Current Zoology, 2024, **70**, 291–297
https://doi.org/10.1093/cz/zoad029
Advance access publication 3 July 2023
Original Article

Isochronous singing in 3 crested gibbon species (*Nomascus* spp.)

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Handling editor: James Hare

Abstract

The search for common characteristics between the musical abilities of humans and other animal species is still taking its first steps. One of the most promising aspects from a comparative point of view is the analysis of rhythmic components, which are crucial features of human communicative performance but also well-identifiable patterns in the vocal displays of other species. Therefore, the study of rhythm is becoming essential to understand the mechanisms of singing behavior and the evolution of human communication. Recent findings provided evidence that particular rhythmic structures occur in human music and some singing animal species, such as birds and rock hyraxes, but only 2 species of nonhuman primates have been investigated so far (*Indri indri* and *Hylobates lar*). Therefore, our study aims to consistently broaden the list of species studied regarding the presence of rhythmic categories. We investigated the temporal organization in the singing of 3 species of crested gibbons (*Nomascus gabriellae, Nomascus leucogenys*, and *Nomascus siki*) and found that the most prominent rhythmic category was isochrony. Moreover, we found slight variation in songs' tempo among species, with *N. gabriellae* and *N. siki* singing with a temporal pattern involving a gradually increasing tempo (a musical *accelerando*), and *N. leucogenys* with a more regular pattern. Here, we show how the prominence of a peak at the isochrony establishes itself as a shared characteristic in the small apes considered so far.

Key words: *accelerando*, isochrony, music, rhythm, singing primates, song, tempo.

Can you imagine a nightingale whistling Beethoven's Ninth Symphony, a woodpecker singing The Rolling Stones' "Can't You Hear Me Knocking," or a chimpanzee drumming at the rhythm of Queen's "We Will Rock You?" Probably not. In fact, what we generally consider as "music" is a social and cultural construct (Honing 2018), which is, however, based on perceptual, motor, and vocal capacities, that have been identified as musicality (Honing et al. 2015; Honing 2018). Once identified, those characteristics and biological and cognitive substrates underlying human musical abilities can be used for cross-species investigation (Fitch 2015).

The last few years have revealed that several species may share the building blocks of musicality with humans. For example, chickadees can discriminate pitch ratios presented at different absolute frequencies (Hoeschele et al. 2012), zebra finches can generalize across different timbres (Spierings and ten Cate 2014), and thrush nightingale songs share an isochronous rhythmic pattern with human music (Roeske et al. 2020). Singing primates, a small circle of primate species that produce modulated songs composed from tens to thousands of vocal units (Haimoff 1986; De Gregorio, Carugati 2022a), have been indicated as among the most promising species to investigate features shared with our musical displays (Ravignani et al. 2014; Levinson 2016). Singing primates tend to live in small social groups, often defending a territory and engaging in loud choruses that propagate for kilometers in the forest (De Gregorio, Carugati 2022a). Singing primates are, in some cases, phylogenetically distant (e.g., 80 mya) and in others within

Received 17 February 2023; accepted 28 June 2023
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the Hominoidea clade (e.g., 20 mya). This phylogenetic distance suggests the possibility of convergent evolution for singing behavior in this taxon (Geissmann 2002). Nevertheless, the lack of knowledge about specific traits often prevents the formulation of further hypotheses.

Past research on 2 nonhuman primate species is particularly relevant here. Previous studies showed that the indri *Indri indri* is currently the only known species that performs duets and choruses (De Gregorio et al. 2019) that display multiple rhythmic categories, as seen in human music (De Gregorio, Valente, et al. 2021a). Rhythmic categories occur when temporal intervals between note onsets assume precise values, rather than being uniformly distributed, and rhythms with a small-integer ratio between these values are common in human music (Savage et al. 2015; Jacoby and McDermott 2017). Besides indris, bioacoustics work on gibbons has shown interactive and individual rhythmic features in their songs. In particular, white-handed gibbons *Hylobates lar* showed a single prominent rhythmic category corresponding to a small-integer ratio, isochrony (Raimondi et al. 2023). The last common ancestor between the white-handed gibbon and modern humans is dated 20 mya (Glazko and Nei 2003), while indris have an evolutionary history separated from humans by about 75 mya (Kumar et al. 2017), making the presence of multiple rhythmic categories in this lemur species even more intriguing. In fact, despite being phylogenetically distant from humans, indri lemurs are currently the nonhuman primates showing multiple rhythmic categories shared with human music, while small apes like the white-handed gibbons show only one.

As the mosaic concerning the occurrence of rhythmic categories within the vocal displays of animals is still largely incomplete, this study aims to extend the currently available knowledge by analyzing the rhythmic categories of 3 species of crested gibbons. Gibbons are one of the few primate families featuring singing species. Hence, mapping rhythmic capacities across gibbon species is crucial to understand whether what was observed in white-handed gibbons generalizes to singing apes.

By studying the singing behavior of 3 species of crested gibbons (*Nomascus gabriellae*, *Nomascus leucogenys*, and *Nomascus siki*), we aimed to understand whether we could find similarities across the rhythmic categories of closely related species. In fact, crested gibbons' common ancestor lived around 1.3 mya, whereas white-handed gibbons' and crested gibbons' common ancestor lived around 8.5 mya (Kumar et al. 2017). Gibbons belonging to the *Nomascus* genus are virtually unstudied in the wild and produce species-specific songs, although songs given by *N. leucogenys*, *N. siki*, and *N. gabriellae* are very similar, and only minor differences were observed (Figure 1; Geissmann 2002; Thinh et al. 2011). Finding that a crested gibbon species would produce nonrandom metrical structures would be relevant not just for our understanding of the species' biology but also for providing a critical piece of information for understanding whether and how conformity of animal rhythms to a small-integer ratio is widespread in the animal kingdom. Furthermore, by examining which primate species, besides humans, have evolved the capacity for musical rhythm, we can create the conditions to test functional hypotheses about why this capacity is adaptive (ten Cate and Healy 2017).

Material and Methods

Observations and recordings

We recorded songs emitted by adult captive gibbons in 2 zoological parks (Supplementary Table S1). At the Pistoia Zoo (Italy), we studied a family group of *N. gabriellae* ($N = 3$, 2 males and 1 female) from October to December 2021. At the Zoological and Botanical Park of Mulhouse (France) from April to June 2022, we recorded a group of *N. gabriellae* ($N = 3$, 2 females and 1 male), a group of *N. leucogenys* ($N = 3$, 2 females and 1 male) and a group of *N. siki* ($N = 3$, 2 females and 1 male).

We recorded songs using both a solid-state recorder (Zoom F1 equipped with a shotgun microphone) and a passive recorder (Audiomoth). The solid-state recorder was employed for the 3 species of *Nomascus* at the Zoological and Botanical Park of Mulhouse. The animals were observed from 0800 to 1600 h CET, each day focusing on 2 species, 1 in the morning and the other in the afternoon, rotating groups each day. The recordist pointed the microphone toward a particular individual and attributed each vocalization to the signaler via the focal animal sampling technique. We also recorded songs through passive recorders (Aumdiomoth) monitoring the groups at Pistoia Zoological Park, with a recording schedule from 0900 to 1400 h CET (low gain, sampling rate: 48 kHz), placing it outside the exhibit of *N. gabriellae* (about 10 m from the animals). Whenever the gibbons sang in the presence of a recordist, we used a digital camera Panasonic Lumix

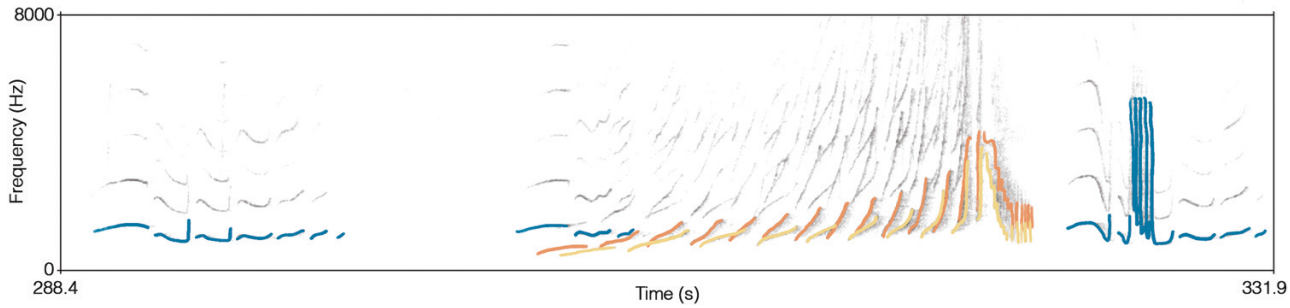

Figure 1 Spectrogram of a song by a group of *Nomascus gabriellae*. The fundamental frequency (f0) of each individual contribution is highlighted with a different colors: the male in blue and the 2 females in orange and yellow, respectively of *N. gabriellae*, highlighting the contributions of the 3 animals to the chorus with different colors.

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DMC-LZ7 to ensure the correct association of the emitter to each vocalization.

Acoustic analyses

We edited and saved the portions of our recordings containing gibbons' songs as single mono audio files (WAV format). Video recordings and focal animal sampling allowed assigning each contribution to a singing individual. An individual contribution comprises all the units emitted by a single individual. We obtained a total of 334 individual contributions; 147 from *N. gabriellae* at the Pistoia Zoological garden, while at Mulhouse Zoological and Botanical Garden, we recorded 79 contributions from *N. gabriellae*, 28 from *N. siki*, and 81 from *N. leucogenys* (Supplementary Table S1). Using the TextGrid tool in Praat (version 6.2.05; Boersma and Weenink 2022), we annotated the onsets and offsets of all the units emitted in each individual contribution to a song. Through a visual inspection of spectrograms, we identified all vocal and nonvocal intervals and measured starting point and duration of each interval (Gamba and Giacoma 2007). Next, using the software RStudio (RStudio Team 2020), we calculated the duration between the onsets of each couple of adjacent notes (inter-onset interval or IOI; hereafter t_k) to evaluate the rhythmic structure of contributions (Sasahara et al. 2015; Gamba et al. 2016; De Gregorio, Carugati, et al. 2021b). We then calculated rhythmic ratios (r_k) by dividing each interval t_k for itself plus the following one: $r_k = t_k/(t_k + t_{k+1})$ (see Roeske et al. 2020 and De Gregorio, Valente, et al. 2021a). Ratios were calculated excluding $t_k < 0.025$ s and >5 s, as these values are hypothesized being the lower and upper limit for meter perception and performance in macaques and humans and the thresholds on other ape species are unknown (Kuhl and Padden 1983; London 2012).

Statistical analyses

We performed all statistical analyses below using RStudio (RStudio Team 2020).

t_k Distribution

To evaluate how subsequent t_k and, consequently, the rhythmic categories were sequentially distributed among gibbons' species, we created a ternary plot (*ggtern* packages; Hamilton and Ferry 2018) for each species. Ternary plots are graphical representations of any 3 components, typically expressed as percentages and whose sum must be 100%. In the case of human music, these plots have been called "time clumping maps," chronotopic maps usually employed in the human music field to capture, in principle, all possible performances of all rhythms of $n + 1$ onset (Desain and Honing 2003). The ternary plots depict a 3-dimensional space: each axis represents 1 t_k, and each area within the graph represents a rhythm resulting from 3 consecutive t_k. Moreover, following the time-clumping map described by Desain and Honing (2003), all points in proximity to an empirical area belong to the same rhythmic category.

Rhythmic categories: r_k distribution

To evaluate the empirical occurrence of small-integer ratios, following the methodology shown in Roeske et al. (2020) and De Gregorio, Valente, et al. (2021a), we divided the ratio distribution into on-integer and off-integer ratio ranges, centering the on-integer ratio range around 1:1 (or 0.50), 1:2 (or 0.33), 1:3 (0.25), 2:1 (0.66), and 3:1 (0.75). The 0.50 value matches isochrony, that is, 2 consecutive intervals have equal duration. According to Roeske et al. (2020), we set the on–off-peak boundaries for the 1:3 ratio at 0.222, 0.235, 0.267, and 0.286; for 1:2 ratio at 0.286, 0.308, and 0.364, 0.400; for 1:1 at 0.400, 0.444, 0.556, and 0.600; for 2:1 at 0.600, 0.636, 0.692, and 0.714; for 3:1 at 0.714, 0.733, 0.765, and 0.778. We then counted all ratios that fell in each on- and off-integer ratio ranges for each contribution and adjusted the count by bin size.

r_k Occurrence

To test whether the values' amount of t_k ratios (r_k) fell statistically more into the on-integer ratio range rather than the off-integer ratio range, we used 3 Generalized Linear Mixed Models (*glmmTMB* package; Brooks et al. 2017), 1 for each of the 3 *Nomascus* species. Before creating the models, we checked the distribution of the response variable (beta) via the package *fitdistrplus* (Delignette-Muller and Dutang 2015) as a suitable theoretical distribution. Next, we entered the r_k adjusted count as a response variable, the r_k bin type (factor levels: OFF1:1, ON1:1, OFF1:2, ON1:2, OFF1:3, ON1:3, OFF2:1, ON2:1, OFF3:1, and ON3:1) as a fixed factor, and individual ID and individual's contribution ID to a song as nested random factors. We then used a post hoc test to perform all pairwise comparisons for all levels of the r_k bin type (*emmeans* package; Lenth 2023). Specifically, this test runs multiple comparisons between the observations that fall on integer and off integer for each integer ratio, with a *P*-value adjustment based on the Tukey method. For all models, we verified the assumption of normality and homogeneity of residuals by visually inspecting the *qqplot* and the residuals' distribution (a function provided by R. Mundry). To test for the significance of our full models, we compared them against null models containing only the random factors (Forstmeier and Schielzeth 2011), with a likelihood ratio test (Anova with argument "Chisq"; Dobson 2002).

Results

t_k Distribution

For *N. gabriellae*, t_k showed a bimodal distribution with a higher peak at 0.870 s and a second peak for shorter t_k at 0.174 s (Figure 2B). In contrast, *N. leucogenys* and *N. siki* had a single peak at 0.392 s (Figure 2G) and 0.481 s (Figure 2L), respectively. Visual inspection of the ternary plots (Figure 2C, 2H, and 2M) indicated a shared pattern in the succession of t_k and, consequently, rhythmic categories. All species shared a higher density of values in the middle of the graphs. Following the time-clumping map (Desain and Honing 2003), rhythmic sequences were marked by 3-time intervals with a reciprocal ratio of 1:1:1, indicating isochrony.

Rhythmic categories: r_k distribution

Visual inspection of r_k types' occurrence indicated a cluster in correspondence of isochronous ratios (1:1 or 0.5) for all 3 gibbon species (Figure 2D, 2I, and 2N). The r_k probability density functions confirmed the results from ternary plots (Figure 1C, 1H, and Figures 1M and 2C, 2H, and 2M), namely that subsequent t_k tends to have the same values, either when focusing on 2 or 3 following intervals of the same individual contribution.

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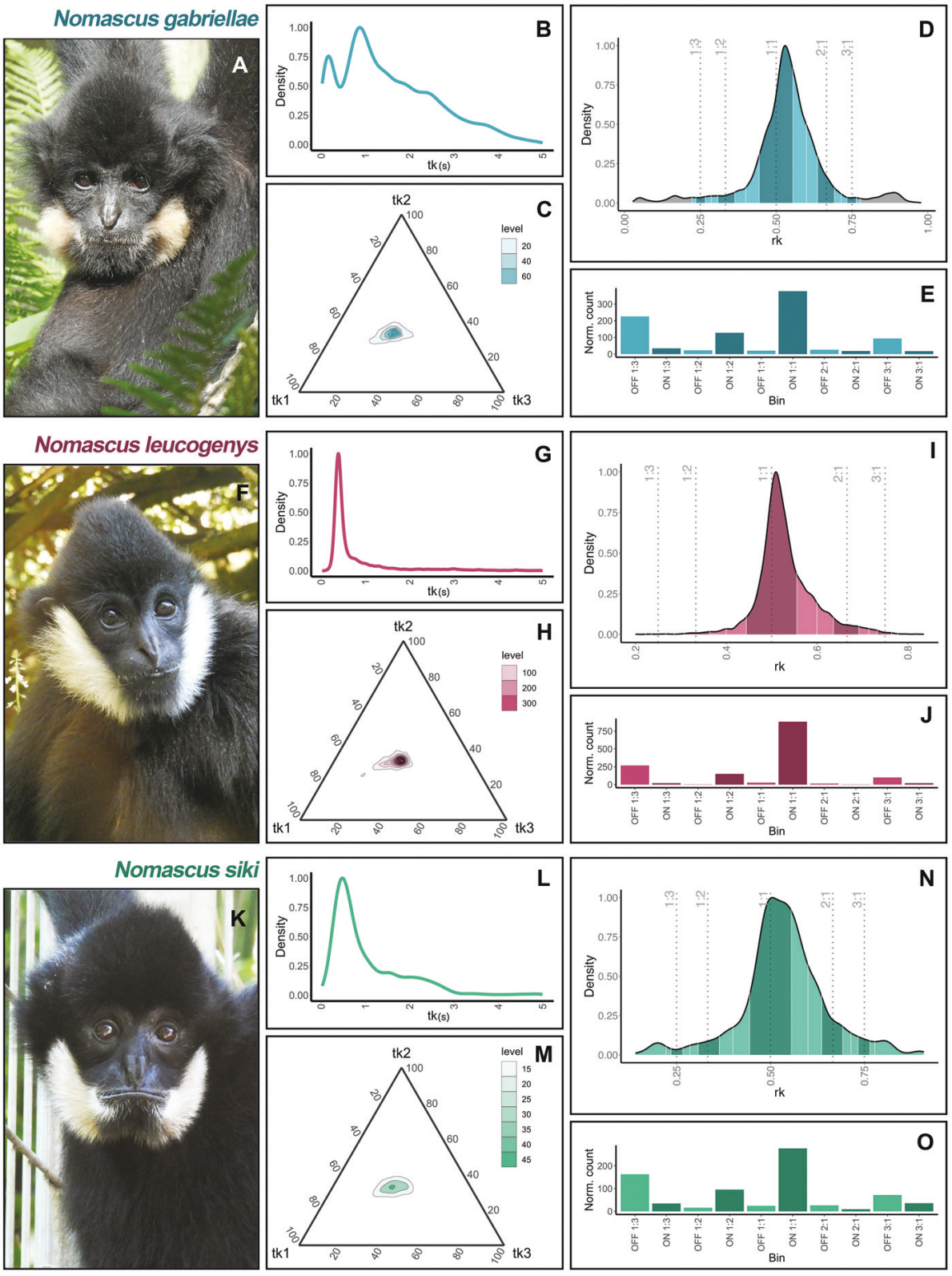

Figure 2 T_k and r_k distribution for the 3 *Nomascus* spp. (A, F, and K) *Nomascus* spp. (B, G, and L) Probability density functions of t_k for each species; (C, H, and M) Ternary plots for the 3 species, each axis represents 1 t_k, and each area within the graph represents a rhythm resulting from 3 consecutive t_k. (D, I, and N) Probability density functions of rhythm ratios (r_k), a shift of central peak to the right of the 1:1 ratio may be diagnostic of an accelerando. (E, J, and O) Bar plot showing the average adjusted r_k occurrence for on-integer (dark colors) and off-integer (light colors) ratio ranges. Photo credits: C. Mancassola.

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Table 1 Post hoc peak-wise comparisons of the GLMMs testing for the effect of r_k bin type (OFF1:1, ON1:1, OFF1:2, ON1:2, OFF1:3, ON1:3, OFF2:1, ON2:1, OFF3:1, and ON3:1) on the r_k-adjusted count in the 3 *Nomascus* spp. Tukey *P*-value adjustment for a 10 estimates comparison

Nomascus gabriellae					
Adjusted *rk* count ~ bin type + (1| ID/IDcontribution)					
Contrast	**Estimate**	***SE***	***df***	***T* ratio**	***P* value**
OFF1:1–ON1:1	−0.522	0.072	2237	−7.269	<0.001
OFF1:2–ON1:2	0.207	0.095	2237	2.185	0.468
OFF1:3–ON1:3	0.017	0.096	2237	0.178	1.000
OFF2:1–ON2:1	0.407	0.088	2237	4.649	<0.001
OFF3:1–ON3:1	0.085	0.096	2237	0.889	0.997
Nomascus leucogenys					
Adjusted *rk* count ~ bin type + (1| ID/ ID contribution)					
Contrast	**Estimate**	***SE***	***df***	***T* ratio**	***P* value**
OFF1:1–ON1:1	−159.778	0.089	797	−17.991	<0.001
OFF1:2–ON1:2	0.135	0.156	797	0.863	0.9974
OFF1:3–ON1:3	0.049	0.157	797	0.311	1.000
OFF2:1–ON2:1	0.552	0.130	797	4.262	<0.001
OFF3:1–ON3:1	0.253	0.156	797	1.618	0.839
Nomascus siki					
Adjusted *rk* count ~ bin type + (1| ID/ IDcontribution)					
Contrast	**Estimate**	***SE***	***df***	***T* ratio**	***P* value**
OFF1:1–ON1:1	−0.964	0.206	267	−4.670	<0.001
OFF1:2–ON1:2	0.095	0.267	267	0.354	1.000
OFF1:3–ON1:3	0.141	0.271	267	0.521	1.000
OFF2:1–ON2:1	0.342	0.249	267	1.374	0.934
OFF3:1–ON3:1	0.171	0.273	267	0.626	1.000

r_k Occurrence and species differences

The 3 models showed, for each species, significant differences in the r_k count depending on the r_k bin types (*N. gabriellae*: Null vs. Full—χ^2 = 1400.514, df = 9, P < 0.001; *N. leucogenys*: Null rss. Full—χ^2 = 829.813, df = 9, P < 0.001; *N. siki*: Null vs. Full—χ^2 = 215.380, df = 9, P < 0.001). The post hoc comparisons showed that the songs of all species were characterized by a prominent isochronous component (P < 0.001, Table 1), but not for 1:2 and 2:1. Note that, *N. gabriellae* and *N. leucogenys* displayed significantly more ratios falling in the 2:1 *off-integer* bin than in the 2:1 *on-integer* one (P < 0.001 for both species, Table 1). The local maxima for the isochrony peak for each species were at 0.503 for *N. gabriellae*, for *N. leucogenys* at 0.501, and 0.505 for *N. siki*.

Discussion

Our work aimed to broaden our knowledge of the occurrence of rhythmic categories in singing primates, particularly investigating the vocal behavior of 3 species of crested gibbons (*Nomascus* spp.). We found that the songs of *N. gabriellae*, *N. siki*, *and N. leucogenys* are characterized by a prominent isochronous component, in agreement with a previous study on lar gibbons (Raimondi et al. 2023). The consistency of distribution of rhythmic ratios among species is even more striking when considering the differences in the distribution of raw intervals, which are not randomly distributed but aggregate around 1 value for *N. leucogenys* and *N. siki* and 2 values for *N. gabriellae*. Although gibbons' songs are strongly genetically determined (Geismann 1984), the concordance in rhythmic structure among different crested gibbon species confirms the strong link among phylogeny, genetic features, and singing behavior in this genus (Geissmann 2002; Konrad and Geissmann 2006; Thinh et al. 2011). Nevertheless, we also found some degree of temporal variability among species, in particular concerning songs tempo: the slight shift of the isochrony peaks over 0.5 in the 3 *Nomascus* spp. seems to indicate that *N. gabriellae* and *N. siki* sing with a temporal pattern imputable to a gradually increasing tempo (a musical *accelerando*), while *N. leucogenys*' singing shows a more regular pattern. However, we cannot infer if these slight differences in tempo could be perceived by the animals as it is known for humans, where the tempo of a song can influence listeners' emotions (van der Zwaag et al. 2011).

Here, we also show how the prominence of a peak at the isochrony establishes itself as a shared characteristic in the small apes considered so far. As Raimondi et al. (2023)

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observed in lar gibbons *H. lar*, we found that crested gibbons showed isochrony as the sole prominent rhythmic category. However, it remains an open question whether isochrony in crested gibbons' songs results from the anatomical constraints influencing call rate and/or is based on a neuronal substrate in the so-called oscillators (Large et al. 2002; Desain and Honing 2003). Results on lar gibbons (Raimondi et al. 2023) would suggest that these 2 aspects might be intertwined, as, in this species, the presence of a strong isochronous rhythm was only partially explained by physiological constraints linked to call rate.

Moreover, even if *Nomascus* spp., as *Hylobates* spp., are phylogenetically closer to humans than indris, all lesser apes investigated so far share less rhythmic categories with human music than lemurs do, as indris produce songs with an additional small-integer ratio (1:2—De Gregorio, Valente, et al. 2021a). The study of rhythmic categories in animals, and in particular in the vocal signals of animals, is becoming increasingly important. For example, studies on male hyraxes have shown that males that vocalize with a more regular isochronous pattern and for longer periods have greater reproductive success and generate offspring that tend to survive longer (Demartsev et al. 2022). Our results complement previous data on lar gibbons, confirming that small apes show only 1 peak in the distribution of rhythmic ratios, corresponding to isochrony. Taking the multiple ratios characterizing popular music (Jacoby and McDermott 2017), we should expect that a small ape, whose evolutionary history diverged later from humans compared to the indris, should feature a higher rhythmic complexity. Two rhythmic categories in the indris correspond significantly with the small-integer ratios 1:2 and 1:1 (De Gregorio, Valente, et al. 2021a).

Thus, 2 questions remain: Which features in the indris singing behavior differ from the crested gibbons? What factors might have favored the evolution of a song showing 2 rhythmic categories in the indris? The first aspect could stem from the extent to which singing results from collective behavior. Evidence in lar and crested gibbons shows that solitary singing is common in males but occurs sometimes in females as well (De Gregorio, Carugati, et al. 2022a). On the other hand, studies on indri have shown that singing is always a collective behavior, rarely emitted by a single individual and potentially occurs as an unanswered duet attempt (De Gregorio, Carugati, et al. 2022a). This aspect seems to be an essential element in distinguishing indri from other singing primates. A second aspect is related to the organization of the chorus and the overlapping of individuals. Nonreproductive gibbons within a group (i.e., offspring of the pair-bonded adults) tend to overlap with the pair (Merker and Cox 1999). Female indris singing template guides the offspring's participation in the song (De Gregorio et al. 2019, De Gregorio, Zanoli, et al. 2022b). Subadults also appear to avoid actively overlapping with their parents' singing (Gamba et al. 2016; De Gregorio, Zanoli, et al. 2022b). We can speculate that this regular alternation of singers in the song and that they take turns but overlap non randomly (Gamba et al. 2016) may have played a role in the evolution of complex rhythmic abilities.

Our findings corroborate the hypothesis that isochrony is a fundamental temporal organization in the singing behavior of primates. The mosaic regarding the rhythmic capabilities of primates is still in its infancy, and future investigations on other singing species and natural populations would constitute a valuable contribution to its construction.

Acknowledgments

We thank the staff at the Zoological institutions, where data were collected for their help and support. We also thank the editor and the reviewers for their helpful suggestions during the revision process.

Funding

This research was supported by the University of Torino. A.R. is funded by the European Union (ERC, TOHR, 101041885). Center for Music in the Brain is funded by the Danish National Research Foundation (DNRF117). The Comparative Bioacoustics Group was funded by Max Planck Group Leader funding to A.R.

Conflict of Interest

The authors declare no conflict of interest.

Authors Contributions

C.D.G. and T.R.: conceptualization. C.D.G. and T.R.: methodology. V.B., C.P., and F.C.: data collection. C.D.G., T.R., and V.B.: investigation. C.D.G. and M.G.: writing—original draft. D.V., F.C., A.R., F.B., L.F., and B.L.: writing—review and editing. T.R.: visualization. All authors contributed to the article and approved the submitted version.

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