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

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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 understanding the mechanisms of singing behaviour 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 two species of non-human primates have been investigated so far (*I. indri* and *H. lar*). Therefore, our study aims to consistently broaden the list of species studied regarding the presence of rhythmic categories. We investigated the temporal organisation in the singing of three species of crested gibbons (*Nomascus gabriellae*, *N. leucogenys*, *N. 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: singing primates, music, tempo, *accelerando*, song, isochrony, rhythm

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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 & 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 et al. 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 kilometres in the forest (De Gregorio et al. 2022a). Singing primates are, in some cases, phylogenetically distant (e.g. 80 mya) and in others within the Hominoidea clade (e.g. 20 mya). This phylogenetic distance suggests the possibility of convergent evolution for singing behaviour in this taxon (Geissmann, 2002). Nevertheless, the lack of knowledge about specific traits often prevents the formulation of further hypotheses.

Past research on two 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 et al. 2021a). Rhythmic categories occur when temporal intervals between note onsets assume precise values, rather than being uniformly distributed, and rhythms with small integer ratio between these values are common in human music (Jacoby & McDermott, 2017; Savage et al. 2015). 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 & 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 non-human 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 analysing the rhythmic categories of three 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 understanding whether what was observed in white-handed gibbons generalises to singing apes.

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By studying the singing behaviour of three species of crested gibbons (*Nomascus gabriellae*, *N. leucogenys*, and *N. 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, while 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 (Geissmann, 2002; Thinh et al. 2011). Finding that a crested gibbon species would produce non-random 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 & Healy, 2017).

Material and Methods

Observations and recordings

We recorded songs emitted by adult captive gibbons in two zoological parks (Table SM1). At the Pistoia Zoo (Italy), we studied a family group of *N. gabriellae* (*N* = 3, two males and one 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 *Nomascus gabriellae* (N = 3, two females and one male), a group of *Nomascus leucogenys* (*N* = 3, two females and one male) and a group of *Nomascus siki* (*N* = 3, two females and one 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 three species of *Nomascus* at the Zoological and Botanical Park of Mulhouse. The animals were observed from 0800 – 1600 hrs CET, each day focusing on two species, one in the morning and the other in the afternoon, rotating groups each day. The recordist pointed the microphone towards a particular individual and attributed each vocalisation 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 – 1400 hrs CET (low gain, sampling rate: 48 kHz), placing it outside the exhibit of *N. gabriellae* (about 10 metres from the animals). Whenever the gibbons sang in the presence of a recordist, we used a digital camera Panasonic Lumix DMC-LZ7 to ensure the correct association of the emitter to each vocalisation.

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. leucogeny*s (Table SM1). Using the TextGrid tool in Praat (version 6.2.05; Boersma & Weenink 2022) we annotated the onsets and offsets of all the units emitted in each individual contribution to a song. Through a

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visual inspection of spectrograms, we identified all vocal and non-vocal intervals and measured starting point and duration of each interval (Gamba & 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 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 et al. (2021a)). Ratios were calculated excluding $t_k < 0.025$ s and > 5 s, as these values are hypothesised being the lower and upper limit for metre perception and performance in macaques and humans and the thresholds on other ape species are unknown (Kuhl & 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 & Ferry, 2018) for each species. Ternary plots are graphical representations of any three components, typically expressed as percentage 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 & Honing, 2003). The ternary plots depict a three-dimensional space: each axis represents one t_k, and each area within the graph represents a rhythm resulting from three consecutive t_k. Moreover, following the time-clumping map described by Desain & Honing (2003), all points in proximity to a 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 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), 3:1 (0.75). The 0.50 value matches isochrony, i.e. two 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, 0.286; for 1:2 ratio at 0.286, 0.308, 0.364. 0.400; for 1:1 at 0.400, 0.444, 0.556, 0.600; for 2:1 at 0.600, 0.636, 0.692, 0.714; for 3:1 at 0.714, 0.733, 0.765, 0.778. We then counted all ratios that fell in each on- and off-integer ratio ranges for each individual 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 three Generalized Linear Mixed Models (GLMM, *glmmTMB* package; Brooks, 2017), one for each of the three *Nomascus* species. Before creating the models, we checked the distribution of the response variable (beta) via the package *fitdistrplus* (Delignette-Muller & Dutang, 2015) as a suitable theoretical distribution. Next, we entered the rk adjusted count as a response variable, the rk bin type (factor levels: OFF1:1, ON1:1, OFF1:2, ON1:2, OFF1:3, ON1:3, OFF2:1, ON2:1, OFF3:1, 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 rk bin type

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(*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, 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 1B). In contrast, *N. leucogenys* and *N. siki* had a single peak at 0.392 s (Figure 1G) and 0.481 s (Figure 1L) respectively. Visual inspection of the ternary plots (Figure 1C, 1H, 1M) 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 & Honing, 2003), rhythmic sequences were marked by three-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 three gibbon species (Figure 1D, I, N). The r_k probability density functions confirmed the results from ternary plots (Fig.1C, H, M), namely that subsequent t_k tend to have the same values, either when focusing on two or three following intervals of the same individual contribution.

r_k occurrence and species differences

The three models showed, for each species, significant differences in the r_k count depending on the r_k bin types (*N. gabriellae*: Null vs Full - $\chi^2 = 1400.514$, $df = 9$, $P < 0.001$; *N. leucogenys*: Null vs Full - $\chi^2 = 829.813$, $df = 9$, $P < 0.001$; *N. siki*: Null vs Full - $\chi^2 = 215.380$, $df = 9$, $P < 0.001$). The post-hoc comparisons showed that the songs of all species were characterised by a prominent isochronous component ($P < 0.001$, Table 1), but not for 1:2, 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 was at 0.503 for *N. gabriellae*, for *N. leucogenys* at 0.501 and at 0.505 for *N. siki*.

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Discussion

Our work aimed to broaden our knowledge of the occurrence of rhythmic categories in singing primates, particularly investigating the vocal behaviour of three species of crested gibbons (*Nomascus* spp.). We found that the songs of *N. gabriellae, N. siki and N. leucogenys* are characterised 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 one value for *N. leucogenys* and *N. siki*, and two 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 between phylogeny, genetic features and singing behaviour in this genus (Geissmann, 2002; Konrad & 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 three *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) observed in lar gibbons (*Hylobates 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 & Kelso, 2002; Desain & Honing, 2003). Results on lar gibbons (Raimondi et al. 2023) would suggest that these two 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 produces songs with an additional small integer ratio (1:2 - De Gregorio 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 vocalise 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 one peak in the distribution of rhythmic ratios, corresponding to isochrony. Taking the multiple ratios characterising 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 et al. 2021a).

Thus, two questions remain: Which features in the indris singing behaviour differ from the crested gibbons? What factors might have favoured the evolution of a song showing two rhythmic categories in the indris? The

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first aspect could stem from the extent to which singing results from collective behaviour. Evidence in lar and crested gibbons shows that solitary singing is common in males but occurs sometimes in females as well (De Gregorio et al. 2022a). On the other hand, studies on indri have shown that singing is always a collective behaviour, rarely emitted by a single individual and potentially occurs as an unanswered duet attempt (De Gregorio 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 organisation of the chorus and the overlapping of individuals. Non-reproductive 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 et al. 2022b). Subadults also appear to avoid actively overlapping with their parents' singing (Gamba et al. 2016, De Gregorio 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 organisation in the singing behaviour 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.

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Authors' contributions

CDG and TR: conceptualization. CDG and TR: methodology. VB, CP, FC: data collection. CDG, TR, VB: investigation. CDG and MG: writing–original draft. DV, FC, AR, FB, LF, BL: writing–review and editing. TR: visualization. All authors contributed to the article and approved the submitted version.

Conflict of Interest

The authors declare no conflict of interest.

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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, ON3:1) on the r_k adjusted count in the three *Nomascus* spp. Tukey p-value adjustment for a 10 estimates comparison.

Nomascus gabriellae

Adjusted r_k 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**	**<.0001**
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	<.0001
OFF3:1-ON3:1	0.085	0.096	2237	0.889	0.997

Nomascus leucogenys

Adjusted r_k count ~ bin type + (1| ID / IDcontribution)

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 r_k 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

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

Figure 2. T_k and r_k distribution for the three *Nomascus* spp. A, F, M) *Nomascus* spp. B, G, L) Probability density functions of t_k for each species; C, H, M) Ternary plots for the three species, each axis represents one t_k, and each area within the graph represents a rhythm resulting from three consecutive tk. D, I, 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, O) Barplot showing the average adjusted r_k occurrence for on-integer (dark colours) and off-integer (light colours) ratio ranges. Photo credits: C. Mancassola.

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Figure 1

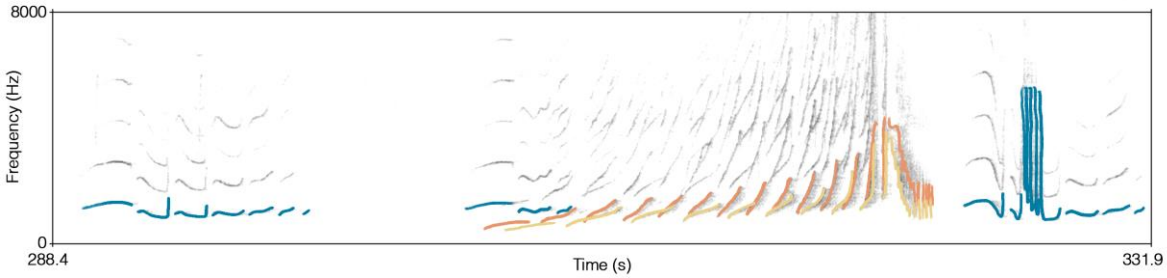

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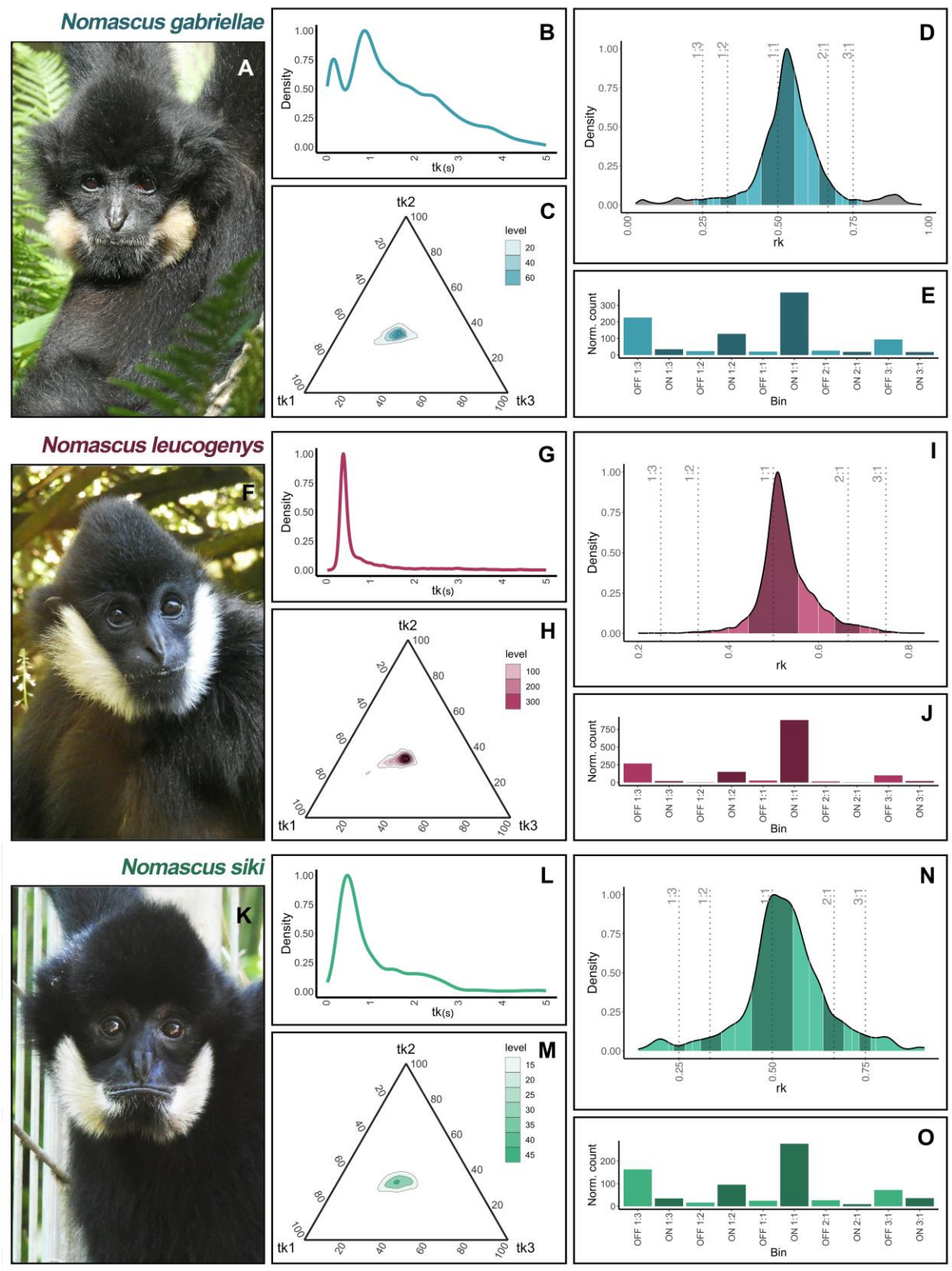
Figure 2



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