Born to sing! Song development in a singing primate

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Abstract

In animal vocal communication, the development of adult-like vocalization is fundamental to interact appropriately with conspecifics. However, the factors that guide ontogenetic changes in the acoustic features remain poorly understood. In contrast with a historical view of nonhuman primate vocal production as substantially innate, recent research suggests that inheritance and physiological modification can only explain some of the developmental changes in call structure during growth. A particular case of acoustic communication is the indris’ singing behavior, a peculiar case among Strepsirrhine primates. Thanks to a decade of intense data collection, this work provides the first long-term quantitative analysis on song development in a singing primate. To understand the ontogeny of such a complex vocal output, we investigated juvenile and sub-adult indris’ vocal behavior, and we found that young individuals started participating in the chorus years earlier than previously reported. Our results indicated that spectro-temporal song parameters underwent essential changes during growth. In particular, the age and sex of the emitter influenced the indris’ vocal activity. We found that frequency parameters showed consistent changes across the sexes, but the temporal features showed different developmental trajectories for males and females. Given the low level of morphological sexual dimorphism and the marked differences in vocal behavior, we hypothesize that factors like social influences and auditory feedback may affect songs’ features, resulting in high vocal flexibility in juvenile indris. This trait may be pivotal in a species that engages in choruses with rapid vocal turn-taking.

Key words: duet, flexibility, juveniles, lemurs, ontogeny, rhythm

During ontogeny, juvenile individuals need to acquire crucial abilities to adult survival, like kin recognition or anti-predatory strategies. In many species, vocalizations undergo developmental changes that transform less structured utterances into fully functional adult calls (Margoliash and Tchernichovski 2015). An ongoing debate focuses on whether vocal developmental changes are determined by genetics and innateness (Mice—Kikusui et al. 2011), by variation in the social environment (Bats-Knörnschild et al. 2011), or by a combination of both.
Studies focused on vocal development in birds showed that vocal production learning is essential to shape adult vocal signals (Rios-Chelén et al. 2012). For instance, studies on parrots’ vocal development, like the green-rumped parrotlet (Forpus passerinus—Berg et al. 2013), demonstrated that, in few weeks, the developmental pattern of their begging call underwent several changes in frequency and duration in order to reach the adult-like output.

Regarding non-human primates, over the past decades, there has been a general agreement that vocal production was largely innate and genetically determined (for review, see Snowdon 1989; Newman 1995; Seyfarth and Cheney 1997; Tomasello 2008). On the other hand, recent studies showed that inheritance and physiological modification could partially explain the developmental changes during growth. In marmosets Callithrix jacchus, the increase of call duration with growth is related to lungs’ growth, which influences the respiration rate and expands the incidence and duration of calls (Zhang and Ghazanfar 2018). Still, parental feedback appeared to influence juvenile vocal ontogeny substantially, while the growth pattern could not explain precisely these changes across development (Takahashi et al. 2015).

Previous studies focused on the variation of infant and juvenile monkeys in acoustic communication (Hammerschmidt et al. 2001; Pistorio et al. 2006; Takahashi et al. 2015), have led researchers to suggest that the expansion of a flexible, juvenile period during individual development may be one of the fundamental steps in the evolution of language (Hage and Nieder 2016). Ontogenetic changes of vocal features were found in all call types of squirrel monkeys (Saimiri sciureus—Hammerschmidt et al. 2001), involving the frequency range and calls duration. In particular, the authors observed that both juvenile and adult form of calls was characterized by high variability, and pointed out that this may be a critical prerequisite for other structural changes during the life span (Hammerschmidt et al. 2001). Indeed, some primates do modify the structure of their vocal output during adulthood (Cebuella pygmaea—Elowson and Snowdon 1994; Snowdon and Elowson 1999; Plecturocebus cupreus—Clink et al. 2019). The work from Seyfarth and Cheney (1986) on vervet monkeys Chlorocebus pygerythrus indicated that, while most of the calls appeared “ready-made,” in some cases animals have to learn “their correct pronunciation,” a process involving, once again, changes in the fundamental frequency and duration of calls and intervals. Hammerschmidt et al. (2000) found a similar effect was found for rhesus macaques’ coo calls Macaca mulatta, which showed changes in the spectro-temporal parameters during development. These authors suggested that practicing may be more important than exposure to an adult model to achieve the adult-like call form.

Although many primates show a certain degree of sex dimorphism in vocal behavior, we have scanty information on how these differences arise during ontogeny, and most studies focused on captive populations of macaques and marmosets. On the one hand, Hammerschmidt et al. (2000) did not find any significant difference in coo calls between male and female rhesus infants or in the development of coo call production.

In this call type, the only sexual dimorphism was found in its usage, with infant females showing a higher emission rate than males (Tomaszycki et al. 2001). On the other hand, screams in the same species are sexually dimorphic in juveniles: in particular, screams of juvenile females were more similar to those of adults than were the screams of juvenile males (Tomaszycki et al. 2005). Similarly, in their first 6 months of life, male and female common marmosets Callithrix jacchus are characterized by different developmental trajectories in terms of the spectral and temporal features of the calls they produce (Pistorio et al. 2006).

Primate vocal communication includes some very diverse acoustic outputs, ranging from low-frequency contact calls (e.g., spider monkeys—Ordoñez-Gómez et al. 2019) to elaborate vocal displays like songs (e.g. indris and gibbons—Geissmann 2000). Elaborate vocal outputs represent challenging cases to study primate vocal ontogeny. Liebal et al. (2013) underlined the difficulty of researching this topic due to mainly methodological constraints: large sample sizes are difficult to obtain from infant and juvenile individuals, especially in the wild, as in most cases mothers give birth to a single infant which has to be followed and studied over a long period. A particular case of vocal communication is the singing behavior of the so-called *vocal primate*: members of the families Pitheciidae, Hylobatidae, Tarsiidae, and Indriidae, utter complex, coordinated vocalizations between 2 or more individuals, composed by a series of vocal elements—termed “units” or “notes”—forming a recognizable pattern in time, known as a *song* (Thorpe 1961; Dahlin and Benedix 2014). Recent research highlighted vocal plasticity and flexibility in primate song’s characteristics (gibbons—Terleph et al. 2018; tarsiers—Clink et al. 2020a; indris—De Gregorio et al. 2019a; titi monkeys—Clink et al. 2019), and it may be of interest to understand how the fully functional adult song develops from life’s early stages.

Almost all the limited information available on song development in singing primates comes from studies on gibbons, which, as all the primates that show singing behavior, are monogamous and characterized by low sexual dimorphism in body size (Leigh and Shea 1995). In general, those works attested that the developmental process leading to the full adult song could last several years (Merker and Cox 1999; Hradec et al. 2017), contrary to what happens with infants’ separation-induced calls, that appeared in early ontogeny with the same spectro-temporal parameters as those produced by older individuals (Nomascus gabriellae—Hradec et al. 2020). This evidence is interesting as it may indicate that the developmental process’s protracted nature does not involve the vocal repertoire of the species but is specific to the song. In particular, Merker and Cox (1999) found that song development in gibbons included an increase in song duration and the appearance of different song portions in different ontogenetic steps; the authors pointed out that the song, at 2.5 years old, was still not fully adult-like. The work of Koda et al. (2013), which proposed the presence of socially mediated vocal flexibility in the song ontogeny, may explain such an extended period of vocal development in gibbons, also suggesting that practice during vocal interaction may be an essential part of the process.

Furthermore, although gibbons’ vocal repertoire is species-specific, it has been reported that immature males can produce female-specific vocalization, called “great calls” (Koda et al. 2014), that showed different acoustic parameters and had a lower number of syllables than those produced by adult females (N. gabriellae—Hradec et al. 2017). Terleph et al. (2016) found that aging in the white-handed gibbon Hylobates lar led females to show lower fundamental frequency in their calls. Besides gibbons, the rate of emission of pulse elements in the titi monkeys’ song decreased, while call duration increased (Clink et al. 2019). The authors mentioned that
this could be an effect of aging, as quickly repeated elements may be challenging to perform.

**Indri indri** is the largest living lemur and the only Strepsirhine primate that produces songs, emitted mostly during the morning (Pollock 1986) and consisting of multiple distinctive unit types. Members of a family group participate in the chorus simultaneously, usually showing duets between males and females in turn. Pollock (1986) reported that juveniles join the chorus after 3 years of age. Songs serve several functions, from inter- and intra-group communication to territory defence (Pollock 1986; Torti et al. 2013) and show a different acoustic structure depending on the context of emission (Torti et al. 2013). Songs may also mediate the formation of new groups (Giacoma et al. 2010; Bonadonna et al. 2014; Gamba et al. 2016) and possess the potential to inform conspecifics about individuals’ genetic relatedness (Torti et al. 2017). Adult songs, which last 113.188 ± 39.682 s (mean ± standard deviation; Gamba et al. 2016), consist of units that are sexually dimorphic: females possess a higher number of unit types, which are also more frequency-modulated (Giacoma et al. 2010). Females’ units also showed a higher fundamental frequency (De Gregorio et al. 2019). Overall, males emit longer units than females (Giacoma et al. 2010), but when considered in detail, only few unit types showed males’ longer duration, likely because units organized in phrases are structurally constrained to phrase length (Gamba et al. 2016). Depending on the level of analysis, males may show a higher pitch (including descending phrase (DP) units only, Gamba et al. 2016) or a lower pitch (once taking into account the different types, e.g., long notes (LN), single notes (SN); De Gregorio et al. 2019). The rhythmic structure of indris’ choruses also appears to be sexually dimorphic (Gamba et al. 2016), with males exhibiting longer intervals between the onset of units compared with females, which instead displayed more flexible intervals between phrases’ units (De Gregorio et al. 2019a). Despite these marked differences, male and female indris are difficult to distinguish morphologically (Pollock 1986), and Dixson (1998) reported no sexual dimorphism in the air sac size. Air sacs have been suggested to play a role in shaping the acoustic and/or temporal communication features (Fitch and Hauser 1995; Hewitt et al. 2002).

This work aims at examining the ontogeny of indris’ song to understand the development of such vocalization. After an intense decade of data collection on wild, free-ranging indri groups, we present the first quantitative analysis on juvenile and sub-adults individuals (following Pollock 1986). Given the importance of practicing or learning in the development of calls in some primates’ species (Seyfarth and Cheney 1986; Hammerschmidt et al. 2000; Koda et al. 2013), understanding if even a Strepsirrhine primate may show some degree of plasticity in the ontogeny of such complex vocal output may be indeed essential. Studies on family-living primates have indicated a more substantial effect of social and environmental factors on the development of vocal signals compared with other non-human primates (for review, see Snowdon 2017). Thus, it is likely that similar processes, together with maturational effects, may also affect the song production of juvenile indris, which join the family chorus for several years and remain in the family group until reaching adulthood.

Given that physical and physiological constraints can influence sound production, we expect that modification of the units’ spectro-temporal parameters will mainly occur during the first years of life because growth rate toward maturity increases consistently from apes to prosimians (Kirkwood 1985). In particular, we predicted that 1) indris will decrease the fundamental frequency during growth since the elongation of vocal folds relates with a lower fundamental frequency (Titze et al. 2016). We also predicted that 2) some temporal features will increase in duration with age: unit duration and phonation amount will be positively affected by lung capacity (Zhang and Ghasanfar 2018). Consequently, we expect that the individual contribution within a song will increase with age. As a previous investigation found that the rhythmic structure of phrases did not change between adults and non-adults (Gamba et al. 2016), we predicted 3) the rhythmic structure of the whole song will be stable during ontogeny and that 4) juvenile indris would show dimorphic acoustic traits that will become more marked during growth. Finally, given the growing evidence showing that juvenile primates are more flexible than conspecific adults (Takahashi et al. 2015), we predicted that 5) juvenile indris would show higher variability in the songs’ spectro-temporal features compared with adults.

### Materials and Methods

#### Observations and recordings

The data were collected in the Maromizaha New Protected Area (18° 56’49” S, 48° 27’53” E), in Eastern Madagascar. We conducted field observations between 6:00 am and 1:00 pm, from 2011 to 2020, for a total of 59 months. We followed 8 habituated groups of wild indris and we recorded their spontaneous songs from a close distance (between 2 and 10 m), using different sound recorders (Sound Devices 702, Olympus S100 and LS05, and Tascam DR-100, DR-40, and DR-05) set at a sampling rate of 44.1 kHz, with a 16-bit amplitude resolution. Semi-directional microphones (ME 67 and AKG CK 98) were oriented toward the singing individuals, and we recognized individuals using natural marks and annotated each emitter’s identity for every unit in the song. We did not use playback or any particular action to avoid altering the natural behavior of the study subjects. For this study, we considered only the individuals we knew or could estimate the date of birth. We provided an

### Table 1. Summary of sex, age, and familiar group of individuals considered in this study

| Individual | Sex | Group | Birthdate |
|------------|-----|-------|-----------|
| Berthe     | F   | 1MZ   | 15 June 2012 |
| Cami       | F   | 1MZ   | 15 May 2017 |
| Fanhy      | F   | 2MZ   | 15 June 2012 |
| Afo        | M   | 2MZ   | 07 July 2014 |
| Tovo       | F   | 2MZ   | 15 July 2016 |
| Zandry     | F   | 3MZ   | 15 May 2010 |
| Faly       | M   | 3MZ   | 31 May 2014 |
| Laro       | M   | 3MZ   | 31 May 2015 |
| Ana        | F   | 3MZ   | 15 May 2017 |
| Gibet      | M   | 4MZ   | 15 June 2012 |
| Meva       | F   | 4MZ   | 15 May 2017 |
| Voary      | M   | 5MZ   | 07 July 2014 |
| Hira       | M   | 6MZ   | 15 July 2014 |
| Zafy       | M   | 8MZ   | 15 May 2012 |
| Mika       | F   | 8MZ   | 07 July 2014 |
| Eme        | M   | 8MZ   | 15 May 2017 |
| Ovy        | M   | 9MZ   | 15 June 2013 |
| Dosy       | F   | 9MZ   | 31 May 2015 |
| Beny       | M   | 9MZ   | 15 June 2017 |
| Maitso     | F   | 10MZ  | 15 May 2010 |

When an accurate birthdate was not known, birthdate was estimated to the 15th day of the respective month.
accurate birthdate for those animals we observed from the day of birth. In contrast, an estimated birthdate (month of birth) refers to a newborn we found during its natal group’s regular sampling. We set the estimated birthdate to the 15th of the actual month of birth, allowing an accuracy of 15 days. We considered juveniles up to 4.5 years because all females dispersed from their natal group at that age. Our dataset comprised 128 choruses, resulting in 140 individual contributions and 2,151 units uttered by 20 individuals (10 males and 10 females). The indris’ age ranged from 0.99 to 4.50 years old for females, and 1.23 to 4.50 years old for males (Table 1).

**Acoustic analyses**

In the indris’ songs, units were mainly organized in phrases, including 2–6 units arranged in sequences of the progressively lower fundamental frequency (and so-called DPs; [Figure 1A]; [Torti et al. 2013]). After a series of roars, harsh emissions that introduce the song, indris uttered some long units (LN), usually longer and less modulated than the units emitted in the DPs. LN preceded a variable number of DPs and SN. We analyzed the songs using the software Praat 6.0.56 ([Boersma and Weenink 2007]) and identified each indri’s contribution using annotations in Praat TextGrids. We labeled units according to their type and position (e.g., being part of a phrase or not) and indicated where intervals occurred between units within a phrase or between different phrases ([Gamba et al. 2016; De Gregorio et al. 2019a]). Each unit type had its code: LN, SN, or according to the phrase type they belong (DP2, DP3, DP4, DP5, DP6 based on the number of units forming the phrase; [Figure 1B]); for the silences, the code identifies the position between (inter) or within (intra) DPs. A unit’s fundamental frequency was then isolated and saved into a single audio file (WAV format). We used a custom
the inter-onset intervals (IOIs) to evaluate the contributions’ rhyth-

m of units (Number of units). We also calculated
cumulative duration of the uttered units (Phonation), and the number
the individual vocal output in a duet/chorus (Contribution), the cu-

Statistical analyses
To investigate developmental changes occurring in juvenile songs’
spectro-temporal features, we used 11 linear mixed models (LMM, 

Table 2. List and abbreviations of the parameters included in the analysis

| Abbreviation | Parameter |
|--------------|-----------|
| Max0 (Hz)    | Maximum fundamental frequency value across the unit |
| Min0 (Hz)    | Minimum fundamental frequency value across the unit |
| Range0 (Hz)  | Max0–Min0 |
| Q50 (Hz)     | Frequency value at the upper limit of the second quartiles of energy |
| MA slope (Hz)| Mean f0 average absolute slope across 25 turning points in the pitch contour |
| Unit duration (s)| Time between the onset and offset of a unit |
| Contribution (s) | Cumulative duration of the units of each individual contribution |
| Phonation (s) | Number of units uttered in each individual contribution |
| Number of units (N) | IOI between 2 subsequent phrases |
| bpIOI (s)    | IOI of 2 following units within a phrase |
| wpIOI (s)    | IOI of 2 following units within a phrase |

Results
Occurrence of different unit types within the song

To understand how song temporal features are affected by
growth, we ran 5 models using contribution, phonation, bpIOI, 
wpIOI, and number of units. As for the spectral parameters, when we used a temporal parameter as the response variable in a particu-
lar model, the others were entered as fixed factors. These models
also included an interaction between sex and age. We used a gen-
eralized LMM (GLMM, glmer function of lme4 package, Bates et al. 2015) with a Poisson distribution for the number of units. In the
models concerning temporal features, we included “age” as a
squared term because it should better fit with the expected growth
rate of Strepsirrhine juveniles (Kirkwood 1985). Moreover, we
know that fast growth rates may correlate with increased body size
and lung capacity (see Ey et al. 2007). We included group ID,
individual ID, contribution ID, and unit type as random factors,
with a nested design. We ruled out correlation among the predictors
by examining the variance inflation factors (vif package; Fox and
Weisberg 2011) and tested the full model’s significance against a
null model including only the random factors using a likelihood
ratio test (see Gamba et al. 2016). We adjusted all the p-values
(padj) using the Benjamini–Hochberg correction, controlling for
false discovery rate.

To determine whether juveniles’ song features were more vari-

cular parameters (range0, max0, min0, Q50, MA slope, number of units, contribution, phonation, wpIOI, bpIOI, and unit duration) and used independent
2-sample t-tests to compare CVs between adults and juveniles. Adult

c parameters were extracted from the datasets of De Gregorio et al. (2019a; 2019).

Considering the 2 sexes, SNs were strongly predominant in
young females between 1 and 2 years old (5.79 ± 2.53 per contribu-
tion), while males of the same age showed this vocal type only spor-
dically (0.13 ± 0.18 per contribution). Both males and females had
lower values of DP2 per contribution at 1 year old, and while males
reached their peak at the age of 2 (2.70 ± 2.05), females reached it
at the age of 4 (2.17 ± 1.34). Phrases composed of 3 and 4 units
(DP3, DP4) were more common in males of 1 year old and while females showed an inversion at the age of 2 and 3 years old, with females
emitting a higher number of this phrase type (1.45 ± 1.23 at 2 years
old; 3.19 ± 1.89 at 3 years old) than males (1.30 ± 1.72 at 2 years
old; 1.26 ± 0.79 at 3 years old). At 4 years old, males emitted again
a higher number of phrases composed of 3 units (2.13 ± 0.61) with
Table 3. Mean number and standard deviation of different vocal types’ occurrence within the song at different ages (tot) and in the 2 sexes (males, females).

| Age | Sex   | Unit   | Tot Males | Females | Tot Females | DP2, phrases composed by 2 units | DP3, phrases composed by 3 units | DP4, phrases composed by 4 units | DP5, phrases composed by 5 units | UnitTot |
|-----|-------|--------|-----------|----------|-------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|---------|
|     |       | 1      | 0.13 ± 0.18 | 0.03 ± 0.20 | 0.16 ± 0.20 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 |
|     |       | 2      | 0.13 ± 0.18 | 0.03 ± 0.20 | 0.16 ± 0.20 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 |
|     |       | 3      | 0.13 ± 0.18 | 0.03 ± 0.20 | 0.16 ± 0.20 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 |
|     |       | 4      | 0.13 ± 0.18 | 0.03 ± 0.20 | 0.16 ± 0.20 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 | 13 ± 4.8 |

Spectral features
The average Q50 value was 808.00 ± 43.01 Hz, showing higher values for males, and it was positively influenced by age in both sexes: the older the indris, the higher the Q50 value (Figure 2A and Supplementary Table SM1). Unit duration influenced this response variable negatively.

The models showed a similar pattern for the minimum (min0) and the maximum (max0) fundamental frequency. While the overall average for max0 was 930.75 ± 53.27 Hz, for min0 was 727.29 ± 41.98 Hz. Moreover, while the individuals’ age negatively influenced min0 (Figure 2B and Supplementary Table SM1), no significant relationship emerged between age and max0. Similarly, unit duration was negatively correlated with max0, but not with min0. From the model also emerged an effect of sex on the average minimum value of fundamental frequency, with females showing higher values than males. Moreover, Q50 appeared to positively affect min0, with higher frequencies corresponding to higher values of Q50, while the range of fundamental frequency was negatively correlated with it.

Considering the range of the fundamental frequency (range0), its average was 203.02 ± 46.01 Hz and were positively influenced by age (Figure 2C and Supplementary Table SM1) and by units’ duration. Also, both max0 and MA slope positively affected the fundamental frequency range. On the contrary, the model showed a negative correlation between the range0 and Q50 value. No significant effect of sex emerged for this response variable.

Concerning the frequency variation along with the unit (MA slope), juvenile indris showed an average of 438.48 ± 131.08 Hz. From the model emerged that the Q50 value positively influenced this variable (Supplementary Table SM2). Max0 and min0 were both significantly correlated with MA slope, but where the first parameter had a positive influence, the second had a negative one. We did not find a significant correlation between age and MA slope. Unit duration negatively affected this response variable.

We did not find a significant effect of the interaction between age and sex on the response variables for all of the spectral features tested (Supplementary Tables SM1 and SM2).

Temporal features
The summary and detailed results of all models can be found in the Supplementary Materials (Supplementary Tables SM1–SM4). The average duration of Phonation was 23,107 ± 7,463 s, with higher values for males. The model showed that the amount of phonation was positively correlated with the duration of individual contribution and number of units. While age itself showed no significant correlation with phonation, the interaction between age and sex...
Figure 2. Effect of age on different spectral features (Hz) as response variable: (A) Q50, (B) minf0, (C) rangef0. Red line represents juvenile females, while blue line represents juvenile males. Dots represent the observed data; shaded areas indicate confidence intervals. Being a plot of the effects resulting from the model, the predictor age must be included as z-transformed.

Figure 3. Effect of the interaction between age and sex on (A) mean phonation duration, (B) mean duration of individual contribution, (C) mean inter-onset-interval between phrases, and (D) unit duration. Red line represents juvenile females, while blue line represents juvenile males. Dots represent the observed data; shaded areas indicate confidence intervals. Being a plot of the effects resulting from the model, the predictor age must be included as z-transformed. * raw P-values of the interaction are 0.046 for Contribution and 0.038 for Phonation; adjusted P-values are, respectively, 0.057 and 0.064.
significantly affected phonation duration. In fact, males showed a decrease in phonation duration with age, contrary to females, which showed an increase instead (Figure 3A and Supplementary Table SM2). Concerning the rhythmic features, the model revealed that the wpIOI positively influenced the phonation, while no significant correlation with bpIOI emerged.

The individual Contribution to the song lasted, on average, 63.883 ± 18.275 s. The duration of the individual contribution was positively correlated with the amount of phonation. Moreover, the model showed that contribution was longer in females. The wpIOI had no significant influence on the response variable, differently from the bpIOI, which was positively correlated with the individual contribution duration. Again, while age was not correlated with the duration of individual contribution, the interaction between sex and age had a significant influence on the response variable, with an increase of the contribution duration for males and a decrease for females as they age (Figure 3B and Supplementary Table SM2).

The mean IOI between different phrases (bpIOI) was 6.097 ± 2.265 s. From the model emerged that this parameter was higher in males, and it showed a significant correlation with the duration of individual contribution and phonation. In particular, while the increase of contribution duration corresponded to longer bpIOI, the phonation was negatively correlated with this parameter. The model did not show significant correlations with the wpIOI and with age. However, the interaction between sex and age negatively influenced the bpIOI: males showed a decrease in their intervals duration with age, while females increased it (Figure 3C and Supplementary Table SM3).

The IOI between different units of the same phrase (wpIOI) was, on average, 2.306 ± 0.304 s. Our results indicated that the duration of the wpIOI was positively influenced by the amount of phonation and was negatively influenced by the number of units emitted. No significant correlations emerged from the other tested variables: sex, age, the interaction between sex and age, the duration of the contribution, and the bpIOI (Supplementary Table SM3).

The songs uttered by juvenile indris were composed, on average, by 16.081 ± 5.612 units, and the number of units was higher in females. Moreover, the number of units increased with longer contribution durations and phonation’s values (Supplementary Table SM4). No significant influence of age and its interaction with sex emerged from the model. The wpIOI and the bpIOI both showed a significant and negative influence on the response variable: the longer the IOIs, the smaller the number of units.

Finally, our study subjects showed a mean value of unit duration of 1.078 ± 0.680 s. The model indicated a general increase in the units’ duration with age, with higher values for males. While Q50 did not significantly influence units’ duration, the min0 and the max0, together with the MA slope, negatively influenced the units’ duration: the higher the value of these parameters, the shorter the units’ duration. Moreover, in this case too, males and female juvenile indris showed different developmental trajectories: while females increased the duration of their units with age, the males decreased it (Figure 3D and Supplementary Table SM2).

Juveniles versus adults variability

When comparing the coefficients of variation, we found that juvenile and adult indris significantly differed for range0 (t = −2.199, df = 16.795, P = 0.033) and for bpIOI (t = −5.321, df = 16.795, P < 0.001), with juveniles showing higher CVs than adults (Figure 4). We did not find significant differences for min0 (t = −0.333, df = 29.450, P = 0.742), max0 (t = −1.532, df = 40.212, P = 0.128), Q50 (t = 1.465, df = 38.420, P = 0.151), MA slope (t = 0.349, df = 41.994, P = 0.728), number of units (t = −0.930, df = 31.691, 0.359), contribution (t = −0.499, df = 30.447, P = 0.621), phonation (t = −0.244, df = 29.670, P = 0.809), wpIOI (t = −1.517, df = 31.986, P = 0.139), and unit duration (t = 0.764, df = 40.970, P = 0.449).

Discussion

We examined how song parameters of juvenile indris change during ontogeny, and we found that age influenced both spectral and temporal features. While the developmental changes in frequency parameters were consistent between sexes, the temporal features showed different developmental trajectories for males and females. Contrary to what was reported by Pollock (1986), who found that juveniles only emitted introductory roars until 3 years of age, we found that female indris started to participate in choruses at 11.88 months, males at 14.76. Moreover, our data indicated that females seem to disperse earlier than males from their natal group: this may suggest that, in this species, females reach maturity earlier than their male counterparts. This finding agrees with what has previously been reported for other primates, where females enter puberty earlier than males (Dixson and Altman 2000; Behringer et al. 2014).

Our results confirmed the presence of vocal sexual dimorphism in I. indri at early stages of development, with males emitting longer but fewer units (in agreement with Giacoma et al. 2010) with higher Q50 values than females (as reported for adult indris: Gamba et al. 2016), who instead have higher values of min0. These findings are in line with what has been suggested by previous research (Giacoma et al. 2010; Gamba et al. 2016), regarding how differences in the contribution of different sexes and age classes to the chorus may act as a cue regarding a group’s composition. Our study confirms a crucial sexual influence on both temporal and spectral features of vocal utterances in juvenile individuals. Interestingly, although a previous work conducted on adult individuals found sex differences in the
fundamental frequency range, with males showing wider ranges than females (Giacoma et al. 2010), we did not detect any sexual dimorphism in this trait in our sample of juvenile indris. Our results also showed that range0 increased with age, and that juvenile individuals emit units with a more variable range of the fundamental frequency compared with adults. Thus, it may be possible that this variability allows juvenile indris to achieve the adult-like form of unit via practice and auditory feedback. Nevertheless, these differences in range0 may indicate that at 4.5 years of age, juveniles are still developing their adult-like units. This process could be due to males exhibiting lower fundamental frequencies with time or juveniles practising units’ delivery, emitting units that better follow the sex-specific modulation with time. Our work also demonstrated that juveniles are more variable in the range of the fundamental frequency than adults, and thus sexual differences may be somehow masked. Moreover, De Gregorio et al. (2019) found sex differences in adults’ min0 only for LN, while our work considered the whole repertoire. This result supports the idea that at 4.5 years of age, indris do not perform the fully developed, adult-like song.

Our results regarding the developmental changes of units’ frequency characteristics were only partially consistent with our first prediction: while the minimum value of f0 decreased with age, the Q50 and the range of f0 showed an increase. Our finding shows that the increase in range0 with age may result from the decrease of min0, as max0 was stable during growth. This effect may, indeed, be explained by the elongation of vocal folds’ length with growth, which leads to the emission of vocalizations characterized by lower frequencies (Titze et al. 2016). The increase of the Q50 value suggests that, in indris, there is a modification of units’ shape, where the min0 of the units shift toward lower values, while the median frequency increases, thus resulting in a higher range of the fundamental frequency. This interpretation is in line with what has previously been reported in squirrel monkeys, whose mean range0 increased with age (Hammerschmidt et al. 2001) and rhesus macaques, whose coo calls exhibited a sharp decrease of f0 during growth (Hammerschmidt et al. 2000). Similar changes of f0 have been found in another singing primate, the white-handed gibbon, where older females showed lower fundamental frequency (Terleph et al. 2016). Our work showed that in indris, juvenile females presented higher values of min0 than males. No differences emerged regarding the max0: the fact that in adults the sexual difference in min0 has been reported only for a particular type of unit (LN), while differences in max0 were present in most units’ type (De Gregorio et al. 2019) can be a further indication that songs’ vocal types undergo essential changes during growth.

Our second prediction that temporal features will show an increase in duration with age was only partially confirmed, as developmental changes in unit duration differed for males and females. We found significantly different developmental trends between males and females in unit duration and IOIs between phrases (bPOI). Moreover, the amount of phonation and individual contribution duration showed a tendency to differ in their developmental process between juvenile males and females. While females showed an increase of unit duration with age, male indris evidenced a decrease, overall, juvenile males emitted longer units than females. This is interesting since the analysis on adult indris’ unit duration that considered the unit type (De Gregorio et al. 2019) as we did in present work evidenced differences only for a limited number of unit type. We can hypothesize that the developmental changes we observed may lead to a reduction in the sex dimorphism in unit duration, that may become more constrained to phrase length as individuals age (Gamba et al. 2016). An increase in units’ duration with age has been reported in titi monkeys’ broadband pulse (Clink et al. 2019), although this species showed no sex differences in the development pattern. This could be because, in titi monkeys, males and females sing the same units, while the indris’ repertoire is strongly dimorphic (Giacoma et al. 2010; Zanoli et al. 2020).

Similar results have been reported on marmosets, which increased their utterances’ duration during the first 2 months of age (Takahashi et al. 2015). However, the authors did not consider a possible effect of sex in the development of vocalizations, and the temporal span they considered is shorter from the one we examined here. Moreover, Takahashi et al. (2015) focused on the transitions between different vocal types (cries and phee) and concluded that their timing was only partially due to maturation, but also affected by parental vocal feedback. This interpretation may be relevant to our findings on the development of temporal parameters. While the increase in units’ duration may be in part due to an increase of lung capacity (Fitch and Hauser 1995), differences between sexes may indicate that vocal plasticity plays an essential role in the process leading to adult vocal output. As reported by De Gregorio et al. (2019a) male and female indris seemed to play a different role in achieving the coordination of utterances, where females showed higher flexibility in the timing of their contribution and males, on the contrary, showed a more fixed pattern. Besides, adult females potentially suffered a higher cost when the number of singers in chorus increases: they had to diminish the phonation to emit a longer contribution, while male singing remained invariant (De Gregorio et al. 2019a). This aspect may explain the differences, even if limited, on unit duration that we found between juvenile and adult females, in agreement with De Gregorio et al. (2019). Our findings support the hypothesis that females’ singing may reflect female dominance by regulating the extent of males’ contribution (Pollock 1979). Therefore, the change in social status and the critical role that female singing has in coordinating male output may explain why we observed that juvenile females’ unit duration increased with age, but adult female’s units are usually shorter than the males’.

Other than unit duration, we also found that IOIs between different phrases changed with age, unlike IOIs between units of the same phrase. Contrary to our third prediction and to what previously found by Gamba et al. (2016) that only considered the IOIs between units, we found that songs’ rhythm changed during development in a sex-specific way. However, as Gamba et al. (2016) reported, we also found that juvenile intervals between units did not differ from adults. Overall, our findings suggest that phrase rhythmic structure is constrained during ontogeny (see also Gamba et al. 2016). Because unit duration increased with age, juvenile indris must then modify the silent gaps between units. In contrast, the rhythmic structure of songs is more flexible (De Gregorio et al. 2019a). Future studies should aim to understand whether the extent to which young and adult indris can control their vocal output can differ and reflect in turn-taking between emitters during the song (Lepilemur edwardsi—Méndez-Cárdenas and Zimmermann 2009; Cercopithecus campbelli—Lemasson and Hausberger 2011; C. jacchus—Takahashi et al. 2013). For marmosets, Chow et al. (2015) conclude that turn-taking is a learned vocal behavior developed under the parents’ tutoring activity, similarly to what Koda et al. (2013) hypothesized for gibbons (Hylobates agilis). Whether or not this tutoring mechanism is present in the indris remains unclear. However, alongside practising, the auditory input may likely be involved in developing such a complex vocal output, which mostly
occurs as a duet or a chorus and requires some degree of coordination among singed (Gamba et al. 2016).

Duration of an individual contribution (overall duration, including the silent gaps) and phonation (the cumulative vocal output) showed a tendency toward different developmental trajectories. We found that while females’ overall duration decreased with age, it increased in males. In contrast, females’ phonation increased with age, and males showed a decrease during ontogeny. These findings differ from adult reproductive indris, where males showed a higher phonation and a shorter individual contribution than females (De Gregorio et al. 2019a). This evidence may indicate that juvenile indris are still developing the fully adult song pattern despite joining the chorus at an early age, a process in which practice may be involved. Our finding also contrasts with the study of female’s great call in gibbons (N. gabbriellae—Merker and Cox 1999), which increased individual contribution during development.

Our study reveals more variability, at least in the range of the fundamental frequency and in the IOI between phrases, in juveniles than adults again suggesting that auditory experience may shape processing of the acoustic stimuli during growth. It is also possible that being dominant and reproductively mature can influence vocal characteristics, as previously reported for indris (Gamba et al. 2016) and other primates (e.g., male baboons, Papio cynocephalus—Fischer et al. 2004). At the same time, taking the role that song may have in the formation of new pairs (Bonadonna et al. 2014; Torti et al. 2017), juvenile females may exploit particular portion of the songs in which overlapping with the adults is less frequent, as previously suggested by Gamba et al. (2016). This result appears in agreement with the observation that overlapping rates decreased with juvenile females’ development (H. lar—Reichard 2003; Koda et al. 2013). This strategy may allow broadcasting more efficiently their unpaired status, resulting in juvenile female songs characterized by lower total duration but higher phonation amount and longer intervals between phrases. On the other hand, we observed that juvenile males might remain in their natal group until 7 years of age: future studies may consider this mechanism to understand whether male singing may show more extended development.

Our study also revealed that the IOIs are sexually dimorphic in juveniles, unlike previous findings on adult indris (De Gregorio et al. 2019a). Duration of the between-phrases IOI in juveniles appeared to be more variable than adults, which instead showed sexually dimorphic wpIOI variability, unlike the juveniles we studied. These differences provide further support to the idea that some factors, other than physiological modification during growth or genetics, may play a role in the development of singing behavior in I. indri.

This species shows a little dimorphism in external morphology (Pollock 1986) and substantial differences in singing behavior (Giacoma et al. 2010). The sub-glottal air sac possessed by indris does not vary in size between males and females (Dixon 1998). Giacoma et al. (2010) results did not support an influence of body size on the f0 values, since both male and female indris utter words characterized by a wide range of f0 values. Indeed, vocal plasticity may be an essential factor in shaping singing behavior, especially in the timing of phrases during vocal development, since animals, like indris, that participate in choruses uttered by several family members need to practice and acquire the ability to perform turn-taking (Gamba et al. 2016; De Gregorio et al. 2019b). Song production can be energetically costly (De Gregorio et al. 2019a; Clink et al. 2020), and an immature vocal apparatus may not be prepared to endure the full adult song, that can reach 110 dB (see Zanoli et al. 2020). In line with the above findings, there was a conspicuous use of SN and short phrases (DP2) in songs produced by indris around 1–2 years old, while reproductively mature animals tended to produce phrases consisting of more units (DP3, DP4). Energetic constraints and development of vocal control may likely drive the emission of different vocal types during growth, and, thus, we hypothesize that vocal plasticity, for example, in the articulation of vocal apparatus or the vocal tract tuning (Gamba et al. 2011), may play an essential role in the development of this complex vocal output. Our results are in line with recent evidence on the primates vocal plasticity and flexibility, which showed a certain degree of control on their vocal production (Terleph et al. 2018), even in juveniles (Koda et al. 2007). Parent tutoring activity, which requires further investigations, and auditory feedback may concur in driving some critical traits of such complex duetting behavior. As pointed out by Chow et al. (2015), some degree of learning may be indeed functional to the ontogeny of a signal that requires the ability to perform turn-taking between callers, as in the case of indris. Moreover, both internal and external factors, from maturation to motivation and social influences, may have a stronger effect on song characteristics than body size (Fitch 1997; Ey et al. 2007), and this may be in line with the fact that vocal development of primate family-living species is susceptible to social and environmental factors (Snowdon 2017).

Flexibility in juvenile primates is a pivotal condition in the evolution of language (Hage and Nieder 2016): as difficult as it is defining the substrates that led to the rise of human language, our work indicates that indeed even in a basal primate as I. indri there is strong evidence for flexibility in the changes during the development of singing behavior.

Authors’ Contributions
C.D.G., F.C., V.E., and M.G. designed the computational framework and analyzed the data. C.D.G., D.V., V.T., T.R., L.M., and J.R. collected the data. C.D.G., F.C., D.V., V.T., and M.G. performed the measurements, C.D.G., F.C., and M.G. wrote the manuscript with support from V.E., D.V., T.R., L.M., and C.G.

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Conflict of Interest

The authors declare no conflict of interest.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

References

Bates D, Maechler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48.

Behringer V, Deschner T, Deimel C, Stevens JM, Hofmann G, 2014. Age-related changes in urinary testosterone levels suggest differences in puberty onset and divergent life history strategies in bonobos and chimpanzees. *Horm Behav* 66:525–533.

Berg KS, Beissinger SR, Bradbury JW, 2013. Factors shaping the ontogeny of liberty onset and divergent life history strategies in bonobos and chimpanzees. *Horm Behav* 66:525–533.

Boersma P, Weenink D, 2007. *PRAAT: Doing Phonetics by Computer*. Version 5.3.51. Available from: http://www.praat.org (accessed 23 March 2017).

Bonadonna G, Torti V, Randrianarison RM, Martinet N, Gamba M, Giacoma C, 2014. Behavioral correlates of extra-pair copulation in *Indri indri*. *Primates* 55:119–123.

Chow CP, Mitchell JF, Miller CT, 2015. Vocal turn-taking in a non-human primate is learned during ontogeny. *Proc Biol Sci* 282:20150069.

Clink DJ, Lau AR, Bales KL, 2019. Age-related changes and vocal convergence in titi monkey duet pulses. *Behaviour* 156:1471–1494.

Clink DJ, Ahmad AH, Klinck H, 2020. Gibbons' aren't singing in the rain: presence and amount of rainfall influences ape calling behavior in Sabah, *Malaysia. Sci Rep* 10:13.

Clink DJ, Tasirin JS, Klinck H, 2020a. Vocal individuality and rhythm in male and female duet contributions of a non-human primate. *Carr Zool* 66:173–186.

Dahlin CR, Benedict L, 2014. Angry birds need not apply: a perspective on the flexible form and multifunctionality of avian vocal duets. *Ethology* 120:1–10.

De Gregorio C, Valente D, Torti V, Zanoli A, Colaci Cirillo D et al., 2019. Male indris determine the rhythmic structure of the song and sustain a divergent line of development. In: Zimmermann E, Newman JD, editors. *Current Topics in Primate Vocal Communication*. Boston: Springer. 73–97.

Dixson A, Altman J, 2000. Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings. *Nature* 403:233–237.

Dixson AF, 1998. *Primate Sexuality*. New York: Oxford University Press.

Elobowon AM, Snowdon CT, 1994. Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Anim Behav* 47:1267–1277.

Ey E, Pfeiferle D, Fischer J, 2007. Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. *Primates* 48:253–267.

Finch WT, 1997. Vocal tract length and formant frequency dispersion correlated with body size in rhesus macaques. *J Acoust Soc Am* 102:1213–1222.

Finch WT, Hauser MD, 1995. Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on “honest” advertisement. *Am J Primatol* 37:191–219.

Fischer J, Kitchen DM, Seyfarth RM, Cheney DL, 2004. Baboon loud calls advertise male quality: acoustic features and their relation to rank, age and exhausition. *Behav Ecol Sociobiol* 56:140–148.

Fox J, Weisberg S, 2011. *Multivariate Linear Models in R. An R Companion to Applied Regression*. Los Angeles: Thousand Oaks.

Gamba M, Favaro L, Torti V, Sorrentino V, Giacoma C, 2011. Vocal tract flexibility and variation in the vocal output in wild indris. *Bioacoustics* 20:251–265.

Gamba M, Torti V, Estienne V, Randrianarison RM, Valente D et al., 2016. The indris have got rhythm! Timing and pitch variation of a primate song examined between sexes and age classes. *Front Neurosci* 10:249.

Geissmann T, 2000. Gibbon songs and human music from an evolutionary perspective. In: Wallin N, Merker B, Brown S, editors. *The Origins of Music*. Cambridge (MA): MIT Press. 103–123.

Giacoma C, Sorrentino V, Rabarivola C, Gamba M, 2010. Sex differences in the song of indri indirs. *Int J Primatol* 31:539–551.

Hage SR, Nieder A, 2016. Dual neural network model for the evolution of speech and language. *Trends Neurosci* 39:813–829.

Hammerschmidt K, Jürgens U, Freundenstein T, 2001. Vocal development in squirrel monkeys. *Behaviour* 138:1179–1204.

Hammerschmidt K, Newman JD, Champoux M, Suomi SJ, 2000. Changes in rhesus macaque ‘coo’ vocalizations during early development. *Ethology* 106:873–886.

Hewitt G, MacLarnon A, Jones KE, 2002. The functions of laryngeal air sacs in primates: a new hypothesis. *Folia Primatol* 73:70–94.

Hradec M, Illmann G, Bolechová P, 2020. A first report of separation calls in southern yellow-cheeked gibbons *Nomascus gabriellae* in captivity. *Primates* 62:3.

Hradec M, Linhart P, Bartoš L, Bolechová P, 2017. The traits of the great calls in the juvenile and adolescent gibbon males *Nomascus gabriellae*. *PLoS ONE* 12:0173939.

Kelley DB, Gorlick DL, 1990. Sexual selection and the nervous system. *BioScience* 40:275–283.

Kirkwood JK, 1985. Patterns of growth in primates. *J Zool* 205:123–136.

Kikusui T, Nakamishii K, Nakagawa R, Nagasawa M, Mogi K et al., 2011. Cross fostering experiments suggest that mice songs are innate. *PLoS ONE* 6:e77721.

Knörnschild M, Nagy M, Metz M, Mayer F, von Helversen O, 2010. Complex vocal imitation during ontogeny in a bat. *BioL Lett* 6:156–159.

Knörnschild M, Nagy M, Metz M, Mayer F, von Helversen O, 2012. Learned vocal group signatures in the polygynous bat *Saccopteryx bilineata*. *Anim Behav* 84:761–769.

Koda H, Lemasson A, Oyakawa C, Pamungkas J, Masataka N, 2013. Possible role of mother–daughter vocal interactions on the development of species-specific song in gibbons. *PLoS ONE* 8:e71432.

Koda H, Masataka N, Kato A, Oyakawa C, 2007. Experimental evidence for the volitional control of vocal production in an immature gibbon. *Behaviour* 144:681–692.

Koda H, Oyakawa C, Kato A, Shimizu D, Koyama Y, Hasegawa S, 2014. Immature male gibbons produce female-specific songs. *Primates* 55:13–17.

Leigh SR, Shea BT, 1995. Ontogeny and the evolution of adult body size dimorphism in apes. *Am J Primatol* 36:37–60.

Lemasson A, Hausberger M, 2011. Acoustic variability and social significance of calls in female Campbell’s monkeys *Cercopithecus campbelli campbelli*. *Carr Zool* 129:3341–3352.

Liebal K, Waller BM, Slocombe KE, Burrows AM, 2013. *Primate Communication: A Multimodal Approach*. Cambridge: Cambridge University Press.

Margolish D, Tchernichovski O, 2015. Marmoset kids actually listen. *Science* 348:1471–1494.

Merker B, Cox C, 1999. Development of the female great call in *Hylobates edwardsi* with early life stress. *Am J Phys Anthropol* 139:523–532.

Newman JD, 1995. Vocal ontogeny in macaques and marmosets: convergent and divergent lines of development. In: Zimmermann E, Newman JD, Jürgens U, editors. *Current Topics in Primate Vocal Communication*. Boston: Springer. 73–97.

Ordoñez-Gómez JD, Santillan-Doherty AM, Hammerschmidt K, 2019. Acoustic variation of spider monkey *Ateles geoffroyi* contact calls is related to caller isolation and affects listeners’ responses. *PLoS ONE* 14:e0213914.
Pistorio AL, Vintch B, Wang X, 2006. Acoustic analysis of vocal development in a New World primate, the common marmoset Callithrix jacchus. *J Acoust Soc Am* 120:1655–1670.

Pollock JL, 1979. Female dominance in *Indri indri*. *Folia Primatol* 31: 143–164.

Pollock JL, 1986. The song of the indris (*Indri indri*; Primates: Lemuroidea): natural history, form, and function. *Int J Primatol* 7:225–264.

Core Team, R, 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Reichard UH, 2003. Social monogamy in gibbons: the male perspective. In: Reichard UH, Boesch C, editors. *Monogamy: Mating Strategies and Partnerships in Birds*. Cambridge: Cambridge University Press. 190–213.

Ríos-Cheleñ AA, Salaberria C, Barbosa I, Macías Garcia C et al., 2012. The learning advantage: bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn. *J Evol Biol* 25:2171

Sasahara K, Tchernichovski O, Takahasi M, Suzuki K, Okanoya K, 2015. A rhythm landscape approach to the developmental dynamics of birdsong. *J R Soc Interface* 12:20150802.

Terleph TA, Malaivijitnond S, Reichard UH, 2016. Age related decline in female lar gibbon great call performance suggests that call features correlate with physical condition. *BMC Evol Biol* 16:4.

Thorpe WH, 1961. *Bird-Song: The Biology of Vocal Communication and Expression in Birds*. New York: Cambridge University Press.

Tomeello M, 2008. *Origins of Human Communication*. Cambridge (MA): MIT Press.

Tomaszyczyk ML, Davis JE, Gouzoules H, Wallen K, 2001. Sex differences in infant rhesus macaque separation–rejection vocalizations and effects of prenatal androgens. *Horm Behav* 39:267–276.

Tomaszyczyk ML, Gouzoules H, Wallen K, 2005. Sex differences in juvenile rhesus macaque *Macaca mulatta* agonistic screams: life history differences and effects of prenatal androgens. *Dev Psychobiol* 47:318–327.

Torti V, Bonadonna G, De Gregorio C, Valente D, Randrianarison RM et al., 2017. An intra-population analysis of the indris’ song dissimilarity in the light of genetic distance. *Sci Rep* 7:12.

Torti V, Gamba M, Rabemananjara ZH, Giacoma C, 2013. The songs of the indris (*Mammalia: primates: Indridae*): contextual variation in the long-distance calls of a lemur. * Ital J Zool* 80:596–607.

Wetzel DM, Kelley DB, 1983. Androgen and gonadotropin effects on male mate calls in South African clawed frogs, Xenopus laevis. *Horm Behav* 17:388–404.

Zanoli A, De Gregorio C, Valente D, Torti V, Bonadonna G et al., 2020. Sexually dimorphic phrase organization in the song of the indris *Indri indri*. *Am J Primatol* 82:e23132.

Zhang YS, Ghazanfar AA, 2018. Vocal development through morphological computation. *PLoS Biol* 16:e2003933.