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(Article begins on next page)

08 January 2022

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Who's got rhythm, and why? One approach to the biology and evolution of musical rhythm consists in finding statistical universals [1]. These are rhythmic features that appear above chance across human musical cultures. One such universal is the production of categorical rhythms, which occurs when note onsets are separated by ~~discrete~~ temporal intervals belonging to few classes [1-3]. Because of categorical rhythms, any song sung (reasonably) faster or slower is still recognizable. Another universal consists in the presence of binary subdivisions, such as those found in the notes of a march [1,3]. A parallel approach to the biology of music focuses on finding similarities and differences across species, so to build evolutionary phylogenies of musical traits [4]. Here we combine these two approaches. We show that complex rhythm categories are not, among mammals, unique to humans [5]; we find that a lemur species displays, in its songs, the isochronous and binary rhythm categories seen in human music.

Beyond melodic features (Figure 1A), individual animal vocalizations have onsets (blue lines in Figure 1C). Two onsets delimit an inter-onset interval (t_k), i.e. the time between the onset of a note and the next one [3,6]. Ratios between these intervals are calculated by dividing an interval by itself plus its adjacent one [5]. Patterns in these ratios may emerge. For instance, two identical intervals generate a 1:1 ratio, and an interval followed by another twice its duration generates a 1:2 ratio. This approach successfully highlighted rhythmic similarities between birdsong and human music [5]. In particular, for the first time in a non-human species, songs of thrush nightingales and zebra finches showed a significant isochronous rhythmic category and a potential bias towards 1:2 categories [5]. This work advanced the hypothesis that rhythmic categories and isochrony should appear in species showing coordinated group singing [5]. Here we test this hypothesis.

We focused on one of the few singing primates, the lemur *Indri indri*, sampling approximately 1% of all living individuals from this critically endangered species. All members of a family group sing in temporally-coordinated duets and choruses [7-8]. Over 12 years, we recorded songs from 20 indri groups living in their natural habitat, the rainforest of Madagascar (Figure 1B and Supplement for details). We extracted temporal features of indris' songs, analyzing inter-onset intervals (Figure 1E) and their ratios (Figure 1D).

First, we find that note onsets are separated by discrete temporal intervals, and ratios of these intervals form three clusters (green density function in Figure 1D). In other words, the intervals between notes bear similarities to the discrete note durations found in human music [2,5], as opposed to being sampled with the same probability among all possible values (yellow line in Figure 1D). Notice that finding these clusters does, in principle, neither imply that they match specific values nor that these values are integer ratios [3].

Second, we find that ratios match two rhythmic categories: isochrony, similar to the pace of a metronome, and 1:2, a fundamentally small integer ratio. We ask whether ratios produced by each individual fall more frequently in the vicinity of a small integer ratio (called on-integer in Figure 1D) or away from it (off-integer) [5]. By pairing the number of on-integer to off-integer ratios produced by each indri, we find that the empirical rhythmic ratios from songs fall statistically more often on small integer ratios than off integer ratios (Figure 1F). In particular, and similarly to songbirds [5], indri songs have a strong, above chance, isochronous component with some tempo flexibility; indris sing at a slightly decreasing isochronous tempo, similar to musical 'ritardando' [5]. Unlike songbirds [5], indris' empirical ratios statistically match the theoretical 1:2 category (but not the 2:1 category, Figure 1F). This provides direct evidence for one musical universal, categorical rhythms, and suggestive evidence for another one, binary subdivisions [1,3]. The production and perception of metrical temporal hierarchies are, to date, aspects of human musicality yet to be found in any non-human species [4]. The binary subdivisions we witness are not direct evidence of meter, though they may result from two nested periodic processes (bottom of Figure 1C).

Third, our data show that, while inter onset intervals differ between males and females (Figure 1E), rhythmic categories are preserved across sexes (see Supplement). This may be relevant to selective hypotheses for music, hypothesizing a role of sexual selection, social bonding, etc. on rhythm origins. Productive inference on how rhythm evolved requires multi-component thinking [4, 6, 9]: rhythm as a whole is a mystery but some of its defining features may be present in other species, as we show here. Male and female indris may produce different singing tempi and interval durations, but rhythmic categories are the same between sexes. This suggests that sexual selection should not affect the evolution of rhythmic categories in indris (while it may play a role in single interval timing) [4].

Why should another mammal, apart from humans, produce categorical rhythms? As the last common ancestor between humans and indris lived 77.5 MYA, this ability may have convergently evolved among singing species, such as songbirds, indris, and humans [10]. As in songbirds, isochrony and rhythmic categories in indris may facilitate song coordination, processing, and potentially learning [4-7]. Alternatively, one hypothesis links isochrony and categorical rhythms to cultural transmission [3,5]. If this holds, and unaware of whether indris show song learning or transmission, our results highlight either an alternative path to isochrony, or the promise of finding cultural transmission in indri.

To conclude, other mammals can spontaneously produce categorical, flexible, and music-like rhythms. Rhythmic universals in other species may be more common than previously surmised. Apart from songbirds, singing mammals are promising species to look for musical universals, offering the advantage of phylogenetic proximity to humans [5]. We encourage more comparative work on indri and other endangered species to gain more data before it is too late to witness their breath-taking singing displays.
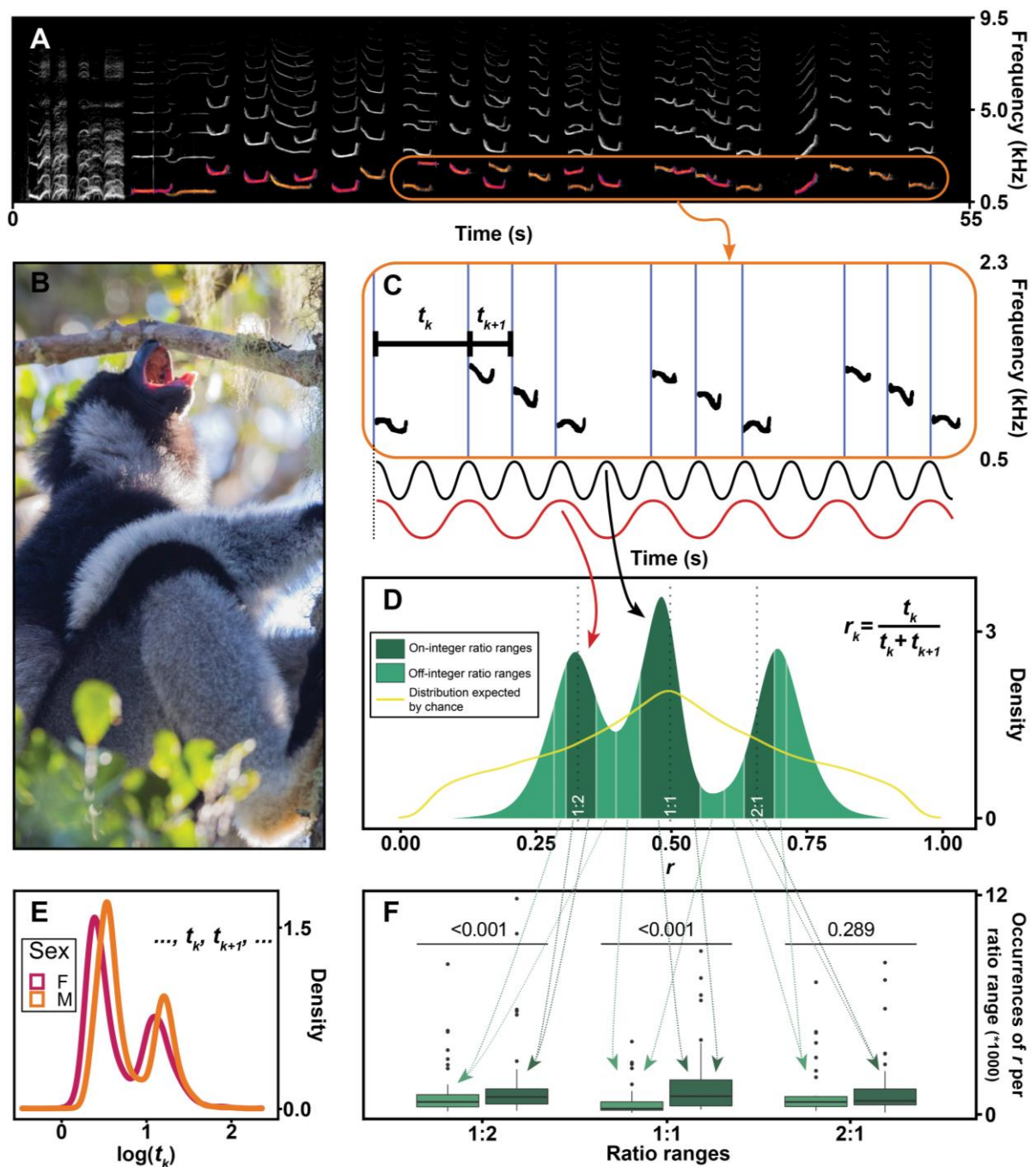
Figure 1. Indris' songs: Extracting individual rhythms from group choruses.

(A) Spectrogram of the indris' song, highlighting the fundamental frequencies of male (orange) and female (pink) notes (iZotope RX). The orange inset highlights the male song portion detailed in C.

(B) Adult male indri singing in the Maromizaha New Protected Area, Madagascar (Credit: Filippo Carugati).

(C) Schematic representation of onsets (solid blue lines) in a male indri song. Pairs of onsets define inter-onset intervals t_k, marked with solid black lines. Sine waves (bottom) exemplify which purported oscillatory processes might generate the rhythmic categories found in the data: 1:1 ratio in black, 1:2 ratio in red.

(D) Probability density function of rhythm ratios (r_k), which we calculated across 39 adult indris and 636 individual contributions to songs. On-integer (dark green) and off-integer (light green) ratio ranges are highlighted. A markedly different null distribution (yellow line, simulated from actual indri data) would be expected in the absence of rhythmic categories.

(E) Probability density function of inter-onset intervals (t_k), depicting dimorphism between sexes (i.e., a statistically significant sex difference, see Supplement).

(F) Boxplots of adjusted r occurrence for on-integer (dark green) and off-integer (light green) ratio ranges. The ratio counts for individual indris constitute the data points for the analysis, and counts are normalized by bin size (see Supplement). Indris significantly produce more on-integer than off-integer ratios for the 1:2 (Wilcoxon signed-rank Test, V = 81, p-values in figure) and the isochronous 1:1 categories (V = 0) but not for the 2:1 category (V = 313).

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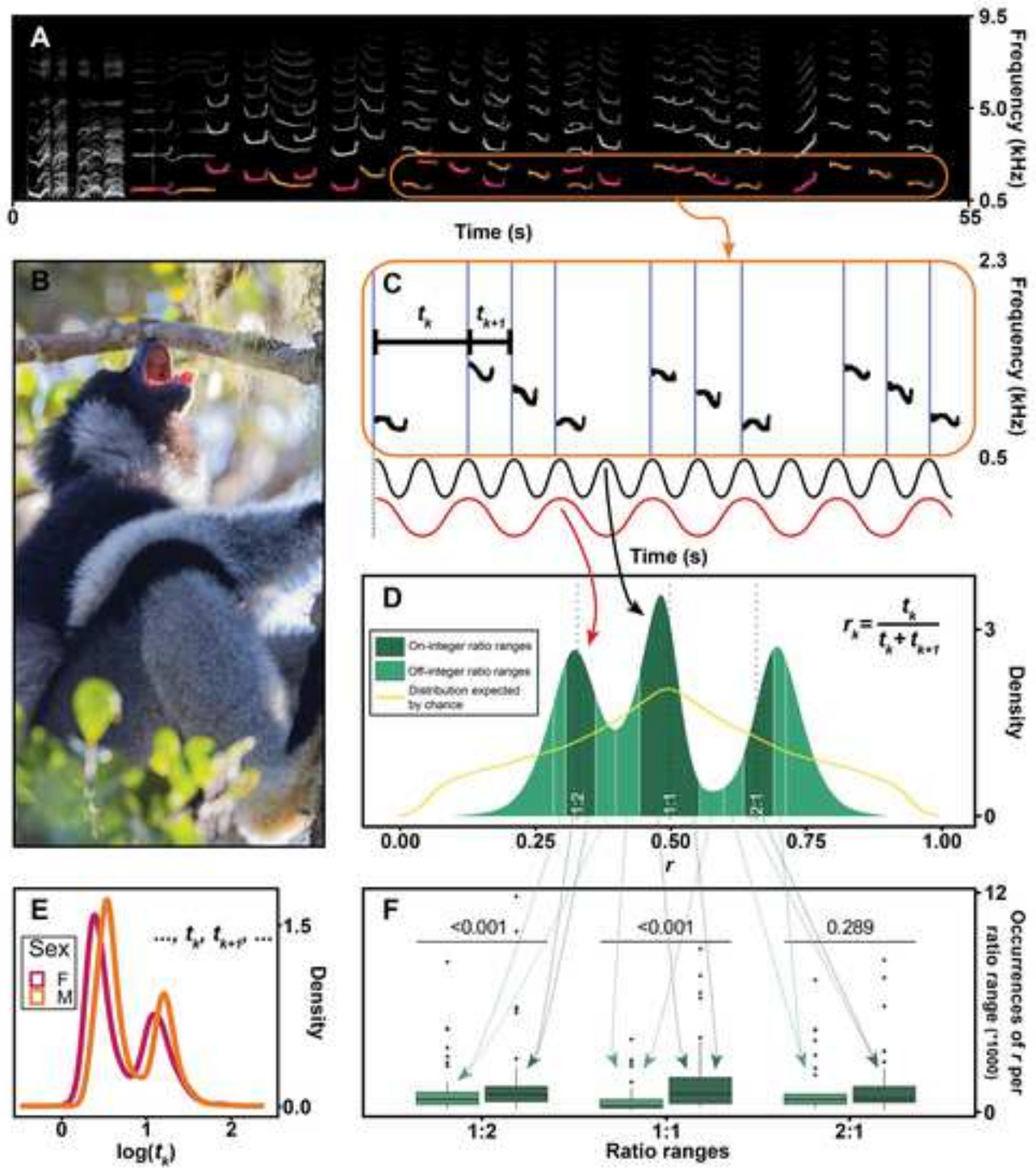
Supplement - Categorical rhythms in a singing primate

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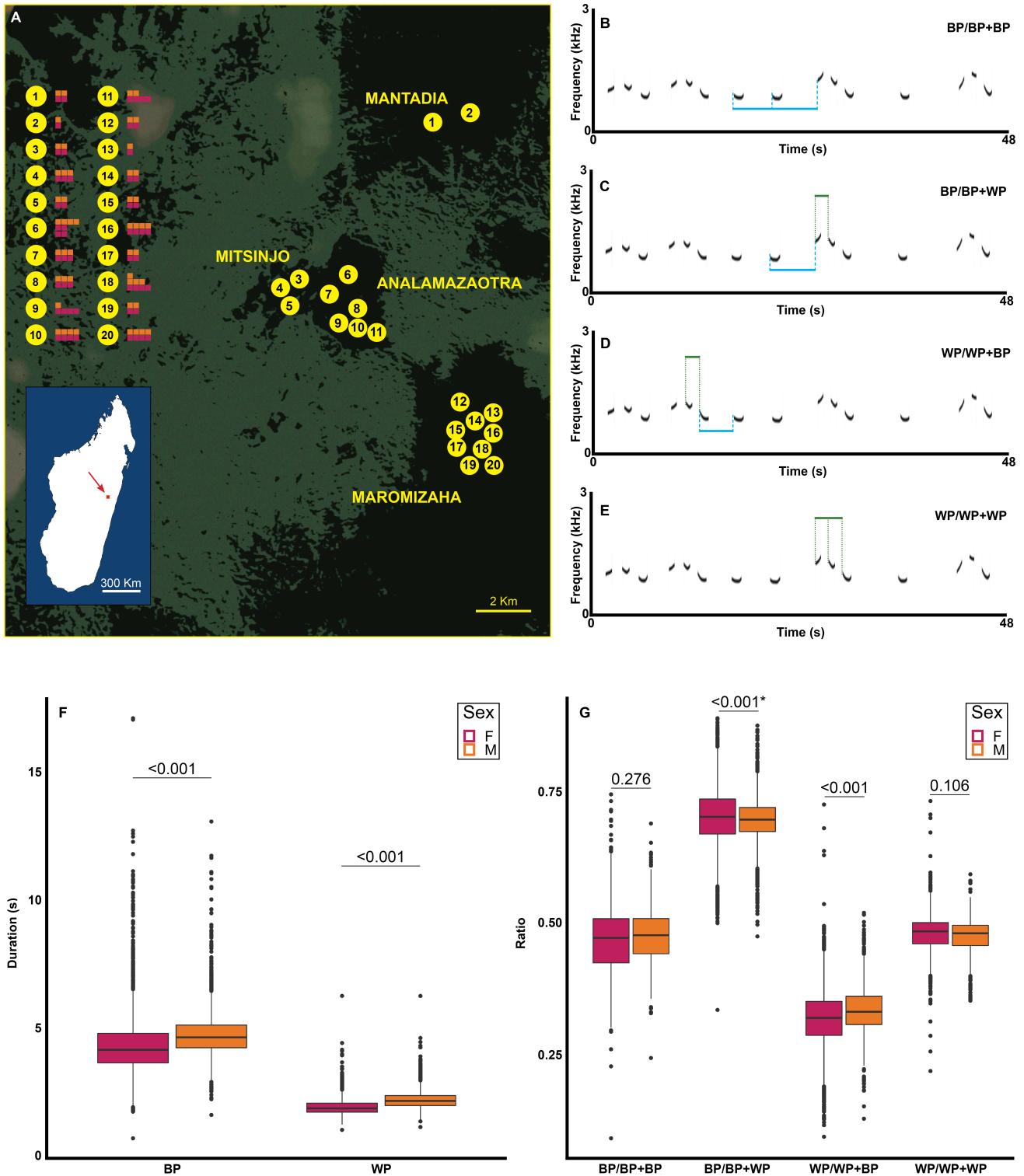
Methods

1. Observations and recordings

Indris (*Indri indri*) are lemurs whose ancestor diverged from ours approximately 77.5 MYA[S1]. 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 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. 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, while isolated units are single notes between two phrases.

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 line 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.

2. Acoustic analyses

We recorded 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 if they occurred between two notes of the *same phrase* ("intra"), or, conversely, if they occurred between two *different phrases* or two different *isolated notes* ("inter"). For each of the above units and intervals, we extracted the timing of the starting point and duration using Praat and saved them to a Microsoft© Excel spreadsheet[S11]. We imported them in R (R Core Team 2017; version 3.4.3) and calculated the inter-onset intervals (t_k, Figure 1C) to evaluate the rhythmic structure of contributions[S12]. Notice that a sequence of n notes will produce n-1 inter-onset intervals, i.e. $t_1,...,t_{n-1}$. Based on previous work[S3,S7], 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, that is, all and only the intervals between notes *within* a phrase) and the between-phrase t_k (BP: Between-Phrase inter-onset intervals, that is, all and only the intervals *between* two different phrases or between two isolated notes).

We then calculated rhythmic ratios r_k following Ref[S14], 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. 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 in Figure 1F. When 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 sexual 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.

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[S15]). 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[S16] to perform all the pairwise comparisons for all the interaction levels between sex and t_k type (multiple contrast package *multcomp* in R).

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[S17]) fitting a beta distribution, continuous between 0 and 1. Beta was chosen via the package *fitdistrplus*[S18] as 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[S16].

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[S19]). To test for significance of our full models[S20] we compared them against null models containing only the random factors, with a likelihood ratio test (Anova with argument test "Chisq"[S21]). 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 Ref[S14], 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, off-integer ratio ranges were centered around 0.285, 0.400, 0.600, and 0.710; the boundaries of all on- and off integer ratio ranges were 0.307, 0.363, 0.444, 0.555, 0.637, and 0.693. All these ratios were calculated according to Ref[S14]. 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[S14]. 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 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[S13], we simulated what would happen if no rhythmic categories existed by sampling inter-onset intervals from uniform distributions and calculating each ratio as in the formula in Figure 1D. In other words, this sampling simulated the distribution of the ratio between one random variable and its sum with another random variable, both random variables being uniform.

Results

1. t_k durations

The average duration of t_k was 2.114 ± 0.298 for WP and 4.651 ± 1.008 for BP. This difference emerged also in Figure 1E, where the probability density function clearly indicated the presence of two clusters in the t_k

duration. Males showed longer t_k than females (Figure S1F, Table S1A), both overall (M = 3.429 ± 1.372, F = 2.919 ± 1.403; p < 0.001) and by t_k type (WP: M = 2.339 ± 0.340, F = 1.899 ± 0.258; p < 0.001; BP: M = 5.002 ± 0.928, F = 4.318 ± 1.083; p <0.001; Table S1D; Figure S1F). WPs had a shorter duration than BPs (p < 0.001; Table S1A). For the comparison between 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.

2. t_k ratios (r_k)

The average of ratios 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 the value of WP/WP+BP between males and females. Notice that this value is always greater than 0.5 because BP>WP. WP/WP+BP corresponds to the third peak in Figure 1D and the third pair of boxplots in Figure 1F, also corresponding to the one non-significant peak out of three. No significant peak in Figure 1D shows sexual dimorphism. In brief, there is little sexual dimorphism in ratios and categories and no dimorphism at all for significant rhythmic categories, speaking *against* sexual selection hypotheses for rhythm.

Summary and details of both models and Tukey tests can be found in table S1.

3. Rhythmic categories: Ratios distribution and their peaks

The evaluation of the occurrence of different r_k types indicated the presence of three clusters (green density function in Figure 1D). The comparison of this density function to the distribution expected by chance (yellow line in Figure 1D) suggested the presence of different rhythmic categories. 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. 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 ratios rather than equally-sized off-integer neighborhoods.

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: $\chi 2 = 24468.48$, df = 3, p < 0.001. (**B**) Influence of the fixed factors on r_k *type*. Full model vs. Null model: $\chi 2 = 30155$, 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.

Acknowledgements

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

An example video is available as supplementary information. Data, code, and custom-written scripts are available from the corresponding author upon request.

Declaration of Interests

The authors declare no competing interests.

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