

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

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

This is a pre print version of the following article:

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1736268> since 2025-01-23T09:46:58Z

Published version:

DOI:10.1002/ajp.23132

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)



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

Journal:	<i>American Journal of Primatology</i>
Manuscript ID	AJP-19-0209.R2
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	25-Mar-2020
Complete List of Authors:	Zanoli, Anna; University of Torino, Life Sciences and Systems Biology De Gregorio, Chiara; University of Torino, Life Sciences and Systems Biology Valente, Daria; University of Torino, Life Sciences and Systems Biology Torti, Valeria; University of Torino, Life Sciences and Systems Biology Bonadonna, Giovanna; University of Torino, Life Sciences and Systems Biology Randrianarison, Rose Marie; GERP (Groupe d'etude et de recherche sur les primates du Madagascar) Giacoma, Cristina; University of Torino, Life Sciences and Systems Biology Gamba, Marco; University of Torino, Life Sciences and Systems Biology
Indicate which taxonomic group was the subject of your study (select all that apply or type another option)::	Prosimians
Keywords:	syntax, language evolution, primates, singing, Levenshtein distance

SCHOLARONE™
Manuscripts

1
2
3
4
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**
8
9 **4**
10 **5**

11 6 Anna Zanolì¹, Chiara De Gregorio¹, Daria Valente¹, Valeria Torti¹, Giovanna

12
13 7 Bonadonna¹, Rose Marie Randrianarison^{2,3}, Cristina Giacomini¹ & Marco Gamba¹
14
15 8

16
17
18 9 ¹Department of Life Sciences and Systems Biology, University of Torino, Torino, Italy

19
20 10 ²Groupe d'Étude et de Recherche sur les Primates de Madagascar (GERP),
21

22 11 Antananarivo, Madagascar

23
24 12 ³Mention d'Anthropobiologie et de Développement Durable (MADD), Université
25

26
27 13 d'Antananarivo, Antananarivo 101, Madagascar
28
29 14
30
31
32
33

34 16 Corresponding Author:

35
36 17 Marco Gamba¹, Department of Life Sciences and Systems Biology, University of
37

38 18 Torino, Via Accademia Albertina 13, 10123 Torino, Italy, Tel. +39 011 6704560
39

40
41 19 Email address: marco.gamba@unito.it
42
43 20
44 21
45 22
46 23
47 24
48 25
49 26
50 27
51 28
52 29
53 30
54 31
55 32
56 33
57 34
58
59
60

1
2
3
4
5
6
7 **35 Abstract**

8
9 **36**
10 **37** Animal acoustic communication often takes the form of complex sequences, composed
11
12 **38** of multiple distinct acoustic units, which can vary in their degree of stereotypy. Studies
13
14 **39** of sequence variation may contribute to our understanding of the structural flexibility of
15
16 **40** primates' songs, which can provide essential ecological and behavioral information about
17
18 **41** variability at the individual, population, and specific level and provide insights into the
19
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
23
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'
29
30 **47** contributions to the song differ in the temporal and frequency structure of song units and
31
32 **48** repertoire size. We calculated the similarity of phrase organization across different
33
34 **49** individual contributions using the Levenshtein distance, a logic distance that expressed
35
36 **50** the minimum cost to convert a sequence into another and can measure differences
37
38 **51** between two sequences of data. We then analyzed the degree of similarity within and
39
40 **52** between individuals and found that: i) the phrase structure of songs varied between
41
42 **53** reproductive males and females: female structuring of the song showed a higher number
43
44 **54** of phrases if compared to males; ii) Male contributions to the song were overall more
45
46 **55** similar to those of other males than were female contributions to the song of other
47
48 **56** females; iii) male contributions were more stereotyped than female contributions, which
49
50 **57** showed greater individual flexibility. The picture emerging from phrase combinatorics in
51
52 **58** the indris is in agreement with previous findings of rhythmic features and song repertoire
53
54
55
56
57
58
59
60

1
2
3
4 59 size of the indris, which also suggested that female songs are potentially less stereotyped
5
6 60 than those of males.
7

8
9 61

10
11 62 Keywords: syntax, language evolution, primates, singing, Levenshtein distance
12

13 63

14
15 64

16
17
18 65 **Research Highlights**

- 19
20
21 66 ● This study demonstrated that male and female adult indris differed in the phrase
22
23 67 organization of their songs.
24
25 68 ● Male contributions to the song were overall more similar to those of other males
26
27
28 69 and more stereotyped than females' ones.
29

30
31 70

32 71 **Graphical Abstract**

33
34 72 Figure 2 works as graphical abstract for this manuscript.
35
36
37
38 73
39
40
41
42 74
43
44
45
46 75
47
48
49
50 76
51
52
53
54 77
55

56
57 78 **Introduction**
58
59
60

1
2
3
4
5 79 Communication between conspecifics often involves the use of vocalizations because
6
7 80 acoustic signals allow encoding a considerable amount of information in a short time
8
9 81 (Bradbury & Vehrencamp, 2011). Animal vocal signals can be emitted in the form of
10
11 82 short vocalizations or given in sequences of variable length (Catchpole & Slater, 2008).
12
13
14 83 In addition to the well-known example of birdsong, other animals such as insects,
15
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
19
20 86 limited ability to concatenate vocal emissions in phrases when compared to humans
21
22 87 (Berwick, Okanoya, Beckers & Bolhuis, 2011), their vocal sequences may contain
23
24 88 information on species and individual identity (e.g., starlings (*Sturnus vulgaris*), wolves
25
26 89 (*Canis lupus*), dolphins (*Tursiops truncatus*), and rock hyraxes (*Procavia capensis*)).
27
28 90 Animal vocal sequences may also encode information about external cues such as
29
30 91 resource availability, e.g., food calls in chimpanzees (*Pan troglodytes*), or predator threats
31
32 92 in marmots (*Marmota* spp.; Kershenbaum et al., 2016).
33
34
35 93 The understanding of the role played by the acoustic sequences in a particular species'
36
37 94 repertoire often involves the comparison of sequences within and between individuals, as
38
39 95 well as within and between groups, so that it is possible to quantify the nature of the
40
41 96 variation and potentially correlate it to ecological and behavioral factors (Kershenbaum
42
43 97 et al., 2014).
44
45 98 So far, the studies of primate call organization focused on contact calls or alarm calls
46
47 99 (Clarke, Reichard & Zuberbühler, 2006) with scarce investigations of song structure
48
49 100 variation within contexts (Torti, Gamba, Rabemananjara & Giacoma, 2013). There is a
50
51 101 lack of information about whether primate males and females combine units in songs
52
53 102 using different phrase combinations. It is essential to examine the sex-dimorphic traits of
54
55
56
57
58
59
60

1
2
3
4
5 103 primate songs because knowledge of sex differences in song organization may be critical
6
7 104 in our understanding of what is biologically informative, especially in sexually
8
9 105 monomorphic species. Moreover, information available on the variability within a species
10
11 106 is very little (Honda & Okanoya, 1999; Takahasi, Yamada & Okanoya, 2010). Few
12
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,
16
17 109 Semple, Ferrer-i-Cancho & Bergman, 2016). While traditional methods may not apply to
18
19 110 a wide array of questions, string metrics can be used to investigate different organizational
20
21 111 levels, are entirely objective, and their results are verifiable (Heeringa, 2004).
22
23
24
25 112 Indris (*Indri indri*, Gmelin, 1788) represent a distinctive species for studying vocal
26
27 113 communication because of their rich repertoire (Maretti, Sorrentino, Finomana, Gamba
28
29 114 & Giacoma, 2010; Valente et al., 2019) and the impressive loud songs, unique among
30
31 115 lemurs (Gamba et al., 2016; Torti et al., 2017), which can be heard at a distance up to 2
32
33 116 km (Pollock, 1986). Data on sound pressure levels revealed that the sound levels of the
34
35 117 indri's song reached 110 dB (estimated at 0.50 m; Torti, *pers. obs.*). This level can be
36
37 118 compared to ring-tailed lemurs (*Lemur catta*), which showed a call amplitude ranging
38
39 119 between 85 and 89 dB (at 1 m, Macedonia, 1993). The song of the indris, which lasts 40-
40
41 120 250 s, consists of a long series of modulated units, organized in phrases (Gamba, Favaro,
42
43 121 Torti, Sorrentino & Giacoma, 2011), uttered simultaneously by males and females,
44
45 122 including juveniles, of the same group (Maretti et al., 2010). These types of units are
46
47 123 emitted exclusively during the song (Valente et al., 2019).
48
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
52
53 126 different contexts showed differences in their temporal structure that are distinguishable
54
55
56
57
58
59
60

1
2
3
4
5 127 by visual inspection of the spectrograms and by ear (Torti et al. 2013). Cohesion songs
6
7 128 were emitted when the individuals of a group were dispersed in their territory, while
8
9 129 advertisement songs were usually given when the animals of the same group were in
10
11
12 130 visual contact at the boundary of their territory (Torti et al., 2013). Cohesion songs were
13
14 131 followed by emitters traveling significantly further than following the advertisement
15
16 132 song, confirming the different functions of the song uttered in different contexts (i.e.,
17
18 133 cohesion songs bring together the members of a group, and advertisement songs inform
19
20
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
24
25 136 qualitatively, in the temporal structure of the units emitted (Giacoma, Sorrentino,
26
27 137 Rabarivola & Gamba, 2010; Sorrentino, Gamba & Giacoma, 2012). Vocal sexual
28
29 138 dimorphism is also present in the modulation of the frequency of vocal utterances, in the
30
31 139 duration of unit types and the rhythmic structure of a contribution (Gamba et al., 2016;
32
33 140 De Gregorio et al., 2018).

34
35
36
37 141 Since the indris' songs can be interpreted as a string of easily identifiable phrases (Gamba
38
39 142 et al., 2016), they represent an ideal case for the study of the variability of phrase
40
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,
46
47 146 Staicer & Inoue, 1991). The LD is a logical distance commonly used to quantify the
48
49 147 difference between two strings of data (e.g., human words, sequences of visual
50
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,
54
55 150 Nerbonne & Baayen, 2014), and it has been applied to animal vocal sequences, but for a
56
57
58
59
60

1
2
3
4
5 151 very limited number of species (Indigo bunting, *Passerina cyanea*, Margoliash et al.,
6
7 152 1991; Willow warbler, *Phylloscopus trochilus*, Gil & Slater, 2000; Humpback whale,
8
9 153 *Megaptera novaeangliae*: Helweg, Cato, Jenkins, Garrigue & McCauley, 1998; Tougaard
10
11
12 154 & Eriksen, 2006; Garland et al., 2012).

13
14 155 Although songs are often referred to as a male's prerogative, we have particular insights
15
16 156 showing that monogamous females may also use the song overlapping male song
17
18 157 functions (e.g., Eastern whip bird (*Psophodes olivaceus*), Rogers, Langmore, & Mulder,
19
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
23
24 160 (*Gymnorhina tibice* Brown & Farabaugh, 1991). Like Eastern whip birds and Australian
25
26 161 magpies, indris are monogamous (Torti et al., 2017; Bonadonna et al., 2019), form groups
27
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
31
32 164 defend resources during group encounters (Torti et al., 2013). Thus, we hypothesized that
33
34 165 the female contribution to the song would be structurally different from that of males.

35
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
39
40 168 territorial model of bird duet evolution (Farabaugh, 1982). In birds, duetting occurs most
41
42 169 commonly where birds hold year-round territories, and it is associated with sexually
43
44 170 monomorphic species that form long-term monogamous pair bonds (Riebel, Odom,
45
46 171 Langmore & Hall, 2019). Indri females showed significantly higher variation in the
47
48 172 rhythm of their contributions to the song and a higher potential to synchronize with males
49
50 173 (De Gregorio et al., 2018). Thus, we hypothesized that the adjustment in the rhythmic
51
52 174 structure of their contribution would also be reflected in a sexually dimorphic phrases
53
54
55
56
57
58
59
60

1
2
3
4 175 combination, where one should expect males to produce songs with a more stereotyped
5
6 176 structure. Similarly to pair living bird species (Rogers et al., 2007), indri females may use
7
8 177 songs for mate guarding and attraction, and song structural variability and complexity
9
10 178 may have evolved to provide conspecifics with information on females' fitness and
11
12
13 179 survival.
14

15 180

16
17
18 181

19
20
21 182

22 23 183 **Methods**

24 25 184 **Observations and recordings**

26
27
28 185 We studied 8 groups (N= 36 individuals) living in the Maromizaha Forest (18°56'49"S,
29
30 186 48°27'53"E). We recorded the animals between 2011 and 2017. We observed one social
31
32 187 group per week, from Monday to Friday approximately from 6 AM to 1 PM, when the
33
34 188 animals usually start resting and sleeping until the day after (Pollock, 1975). All
35
36 189 recordings were carried out without the use of playback stimuli, and nothing was done to
37
38 190 modify the behavior of the indris. We recorded 142 songs, consisting of duets and
39
40 191 choruses with a maximum of five individuals singing in the same song. For the analysis,
41
42 192 we only considered the contribution of the reproductive individuals, for a total of 17 focal
43
44 193 animals from eight social groups: nine reproductive adult males, and eight reproductive
45
46 194 adult females. An example of an indri song and the singers' contributions is shown in
47
48 195 Figure 1. The different number of males and females is motivated by the fact that, during
49
50 196 the study period, the reproductive male of a group changed. All the songs were recorded
51
52 197 using solid-state recorders (Olympus LS05, Tascam DR-100, Tascam DR-05) with a
53
54 198 sampling rate of 44.1 kHz (16-bit depth) during all the recording sessions. When
55
56
57
58
59
60

1
2
3
4
5
6
7 199 recording the songs, we were always at a distance between 2 and 20 m from the animals,
8
9 200 with the microphone oriented toward the focal singing individuals. We always kept visual
10
11 201 contact with the vocalizing animals and maximized our efforts to face the focal animals
12
13
14 202 during the emission of the song. Since indri songs emitted in different contexts have
15
16 203 different acoustic structure, in order to avoid any bias due to these differences, we
17
18 204 considered, from multiple years, only those songs that were labeled as advertisement
19
20 205 songs and were recorded in the same context (Torti et al., 2013). Using the focal animal
21
22 206 sampling technique (Altmann, 1974), we were able to attribute each vocalization to its
23
24 207 signaler. We will refer to every individual uttered portion within a song or a chorus as an
25
26 208 ‘individual contribution’.

27
28
29
30
31 209 During this study, we did not have any physical contact with the animals, and we recorded
32
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
46
47 217 collaborators only.

48
49
50
51
52
53 218 We adhered to applicable international, national, and/or institutional guidelines for the
54
55 219 study on animals and nonhuman primates, including the American Society of
56
57 220 Primatologist (ASP) Principle for the Ethical Treatment of nonhuman Primates, and the
58
59
60

1
2
3
4
5 221 European Union directive guidelines for the study on animals and nonhuman primates
6
7 222 (Directive 2010/63/EU). The study did not require IACUC approval.
8
9

10
11 223 **Acoustic and statistical analyses**
12

13
14 224 We edited segments containing indri songs using Praat 6.0.30 (Boersma & Weenink
15
16 225 2008) and BORIS 5.1 (Friard & Gamba 2016). For each recorded song, we created a
17
18 226 spectrogram with a view range between 0 and 5000 Hz, a window length of 0.09 s, and a
19
20 227 dynamic range of 65.0 dB. We saved each song in a single audio file in WAV format
21
22 228 (Waveform audio file format). We saved the information related to the identity of each
23
24 229 singer in a Praat textgrid. We then labeled all the vocal units (each single sound
25
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,
29
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
33
34 234 temporal structure that are distinguishable by visual inspection of the spectrograms and
35
36 235 by ear (Torti et al. 2013). We considered phrases consisting of two (DP2), three (DP3),
37
38 236 four (DP4), five (DP5), and six (DP6) units. This information was saved in Praat and
39
40 237 exported to a Microsoft© Excel spreadsheet (Gamba, Friard & Giacoma, 2012). Since all
41
42 238 the steps of the labeling process have been done by a single operator (A.Z.), we avoided
43
44 239 the possibility of encountering errors due to observer differences. To understand whether
45
46 240 there were differences in song structure between sexes, we investigated the DPs similarity
47
48 241 in each contribution. We transformed each contribution in a string of labels separated by
49
50 242 a break symbol (e.g., DP2|DP3|DP4|DP3). The resulting string represents the
51
52 243 concatenation of the phrases uttered within a contribution (and it is a measure of phrase
53
54
55
56
57
58
59
60

1
2
3
4
5
6 244 organization). From the 142 songs, we obtained 142 strings for females (with an average
7
8 245 of 17.88 songs per individual, SD = 5.44), and 119 strings for males (with an average of
9
10 246 13.22 songs per individual, SD = 5.91). Using R (R Core Team, 2015; version 3.3.3), we
11
12 247 calculated the Levenshtein distance (LD) for each pair of strings
13
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
17
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,
21
22 252 1985). We obtained a squared matrix consisting of the distances between each pair of
23
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
27
28 255 purpose, we ran Mantel tests (9999 randomizations) using a matrix featuring the average
29
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
33
34 258 (package *vegan* in R; Oksanen et al., 2013). When investigating differences at the group
35
36 259 level or within-sex, we used the non-parametric paired samples Wilcoxon test to compare
37
38 260 the average individual LDs of each member of a pair or the within- versus between-
39
40 261 individual LDs because, with such a small sample size, the Mantel test is not
41
42 262 recommended (Legendre & Fortin, 1989). Only for the Wilcoxon test, the group in which
43
44 263 the male changed was entered twice, considering the two pairs as different groups. We
45
46 264 obtained a lower number of male contributions because the reproductive females also
47
48 265 engaged in duets with immature male offspring (N = 23).
49
50
51
52
53
54
55
56
57
58 266
59
60

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 ($LD_{\text{females}} = 7.386$
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

1
2
3
4
5 289 those of males. The LDs showed that the between-individual stereotypy of male
6
7 290 contributions was higher than females' one. Males, therefore, appeared to produce songs
8
9 291 that are overall more similar to those of other males. In agreement with previous studies
10
11 292 that reported sexual dimorphism in the overall timing and repertoire size (Giacoma et al.,
12
13 293 2010), and in the frequency modulation, duration and rhythm (Gamba et al., 2016; Torti
14
15 294 et al., 2017, De Gregorio et al., 2018), we found that male and female indris also differed
16
17 295 in the phrase organization of their songs. Female structuring of the song showed a higher
18
19 296 number of phrases if compared to males, independently of the phrases being of the same
20
21 297 or different type. This result is in line with previous studies on family-living and pair-
22
23 298 bonded primate and bird species (Deputte, 1982; Savage, Snowdon, Giraldo & Soto,
24
25 299 1996; Snowdon, 2017; Riebel et al., 2019; Levin, 1996a; 1996b), endorsing that in a
26
27 300 socially monogamous, monomorphic species which holds year-round territories, sex
28
29 301 differences in vocal output are frequent (Marshall & Marshall, 1976). Furthermore,
30
31 302 despite the fact that songs are considered to be males' peculiar features (Cowlshaw,
32
33 303 1996), our results confirm that also monogamous females use songs and that female song
34
35 304 can be more elaborate than those of males. Female song phrase concatenation is more
36
37 305 complex than males' because even if males are playing the primary role in territorial
38
39 306 defense, females' role in territorial disputes can be essential. Female songs may be critical
40
41 307 for advertising their identity as well as resources holding potential. For instance, vocal
42
43 308 fights, in which females and males are singing together, are often sufficient to resolve
44
45 309 group encounters, reducing the occurrence of physical fights (Bonadonna et al., 2020).
46
47 310 Future studies may investigate whether female dispersal distance and territorial changes
48
49 311 over the years may contribute to a deeper understanding of this sex-dimorphic variation.
50
51 312 Expanding previous findings that showed how indri female contribution to the song was
52
53
54
55
56
57
58
59
60

1
2
3
4
5 313 more varied in the rhythm (De Gregorio et al., 2018), we showed that the combination
6
7 314 and repertoire of the phrases are also more extensive than those shown by males. Females
8
9 315 not only have a broader repertoire of units, but they also emit descending phrases that we
10
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
16
17 319 assessed at a distance by conspecifics.

20
21 320 In agreement with previous findings on the different role of males and females during the
22
23 321 song (Giacoma et al., 2010), we found that female song is potentially more distinctive
24
25 322 than the male one. These results are in agreement with previous findings on birds (Brown
26
27 323 & Farabaugh, 1991), confirming that in those species in which females are involved in
28
29 324 territorial defense, their repertoires are as large or larger than those of males, on the level
30
31 325 of both units and phrases. Territorial defense is crucial for survival and reproduction in
32
33 326 pair-bonding species that occupy stable territories, and even if female involvement in
34
35 327 territorial defense is different from that of the reproductive male, they participate in
36
37 328 joining with their partner. An increasing body of literature (e.g., Hall, Rittenbach, &
38
39 329 Vehrencamp, 2015) supported the view that same-sex competition is the primary driver
40
41 330 of female song elaboration. It can be the case of the indris, where females may benefit
42
43 331 from multiple mating partners to increase tolerance by neighboring males (Bonadonna et
44
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
50
51 335 a critical role in determining the characteristics of DPs in males, whereas it may have a
52
53 336 lesser impact on female songs (Torti et al., 2017). A more variable song structure may
54
55
56
57
58
59
60

1
2
3
4 337 add up to a more flexible structuring of the phrase notes, but further investigations are
5
6 338 needed.

7
8
9 339 This work also expands on and complements previous studies on humpback whales
10
11 340 (Helweg et al., 1998; Tougaard & Eriksen, 2006; Garland et al., 2012), showing that the
12
13 341 Levenshtein distance is simple, efficiently computable and highly applicable to any
14
15 342 behavioral data that are produced in a sequence. Our results confirmed that the
16
17 343 Levenshtein distance method is a simple but powerful technique that can be applied to
18
19 344 assess stereotypy or divergence between sexes.
20
21
22
23
24
25
26
27

28 346 **Acknowledgements**

29
30
31 347 We thank two anonymous Reviewers and the Editor for their careful reading of our
32
33 348 manuscript and their many insightful comments and suggestions. This research was
34
35 349 supported by Università degli Studi di Torino and by grants from the Parco Natura Viva—
36
37 350 Centro Tutela Specie Minacciate. We are grateful to GERP and Dr Jonah Ratsimbazafy.
38
39 351 We thank Dr, Cesare Avesani Zaborra and Dr Caterina Spiezio for helping us with the
40
41 352 organization of the field station in Maromizaha. We are grateful to the researchers and
42
43 353 the international guides, for their help and logistical support. We also thank San Diego
44
45 354 Zoo Global, LDVI, Dr Chia L. Tan.
46
47
48
49
50

51 355

52
53
54 356

55
56
57
58 357
59
60

358 **References**

- 359 Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49,
360 227-267. DOI: 10.1163/156853974X00534
- 361 Berwick, R. C., Okanoya, K., Beckers, G. J. L., & Bolhuis, J. J. (2011). Songs to
362 syntax: the linguistics of birdsong. *Trends in Cognitive Sciences*, 15, 113-121. DOI:
363 10.1016/j.tics.2011.01.002
- 364 Boersma, P., & Weenink, D. (2005). Praat: doing phonetics by computer [Computer
365 program].
- 366 Bonadonna, G., Torti, V., Sorrentino, V., Randrianarison, R. M., Zaccagno, M., Gamba,
367 M., & Giacoma, C. (2017). Territory exclusivity and intergroup encounters in the indris
368 (Mammalia: Primates: Indridae: *Indri indri*) upon methodological tuning. *The European*
369 *Zoological Journal*, 84, 238-251. DOI: 10.1080/24750263.2017.1318184
- 370 Bonadonna, G., Torti, V., De Gregorio, C., Valente, D., Randrianarison, R. M., Pozzi,
371 L., M., Gamba, M., & Giacoma, C. (2019). Evidence of genetic monogamy in the lemur
372 Indri (*Indri indri*). *American Journal of Primatology*, 81(6), e22993. DOI:
373 10.1002/ajp.22993
- 374 Bonadonna, G., Zaccagno, M., Torti, V., Valente, D., De Gregorio, C., Randrianarison,
375 R. M., ... & Giacoma, C. (2020). Intra-and Intergroup Spatial Dynamics of a Pair-Living
376 Singing Primate, Indri indri: A Multiannual Study of Three Indri Groups in
377 Maromizaha Forest, Madagascar. *International Journal of Primatology*, 1-22. DOI:
378 10.1007/s10764-019-00127-5

- 1
2
3
4 379 Bradbury, J.W., & Vehrencamp, S.L. (2011). Principles of animal communication.
5
6 380 Sinauer, Sunderland.
7
8
9
10 381 Brown, E. D., & Farabaugh, S. M. (1991). Song sharing in a group-living songbird, the
11
12 382 Australian magpie, *Gymnorhina tibicen*. Part III. Sex specificity and individual
13
14 383 specificity of vocal parts in communal chorus and duet songs. *Behaviour*, 118, 244-274.
15
16
17
18 384 Catchpole, C. K., & Slater, P. J. R. (2008). Bird song: biological themes and variations.
19
20 385 Cambridge University Press, Cambridge.
21
22
23 386 Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild
24
25 387 gibbon songs. *PloS one*, 1(1), e73. DOI: 10.1371/journal.pone.0000073
26
27
28
29 388 Cowlshaw, G. U. Y. (1996). Sexual selection and information content in gibbon song
30
31 389 bouts. *Ethology*, 102(2), 272-284. DOI: 10.1111/j.1439-0310.1996.tb01125.x
32
33
34
35 390 De Gregorio, C., Zanolli, A., Valente, D., Torti, V., Bonadonna, G., Randrianarison, R.
36
37 391 M., Giacoma, C., & Gamba, M. (2019). Female indris determine the rhythmic structure
38
39 392 of the song and sustain a higher cost when the chorus size increases. *Current Zoology*,
40
41 393 65, 89-97. DOI: 10.1093/cz/zoy058
42
43
44
45 394 Deputte, B. L. (1982). Duetting in male and female songs of the white-cheeked gibbon
46
47 395 (*Hylobates concolor leucogenys*). In C. T. Snowdon, C. H. Brown, & M. R. Petersen
48
49 396 (Eds.), *Primate communication* (pp. 67–93). New York: Cambridge University Press.
50
51
52
53 397 Farabaugh, S. M. (1982). The ecological and social significance of duetting. In: D. E.
54
55 398 Kroodsma & E. H. Miller (Eds.), *Acoustic Communication in Birds Vol. 2.* (pp. 85-124).
56
57
58 399 New York, USA: Academic Press.
59
60

- 1
2
3
4
5
6
7 400 Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging
8
9 401 software for video/audio coding and live observations. *Methods in Ecology and*
10
11 402 *Evolution*, 7, 1325–1330. DOI:10.1111/2041-210X.12584
12
13
14
15 403 Gamba, M., Favaro, L., Torti, V., Sorrentino, V., & Giacoma, C. (2011). Vocal tract
16
17 404 Flexibility and variation in the vocal output in wild indris. *Bioacoustics*, 20, 251-265.
18
19 405 DOI: 10.1080/09524622.2011.9753649
20
21
22
23 406 Gamba, M., Friard, O., & Giacoma, C. (2012). Vocal tract morphology determines
24
25 407 species-specific features in vocal signals of lemurs (*Eulemur*). *International Journal of*
26
27 408 *Primatology*, 33(6), 1453-1466. DOI:10.1007/s10764-012-9635-y
28
29
30
31 409 Gamba, M., Torti, V., Estienne, V., Randrianarison, R. M., Valente, D., Rovara, P., &
32
33 410 Giacoma, C. (2016). The indris have got rhythm! Timing and pitch variation of a
34
35 411 primate song examined between sexes and age classes. *Frontiers in neuroscience*, 10,
36
37 412 249. DOI: 10.3389/fnins.2016.00249
38
39
40
41
42 413 Garland, E. C., Lilley, M. S., Goldizen, A. W., Rekdahl, M. L., Garrigue, C., & Noad,
43
44 414 M. J. (2012). Improved versions of the Levenshtein distance method for comparing
45
46 415 sequence information in animals' vocalisations: tests using humpback whale song.
47
48 416 *Behaviour*, 149, 1413–1441. DOI: 10.1163/1568539X-00003032
49
50
51
52 417 Giacoma, C., Sorrentino, V., Rabarivola, C., & Gamba, M. (2010). Sex differences in
53
54 418 the song of *Indri indri*. *International Journal of Primatology*, 31, 539-551. DOI:
55
56 419 10.1007/s10764-010-9412-8
57
58
59
60

- 1
2
3
4 420 Gil, D., & Slater, P. J. (2000). Song organisation and singing patterns of the willow
5
6 421 warbler, *Phylloscopus trochilus*. *Behaviour*, 137(6), 759-782.
7
8
9
10 422 Gooskens, C. & Heeringa, W. (2004). Perceptive evaluation of Levenshtein dialect
11
12 423 distance measurements using Norwegian dialect data. *Language variation and change*,
13
14 424 16, 189-207. DOI: 10.1017/S0954394504163023
15
16
17
18 425 Gmelin, J. F. (1788). *Systema naturæ: per Regna tria naturæ, secundum classes*,
19
20 426 *ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (Vol. 1, No.
21
22 427 6). Beer.
23
24
25
26 428 Gustison, M. L., Semple, S., Ferrer-i-Cancho, R., & Bergman, T. J. (2016). Gelada
27
28 429 vocal sequences follow Menzerath's linguistic law. *Proceedings of the National*
29
30 430 *Academy of Sciences*, 113, E2750-E2758. DOI: 10.1073/pnas.1522072113
31
32
33
34 431 Hall, M. L., Rittenbach, M. R., & Vehrencamp, S. L. (2015). Female song and vocal
35
36 432 interactions with males in a neotropical wren. *Frontiers in Ecology and Evolution*, 3,
37
38 433 12. DOI: 10.3389/fevo.2015.00012
39
40
41
42 434 Heeringa, W. J. (2004). Measuring dialect pronunciation differences using Levenshtein
43
44 435 distance (Doctoral dissertation, University Library Groningen).
45
46
47
48 436 Helweg, D. A., Cato, D. H., Jenkins, P. F., Garrigue, C., & McCauley, R. D. (1998).
49
50 437 Geographic variation in South Pacific humpback whale songs. *Behaviour*, 135, 1-27.
51
52 438 DOI: 10.1163/156853998793066438
53
54
55
56 439 Honda, E. & Okanoya, K. (1999). Acoustical and syntactical comparisons between
57
58 440 songs of the white-backed Munia (*Lonchura striata*) and its domesticated strain, the
59
60

- 1
2
3
4
5
6 441 Bengalese finch (*Lonchura striata* var. *domestica*). *Zoological Science*, 16, 319-326.
7
8 442 DOI: 10.2108/zsj.16.319
9
10
11
12 443 Kershenbaum, A., Blumstein, D. T., Roch, M. A., Akçay, Ç., Backus, G., Bee, M. A., ...
13
14 444 & Coen, M. (2016). Acoustic sequences in non-human animals: a tutorial review and
15
16 445 prospectus. *Biological Reviews*, 91(1), 13-52. DOI: [10.1111/brv.12160](https://doi.org/10.1111/brv.12160)
17
18
19
20 446 Kershenbaum, A. & Garland, E. C. (2015). Quantifying similarity in animal vocal
21
22 447 sequences: which metric performs best? *Methods in Ecology and Evolution*, 6, 1452-
23
24 448 1461. DOI: [10.1111/2041-210X.12433](https://doi.org/10.1111/2041-210X.12433)
25
26
27
28 449 Kershenbaum, A., Bowles, A. E., Freeberg, T. M., Jin, D. Z., Lameira, A. R., & Bohn,
29
30 450 K. (2014). Animal vocal sequences: not the Markov chains we thought they
31
32 451 were. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792), 20141370.
33
34 452 DOI: [10.1098/rspb.2014.1370](https://doi.org/10.1098/rspb.2014.1370)
35
36
37
38 453 Kohonen, T. (1985). Median strings. *Pattern Recognition Letters*, 3, 309-313. DOI:
39
40 454 [10.1016/0167-8655\(85\)90061-3](https://doi.org/10.1016/0167-8655(85)90061-3)
41
42
43
44 455 Krull, C. R., Ranjard, L., Landers, T. J., Ismar, S. M., Matthews, J. L., & Hauber, M. E.
45
46 456 (2012). Analyses of sex and individual differences in vocalizations of Australasian
47
48 457 gannets using a dynamic time warping algorithm. *The Journal of the Acoustical Society*
49
50 458 *of America*, 32, 1189- 98. DOI: [10.1121/1.4734237](https://doi.org/10.1121/1.4734237)
51
52
53
54 459 Legendre, P., & Fortin, M. J. (1989). Spatial pattern and ecological
55
56 460 analysis. *Vegetatio*, 80(2), 107-138.
57
58
59
60

- 1
2
3
4
5
6
7
8 461 Levin, R. N. (1996a). Song behaviour and reproductive strategies in a duetting wren,
9
10 462 *Thryothorus nigricapillus*: I. Removal experiments. *Animal Behaviour*, 52, 1093-1106.
11
12
13 463 DOI: 10.1006/anbe.1996.0257
14
15
16 464 Levin, R. N. (1996b). Song behaviour and reproductive strategies in a duetting wren,
17
18 465 *Thryothorus nigricapillus*: II Playback experiments. *Animal Behaviour*, 52, 1107-1117.
19
20
21 466 DOI: 10.1006/anbe.1996.0258
22
23
24 467 Logue, D. M., & Gammon, D. E. (2004). Duet song and sex roles during territory
25
26 468 defence in a tropical bird, the black-bellied wren, *Thryothorus fasciatoventris*. *Animal*
27
28 469 *Behaviour*, 68(4), 721-731. DOI: 10.1016/j.anbehav.2003.10.026
29
30
31
32 470 Macedonia, J. M. (1993). The vocal repertoire of the ring-tailed lemur (Lemur
33
34 471 catta). *Folia primatologica*, 61(4), 186-217.
35
36
37
38 472 Maretti, G., Sorrentino, V., Finomana, A., Gamba, M., & Giacomini, C. (2010). Not just
39
40 473 a pretty song: an overview of the vocal repertoire of *Indri indri*. *Journal of*
41
42 474 *Anthropological Sciences*, 88, 151-165.
43
44
45
46 475 Margoliash, D., Staicer, C. A., & Inoue, S. A. (1991). Stereotyped and plastic song in
47
48 476 adult indigo buntings, *Passerina cyanea*. *Animal Behaviour*, 42, 367-388. DOI:
49
50 477 10.1016/S0003-3472(05)80036-3
51
52
53
54 478 Marshall, J. T., & Marshall, E. R. (1976). Gibbons and their territorial songs. *Science*,
55
56 479 193, 235-237.
57
58
59
60

- 1
2
3
4 480 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., ...
5
6 481 & Oksanen, M. J. (2013). Package 'vegan'. *Community ecology package, version, 2(9)*,
7
8 482 1-295.
9
10
11
12 483 Pollock, J. I. (1975). *The social behaviour and ecology of Indri indri* (Doctoral
13
14 484 dissertation, University of London).
15
16
17
18 485 Pollock, J. I. (1986). The song of the Indris (*Indri indri*; Primates: Lemuroidea): natural
19
20 486 history, form and function. *International Journal of Primatology, 7*, 225–267. DOI:
21
22 487 10.1007/BF02736391
23
24
25
26 488 R Core Team (2015). *R: A Language and Environment for Statistical Computing*.
27
28 489 Vienna: R Foundation for Statistical Computing. Available online at: [http://www.R-
31
32
33
34 491 Riebel, K., Odom, K. J., Langmore, N. E., & Hall, M. L. \(2019\). New insights from
35
36 492 female bird song: towards an integrated approach to studying male and female
37
38 493 communication roles. *Biology letters, 15\(4\)*, 20190059. DOI: 10.1098/rsbl.2019.0059
39
40
41
42 494 Rogers, A. C., Langmore, N. E., & Mulder, R. A. \(2007\). Function of pair duets in the
43
44 495 eastern whipbird: cooperative defense or sexual conflict?. *Behavioral Ecology, 18\(1\)*,
45
46 496 182-188. DOI:10.1093/beheco/arl070
47
48
49
50 497 Savage, A., Snowdon, C. T., Giraldo, H., & Soto, H. \(1996\). Parental care patterns and
51
52 498 vigilance in wild cotton-top tamarins \(*Saguinus oedipus*\). In M. Norconk, A.
53
54 499 Rosenberger, & P. A. Garber \(Eds.\), *Adaptive radiations of neotropical primates* \(pp.
55
56 500 187–199\). New York: Plenum Press.
57
58
59
60](http://www.R-
29
30 490 project.org/)

- 1
2
3
4 501 Snowdon, C. T. (2017). Vocal communication in family-living and pair-bonded
5
6 502 primates. In *Primate Hearing and Communication* (pp. 141-174). Springer, Cham.
7
8
9
10 503 Sorrentino, V., Gamba, M., & Giacoma, C. (2012). A quantitative description of the
11
12 504 vocal types emitted in the indri's song. *Leaping ahead: advances in prosimian biology*,
13
14 505 315-322. DOI: 10.1007/978-1-4614-4511-1_35
15
16
17
18 506 Takahasi, M., Yamada, H., & Okanoya, K. (2010). Statistical and Prosodic Cues for
19
20 507 Song Segmentation Learning by Bengalese Finches (*Lonchura striata* var. *domestica*).
21
22 508 *Ethology*, 116, 481–489. DOI: 10.1111/j.1439-0310.2010.01772.x
23
24
25
26 509 Thalmann, U., Geissmann, T., Simona, A., & Mutschler, T. (1993). The indris of
27
28 510 Anjanaharibe-Sud, northeastern Madagascar. *International Journal of*
29
30 511 *Primatology*, 14(3), 357-381.
31
32
33
34 512 Torti, V., Gamba, M., Rabemananjara, Z. H., & Giacoma, C. (2013). The songs of the
35
36 513 indris (Mammalia: Primates: Indridae): contextual variation in the long-distance calls of
37
38 514 a lemur. *Italian Journal of Zoology*, 80, 596-607. DOI: 10.1080/11250003.2013.845261
39
40
41
42 515 Torti, V., Bonadonna, G., De Gregorio, C., Valente, D., Randrianarison, R. M., Friard,
43
44 516 O., ... Giacoma, C. (2017). An intra-population analysis of the indris' song dissimilarity
45
46 517 in the light of genetic distance. *Scientific reports*, 7, 10140. DOI: 10.1038/s41598-017-
47
48 518 10656-9
49
50
51
52 519 Tougaard, J., & Eriksen, N. (2006) Analysing differences among animal songs
53
54 520 quantitatively by means of the Levenshtein distance measure. *Behaviour*, 143, 239-252.
55
56
57 521 DOI: 10.1163/156853906775900685
58
59
60

- 1
2
3
4 522 Valente, D., De Gregorio, C., Torti, V., Miaretsoa, L., Friard, O., ... Gamba M. (2019).
5
6 523 Finding Meanings in low dimensional structures: Stochastic Neighbor Embedding
7
8 524 applied to the analysis of *Indri indri* vocal repertoire. *Animals*, 9, 5, 243. DOI:
9
10 525 10.3390/ani9050243
11
12
13
14 526 van der Loo, M. (2014). The stringdist package for approximate string matching. *The R*
15
16 527 *Journal*, 6, 111-122. <https://CRAN.R-project.org/package=stringdist>
17
18
19
20 528 Wei, T., & Simko, V. (2017). R package "corrplot": Visualization of a Correlation
21
22 529 Matrix. <https://github.com/taiyun/corrplot>
23
24
25
26 530 Wieling, M., Montemagni, S., Nerbonne, J., & Baayen, R. H. (2014). Lexical
27
28 531 differences between Tuscan dialects and standard Italian: Accounting for geographic
29
30 532 and sociodemographic variation using generalized additive mixed modeling. *Language*,
31
32 533 90, 669-692. DOI: 10.1353/lan.2014.0064
33
34
35
36 534
37
38
39
40 535
41
42
43 536
44
45
46
47 537
48
49
50 538
51
52
53 539
54
55
56
57 540
58
59
60

1
2
3
4 541 **Figure legend:**
5
6

7 542 *Figure 1: Spectrographic and schematic representation of an indri song.* Spectrograms
8
9 543 of an indri song (a) showing a typical sequence of units given by one male and one
10
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).
24
25
26
27
28

29 551 *Figure 2: The Levenshtein Distances showing song structuring in male and female*
30
31 552 *indris of the studied groups.* Individuals are shown on the vertical axis; sexes are shown
32
33 553 on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker
34
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).
40
41
42
43

44 557 *Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight*
45
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
49
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
55
56 563 Standard Deviation.
57
58
59
60

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

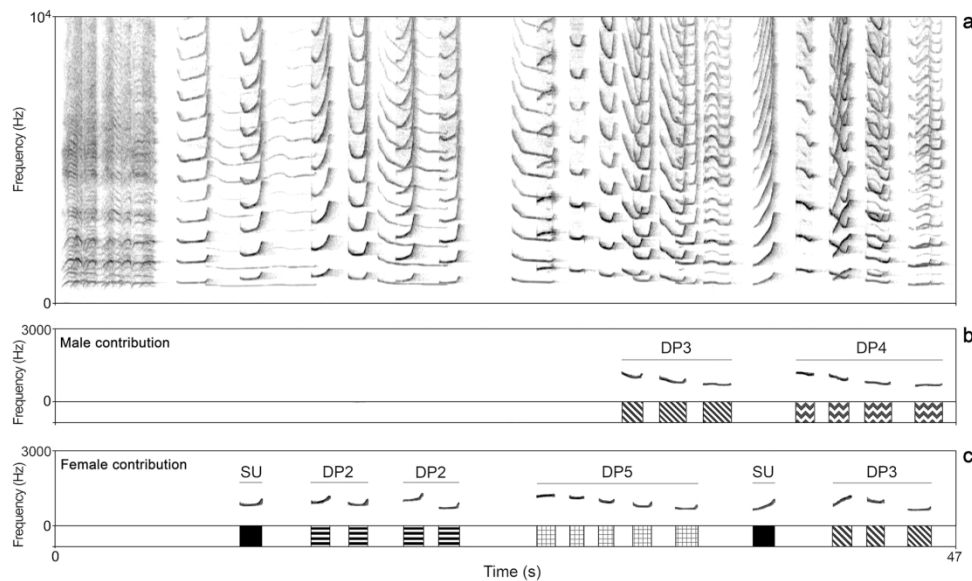


Figure 1: Spectrographic and schematic representation of an indri song. Spectrograms of an indri song (a) showing a typical sequence of units given by one male and one female. Schematic representation of the fundamental frequency of the descending phrase units given by one male (b) and one female (c).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

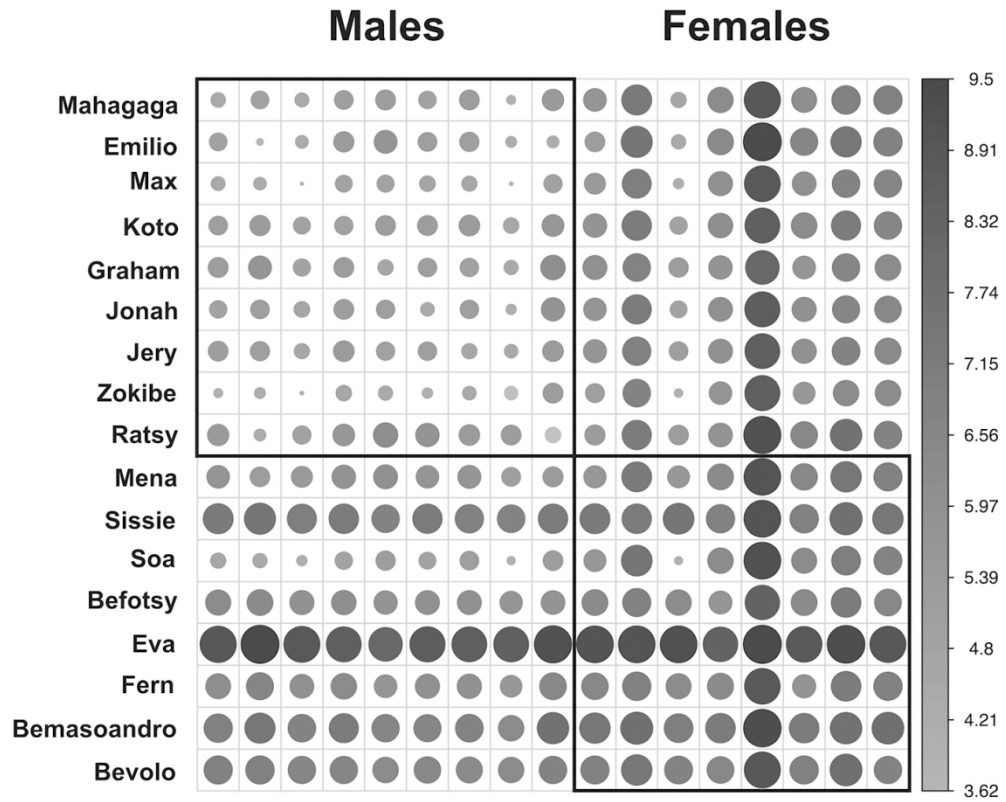


Figure 2: The Levenshtein Distances showing song structuring in male and female indris of the studied groups. Individuals are shown on the vertical axis; sexes are shown on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker and bigger the dots, the higher are the distances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

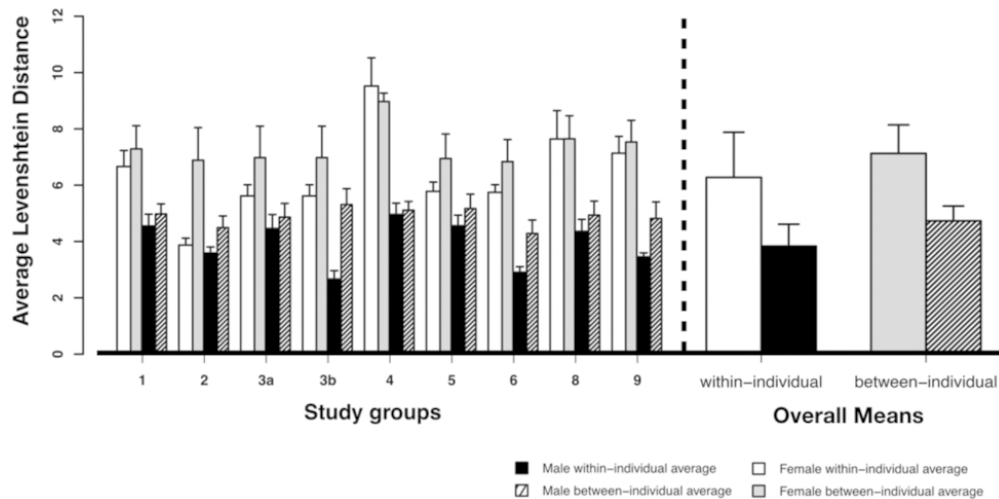


Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight studied groups. Bar plot describing the individual and overall degree of stereotypy and variability expressed by the average Levenshtein Distances (LDs). Within-individual LDs are reported for females (white bars) and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

1
2
3
4
5 **Sexually dimorphic phrase organization in the song of the indris (*Indri indri*)**

6
7
8 **Running title: Phrase organization in the indris**

9
10
11 Anna Zanolì¹, Chiara De Gregorio¹, Daria Valente¹, Valeria Torti¹, Giovanna

12
13 Bonadonna¹, Rose Marie Randrianarison^{2,3}, Cristina Giacomini¹ & Marco Gamba¹

14
15
16
17
18 ¹ Department of Life Sciences and Systems Biology, University of Torino, Torino, Italy

19
20 ² Groupe d'Étude et de Recherche sur les Primates de Madagascar (GERP),

21
22 Antananarivo, Madagascar

23
24 ³ Mention d'Anthropobiologie et de Développement Durable (MADD), Université

25
26 d'Antananarivo, Antananarivo 101, Madagascar

27
28
29
30
31
32
33
34 Corresponding Author:

35
36 Marco Gamba¹, Department of Life Sciences and Systems Biology, University of

37
38 Torino, Via Accademia Albertina 13, 10123 Torino, Italy, Tel. +39 011 6704560

39
40
41 Email address: marco.gamba@unito.it

1
2
3
4
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**
11
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**
15
16 42 **mechanisms and drivers responsible for the evolutionary change of communicative traits.**
17
18 43 ~~Several methods have been used for investigating different levels of structural~~
19
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
25
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
35
36 52 expressed the minimum cost to convert a sequence into another and can measure
37
38 53 differences between two sequences of data. We then analyzed the degree of similarity
39
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**
43
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**
47
48 58 **females;** iii) **male contributions were more stereotyped than female contributions, which**
49
50 59 **showed greater individual flexibility.** The picture emerging from phrase combinatorics in
51
52
53
54
55
56
57
58
59
60

1
2
3
4 60 the indris is in agreement with previous findings of rhythmic features and song repertoire
5
6 61 size of the indris, which also suggested that female songs are potentially less stereotyped
7
8
9 62 than those of males.

10
11 63 Keywords: syntax, language evolution, primates, singing, Levenshtein distance
12
13
14
15
16
17
18
19

64

65

66 **Research Highlights**

- 20
21 67 ● This study demonstrated that male and female adult indris differed in the phrase
22
23 68 organization of their songs.
24
25
26 69 ● Male contributions to the song were overall more similar to those of other males
27
28 70 and more stereotyped than females' ones.
29

30
31
32
33

72 **Graphical Abstract**

34
35 73 Figure 2 works as graphical abstract for this manuscript.
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

74

75

76

77

78

79

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

1
2
3
4
5 104 using different phrase combinations. It is essential to examine the sex-dimorphic traits of
6
7 105 primate songs because knowledge of sex differences in song organization may be critical
8
9 106 in our understanding of what is biologically informative, especially in sexually
10
11 107 monomorphic species. Moreover, information available on the variability within a species
12
13
14 108 is very little (Honda & Okanoya, 1999; Takahasi, Yamada & Okanoya, 2010). Few
15
16 109 investigations on primate vocal sequences are currently available and none of them are
17
18 110 evaluating the stereotypy of song structure between sexes using a string metric (Gustison,
19
20 111 Semple, Ferrer-i-Cancho & Bergman, 2016). While traditional methods may not apply to
21
22 112 a wide array of questions, string metrics can be used to investigate different organizational
23
24 113 levels, are entirely objective, and their results are verifiable (Heeringa, 2004).
25
26
27 114 Indris (*Indri indri*, Gmelin, 1788) represent a distinctive species for studying vocal
28
29 115 communication because of their rich repertoire (Maretti, Sorrentino, Finomana, Gamba
30
31 116 & Giacoma, 2010; Valente et al., 2019) and the impressive loud songs, unique among
32
33 117 lemurs (Gamba et al., 2016; Torti et al., 2017), which can be heard at a distance up to 2
34
35 118 km (Pollock, 1986). Data on sound pressure levels revealed that the sound levels of the
36
37 119 indri's song reached 110 dB (estimated at 0.50 m; Torti, *pers. obs.*). This level can be
38
39 120 compared to ring-tailed lemurs (*Lemur catta*), which showed a call amplitude ranging
40
41 121 between 85 and 89 dB (at 1 m, Macedonia, 1993). The song of the indris, which lasts 40-
42
43 122 250 s, consists of a long series of modulated units, organized in phrases (Gamba, Favaro,
44
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).
50
51 126 Previous research showed that the indris can emit songs in different contexts and that the
52
53 127 song can elicit different behaviors depending on its acoustic structure. Songs given in
54
55
56
57
58
59
60

1
2
3
4
5 128 different contexts showed differences in their temporal structure that are distinguishable
6
7 129 by visual inspection of the spectrograms and by ear (Torti et al. 2013). Cohesion songs
8
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
16
17 134 song, confirming the different functions of the song uttered in different contexts (i.e.,
18
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
22
23 137 that male and female contributions to the song differ, both quantitatively and
24
25 138 qualitatively, in the temporal structure of the units emitted (Giacoma, Sorrentino,
26
27 139 Rabarivola & Gamba, 2010; Sorrentino, Gamba & Giacoma, 2012). Vocal sexual
28
29 140 dimorphism is also present in the modulation of the frequency of vocal utterances, in the
30
31 141 duration of unit types and the rhythmic structure of a contribution (Gamba et al., 2016;
32
33 142 De Gregorio et al., 2018).
34
35 143 Since the indris' songs can be interpreted as a string of easily identifiable phrases (Gamba
36
37 144 et al., 2016), they represent an ideal case for the study of the variability of phrase
38
39 145 concatenation in primate songs. Among the methods for investigating different levels of
40
41 146 structural variation in acoustic displays, we chose the Levenshtein distance, which is a
42
43 147 quantitative method for measuring the similarity of sequences (hereafter LD; Margoliash,
44
45 148 Staicer & Inoue, 1991). The LD is a logical distance commonly used to quantify the
46
47 149 difference between two strings of data (e.g., human words, sequences of visual
48
49 150 movements or sequences of song themes; Gooskens & Heeringa, 2004). This technique
50
51 151 has often been used to measure similarity in human dialects (Wieling, Montemagni,
52
53
54
55
56
57
58
59
60

1
2
3
4
5 152 Nerbonne & Baayen, 2014), and it has been applied to animal vocal sequences, but for a
6
7 153 very limited number of species (Indigo bunting, *Passerina cyanea*, Margoliash et al.,
8
9 154 1991; Willow warbler, *Phylloscopus trochilus*, Gil & Slater, 2000; Humpback whale,
11
12 155 *Megaptera novaeangliae*: Helweg, Cato, Jenkins, Garrigue & McCauley, 1998; Tougaard
13
14 156 & Eriksen, 2006; Garland et al., 2012).

15
16 157 Although songs are often referred to as a male's prerogative, we have particular insights
17
18 158 showing that monogamous females may also use the song overlapping male song
19
20 159 functions (e.g., Eastern whip bird (*Psophodes olivaceus*), Rogers, Langmore, & Mulder,
21
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
25
26 162 (*Gymnorhina tibice* Brown & Farabaugh, 1991). Like Eastern whip birds and Australian
27
28 163 magpies, indris are monogamous (Torti et al., 2017; Bonadonna et al., 2019), form groups
29
30 164 that occupy non-overlapping areas in the forest (Bonadonna et al., 2017), and use the
31
32 165 songs to inform neighboring groups about the occupation of a territory and to actively
33
34 166 defend resources during group encounters (Torti et al., 2013). Thus, we hypothesized that
35
36 167 the female contribution to the song would be structurally different from that of males.

37
38 168 Studies of song structure in bird duets also suggested that females' songs would be more
39
40 169 acoustically variable than that of males (Logue & Gammon, 2004), in line with the
41
42 170 territorial model of bird duet evolution (Farabaugh, 1982). In birds, duetting occurs most
43
44 171 commonly where birds hold year-round territories, and it is associated with sexually
45
46 172 monomorphic species that form long-term monogamous pair bonds (Riebel, Odom,
47
48 173 Langmore & Hall, 2019). Indri females showed significantly higher variation in the
49
50 174 rhythm of their contributions to the song and a higher potential to synchronize with males
51
52 175 (De Gregorio et al., 2018). Thus, we hypothesized that the adjustment in the rhythmic
53
54
55
56
57
58
59
60

1
2
3
4 176 structure of their contribution would also be reflected in a sexually dimorphic phrases
5
6 177 combination, where one should expect males to produce songs with a more stereotyped
7
8 178 structure. Similarly to pair living bird species (Rogers et al., 2007), indri females may use
9
10 179 songs for mate guarding and attraction, and song structural variability and complexity
11
12
13 180 may have evolved to provide conspecifics with information on females' fitness and
14
15 181 survival.
16
17
18 182
19
20
21 183
22
23 184
24
25

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

1
2
3
4
5 200 sampling rate of 44.1 kHz (16-bit depth) during all the recording sessions. When
6
7 201 recording the songs, we were always at a distance between 2 and 20 m from the animals,
8
9 202 with the microphone oriented toward the focal singing individuals. We always kept visual
10
11 203 contact with the vocalizing animals and maximized our efforts to face the focal animals
12
13 204 during the emission of the song. Since indri songs emitted in different contexts have
14
15 205 different acoustic structure, in order to avoid any bias due to these differences, we
16
17 206 considered, from multiple years, only those songs that were labeled as advertisement
18
19 207 songs and were recorded in the same context (Torti et al., 2013). Using the focal animal
20
21 208 sampling technique (Altmann, 1974), we were able to attribute each vocalization to its
22
23 209 signaler. We will refer to every individual uttered portion within a song or a chorus as an
24
25 210 ‘individual contribution’.

26
27
28
29
30
31 211 During this study, we did not have any physical contact with the animals, and we recorded
32
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°
36
37 214 274/11/MEF/SG/D GF/DCB.SAP/SCB, 2012 N°245/12/MEF/SG/DGF/DCB.SAP/SCB,
38
39 215 2014 - N°066/14/MEF/SG/DGF/DCB.SAP/SCB, 2015 - N° 180/ 15/ MEEMF/ SG/ DGF/
40
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
46
47 219 collaborators only.

48
49
50
51
52
53 220 We adhered to applicable international, national, and/or institutional guidelines for the
54
55 221 study on animals and nonhuman primates, including the American Society of
56
57 222 Primatologist (ASP) Principle for the Ethical Treatment of nonhuman Primates, and the
58
59
60

1
2
3
4
5 223 European Union directive guidelines for the study on animals and nonhuman primates
6
7 224 (Directive 2010/63/EU). The study did not require IACUC approval.
8
9

10
11 225 **Acoustic and statistical analyses**
12

13
14 226 We edited segments containing indri songs using Praat 6.0.30 (Boersma & Weenink
15
16 227 2008) and BORIS 5.1 (Friard & Gamba 2016). For each recorded song, we created a
17
18 228 spectrogram with a view range between 0 and 5000 Hz, a window length of 0.09 s, and a
19
20 229 dynamic range of 65.0 dB. We saved each song in a single audio file in WAV format
21
22 230 (Waveform audio file format). We saved the information related to the identity of each
23
24 231 singer in a Praat textgrid. We then labeled all the vocal units (each single sound
25
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,
29
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**
33
34 236 **temporal structure that are distinguishable by visual inspection of the spectrograms and**
35
36 237 **by ear (Torti et al. 2013).** We considered phrases consisting of two (DP2), three (DP3),
37
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
47
48 243 in each contribution. We transformed each contribution in a string of labels separated by
49
50 244 a break symbol (e.g., DP2|DP3|DP4|DP3). The resulting string represents the
51
52 245 concatenation of the phrases uttered within a contribution (and it is a measure of phrase
53
54
55
56
57
58
59
60

1
2
3
4
5
6 246 organization). From the 142 songs, we obtained 142 strings for females (with an average
7
8 247 of 17.88 songs per individual, SD = 5.44), and 119 strings for males (with an average of
9
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
19
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
23
24 255 strings, then averaged LDs and calculated within- and between-individual means (Fig. 2),
25
26 256 to investigate whether females and males differed in their degree of variation. For this
27
28 257 purpose, we ran Mantel tests (9999 randomizations) using a matrix featuring the average
29
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
43
44 265 the male changed was entered twice, considering the two pairs as different groups. We
45
46 266 obtained a lower number of male contributions because the reproductive females also
47
48 267 engaged in duets with immature male offspring (N = 23).
49
50
51
52
53
54
55
56
57
58 268
59
60

269 **Results**

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 ($LD_{\text{females}} = 7.386$
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

1
2
3
4
5 291 those of males. The LDs showed that the between-individual stereotypy of male
6
7 292 contributions was higher than females' one. Males, therefore, appeared to produce songs
8
9 293 that are overall more similar to those of other males. In agreement with previous studies
10
11 294 that reported sexual dimorphism in the overall timing and repertoire size (Giacoma et al.,
12
13 295 2010), and in the frequency modulation, duration and rhythm (Gamba et al., 2016; Torti
14
15 296 et al., 2017, De Gregorio et al., 2018), we found that male and female indris also differed
16
17 297 in the phrase organization of their songs. Female structuring of the song showed a higher
18
19 298 number of phrases if compared to males, independently of the phrases being of the same
20
21 299 or different type. This result is in line with previous studies on family-living and pair-
22
23 300 bonded primate and bird species (Deputte, 1982; Savage, Snowdon, Giraldo & Soto,
24
25 301 1996; Snowdon, 2017; Riebel et al., 2019; Levin, 1996a; 1996b), endorsing that in a
26
27 302 socially monogamous, monomorphic species which holds year-round territories, sex
28
29 303 differences in vocal output are frequent (Marshall & Marshall, 1976). Furthermore,
30
31 304 despite the fact that songs are considered to be males' peculiar features (Cowlshaw,
32
33 305 1996), our results confirm that also monogamous females use songs and that female song
34
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**
38
39 308 **defense, females' role in territorial disputes can be essential. Female songs may be critical**
40
41 309 **for advertising their identity as well as resources holding potential. For instance, vocal**
42
43 310 **fight, in which females and males are singing together, are often sufficient to resolve**
44
45 311 **group encounters, reducing the occurrence of physical fights (Bonadonna et al., 2020).**
46
47 312 **Future studies may investigate whether female dispersal distance and territorial changes**
48
49 313 **over the years may contribute to a deeper understanding of this sex-dimorphic variation.**
50
51 314 Expanding previous findings that showed how indri female contribution to the song was
52
53
54
55
56
57
58
59
60

1
2
3
4
5 315 more varied in the rhythm (De Gregorio et al., 2018), we showed that the combination
6
7 316 and repertoire of the phrases are also more extensive than those shown by males. Females
8
9 317 not only have a broader repertoire of units, but they also emit descending phrases that we
10
11 318 did not observe in males (e.g., descending phrases of six units). Considering those
12
13
14 319 previous findings, our results may suggest that the differences in song structuring could
15
16 320 be used to convey information about the sex and the status of the singers that can be
17
18
19 321 assessed at a distance by conspecifics.

20
21 322 In agreement with previous findings on the different role of males and females during the
22
23 323 song (Giacoma et al., 2010), we found that female song is potentially more distinctive
24
25 324 than the male one. These results are in agreement with previous findings on birds (Brown
26
27
28 325 & Farabaugh, 1991), confirming that in those species in which females are involved in
29
30 326 territorial defense, their repertoires are as large or larger than those of males, on the level
31
32 327 of both units and phrases. Territorial defense is crucial for survival and reproduction in
33
34 328 pair-bonding species that occupy stable territories, and even if female involvement in
35
36 329 territorial defense is different from that of the reproductive male, they participate in
37
38 330 joining with their partner. An increasing body of literature (e.g., Hall, Rittenbach, &
39
40 331 Vehrencamp, 2015) supported the view that same-sex competition is the primary driver
41
42 332 of female song elaboration. It can be the case of the indris, where females may benefit
43
44 333 from multiple mating partners to increase tolerance by neighboring males (Bonadonna et
45
46 334 al., 2014). **As mentioned above,** females can advertise the occupancy of an area as well
47
48 335 as their quality and resource-holding potential. In support of the higher variability in
49
50 336 female song structure, there is also the recent **evidence that genetic relatedness may play**
51
52 337 a critical role in determining the characteristics of DPs in males, whereas it may have a
53
54 338 lesser impact on female songs (Torti et al., 2017). A more variable song structure may
55
56
57
58
59
60

1
2
3
4 339 add up to a more flexible structuring of the phrase notes, but further investigations are
5
6 340 needed.

7
8
9 341 This work also expands on and complements previous studies on humpback whales
10
11 342 (Helweg et al., 1998; Tougaard & Eriksen, 2006; Garland et al., 2012), showing that the
12
13 343 Levenshtein distance is simple, efficiently computable and highly applicable to any
14
15 344 behavioral data that are produced in a sequence. Our results confirmed that the
16
17 345 Levenshtein distance method is a simple but powerful technique that can be applied to
18
19 346 assess stereotypy or divergence between sexes.
20
21
22
23
24
25 347

26 27 28 348 **Acknowledgements**

29
30
31 349 We thank two anonymous Reviewers and the Editor for their careful reading of our
32
33 350 manuscript and their many insightful comments and suggestions. This research was
34
35 351 supported by Università degli Studi di Torino and by grants from the Parco Natura Viva—
36
37 352 Centro Tutela Specie Minacciate. We are grateful to GERP and Dr Jonah Ratsimbazafy.
38
39 353 We thank Dr, Cesare Avesani Zaborra and Dr Caterina Spiezio for helping us with the
40
41 354 organization of the field station in Maromizaha. We are grateful to the researchers and
42
43 355 the international guides, for their help and logistical support. We also thank San Diego
44
45 356 Zoo Global, LDVI, Dr Chia L. Tan.
46
47
48
49
50
51 357
52
53
54
55 358
56
57
58 359
59
60

360 **References**

- 361 Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49,
362 227-267. DOI: 10.1163/156853974X00534
- 363 Berwick, R. C., Okanoya, K., Beckers, G. J. L., & Bolhuis, J. J. (2011). Songs to
364 syntax: the linguistics of birdsong. *Trends in Cognitive Sciences*, 15, 113-121. DOI:
365 10.1016/j.tics.2011.01.002
- 366 Boersma, P., & Weenink, D. (2005). Praat: doing phonetics by computer [Computer
367 program].
- 368 Bonadonna, G., Torti, V., Sorrentino, V., Randrianarison, R. M., Zaccagno, M., Gamba,
369 M., & Giacoma, C. (2017). Territory exclusivity and intergroup encounters in the indris
370 (Mammalia: Primates: Indridae: *Indri indri*) upon methodological tuning. *The European*
371 *Zoological Journal*, 84, 238-251. DOI: 10.1080/24750263.2017.1318184
- 372 Bonadonna, G., Torti, V., De Gregorio, C., Valente, D., Randrianarison, R. M., Pozzi,
373 L., M., Gamba, M., & Giacoma, C. (2019). Evidence of genetic monogamy in the lemur
374 Indri (*Indri indri*). *American Journal of Primatology*, 81(6), e22993. DOI:
375 10.1002/ajp.22993
- 376 Bonadonna, G., Zaccagno, M., Torti, V., Valente, D., De Gregorio, C., Randrianarison,
377 R. M., ... & Giacoma, C. (2020). Intra-and Intergroup Spatial Dynamics of a Pair-Living
378 Singing Primate, *Indri indri*: A Multiannual Study of Three Indri Groups in
379 Maromizaha Forest, Madagascar. *International Journal of Primatology*, 1-22. DOI:
380 10.1007/s10764-019-00127-5

- 1
2
3
4 381 Bradbury, J.W., & Vehrencamp, S.L. (2011). Principles of animal communication.
5
6 382 Sinauer, Sunderland.
7
8
9
10 383 Brown, E. D., & Farabaugh, S. M. (1991). Song sharing in a group-living songbird, the
11
12 384 Australian magpie, *Gymnorhina tibicen*. Part III. Sex specificity and individual
13
14 385 specificity of vocal parts in communal chorus and duet songs. *Behaviour*, 118, 244-274.
15
16
17 386 Catchpole, C. K., & Slater, P. J. R. (2008). Bird song: biological themes and variations.
18
19 387 Cambridge University Press, Cambridge.
20
21
22
23 388 Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild
24
25 389 gibbon songs. *PloS one*, 1(1), e73. DOI: 10.1371/journal.pone.0000073
26
27
28
29 390 Cowlshaw, G. U. Y. (1996). Sexual selection and information content in gibbon song
30
31 391 bouts. *Ethology*, 102(2), 272-284. DOI: 10.1111/j.1439-0310.1996.tb01125.x
32
33
34
35 392 De Gregorio, C., Zanolli, A., Valente, D., Torti, V., Bonadonna, G., Randrianarison, R.
36
37 393 M., Giacoma, C., & Gamba, M. (2019). Female indris determine the rhythmic structure
38
39 394 of the song and sustain a higher cost when the chorus size increases. *Current Zoology*,
40
41 395 65, 89-97. DOI: 10.1093/cz/zoy058
42
43
44
45 396 Deputte, B. L. (1982). Duetting in male and female songs of the white-cheeked gibbon
46
47 397 (*Hylobates concolor leucogenys*). In C. T. Snowdon, C. H. Brown, & M. R. Petersen
48
49 398 (Eds.), *Primate communication* (pp. 67–93). New York: Cambridge University Press.
50
51
52
53 399 Farabaugh, S. M. (1982). The ecological and social significance of duetting. In: D. E.
54
55 400 Kroodsma & E. H. Miller (Eds.), *Acoustic Communication in Birds Vol. 2.* (pp. 85-124).
56
57 401 New York, USA: Academic Press.
58
59
60

- 1
2
3
4
5
6
7 402 Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging
8
9 403 software for video/audio coding and live observations. *Methods in Ecology and*
10
11 404 *Evolution*, 7, 1325–1330. DOI:10.1111/2041-210X.12584
12
13
14
15 405 Gamba, M., Favaro, L., Torti, V., Sorrentino, V., & Giacoma, C. (2011). Vocal tract
16
17 406 Flexibility and variation in the vocal output in wild indris. *Bioacoustics*, 20, 251-265.
18
19 407 DOI: 10.1080/09524622.2011.9753649
20
21
22
23 408 Gamba, M., Friard, O., & Giacoma, C. (2012). Vocal tract morphology determines
24
25 409 species-specific features in vocal signals of lemurs (*Eulemur*). *International Journal of*
26
27 410 *Primatology*, 33(6), 1453-1466. DOI:10.1007/s10764-012-9635-y
28
29
30
31 411 Gamba, M., Torti, V., Estienne, V., Randrianarison, R. M., Valente, D., Rovara, P., &
32
33 412 Giacoma, C. (2016). The indris have got rhythm! Timing and pitch variation of a
34
35 413 primate song examined between sexes and age classes. *Frontiers in neuroscience*, 10,
36
37 414 249. DOI: 10.3389/fnins.2016.00249
38
39
40
41
42 415 Garland, E. C., Lilley, M. S., Goldizen, A. W., Rekdahl, M. L., Garrigue, C., & Noad,
43
44 416 M. J. (2012). Improved versions of the Levenshtein distance method for comparing
45
46 417 sequence information in animals' vocalisations: tests using humpback whale song.
47
48 418 *Behaviour*, 149, 1413–1441. DOI: 10.1163/1568539X-00003032
49
50
51
52 419 Giacoma, C., Sorrentino, V., Rabarivola, C., & Gamba, M. (2010). Sex differences in
53
54 420 the song of *Indri indri*. *International Journal of Primatology*, 31, 539-551. DOI:
55
56 421 10.1007/s10764-010-9412-8
57
58
59
60

- 1
2
3
4 422 Gil, D., & Slater, P. J. (2000). Song organisation and singing patterns of the willow
5
6 423 warbler, *Phylloscopus trochilus*. *Behaviour*, 137(6), 759-782.
7
8
9
10 424 Gooskens, C. & Heeringa, W. (2004). Perceptive evaluation of Levenshtein dialect
11
12 425 distance measurements using Norwegian dialect data. *Language variation and change*,
13
14 426 16, 189-207. DOI: 10.1017/S0954394504163023
15
16
17
18 427 Gmelin, J. F. (1788). *Systema naturæ: per Regna tria naturæ, secundum classes*,
19
20 428 *ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (Vol. 1, No.
21
22 429 6). Beer.
23
24
25
26 430 Gustison, M. L., Semple, S., Ferrer-i-Cancho, R., & Bergman, T. J. (2016). Gelada
27
28 431 vocal sequences follow Menzerath's linguistic law. *Proceedings of the National*
29
30 432 *Academy of Sciences*, 113, E2750-E2758. DOI: 10.1073/pnas.1522072113
31
32
33
34 433 Hall, M. L., Rittenbach, M. R., & Vehrencamp, S. L. (2015). Female song and vocal
35
36 434 interactions with males in a neotropical wren. *Frontiers in Ecology and Evolution*, 3,
37
38 435 12. DOI: 10.3389/fevo.2015.00012
39
40
41
42 436 Heeringa, W. J. (2004). Measuring dialect pronunciation differences using Levenshtein
43
44 437 distance (Doctoral dissertation, University Library Groningen).
45
46
47
48 438 Helweg, D. A., Cato, D. H., Jenkins, P. F., Garrigue, C., & McCauley, R. D. (1998).
49
50 439 Geographic variation in South Pacific humpback whale songs. *Behaviour*, 135, 1-27.
51
52 440 DOI: 10.1163/156853998793066438
53
54
55
56 441 Honda, E. & Okanoya, K. (1999). Acoustical and syntactical comparisons between
57
58 442 songs of the white-backed Munia (*Lonchura striata*) and its domesticated strain, the
59
60

- 1
2
3
4
5
6 443 Bengalese finch (*Lonchura striata* var. *domestica*). *Zoological Science*, 16, 319-326.
7
8 444 DOI: 10.2108/zsj.16.319
9
10
11
12 445 Kershenbaum, A., Blumstein, D. T., Roch, M. A., Akçay, Ç., Backus, G., Bee, M. A., ...
13
14 446 & Coen, M. (2016). Acoustic sequences in non-human animals: a tutorial review and
15
16 447 prospectus. *Biological Reviews*, 91(1), 13-52. DOI: [10.1111/brv.12160](https://doi.org/10.1111/brv.12160)
17
18
19
20 448 Kershenbaum, A. & Garland, E. C. (2015). Quantifying similarity in animal vocal
21
22 449 sequences: which metric performs best? *Methods in Ecology and Evolution*, 6, 1452-
23
24 450 1461. DOI: [10.1111/2041-210X.12433](https://doi.org/10.1111/2041-210X.12433)
25
26
27
28 451 Kershenbaum, A., Bowles, A. E., Freeberg, T. M., Jin, D. Z., Lameira, A. R., & Bohn,
29
30 452 K. (2014). Animal vocal sequences: not the Markov chains we thought they
31
32 453 were. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792), 20141370.
33
34 454 DOI: [10.1098/rspb.2014.1370](https://doi.org/10.1098/rspb.2014.1370)
35
36
37
38 455 Kohonen, T. (1985). Median strings. *Pattern Recognition Letters*, 3, 309-313. DOI:
39
40 456 [10.1016/0167-8655\(85\)90061-3](https://doi.org/10.1016/0167-8655(85)90061-3)
41
42
43
44 457 Krull, C. R., Ranjard, L., Landers, T. J., Ismar, S. M., Matthews, J. L., & Hauber, M. E.
45
46 458 (2012). Analyses of sex and individual differences in vocalizations of Australasian
47
48 459 gannets using a dynamic time warping algorithm. *The Journal of the Acoustical Society*
49
50 460 *of America*, 32, 1189- 98. DOI: [10.1121/1.4734237](https://doi.org/10.1121/1.4734237)
51
52
53
54 461 Legendre, P., & Fortin, M. J. (1989). Spatial pattern and ecological
55
56 462 analysis. *Vegetatio*, 80(2), 107-138.
57
58
59
60

- 1
2
3
4
5
6
7
8 463 Levin, R. N. (1996a). Song behaviour and reproductive strategies in a duetting wren,
9
10 464 *Thryothorus nigricapillus*: I. Removal experiments. *Animal Behaviour*, 52, 1093-1106.
11
12
13 465 DOI: 10.1006/anbe.1996.0257
14
15
16 466 Levin, R. N. (1996b). Song behaviour and reproductive strategies in a duetting wren,
17
18 467 *Thryothorus nigricapillus*: II Playback experiments. *Animal Behaviour*, 52, 1107-1117.
19
20
21 468 DOI: 10.1006/anbe.1996.0258
22
23
24 469 Logue, D. M., & Gammon, D. E. (2004). Duet song and sex roles during territory
25
26 470 defence in a tropical bird, the black-bellied wren, *Thryothorus fasciatoventris*. *Animal*
27
28 471 *Behaviour*, 68(4), 721-731. DOI: 10.1016/j.anbehav.2003.10.026
29
30
31
32 472 Macedonia, J. M. (1993). The vocal repertoire of the ring-tailed lemur (Lemur
33
34 473 catta). *Folia primatologica*, 61(4), 186-217.
35
36
37
38 474 Maretti, G., Sorrentino, V., Finomana, A., Gamba, M., & Giacomini, C. (2010). Not just
39
40 475 a pretty song: an overview of the vocal repertoire of *Indri indri*. *Journal of*
41
42 476 *Anthropological Sciences*, 88, 151-165.
43
44
45
46 477 Margoliash, D., Staicer, C. A., & Inoue, S. A. (1991). Stereotyped and plastic song in
47
48 478 adult indigo buntings, *Passerina cyanea*. *Animal Behaviour*, 42, 367-388. DOI:
49
50 479 10.1016/S0003-3472(05)80036-3
51
52
53
54 480 Marshall, J. T., & Marshall, E. R. (1976). Gibbons and their territorial songs. *Science*,
55
56 481 193, 235-237.
57
58
59
60

- 1
2
3
4 482 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., ...
5
6 483 & Oksanen, M. J. (2013). Package 'vegan'. *Community ecology package, version, 2(9)*,
7
8 484 1-295.
- 10
11
12 485 Pollock, J. I. (1975). *The social behaviour and ecology of Indri indri* (Doctoral
13
14 486 dissertation, University of London).
- 16
17
18 487 Pollock, J. I. (1986). The song of the Indris (*Indri indri*; Primates: Lemuroidea): natural
19
20 488 history, form and function. *International Journal of Primatology, 7*, 225–267. DOI:
21
22 489 10.1007/BF02736391
- 24
25
26 490 R Core Team (2015). *R: A Language and Environment for Statistical Computing*.
27
28 491 Vienna: R Foundation for Statistical Computing. Available online at: [http://www.R-](http://www.R-project.org/)
29
30 492 [project.org/](http://www.R-project.org/)
- 32
33
34 493 Riebel, K., Odom, K. J., Langmore, N. E., & Hall, M. L. (2019). New insights from
35
36 494 female bird song: towards an integrated approach to studying male and female
37
38 495 communication roles. *Biology letters, 15(4)*, 20190059. DOI: 10.1098/rsbl.2019.0059
- 40
41
42 496 Rogers, A. C., Langmore, N. E., & Mulder, R. A. (2007). Function of pair duets in the
43
44 497 eastern whipbird: cooperative defense or sexual conflict?. *Behavioral Ecology, 18(1)*,
45
46 498 182-188. DOI:10.1093/beheco/arl070
- 48
49
50 499 Savage, A., Snowdon, C. T., Giraldo, H., & Soto, H. (1996). Parental care patterns and
51
52 500 vigilance in wild cotton-top tamarins (*Saguinus oedipus*). In M. Norconk, A.
53
54 501 Rosenberger, & P. A. Garber (Eds.), *Adaptive radiations of neotropical primates* (pp.
55
56 502 187–199). New York: Plenum Press.

- 1
2
3
4 503 Snowdon, C. T. (2017). Vocal communication in family-living and pair-bonded
5
6 504 primates. In *Primate Hearing and Communication* (pp. 141-174). Springer, Cham.
7
8
9
10 505 Sorrentino, V., Gamba, M., & Giacoma, C. (2012). A quantitative description of the
11
12 506 vocal types emitted in the indri's song. *Leaping ahead: advances in prosimian biology*,
13
14 507 315-322. DOI: 10.1007/978-1-4614-4511-1_35
15
16
17
18 508 Takahasi, M., Yamada, H., & Okanoya, K. (2010). Statistical and Prosodic Cues for
19
20 509 Song Segmentation Learning by Bengalese Finches (*Lonchura striata* var. *domestica*).
21
22 510 *Ethology*, 116, 481–489. DOI: 10.1111/j.1439-0310.2010.01772.x
23
24
25
26 511 Thalmann, U., Geissmann, T., Simona, A., & Mutschler, T. (1993). The indris of
27
28 512 Anjanaharibe-Sud, northeastern Madagascar. *International Journal of*
29
30 513 *Primatology*, 14(3), 357-381.
31
32
33
34 514 Torti, V., Gamba, M., Rabemananjara, Z. H., & Giacoma, C. (2013). The songs of the
35
36 515 indris (Mammalia: Primates: Indridae): contextual variation in the long-distance calls of
37
38 516 a lemur. *Italian Journal of Zoology*, 80, 596-607. DOI: 10.1080/11250003.2013.845261
39
40
41
42 517 Torti, V., Bonadonna, G., De Gregorio, C., Valente, D., Randrianarison, R. M., Friard,
43
44 518 O., ... Giacoma, C. (2017). An intra-population analysis of the indris' song dissimilarity
45
46 519 in the light of genetic distance. *Scientific reports*, 7, 10140. DOI: 10.1038/s41598-017-
47
48 520 10656-9
49
50
51
52 521 Tougaard, J., & Eriksen, N. (2006) Analysing differences among animal songs
53
54 522 quantitatively by means of the Levenshtein distance measure. *Behaviour*, 143, 239-252.
55
56
57 523 DOI: 10.1163/156853906775900685
58
59
60

- 1
2
3
4 524 Valente, D., De Gregorio, C., Torti, V., Miaretsoa, L., Friard, O., ... Gamba M. (2019).
5
6 525 Finding Meanings in low dimensional structures: Stochastic Neighbor Embedding
7
8 526 applied to the analysis of *Indri indri* vocal repertoire. *Animals*, 9, 5, 243. DOI:
9
10 527 10.3390/ani9050243
11
12
13
14 528 van der Loo, M. (2014). The stringdist package for approximate string matching. *The R*
15
16 529 *Journal*, 6, 111-122. <https://CRAN.R-project.org/package=stringdist>
17
18
19
20 530 Wei, T., & Simko, V. (2017). R package "corrplot": Visualization of a Correlation
21
22 531 Matrix. <https://github.com/taiyun/corrplot>
23
24
25
26 532 Wieling, M., Montemagni, S., Nerbonne, J., & Baayen, R. H. (2014). Lexical
27
28 533 differences between Tuscan dialects and standard Italian: Accounting for geographic
29
30 534 and sociodemographic variation using generalized additive mixed modeling. *Language*,
31
32 535 90, 669-692. DOI: 10.1353/lan.2014.0064
33
34
35
36 536
37
38
39
40 537
41
42
43 538
44
45
46
47 539
48
49
50 540
51
52
53 541
54
55
56
57 542
58
59
60

1
2
3
4 **543 Figure legend:**
5
6

7 *544 Figure 1: Spectrographic and schematic representation of an indri song.* Spectrograms
8
9 *545 of an indri song (a) showing a typical sequence of units given by one male and one*
10
11 *546 female. Schematic representation of the fundamental frequency of the descending*
12
13 *547 phrase units given by one male (b) and one female (c). Box fill patterns denote the*
14
15 *548 phrase type: black boxes mark single units (SU), horizontal lines boxes mark DP2,*
16
17 *549 diagonal lines boxes mark DP3, wavy lines boxes mark DP4, and checkered boxes mark*
18
19 *550 DP5. The spectrograms were generated in Praat with the following parameters: window*
20
21 *551 length: 0.05 s; dynamic range: 50 dB; frequency range: 0 to 10.000 Hz (a), 0 to 3.000*
22
23 *552 Hz (b,c).*
24
25
26
27
28

29 *553 Figure 2: The Levenshtein Distances showing song structuring in male and female*
30
31 *554 indris of the studied groups.* Individuals are shown on the vertical axis; sexes are shown
32
33 *555 on the horizontal axis. Dot size and color refer to the Levenshtein Distance: the darker*
34
35 *556 and bigger the dots, the higher are the distances between the individual contributions to*
36
37 *557 the song. This plot was generated using the R package corrplot (vers. 0.84; Wei &*
38
39 *558 Simko, 2017).*
40
41
42
43

44 *559 Figure 3: The average Levenshtein Distance among sexes and individuals, in the eight*
45
46 *560 studied groups.* Bar plot describing the individual and overall degree of stereotypy and
47
48 *561 variability expressed by the average Levenshtein Distances (LDs). Within-individual*
49
50 *562 LDs are reported for females (white bars) and males (black bars), as well as between-*
51
52 *563 individual LDs (grey bars for females, striped bars for males). Group 3 is reported twice*
53
54 *564 because the male of the reproductive pairs changed in 2014. Capped lines represent*
55
56 *565 Standard Deviation.*
57
58
59
60