Supplemental Information: Categorical rhythms in a singing primate

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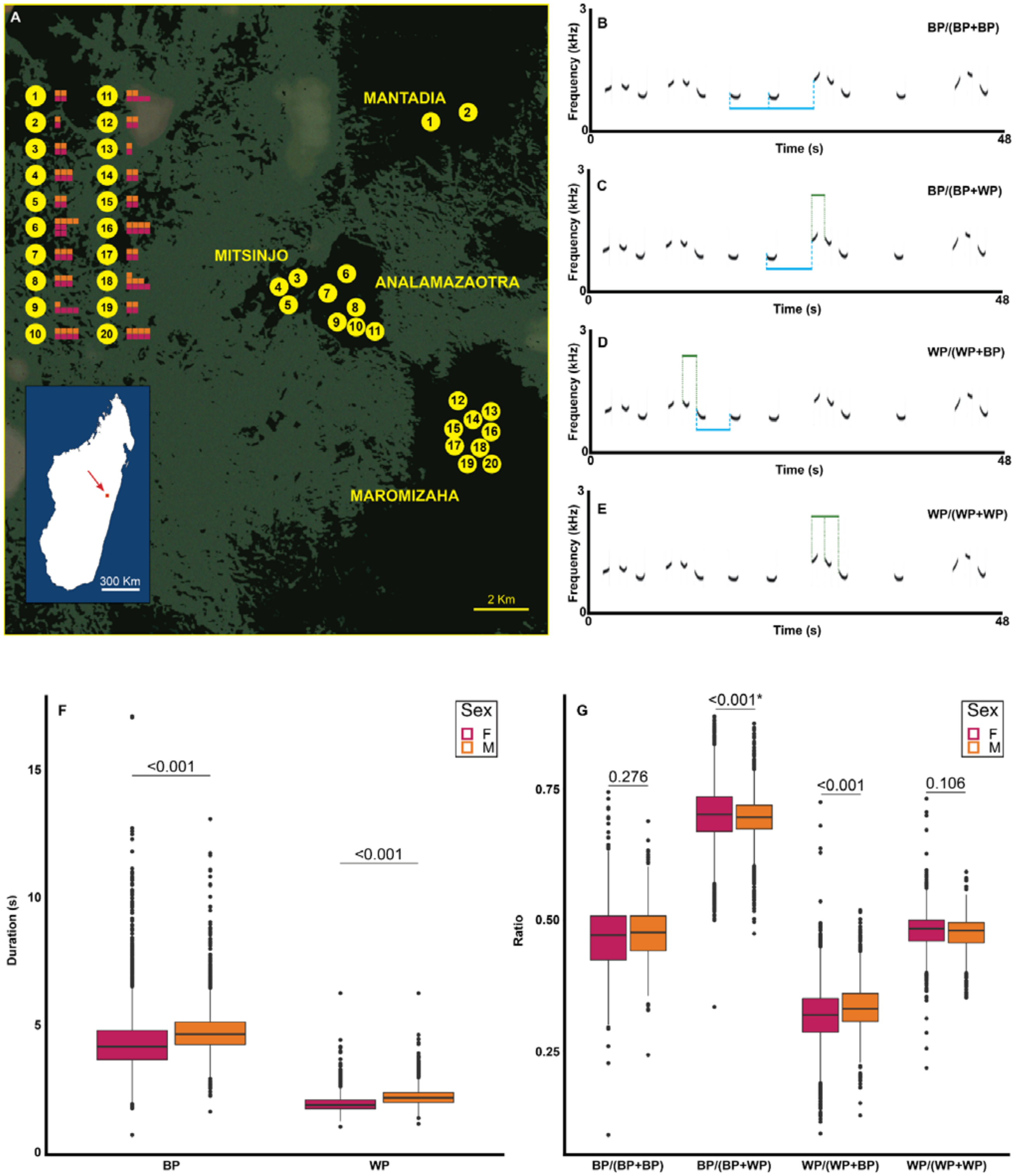

Figure S1. Song recording locations, with schematic representation of durations and ratios types and their values. (A) Map showing the four sites where indris were recorded. Yellow numbered circles represent the ID of the familiar group sampled. Colored lines next to the circles indicate that a reproductive male (orange) or female (pink) belonged to that group; the number of squares in each bar denotes the number of years that individual was recorded. **(B)** Schematic representation of a “BP/(BP+BP)” r_k type; the light blue line indicates two BP intervals: a t_k between two isolated notes, and a t_k between an isolated note and the first note of a phrase. **(C)** Schematic representation of a “BP/(BP+WP)” r_k type; the light blue line indicates a BP interval, and the green line indicates a WP interval: a t_k between an isolated note and the first note of a phrase, and a t_k between the first two notes of the same phrase. **(D)** Schematic representation of a “WP/(WP+BP)” r_k type; the light blue line indicates the BP interval, the green line indicates the WP interval: a t_k between two notes of the same phrase, and a t_k between a note belonging to a phrase and an isolated note. **(E)** Schematic representation of a “WP/(WP+WP)” r_k type; the green line indicates two WP intervals: in this case a t_k between the first and second note of the same phrase, and a t_k between the second and third note of the same phrase. **(F)** Boxplots of t_k duration by type. Notice that the WP boxplots here correspond to the first and second peaks in Figure 1E, and the BP boxplots here correspond to the third and fourth peaks in Figure 1E. **(G)** Boxplots of r_k values by type. The * denotes that, although the Tukey test is statistically significant, the difference is negligible because of the small effect size of the comparison.

A	**[LMM] Response Δ**		**Fixed Factor**	**Random Factors**	**Package**	
	t_k duration		Sex * t_k type	ID Individual, ID contribution	lme4	
Predictors		*Estimate*	*SE*	*df*	*t*	*p*
(Intercept)		1.423	0.028	[a]	[a]	[a]
WP[b]		-0.080	0.038	13770	-207.956	**<0.001**
M[b,c]		0.163	0.033	40.130	5.443	**<0.001**
WP*M[b,c]		0.037	0.006	13760	5.875	**<0.001**
B	**[GLMM] Response Δ**		**Fixed Factor**	**Random Factors**	**Package**	
	r_k		Sex * r_k type	ID Individual, ID contribution	glmmTMB	
Predictors		*Estimate*	*SE*	*z*	*p*	
(Intercept)		-0.130	0.008	[a]	[a]	
BP/(BP+WP)[b]		0.982	0.009	105.460	**<0.001**	
WP/(BP+WP)[b]		-0.632	0.009	-68.020	**<0.001**	
WP/(WP+WP)[b]		0.046	0.009	4.860	**<0.001**	
M[b,c]		0.034	0.015	2.300	**0.021**	
BP/(BP+WP)*M[b,c]		-0.069	0.016	-4.170	**<0.001**	
WP/(BP+WP)*M[b,c]		0.040	0.016	2.430	**0.015**	
WP/WP+WP*M[b,c]		-0.054	0.016	-3.270	**0.001**	
C			**[Tukey Test] r_k type**		**Package:** multcomp	
		Estimate	*SE*	*z*	*p*	
BP/(BP+WP) - BP/(BP+BP)		0.982	0.009	105.457	**<0.001**	
WP/(WP+BP) - BP/(BP+BP)		-0.632	0.009	-68.021	**<0.001**	
WP/(WP+WP) - BP/(BP+BP)		0.045	0.009	4.858	**<0.001**	
WP/(WP+BP) - BP/(BP+WP)		-1.614	0.006	-259.709	**<0.001**	
WP/(WP+WP) - BP/(BP+WP)		-0.936	0.006	-144.786	**<0.001**	
WP/(WP+WP) - WP/(WP+BP)		0.677	0.006	105.373	**<0.001**	
D			**[Tukey Test] t_k type * Sex**		**Package:** multcomp	
		Estimate	*SE*	*z*	*p*	
(F:F) WP-BP		-0.796	-0.796	-207.956	**<0.001**	
(M:F) BP-BP		0.163	0.038	5.443	**<0.001**	
(M:F) WP-BP		-0.596	0.030	-19.994	**<0.001**	
(M:F) BP-WP		0.958	0.030	32.090	**<0.001**	
(M:F) WP-WP		0.199	0.030	6.697	**<0.001**	
(M:M) WP-BP		-0.759	0.005	-153.539	**<0.001**	
E			**[Tukey Test] r_k type * Sex**		**Package**: multcomp	
		Estimate	*SE*	*z*	*p*	
(M:F) BP/(BP+BP)-BP/(BP+BP)		-0.796	-0.796	-207.956	0.276	
(M:F) BP/(BP+WP)-BP/(BP+WP)		0.163	0.038	5.443	**<0.001**	
(M:F) WP/(WP+BP)-WP/(WP+BP)		-0.596	0.030	-19.994	**<0.001**	
(M:F)WP/(WP+WP)-WP/(WP+WP)		0.958	0.030	32.090	0.106	

Table S1. Summary and details of models and Tukey tests. **(A)** Influence of the fixed factors on t_k *duration*. Full model vs. Null model: $\chi2 = 24468.48$, df = 3, p < 0.001. **(B)** Influence of the fixed factors on r_k *type*. Full model vs. Null model: $\chi2$ =

30155, df = 11, p < 0.001. (**C**) Results of the Tukey test for r_k *type*. (**D**) Results of the Tukey test for the interaction between t_k *type* and *sex*. (**E**) Results of the Tukey test for the interaction between r_k *type* and *sex*. [a] Not shown as not having a meaningful interpretation. [b] Estimate ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor. [c] This predictor was dummy coded, with "SexF," being the reference category. Statistically significant values are indicated in bold; M: males; F: females.

Supplemental Experimental Procedures

1. Observations and recordings

Indris (*Indri indri*) are lemurs whose ancestor diverged from ours approximately 77.5 MYA[S1]; phylogenetically, they are one of the farthest primate species from humans. Indris are classified as 'critically endangered' by the IUCN Red List of Threatened Species[S2]. While their population size is currently unknown, it has been estimated that only around 1000 - 10000 individuals remain in the wild[S3]. Indris have never been successfully bred in captivity[S4].

We recorded songs produced by 20 indri groups (39 individuals) living in four different rainforest patches in Madagascar (Figure S1A): six groups in the Analamazaotra Reserve (Andasibe-Mantadia National Park, 18°56' S, 48° 25' E), two groups in Mantadia (Andasibe-Mantadia National Park), three groups in the Mitsinjo Station Forestière (18°56'S, 48°4' E), and nine groups in the Maromizaha Forest (18°56'49" S, 48°27'53"E). Genetic analyses on seven groups inhabiting Maromizaha Forest confirmed that indris live in groups composed of an unrelated mating pair plus one to three individuals, usually their offspring[S5].

We collected data in the field from 2005 to 2016 for a total of 41 months. We observed one group per day from 06:00 a.m. to 1:00 p.m., using natural marks to identify each individual. Our analyses focused on adult reproductive individuals because temporal features in the vocalizations of adult reproductive indris may differ from those found in young or non-reproductive individuals[S6,S7].

We recorded songs using solid-state recorders (SoundDevices 702, Olympus S100 and LS05, and Tascam DR-100, DR-40, and DR-05) equipped with Sennheiser (ME 66 and ME 67) or AKG (CK 98) shotgun microphones. We set the recorders at a sampling rate of 44.1 kHz and an amplitude resolution of 16 bits during all the recording sessions. We recorded the animals at a distance ranging from 2 to 20 meters, with the microphone aimed at the focal singing animals. The recordist pointed the microphone towards a particular individual and attributed each vocalization to the signaler via the focal animal sampling technique[S8]. Songs can take the form of duets when two indris (usually the reproductive pair) sing together, or choruses, when one or more non-reproductive individuals join the pair in singing. An illustrative video can be found online at https://youtu.be/4w04ohzB40g. In the indris' songs, notes can be either organized in phrases or produced as isolated units. Phrases are characterized by adjacent units with a descending frequency pattern and separated by silent intervals. Isolated units are single notes between two phrases (Figure 1C, Figure S1B-E). A new phrase starts when the starting fundamental frequency of a note is higher than the ending fundamental frequency of the preceding one.

2. Acoustic analyses

From group recordings of 346 duets and choruses we extracted a total of 636 individual contributions uttered by 39 reproductive indris, 20 females and 19 males. Using Praat 5.3.46[S9], we edited and saved the recorded portion containing the indris' song as a single mono audio file (WAV format). Using field notes and video recordings, we then identified, annotated, and saved the onsets and offsets of each note for each individual as a Praat textgrid. We identified units and silences via visual inspection of the spectrograms. We labeled the notes, differentiating if they were organized in a sequence or produced as isolated units. Our analysis does not include 'roars', which are harsh and chaotic emissions that usually introduce the song[S10].

We then labeled the silent portions of the individual contributions, differentiating silences depending on whether they occurred between two notes of the *same phrase*, vs. between two *different phrases* or two different *isolated notes*. For each of the above units and intervals, we extracted the timing of note onsets and duration using

Praat. We imported them in R (R Core Team 2017; version 3.4.3) and calculated the inter-onset intervals (t_k, Figure 1C) based on onsets to evaluate the rhythmic structure of contributions[S11]. Based on previous work[S7,S12], we used the information on notes and silences type (belonging to a phrase or an isolated note) to calculate two types of t_k. The within-phrase t_k (WP: Within-Phrase inter-onset intervals) are all and only the intervals between notes *within* a phrase (roughly mapping to the two leftmost peaks in Figure 1E). The between-phrase t_k (BP: Between-Phrase inter-onset intervals) are all and only the intervals *between* two different phrases or between two isolated notes (roughly mapping to the two rightmost peaks in Figure 1E). Note that a sequence of *n* notes will produce *n-1* inter-onset intervals, i.e. $t_1,...,t_{n-1}$.

We then calculated rhythmic ratios r_k following the methodology of Roeske et al.[S13], namely by dividing each t_k for its duration plus the duration of the following interval: $r_k = t_k /(t_k+t_{k+1})$. Since each t_k can either be a WP or a BP, we obtained four ratio types: WP/(WP+WP), WP/(WP+BP), BP/(WP+BP) and BP/(BP+BP), depending on the type of two adjacent t_k. These four ratio types and their corresponding intervals in indris' songs are depicted in Figure S1B-E (and their pooled distribution in Figure 1D). Further analyses were performed both on the t_k values and their ratios r_k.

3. Statistical analysis

Four main analyses were performed. All statistical analyses in 3.1-3.3 below were performed in R (R Core Team 2017; version 3.4.3). Analyses in 3.1 aimed at statistically substantiating the intuition in Figure 1E, namely that the distributions of t_k durations have 4 distinct peaks, potentially different by sex and t_k type. Analyses in 3.2 aimed at testing this same hypothesis on the r_k data. Analyses in 3.3 correspond to, and provide details for, the main result reported in the manuscript and Figure 1F. Compared to 3.3, analyses in 3.2 afford the possibility of zooming in on the overall pattern of ratios and analyzing them by sex and ratio type. In addition, comparison between results in 3.1 and 3.2 allow inference on potential sex differences in durations and/or ratios. Finally, the simulation described in 3.4 aimed at providing a plausible baseline scenario of how empirical ratios would look if indris had no rhythmic categories. While density functions (Figure 1D and 1E) were calculated for illustrative purposes, all statistical analyses were based on the original data points, not the smoothed, continuous density functions.

3.1. t_k durations

We tested whether sex and the type of t_k statistically predicted the inter-onset interval duration, using a Linear Mixed Model (LMM, lmer function of lme4 package[S14]). Before fitting the models, t_k duration was log-transformed ($\log_e$) because it was not normally distributed. We entered the values of t_k as response variable, and sex of the emitter, t_k type (WP and BP) and their interaction as fixed factors. We included the individual's identity and the specific song contribution from which we extracted the t_k as nested random factors. We used the Tukey test[S15] to perform all the pairwise comparisons for all the interaction levels between sex and t_k type (multiple contrast package *multcomp* in R). Finally, we used a two-sample Kolmogorov-Smirnov test in order to test if the two-peak distribution of our observed t_k durations (Fig. 1E) would differ from a random, uniformly distributed one, generated based on the upper and lower limit of the real distribution and containing the same number of observations (N= 14192).

3.2. t_k ratios (r_k)

To test whether the values of t_k ratios (r_k) were statistically influenced by the sex of the singer and the r_k type (WP/(WP+WP), WP/(WP+BP), BP/(WP+BP), and BP/(BP+BP)), we used a Generalised Linear Mixed Model (GLMM, *glmmTMB* package[S16]) fitting a beta distribution, continuous between 0 and 1. Beta was chosen via the package *fitdistrplus*[S17] as a suitable theoretical distribution. The values of r_k were entered in the model as response variable, and sex of the emitter, r_k type, and their interaction as fixed factors. We included the individual identity and the specific song contribution from which we extracted the ratios r_k as nested random factors. We used the Tukey test (within the multiple contrast package *multcomp* in R) to perform all pairwise comparisons for all levels of the interaction between sex and r_k type and for all levels of r_k type[S15].

For both models, we verified the assumptions of normality and homogeneity of residuals by visually inspecting the *qqplot* and the residuals' distribution (a function provided by R. Mundry). We also excluded the presence of collinearity among predictors based on variance inflation factors (*vif* package[S18]). To test for significance of our full models[S19] we compared them against null models containing only the random factors, with a likelihood ratio test (Anova with argument test "Chisq"[S20]). We report estimates, standard error (S.E.), z- and p-values for the Tukey tests (Table S1C-E).

Finally, we used Cohen's d test to compute the magnitude of the effect size for the Tukey tests' comparisons between different types of durations and ratios between the two sexes.

3.3. Rhythmic categories: Ratios distribution and their peaks

To evaluate the empirical occurrence of small integer ratios, following the methodology of Roeske et al.[S13], we divided the ratio distribution into on-integer and off-integer ratio ranges, centering the on-integer ratio ranges around 1:2 (or 0.333; a fundamentally small integer ratio), 1:1 (or 0.500; corresponding to isochrony), and 2:1 (or 0.666; a fundamentally small integer ratio). While the 1:1 ratio corresponds to two intervals of equal duration, the 1:2 and 2:1 ratios correspond to the second interval being, respectively, double and half the duration of the first.

Conversely, again following the methodology of Roeske et al.[S13], off-integer ratio ranges were centered around 1:3.5 (or 0.285), 1:2.5 (or 0.400), 1-1:2.5 (or 0.600), and 1-1:3.5 (or 0.710); the boundaries of all on- and off integer ratio ranges were 1:3.25 (or 0.307), 1:2.75 (or 0.363), 1:2.25 (or 0.444), 1-1:2.25 (or 0.555), 1-1:2.75 (or 0.637), and 1-1:3.25 (or 0.693). All these ratios were those used by Roeske et al.[S13]. We then counted all occurrences of ratio values that fell in each on- and off-integer ratio range for each individual, and we normalized these counts according to the size of their range on the x-axis[S13]. Notice, for instance, how the on-integer ratio range of 1:2 in Figure 1D is narrower than the 1:1 range; normalization allowed to correct and account for this and other inequalities. The Shapiro-Wilk tests confirmed that our count data did not follow a normal distribution, so we compared on-integer and off-integer ratio ranges using three (paired) Wilcoxon signed-rank tests.

3.4. Simulated ratio distribution

For reference, we simulated the null ratio distribution N expected by chance. The yellow line in Figure 1D is based on 100,000 simulated ratios produced using a custom script in Python 2.7.10. Based on the upper (681 msec) and lower (17089 msec) bound of inter-onset intervals naturally produced by indri[S12], we simulated what would happen if no rhythmic categories existed by sampling inter-onset intervals from two uniform distributions U and V with bounds at 681 and 17089 msec and calculating each ratio as in the formula in Figure 1D. In other words, this sampling simulated the distribution N of the ratio between one random variable U and its sum with another random variable V, both random variables being uniform.

Finally, to understand if the simulated ratio distribution (yellow line in Figure 1D) significantly differed from the empirical one, we resampled 17100 observations (the number of observations in our dataset) from the 100,000 simulated ones. This was done 1000 times, and every resampled distribution was compared with the empirical one using Kolmogorov-Smirnov tests in R.

<u>Supplemental Results</u>

1. t_k durations

The average duration of t_k was 2.114 ± 0.298s for WP and 4.651 ± 1.008s for BP. This difference is also visible in Figure 1E, where the probability density function clearly shows the presence of two clusters in each distribution of the t_k durations. Males showed longer t_k than females (Figure S1F, Table S1A), both overall (M = 3.429 ± 1.372s, F = 2.919 ± 1.403s; $p < 0.001$) and by t_k type (WP: M = 2.339 ± 0.340s, F = 1.899 ± 0.258s; $p < 0.001$; BP: M = 5.002 ± 0.928s, F = 4.318 ± 1.083s; $p < 0.001$; Table S1D; Figure S1F). WPs had a shorter duration than BPs ($p < 0.001$; Table S1A). When comparing the two sexes, Cohen's d was 1.477 for WP and 0.679 for BP, confirming that the significant sexual differences were non-negligible. In brief, there is both a sexual dimorphism in durations and a significant difference between the t_k types BP and WP, exemplified as the four peaks in Figure 1E. Finally, the two-sample Kolmogorov-Smirnov test confirmed that the distribution of observed t_k durations significantly differed from a null uniform one with the same boundary values ($D = 0.656$, $p < 0.001$)

2. t_k ratios (r_k)

The average ratio r_k was 0.499 ± 0.161. Our model showed significant differences among r_k types (Table S1B), and the Tukey test confirmed that all four r_k types differed significantly ($p < 0.001$, for every comparison; Table S1C). The average WP/(WP+BP) was 0.324 ± 0.054, WP/(WP+WP) was 0.477 ± 0.033, BP/(BP+WP) was 0.698 ± 0.054, and BP/(BP+BP) was 0.470 ± 0.068. Notice how both values linked to isochrony (BP/BP+BP and WP/WP+WP) are slightly smaller than 0.5, suggesting increasing duration of adjacent intervals, i.e. ritardando.

Males presented overall higher ratio values than females ($p = 0.021$; Table S1B). However, the Tukey test indicated no significant sex differences for the ratios types linked to isochrony (BP/(BP+BP), $p = 0.276$; WP/(WP+WP), $p = 0.106$; Table S1E) emerged. Instead, we did find sexual dimorphism in r_k type WP/(WP+BP), where males showed lower values than females ($p < 0.001$), and in BP/(BP+WP), where males were the ones showing higher values ($p < 0.001$). When comparing between sexes, Cohen's d was 0.152 for WP/(WP+WP), 0.059 for BP/(BP+BP), 0.278 for WP/(WP+BP). Instead, it was 0.111 for BP/(BP+WP), suggesting that this difference between males and females is negligible, even if it is statistically significant (Figure S1G). Therefore, the only actual (significant and non-negligible) difference in r_k types concerns WP/(WP+BP) values between males and females. WP/(WP+BP) corresponds to the first peak in Figure 1D and the first pair of boxplots in Figure 1F. The two significant peaks in Figure 1D characterize the 1:1 and the 1:2 ratio; the latter is sexually dimorphic and with higher values in males (third pair of boxplots in Figure S1G). This necessarily implies that the last inter-onset interval within a phrase is longer in males. In brief, there is little sexual dimorphism in ratios and categories and no dimorphism at all for significant rhythmic categories but the 1:2 ratio. On the one hand, this speaks *against* sexual selection hypotheses for isochrony; on the other hand, sexual selection might be responsible for longer intervals in males.

Summary and details of both models and Tukey tests appear in Table S1.

3. Rhythmic categories: Ratios distribution and their peaks

Visual inspection of the occurrence of different r_k types indicated a possible presence of three clusters (green density function in Figure 1D). Statistical comparison between data points from this density function confirmed and refined this intuition. The dependent 2-group Wilcoxon tests between on-integer and off-integer ratio ranges (Figure 1F) confirmed that indris produce songs characterized by at least two rhythmic categories: isochrony, corresponding to 1:1 ratio ($p < 0.001, V = 0$) and a 1:2 ratio ($p < 0.001$, $V = 81$). A V value of 0 for the isochronous 1:1 categories means that each of the 39 indris produced more on-integer than off-integer ratios, not only statistically but also numerically at an individual level. However, we did not find significant differences between on-integer and off integer ratio ranges for 2:1 ($p = 0.289$, $V = 313$). In other words, the first and second (but not the third) peaks in Figure 1D result from indris producing ratios falling on small on-integer ratio neighborhoods rather than equally-sized off-integer neighborhoods.

4. Simulated ratio distribution

The results of the Kolmogorov-Smirnov two-sample test showed that the 1000 resampled ratio distributions were significantly different from the empirical real ratio distribution: all $0.109 < D < 0.127$, all $p < 0.001$. In other words, statistical comparison between data points from the empirical distribution and data points from the distribution expected by chance (yellow line in Figure 1D) suggested that our empirical ratios differed from those expected by chance.

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Author Contributions

Conceptualization, C.D.G., D.V., T.R., A.R. and M.G.; Methodology, C.D.G., D.V., T.R., A.R., O.F. and M.G.; Investigation, C.D.G., D.V., V.T., T.R. and L.M.; Writing – Original Draft, A.R. and C.D.G.; Writing – Review & Editing, M.G., V.T., T.R., D.V. and L.M.; Visualization, C.D.G., D.V., T.R., A.R. and M.G.; Supervision, M.G. and C.G.

Data and Code Availability

Data, code, and custom-written scripts are available from the corresponding author upon request.

Declaration of Interests

The authors declare no competing interests.

Supplemental References

S1. Masters, J.C., Silvestro, D., Génin, F., and DelPero, M. (2013). Seeing the wood through the trees: the current state of higher systematics in the Strepsirhini. Folia Primatol. *84*, 201-19.

S2. King, T., Dolch, R., Randriahaingo, H.N.T., Randrianarimanana, L., and Ravaloharimanitra, M. (2020). *Indri indri*. The IUCN Red List of Threatened Species 2020: e.T10826A115565566. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T10826A115565566.en

S3. Andriaholinirina, N., Baden, A., Blanco, M., Chikhi, L., Cooke, A., Davies, N., Dolch, R., Donati, G., Ganzhorn, J., Golden, C., Groeneveld, L.F., Hapke, A., Irwin, M., Johnson, S., Kappeler, P., King, T., Lewis, R., Louis, E.E., Markolf, M., Mass, V., Mittermeier, R.A., Nichols, R., Patel, E., Rabarivola, C.J., Raharivololona, B., Rajaobelina, S., Rakotoarisoa, G., Rakotomanga, B., Rakotonanahary, J., Rakotondrainibe, H., Rakotondratsimba, G., Rakotondratsimba, M., Rakotonirina, L., Ralainasolo, F.B., Ralison, J., Ramahaleo, T., Ranaivoarisoa, J.F., Randrianahaleo, S.I., Randrianambinina, B., Randrianarimanana, L., Randrianasolo, H., Randriatahina, G., Rasamimananana, H., Rasolofoharivelo, T., Rasoloharijaona, S., Ratelolahy, F., Ratsimbazafy, J., Ratsimbazafy, N., Razafindraibe, H., Razafindramanana, J., Rowe, N., Salmona, J., Seiler, M., Volampeno, S., Wright, P., Youssouf, J., Zaonarivelo, J., and Zaramody, A. (2020). *Indri indri*. The IUCN Red List of Threatened Species. Version 2020-3. https://www.iucnredlist.org

S4. Britt, A., Randriamandratonirina, N.J., Glasscock, K.D., and Iambana, B.R. (2002). Diet and feeding behaviour of *Indri indri* in a low-altitude rain forest. Folia Primatol. *73*, 225–239.

S5. Torti, V., Bonadonna, G., De Gregorio, C., Valente, D., Randrianarison, R.M., Friard, O., Pozzi, L., Gamba, M., and Giacoma, C. (2017). An intra-population analysis of the indris' song dissimilarity in the light of genetic distance. Sci. Rep. *7*, 10140.

S6. Gamba, M., Torti, V., Estienne, V., Randrianarison, R.M., Valente, D., Rovara, P., Bonadonna, G., Friard, O., and Giacoma, C. (2016). The indris have got rhythm! Timing and pitch variation a primate song examined between sexes and age classes. Front. Neurosci. *10*, 249.

S7. De Gregorio, C., Carugati, F., Estienne, V., Valente, D., Raimondi, T., Torti, V., Miaretsoa, L., Ratsimbazafy, J., Gamba, M., and Giacoma, C. (2021). Born to sing! Song development in a singing primate. Curr. Zool., zoab018.

S8. Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour *49*, 227–267.

S9. Boersma, P., and Weenink, D. (2008). Praat: Doing Phonetics by Computer (Computer Program). Available online at: http://www.praat.org

S10. Pollock, J. I. (1986). The song of the indris (*Indri indri*; Primates: Lemuroidea): natural history, form, and function. Int. J. Primatol. *7*, 225-264.

S11. Sasahara, K., Tchernichovski, O., Takahasi, M., Suzuki K, and Okanoya K. (2015). A rhythm landscape approach to the developmental dynamics of birdsong. J. R. Soc. Interface *12*, 20150802.

S12. De Gregorio, C., Zanoli, A., Valente, D., Torti, V., Bonadonna, G., Randrianarison, R.M., Giacoma, C., and Gamba, M. (2019). Female indris determine the rhythmic structure of the song and sustain a higher cost when the chorus size increases. Curr. Zool. *65*, 89-97.

S13. Roeske, T. C., Tchernichovski, O., Poeppel, D., and Jacoby, N. (2020). Categorical rhythms are shared between songbirds and humans. Curr. Biol. *30*, 3544-3555.

S14. Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. J. Stat. Softw. *67*, 1–48.

S15. Bretz, F., Hothorn, T., and Westfall, P. (2010). Multiple Comparisons Using R (Chapman and Hall/CRC Press).

S16. Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., and Bolker, B.M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R. J. *9*, 378–400.

S17. Delignette-Muller, M.L., and Dutang, C. (2015). fitdistrplus: An R Package for Fitting Distributions. J. Stat. Softw. *64*, 1–34.

S18. Fox, J., and Weisberg, S. (2011). An R companion to applied regression (SAGE Publications, Inc).

S19. Forstmeier, W., and Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav. Ecol. Sociobiol. *65*, 47–55.

S20. Dobson, A. J. (2002). An Introduction to Generalized Linear Models (Chapman and Hall/CRC Press).