

Article

Born to sing! Song development in a singing primate

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Handling editor: James Hare

Received on 23 October 2020; accepted on 1 March 2021

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.

2012) or in the internal environment, such as changes in hormone levels (Wetzel and Kelley 1983; Frogs-Kelley and Gorlick 1990); finally, they may be the result of a learning process (Bats-Knörnschild et al. 2010).

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 *C. 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—Ordóñez-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 *singing primates*: 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 Benedict 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 whole 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 sex-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

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
Fanihy	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
Gibbet	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
Maintso	F	10MZ	15 May 2010

When an accurate birthdate was not known, birthdate was estimated to the 15th day of the respective month.

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 Strepsirrhine 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 \pm 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 Dixon (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 Ghazanfar 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 ($18^{\circ} 56'49''$ S, $48^{\circ} 27'53''$ 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 playbacks 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

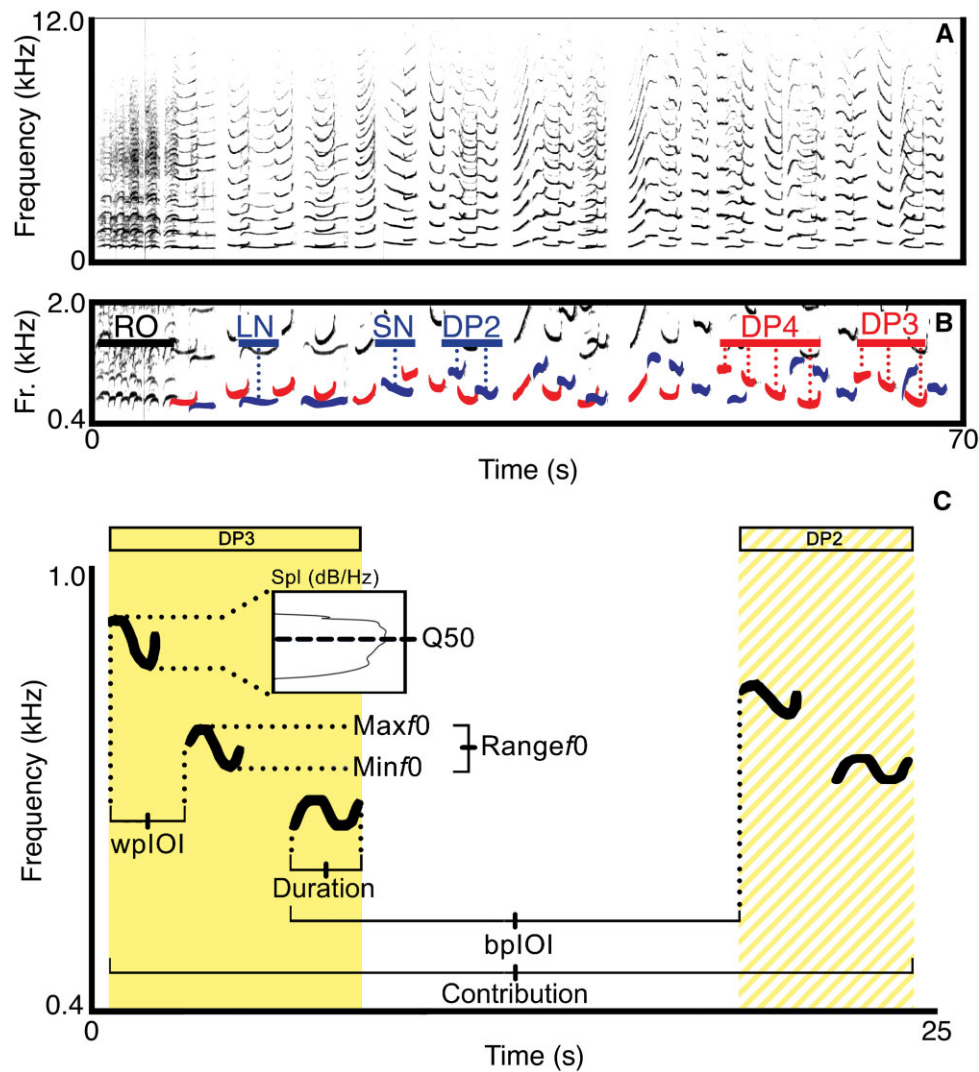


Figure 1. (A) A spectrogram of the indris' song. (B) A spectrogram of the song in which the singing of males (blue) and females (red) is highlighted. The different elements and phrases are also shown: roars (RO—*not included in the analysis*), a LN, a single note (SN), DPs made of 2 (DP2), 3 (DP3), or 4 (DP4) units. (C) Schematic representation of a spectrogram describing the acoustic parameters we collected. Temporal features included the duration of a unit (Duration), the duration of the individual contribution to the song (Contribution), the IOI between 2 consequent units (wplOI) and phrases (bpIOI). Phonation not represented as consisting in the cumulative duration of units in a contribution. Spectral features included the maximum, minimum, and range value of each unit's fundamental frequency (respectively, maxf0, minf0, Rangef0), the upper limit of the second quartile of energy in the spectrum (Q50). The sound spectrum displays sound pressure level (Spl) on the x-axis, frequency on the vertical axis. We did not show the mean absolute slope as it is the average absolute slope across 25 turning points in the pitch contour.

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 accordingly 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

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

Abbreviation	Parameter
Maxf0 (Hz)	Maximum fundamental frequency value across the unit
Minf0 (Hz)	Minimum fundamental frequency value across the unit
Rangef0 (Hz)	Maxf0–Minf0
Q50 (Hz)	Frequency value at the upper limit of the second quartiles of energy
MA slope (Hz)	Mean f_0 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)	Total duration of an individual vocal output in a duet/chorus, from the first its first note to its last one
Phonation (s)	Cumulative duration of the units of each individual contribution
Number of units (N)	Number of units uttered in each individual contribution
bpIOI (s)	IOI between 2 subsequent phrases
wpIOI (s)	IOI of 2 following units within a phrase

Praat script to extract the duration and 5 spectral measurements from each unit (Figure 1C and Table 2): the frequency at the upper limit of the second quartile of energy (Q50), the maximum and minimum of the fundamental frequency (maxf0 and minf0, respectively), the difference between the maximum and minimum fundamental frequency (rangef0), and the fundamental frequency mean absolute slope, a measure of the frequency variation along with the unit (MA slope). We then calculated the total duration of the individual vocal output in a duet/chorus (Contribution), the cumulative duration of the uttered units (Phonation), and the number of units in each contribution (Number of units). We also calculated the inter-onset intervals (IOIs) to evaluate the contributions' rhythmic structure (Sasahara et al. 2015). Namely, we considered the within-phrase IOI (wpIOI) and the between-phrase IOI (bpIOI). For all parameters (Table 2), we calculated the mean and the standard deviation.

Statistical analyses

To investigate developmental changes occurring in juvenile songs' spectro-temporal features, we used 11 linear mixed models (LMM, *lmer* function of *lme4* package, Bates et al. 2015) in R (R Core Team 2017; version 3.4.3). We used the subjects' age at the moment of recording (hereafter only “age”) as a fixed factor in all models. Before fitting the models, bpIOI and wpIOI were log-transformed since they did not show a normal distribution and all continuous variables were z -transformed. We ran 5 models using Q50, maxf0, minf0, rangef0, and MA slope as response variables. Since we could not assume that duration was not affecting spectral features, we included duration as a predictor, and we then ran an additional model with unit duration as the response variable. Each model featured one of the above parameters as the response variable, and all the others as fixed factors altogether with an interaction between age and sex.

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 particular model, the others were entered as fixed factors. These models also included an interaction between sex and age. We used a generalized 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 variable than adults, we calculated the individual mean of the coefficient of variation (CV) for each parameter considered in our models (rangef0, minf0, maxf0, 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 song parameters were extracted from the datasets of De Gregorio et al. (2019a; 2019).

Results

Occurrence of different unit types within the song

The occurrence of different unit types at different age and sex, summarized in Table 3, indicated that the mean number of SN emitted in the individual contribution to the song decreased with age, while the phrases composed by 2 units (DP2) showed a more variable trend, with a lower value at 1 year old and a higher one at 4 years old. Both phrases including 3 and 4 units (DP3, DP4) increased in number with age, while DP5 were more common at 1 year old and generally scarce compared with the other vocal types. The mean number of LN emitted per contribution remained more stable across years than phrases and SN, while the mean total number of units (Unit^{tot}) emitted per contribution increased with age.

Considering the 2 sexes, SNs were strongly predominant in young females between 1 and 2 years old (5.79 ± 2.53 per contribution), while males of the same age showed this vocal type only sporadically (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 (1.88 ± 0.18 for DP3; 0.38 ± 0.53 for DP4) than females of the same age (0.21 ± 0.29 for DP3; 0.17 ± 0.24 for DP4). For DP3, the trend 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)

Vocal type	1			2			3			4		
	Tot	Males	Females	Tot	Males	Females	Tot	Males	Females	Tot	Males	Females
SN	2.47 ± 2.89	0.13 ± 0.18	5.79 ± 2.53	2.38 ± 2.33	2.20 ± 1.30	2.51 ± 2.97	1.73 ± 1.27	1.53 ± 1.17	2.02 ± 1.55	1.36 ± 0.67	1.48 ± 0.60	1.21 ± 0.80
DP2	0.61 ± 0.78	1.38 ± 0.53	0.71 ± 1.00	2.29 ± 1.87	2.70 ± 2.05	2.00 ± 1.83	1.68 ± 1.19	1.43 ± 1.07	2.06 ± 1.42	2.14 ± 1.21	2.12 ± 1.23	2.17 ± 1.34
DP3	0.53 ± 0.72	1.88 ± 0.18	0.21 ± 0.29	1.39 ± 1.38	1.30 ± 1.72	1.45 ± 1.23	2.03 ± 1.59	1.26 ± 0.79	3.19 ± 1.89	1.74 ± 0.87	2.13 ± 0.61	1.26 ± 0.95
DP4	0.18 ± 0.31	0.38 ± 0.53	0.17 ± 0.24	0.52 ± 0.53	0.70 ± 0.67	0.39 ± 0.40	0.63 ± 0.90	0.74 ± 1.15	0.46 ± 0.42	0.65 ± 0.91	0.89 ± 1.14	0.37 ± 0.51
DP5	0.10 ± 0.20	0.25 ± 0.35	0.04 ± 0.06	0.01 ± 0.04	-	0.02 ± 0.05	0.03 ± 0.08	0.04 ± 0.10	-	0.03 ± 0.12	-	0.08 ± 0.17
LN	1.68 ± 1.52	2.63 ± 0.53	0.92 ± 1.30	2.00 ± 1.30	2.80 ± 1.35	1.42 ± 0.98	2.11 ± 1.31	2.78 ± 1.03	1.10 ± 1.06	2.44 ± 1.73	2.60 ± 1.69	2.25 ± 1.95
UNIT ^{tot}	8.17 ± 6.48	13.88 ± 4.07	9.63 ± 7.95	15.27 ± 6.05	17.10 ± 5.48	13.96 ± 6.50	15.93 ± 5.65	14.11 ± 5.68	18.65 ± 5.03	16.08 ± 7.28	18.28 ± 8.78	13.44 ± 4.47

DP2, phrases composed by 2 units; DP3, phrases composed by 3 units; DP4, phrases composed by 4 units; DP5, phrases composed by 5 units; and unit^{tot}, mean value of number of units emitted per individual contribution.

respect to females (1.26 ± 0.95). Concerning DP4s, males showed higher values than females at all developmental stages; in particular, while the mean number of DP4 emitted by males increased with age, for females increased until 3 years old and then decreased. The number of DP5, although generally low, had a peak in males at 1 year old (0.25 ± 0.35). Moreover, this vocal type was absent in males aged 2 and 4 years old and females aged 3 years old. DP6s are not reported in the table since we recorded a single case emitted by a female at 4.5 years old.

The number of LN was always higher in males than females and, regarding the mean number of units emitted in an individual contribution (Unit^{tot}), males had their peak at 4 years old (18.28 ± 8.78) while females at 3 years old (18.56 ± 5.03).

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 (minf0) and the maximum (maxf0) fundamental frequency. While the overall average for maxf0 was 930.75 ± 53.27 Hz, for minf0 was 727.29 ± 41.98 Hz. Moreover, while the individuals' age negatively influenced minf0 (Figure 2B and Supplementary Table SM1), no significant relationship emerged between age and maxf0. Similarly, unit duration was negatively correlated with minf0, but not with maxf0. 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 minf0, 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 (rangef0), 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 maxf0 and MA slope positively affected the fundamental frequency range. On the contrary, the model showed a negative correlation between the rangef0 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). Maxf0 and minf0 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

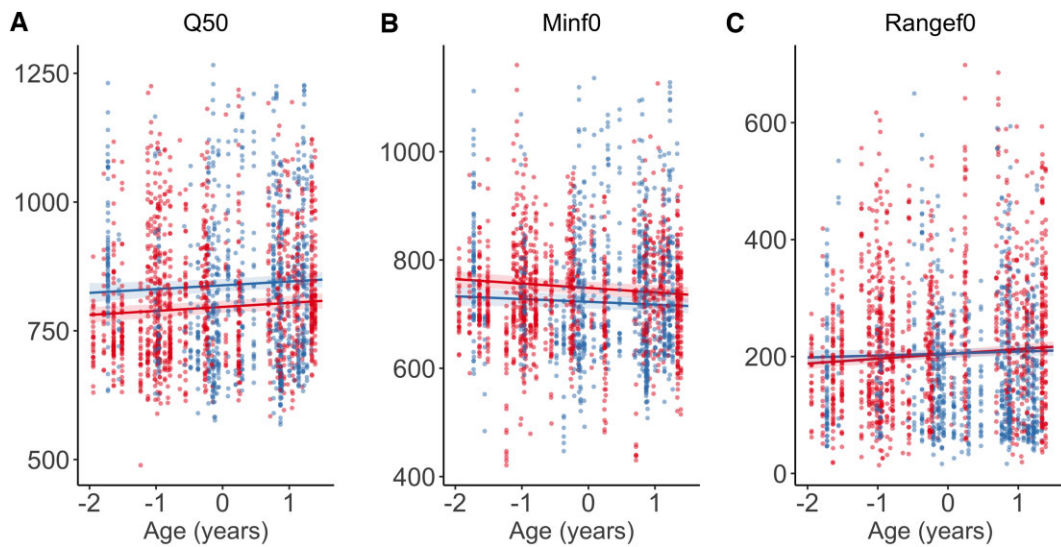


Figure 2. Effect of age on different spectral features (Hz) as response variable: (A) Q50, (B) min f_0 , (C) range f_0 . Red line represents juvenile females, while blue line represents juvenile males. Dots represent the observed data; shaded areas indicate confidence intervals. Being a plot of the effects resulting from the model, the predictor age must be included as z-transformed.

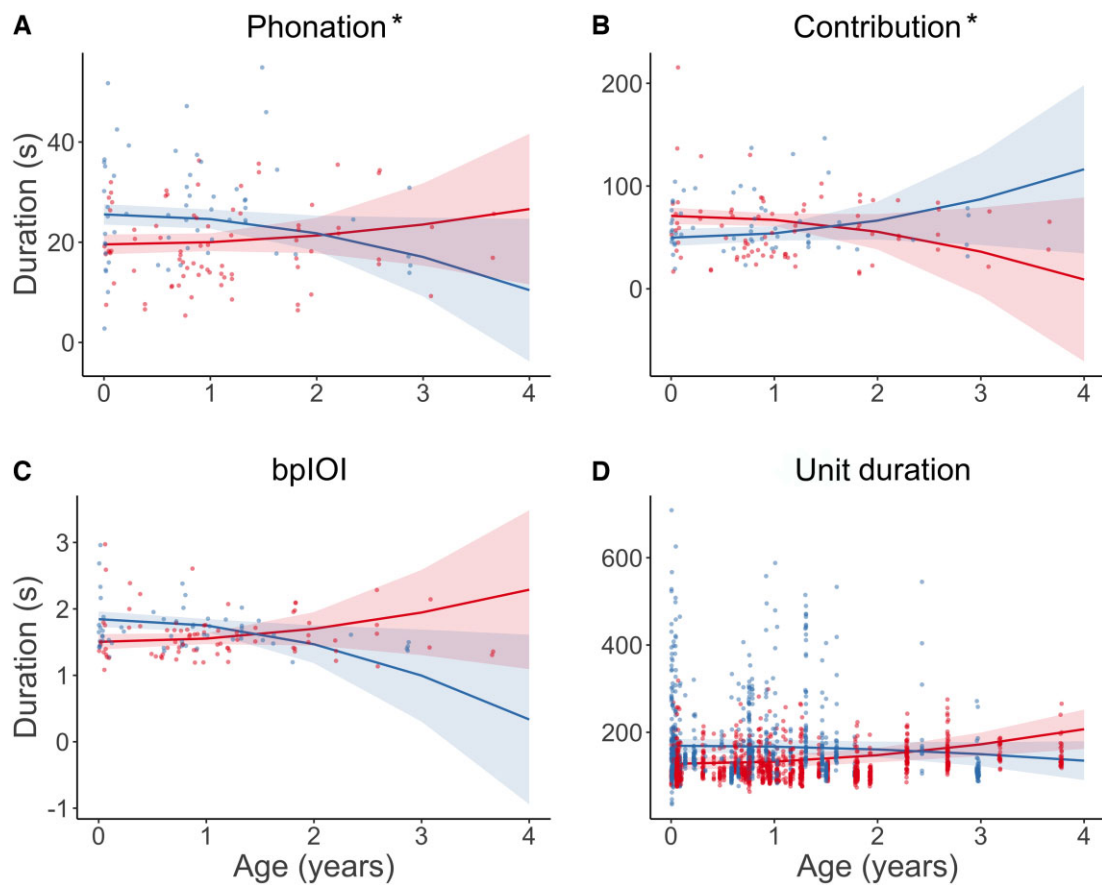


Figure 3. Effect of the interaction between age and sex on (A) mean phonation duration, (B) mean duration of individual contribution, (C) mean inter-onset-interval between phrases, and (D) unit duration. Red line represents juvenile females, while blue line represents juvenile males. Dots represent the 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 minf0 and the maxf0, 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 rangef0 ($t = -2.199$, $df = 16.795$, $P = 0.033$) 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 minf0 ($t = -0.333$, $df = 29.450$, $P = 0.742$), maxf0 ($t = -1.552$, $df = 40.212$,

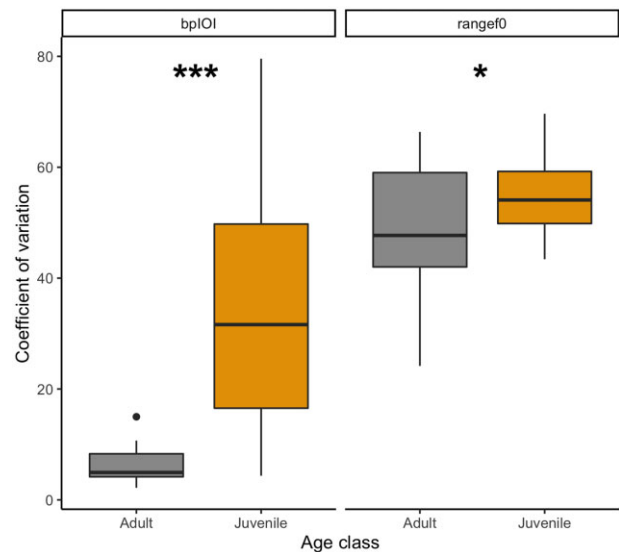


Figure 4. Boxplot of the CV of bpIOI and rangef0 in the age classes (adults in gray and juveniles in orange). The values shown are calculated from the average individual means; t-test significance at $P < 0.001$ is denoted by ***, at $P = 0.033$ is denoted by *.

$P = 0.128$), Q50 ($t = 1.465$, $df = 38.420$, $P = 0.151$), MA slope ($t = 0.349$, $df = 41.994$, $P = 0.728$), number of units ($t = -0.930$, $df = 31.691$, $P = 0.359$), 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 Altmann 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 minf0. 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 $\text{range}f_0$ 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 $\text{range}f_0$ 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' $\text{min}f_0$ 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 f_0 decreased with age, the Q50 and the range of f_0 showed an increase. Our finding shows that the increase in $\text{range}f_0$ with age may result from the decrease of $\text{min}f_0$, as $\text{max}f_0$ 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 $\text{min}f_0$ 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 $\text{range}f_0$ increased with age (Hammerschmidt et al. 2001) and rhesus macaques, whose *coo* calls exhibited a sharp decrease of f_0 during growth (Hammerschmidt et al. 2000). Similar changes of f_0 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 $\text{min}f_0$ than males. No differences emerged regarding the $\text{max}f_0$: the fact that in adults the sexual difference in $\text{min}f_0$ has been reported only for a particular type of unit (LN), while differences in $\text{max}f_0$ 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 (bpIOI). 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 singers (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. gabriellae*—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 (Dixson 1998). Giacoma et al. (2010) results did not support an influence of body size on the f_0 values, since both male and female indris utter units characterized by a wide range of f_0 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 primate 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., V.T., T.R., L.M., and C.G.

Acknowledgments

The authors want to thank the local field guides and the field assistants helping during the data collection. They are also grateful to GERP (Groupe d'Étude et des Recherches sur les Primates de Madagascar) for their support during the field activities and to Dr. Cesare Avesani Zaborra and Dr. Caterina Spiezio for the financial and technical support. They also thank Prof. Daniel Chamberlain for his helpful suggestions on statistical analyses. Finally, they thank the anonymous reviewers for their careful reading of our manuscript and their many insightful comments and suggestions. They have received permits for this research, each year, from "Direction des Eaux et Forêts" and "Madagascar National Parks" (formerly ANGAP) [2011 (N°274/11/MEF/SG/DGF/DCB.SAP/SCB), 2012 (N°245/12/MEF/SG/DGF/DCB.SAP/SCB), 2014 (N°066/14/MEF/SG/DGF/DCB.SAP/SCB), 2015 (N°180/15/MEEMF/SG/DGF/DAPT/SCBT), 2016 (N°98/16/MEEMF/SG/DGF/DAPT/SCB.Re and N°217/16/MEEMF/SG/DGF/DSAP/SCB.Re)], 2017 (73/17/MEEMF/SG/DGF/DSAP/SCB.RE). 2018: 91/18/MEEMF/SG/DGF/DSAP/SCB.Re; 2019: 118/19/MEDD/SG/DGEF/DSAP/DGRNE and 284/19/MEDD/SG/DGEF/DSAP/DGRNE; 2019/2020: 338/19/MEDD/SG/DGEF/DSAP/DGRNE]. Data collection did not require a permit for 2013 because it has been performed by Malagasy citizens only.

Funding

This research was supported by the University of Torino and the Parco Natura Viva—Centro Tutela Specie Minacciate, with the financial assistance

of the European Union, through the Project BIRD (ACP SandT Program, Contract FED/2009/217077).

Conflict of Interest

The authors declare no conflict of interest.

Supplementary Material

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

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