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The origins of musicality in the motion of primates

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Abstract

Animals communicate acoustically to report location, identity, and emotive state to conspecifics. Acoustic signals can also function as displays to potential mates and as territorial advertisement. Music and song are terms often reserved only for humans and birds, but elements of both forms of acoustic display are also found in non-human primates. While culture, bonding, and side-effects all factor into the emergence of musicality, biophysical insights into what might be signaled by specific acoustic features are less well understood.

Objectives: Here we probe the origins of musicality by evaluating the links between musical features (structural complexity, rhythm, interval, and tone) and a variety of potential ecological drivers of its evolution across primate species. Alongside other hypothesized causes (e.g. territoriality, sexual selection), we evaluated the hypothesis that perilous arboreal locomotion might favor musical calling in primates as a signal of capacities underlying spatio-temporal precision in motor tasks.

Materials and Methods: We used musical features found in spectrographs of vocalizations of 58 primate species and corresponding measures of locomotion, diet, ranging, and mating. Leveraging phylogenetic information helped us impute missing data and control for relatedness of species while selecting among candidate multivariate regression models.

Results: Results indicated that rapid inter-substrate arboreal locomotion is highly correlated with several metrics of music-like signaling. Diet, alongside mate-choice and range size, emerged as factors that also correlated with complex calling patterns.

Discussion: These results support the hypothesis that musical calling may function as a signal, to neighbors or potential mates, of accuracy in landing on relatively narrow targets.

KEYWORDS
adaptation, brachiation, evolution, jumping, pair-bonding, singing

1 | INTRODUCTION

The origin of human music is an enduring mystery that remains elusive partly because current explanations are often confounded by a seemingly unavoidable circularity in definitions and a lack of consensus on evolutionary causality (Schruth et al., 2021). Our species has an unusual ability to adapt in diverse ways—that is, via cultural as well as genetic, cognitive, and ecological means (Smith, 2011). Many correspondingly diverse mechanisms for music's origins have been proposed including sexual selection (Darwin, 1871; Miller, 2000), coalitional or intergroup competition (Hagen & Bryant, 2003), cultural evolution (Fitch, 2017; Savage, 2019), as well as gene-culture co-evolution (Cross, 2003) or dual inheritance (Henrich & McElreath 2012). Similar diversity also adheres to definitions of the musical units of investigation: these include "song" as relatively complex calls used in conspecific interactions (Beecher & Brenowitz, 2005), "complex acoustic display" (Templeton et al., 2011), or "learned complex calls" (Fitch, 2015); music as "information rich holistic patterns" (Roederer, 1984), or "creative orderly, organized, structured sequences with repeatable distinctive patterns" (Marler, 2000); and musicality as a neurobiologically constrained and spontaneous capacity to receive and produce such stimuli (Honing et al., 2015; Morley, 2002, 2012). A lack of clarity concerning the whats (outcomes and inputs) and hows (level, unit, tempo, and mode) of the evolution of musicality, however, has thus far hindered rigorous testing of theories on its origins (Schruth et al., 2021).

Musical behavior, in humans, is as motivated by acquired culture as inherited biology (Cross & Morley, 2010). Ideas on biologically adaptive function typically include social bonding, (sexual or group) signaling, or by-product accounts (Dissanayake, 2009; Hagen & Bryant, 2003; Mithen, 2006; Pinker, 1997). Social bonding theories run the full gamut of possible social coteries—ranging from the mother-infant pair (Dissanayake, 2000; Trehub & Trainor, 1998) to large groups (Brown, 2000; Cross & Morley, 2009). Signaling theories have existed since Darwin suggested that musical notes and rhythm functioned as signals to mates during courtship (Darwin, 1871), a theory others have endorsed (Dunbar, 2012; Miller, 2000). The role of bird song in advertising territorial claims has also long been recognized (Catchpole & Slater 2008). Recent efforts have proposed that coordinated musical displays by larger human groups could signal cohesion and commitment by competing coalitions (Hagen & Bryant, 2003). By-product theories constitute a third category of ideas exploring musical evolution as a side-effect of other traits. This has been most famously monikered as the auditory cheesecake hypothesis (Pinker, 1997), whereby music evolved as an exploitative side-effect of listeners' sensitivities and curiosity for singular "attention worthy" sound patterns (Pinker, 1997). Preferences for such complex "psuedo-musical" sounds could have piggybacked on naturally selected faculties for language in hominins or auditory scene analysis in primates, in sensing contours of purposeful speech or randomly produced environmental sounds.

Obstruction of line-of-sight by vegetation is thought to selectively act on vocal communication in arboreal animals (Krause, 1993; Slater, 2000). That is, animals living in densely vegetated habitats should evolve to produce highly intervalic, low frequency tones in their calls in order to circumvent acoustic impediments inherent to living in the forest (Ey & Fischer, 2009; Hansen, 1979; Morton, 1975). Some species have developed even more complex calls into elaborate vocal displays which advertise territorial defensibility (Goustard, 1984; Kroodsma & Byers, 1991; Marshall & Marshall, 1976; Nice, 1941; Pollock, 1986). Often, however, song-like calls simply act to advertise presence and communicate identity or location to conspecifics, especially in noisy or foliage distorted habitats (Rogers & Kaplan, 2002). Yet human musicality presents a puzzle as we do not typically face similar constraints, having adapted to more open habitats since the Pliocene (Grove, 2011). While humans are nearly unique in being both musical and terrestrial, other species that exhibit music-like behavior (e.g. songbirds) are overwhelmingly arboreal (Brown & Jordania, 2013). In primates, calls associated with such display contexts feature structures with a great diversity of repeated syllables (Schruth et al., 2021), perhaps suggestive of a function that is driven by signaling of abstract contour perception during interaction with habitat (e.g. visual branch resolution) as we further explain and develop here.

We suggest that an investigation into the adaptive causes of hominin musicality could benefit from ecological insights on primate behavior and the perspective of signaling theory. We also advocate for an understanding of such contexts and roles as separate from "the acoustic features themselves" (Merriam & Merriam, 1964). Settings ranging from more subdued communication during familial foraging to more exuberant calls for mating or intergroup spacing, for example, may have driven uniqueness in call structure (Schruth et al., 2021). Here we examine vocalizations of extant primates in relation to forms of locomotion through arboreal substrate. The primacy of vocalization in arboreal environments could derive from several factors, including visual occlusion, olfactory diminution, and predation reduction (Schruth & Jordania, 2020). In past work we revisited the controversial idea that tree climbing spawned the modern primate form (Jones, 1916; Smith, 1924), and the related hypothesis that a more active form of capering between branches selected for cranial traits adaptive for arboreal (Clark, 1959) or otherwise gravitationally challenging settings (Schruth, 2021b). Here we build on these arguments by extrapolating to signaling, by suggesting that such rapid movement through these arboreal habitats favored the development of acoustic signals to conspecifics—both to potential mates and resource competitors—that serve as *indicators* of underlying cognitive abilities to successfully engage in such locomotion.

Employing a behavioral ecology framework (Fox & Westneat, 2010), we model the fit of musical behavior to both physical and social context. We know that certain social relationships have strong associations with musical behavior (Haimoff, 1986). For example, pair bonding and mother infant attachment are thought to benefit from music-like interaction (Dissanayake, 2008; Savage et al., 2020; Trehub & Trainor, 1998). We considered the full spectrum of mate choice behaviors—including courtship, transfer, pairing, copulation, fertilization, and parenting (Brooks et al., 2010; Dissanayake, 2008; Savage, 2019)—to better accommodate these influences on musicality. Accordingly, we considered assessments of mating system, group size, and social permeability as essential factors that mediate between signals of individual senders and any number of signal receivers. Primarily, however, we investigated possible selection for habitat-interactive *survival* traits (e.g., locomotor agility) signaled by these senders of musical displays, complementing more typical attention to social and reproductive traits (e.g. mating).

Musicality and motion (e.g. dance) have a deeply entangled history (Camurri et al., 2004; Clayton et al., 2020; Dunbar, 2012; Hagen & Bryant, 2003). We focus here on ideas involving motor control (Calvin, 1982; Pinker, 1997; Roederer, 1982) utilized for more refined musical dexterity (Nettl, 1983; Sacks, 2007) as well as pattern matching (Roederer, 1984) and auditory grouping (Bregman, 1990; ten Cate & Spierings, 2019) used in musical motif appreciation. Specifically, we propose that musical displays could signal maturation of generalized cognition for contour comparison used in fine motor control as well as rapid, recurrent, and especially binocular visual focus. In primates, such coordination enables inter-branch leaping and arm-swinging for acrobatic arboreal locomotion. In humans, this spatial-dimensional cognition also overlaps with many auditory-musical behaviors, such as auditory interval assessment (Bonetti & Costa, 2019; Melara & O'Brien, 1987; Rusconi et al., 2006), but we are most interested in correlates of more melodic aspects of musical processing. Brain imaging studies typically locate music and melody perception in higher-cortical areas such as the insula (Blood & Zatorre, 2001) and temporal lobe (Morley, 2002, 2012) but more ancient areas have also been implicated (Harvey, 2017). These (para-) limbic areas, including the hippocampus (Levitin, 2006) and schizocortex (Schruth, 2022a), facilitate spatial and navigational processing (Save & Poucet, 2000). Similar connections between song and equivalent brain structures in birds have also recently been observed (Nicholson et al., 2018; Pidoux et al., 2018). Thus there appears to be two, perhaps interdependent, neural mechanisms relevant to musical signaling: one processing abstract auditory input for orientation in space and the other modulating fine motor control of eyes to resolve binocular input and coordinate limb placement. Each may undergird our hypothesized connection between call musicality and the precision of motive landing in space and time (Schruth, 2021c). This notion is supported by additional evidence of visual and motor control areas correlating with musical calling (Schruth, 2022c).

Primates capable of rapid gap-spanning movement between arboreal structures use fine ocular-motor control for visually resolving and efficiently landing on intended targets, and such abilities plausibly correspond to auditory grouping and laryngeal-motor control for learning and producing elaborate acoustical displays. We hypothesized that these proto-musical displays were evolutionary elaborated to serve as honest signals to conspecific receivers. Thus, aptitudes for difficult aerial sensory-motor tasks, such as landing with velocity in complex branching substrate or on mobile prey, could be efficiently and remotely signaled to others. Senders and receivers could mutually benefit from such honest signals (Enquist et al., 2010) in a number of ways involving resource spacing, conflict avoidance, or adaptive mating arrangements (Mitani, 1985). Neighbors endowed with capabilities for efficient matching of arbitrary conformations of substrate during aerial locomotion could recognize high-quality calls by others, and ascertain that encroaching on their territories could be costly. Alternatively, elaborate calls could signal desirable mates with high genotypic or phenotypic quality. In summary, we hypothesize that arboreal primates frequently became at least moderately acrobatic in order to rapidly and efficiently traverse gaps in substrate, which selected for the motor control and spatial cognition discussed above. Here we further propose that the selection for honest signals to advertise abilities to engage in such high-speed aerial locomotion also favored the evolutionary elaboration of complex vocal displays—that is, proto-musicality.

The evidence for musical behavior in the archeological record is slim (Zhang et al., 1999) and virtually non-existent in the paleontological record, making the testing of evolutionary hypotheses difficult. Alternatively, researchers might utilize modern day analogs to either reconstruct or statistically infer what ancestral calls may have been like (Wich & Nunn, 2002). Unfortunately, few primate genera are considered to have musical song-like qualities (Geissmann, 2000); thus binary categorizations make ancestral reconstruction problematic and obscure the potential gradual evolution of musicality. Accordingly, instead of traditional binary classifications, we used four related versions of a continuous measure of musicality, the acoustic reappearance diversity index (ARDI). ARDI is a simple, and therefore more universally applicable, measure that estimates of the number of syllables that typically reappear within a call. ARDI was derived from analysis of ethnomusicologically prevalent acoustic features observed in primate calls (Schruth et al., 2021). It thus constitutes a measure of vocal complexity approximating protomusical behavior. We investigate the territorial, mating, and locomotion based hypotheses outlined above by analyzing ARDI variants and individual feature scores alongside control data using plots, cross-tabulations, and phylogenetic regression modeling—comparing results with insights from other musical species.

2 | MATERIALS AND METHODS

We collected spectrographic vocal repertoires from the literature by searching Web of Science Citation Index (Garfield, 1970) using the partial search terms “spectro* AND primate* AND <genus>” with asterisks indicating wild cards. Subsequent searches via Google Scholar (Acharya & Verstak, 2004) helped to fill in gaps by finding studies on species from genera with sparse representation in the larger dataset. In total 832 vocalizations from 60 species were collected corresponding to 39 genera and all but one primate family. Spectrograms were cropped out of their axes, renamed, and anonymized before scoring—using a globally identifiable numbering scheme.

Scoring took place over the course of two days using bird call examples as training materials. Each of the five scorers had a different ordered spreadsheet of calls and scored, on a 1–10 scale, six different acoustic features: tone, (within-unit) interval, (monotonic) rhythm, repetition, transposition (both between units), and syllable count (Schruth, 2020b). Scores were consistent across scorers, with reliabilities ranging from 0.7 to 0.9, using Cronbach's alpha measure (Cronbach, 1970). These scores were then converted to a single number per vocalization by averaging between the scorers resulting in a total of 832 scores for six different features. This matrix was then input into PCA software (R Core Team, 2018) to help reduce the six variables into a more manageable number of variables for further analysis. PCA results suggested retaining four eigenvectors ($\lambda > 0.7$) (Jolliffe, 1972) most strongly associated with repetition, transposition, and syllable count—the last of which is a commonly measured feature of avian songs (Botero et al., 2008; Wildenthal, 1965). We reasoned that repetition and transposition are mutually exclusive and could be combined into a single measure of *redundancy*. Reappearance, in turn, was then multiplied by the unique syllable count to create a reappearance weighted measure of spectral shape diversity. This simple formula (as ARDI)—composed of the per vocalization averages for each of these three feature scores—corresponded well to vocalizations designated by primary researchers as "song" or "musical" (Schruth et al., 2021). Since rhythm was not retained by our PCA reduction procedure, however, the resulting index is admittedly more focused on transpositionally melodic [than more rhythmically complex or even song-like] calls (Schruth et al., 2021). Details of the PCA variable reduction, along with data and code (https://osf.io/hszaq/), are available online (Schruth, 2019b).

As the current project is more geared towards applicability of primate evolution towards more human like music, however, we have also derived three ARDI variants that individually incorporate the previously unincorporated features of rhythm (ArRDI), interval (ARDiI) and tone (ARDtI). These variants were calculated by rescaling ARDI by each feature using

$$\mathrm{ARDI}_f = \mathrm{ARDI} \times (a + (f - q_2(f)) \times (\mathrm{b} - a)/(\max(f) - \min(f))), \qquad (1)$$

where q_2 is the second quintile of f, and where f is one of the three non-ARDI musical features of rhythm, tone, or interval. Constants were set as $a = 0.1$ and $b = 1$ with an additional correction factor of 0.2 lastly added to all variants to render them non-negative. This rescaling, resulting in a mean closer to one and a more Gaussian distribution, was then multiplied by the original ARDI measure (Equation 1). These three variants, like ARDI, have convenient properties of being continuous and quantitative. These simple extensions have the additional advantage of potentially providing insight into influences of other features of human music not yet formally incorporated into ARDI. As an additional check beyond these ARDI variant formulations, we also performed simple correlation analysis of individual feature scores on possible associations with predictor variables.

Locomotion data was collated from the primate literature in a search procedure analogous to that employed for the spectrographic data—using "locomot* primate* <genus>" search terms—as detailed above. In total the locomotion data set contained 54 different genera and 112 species. Studies were required at a minimum to have a quantitative estimate for leaping. However, all other modes of locomotion were tabulated as well. Leaping and swinging percentages were cross-checked and verified against secondary compilations of locomotion (Rowe & Meyers, 2017). Leaping was coded as a composite variable combined with jump, air, and drop modes. Swinging was also composite with armswing and other suspensory modes. Full details of the data collection procedure are available elsewhere (Schruth, 2021b) and the full data-set can also be found online (Schruth, 2019a).

Control variables were coded as follows: *wooded* included all but geladas, baboons, and vervets, *monogamy* included both "strict" and "socially" forms (Fuentes, 1998), and *group size* estimates came mostly from a single source (Lehmann et al., 2007). *Arboreal* was taken as a binary measure indicating a habit of predominantly living in trees. *Carry* was formulated in order to assess the degree of mislanding-risk corresponding to various stages of ventral *infant* fur-cling carrying. It is an ordinal measure derived by the addition of two independent datasets on primate *infant* carrying (Nakamichi & Yamada, 2009; Ross, 2001) via an algorithm (Schruth, 2023):

$$\text{carry} = \text{park}\,[0],\ \text{ride}\,[2],\ \text{or mix}\,[1] + \text{dorsal}\,[1],\ \text{ventral}\,[3],\ \text{or mix}\,[2] \qquad (2)$$

Since dorsal versus ventral riding information was not available for non-anthropoids in the latter study, those that were known to carry, Indri [+3] and lorises [+1 or +2], were individually appraised for such information using additional sources (Ehrlich & Macbride, 1989; Quinn & Wilson, 2002; Radhakrishna & Singh, 2004). Other assessments were coded in post-hoc using more recent observations on *infant* carrying in strepsirrhines (Peckre et al., 2016).

We coded binary measures of feeding, including *fruit*, *mammals*, and *insects*, as presence or absence of a substantial amount of such food items in the diet of each primate. Full details on collection of these control data are available elsewhere (Schruth et al., 2021). Additional variables—including *home range* (measured in hectares), *sex ratio*, *canine dimorphism*, and *female transfer* (aka *dispersal*)—were merged in from a single study (Wich and Nunn, 2002). The average of female and male mass was used as a single value of *mass* for each species. Home range, like mass, was log transformed to normalize the distribution. *Daily path length [DPL]* (measured in kilometers traveled) was taken from a single source (Wheeler et al., 2011). The merging of these numerous datasets, each arranged according to unique dimensions, inevitably resulted in missing data-value issues, leading to the development of new tools (Schruth, 2022b) to merge, update, check, accommodate, and partially control for such imperfect input to our regression models. Some of these variables with higher levels of missing data (e.g. *group size*, *home range*, *and female dispersal*) were augmented using entries (e.g., "emigration" for the latter of these) in a single secondary source (Rowe & Meyers, 2017).

We used multivariate least-squares regression (R Core Team, 2018) to compare our ARDI proto-musicality variable with numerous candidate ecological variables ($n = 58$ species). We controlled for non-independence of data collected at terminal nodes of the evolutionary tree, as closely related species should not be considered independent points (Felsenstein, 1985). We used the *phytools* R-package (Revell, 2012) to assess the phylogenetic signal [*lambda*] of ARDI in the primate tree across all of the ARDI outcome variants (Table S1). These estimates (mean *lambda* $= 0.83$, $n = 58$) were used in the subsequent regression analyses. Such regressions were facilitated by phylogenetic generalized least-squares modeling (PGLS) (*caper* v. 0.5.2) whereby non-independence of terminal nodes were controlled for via appropriate tree transformations (Orme et al., 2013).

We used an information theoretic approach for selecting models (Garamszegi, 2011; Symonds & Moussalli, 2011), by permuting over all possible variable combinations for all model lengths. The pool of ($q = 20$) possible predictor variables considered included: *arboreal*, *wooded*, *daily path length* [DPL], *home range*, *territorial*, *nocturnal*, *group size*, *canine dimorphism*, *sex ratio*, *female dispersal*, *monogamy*, *infant*

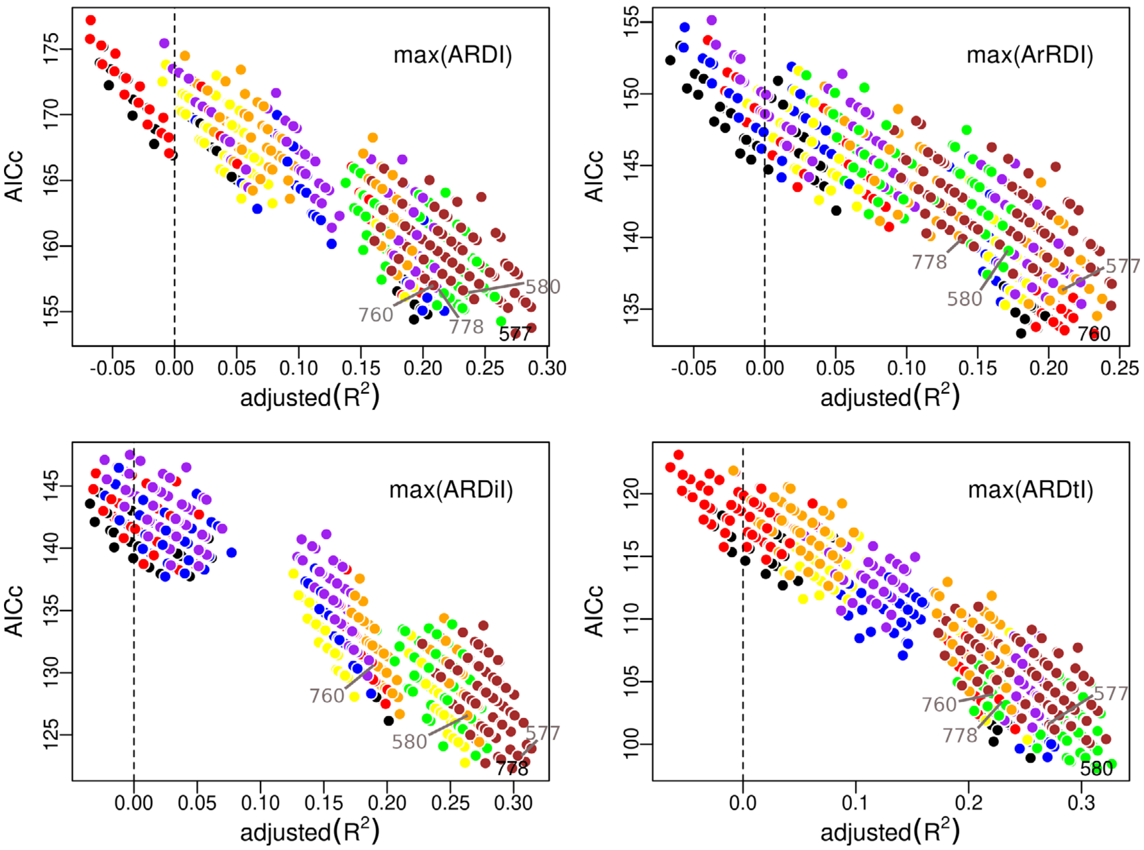


FIGURE 1 Coefficient of determination vs information criterion for all model compositions. Phylogenetically controlled multivariate regression models (circles) are plotted by performance according to information theory (AICc) and the coefficient of determination (adjusted R^2). All four analysis runs appear as diagonal clusters of colored circles in four seperate panels. The "best" models (black numbers) for each run was selected using the lowest AICc and appear in the lower right of these point clouds—each corresponding to a different variant of the Acoustic Reappearance Diversity Index (ARDI). Models that were selected via AIC across the other three ARDI runs are approximately demarcated via lighter lines and numbers (both gray). The *leap* and *swing* including models are colored blue and yellow, or green for both (#580). Insectivory containing models were colored red (#760). Insectivory and swinging models were colored orange. Models containing all three (#577 and #778) were colored brown. We note that in the far right disaccordant selection (green #580 & red #760) panels, many of the most motion relevant models (brown points) are also nearby, with comparably low AIC and slightly higher R^2.

carrying, *mass*, *claws*, *prehensile*, *insect*ivory, *carnivory*, *fug*ivory, as well as *leaping* and *swinging*. In order to circumvent convergence errors, the initial tree transformation parameters considered were constrained between 0.4 and 2.8 for both *kappa* and *delta*. After iterating through initial PGLS runs using a subset of these variables, we averaged the maximum likelihood estimates of all possible tree transformation parameter estimates in order to obtain a static set for each ARDI variant with means of *kappa* $= 1.8$ and *delta* $= 1.3$, for the final PGLS analyses (Schruth, 2021a). This fixed four-fold matrix of these three PGLS parameters (Table S1) was used to transform our phylogenetic tree into four static versions (Figure S1) for the final estimation run over all 1023 possible models on a select subset of covariates.

During this initial model building process, some binary variables (e.g. *nocturnal and wooded*) were excluded to facilitate model inclusion. Further computational constraints inherent to regressing such a large combination of model covariates during these tree parameter estimation runs required culling the original 20 candidate variables—using inspections of covariate estimation and their variances from ANOVA. The resulting reduced set ($q = 10$) of predictor variables additionally excluded *territorial*, *sex ratio*, *canine dimorphism*, *claws*, *prehensile*, *frugivory*, and *carnivory*. *DPL* was subsequently removed because it was found to have unacceptably high levels of missingness (>30%). For those remaining covariates with acceptable levels of missing data, we performed phylogenetic imputation using the '*phylopars*' function of the *Rphylopars* package (Goolsby et al., 2017).

The compositions of remaining variables were determined using a model selection procedure (Figure 1) that minimized sample-size corrected Akaike's information criterion (AICc) for regressions on each ARDI variant. The *t*-values are plotted in addition to AICc and R^2 information (Figures 1, 2). To further qualify this selection procedure, we assessed the uncertainty of estimated parameters. The estimates of uncertainty of estimated parameters were assessed using AICc-weighted sampling variance calculations (Burnham & Anderson, 2000). We also tabulated the presence and absence percentages for each covariate in the selected

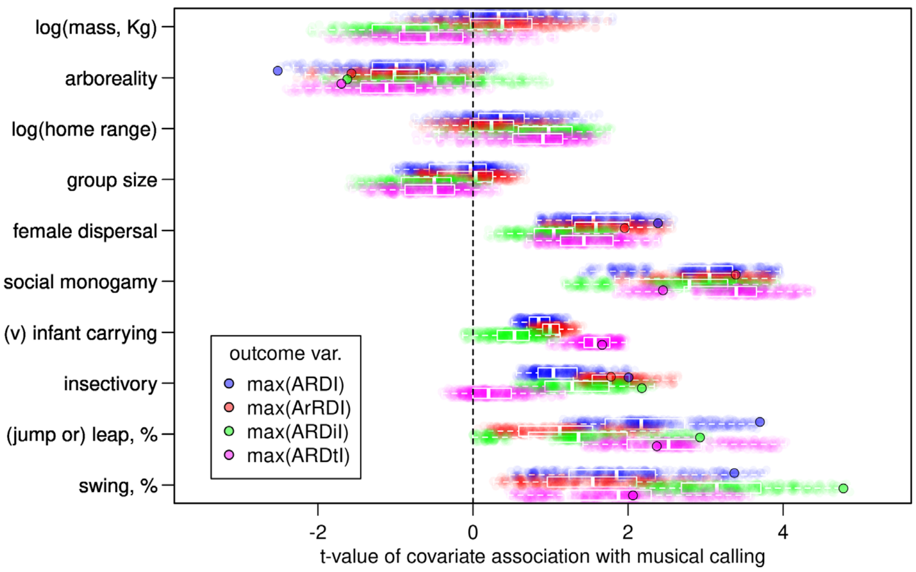


FIGURE 2 Distribution of *t*-values of covariates of AIC-selected models across all multivariate phylogenetic generalized least-squares (PGLS) regressions. Predictor covariates were compared to four musicality metrics using PGLS multivariate regression modeling. Distributions of individual *t*-values of covariate parameter estimates (circles) highlight 18 select estimates (black borders) belonging to the (four) lowest AICc models selected from all 1023 possible models (horizontal streaks) for each of the four Acoustic Reappearance Diversity Index (ARDI) variant outcome variables. Coefficients are plotted as *t*-values across the x-axis while covariate names appear as categories across the *y*-axis. The *y*-positions of these coefficients were randomly jittered and dodged away from each other (within and between runs respectively) and color-coded to indicate the outcome variable. Box plot outlines (in white) of interquartile range for each distribution appear over the top of each respective point cloud. Variables corresponding to morphology and habitat are at the top, social factors are in the middle, and motion-related variables appear at the bottom. These four outcome variables correspond to four different variants of ARDI—where rhythm (*r*), interval (*i*), and tone (*t*) were each normalized and multiplied against ARDI.

TABLE 1 Presence, importance, and error of covariates included in lowest AIC selected models from each ARDI variant analysis runs.

	Presence	Importance	Error
Arboreality	100%	0.00	0.091
Log (mass, Kg)	0%	0.67	0.034
Group size	0%	0.54	0.001
Log (home range, ha)	0%	0.98	0.012
Female dispersal	50%	1.00	0.063
Social monogamy	50%	1.00	0.155
(*v*) Infant carrying	25%	0.99	0.007
Insectivory	75%	0.92	0.073
Swing, %	75%	1.00	0.402
(Jump or) Leap, %	75%	1.00	0.370

models (Table 1) and analyzed the relative 'importance' of parameters (Burnham & Anderson, 2000).

3 | RESULTS

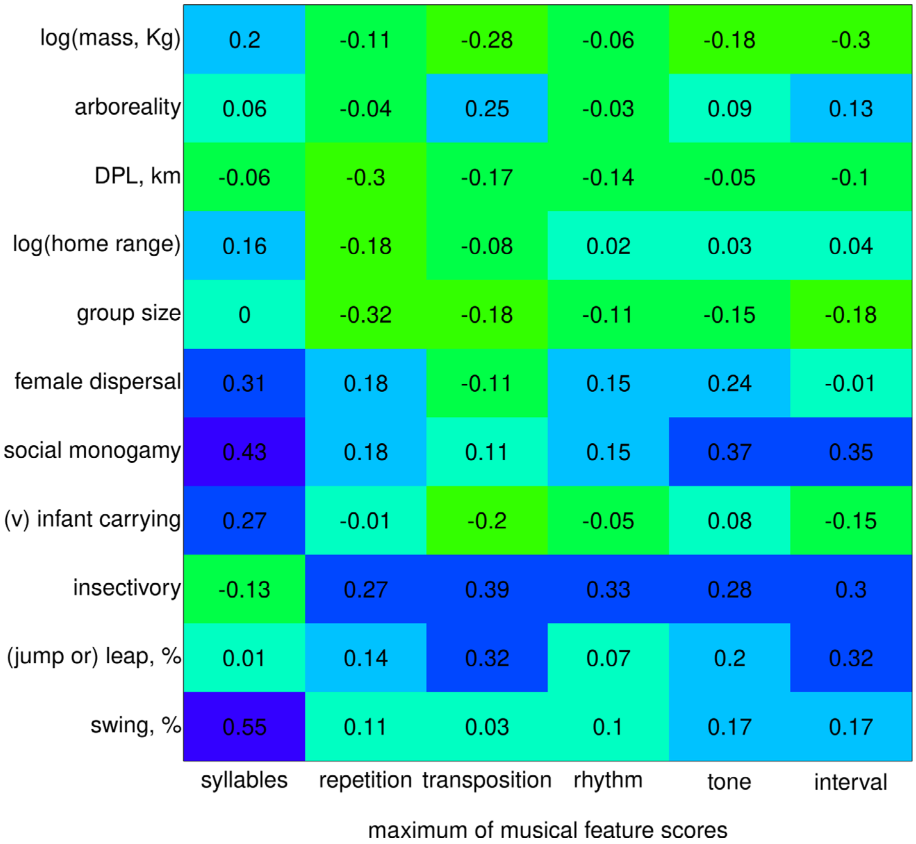
Our results suggest that manifestations of discontiguous motion and socio-positional coordination, including challenging locomotive and dietary targeting and egalitarian mate choice factors, are credibly associated with musical calling. Locomotion, *female dispersal*, and *monogamy* exhibited the most dramatic positive associations with protomusical calling as assessed by all four ARDI variants (Table 2, Figure 2). Compared to non-, monogamous species had vocal displays with an additional reappearing syllable ($\beta \sim 0.7 \pm 0.2$; $p \sim 0.01$). *Leap*ing and *swing*ing had an approximately two-fold greater effect than *monogamy*—with additional reappearing syllables in the most music-like call as a function of both leaping bouts ($\beta \sim 2 \pm 0.8$; $p \sim 0.01$) and swinging bouts ($\beta \sim 2.2 \pm 0.4$; $p \sim 0.02$). The importance of the *monogamy* (Figures 3, S3) and locomotion variables is evidenced by their significant deviations from zero under most models including the model with the highest R^2 and lowest AIC (Table 1). Habitat defense variables such as *home range* had largely positive associations with musical calling, but did not appear in any of the four selected models. *Arboreality* ($\beta \sim -0.5 \pm 0.3$; $p \sim 0.09$) was negatively associated—likely because of masking by our two continuous locomotion variables (Figure S3). *Female dispersal* was consistently positively associated ($\beta \sim 0.6 \pm 0.1$; $p \sim 0.04$) with musical calling. Variables less directly associated with motive landing, such as *infant carrying* ($\beta \sim 0.08 \pm 0.01$; $p \sim 0.1$) and *insectivory* ($\beta \sim 0.6 \pm 0.07$, $p \sim 0.05$), were also associated with musical calling. The only covariates with unresolved directionality were *group size* and *body mass*.

Home range and *infant carrying* had mid-range *t*-values that showed signs of approaching significance. Model selection (Table 2) also highlighted locomotion variables and insectivory, with the

TABLE 2 Regression results for AIC-selected models across all four musicality variants. For each ARDI variant (columns), parameter estimates (and their *p*-values) are reported for the lowest (corrected) AICs of all possible phylogenetic least squares regression models derived from the ten covariates listed here (rows).

	ARDI	ArRDI	ARDiI	ARDtI
Model number	577	760	778	580
R^2 (adjusted)	0.34 (0.28)	0.29 (0.23)	0.35 (0.30)	0.37 (0.31)
AIC (AICc)	152 (153)	132 (133)	121 (122)	96 (98)
Log (mass, Kg)				
Arboreality	−0.88 (0.015)*	−0.42 (0.123)	−0.38 (0.111)	−0.33 (0.096)
Log (home range, ha)				
Group size				
Female dispersal	0.71 (0.021) *	0.50 (0.056)		
Social monogamy		0.84 (0.001)**		0.54 (0.018)*
(v) Infant carrying				0.08 (0.102)
Insectivory	0.74 (0.050)*	0.56 (0.081)	0.64 (0.034)*	
(Jump or) Leap, %	2.90 (0.001)***		1.68 (0.005)**	1.35 (0.022)*
Swing, %	2.63 (0.001)**		2.76 (0.000)***	1.16 (0.044)*

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.



	syllables	repetition	transposition	rhythm	tone	interval
log(mass, Kg)	0.2	-0.11	-0.28	-0.06	-0.18	-0.3
arboreality	0.06	-0.04	0.25	-0.03	0.09	0.13
DPL, km	-0.06	-0.3	-0.17	-0.14	-0.05	-0.1
log(home range)	0.16	-0.18	-0.08	0.02	0.03	0.04
group size	0	-0.32	-0.18	-0.11	-0.15	-0.18
female dispersal	0.31	0.18	-0.11	0.15	0.24	-0.01
social monogamy	0.43	0.18	0.11	0.15	0.37	0.35
(v) infant carrying	0.27	-0.01	-0.2	-0.05	0.08	-0.15
insectivory	-0.13	0.27	0.39	0.33	0.28	0.3
(jump or) leap, %	0.01	0.14	0.32	0.07	0.2	0.32
swing, %	0.55	0.11	0.03	0.1	0.17	0.17

FIGURE 3 Correlation of individual feature scores versus key predictor variables. In addition to using variants of the composite Acoustic Reappearance Diversity Index (ARDI) scores, the species-level maximum of individual musical feature scores were compared to our panel of key predictor variables. The above matrix illustrates strongly positive correlations (darker blues) as well as strongly negative correlations (darker greens) and all the shades in between. Locomotion and mating variables were the predictors most consistently positively associating with all six scores on structural acoustic features prevalent in human music.

combination of all three appearing in half of the four selected variant models. The highest adjusted R^2 model (and lowest overall AICc) of all modeling runs, for max(ARDtI), included *leaping*, *swinging*, *ventral infant carrying*, but not *insectivory*. The separation of modeling runs on ARDI and its scalar derived variants yielded mildly surprising results. First, we note that ARDI had a much lower phylogenetic signal (as measured by lambda of 0.73) than any of its variants (and 12% lower than the average). We were surprised then to discover how similar each variant was to the original ARDI version (Figure 2). However, we have also demonstrated there are likely differences in venturing beyond just repeated or transposed syllable counts. Rhythm, when multiplied to our base metric, as ArRDI, appears to associate more strongly with mate selection (than locomotion) effects on musical calling. Interval, when multiplied into our metric [ARDiI], reduced the association with mate selection factors and increased the association with *swinging* locomotion. Tone, when multiplied into our metric (ARDtI), yielded results suggesting more equanimity of multi-causality across our mate selection and locomotion covariates than either of the other two scalar-multiplier versions of ARDI.

Mass and *group size* did not appear in any of the selected models, both of them indecisively straddling the zero line in our *t*-value plot (Figure 2). Arboreality, on the other extreme, appeared in all four selected models, though with a decidedly negative, but likely masked, association with musical calling (see Table 1 versus Figure S3). Mate choice covariates only appeared in two of the four selected models whereas *infant carrying* only appeared in one (Table 1). Uncertainty of the selected models' parameter estimators were surprisingly low—*infant carrying*, and *group size* were the lowest while the locomotion variables were highest (Table 1). Importance of selected covariates was highest for the movement, mating, and range size variables and lowest for *arboreality* (Table 1).

Correlations of individual feature scores with predictor variables (Figure 3) revealed more nuanced associations that may have been obscured by the amalgamative ARDI scores. *Insectivory*, *leaping*, and *arboreality* had the strongest positive correlations with transposition of intervals, indicative of a motor control signaling connection with those motive landing contexts. The mate-choice variables of *female dispersal* and social *monogamy* were most strongly associated with almost all features but especially a greater number of temporally structured tonal syllables, suggesting the importance of discrete acoustic symbols replacing chemical sexual signals. The most consistently correlating variables—the two locomotion variables and *monogamy*—indicate that musicality, especially in spectral forms, may evolve as spatially efficient signals for acquiring long term mates in species who are chemically partitioned, in particular, by trees. Analogous correlation analysis between these individual acoustic feature scores, as correlated with individual locomotor modes (Figure S4) revealed confirmatory results. *Brachiation* had strong correlations with all six musical features, nearly twice as high as *arm-swinging*. *Leap* and *drop* had generally positive associations but *leap-drop* was by far the strongest and most consistent.

In all, positive *monogamy* and *female dispersal* parameters support mate selection, and *home range* supports territoriality, as the primary direct social functions for musical calling. Simultaneously, the three motion related covariates support motive limb placement as the underlying *individual*-level trait indirectly advertised via such social signals. Positive *home range* associations suggest musical calls could help maintain spacing from afar—leveraging the efficiency of vocal articulation instead of closer-range chemical scent sources. Most corroborative were the consistent selection for low-AIC models that included both *leap*, *swing*. and *insectivory* (brown points in Figure 1) and individual correlations of *leap-drop* and *brachiation* with all individual musical feature scores.

4 | DISCUSSION

In conclusion, acrobatic aerial locomotion (e.g. leaping and swinging)—heightened by the characteristically precarious habitats of arboreal primates (e.g. terminal branches)—may have favored the evolution of proto-musical displays. More general forms of rapid locomotor limb placement (e.g. repetitious insectivory), also appear to associate with precise and discrete calling patterns. We argue for the importance of such (repetitively) discontiguous locomotion in explaining the evolution of proto-musicality on several grounds. Primarily, habitual arboreal locomotion tends to impede visual and chemical communication between individuals (Schruth, 2021d)—such as mated pairs or mothers and infants (Schruth, 2022a). Crossing arboreal gaps likely further incentivized discrete, reappearing, and complex sounds—compensating for this diminution of communication via olfactory, visual, and direct contact (Schruth, 2021d), especially with weaning infants. And rather than musicality associated with dependent offspring serving as signals of continued parental attention (Mehr et al., 2021), we suggest that primates' long life-histories—with prolonged weaning, tutelage, and attachment—instead drives signaling of offspring call maturity. Once fully developed spatio-motor control and perception link locomotion and musicality, the latter could come to serve as an honest signal of the former. Signaling such skill via elaborate proto-musical calls would benefit both senders and receivers in the context of mate choice and resource competition.

Our analysis here also corroborates longer-term mate-choice factors as tying into our proposed motion-based co-evolutionary dynamic—as evinced by the positive associations with monogamy (Schruth et al., 2019) and female dispersal (Table S2, Figure S2). Positive associations of musicality with female dispersal could boster hypotheses highlighting the difficulties of mate-guarding in three-dimensional habitats (Verpooten, 2021). However, our individual feature score results single out *monogamy* as the main variable that co-varies most strikingly with all six musical feature scores (Figure 3). Therefore, our results more convincingly support mate *choice* hypotheses (Darwin, 1871; Miani, 2016; Miller, 2000; Ravignani, 2018a) than mate *guarding* hypotheses. We propose that the stakes are much higher in the acquisition of long term mates for species that have longer and slower life histories—where parity is small and infants are carried for longer periods of time before being weaned (Jones, 2011). Overall, *monogamy* was the most consistent predictor across all of our musical measures, but *home range* was also positively associated. Range spacing likely enriches reproductive engagement, enabling such low parity species to secure partnerships with protective and care-capable long-term mates (Schruth, 2022c). While *home range* and *mate choice* may seem independent, they are plausibly interconnected through density dependence factors underlying reproductive rate regulation (Roughgarden, 1971) and [anti-predation] contest assistance (van Schaik et al., 2022).

It is possible that music-like behaviors could also serve as signals of spatial ability in other taxonomic groups. For example, the avian clade, *Passeriformes*, is also known as ‘songbirds’ (Gill, 1995), because it contains thousands of species with highly-developed vocal communication systems and specialized cognition for song learning that facilitate flexibility and complexity of signals (Catchpole and Slater, 2008). Songbirds also tend to form monogamous pairs, potentially lending support to analogous observations concerning egalitarian mating systems in musical primates. These species are also referred to as 'perching birds' because they have long and flexible toes that, along with flying, enable perching on thin branches (Gill, 1995), allowing them to exploit spatially complex, three-dimensional environments. Admittedly, factors other than habitat—such as sex, and body size—also show strong effects on singing behavior (Mikula et al., 2020). However, analysis of correspondence between song to call ratio and dietary targets—that are small, such as seeds, fruit, and insects, or displaced, such as flies, foliage, and [attached] fruit—also support motion-based influences on musical calling (Schruth, 2022a). Thus, we hypothesize that musical calling could function as a signal of underlying abilities for precise coordination between vision and motion in passerines as well as primates.

In addition to branch-landing in primates and birds, these selective influences of time-sensitive motive landing could apply to many other animals locomoting along perilous trajectories. Many arthropods, bats, penguins, seals, and cetaceans could be considered to have proto-musical calls (Aubin & Jouventin, 2002; Hoeschele et al., 2015; McDermott, 2008; Ravignani, 2018b) and many of these species also possess spatially challenging locomotion, in the form of flight or swimming. For example, many arthropods and passeriforms land by grasping slender grasses or thin terminal branches. Aquatic species, like penguins, seals, or whales that must keep track of the precise location of the surface to return to breathe, could face similar spatial challenges such as tracking and honing in three dimensions. This could be particularly true for whales that feed near polar ice sheets (Schruth & Jordania, 2020) and may have frequently breathed using polynyas in such ice sheets during the more heavily glaciated Pleistocene. As with primates, signals advertising an individual's competency in transitioning throughout and between such spatially complex and narrowly delineated ecotones could have served as a primary selection pressure for the co-evolution of musical calling and locomotion.

In strictly terrestrial primates, previously evolved associations between musical calling and locomotion appear to have atrophied. This is best illustrated using the counter-example of cheek-pouch monkeys (subfamily *Cercopithecinae*) few of which are musical, leapers, or monogamous (Schruth, 2020a). A notable exception is the one "musical call" of the (terrestrial and arboreal) long-tailed macaques—who exhibit an extraordinary array of atypical behaviors such as cliff climbing, swimming, and stone-tool use (Dzulhelmi et al., 2019; Malaivijitnond et al., 2007). Among anthropoids, only the monogamous and swinging lesser apes seem to share our aptitudes for spectral musicality, we argue here as being ancestral. All three other genera of hominoid presumably lost this trait which hylobatids seemingly retained through the Miocene. The discovery of *Ardipithecus ramidus*—a putative singer (Clark & Henneberg, 2017)—illuminates the possibility that our ancestors may have been largely arboreal as recently as four million years ago (Fruth et al., 2018; Lovejoy, 2009; Lovejoy et al., 2009). However, the link between arboreal locomotion and musical calling is contradicted by our own genus, which is both more terrestrial and musical than other hominoids. Indeed, humans are outliers among mostly non-terrestrial examples of musical behavior. Human musicality could instead be related to other grounded behaviors such as larger groups (Merker, 1999; Mithen, 2006), language (Livingstone, 1973; Pinker, 1997), or dance (Hagen & Bryant, 2003). Our results highlighting both phyletic depth of this trait in primates and the acoustic redundancies inherent to musical calls (e.g. reappearance of syllables), however, make these terrestrial hypotheses less chronologically compelling.

In light of the negative correlations reported here, *arboreality* appears to be only a causally latent factor that could indirectly drive musical behavior in non-human primates via a contingent link to acrobatic locomotion. What then might account for the paradoxical *increase* in musical behavior in the resolutely terrestrial Homo? It is plausible that ballistics, in the form of accurate throwing (e.g. rocks, spears), could pose selection pressures similar to those for aerial or other rapid motive landing locomotion. Humans throw things from great distance, with high momentum, and more accurately than any other species (Bingham, 1999). More generally, tool use is also known to be a primary defining characteristic of the genus Homo. The main evidence for hammering and throwing, dating back to Middle Paleolithic, occurs in stone tool industries (Semaw et al., 1997), and spear manufacture (Thieme, 1997). These characteristically human activities could have co-opted the Miocene adaptations of suspensory arm-swinging. In addition, territorial signaling (Hagen & Bryant, 2003; Hagen & Hammerstein, 2009; Mehr et al., 2021), linked to trophic dominance by hominins over seasonal resources (e.g. game), could be derived from analogous behaviors of ancestral hominoids tens of millions of years previously. Both factors may have acted as evolutionary drivers of acoustic status displays (Mazur, 1985) targeted towards conspecific mates and neighbors. Thus, locomotion and other complex motor skills may have engendered neurological changes that overlapped with complex calling (Schruth, 2022c). Whether or not musical calling signals brachiational skill in other hominoids, we are compelled to consider that precision limb swinging—via hammering, skirmishing, throwing, or even rapid and laden bipedalism across irregular footholds—could have co-evolved with increasingly complex musical calling in hominins.

Singing entails micro-athletic regulation of the musically facilitative muscles (Nettl, 1983; Sacks, 2007) in the vocal apparatus as well as memory to match current *auditory* inputs with previous utterances (Roederer, 1984). Possibly analogous pattern-matching also occurs between disparate *visual* inputs for modulating rectus muscle control over eye position in actuating stereoscopic vision. In primates, this could manifest as part of hand-eye coordination for grasp placement adjustments (Schruth et al., 2020), for landing clawless grasps on substrate with velocity (e.g. while completing aerial-spectrum locomotor bouts). Even further extrapolations of musical behavior as a motor control signal include that of fine finger movements, perhaps for highly repetitive extractive foraging or intricate crafting by hominins. It is also tempting to envision scenarios where performance drumming manifestations, of *rhythmic* musicality, could signal butchering capacities (Jordania, 2008) to other long-distance scavenging parties of lithically productive hominins, dispersed across semi-terrestrial savanah-woodland habitats.

In sum, we have presented evidence supporting a history of coevolution between rapid locomotor emplacement and music-like vocalizations, spanning phylogenetically disparate primate taxa from duetting insectivorous tarsiers to the canopy singing indri. The majority of such primates exhibit egalitarian mating systems and tend to occupy larger home ranges. However, evidence presented here reveals even more robust links between musicality and motion. We argue for an adaptive continuity over the entire era since primates began, featuring locomotor forms such as leaping between vertical trunks of trees, vaulting from boughs in the canopy, and rapid brachiating between branches. We also suggested a plausible transition scenario to humans: from branch landing in apes, to throwing in australopithecines, to stone hammering in *Homo*, and perhaps even to smaller-scale digital dexterity for more delicate crafting in *sapiens*. In short, the curious case of human music appears to have deep (Schruth, 2020a) and multi-causal evolutionary roots, consistent with a complex socio-positionally and visuo-spatially adaptive past.

AUTHOR CONTRIBUTIONS

David M. Schruth: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); resources (lead); software (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Christopher Templeton:** Supervision (supporting); writing – review and editing (supporting). **Darryl J. Holman:** Conceptualization (supporting); data curation (supporting); funding acquisition (supporting); resources (lead); supervision (supporting); writing – review and editing (supporting). **Eric Smith:** Supervision (supporting); writing – review and editing (supporting).

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DATA AVAILABILITY STATEMENT

We have made the vocalization, locomotion, and control data available on the OSF website primarily via the following two project pages: http://osf.io/bvsfz and http://osf.io/cd68q. Also, our new 'mmodely' package for averaging and selection of phylogenetic regression models has been uploaded to CRAN (at https://cran.r-project.org/web/packages/mmodely/index.html).

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