of the song; Thalmann, Geissmann, Simona & Mutschler,

233   1993) according to their belonging to a song portion (long notes or descending phrases,

234   see Torti et al., 2013 for details) and to a descending phrase (hereafter, DP; see Torti et

235   al., 2017 for details). Songs given in different contexts showed differences in their

236   temporal structure that are distinguishable by visual inspection of the spectrograms and

237   by ear (Torti et al. 2013). We considered phrases consisting of two (DP2), three (DP3),

238   four (DP4), five (DP5), and six (DP6) units. This information was saved in Praat and

239   exported to a Microsoft© Excel spreadsheet (Gamba, Friard & Giacoma, 2012). Since all

240   the steps of the labeling process have been done by a single operator (A.Z.), we avoided

241   the possibility of encountering errors due to observer differences. To understand whether

242   there were differences in song structure between sexes, we investigated the DPs similarity

243   in each contribution. We transformed each contribution in a string of labels separated by

244   a break symbol (e.g., DP2|DP3|DP4|DP3). The resulting string represents the

245   concatenation of the phrases uttered within a contribution (and it is a measure of phrase

246 organization). From the 142 songs, we obtained 142 strings for females (with an average

247 of 17.88 songs per individual, SD = 5.44), and 119 strings for males (with an average of

248 13.22 songs per individual, SD = 5.91). Using R (R Core Team, 2015; version 3.3.3), we

249 calculated   the   Levenshtein   distance   (LD)   for   each   pair   of   strings

250 (package *stringdist* 0.9.4.2 in R; van der Loo, 2014) because this methodology provides

251 a robust quantitative approach for the study of animal acoustic sequences (Kershenbaum

252 & Garland, 2015). The distance calculates the minimum number of necessary changes

253 (insertions, deletions, and substitutions) to transform one string into another (Kohonen,

254 1985). We obtained a squared matrix consisting of the distances between each pair of

255 strings, then averaged LDs and calculated within- and between-individual means (Fig. 2),

256 to investigate whether females and males differed in their degree of variation. For this

257 purpose, we ran Mantel tests (9999 randomizations) using a matrix featuring the average

258 individual means against a model matrix consisting of 0 when the corresponding

259 individuals were of the same sex (Krull et al., 2012), and 1 when they were opposite sexes

260 (package *vegan* in R; Oksanen et al., 2013). When investigating differences at the group

261 level or within-sex, we used the non-parametric paired samples Wilcoxon test to compare

262 the average individual LDs of each member of a pair or the within- versus between-

263 individual LDs because, with such a small sample size, the Mantel test is not

264 recommended (Legendre & Fortin, 1989). Only for the Wilcoxon test, the group in which

265 the male changed was entered twice, considering the two pairs as different groups. We

266 obtained a lower number of male contributions because the reproductive females also

267 engaged in duets with immature male offspring (N = 23).

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Results

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270   We analyzed 261 individual contributions consisting of a total of 2018 phrases. We

271   obtained 77 ± 21 (mean $\pm$ standard deviation) phrases per male and 78 ± 23 phrases per

272   female. We found that average phrase duration was 1.285 s (range: 0.380 - 3.000 s). The

273   number of phrases in the individual song ranged between 2 and 27.

274   We found a significant difference between the LDs calculated for males and females,

275   where females showed higher average individual means than males (Mantel test: r =

276   0.167, P = 0.002; Fig. 2). In all groups, the females had higher LDs (LD = 6.497 + 1.674)

277   than males (LD = 3.946 + 0.814), showing that female contribution to the song was less

278   stereotyped (Fig. 3, Wilcoxon paired test: V = 0, df = 7; P = 0.008). It is noticeable that

279   the individuals Eva, which sang with three different males and had a high number of

280   recordings (N=39), showed remarkable differences compared to other females. Both

281   females and males showed a higher variability at between-individuals ($LD_{females}$ = 7.386

282   + 0.709, LD_{males} = 4.885 + 0.325) than within-individual level (Fig. 3), except for the

283   females of groups 4 and 8. Overall, we found a significant difference between within- and

284   between-individual LDs (Wilcoxon paired test: V = 0, df = 7; P = 0.008).

Discussion

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286   We examined differences in the order of phrases emitted during the songs by reproductive

287   male and female indris living in the same population. We hypothesized that female

288   contributions to the song may function differently in phrase concatenation from those of

289   males. We found support for our predictions. The phrase structure of songs indeed

290   differed between males and females, and female contributions were less stereotyped than

291 those of males. The LDs showed that the between-individual stereotypy of male

292 contributions was higher than females' one. Males, therefore, appeared to produce songs

293 that are overall more similar to those of other males. In agreement with previous studies

294 that reported sexual dimorphism in the overall timing and repertoire size (Giacoma et al.,

295 2010), and in the frequency modulation, duration and rhythm (Gamba et al., 2016; Torti

296 et al., 2017, De Gregorio et al., 2018), we found that male and female indris also differed

297 in the phrase organization of their songs. Female structuring of the song showed a higher

298 number of phrases if compared to males, independently of the phrases being of the same

299 or different type. This result is in line with previous studies on family-living and pair-

300 bonded primate and bird species (Deputte, 1982; Savage, Snowdon, Giraldo & Soto,

301 1996; Snowdon, 2017; Riebel et al., 2019; Levin, 1996a; 1996b), endorsing that in a

302 socially monogamous, monomorphic species which holds year-round territories, sex

303 differences in vocal output are frequent (Marshall & Marshall, 1976). Furthermore,

304 despite the fact that songs are considered to be males' peculiar features (Cowlishaw,

305 1996), our results confirm that also monogamous females use songs and that female song

306 can be more elaborate than those of males. Female song phrase concatenation is more

307 complex than males' because even if males are playing the primary role in territorial

308 defense, females' role in territorial disputes can be essential. Female songs may be critical

309 for advertising their identity as well as resources holding potential. For instance, vocal

310 fights, in which females and males are singing together, are often sufficient to resolve

311 group encounters, reducing the occurrence of physical fights (Bonadonna et al., 2020).

312 Future studies may investigate whether female dispersal distance and territorial changes

313 over the years may contribute to a deeper understanding of this sex-dimorphic variation.

314 Expanding previous findings that showed how indri female contribution to the song was

315   more varied in the rhythm (De Gregorio et al., 2018), we showed that the combination

316   and repertoire of the phrases are also more extensive than those shown by males. Females

317   not only have a broader repertoire of units, but they also emit descending phrases that we

318   did not observe in males (e.g., descending phrases of six units). Considering those

319   previous findings, our results may suggest that the differences in song structuring could

320   be used to convey information about the sex and the status of the singers that can be

321   assessed at a distance by conspecifics.

322   In agreement with previous findings on the different role of males and females during the

323   song (Giacoma et al., 2010), we found that female song is potentially more distinctive

324   than the male one. These results are in agreement with previous findings on birds (Brown

325   & Farabaugh, 1991), confirming that in those species in which females are involved in

326   territorial defense, their repertoires are as large or larger than those of males, on the level

327   of both units and phrases. Territorial defense is crucial for survival and reproduction in

328   pair-bonding species that occupy stable territories, and even if female involvement in

329   territorial defense is different from that of the reproductive male, they participate in

330   joining with their partner. An increasing body of literature (e.g., Hall, Rittenbach, &

331   Vehrencamp, 2015) supported the view that same-sex competition is the primary driver

332   of female song elaboration. It can be the case of the indris, where females may benefit

333   from multiple mating partners to increase tolerance by neighboring males (Bonadonna et

334   al., 2014). As mentioned above, females can advertise the occupancy of an area as well

335   as their quality and resource-holding potential. In support of the higher variability in

336   female song structure, there is also the recent evidence that genetic relatedness may play

337   a critical role in determining the characteristics of DPs in males, whereas it may have a

338   lesser impact on female songs (Torti et al., 2017). A more variable song structure may

339 add up to a more flexible structuring of the phrase notes, but further investigations are

340 needed.

341 This work also expands on and complements previous studies on humpback whales

342 (Helweg et al., 1998; Tougaard & Eriksen, 2006; Garland et al., 2012), showing that the

343 Levenshtein distance is simple, efficiently computable and highly applicable to any

344 behavioral data that are produced in a sequence. Our results confirmed that the

345 Levenshtein distance method is a simple but powerful technique that can be applied to

346 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.