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(Article begins on next page)



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

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5 **1 Sexually dimorphic phrase organization in the song of the indris (*Indri indri*)**

6 **2**  
7 **3 Running title: Phrase organization in the indris**  
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7 **35 Abstract**

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9 **36**  
10 **37** Animal acoustic communication often takes the form of complex sequences, composed  
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12 **38** of multiple distinct acoustic units, which can vary in their degree of stereotypy. Studies  
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14 **39** of sequence variation may contribute to our understanding of the structural flexibility of  
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16 **40** primates' songs, which can provide essential ecological and behavioral information about  
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18 **41** variability at the individual, population, and specific level and provide insights into the  
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20 **42** mechanisms and drivers responsible for the evolutionary change of communicative traits.  
21  
22 **43** We studied intra and inter-individual variation in the song structuring of a singing  
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24 **44** primate, the indri (*Indri indri*). Indri groups emit duets and choruses in which they  
25  
26 **45** combine long notes, short single units, and phrases consisting of a variable number of  
27  
28 **46** units (from two to six) with slightly descending frequency. Males' and females'  
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30 **47** contributions to the song differ in the temporal and frequency structure of song units and  
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32 **48** repertoire size. We calculated the similarity of phrase organization across different  
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34 **49** individual contributions using the Levenshtein distance, a logic distance that expressed  
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36 **50** the minimum cost to convert a sequence into another and can measure differences  
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38 **51** between two sequences of data. We then analyzed the degree of similarity within and  
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40 **52** between individuals and found that: i) the phrase structure of songs varied between  
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42 **53** reproductive males and females: female structuring of the song showed a higher number  
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44 **54** of phrases if compared to males; ii) Male contributions to the song were overall more  
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46 **55** similar to those of other males than were female contributions to the song of other  
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48 **56** females; iii) male contributions were more stereotyped than female contributions, which  
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50 **57** showed greater individual flexibility. The picture emerging from phrase combinatorics in  
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52 **58** the indris is in agreement with previous findings of rhythmic features and song repertoire  
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4 59 size of the indris, which also suggested that female songs are potentially less stereotyped  
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6 60 than those of males.  
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10  
11 62 Keywords: syntax, language evolution, primates, singing, Levenshtein distance  
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18 65 **Research Highlights**

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21 66 ● This study demonstrated that male and female adult indris differed in the phrase  
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23 67 organization of their songs.  
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25 68 ● Male contributions to the song were overall more similar to those of other males  
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28 69 and more stereotyped than females' ones.  
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32 71 **Graphical Abstract**

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34 72 Figure 2 works as graphical abstract for this manuscript.  
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57 78 **Introduction**  
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5 79 Communication between conspecifics often involves the use of vocalizations because  
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7 80 acoustic signals allow encoding a considerable amount of information in a short time  
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10 81 (Bradbury & Vehrencamp, 2011). Animal vocal signals can be emitted in the form of  
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12 82 short vocalizations or given in sequences of variable length (Catchpole & Slater, 2008).  
13  
14 83 In addition to the well-known example of birdsong, other animals such as insects,  
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16 84 amphibians, and mammals (including bats, rodents, primates, and cetaceans) also emit  
17  
18 85 complex acoustic sequences (Kershenbaum et al., 2016). Although animals showed a  
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20 86 limited ability to concatenate vocal emissions in phrases when compared to humans  
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22 87 (Berwick, Okanoya, Beckers & Bolhuis, 2011), their vocal sequences may contain  
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24 88 information on species and individual identity (e.g., starlings (*Sturnus vulgaris*), wolves  
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26 89 (*Canis lupus*), dolphins (*Tursiops truncatus*), and rock hyraxes (*Procavia capensis*)).  
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28 90 Animal vocal sequences may also encode information about external cues such as  
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30 91 resource availability, e.g., food calls in chimpanzees (*Pan troglodytes*), or predator threats  
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32 92 in marmots (*Marmota* spp.; Kershenbaum et al., 2016).  
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37 93 The understanding of the role played by the acoustic sequences in a particular species'  
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39 94 repertoire often involves the comparison of sequences within and between individuals, as  
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41 95 well as within and between groups, so that it is possible to quantify the nature of the  
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43 96 variation and potentially correlate it to ecological and behavioral factors (Kershenbaum  
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45 97 et al., 2014).  
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48 98 So far, the studies of primate call organization focused on contact calls or alarm calls  
49  
50 99 (Clarke, Reichard & Zuberbühler, 2006) with scarce investigations of song structure  
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52 100 variation within contexts (Torti, Gamba, Rabemananjara & Giacoma, 2013). There is a  
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54 101 lack of information about whether primate males and females combine units in songs  
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56 102 using different phrase combinations. It is essential to examine the sex-dimorphic traits of  
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5 103 primate songs because knowledge of sex differences in song organization may be critical  
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7 104 in our understanding of what is biologically informative, especially in sexually  
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9 105 monomorphic species. Moreover, information available on the variability within a species  
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11 106 is very little (Honda & Okanoya, 1999; Takahasi, Yamada & Okanoya, 2010). Few  
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13 107 investigations on primate vocal sequences are currently available and none of them are  
14  
15 108 evaluating the stereotypy of song structure between sexes using a string metric (Gustison,  
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17 109 Semple, Ferrer-i-Cancho & Bergman, 2016). While traditional methods may not apply to  
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19 110 a wide array of questions, string metrics can be used to investigate different organizational  
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21 111 levels, are entirely objective, and their results are verifiable (Heeringa, 2004).  
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25 112 Indris (*Indri indri*, Gmelin, 1788) represent a distinctive species for studying vocal  
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27 113 communication because of their rich repertoire (Maretti, Sorrentino, Finomana, Gamba  
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29 114 & Giacoma, 2010; Valente et al., 2019) and the impressive loud songs, unique among  
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31 115 lemurs (Gamba et al., 2016; Torti et al., 2017), which can be heard at a distance up to 2  
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33 116 km (Pollock, 1986). Data on sound pressure levels revealed that the sound levels of the  
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35 117 indri's song reached 110 dB (estimated at 0.50 m; Torti, *pers. obs.*). This level can be  
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37 118 compared to ring-tailed lemurs (*Lemur catta*), which showed a call amplitude ranging  
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39 119 between 85 and 89 dB (at 1 m, Macedonia, 1993). The song of the indris, which lasts 40-  
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41 120 250 s, consists of a long series of modulated units, organized in phrases (Gamba, Favaro,  
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43 121 Torti, Sorrentino & Giacoma, 2011), uttered simultaneously by males and females,  
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45 122 including juveniles, of the same group (Maretti et al., 2010). These types of units are  
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47 123 emitted exclusively during the song (Valente et al., 2019).  
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49 124 Previous research showed that the indris can emit songs in different contexts and that the  
50  
51 125 song can elicit different behaviors depending on its acoustic structure. Songs given in  
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53 126 different contexts showed differences in their temporal structure that are distinguishable  
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5 127 by visual inspection of the spectrograms and by ear (Torti et al. 2013). Cohesion songs  
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7 128 were emitted when the individuals of a group were dispersed in their territory, while  
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9 129 advertisement songs were usually given when the animals of the same group were in  
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12 130 visual contact at the boundary of their territory (Torti et al., 2013). Cohesion songs were  
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14 131 followed by emitters traveling significantly further than following the advertisement  
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16 132 song, confirming the different functions of the song uttered in different contexts (i.e.,  
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18 133 cohesion songs bring together the members of a group, and advertisement songs inform  
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21 134 neighbors about the sex, age, and status of singing individuals). Other studies have shown  
22  
23 135 that male and female contributions to the song differ, both quantitatively and  
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25 136 qualitatively, in the temporal structure of the units emitted (Giacoma, Sorrentino,  
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27 137 Rabarivola & Gamba, 2010; Sorrentino, Gamba & Giacoma, 2012). Vocal sexual  
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29 138 dimorphism is also present in the modulation of the frequency of vocal utterances, in the  
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31 139 duration of unit types and the rhythmic structure of a contribution (Gamba et al., 2016;  
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33 140 De Gregorio et al., 2018).

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37 141 Since the indris' songs can be interpreted as a string of easily identifiable phrases (Gamba  
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39 142 et al., 2016), they represent an ideal case for the study of the variability of phrase  
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41 143 concatenation in primate songs. Among the methods for investigating different levels of  
42  
43 144 structural variation in acoustic displays, we chose the Levenshtein distance, which is a  
44  
45 145 quantitative method for measuring the similarity of sequences (hereafter LD; Margoliash,  
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47 146 Staicer & Inoue, 1991). The LD is a logical distance commonly used to quantify the  
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49 147 difference between two strings of data (e.g., human words, sequences of visual  
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51 148 movements or sequences of song themes; Gooskens & Heeringa, 2004). This technique  
52  
53 149 has often been used to measure similarity in human dialects (Wieling, Montemagni,  
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55 150 Nerbonne & Baayen, 2014), and it has been applied to animal vocal sequences, but for a  
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5 151 very limited number of species (Indigo bunting, *Passerina cyanea*, Margoliash et al.,  
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7 152 1991; Willow warbler, *Phylloscopus trochilus*, Gil & Slater, 2000; Humpback whale,  
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9 153 *Megaptera novaeangliae*: Helweg, Cato, Jenkins, Garrigue & McCauley, 1998; Tougaard  
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12 154 & Eriksen, 2006; Garland et al., 2012).

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14 155 Although songs are often referred to as a male's prerogative, we have particular insights  
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16 156 showing that monogamous females may also use the song overlapping male song  
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18 157 functions (e.g., Eastern whip bird (*Psophodes olivaceus*), Rogers, Langmore, & Mulder,  
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20 158 2007; Levin, 1996a; 1996b). Females may use songs for mate attraction (Rogers et al.,  
21  
22 159 2007), and they may even show a more elaborated song repertoire (Australian magpies  
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24 160 (*Gymnorhina tibice* Brown & Farabaugh, 1991). Like Eastern whip birds and Australian  
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26 161 magpies, indris are monogamous (Torti et al., 2017; Bonadonna et al., 2019), form groups  
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28 162 that occupy non-overlapping areas in the forest (Bonadonna et al., 2017), and use the  
29  
30 163 songs to inform neighboring groups about the occupation of a territory and to actively  
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32 164 defend resources during group encounters (Torti et al., 2013). Thus, we hypothesized that  
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34 165 the female contribution to the song would be structurally different from that of males.

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36 166 Studies of song structure in bird duets also suggested that females' songs would be more  
37  
38 167 acoustically variable than that of males (Logue & Gammon, 2004), in line with the  
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40 168 territorial model of bird duet evolution (Farabaugh, 1982). In birds, duetting occurs most  
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42 169 commonly where birds hold year-round territories, and it is associated with sexually  
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44 170 monomorphic species that form long-term monogamous pair bonds (Riebel, Odom,  
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46 171 Langmore & Hall, 2019). Indri females showed significantly higher variation in the  
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48 172 rhythm of their contributions to the song and a higher potential to synchronize with males  
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50 173 (De Gregorio et al., 2018). Thus, we hypothesized that the adjustment in the rhythmic  
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52 174 structure of their contribution would also be reflected in a sexually dimorphic phrases  
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4 175 combination, where one should expect males to produce songs with a more stereotyped  
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6 176 structure. Similarly to pair living bird species (Rogers et al., 2007), indri females may use  
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8 177 songs for mate guarding and attraction, and song structural variability and complexity  
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10 178 may have evolved to provide conspecifics with information on females' fitness and  
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13 179 survival.  
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## 23 183 **Methods**

### 24 184 **Observations and recordings**

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26 185 We studied 8 groups (N= 36 individuals) living in the Maromizaha Forest (18°56'49"S,  
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28 186 48°27'53"E). We recorded the animals between 2011 and 2017. We observed one social  
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31 187 group per week, from Monday to Friday approximately from 6 AM to 1 PM, when the  
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33 188 animals usually start resting and sleeping until the day after (Pollock, 1975). All  
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35 189 recordings were carried out without the use of playback stimuli, and nothing was done to  
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37 190 modify the behavior of the indris. We recorded 142 songs, consisting of duets and  
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39 191 choruses with a maximum of five individuals singing in the same song. For the analysis,  
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41 192 we only considered the contribution of the reproductive individuals, for a total of 17 focal  
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43 193 animals from eight social groups: nine reproductive adult males, and eight reproductive  
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45 194 adult females. An example of an indri song and the singers' contributions is shown in  
46  
47 195 Figure 1. The different number of males and females is motivated by the fact that, during  
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49 196 the study period, the reproductive male of a group changed. All the songs were recorded  
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51 197 using solid-state recorders (Olympus LS05, Tascam DR-100, Tascam DR-05) with a  
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53 198 sampling rate of 44.1 kHz (16-bit depth) during all the recording sessions. When  
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7 199 recording the songs, we were always at a distance between 2 and 20 m from the animals,  
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9 200 with the microphone oriented toward the focal singing individuals. We always kept visual  
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11 201 contact with the vocalizing animals and maximized our efforts to face the focal animals  
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14 202 during the emission of the song. Since indri songs emitted in different contexts have  
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16 203 different acoustic structure, in order to avoid any bias due to these differences, we  
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18 204 considered, from multiple years, only those songs that were labeled as advertisement  
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20 205 songs and were recorded in the same context (Torti et al., 2013). Using the focal animal  
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22 206 sampling technique (Altmann, 1974), we were able to attribute each vocalization to its  
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24 207 signaler. We will refer to every individual uttered portion within a song or a chorus as an  
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26 208 ‘individual contribution’.

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31 209 During this study, we did not have any physical contact with the animals, and we recorded  
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33 210 only spontaneously emitted songs. We have received permits for this research, each year,  
34  
35 211 from “Direction des Eaux et Forêts” and “Madagascar National Parks”: 2011 - N°  
36  
37 212 274/11/MEF/SG/D GF/DCB.SAP/SCB, 2012 N°245/12/MEF/SG/DGF/DCB.SAP/SCB,  
38  
39 213 2014 - N°066/14/MEF/SG/DGF/DCB.SAP/SCB, 2015 - N° 180/ 15/ MEEMF/ SG/ DGF/  
40  
41 214 DAPT/ SCBT; 2016 - N° 98/ 16/ MEEMF/ SG/ DGF/ DAPT/ SCB.Re and N° 217/  
42  
43 215 16/MEEMF/ SG/ DGF/ DSAP/ SCB.Re, 2017 - 73/17/MEEF/SG/DGF/DSAP/SCB.RE.  
44  
45 216 The data collection in 2013 did not require a permit because performed by our Malagasy  
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47 217 collaborators only.

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53 218 We adhered to applicable international, national, and/or institutional guidelines for the  
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55 219 study on animals and nonhuman primates, including the American Society of  
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57 220 Primatologist (ASP) Principle for the Ethical Treatment of nonhuman Primates, and the  
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5 221 European Union directive guidelines for the study on animals and nonhuman primates  
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7 222 (Directive 2010/63/EU). The study did not require IACUC approval.  
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11 223 **Acoustic and statistical analyses**  
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14 224 We edited segments containing indri songs using Praat 6.0.30 (Boersma & Weenink  
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16 225 2008) and BORIS 5.1 (Friard & Gamba 2016). For each recorded song, we created a  
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18 226 spectrogram with a view range between 0 and 5000 Hz, a window length of 0.09 s, and a  
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20 227 dynamic range of 65.0 dB. We saved each song in a single audio file in WAV format  
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22 228 (Waveform audio file format). We saved the information related to the identity of each  
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24 229 singer in a Praat textgrid. We then labeled all the vocal units (each single sound  
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26 230 constituting the modulated part of the song; Thalmann, Geissmann, Simona & Mutschler,  
27  
28 231 1993) according to their belonging to a song portion (long notes or descending phrases,  
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30 232 see Torti et al., 2013 for details) and to a descending phrase (hereafter, DP; see Torti et  
31  
32 233 al., 2017 for details). Songs given in different contexts showed differences in their  
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34 234 temporal structure that are distinguishable by visual inspection of the spectrograms and  
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36 235 by ear (Torti et al. 2013). We considered phrases consisting of two (DP2), three (DP3),  
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38 236 four (DP4), five (DP5), and six (DP6) units. This information was saved in Praat and  
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40 237 exported to a Microsoft© Excel spreadsheet (Gamba, Friard & Giacoma, 2012). Since all  
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42 238 the steps of the labeling process have been done by a single operator (A.Z.), we avoided  
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44 239 the possibility of encountering errors due to observer differences. To understand whether  
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46 240 there were differences in song structure between sexes, we investigated the DPs similarity  
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48 241 in each contribution. We transformed each contribution in a string of labels separated by  
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50 242 a break symbol (e.g., DP2|DP3|DP4|DP3). The resulting string represents the  
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52 243 concatenation of the phrases uttered within a contribution (and it is a measure of phrase  
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6 244 organization). From the 142 songs, we obtained 142 strings for females (with an average  
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8 245 of 17.88 songs per individual, SD = 5.44), and 119 strings for males (with an average of  
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10 246 13.22 songs per individual, SD = 5.91). Using R (R Core Team, 2015; version 3.3.3), we  
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12 247 calculated the Levenshtein distance (LD) for each pair of strings  
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14 248 (package *stringdist* 0.9.4.2 in R; van der Loo, 2014) because this methodology provides  
15  
16 249 a robust quantitative approach for the study of animal acoustic sequences (Kershenbaum  
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18 250 & Garland, 2015). The distance calculates the minimum number of necessary changes  
19  
20 251 (insertions, deletions, and substitutions) to transform one string into another (Kohonen,  
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22 252 1985). We obtained a squared matrix consisting of the distances between each pair of  
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24 253 strings, then averaged LDs and calculated within- and between-individual means (Fig. 2),  
25  
26 254 to investigate whether females and males differed in their degree of variation. For this  
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28 255 purpose, we ran Mantel tests (9999 randomizations) using a matrix featuring the average  
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30 256 individual means against a model matrix consisting of 0 when the corresponding  
31  
32 257 individuals were of the same sex (Krull et al., 2012), and 1 when they were opposite sexes  
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34 258 (package *vegan* in R; Oksanen et al., 2013). When investigating differences at the group  
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36 259 level or within-sex, we used the non-parametric paired samples Wilcoxon test to compare  
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38 260 the average individual LDs of each member of a pair or the within- versus between-  
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40 261 individual LDs because, with such a small sample size, the Mantel test is not  
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42 262 recommended (Legendre & Fortin, 1989). Only for the Wilcoxon test, the group in which  
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44 263 the male changed was entered twice, considering the two pairs as different groups. We  
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46 264 obtained a lower number of male contributions because the reproductive females also  
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48 265 engaged in duets with immature male offspring (N = 23).  
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## 267 **Results**

268 We analyzed 261 individual contributions consisting of a total of 2018 phrases. We  
269 obtained  $77 \pm 21$  (mean  $\pm$  standard deviation) phrases per male and  $78 \pm 23$  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 ( $LD_{\text{females}} = 7.386$   
280  $+ 0.709$ ,  $LD_{\text{males}} = 4.885 + 0.325$ ) 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

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5 289 those of males. The LDs showed that the between-individual stereotypy of male  
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7 290 contributions was higher than females' one. Males, therefore, appeared to produce songs  
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9 291 that are overall more similar to those of other males. In agreement with previous studies  
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11 292 that reported sexual dimorphism in the overall timing and repertoire size (Giacoma et al.,  
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13 293 2010), and in the frequency modulation, duration and rhythm (Gamba et al., 2016; Torti  
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15 294 et al., 2017, De Gregorio et al., 2018), we found that male and female indris also differed  
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17 295 in the phrase organization of their songs. Female structuring of the song showed a higher  
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19 296 number of phrases if compared to males, independently of the phrases being of the same  
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21 297 or different type. This result is in line with previous studies on family-living and pair-  
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23 298 bonded primate and bird species (Deputte, 1982; Savage, Snowdon, Giraldo & Soto,  
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25 299 1996; Snowdon, 2017; Riebel et al., 2019; Levin, 1996a; 1996b), endorsing that in a  
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27 300 socially monogamous, monomorphic species which holds year-round territories, sex  
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29 301 differences in vocal output are frequent (Marshall & Marshall, 1976). Furthermore,  
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31 302 despite the fact that songs are considered to be males' peculiar features (Cowlshaw,  
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33 303 1996), our results confirm that also monogamous females use songs and that female song  
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35 304 can be more elaborate than those of males. Female song phrase concatenation is more  
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37 305 complex than males' because even if males are playing the primary role in territorial  
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39 306 defense, females' role in territorial disputes can be essential. Female songs may be critical  
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41 307 for advertising their identity as well as resources holding potential. For instance, vocal  
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43 308 fights, in which females and males are singing together, are often sufficient to resolve  
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45 309 group encounters, reducing the occurrence of physical fights (Bonadonna et al., 2020).  
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47 310 Future studies may investigate whether female dispersal distance and territorial changes  
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49 311 over the years may contribute to a deeper understanding of this sex-dimorphic variation.  
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51 312 Expanding previous findings that showed how indri female contribution to the song was  
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5 313 more varied in the rhythm (De Gregorio et al., 2018), we showed that the combination  
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7 314 and repertoire of the phrases are also more extensive than those shown by males. Females  
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9 315 not only have a broader repertoire of units, but they also emit descending phrases that we  
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11 316 did not observe in males (e.g., descending phrases of six units). Considering those  
12  
13 317 previous findings, our results may suggest that the differences in song structuring could  
14  
15 318 be used to convey information about the sex and the status of the singers that can be  
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17 319 assessed at a distance by conspecifics.

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21 320 In agreement with previous findings on the different role of males and females during the  
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23 321 song (Giacoma et al., 2010), we found that female song is potentially more distinctive  
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25 322 than the male one. These results are in agreement with previous findings on birds (Brown  
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27 323 & Farabaugh, 1991), confirming that in those species in which females are involved in  
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29 324 territorial defense, their repertoires are as large or larger than those of males, on the level  
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31 325 of both units and phrases. Territorial defense is crucial for survival and reproduction in  
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33 326 pair-bonding species that occupy stable territories, and even if female involvement in  
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35 327 territorial defense is different from that of the reproductive male, they participate in  
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37 328 joining with their partner. An increasing body of literature (e.g., Hall, Rittenbach, &  
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39 329 Vehrencamp, 2015) supported the view that same-sex competition is the primary driver  
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41 330 of female song elaboration. It can be the case of the indris, where females may benefit  
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43 331 from multiple mating partners to increase tolerance by neighboring males (Bonadonna et  
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45 332 al., 2014). As mentioned above, females can advertise the occupancy of an area as well  
46  
47 333 as their quality and resource-holding potential. In support of the higher variability in  
48  
49 334 female song structure, there is also the recent evidence that genetic relatedness may play  
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51 335 a critical role in determining the characteristics of DPs in males, whereas it may have a  
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53 336 lesser impact on female songs (Torti et al., 2017). A more variable song structure may  
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4 337 add up to a more flexible structuring of the phrase notes, but further investigations are  
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6 338 needed.

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9 339 This work also expands on and complements previous studies on humpback whales  
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11 340 (Helweg et al., 1998; Tougaard & Eriksen, 2006; Garland et al., 2012), showing that the  
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13 341 Levenshtein distance is simple, efficiently computable and highly applicable to any  
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15 342 behavioral data that are produced in a sequence. Our results confirmed that the  
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17 343 Levenshtein distance method is a simple but powerful technique that can be applied to  
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19 344 assess stereotypy or divergence between sexes.  
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4 **541 Figure legend:**  
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7 **542 Figure 1: Spectrographic and schematic representation of an indri song.** Spectrograms  
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9 **543** of an indri song (a) showing a typical sequence of units given by one male and one  
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11 **544** female. Schematic representation of the fundamental frequency of the descending  
12  
13 **545** phrase units given by one male (b) and one female (c). Box fill patterns denote the  
14  
15 **546** phrase type: black boxes mark single units (SU), horizontal lines boxes mark DP2,  
16  
17 **547** diagonal lines boxes mark DP3, wavy lines boxes mark DP4, and checkered boxes mark  
18  
19 **548** DP5. The spectrograms were generated in Praat with the following parameters: window  
20  
21 **549** length: 0.05 s; dynamic range: 50 dB; frequency range: 0 to 10.000 Hz (a), 0 to 3.000  
22  
23 **550** Hz (b,c).  
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29 **551 Figure 2: The Levenshtein Distances showing song structuring in male and female**  
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31 **552** *indris of the studied groups.* Individuals are shown on the vertical axis; sexes are shown  
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33 **553** on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker  
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35 **554** and bigger the dots, the higher are the distances between the individual contributions to  
36  
37 **555** the song. This plot was generated using the R package *corrplot* (vers. 0.84; Wei &  
38  
39 **556** Simko, 2017).  
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44 **557 Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight**  
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46 **558** *studied groups.* Bar plot describing the individual and overall degree of stereotypy and  
47  
48 **559** variability expressed by the average Levenshtein Distances (LDs). Within-individual  
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50 **560** LDs are reported for females (white bars) and males (black bars), as well as between-  
51  
52 **561** individual LDs (grey bars for females, striped bars for males). Group 3 is reported twice  
53  
54 **562** because the male of the reproductive pairs changed in 2014. Capped lines represent  
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56 **563** Standard Deviation.  
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**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.

For Peer Review

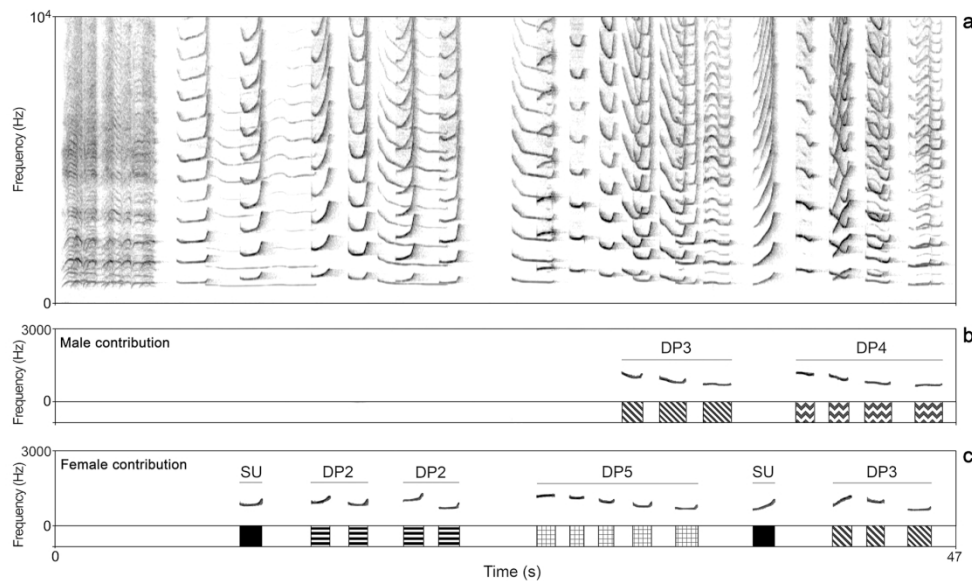


Figure 1: Spectrographic and schematic representation of an indri song. Spectrograms of an indri song (a) showing a typical sequence of units given by one male and one female. Schematic representation of the fundamental frequency of the descending phrase units given by one male (b) and one female (c). 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).

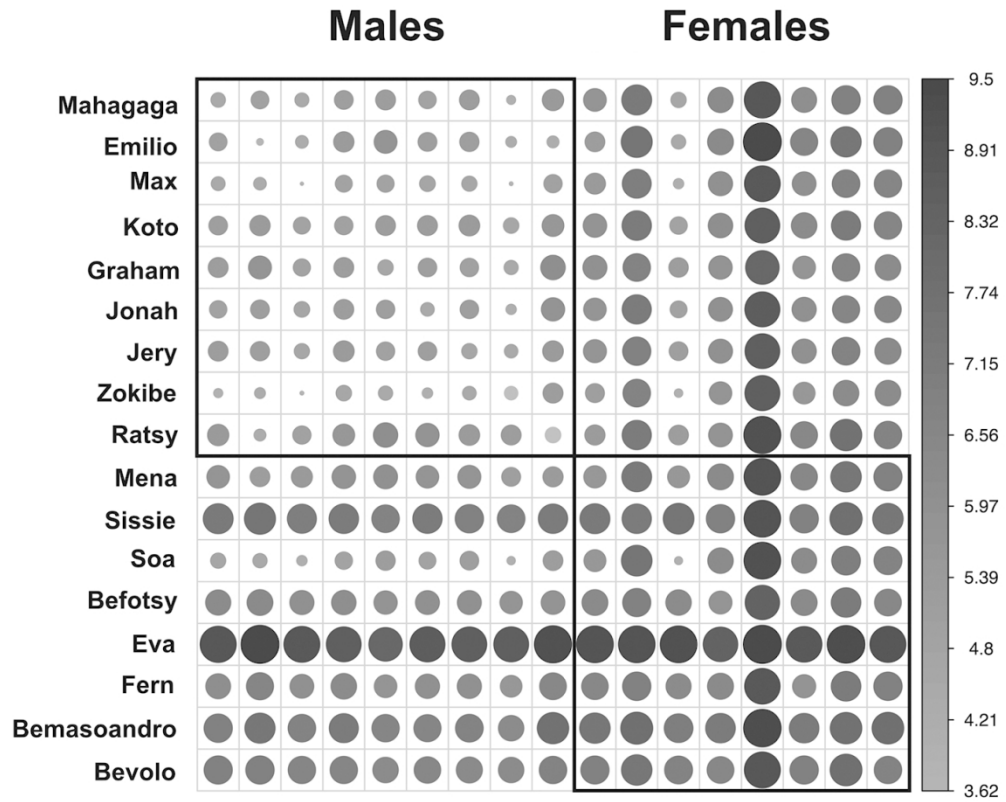


Figure 2: The Levenshtein Distances showing song structuring in male and female indris of the studied groups. Individuals are shown on the vertical axis; sexes are shown on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker and bigger the dots, the higher are the distances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

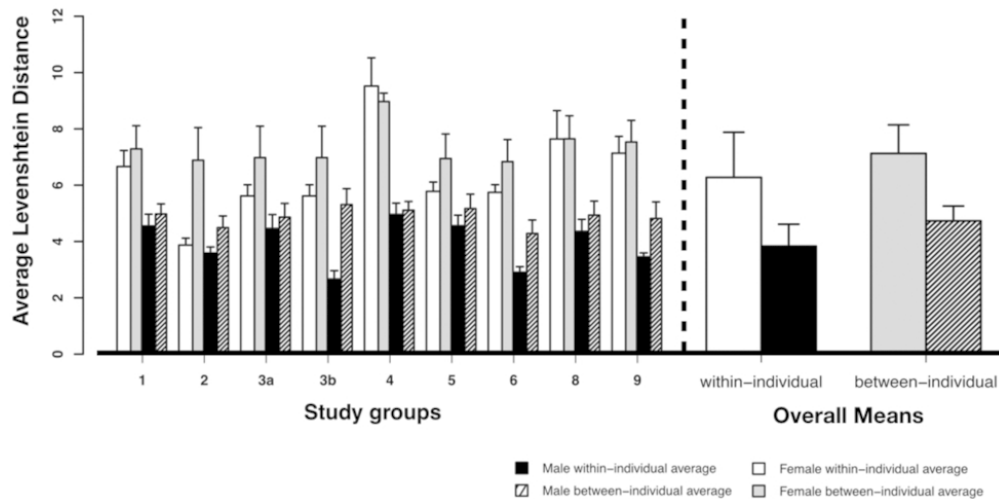


Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight studied groups. Bar plot describing the individual and overall degree of stereotypy and variability expressed by the average Levenshtein Distances (LDs). Within-individual LDs are reported for females (white bars) and 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.

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

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

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13 Bonadonna<sup>1</sup>, Rose Marie Randrianarison<sup>2,3</sup>, Cristina Giacomini<sup>1</sup> & Marco Gamba<sup>1</sup>

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5 **35 Abstract**

6 36  
7 37 Animal acoustic communication often takes the form of complex sequences, composed  
8  
9 38 of multiple distinct acoustic units, which can vary in their degree of stereotypy. **Studies**  
10 39 **of sequence variation may contribute to our understanding of the structural flexibility of**  
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12 40 **primates' songs, which can provide essential ecological and behavioral information about**  
13  
14 41 **variability at the individual, population, and specific level and provide insights into the**  
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16 42 **mechanisms and drivers responsible for the evolutionary change of communicative traits.**  
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18 43 ~~Several methods have been used for investigating different levels of structural~~  
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20 44 ~~information and sequence similarity in acoustic displays.~~ We studied intra and inter-  
21  
22 45 individual variation in the song structuring of a singing primate, the indri (*Indri indri*),  
23  
24 46 ~~which inhabits the montane rain forests of Madagascar.~~ Indri groups emit duets and  
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26 47 **choruses in which they** combine long notes, short single units, and phrases **consisting of**  
27  
28 48 **a variable number of units (from two to six) with slightly descending frequency.** Males'  
29  
30 49 and females' contributions to the song differ in the temporal and frequency structure of  
31  
32 50 song units and repertoire size. We calculated the similarity of phrase organization across  
33  
34 51 different individual contributions using the Levenshtein distance, a logic distance that  
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36 52 expressed the minimum cost to convert a sequence into another and can measure  
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38 53 differences between two sequences of data. We then analyzed the degree of similarity  
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40 54 within and between individuals and found that: i) the phrase structure of songs varied  
41  
42 55 between reproductive males and females: **female structuring of the song showed a higher**  
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44 56 **number of phrases if compared to males;** ii) **Male contributions to the song were overall**  
45  
46 57 **more similar to those of other males than were female contributions to the song of other**  
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48 58 **females;** iii) **male contributions were more stereotyped than female contributions, which**  
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50 59 **showed greater individual flexibility.** The picture emerging from phrase combinatorics in  
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4 60 the indris is in agreement with previous findings of rhythmic features and song repertoire  
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6 61 size of the indris, which also suggested that female songs are potentially less stereotyped  
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8 62 than those of males.  
9

10 63 Keywords: syntax, language evolution, primates, singing, Levenshtein distance  
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### 18 66 **Research Highlights**

- 19  
20 67 ● This study demonstrated that male and female adult indris differed in the phrase  
21  
22 68 organization of their songs.
- 23  
24 69 ● Male contributions to the song were overall more similar to those of other males  
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26 70 and more stereotyped than females' ones.  
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### 30 71 31 72 **Graphical Abstract**

32 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

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5 104 using different phrase combinations. It is essential to examine the sex-dimorphic traits of  
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7 105 primate songs because knowledge of sex differences in song organization may be critical  
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9 106 in our understanding of what is biologically informative, especially in sexually  
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11 107 monomorphic species. Moreover, information available on the variability within a species  
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14 108 is very little (Honda & Okanoya, 1999; Takahasi, Yamada & Okanoya, 2010). Few  
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16 109 investigations on primate vocal sequences are currently available and none of them are  
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18 110 evaluating the stereotypy of song structure between sexes using a string metric (Gustison,  
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20 111 Semple, Ferrer-i-Cancho & Bergman, 2016). While traditional methods may not apply to  
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22 112 a wide array of questions, string metrics can be used to investigate different organizational  
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24 113 levels, are entirely objective, and their results are verifiable (Heeringa, 2004).  
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27 114 Indris (*Indri indri*, Gmelin, 1788) represent a distinctive species for studying vocal  
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29 115 communication because of their rich repertoire (Maretti, Sorrentino, Finomana, Gamba  
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31 116 & Giacoma, 2010; Valente et al., 2019) and the impressive loud songs, unique among  
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33 117 lemurs (Gamba et al., 2016; Torti et al., 2017), which can be heard at a distance up to 2  
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35 118 km (Pollock, 1986). Data on sound pressure levels revealed that the sound levels of the  
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37 119 indri's song reached 110 dB (estimated at 0.50 m; Torti, *pers. obs.*). This level can be  
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39 120 compared to ring-tailed lemurs (*Lemur catta*), which showed a call amplitude ranging  
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41 121 between 85 and 89 dB (at 1 m, Macedonia, 1993). The song of the indris, which lasts 40-  
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43 122 250 s, consists of a long series of modulated units, organized in phrases (Gamba, Favaro,  
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45 123 Torti, Sorrentino & Giacoma, 2011), uttered simultaneously by males and females,  
46  
47 124 including juveniles, of the same group (Maretti et al., 2010). These types of units are  
48  
49 125 emitted exclusively during the song (Valente et al., 2019).  
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51 126 Previous research showed that the indris can emit songs in different contexts and that the  
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53 127 song can elicit different behaviors depending on its acoustic structure. Songs given in  
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5 128 different contexts showed differences in their temporal structure that are distinguishable  
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7 129 by visual inspection of the spectrograms and by ear (Torti et al. 2013). Cohesion songs  
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9 130 were emitted when the individuals of a group were dispersed in their territory, while  
10  
11 131 advertisement songs were usually given when the animals of the same group were in  
12  
13 132 visual contact at the boundary of their territory (Torti et al., 2013). Cohesion songs were  
14  
15 133 followed by emitters traveling significantly further than following the advertisement  
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17 134 song, confirming the different functions of the song uttered in different contexts (i.e.,  
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19 135 cohesion songs bring together the members of a group, and advertisement songs inform  
20  
21 136 neighbors about the sex, age, and status of singing individuals). Other studies have shown  
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23 137 that male and female contributions to the song differ, both quantitatively and  
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25 138 qualitatively, in the temporal structure of the units emitted (Giacoma, Sorrentino,  
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27 139 Rabarivola & Gamba, 2010; Sorrentino, Gamba & Giacoma, 2012). Vocal sexual  
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29 140 dimorphism is also present in the modulation of the frequency of vocal utterances, in the  
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31 141 duration of unit types and the rhythmic structure of a contribution (Gamba et al., 2016;  
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33 142 De Gregorio et al., 2018).  
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35 143 Since the indris' songs can be interpreted as a string of easily identifiable phrases (Gamba  
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37 144 et al., 2016), they represent an ideal case for the study of the variability of phrase  
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39 145 concatenation in primate songs. Among the methods for investigating different levels of  
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41 146 structural variation in acoustic displays, we chose the Levenshtein distance, which is a  
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43 147 quantitative method for measuring the similarity of sequences (hereafter LD; Margoliash,  
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45 148 Staicer & Inoue, 1991). The LD is a logical distance commonly used to quantify the  
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47 149 difference between two strings of data (e.g., human words, sequences of visual  
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49 150 movements or sequences of song themes; Gooskens & Heeringa, 2004). This technique  
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51 151 has often been used to measure similarity in human dialects (Wieling, Montemagni,  
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5 152 Nerbonne & Baayen, 2014), and it has been applied to animal vocal sequences, but for a  
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7 153 very limited number of species (Indigo bunting, *Passerina cyanea*, Margoliash et al.,  
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9 154 1991; Willow warbler, *Phylloscopus trochilus*, Gil & Slater, 2000; Humpback whale,  
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12 155 *Megaptera novaeangliae*: Helweg, Cato, Jenkins, Garrigue & McCauley, 1998; Tougaard  
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14 156 & Eriksen, 2006; Garland et al., 2012).

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16 157 Although songs are often referred to as a male's prerogative, we have particular insights  
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18 158 showing that monogamous females may also use the song overlapping male song  
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20 159 functions (e.g., Eastern whip bird (*Psophodes olivaceus*), Rogers, Langmore, & Mulder,  
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22 160 2007; Levin, 1996a; 1996b). Females may use songs for mate attraction (Rogers et al.,  
23  
24 161 2007), and they may even show a more elaborated song repertoire (Australian magpies  
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26 162 (*Gymnorhina tibice* Brown & Farabaugh, 1991). Like Eastern whip birds and Australian  
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28 163 magpies, indris are monogamous (Torti et al., 2017; Bonadonna et al., 2019), form groups  
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30 164 that occupy non-overlapping areas in the forest (Bonadonna et al., 2017), and use the  
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32 165 songs to inform neighboring groups about the occupation of a territory and to actively  
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34 166 defend resources during group encounters (Torti et al., 2013). Thus, we hypothesized that  
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36 167 the female contribution to the song would be structurally different from that of males.

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38 168 Studies of song structure in bird duets also suggested that females' songs would be more  
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40 169 acoustically variable than that of males (Logue & Gammon, 2004), in line with the  
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42 170 territorial model of bird duet evolution (Farabaugh, 1982). In birds, duetting occurs most  
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44 171 commonly where birds hold year-round territories, and it is associated with sexually  
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46 172 monomorphic species that form long-term monogamous pair bonds (Riebel, Odom,  
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48 173 Langmore & Hall, 2019). Indri females showed significantly higher variation in the  
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50 174 rhythm of their contributions to the song and a higher potential to synchronize with males  
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52 175 (De Gregorio et al., 2018). Thus, we hypothesized that the adjustment in the rhythmic  
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4 176 structure of their contribution would also be reflected in a sexually dimorphic phrases  
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6 177 combination, where one should expect males to produce songs with a more stereotyped  
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8 178 structure. Similarly to pair living bird species (Rogers et al., 2007), indri females may use  
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10 179 songs for mate guarding and attraction, and song structural variability and complexity  
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12 180 may have evolved to provide conspecifics with information on females' fitness and  
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14 181 survival.  
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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

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5 200 sampling rate of 44.1 kHz (16-bit depth) during all the recording sessions. When  
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7 201 recording the songs, we were always at a distance between 2 and 20 m from the animals,  
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9 202 with the microphone oriented toward the focal singing individuals. We always kept visual  
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11 203 contact with the vocalizing animals and maximized our efforts to face the focal animals  
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13 204 during the emission of the song. Since indri songs emitted in different contexts have  
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15 205 different acoustic structure, in order to avoid any bias due to these differences, we  
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17 206 considered, from multiple years, only those songs that were labeled as advertisement  
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19 207 songs and were recorded in the same context (Torti et al., 2013). Using the focal animal  
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21 208 sampling technique (Altmann, 1974), we were able to attribute each vocalization to its  
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23 209 signaler. We will refer to every individual uttered portion within a song or a chorus as an  
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25 210 ‘individual contribution’.

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31 211 During this study, we did not have any physical contact with the animals, and we recorded  
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33 212 only spontaneously emitted songs. We have received permits for this research, each year,  
34  
35 213 from “Direction des Eaux et Forêts” and “Madagascar National Parks”: 2011 - N°  
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37 214 274/11/MEF/SG/D GF/DCB.SAP/SCB, 2012 N°245/12/MEF/SG/DGF/DCB.SAP/SCB,  
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39 215 2014 - N°066/14/MEF/SG/DGF/DCB.SAP/SCB, 2015 - N° 180/ 15/ MEEMF/ SG/ DGF/  
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41 216 DAPT/ SCBT; 2016 - N° 98/ 16/ MEEMF/ SG/ DGF/ DAPT/ SCB.Re and N° 217/  
42  
43 217 16/MEEMF/ SG/ DGF/ DSAP/ SCB.Re, 2017 - 73/17/MEEF/SG/DGF/DSAP/SCB.RE.  
44  
45 218 The data collection in 2013 did not require a permit because performed by our Malagasy  
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47 219 collaborators only.

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53 220 We adhered to applicable international, national, and/or institutional guidelines for the  
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55 221 study on animals and nonhuman primates, including the American Society of  
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57 222 Primatologist (ASP) Principle for the Ethical Treatment of nonhuman Primates, and the  
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5 223 European Union directive guidelines for the study on animals and nonhuman primates  
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7 224 (Directive 2010/63/EU). The study did not require IACUC approval.  
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11 225 **Acoustic and statistical analyses**  
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14 226 We edited segments containing indri songs using Praat 6.0.30 (Boersma & Weenink  
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16 227 2008) and BORIS 5.1 (Friard & Gamba 2016). For each recorded song, we created a  
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18 228 spectrogram with a view range between 0 and 5000 Hz, a window length of 0.09 s, and a  
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20 229 dynamic range of 65.0 dB. We saved each song in a single audio file in WAV format  
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22 230 (Waveform audio file format). We saved the information related to the identity of each  
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24 231 singer in a Praat textgrid. We then labeled all the vocal units (each single sound  
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26 232 constituting the modulated part of the song; Thalmann, Geissmann, Simona & Mutschler,  
27  
28 233 1993) according to their belonging to a song portion (long notes or descending phrases,  
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30 234 see Torti et al., 2013 for details) and to a descending phrase (hereafter, DP; see Torti et  
31  
32 235 al., 2017 for details). **Songs given in different contexts showed differences in their**  
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34 236 **temporal structure that are distinguishable by visual inspection of the spectrograms and**  
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36 237 **by ear (Torti et al. 2013).** We considered phrases consisting of two (DP2), three (DP3),  
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38 238 four (DP4), five (DP5), and six (DP6) units. This information was saved in Praat and  
39  
40 239 exported to a Microsoft© Excel spreadsheet (Gamba, Friard & Giacoma, 2012). Since all  
41  
42 240 the steps of the labeling process have been done by a single operator (A.Z.), we avoided  
43  
44 241 the possibility of encountering errors due to observer differences. To understand whether  
45  
46 242 there were differences in song structure between sexes, we investigated the DPs similarity  
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48 243 in each contribution. We transformed each contribution in a string of labels separated by  
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50 244 a break symbol (e.g., DP2|DP3|DP4|DP3). The resulting string represents the  
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52 245 concatenation of the phrases uttered within a contribution (and it is a measure of phrase  
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6 246 organization). From the 142 songs, we obtained 142 strings for females (with an average  
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8 247 of 17.88 songs per individual, SD = 5.44), and 119 strings for males (with an average of  
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10 248 13.22 songs per individual, SD = 5.91). Using R (R Core Team, 2015; version 3.3.3), we  
11  
12 249 calculated the Levenshtein distance (LD) for each pair of strings  
13  
14 250 (package *stringdist* 0.9.4.2 in R; van der Loo, 2014) because this methodology provides  
15  
16 251 a robust quantitative approach for the study of animal acoustic sequences (Kershenbaum  
17  
18 252 & Garland, 2015). The distance calculates the minimum number of necessary changes  
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20 253 (insertions, deletions, and substitutions) to transform one string into another (Kohonen,  
21  
22 254 1985). We obtained a squared matrix consisting of the distances between each pair of  
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24 255 strings, then averaged LDs and calculated within- and between-individual means (Fig. 2),  
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26 256 to investigate whether females and males differed in their degree of variation. For this  
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28 257 purpose, we ran Mantel tests (9999 randomizations) using a matrix featuring the average  
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30 258 individual means against a model matrix consisting of 0 when the corresponding  
31  
32 259 individuals were of the same sex (Krull et al., 2012), and 1 when they were opposite sexes  
33  
34 260 (package *vegan* in R; Oksanen et al., 2013). When investigating differences at the group  
35  
36 261 level or within-sex, we used the non-parametric paired samples Wilcoxon test to compare  
37  
38 262 the average individual LDs of each member of a pair or the within- versus between-  
39  
40 263 individual LDs because, with such a small sample size, the Mantel test is not  
41  
42 264 recommended (Legendre & Fortin, 1989). Only for the Wilcoxon test, the group in which  
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44 265 the male changed was entered twice, considering the two pairs as different groups. We  
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46 266 obtained a lower number of male contributions because the reproductive females also  
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48 267 engaged in duets with immature male offspring (N = 23).  
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## 269 **Results**

270 We analyzed 261 individual contributions consisting of a total of 2018 phrases. We  
271 obtained  $77 \pm 21$  (mean  $\pm$  standard deviation) phrases per male and  $78 \pm 23$  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 ( $LD_{\text{females}} = 7.386$   
282  $+ 0.709$ ,  $LD_{\text{males}} = 4.885 + 0.325$ ) 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:  $V = 0$ ,  $df = 7$ ;  $P = 0.008$ ).

## 285 **Discussion**

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

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5 291 those of males. The LDs showed that the between-individual stereotypy of male  
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7 292 contributions was higher than females' one. Males, therefore, appeared to produce songs  
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9 293 that are overall more similar to those of other males. In agreement with previous studies  
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11 294 that reported sexual dimorphism in the overall timing and repertoire size (Giacoma et al.,  
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13 295 2010), and in the frequency modulation, duration and rhythm (Gamba et al., 2016; Torti  
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15 296 et al., 2017, De Gregorio et al., 2018), we found that male and female indris also differed  
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17 297 in the phrase organization of their songs. Female structuring of the song showed a higher  
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19 298 number of phrases if compared to males, independently of the phrases being of the same  
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21 299 or different type. This result is in line with previous studies on family-living and pair-  
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23 300 bonded primate and bird species (Deputte, 1982; Savage, Snowdon, Giraldo & Soto,  
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25 301 1996; Snowdon, 2017; Riebel et al., 2019; Levin, 1996a; 1996b), endorsing that in a  
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27 302 socially monogamous, monomorphic species which holds year-round territories, sex  
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29 303 differences in vocal output are frequent (Marshall & Marshall, 1976). Furthermore,  
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31 304 despite the fact that songs are considered to be males' peculiar features (Cowlshaw,  
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33 305 1996), our results confirm that also monogamous females use songs and that female song  
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35 306 can be more **elaborate** than those of males. **Female song phrase concatenation is more**  
36  
37 307 **complex than males' because even if males are playing the primary role in territorial**  
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39 308 **defense, females' role in territorial disputes can be essential. Female songs may be critical**  
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41 309 **for advertising their identity as well as resources holding potential. For instance, vocal**  
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43 310  **fights, in which females and males are singing together, are often sufficient to resolve**  
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45 311 **group encounters, reducing the occurrence of physical fights (Bonadonna et al., 2020).**  
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47 312 **Future studies may investigate whether female dispersal distance and territorial changes**  
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49 313 **over the years may contribute to a deeper understanding of this sex-dimorphic variation.**  
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51 314 Expanding previous findings that showed how indri female contribution to the song was  
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5 315 more varied in the rhythm (De Gregorio et al., 2018), we showed that the combination  
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7 316 and repertoire of the phrases are also more extensive than those shown by males. Females  
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9 317 not only have a broader repertoire of units, but they also emit descending phrases that we  
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11 318 did not observe in males (e.g., descending phrases of six units). Considering those  
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14 319 previous findings, our results may suggest that the differences in song structuring could  
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16 320 be used to convey information about the sex and the status of the singers that can be  
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19 321 assessed at a distance by conspecifics.

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21 322 In agreement with previous findings on the different role of males and females during the  
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23 323 song (Giacoma et al., 2010), we found that female song is potentially more distinctive  
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25 324 than the male one. These results are in agreement with previous findings on birds (Brown  
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27 325 & Farabaugh, 1991), confirming that in those species in which females are involved in  
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29 326 territorial defense, their repertoires are as large or larger than those of males, on the level  
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31 327 of both units and phrases. Territorial defense is crucial for survival and reproduction in  
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33 328 pair-bonding species that occupy stable territories, and even if female involvement in  
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35 329 territorial defense is different from that of the reproductive male, they participate in  
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37 330 joining with their partner. An increasing body of literature (e.g., Hall, Rittenbach, &  
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39 331 Vehrencamp, 2015) supported the view that same-sex competition is the primary driver  
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41 332 of female song elaboration. It can be the case of the indris, where females may benefit  
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43 333 from multiple mating partners to increase tolerance by neighboring males (Bonadonna et  
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45 334 al., 2014). **As mentioned above,** females can advertise the occupancy of an area as well  
46  
47 335 as their quality and resource-holding potential. In support of the higher variability in  
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49 336 female song structure, there is also the recent **evidence that genetic relatedness may play**  
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51 337 a critical role in determining the characteristics of DPs in males, whereas it may have a  
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53 338 lesser impact on female songs (Torti et al., 2017). A more variable song structure may  
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4 339 add up to a more flexible structuring of the phrase notes, but further investigations are  
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6 340 needed.

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9 341 This work also expands on and complements previous studies on humpback whales  
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11 342 (Helweg et al., 1998; Tougaard & Eriksen, 2006; Garland et al., 2012), showing that the  
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13 343 Levenshtein distance is simple, efficiently computable and highly applicable to any  
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15 344 behavioral data that are produced in a sequence. Our results confirmed that the  
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17 345 Levenshtein distance method is a simple but powerful technique that can be applied to  
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19 346 assess stereotypy or divergence between sexes.  
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4 **543 Figure legend:**  
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7 *544 Figure 1: Spectrographic and schematic representation of an indri song.* Spectrograms  
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9 *545 of an indri song (a) showing a typical sequence of units given by one male and one*  
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11 *546 female. Schematic representation of the fundamental frequency of the descending*  
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13 *547 phrase units given by one male (b) and one female (c). Box fill patterns denote the*  
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15 *548 phrase type: black boxes mark single units (SU), horizontal lines boxes mark DP2,*  
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17 *549 diagonal lines boxes mark DP3, wavy lines boxes mark DP4, and checkered boxes mark*  
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19 *550 DP5. The spectrograms were generated in Praat with the following parameters: window*  
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21 *551 length: 0.05 s; dynamic range: 50 dB; frequency range: 0 to 10.000 Hz (a), 0 to 3.000*  
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23 *552 Hz (b,c).*  
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29 *553 Figure 2: The Levenshtein Distances showing song structuring in male and female*  
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31 *554 indris of the studied groups.* Individuals are shown on the vertical axis; sexes are shown  
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33 *555 on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker*  
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35 *556 and bigger the dots, the higher are the distances between the individual contributions to*  
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37 *557 the song. This plot was generated using the R package corrplot (vers. 0.84; Wei &*  
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39 *558 Simko, 2017).*  
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44 *559 Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight*  
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46 *560 studied groups.* Bar plot describing the individual and overall degree of stereotypy and  
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48 *561 variability expressed by the average Levenshtein Distances (LDs). Within-individual*  
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50 *562 LDs are reported for females (white bars) and males (black bars), as well as between-*  
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52 *563 individual LDs (grey bars for females, striped bars for males). Group 3 is reported twice*  
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54 *564 because the male of the reproductive pairs changed in 2014. Capped lines represent*  
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56 *565 Standard Deviation.*  
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