Ecological pressures selecting for singing behavior in primates

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Abstract

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This dissertation explores the social, behavioral, and habitat based influences on the evolution of elaborate vocalizations in primates. The goals of this project were to merge and test hypotheses derived from both the primate morphological origins literature and the musical behavior origins literature. Theoretical elements from the leaping and arboreal hypotheses from the primate origins literature were brought to bear on vocal display data from extant primates and on theories on the function of song in animals and music in humans. Specifically, I used computational statistical techniques to test the dual hypotheses that precision limb landing, as required in navigating complex arboreal topologies, could have not only shaped primate morphology, but also evolutionarily shaped their vocal signaling behaviors. I also tested other theories from the literature on both animal communication (e.g. the acoustic adaptation hypothesis) and human music (e.g. coalition signaling as well as group and pair bonding). I collected behavioral data, for as many species (*n*) as possible, from the primary primate behavioral literature, including vocalization (*n*=68), locomotion (*n*=99), and socio-ecological regression control variables. Data were then analyzed in three separate substantive chapters. First, in chapter 2, spectrographic vocalizations were scored manually along ethnomusicologically universal acoustic parameters and subsequently reduced into a univariate *acoustic reappearance diversity index* [ARDI], reflecting call elaborateness. Second, in chapter 3, quantitative locomotion activity data (e.g. leaping and swinging percentages) were harvested from the positional behavior primary literature in order to both estimate its ancestral influence on morphology as well as to create

better (non-binary) predictor variables for testing vocal display origin theories. Third, in chapter 4, I tested for my hypothesized co-evolutionary relationship while controlling for phylogeny. ARDI was highest in smaller, socially monogamous, and forest living groups, as well as positively associated with swinging and leaping. These results are consistent with the dual hypothesis that both elaborate vocal displays and vision changes in primates could have evolved as a result of increased demand for precision limb landing locomotion. In chapter 5, I discuss the limitations and drawbacks as well as the theoretical significance, scientific relevance, broader implications, and ideas for future research.

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Dedication

To my family, who encouraged
a harmonious balance between earnestness and peregrination
in all aspects of life.

Chapter 1 – Introduction

Problem Statement: *The puzzling ubiquity of animal song and human music*

Why do animals sing? And why is human musical behavior so mysterious? Music has historically been characterized as a uniquely human trait. It is practiced as a part of many human courtship and mating rituals such as dance and marriage. It is also frequently an integral part of military and sporting events. In western society, it is also increasingly part of most personal entertainment budgets. It drives a substantial portion of the innovation underlying the computing revolution and accompanies most of the movies, television, and internet-based video media we consume in the form of soundtracks. Yet the point of music—why it exists at all—is still poorly understood.

Music-like behavior, in the form of song, has evolved in arthropods and vertebrates such as birds, cetaceans, and many primate genera. Explanations for the underlying cause of such ubiquity range from arguments based in habitat acoustics to those based on social interactions. Some of the more pertinent social theories, to which I will later return, explore the emotional impact of regulation and infant development (Dissanayake, 2000), sexual advertisement (Miller, 2000), group selection (Brown, 2000), and coalition signaling (Hagen and Bryant, 2003). Few of these theories, however, investigate how specific features of the environment influence individual acoustic features of song.

Many primates engage in numerous forms of acoustic display behavior: they loud call, long call, chorus, duet, and sing. The proximate causes of these calls have been widely characterized previously, but their ultimate function—an understanding why specific acoustic features of display calls were ecologically selected for in the first place—has not been systematically explored. As primates became predation-avoiding arboreal specialists, they likely evolved forms of high-speed, and potentially high-impact, locomotion to adeptly maneuver their way through complex terminal-branch habitats. I proposed that this shift in locomotion not only increased demand for precision in grasp landing but was also accompanied by evolution of elaborately precise vocal displays where the latter could act as signals of the underlying cognition required for the former.

Testing this idea entailed the development and comparison of these two datasets in several inter-related steps. First I defined song by quantifying the aesthetic quality of elaborate acoustic utterances based on human universals and avian display call features. Secondly, I used a literature-based collection of locomotor data both to infer ancestral frequencies of high-risk, precision grasp landed locomotion, and, as an aside, to explore its relationship with the origins of primate visual-cranial morphology. Lastly, I tested for a co-evolutionary relationship between these two new continuous indexes of locomotor and vocal behavior while controlling for other socio-ecological factors.

Background: *Ethnomusicological universals, music origins, and acoustic adaptation*

This dissertation explored the idea that musical behavior ultimately derives from the evolutionary pressures of habitat in addition to more proximate social causes (Roederer, 1984). A first step in entertaining such a notion entailed honing in on an operational definition of “elaborate” musical behavior. Since defining this aesthetic standard potentially involved a moderate amount of subjectivity, it was important to systematically examine the aesthetic universals of our own species first. Universal acoustic features such as periodic tone of acoustic units, intervallic variation in tones within and across units, as well as higher order inter-unit patterns such as repetition, transposition, and rhythm might all be present at an utterance level (Nettl, 1983, p. 39).

The field of evolutionary musicology expands the applicability of these features broadly beyond our species: applying our own acoustic aesthetic universals to taxa as diverse as birds, cetaceans, and many primates. Broadening this definition, however, rarefies the solution from beyond our own origins to one which could also resolve origins questions in these other taxa—most of whom do not share many of the postulated co-evolutionary behaviors thought to be uniquely human (Mache, 2000). Any origins theory involving a universally selective ecology should explain not only human music but somehow also bird, cetaceans, and primate song—as universal features of human music share many features with the elaborate acoustic displays of all these taxa.

Many have theorized that sociality (e.g. sexual selection, group and pair bonding) has driven the evolution of song (Bispham, 2009; Darwin, 1871; Haimoff, 1986). Although a minimally dyadic (sender-receiver) sociality is undeniably a prerequisite for any display, it fails to explain how individual, unaccompanied elaborate solo-performances are rewarded and selected for *within* said groups. Furthermore, social-based theories usually neglect ultimate ecological considerations (e.g. arboreal risk) that can also exert selection pressures.

In birds, sound is used as a way to signal to conspecifics in ways that the other senses cannot. Sight and smell do not have the same range under wind ventilated conditions and in a disconnected canopy environment in which birds [and primates] evolved (Slater, 2000). Similar arguments could perhaps be made for cetaceans in diluted oceanic environments where chemical, olfaction based signals become diffuse and scrambled over long distances. Sound can travel fast day and night, go around obstacles, is detectable at long range, and can encode complex, changing messages making it an ideal medium for rapidly assessing a potential mate during seasonal breeding (Slater, 2000). Within this signaling medium, song birds (Passeriformes) with large and elaborate acoustic repertoires tend to be more attractive to mates. (Slater, 2000).

Although their research is further developed than primatological efforts, bird song researchers still usually focus adaptive studies on a single acoustic feature at a time. Features such as *trill rate* (Ballentine, 2004), *song bout length* (Farrell et al., 2012), *repertoire size* (Boogert et al., 2011; Hasselquist et al., 1996), *complexity* (Boogert et al., 2008; Nowicki and Searcy, 2004), and *consistency* (Brown and Handford, 2000) are typically assessed individually. Song *complexity* (measured by counting syllables or songs) and *consistency* likely satisfy an innovation versus familiarity equilibrium that is expected by receivers of these displays, but these two features have not, to my knowledge, been studied in combination. And there are no studies that have been able to combine these features together in such a way that acoustical elaborateness can collectively serve as a single outcome variable in a controlled statistical model that takes both behavior and habitat into account.

The most promising habitat based theory on the origin of song focuses on the relationship between acoustics and forest composition. This “acoustic adaptation hypothesis” [AAH] (Morton, 1975) predicts that low frequency, intervalic tones should better penetrate complex vegetation (Hansen, 1979). This low frequency prediction has been confirmed in primates (Mitani and Stuht, 1998). Higher order acoustic complexity, however, has not been well studied as being possibly connected with habitat complexity. The intervalic predictions of AAH, for example, derive from a propagation perspective and fail to address the possibility that such tonal variation might instead serve as cognitive signals.

Few have postulated a zoologically broad, spatial-relativistic connection between vocal display and movement through habitat (Brown and Jordania, 2013). And some biomusicologists only poetically hint at music’s spatial “transposable aboutness” (Cross, 2001) potentially alluding to the idea that an animal’s use of transposition of melodic intervals is somehow analogous to relativistic movement through a three-dimensional habitat. Spatial-navigation selection pressures have been corroborated in neuro-behavioral studies of a possible musical-spatial processing overlap in both humans (Dehaene et al., 2003) and songbirds (Boogert et al., 2011; Feenders, 2008). But very few to date have explored this in both a multi-feature and ultimate-cause adaptionist framework, as was done here.

A classic theory on the origins of primates, coincidentally, rests upon analogous reasoning between habitat dimensionality driving behavioral (and morphological) evolution. The so-called “arboreal theory” suggests that arboreal life selected for grasping hands and a shift from smell to vision —including convergent orbital apertures and stereoscopic depth perception for frequent leaping (Jones, 1916; Smith, 1924). Primates that evolved these anatomical changes were better able to assess and complete leaps between arboreal supports to both forage and avoid predation.

Theoretical Foundations: *Behavioral ecology, mate choice, and signaling theory*

The line of reasoning considered here borrows key theoretical elements from the field of behavioral ecology where evolved animal behavior can be understood as responses to ecological influences (Fox and Westneat, 2010). Behavioral ecology, like ethology, helps explain biological traits using both proximate (mechanistic and developmental) and ultimate (phylogenetic and adaptive) causes (Mayr and Provine, 1981; Tinbergen, 1963). Co-evolutionary interplay, such as environmental or social influences on behavior, can be tabulated and controlled for in phylogenetic analyses (Fox and Westneat, 2010; Winterhalder and Smith, 1992), perhaps also enabling inference of ancestral ecological forces.

Behavioral ecologists do not typically include genetic, developmental, or often-times even evolutionary mechanisms in their models. Adaptive facets of phenotype are regarded as heritable and testable without necessarily knowing the details of the mechanistic pathways that gave rise to them (Reeve and Sherman, 1993). The adaptationist approach focuses on how phenotype fits an environment as a result of evolution by natural selection (Reeve and Sherman, 1993). And while three criteria—trait variation, environmental contexts, and a fitness measure—are required for demonstrating adaptation (Reeve and Sherman, 1993), merely showing an association between the first two of these can be evolutionarily informative (Fox and Westneat, 2010), particularly if many data points, at the species level, for example, are separated over millions of years of phylogenetic time.

From this adaptationist foundation, I investigated the mystery of song origins by building a model using signaling theory (Grafen, 1990; Zahavi, 1975). Signaling theory explores the communication strategies between individuals: both senders of signals and receivers of signals

(Irschick, 2015). Signals evolve when the information content of the signal[1] somehow increases fitness of the sender-receiver dyad: senders benefit when they can modify receiver behavior to improve their own fitness and receivers benefit when the signaler, for example, honestly conveys information that improves receiver fitness (Enquist et al., 2010). Honest signaling can be classified under costly signaling theory, as a special case, when deception is more costly than honest signals (Grafen, 1990; Zahavi, 1975). Sexual selection, a component of mate choice[2], is a commonly invoked mechanism of how such an signaling system might evolve. While these social mechanisms may initiate the prolonged social bonds that enable deffered direct benefits (Brooks et al., 2010), such as cooperative rearing or defense, I also investigated the environmentally relevant honesty[3] of signals by also exploring habitat effects. My aim was not to discount the important and inherent sociality of singing, but to instead simultaneously focus more intently on the micro-level acoustics of this social signal itself as well as the macro level environmental context, i.e. what the acoustic structure implies about habitat structure.

As mentioned above, I merged existing origins theories—both on arboreal drivers of primate evolution and social functions of song—and re-constructed them together under a more quantifiable framework. Specifically I hypothesized that elaborate song-like acoustic displays evolved as signals of *dimensional precision* required for complex aerial sensory-motor tasks. Landing, with velocity, an appendage on a tree limb in a complex canopy habitat, for example, requires precision in last minute spatial and temporal adjustments when substrate orientation and position are unpredictable. Primate songs could serve as honest signals of this landing ability in species that frequently traverse via risky aerially discontinuous paths through complex and gapped arboreal habitats.

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1 A signal is defined as any behavior (**a)** that alters receiver behavior (**b**), where **a** evolved to create **b**, and **a** is effective because **b** is also an evolved response (Maynard Smith and Harper, 2003)

2 Mate choice is any behavior that changes the likelihood of mating. Its scope has been expanded recently to include courtship, copulation, fertilization, and even parenting (Brooks et al., 2010)

3 Due to limited variation in primate calls, a constraint or performance-based “index” is arguably more appropriate nomenclature than a handicap-based, a costly or “honest” signal (Enquist et al., 2010)

Study Population: *Modern distribution, defining traits, and origins of primates*

The Primate order consists of 14 different families, over 50 genera, and hundreds of species. Geographically, these animals live in nearly every rain forest, and many other habitats, in nearly half of the continents on the planet, primarily South America, Africa, and Asia. Understandably, such a global radiation has resulted in an enormous diversity of adaptations to the various geographies, weather patterns, and corresponding radiations of flora (Swindler, 1998). Their enormous morphological and behavioral diversity, makes extant primates excellent study system for addressing evolutionary questions. Specifically, these data offer an exciting opportunity to test co-evolutionary theories surrounding locomotion and vocalization (Fitch, 2006). Primates are numerous and phyletically broad enough to provide statistical power and time span over which this (likely slow) co-evolutionary process can be meaningfully assessed. Lastly, while an influx of genetic data has recently reshuffled older morphological understandings of phyletic relationships, these doubly informed phylogenies currently puts us in a better position to control for effects of shared ancestry.

Members of the primate order are distinguished by a suite of traits which typically includes grasping appendages, unspecialized dentition, a claw-less hallux, longer hind limbs, orbital aperture convergence, a reduced olfactory apparatus, and an enlarged cranium relative to body size (Cartmill, 2012; Silcox et al., 2007). These traits likely gradually evolved, in piecemeal fashion, over the course of tens of millions of years during the late Cretaceous and early Paleocene Epochs more than 50 million years ago (Cartmill, 2012). During this time, angiosperms, flowering plants and trees, were evolving and radiating concomitantly with the various diversifying mammalian orders, with primates adapting to the newly vertically expanding dietary niche of the terminal branch milieu (Cartmill, 1972).

Correspondingly, there are numerous other theories that could explain many of these features such as visually directed reach/grasp predation (Cartmill, 1972), grasp-leap locomotion (Szalay and

Dagosto, 1980), primate-angiosperm co-evolution (Sussman, 1991), nocturnal leaping (Crompton, 1995), and the snake detection theory (Isbell, 2006). Ideally, a compelling theory would explain most, if not all, of the unique arboreal specializations of early euprimates (Szalay and Dagosto, 1988). Frequent landing of leaps, as necessitated in a strictly arboreal, terrestrial-predation avoidance and subsistence strategy, seems to explain most of these primate features simultaneously.

If primate morphology could have been driven primarily by leaping, it seems reasonable that other behaviors might also be attributable to it. Although song is widely thought to have independently and convergently evolved in primates and other groups of vertebrates, whether song is plesiomorphic (ancestral) or homoplasic (convergent) in the primate order itself remains unresolved. The key aim of this dissertation was to argue for the former, that the same complex arboreal environment that selected for primate morphology and leaping behavior, might also have selected for elaborate musical display behavior in the form of singing.

Hypotheses: *Precision limb and note landing versus phylogenetic stochastisity*

I merged and extended these previously advanced spatial, sensory, motor control, and social theories (Cross, 2001; Merchant and Honing, 2014; Pinker, 1997, p. 534) and subsumed them under a more quantitatively testable evolutionary framework (Paradis et al., 2004). In the vein of more motor control and pattern recognition (Roederer, 1984) based ideas, I hypothesized that song-like acoustic displays—those with a diverse clustering of acoustic units—evolved as signals of dimensional precision in spatial-motor tasks. Gravitationally time-sensitive, limb-landed locomotion—as executed during aerial bouts through complex canopy habitats, for example, where substrate orientation and position can be unpredictable—could have naturally selected for the cognition underlying sensory-motor precision. Primate song-like behavioral outputs could serve as honest signals of both fine (vocal and orbital) and coarse (skeletal) motor control required by species that frequently traverse via aerially discontinuous paths through complexly gapped canopy habitats.

This hypothesis was broken down into corollary hypotheses which I explored:

a. Strictly arboreal life selected for morphological changes to improve precision limb landing (specifically in the form of leap landing).
b. Precision limb landing necessitated cognitive improvements for precision comparison abilities (e.g. of abstract shapes across [audio or visual] sensory inputs)
c. This precision comparison ability can be communicated via elaborate display calls to potential mates and territorially adjacent conspecifics

Specific, testable predictions derived from these hypotheses were as follows:

1. Strictly arboreal primates should leap more between branches and across canopy gaps (a)
2. Leaping and swinging primates should have more convergent ocular apertures (a & b)
3. Precision comparison abilities should manifest as elaborate calling (c)
4. Leaping should associate strongly with elaborate calling (c)
5. Strictly terrestrial animals should have a less elaborate calls (a, b, c)

As mentioned above, behavioral ecologists are able to test adaptive hypotheses without knowing the genetic or cognitive inner-workings of the organisms they study. Specifically, I did not collect DNA, or quantify gene expression, or hormone levels, nor did I collected new brain lobe volume data even though much of it could have been quite useful for further understanding of mechanisms. I assumed that these mechanism would remain unknown (Reeve and Sherman, 1993) for the duration of this naturalistic experiment. Instead I tabulated the externally measurable phenotypes of locomotion and vocalization (primarily) as well as other socio-ecological controls such as activity period, mating system, habitat, physiology, territoriality, and diet all as inputs and outputs of an otherwise mechanistically unknown system.

Data & Definitions: *from the acoustics and positional behavior literature*

In addition to using published datasets as control variables for comparison in all three substantive chapters, I gathered evidence to test my theory by looking at both predetermined categorical measures from secondary sources as well as harvesting new high-resolution vocalization and locomotion data sets from the primary literature.

Vocalization Data: I collected published spectrograms[4] from primate studies usually in the form of vocalization repertoires as well as contexts and types of vocalizations. The categorical data helped to verify the spectrographically derived elaborateness index we derive in chapter 2. The spectrographic studies were found using search engines with "vocal* AND repertoire* AND [primate genus]." Search focus within each genus was discontinued after a sufficient number of species from each were obtained. From a potential pool of over 300 possible leads: I scanned 61 books and downloaded 67 manuscripts to obtain more than 80 species' spectrographic vocalizations. The current dataset includes 1297 different spectrograms for 61 species representing 40 genera from 58 sources.

Spectrogram Scoring: using human music universals (Brown and Jordania, 2013; Nettl, 2000) and the principles of acoustics (Roederer, 2008) as a guide, I selected six structural features as scoring parameters: tone, interval, rhythm, repetition, transposition, and variation. Training materials for these features were developed and verified using definitions from multiple sources including online dictionaries and encyclopedias and some of my own specialized knowledge of acoustics. Vocalizations

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[4] Spectrograms, also called sonograms or spectrographs, are plots of acoustic energy in two or three dimensions: time (x-axis) versus frequency (y-axis) versus amplitude (pixel darkness).

were scored for each of the six musical features in a random order and blind to species. Each of the six features was scored on a scale of 0 (lowest) to 10 (highest), except for variation which was scored as a count of unique syllable shapes. Further details can be found in Chapter 2.

Locomotion Data: I performed online searches for positional and locomotor studies that could provide numerical estimates of acrobatic behavior. I generally used broad search terms such as “locomot* OR position* AND primate*”, but additional more specific searches were also made for genera that did not have a representative species already in the dataset. I downloaded 99 of these sources from academic journals, books, and theses. The only criterion for rejecting a study was an inability to obtain a solid quantitative estimate for leaping.

Locomotion Categories: I extracted quantitative locomotor data from primary sources — sorting and tabulating the locomotor data from individual primate species’ studies into general locomotion categories. Since many of these studies observed several species simultaneously and other studies were similarly overlapping, estimates for the same species over multiple studies were averaged. For some species whose daily motion tended not to warrant quantitative study, a proxy description (e.g. “strictly terrestrial”) was used to assign a zero value for leaping and swinging. I calculated and re-partitioned the published distributions of locomotor frequencies into two main categories, “***swing”*** including *brachiate*[5], *semi-brachiate*, *arm-swing*, *tension*, *suspensory torso-orthograde*, *suspensory* and “***leap”*** including *leap*, *vertical cling leap*, and *bound leap*, *jump*, *drop*, *leap/drop*, *airborne*. Other positional behaviors such as postures (e.g. those observed during feeding, resting, etc.) were, for the vast majority of species, not tabulated.

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5 Brachiation is a form of torso-orthograde suspensory arm-swinging locomotion, performed primarily by apes, where the hands are deployed overhead, attached to a branch above them, for use in successive angular momentum driven swings to propel the body forward.

Methodology: *Ancestral character estimation, PCA, and phylogenetic regression*

Although ancient behavioral data are inherently impossible to observe directly, some locomotor behavior can be inferred via observation of skeletal changes that occurred between related species over millions of years of evolutionary time. Modern computational algorithms allow us to utilize the multitude of behavioral data available on extant primates to estimate ancestral behavior (Paradis et al., 2004). This and other related methods can be used for not only locomotor behavior but arguably for many other less physically preservable activities such as vocalization.

Ancestral Character Estimation: I used the ancestral character estimation (*ACE*) function in the *ape* R-package (Paradis et al., 2004) on the tabulated leap and swing percentages to triangulate, from the modern primate data set, an understanding of how early primates might have moved. I performed a root phylogenetic mean calculation to find these ancestral values as well as interpolate the internal node values between ancestral and extant primates to create a cladographic visualization.

Photogenic Tree: For the purposes of visualization, ancestral character estimation, and statistical control in regression modeling, I used a phylogenetic tree. Specifically, I used a RAxML phylogram based on a concatenation of 69 nuclear and ten mitochondrial genes (Springer et al., 2012).

Phylogenetically Controlled Regression: To computationally assess the relationship between risky aerial locomotion and elaborate acoustic display while controlling for counfonding vairables, I performed phylogenetic regression. This method tests for association between evolved characters of terminal data points in a phylogenetic tree while controlling for their non-independence due to a shared lineage. The specific method, phylogenetic generalized least squares (PGLS), is available via the *pgls* function from the *caper* R-package (Orme, 2012). This function's requirement for the outcome to be a single variable was main motivation for developing the continuous and univariate index (ARDI).

Principal Components Analysis: PCA is an exploratory statistical procedure that orthogonality transforms a dataset (of *n* observations on *p* possibly correlated variables) into a set of linearly uncorrelated principal components (Dunteman, 1989). I used the loadings, or weights, or correlations of the original six variables with each of these six derived components as a guide in choosing the subset of variables to retain which encapsulated most of the variation. I selected the variables with the highest loading in the retained components—discarding those variables associated with low eigenvalue components (Jolliffe, 1972). The retained components of transposition, repetition, and syllable count were combined to create an Acoustic Reappearance Diversity Index [ARDI] which could then be used as an outcome variable in the multi-variate regressions.

Organization of Chapters

The dissertation is a collection of three substantive chapters flanked on either side by introduction and conclusion chapters. The first of these three middle chapters used a literature-based dataset (of spectrographic vocal repertoires of primates) to both develop a new way of quantifying elaborate display calls and to use these data to shed light upon the question of convergent or ancestral primate singing. The second chapter explored a literature based locomotion dataset and used it to quantitatively explore the century old question of primate origins surrounding, specifically, which ecological forces helped to select for convergent orbits. The third substantive chapter then utilized these two new datasets by incorporating them in a phylogenetically controlled regression model. The final chapter reviewed the leaping and grasping based origins of primates and how these ecologically mediating behaviors may have influenced developmental, mating, and group level selection for vocal behavior. I also review the novel contributions of this work including two new datasets, ARDI, locomotion estimates, and the test results of both sets of origins theories. Finally, I review the implications of these findings in the light of human music making.

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Chapter 2 – The acoustic reappearance diversity index: from primate song to human music

Abstract

Musical behavior is likely as old as our species with song-like calls possibly originating tens of millions of years ago when primates were first radiating across the globe. Early singing likely evolved into the music of modern humans via multiple selective events, but efforts to disentangle these influences have been stifled by challenges to precisely define this behavior in a broadly applicable way. Detailed here is a method to quantify the elaborateness of acoustic displays using published spectrograms (*n*=832 calls) from the literature on primate vocalizations. Each spectrogram was scored by five trained analysts via visual assessments along six musically relevant acoustic parameters: *tone, interval, transposition, repetition, rhythm*, and *syllabic variation*. Principal Components Analysis (PCA) was used to reduce this multivariate assessment into a simplified measure of musical elaborateness. The resulting "acoustic reappearance diversity index" [ARDI] simultaneously captures syllabic variation and spectral/temporal redundancy in a single continuous variable. The potential utility of this index is demonstrated by applying it to several social and habitat-based theories of acoustic display origins. Our results confirm that primate species living in small, monogamous groups have song-like calls, while forest habitat had a less pronounced association.

Introduction

Elaborate acoustic display, including song and other musical behaviors, has independently evolved in several vertebrate (Hauser and McDermott, 2003) and some arthropod (Pollack, 1980) clades. However, the historical selection pressures that gave rise to this behavior, and its current evolutionary function, are less well established than its ubiquity. Delineating the emergence of human music, for example, is challenged by its acoustic ephemerality and a paucity of artifacts—although fossil musical instruments have been unearthed (Conard et al., 2009). Consequently, we have few clues available to resolve if human music is truly novel or merely an evolutionary continuation of the song-like calls of non-human primates such as those of the lesser apes. Alternatively, researchers can leverage statistical tools to investigate ultimate evolutionary function and mechanism by using behavioral data among living organisms (Fitch, 2015).

A number of explanations have been proposed for the evolution of musicality. The primary habitat-based theory, the acoustic adaptation hypothesis (AAH) (Hansen, 1979; Mitani and Stuht, 1998; Morton, 1975), makes two predictions about how the structure of flora drives the evolution of the vocalizations of the inhabiting fauna. First, it predicts that low-frequency vocalizations will increase as vegetation density increases (Hansen, 1979). This has been previously demonstrated in primates (Mitani and Stuht, 1998). The second prediction is that there will be more inter-element intervals as vegetation structure becomes more complex (Hansen, 1979). AAH has been modestly supported over the years, but its explanation of song is only weakly supported (Boncoraglio and Saino, 2007).

Theories about a social function of musical behavior lie on a continuum ranging from the affiliative and parental (e.g. lullabies) to the more aggressive and territorial (e.g. loud calls) with mating calls, or “love songs,” lying somewhere in-between (Lehmann et al., 2009). These include: emotion regulation (Roederer, 1984) and language acquisition (Dissanayake, 2000; Patel, 2008; Trehub and

Trainor, 1998), emotional communication (Altenmüller, Schmidt, and Zimmermann 2013; Snowden 2015), pair bonding (Geissmann, 1993), sexual advertisement (Darwin, 1871; Miller, 2000), group cohesion (Roederer, 1984), group selection (Brown, 2000), and coalition signaling (Hagen and Bryant, 2003). We suggest that these approaches to musical behavior fall short of fully disentangling the mystery of function because they lack a quantitative, acoustic features based definition.

Historically, the critical testing of these theories has involved focusing too narrowly on specific features (e.g. call frequency) in the case of habitat selection (Boncoraglio and Saino, 2007; Mitani and Stuht, 1998) or using extremely broad, binary aesthetic assessments—in the case of social selection (Hagen and Bryant, 2003). Contrary to the notion of a strict boundary between musical and non-musical, we argue here that musical behavior is a spectrum phenomenon (Nettl, 2015, p. 459). Music is also an emergent phenomenon most appreciated for the interaction of components that *synergistically* affect listeners. Few studies have attempted to combine these multiple features of acoustic display signal to more objectively encompass an essential musicality—efforts at a definition have understandably been challenged by imprecision (Kondik, 2010), circularity (Fitch, 2015), and ambiguity (e.g. the purposefully poetic “transposable aboutness” in Cross, 2001). Although there have been efforts to investigate the relationship between specific acoustic features of music and specific selective forces (Miller, 2000), few have focused on features of musical *performance* (Kondik, 2010) and many approaches (Hagen and Bryant, 2003; Miller, 2000; Pinker, 1997) only study western music *listeners,* a culture where they vastly outnumber performers (Cross, 2011).

We endeavor to construct a neutral formulation of these acoustic features (the signal itself) based mostly on human music universals (Mache, 2000). We do so by first distinguishing “utterance level” features—those present in every piece or performance—from “conserved” or “common” features—those present at some level in a musical system or culture (Nettl, 1983). Non-vocal modes of generation (e.g. via instruments) and cultural musical contexts (e.g. dance and rituals) are common human universals (Brown and Jordania, 2013), but they are rare in other vertebrates. These contexts are even considered inseparable from music to the degree that an ethnomusicological definition is nearly impossible without mentioning them (Nettl, 2015, pp. 6, 232, 242). Definitions of *song*, likewise, are not typically disassociated from references to ecological context (Beecher and Brenowitz, 2005; Searcy and Andersson, 1986). A context is not inherently acoustic itself, however, and might best be reconsidered as a co-evolutionary *influence* on acoustic display. Accordingly, we focus initial index construction efforts on only *structural* universals (e.g. pitch, rhythm, melody, and form) from human music (Brown and Jordania, 2013). Contexts can instead be tested later as potential influences on this independently constructed acoustic-based index. Our approach differs from previous work (Hauser and McDermott, 2003; McDermott and Hauser, 2005), in that features need not be uniquely human, just universally so. In addition, have omitted certain universals studies (Stevens and Byron, 2009), in order to focus our analysis on the vocalizations produced by the senders (e.g. tone) rather than the audio perceived by the receivers (e.g. pitch) of musical signals.

Evolutionary bioacoustics outside our own species (e.g. in *Aves*) has historically focused less on rhythm and pitch than more spectrally complex aspects of display. Examples of these latter approaches include between-song structural consistency measures such as typicality, the similarity of a song's features with the songs of others, and stereotypy, consistency in one's own songs (Searcy and Nowicki, 2010). Other, within-song focused signaling features (e.g. song rate, length, and size) relate more to mate choice preferences for output, performance, or complexity (Searcy and Nowicki, 2010). Here we aim to explore aesthetic feature combinations that span multiple of these broad (within-song) signaling categories simultaneously. Song analysis can entail visual quantification of putative aesthetic features, of possible signaling importance, present in spectrograms[1] (Fig. 1). Various within-song measures, such as unit consistency (Brown and Handford, 2000; Lambrechts, 1996), trill rate

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[1] plots of acoustic energy over both time and frequency

(Ballentine, 2004), repertoire size (Boogert et al., 2008; Hasselquist et al., 1996), song bout length (Farrell et al., 2012), and complexity (Boogert et al., 2008; Nowicki and Searcy, 2004), overlap well with the utterance level universals we use. Categorizing behaviors as “complex,” while preserving mystique, might also, paradoxically, act to discourage deeper understanding of such phenomena (Mace and Holden, 2005). While we are partial to the category of “complexity,” we aspire to transcend its potentially ambiguous connotation by developing a sophisticated and concrete multi-feature index.

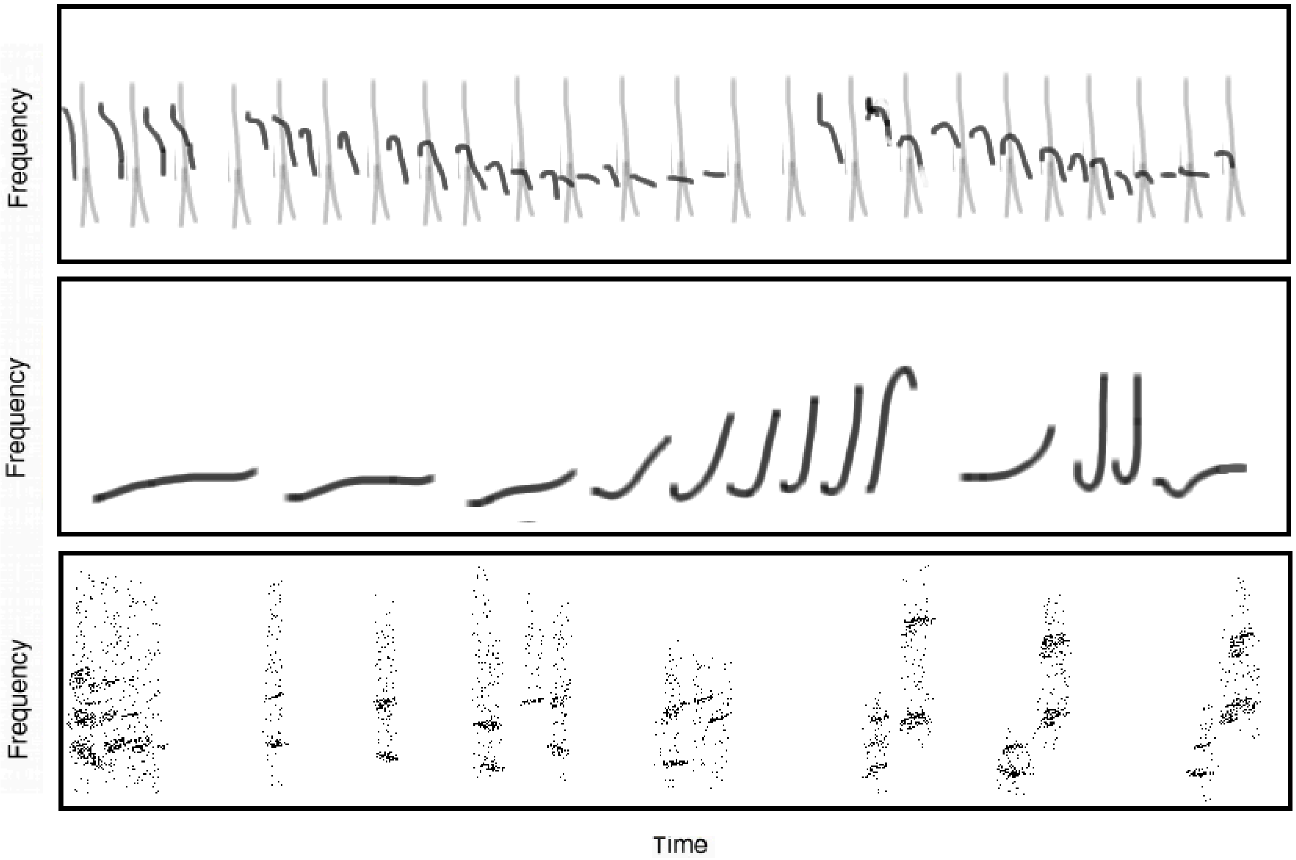

Figure 1. Spectrograms of various elaborate primate calls. Redrawn spectrographic representations of three species calls with corresponding acoustic reappearance diversity scores (averaged across 5 independent visual assessments) formulated as syllables * (Pr(repetition) + Pr(transposition)) where Pr is a proportion**. (top)** *Tarsius spectrum* 4.8 * (0.86 + 0.4) = 6.1; **(middle)** *Nomascus concolor* 5.4* (0.48 + 0.18) = 3.6 **(bottom);** *Lepilemur edwardsi* 2.8 * (0.72+ 0.1) = 2.3. Figures redrawn from Nietsch 2003, Geissmann 2000, and Gosset 2003 respectively (consult the references listed in the vocalization source list below).

Terminology differs between human and avian bodies of literature, but many of the aesthetic features from both seem to group nicely into two broader categories—first, a similarity among units, and second, a diversity among units. These can be measured, for example, by a consistency of repeated units or number of different units respectively. These more melodic and form-related elements might best be included at the more universal *utterance* level of acoustic musicality. The less common system-level universals of rhythm and tone (e.g. pitch) may not be as efficient at explaining more diverse aspects of proto-musicality. Human musical utterances consist of multiple, discrete units (e.g. notes, chords, phrases) that both vary (in pitch, tempo, or texture) and repeat (Brown and Jordania, 2013; Nettl, 1983, p. 39) (Table 1: utterance). There is disagreement as to whether pitch, a constituent of tone[2] (Helmholtz, 1885, p. 10), and rhythm are required features at this first, most basic level of musical organization (Table 1: system). Whereas rhythm and pitch are prevalent in both human music and animal song, they may not be universally common features of all elaborate vocal utterances.

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[2] Tone is sometimes used synonymously with frequency, pitch, or (musical) note. Under the convention used here, however, tone, is arguably more closely associated with the word *tonal* and is used as an indication of how far a sound might lie along a spectrum ranging from less structured or possibly noisy (or even *atonal*) sounds to more *tonal* and harmonically-structured sounds. It lies at the top of a hierarchy which includes timbre, loudness, duration, and pitch as underlying attributes (see Table 2). While pitch and tone are sometimes used interchangeably, as pitch is a prerequisite of tone, other factors (brevity, noise, and softness) can also nullify an observation of a sound being tonal.

Table 1. Gradient of music universals across different studies.

Nettl 1983			Brown & Jordania 2011		this study	
universal type	level	feature	**type:** feature	level	**feature**	abbreviated definition (or explanation)
instant	**0**	(“unmeaningful” / “unhelpful”)	NA		NA	*(minimal duration / multiple units required)*
utterance	**1**	well marked smaller **units**	**P1:** discrete (pitches)	1	(units)	*(unblind count performed by researcher)*
		clear beginning & end	**F1:** beginning, middle (& end)	2	NA	*(determined by primary researchers)*
		Redundancy / Variation balance				
		repetition	**F2:** (internal) repetition w/ variation	2	**repetition**	unit reappearance across time
		variety: textural variety: melodic	**M1:** (melodic) phrase organization	1	**variation**	unique unit “shape” count
			E1: arousal factor:register	1	**interval**	frequency change (within unit)
		variety: rhythmic	**E1:** arousal factor:tempo	1	*****	*(less applicable for short phrases)*
			E1: arousal factor:amplitude	1	*****	*(difficult spectrographic assessment)*
			P10: relative pitch (transposability)	1	**transposition**	unit reappearance across frequency (& time)
system	**2**	**rhythmic** structure (dynamic stress)	**R1:** isometric rhythm **R5:** divisional durational structure	2 2	**rhythm**	closeness to perfectly isometric temporal spacing of units
		tonal (~Maj 2nd, descend. pitch end)	**P2:** octave equivalence **P3:** scales **M2:** hierarchical tone organization	1 1	**tone**	evidence of a main frequency or harmonic banding pattern

There are two main levels of human music universality, utterance and system, which will most help us in defining song. The current study attempts to understand utterance level universals. Two previous studies, however, were somewhat ambiguous in determining the level at which the certain features might lie. After the requirement for *discrete units*, *repetition* and *variation* are the most obvious utterance-level universals, and *pitch* and *rhythm* are included at the system level, whereas *transposition* likely lies in-between these other two pairs. Bolded letter abbreviations for the Brown & Jordania’s study are uncompressed as follows: **P**=pitch, **F**=form, **M**=melody, **E**=emotional/arousal factor, and **R**=rhythm. The top two most universal sub-features (bold numbers) of each category in Brown & Jordania’s study are listed here, with exceptions of the added **R5**, **P3**, and **P10** and the omitted **R2**, to more closely align these with the features selected for the present study. ‡While we recognize “discrete pitches” as being ranked highly by Brown & Jordania, we argue for “discrete” as fitting best at the utterance level and “pitched” as fitting best at the system level. *Note additionally that variation in duration, tempo, and amplitude were not tabulated for this study.

To shed light on this debate, we developed an impartial formulation by collecting spectrograms of vocalizations from 55 primate species and then scored them on six musically relevant acoustic parameters—at both the *utterance* and *system* levels. We then performed a principal components analysis (PCA) informed variable reduction on these six acoustic feature scores. The contrasting utterance-level acoustic music universals of syllabic diversity and reappearance were retained and combined into a univariate measure of proto-musicality that detects song-like elaborateness from any acoustic utterance. The resultant “acoustic reappearance diversity index” is defined (Schruth et al., 2019) as the expected number of unique spectral shapes or “syllables” that reappear within a call (either by repetition or transposition). We demonstrate the utility of this metric by applying it to key ideas from the two theoretical bodies mentioned above: both adaptation to habitat acoustics and selection based on social influences.

Methods & Analysis

Vocalization data collection

As an alternative to analyzing raw audio recordings, which are often unavailable, we used published spectrograms: plots of acoustic energy where x=time and y=frequency (Fig. 1). We sampled spectrographic studies from nearly all families in the primate family tree, where each vocalization collection was individually culled and classified by primatologists focusing on select species. We primarily focused on collecting *continuous* data, from spectrographic vocalization repertoires (for 62 species), and only secondarily on *categorical* call type data (e.g. *loud call*, *long call*, *chorus*, *song*, *duet*) from text descriptions of vocalizations (for 199 species) (Mitani and Stuht, 1998; Wich and Nunn, 2002). The spectrographic studies studied individual species and were all published in English before 2014. The categorical data (e.g. name, type, and context) were additionally used to verify the multivariate analysis on the variables derived from the spectrographic dataset.

For the quantitative analysis, we searched for publications meeting the above criteria by querying on-line search engines (ISI Web of Knowledge and Google Scholar) to locate these vocal repertoires. Initially this involved hand-entering “vocal* AND repertoire* AND [primate genus]” as an all-field query into the journal article search feature of Web of Science citation index online. Use of this text-based meta-database (limited to title, abstract, and keyword fields), however, could not easily detect presence of “spectrograms” as this particular keyword usually only appears in captions or methods sections. High sensitivity search focus within each genus was discontinued after a sufficient number of species from each were obtained. Additional search efforts were instead redirected toward more sparsely studied corners of the primate family tree using reference cross-checks and review article citations.

In general, studies were catalogs of individual species behavior rather than developmental, experimental, or species comparative studies. For each species studied, articles had to include spectrographic depictions for multiple calls, in order to obtain a variance estimate of each species’ song index. A primary objective was to obtain “complete repertoire” studies and, as a result, over 2/3rds of accepted studies had more than 10 different calls (*n*=45 species). Some exceptions were made for species with (an) obvious, stand-out display call(s) (e.g. gibbon songs) that were otherwise relatively non-vocal (*n*=5). Some other exceptional non-repertoire focused studies (e.g. long calls, loud calls) were also included (*n*=5). Because the main goal was to let acoustic features predict song-like calls independent of researcher call designation, we did not include any other studies on just a single call type (e.g. contact, food, alarm). A single study (Harcourt 1993) that was neither a full-repertoire nor a loud-call study on the “close calls” of the gorilla was used as studies with a larger variety of calls were not found.

We scanned 61 books and downloaded 67 PDFs to obtain spectrographic vocalizations from more than 80 species and over 300 total leads on possibly relevant studies. Only a single spectrographic study for each species was used in the data-set, so that some studies of the same species were removed (*n*=53). In these cases, we retained the higher quality studies: those with more vocalizations described, more modern recording and analysis tools, higher quality spectrograms, more sophisticated call classification technique, or ones that were more recently published. The final collection of spectrograms was extracted from 58 sources resulting in 1,297 different spectrograms for 61 species representing 40 genera.

For 44 studies in electronic format, images were obtained as screen captures at 100% zoom. For the remaining species, we scanned spectrograms from printed articles at 300dpi as grayscale 8-bit depth bitmaps to provide similar resolution. We also used image editing software to manually clean and standardize the spectrograms by removing axes, labels, and any annotative markings. Careful effort was made to avoid truncating any features of calls that weren't already constrained by the plot margins as delineated by the original authors.

Vocalizations were grouped into 842 species-specific note, phrase, and song types as assigned by the original authors themselves. We included as separate vocal types both single unit and repeated unit vocalizations, if the primary authors had also done so. Ten vocalizations (from three different studies) did not meet the minimal study acceptance criteria above, leaving 832 scored vocalizations (corresponding to 1287 spectrograms from 55 sources).

Spectrogram scoring

We used simple human music universals (Brown and Jordania, 2013; Nettl, 1983) and the principles of acoustics (Roederer, 2008) to guide us in selecting a total of six structural features as scoring parameters: variation, repetition, transposition, rhythm, tone, and interval. Spectrographic interpretations of definitions used are abbreviated as follows (see Table 2 for full details):

tone: the presence of clean harmonics with distinct, horizontally-parallel bands

interval: a sloping, jagged, or curving, rather than static, fundamental frequency

rhythm: a regular recurrence or pattern of [vocal] units over time

repetition: similarity in [vocal] units repeated across time

transposition: similarity in [vocal] units of different frequencies (and at different times)

variation: number of distinct [vocal] unit types or shapes ("syllables") within a call

Observers were trained for one hour on feature definitions[3] and how to identify and quantify them spectrographically. These song sub-components proved rather difficult to impartially define themselves and were subsequently verified using entries (Table S1) in hard-copy encyclopedias (Hughes et al., 1966; Randel, 2003). Manual scoring was performed blindly without reference to the species. Vocalizations were scored for each of the six musical features in a random order of species. Each of the six features was scored on a scale of 0 (lowest) to 10 (highest), except for variation which was scored as a count of unique syllable shapes. Vocalizations with multiple spectrograms (*n*=221 or 26.6%) were separately analyzed and then averaged to calculate the final measure for that vocalization type. This matrix of ordinal scores was then averaged across the individual scorers. Finally, for the PCA analysis, these scores were scaled to continuous values between 0 and 1. These spectrographic scores, vocalization source information, and categorical call type data have been archived on-line[4].

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[3] Retrieved Jan. 20, 2014. from:
Wikipedia.*com*, from https://en.wikipedia.com/wiki/ { exceptions to feature spellings include "transposition_(music)," "interval_(music)," "repetition (music)," and "musical tone" } and from *Merriam-Webster.com*, https://www.merriam-webster.com/dictionary/ { all same except "transpose"}

[4] ProQuest Dissertations & Theses https://www.proquest.com/products-services/dissertations/

Table 2. Vocalization spectrogram component definitions and scoring key.

acoustic feature	definition	spectrographic	scoring
tone	a steady, regular, or periodic sound characterized by its pitch (or perceived frequency), intensity, duration, and timbre	presence of a clean, high-contrast fundamental frequency and/or harmonics	low={noisy, pixelated, grey} high={clean, clear, black & white}
interval	the difference between two (successively sounding) tones. The ratio between two sonic frequencies	the presence of sloping or curving (rather than static) fundamental frequency within units	low={flat or noisy} high={sloped, jagged or curvey}
rhythm	a regular recurrence or pattern in time--a movement marked by the regulated succession of strong and weak elements, or of opposite or different conditions	the regularity of spacing between units over time	low={unpredictable horizontal spacing of units} high={evenly spaced repeats, scale or syllables}
repetition	restatement [over time], such as the restatement of an utterance, phrase, or theme.	reappearance of a syllable at the *same* frequency across time	low={isolate, unique} high={all units match many other units horizontally}
transposition	moving a (collection of) note(s) up or down in pitch by a constant interval	reappearance of a syllable at *different* frequencies over time	low={flat progression} high={all units match other units after shifting vertically and horizontally}
syllable(s)	a unit of organization for a sequence of speech sounds. Typically made up of a syllable nucleus (most often a vowel) with optional initial and final margins (typically, consonants).	a count of the number of distinct unit shapes within a call	low={one unit shape type} high={many unit shape types}

Listed here are the six universal acoustic music features, their composite definitions[3], and a spectrographically relevant interpretation for scoring purposes. The first five dimensions were scored on a scale of 1 (lowest) to 10 (highest), while syllable was scored as a count of different spectral shapes. This matrix, along with pictures of the original dictionary and encyclopedia definitions, and a small set of non-primate spectrographic examples, constituted the materials provided to scorers during the hour-long computer lab training session. These features *themselves* proved difficult to precisely and impartially define and, consequently, were derived and verified using multiple independent sources including dictionaries and encyclopedias (Table S1), both on-line and in book format.

Principal components and dimension reduction analysis

We used PCA as a guide in reducing the acoustic feature scores from six to just three variables that could then be combined into a single multivariate elaborateness index. In this dataset, for example, repetition and rhythm are highly correlated with each other as are tone and interval (Supplemental Fig. 1). These two variable pairs are therefore strong candidates for reduction where one variable from each pair is kept as a proxy for both variables in the pair. The end goal of this reduction was to both eliminate redundancy and gain access to statistical analysis programs and functions that required a univariate parameter as input. Using PCA to inform a dimensionality reduction also had several additional advantages ranging from alleviating visualization issues to addressing multicoleniarity of variables (George Dunteman, 1989).

PCA is an exploratory statistical procedure that orthogonally transforms a dataset (of n observations on p possibly correlated variables) into a set of linearly uncorrelated principal components (George Dunteman, 1989). In this case, p corresponds to six music universal feature scores and n equals 829 primate vocalizations. The loadings (i.e. weights, or correlations) of the original p=6 variables with each of the components, are a useful way to systematically translate between the original variables and these main variance-explaining best-fit lines. The loadings were used as a guide in selecting a subset of variables that encapsulate most of the variation. This involved selecting the variables with the highest loading (α_0), or contribution, in the retained components ($\alpha_0 > 80\%$) and discarding those variables associated with low eigenvalue ($\lambda_0 < 0.7$) components (Jolliffe, 1972).

Index development, verification, and demonstration

We used a probability argument to develop an index that most efficiently captures acoustic elaborateness at the utterance level. We also used theoretical arguments—invoking norms from avian bioacoustic research, human music history, and ethnomusicological works (Brown and Jordania, 2013; Nettl, 1983)—to support the acoustic feature selection. For verification, we performed Mann-Whitney U tests and Pearson’s Rank of the index against established call names and contexts. We also illustrate the utility of the resulting index by examining theories of song and music evolution.

Results and Discussion

Scorer consistency

Scores were fairly similar across individual observers (average standard deviations were all under 2 out of 10) with syllable and transposition having the lowest deviations (both under 0.6). Interclass reliability scores, were all significantly positively correlated between observers (average *ICC* = 0.09) with transposition and rhythm having the lowest ICCs (both under 0.017). Pairwise comparisons suggested that rhythm and transposition were the most reliable and perhaps the least ambiguous features to score. Either reducing these categories to fewer, perhaps binary, categories or normalizing them to the same mean would likely help improve their similarity, consistency, and reliability (Supplemental Fig. 2). Though these measures are suggestive of not being ideal for applications that require *discrete* outcomes, we moved forward, regardless, in using the underlying scores, in this more exploratory setting, to inform variable selection and subsequent construction of our *continuous* index.

PCA results

The results of the PCA (Table 3) suggest that PC1 (the best-fitting variance-minimizing line) is one that delineates along a continuum from signal-rich, song-like calls to acoustically noisy and single unit calls (Fig. 2 a and b respectively). We hereafter refer to this as the “signal content” component. All loadings in this component are negative suggesting that all six features contribute to explaining the signal content component and are helpful in assessing acoustic musicality. This first signal content component explains 43% of the variance (Table 3).

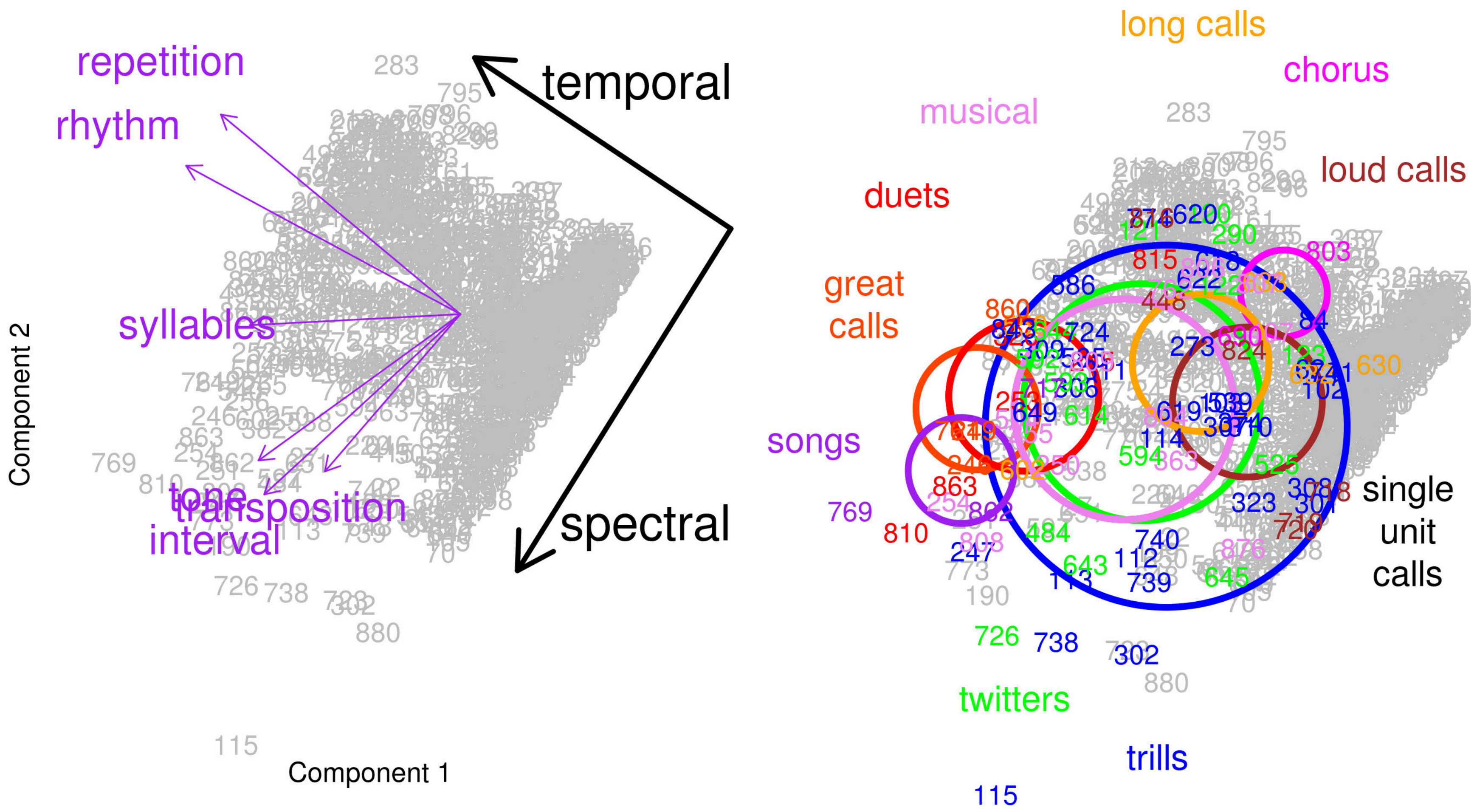


Figure 2. Principal Components Analysis [PCA] of six acoustic display aspects of primate calls.
PCA on six acoustic music universals (tone, interval, and rhythm, repetition, transposition, and syllable count) where each numbered point above represents one of 823 unique primate vocalizations**.** **(left)** Each of the six arrow-head coordinates represents the loadings (contributions) of each of these acoustic feature scores towards PC1 and PC2 (also see Table 3). The three distinct clusters formed by these PC loading coordinates suggests a possible reduction in dimensionality down to just three proxy measures – a diversity measure: syllable count (left) and two redundancy measures: temporal (top) and spectral (bottom) **(right)** Using the same underlying numbered point positions of calls, primary study author determined call types labels and rings (color online) point out their approximate clustering ranges, scaled to relative number of calls. The plot suggests that song like calls (right: far left) are distinctly more signal rich than long calls, loud calls, or choruses (right: far right).

Table 3. Results of the principal components analysis of music universals on primate calls.

	Component					
Acoustic Feature	**1**	**2**	**3**	**4**	**5**	**6**
syllables	-0.40	-0.03	-0.19	**0.87**	-0.17	0.08
repetition	-0.46	**0.53**	0.07	-0.23	0.04	0.67
transposition	-0.26	-0.42	**-0.79**	-0.33	-0.05	0.13
rhythm	-0.52	0.40	-0.09	-0.17	0.09	**-0.72**
tone	-0.39	-0.39	0.46	-0.22	-0.66	-0.03
interval	-0.37	-0.48	0.33	0.02	**0.72**	0.05

	1	**2**	**3**	**4**	**5**	**6**
Loadings (eigenvalues)	2.55	1.29	0.83	0.71	0.49	0.13
Proportion Variance	0.43	0.22	0.14	0.12	0.08	0.02
Cumulative Variance	0.43	0.64	0.78	0.90	0.98	1.00

The Principal Components Analysis of human-music acoustic universals (p=6) applied to primate calls (n=826), suggests that repetition, transposition, and syllable count are the most variance explaning. The feature score loadings (top table) contains each features' correlations with the components: PC1 (signal content) explains 43% of overall variance and indicates that all six parameters contribute to a call's signal content; PC2 (degree of temporal versus spectral redundancy: 22% of total var.) highlights the high loading of repetition (53% corr.). PC3 (14% of var.) and PC4 (12% of var.) have top loadings of transposition (79% corr.) and syllable count (87% corr.), respectively, of feature score correlation with each component. Loadings which were highest in absolute value both across features and across components were highlighted in bold (PC1 had no such value).

The second component, which minimizes the variance between the first component and the residuals of that component's fit, is one that differentiates between types of redundancy: temporal versus spectral (Fig. 2 a and b: top and bottom respectively). The highly correlated time domain measures of rhythm and repetition both have positive loadings and the spectral domain measures of tone, interval, and transposition all have negative loadings along PC2.

A pronounced inflection point in eigenvalues between these first two components (PC1: signal content: λ=2.56 and PC2: redundancy: λ=1.3) and the rest suggests that we might focus primarily on the former and less on the latter. The third and fourth components, however, do explain a good proportion of the overall variance—raising it 25.5% from 64% to 90%—and the eigenvalues (λ_0) are all above 0.7 and suggest retention (Jolliffe, 1972). These two components are harder to interpret than the first two (signal content and redundancy type), but the loadings' correlations, of each parameter with each component, are informative. The single highest loading for each of these two components are, interestingly, transposition (79% loading correlation) and syllable (87% loading correlation). They explain 13.8% (PC3) and 11.7% (PC4) respectively of overall variance—after 42.5% (PC1) and 21.6%

(PC2).

Syllable count is the most unambiguously neutral in PC2 (redundancy) and clearly collimate with PC1 (signal content) suggesting it could be an efficient indicator of complex calls. As mentioned above, it was also the highest loading feature in the 4th component—one which explains 12% of the variance of the overall dataset. Syllable diversity's prominence is not that surprising as its analog (repertoire size) is a commonly used metric for display quality in avian acoustic research (Boogert et al., 2011; Moore et al., 2011).

Repetition and rhythm had similar loadings in PC1 and PC2 (Fig. 2a) suggesting a collapsing of them into a single variable to reduce collinearity. Rhythm was indicated as being important, but it was excluded from the index due to its high association (72%) with discarded PC6 (λ=0.13). Only one of these two features was retained, as either one could serve as a rough proxy for time-domain redundancy. Repetition is more elemental (as it is often a prerequisite for rhythm) and is thus considered to be further justified for retention in the index. We offer additional rationale below in arguing for rhythm’s proper classification as a musical *system level* universal (also see Table 1).

The PC1 and PC2 loadings for tone, interval, and transposition similarly overlap with each other in the PCA analysis (Fig. 2 a and b bottom) and could be reduced to a single representative non-co-linear variable representing frequency domain redundancy. Interval was difficult to properly assess as were other (unmeasured) emotive/arousal universals (e.g. tempo and amplitude variation). As it had the highest loading with the discarded fifth component (λ=0.49), interval was ruled out. Pitch, like rhythm, has an unclear position in the gradient of musical universality somewhere between utterance and system level universals (Brown and Jordania, 2013; Nettl, 1983), and it is possible that tonal (pitched) units should not be categorically required in an utterance level definition (Table 1). Transposition, with its high loading on the third component, was selected to serve a proxy for both pitch and interval.

Towards a univariate quantitative index

The topic of musical quality can be polarizing (Cross, 2011; Fitch, 2015) and features such as pitch (e.g. tonal versus atonal music) and rhythm (e.g. melodic versus rhythmic music) are likely candidates for inciting disagreement. Perennial controversy surrounding these features hints that they are not necessarily simultaneously required as part of a universal definition. Our PCA results correspondingly suggest we can be less concerned with these two features as they can be proxied by the spectral and temporal redundancy measures of transposition and repetition. These features' components together explain over a third of the total variance, whereas the rhythm-associated component explains less than three percent.

Music has more simply and broadly been encapsulated as "an unusual combination of order and chaos" or an emergent balancing of "[ritualization with innovation]" (Miller, 2000, p. 433), "redundancy balanced by variety" (Nettl, 1983, p. 39), and as formalization and repetition versus exaggeration and elaboration (Dissanayake, 2008). It is an art form which sets up expectations via reappearing motifs and then morphs them into variants that act to pleasantly surprise listeners. Variety unquestioningly provides the combinatoric uniqueness underlying musical novelty and interest. But its counterpart, repetition, though it provides baseline temporal acoustic scaffolding, still remains a relatively unsolved mystery in musicological research.

We need only include this minimum set of acoustic universals, as we are most interested in detecting song at the most abstract, general levels. And we could require the two simplest and yet nicely contrasting and balancing features of redundancy (sometimes measured as *consistency*) and variation (often proxied by *size* or *complexity*) of syllables within an utterance—especially given the (avian/human) quality metric overlap discussed in the introduction. The PCA nicely corroborates this theoretical argument for a simple inclusion of just these few non-collinear variables. However, we still need to further quantitatively combine them, if we are to obtain a single outcome measure of acoustic elaborateness. Below, we provide the mathematical rationale for adding the two reappearance probabilities together and then multiplying the result by syllable count.

These two (within-utterance) features can be quantitatively defined as follows: *variation as* a count of the number of distinct syllables and *redundancy* as reappearance of syllables across time—either at the same frequency, in the case of repetition, or at different frequencies, in the case of transposition. Mathematically, we need to determine which operations to use when combining these together. As for combining repetition and transposition, we can re-purpose the addition rule of probability theory (Freedman et al., 2008) that states that for two events, A and B:

$$P(A \text{ or } B) = P(A) + P(B) - P(A \text{ and } B) \text{ (Eq. 1a).}$$

The last term can be set to zero due to mutually exclusivity (Freedman et al., 2008) of the repetition and transposition of any given vocal unit. That is, it's impossible to both repeat, in time, and transpose, in frequency, a unit across an entire call. And since these two feature scores also happen to be easy to scale into probabilities, as they are already recorded on a scale of 1 to 10, the probability of unit reappearance as the sum of the two terms can be written as:

$$P(\textit{reappearance}) = P(\textit{repetition}) + P(\textit{transposition}) - 0 \text{ (Eq. 1b).}$$

For integrating this new reappearance probability into our index, we can model the index (which requires both unit reappearance and syllabic diversity) as an expectation (Freedman et al., 2008) written like so:

$$E(X) = \sum(x_i \times P(X = x_i)) \text{ (Eq. 2a)}$$

where X is a random variable that serves as an indicator of reappearance. It is a binary (yes or no) variable that answers the question: does this unique syllable [i] occur elsewhere in the utterance? The probability term can be removed from the summation because it is uniform across the entire call (scoring was assessed on entire calls and not individual units). The equation, within the context of this study, then simply becomes the count of unique syllables times the overall probability of syllable recurrence within the utterance:

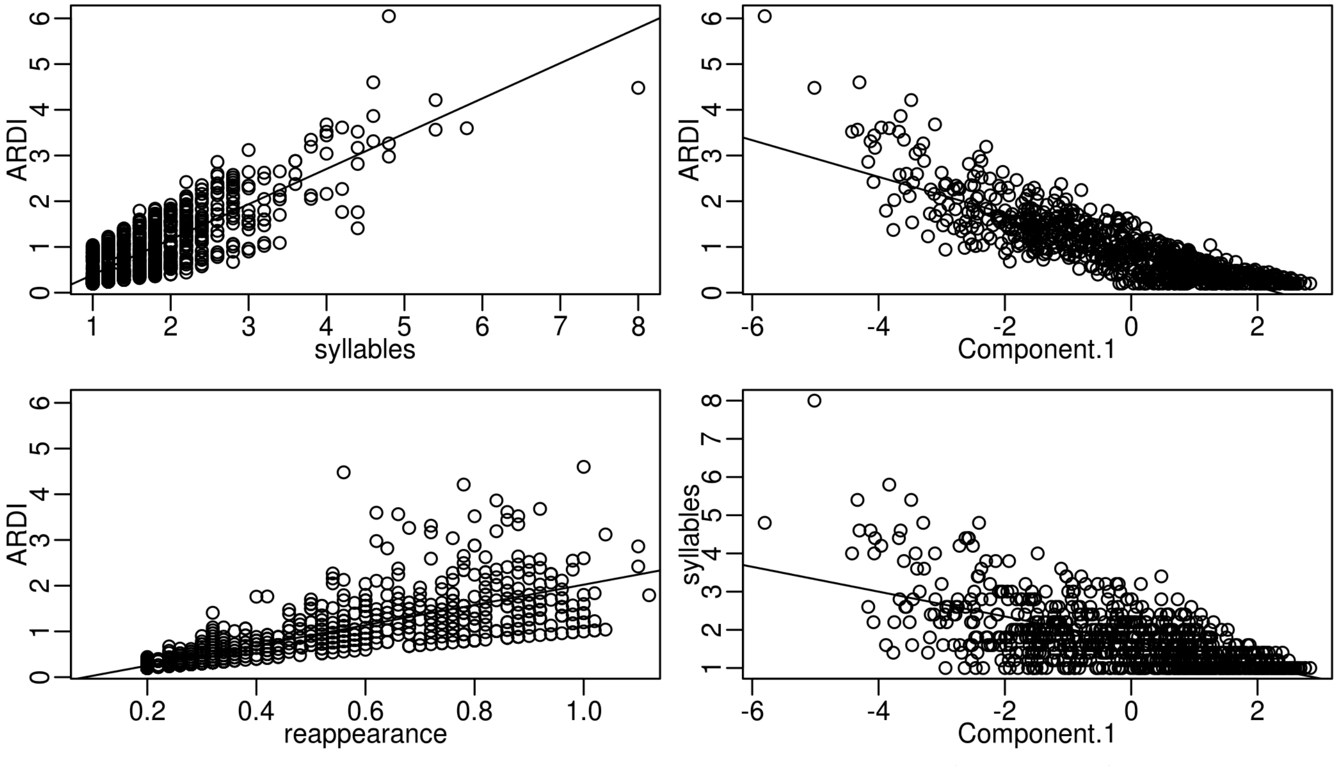
$$E(X) = N \times P(X) = \sum(x_i) \times P(X = x_i) \text{ (Eq. 2b).}$$

Rewritten with the full names of the two main components, this expectation looks like:

$$E(\textit{number of syllables reappearing}) = \textit{syllable count} \times P(\textit{reappearance}) \text{ (Eq. 2c).}$$

This use of multiplication is an elegant and mathematically certain way to require that each of these elements co-exist within every musical utterance; *multiplication* of the two individual feature scores of syllable and reappearance guarantees a score of zero if either feature is scored as zero (Equation 2c).

Figure 3. Component 1 compared with ARDI and its two main underlying feature scores.



Our musical elaborateness measure, ARDI, incorporates a representative from each of the three main loading clusters from the PCA (Figure 2) and correlates strongly with the first component (ρ=-0.85, n=832, Pearson) as all three of these clusters are negative along PC1. While it's possible, and arguably more simple, to use just component 1 (the main variance explaining signal content PCA component), the plots above show that our more theory-based formulation has cleaner correlations with both syllable and reappearance. ARDI also has a stronger correlation with syllable (ρ=0.83, n=832, Pearson) than component 1 does (ρ=-0.64, n=832, Pearson). Furthermore, ARDI is more theoretically driven, incorporates additionally explanatory factors, and more readily lends itself to easy interpretation.

Corroboration of the index

We demonstrate use of the acoustic reappearance diversity index by examining its correlation with vocalization categories and contexts. The appropriateness of the composite index was suggested by its assignment of relatively higher values to vocalizations categorized as *display* (Mann-Whitney U test, *n*=829, *W*=3581, *p*<0.0001) or those described as *song, duet, trio, chorus, great, music, scale, coda*, *intro,* or *interlude* (Pearson's rank, *n*=829, *r*=0.49). Visual evidence of the latter of these correlations is available by inspecting the overlay of these song names on the PCA plot (Fig. 2b). The correlation between higher acoustic reappearance diversity index values with classifications such as *duet* or *song* (Wilcox-test: *n*=58, *W*=91, p<0.007; Fig. 4) verified this composition of features in the composite score. Similarly, higher scores also associate with primary author determined call contexts such as “display” and “sociosexual” (Fig. 5). These scores are univariate, continuous, blindly scored, and conform to expert-determined names and contexts.

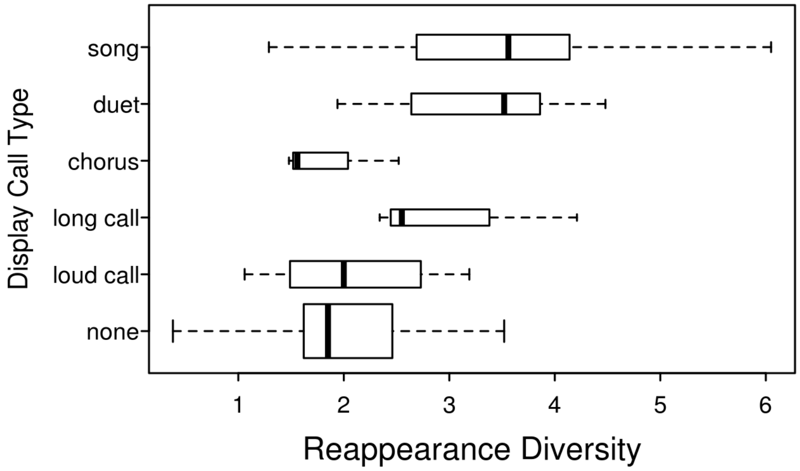


Figure 4. Acoustic reappearance diversity scores versus display call type. Acoustic reappearance diversity is a univariate measure of the expected number of times a unique syllable reappears within a single call or song. This measure has a high correspondence with duet or song calls versus other types of calls.

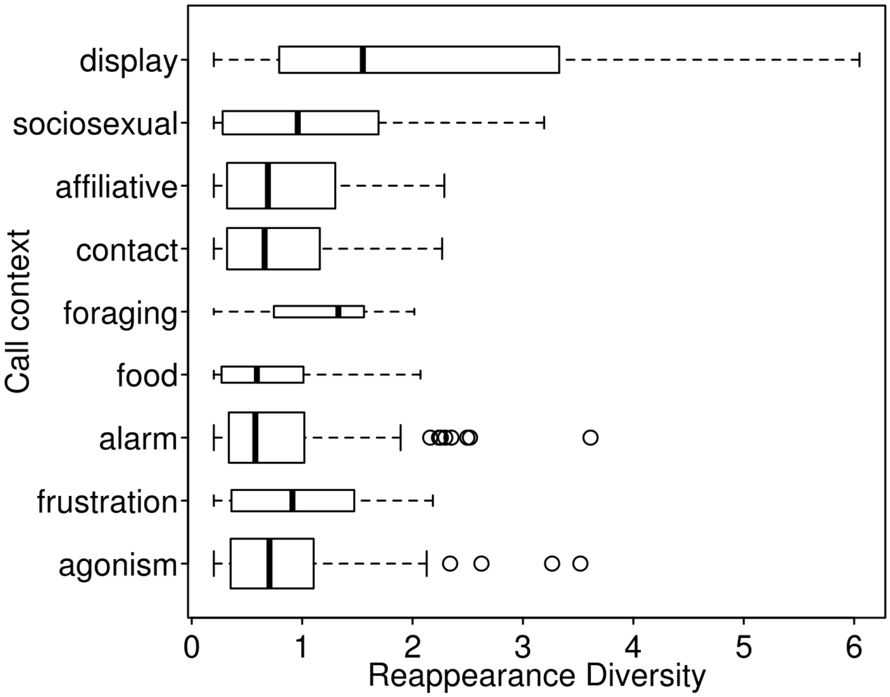


Figure 5. Acoustic reappearance diversity scores versus call level controls (context). Display calls are the primary vocalization context which appear to strongly associate with higher acoustic reappearance diversity. This suggests that the reappearance diversity measure could serve well as an indicator of elaborate display calls. Note: display included territorial, contact included: abandonment, contact, isolation, exploration, location; frustration included agitation, discomfort, and upset; alarm included: fear, disturbance, distress, alert, and arousal; agonism included ,threat, warning, and mobbing; affiliative included play, submission, greeting, social, mothering, and grooming; sociosexual included copulation, mating, and sexual.

These results seem to corroborate our index formulation, but there admittedly exists potential western bias in that both primary researchers (who named and classified the calls) as well the five trained scorers (using English definitions) are mostly culturally Western and primarily English speaking. Thus, there remains some circularity in validating an index built upon Western feature definitions, scored by mostly Western students, using western researcher determined call names. Although future studies could include more scorer diversity, it is unlikely that this would have a significant impact on the results as we attempted to be as objective and blind as possible. Although we may not have completely avoided all forms of definitional circularity, we have tried our best to minimize these self-fulfilling influences.

Akin to concerns that the limits of what is considered to be musical exists within certain “perceptual bands” of frequency, amplitude, and temporal patterning (Nettl, 1983, p. 39), we admit that our model breaks down when extrapolated to its extremes. That is, our index likely has a parabolic, rather than linear, relationship with actual perceived quality of acoustic display. At low to mid levels of acoustic reappearance diversity, the index should perform fairly well, but at higher levels, it is likely to be less useful. At these extremes, listeners cannot appreciate the increasing levels of elaborateness because their auditory perception circuitry becomes overwhelmed by either processing utterances that reappear too closely together in time or are over-populated by too many different types of syllables of which to keep track.

Testing habitat acoustics and social effects using a species-level index

We used a single index value for each species to explore questions about music and song origins. A box plot of all species in the study illustrates the range of possible scores within a species from which the top score was selected (Fig. 6). The maximum score for each species was used, because we are interested ultimately in the highest level of possible performance in the display calls of species. This “acoustic reappearance diversity index” (highest score per species) formulation showed negligible correlation with many possible study and species level predictor variables, but significant exceptions, such as habitat, monogamy (Fig. 7) and group size (Fig. 8), are discussed hereafter. Using the average ARDI score for each species had results similar to, but less significant than, using the maximum.

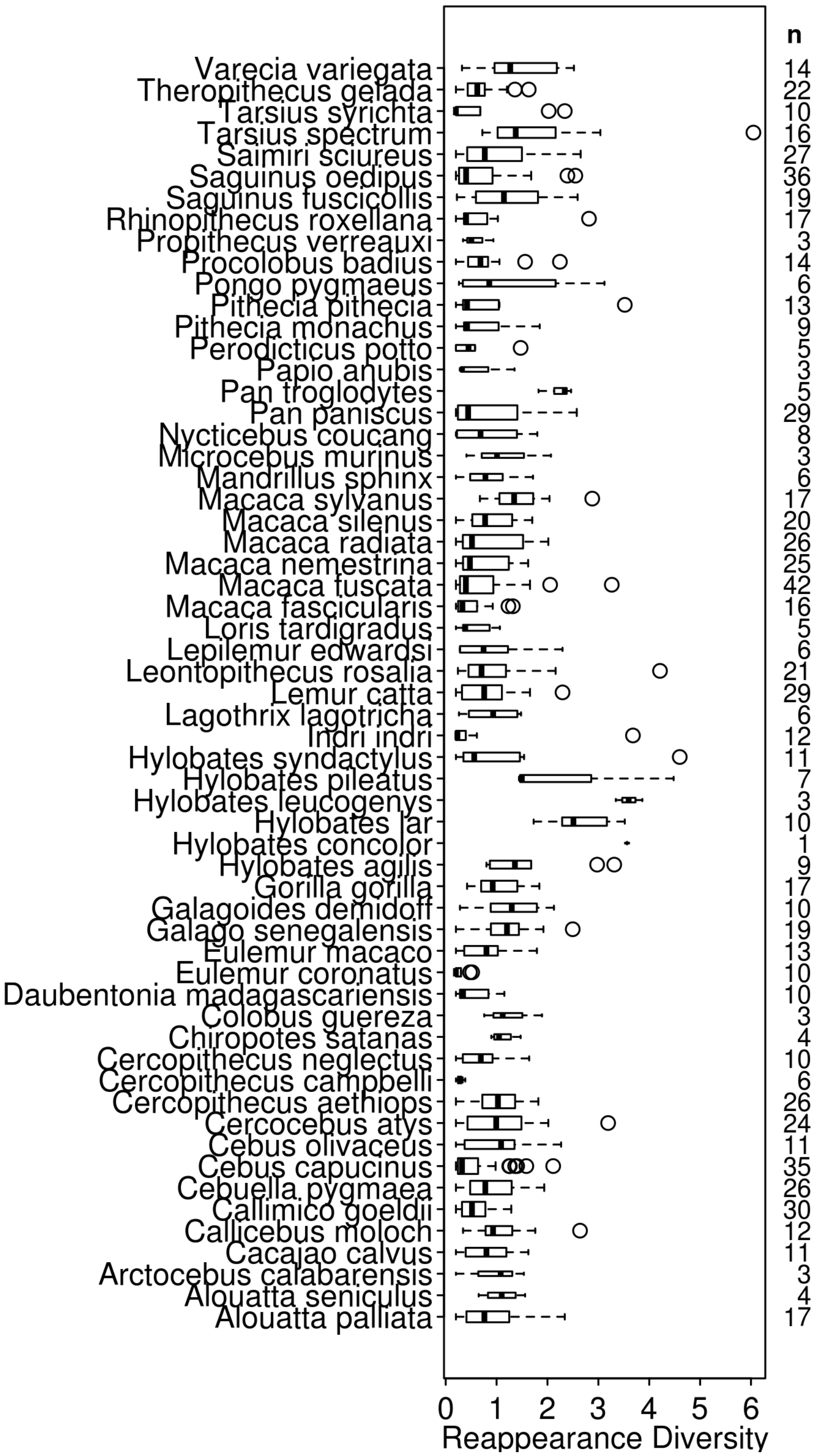


Figure 6. Species level reappearance diversity scores distributions. These box plots demonstrate how species can have a great array of calls (total count of calls in repertoire listed under "**n**" on right hand side) whose reappearance diversity scores are quite low but have a stand-out call (e.g. *Indrii*'s song) which scores exceptionally high.

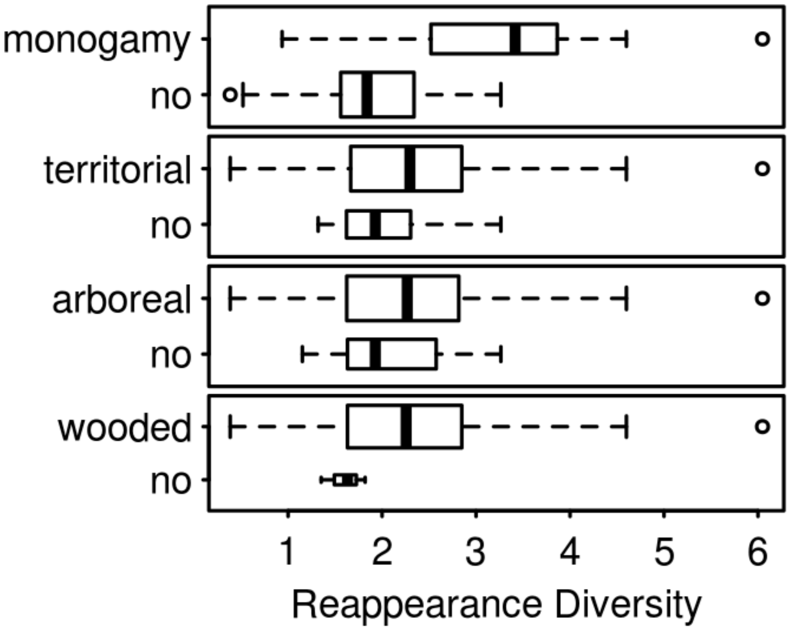


Figure 7. Acoustic reappearance diversity scores versus socioecological controls. The evolutionary emergence of musical behavior has a variety of suggested hypotheses ranging from territorial defense to an acoustic adaptation to pair-bonding. While the score disparity between wooded and non-wooded habitats lends support to the acoustic adaptation hypothesis only monogamy appears to have a strong association with acoustic reappearance diversity.

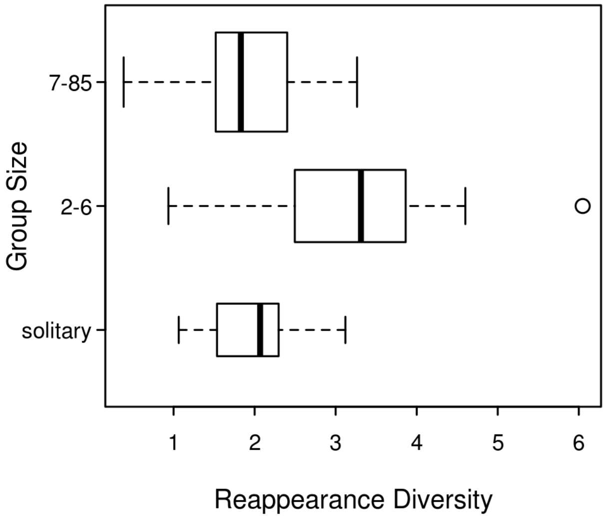


Figure 8. Box plots of reappearance diversity scores versus typical group size per species. Plotting group size categorically, higher acoustic reappearance diversity scores predominate in small group size species (e.g. monogamous, duetting primates such as gibbons, tarsiers, and callitrichids)

The first hypothesis we considered was that of acoustic adaptation (AAH). We were not able to test the fundamental-frequency based component of AAH as we had focused on tabulating more relativistic song-like parameters. The data presented here do, however, suggest mild support for the second part of the AAH regarding inter-element intervals. Species living in forest habitats had a call with 0.75 (on average) more reappearing syllables (*t*=3.77, *df*=9.74, *p*=0.004) which seems to suggest that changes in habitat acoustics could moderately effect song elaborateness (Fig. 7). Richer variable types, beyond our merely binary arboreality measure are, however, needed to explore effects of higher dimensional wooded habitats and associated behaviors.

The second hypothesis we tested concerned effects of sociality on elaborate acoustic display behavior. Our index and data-set support the prevailing view of monogamy as being an important coevolutionary factor (Fig. 7). Monogamous species had 1.2 (on average) more reappearing syllables for their most-elaborate call. We found less support for a strictly positive linear correlation with group size, but our metric does indicate that species living in small-sized groups (*n*=2 to 6) possessed more song like calls (Fig. 8). Compared with large groups or solitary species, small groups had almost 50% more reappearing syllables (on average) in their most-elaborate call (*t*=3.58, *df*=20.1, *p*=0.002). Although testing all social influences is out of the scope of the present work, our approach here suggests that smaller, more intimate groups merit further, more detailed investigation.

Conclusion

Song appears to be detectable using the combination of a simple (syllabic) diversity measure and a redundancy proxy measure—one that captures either spectral or temporal patterning. Our PCA-determined formulation corroborates a human music universals scheme (Nettl, 1983) that emphasizes repetition and variation of discrete units as foundational. Correspondingly, the definition of animal song might not need to be complicated by pitch and rhythm as feature requirements—although "acoustic reappearance diversity" could be re-construed and rarefied to capture them anyway (see Fig. 9). Furthermore, we have similarly argued that music should not be delimited by non-acoustic universals such as mode of generation or context, despite the fact that many cultures, for example, consider elaborate acoustic display as inseparable from dance.

We've argued that the boundary between music and song is not black and white. Like others before, we note that the definition of music should not be limited to discrete categories (Nettl, 2015, p. 459) of music versus non-music. Similarly, the acoustic reappearance diversity measure can be easily adapted from a form using few (often vocal) sources, in the case of song, to a more multi-component (often instrumental) form, in the case of music. Here we have developed an acoustic display index that portrays musicality as lying upon a broadly applicable continuum.

Our simplified utterance-level index shows an association with small, family-sized groups. Less simplistic, beyond utterance-level definitions of music (e.g. those including isometric rhythms, pitch-blending, and harmony), however, should prove to correspond with later co-evolutionary selection pressures such as coordinated group action (Brown 2000). Further such studies will be useful in assessing influences of ulterior events in the evolution of hominid musicality—those in the last 5 million years (Mithen, 2006). It seems, however, that large group social contexts were likely not necessary as initial drivers of ancient primate song co-evolution (see chorus opposite of song in Fig. 2). Instead, coordinated musical display of modern humans likely evolved piecemeal from an "existing substrate" (Nettl 2015). This existing substrate was likely the elaborate duet advertisements of small, group-living and socially monogamous hominoids. Their displays in turn, likely also evolved piecemeal from even simpler, more solitary display calls of ancient primates.

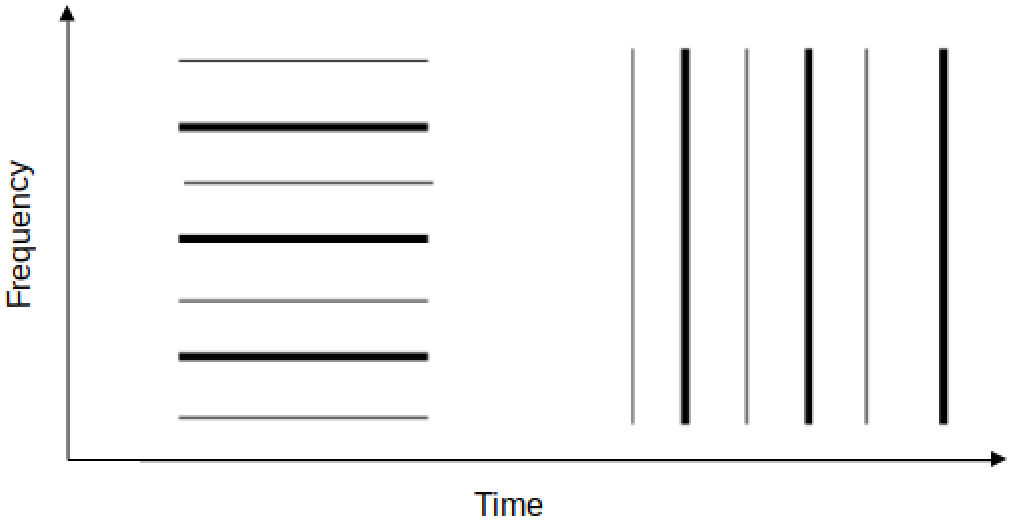


Figure 9. Acoustic reappearance diversity (in amplitude) also captures harmony and rhythm. A highly-simplified illustration of how "acoustic reappearance diversity" could be construed as a general enough construct to encapsulate aspects of both pitched and rhythmic musicality, despite the fact that it was not formulated using either. LEFT: A pitched matched harmonic sound with two different overlapping harmonic series (the higher frequency tone is bolded as it overlaps with the harmonics of the lower frequency tone one octave below it). RIGHT: A rhythmic pattern with stresses, in bold, every other beat. This illustration is only a very simple demonstration of how our index could be expanded beyond the syllable or utterance level to incorporate higher system level universals. In the example above, it is expanded to include reappearing diversity of ***amplitude*** across both frequency (left) and time (right). The reappearance diversity index could also conceivably be expanded to include much higher-order and complex attributes such as musical motif patterning or song repertoire typicality.

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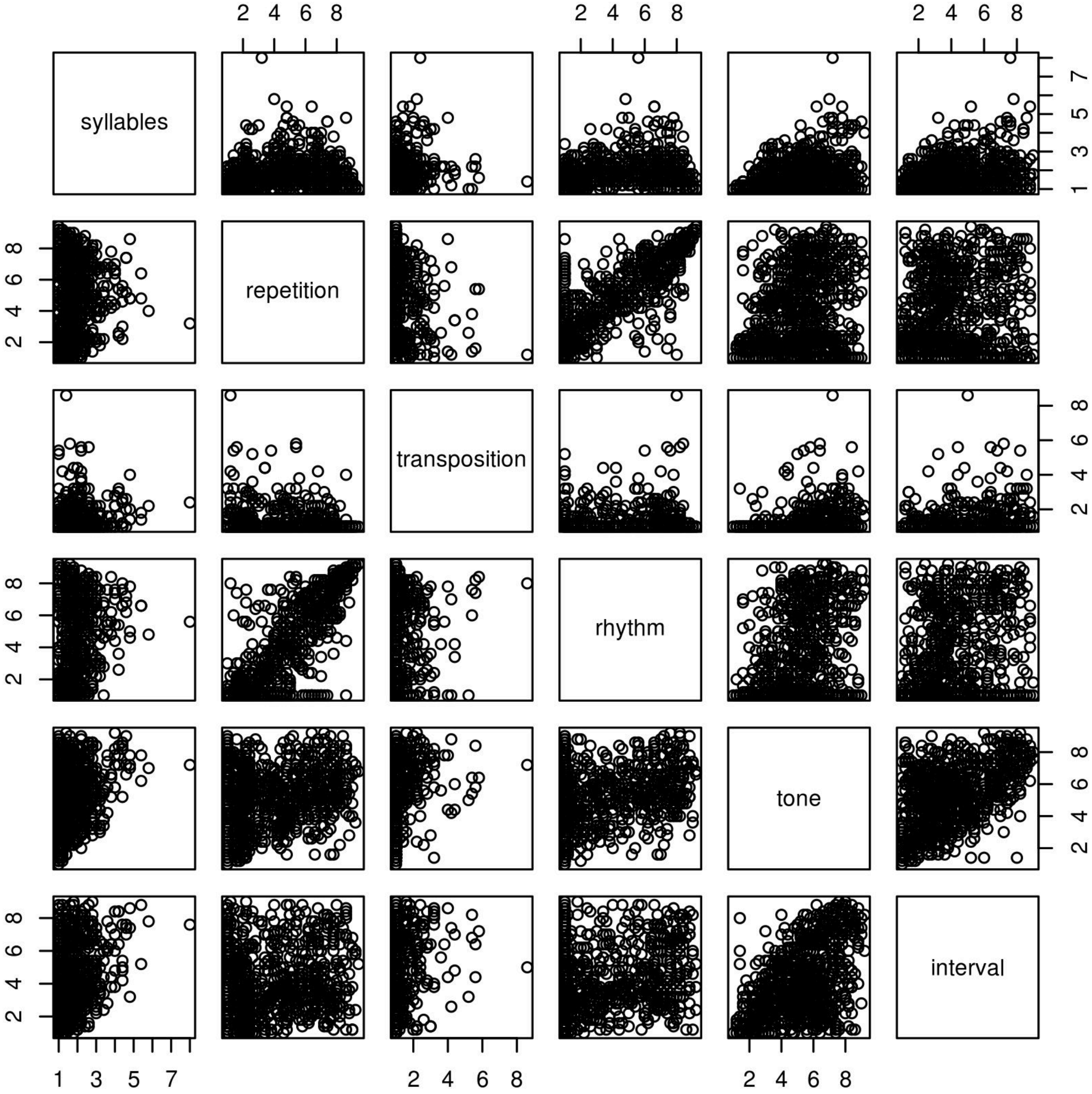
Table S1. Feature definitions used in training along side the dictionary and encyclopedia versions

	current study	**Taylor 1966**	**Randel 2003**	**M&W 2014**	**en.wikipedia.org 2014**
tone	a steady, regular, or periodic sound characterized by its pitch (or perceived frequency), intensity, duration, and timbre	**1**. a sound of musical quality and regular vibration as opposed to noise; **2**. a sound of definite pitch or quality; The investigation of vibrations, or values, tone-relationships	***tone***: **1**. a sound of definite pitch [ ] **3.** character of sound achieved in performance of an instrument**;** ***tonality***: in western music, the organized relationships of tones with reference to [a tonic],and [a scale]	the quality of sound produced By a musical instrument or singing voice: [**2**: a sound of definite pitch and vibration]	***musical*** **tone**: a steady periodic sound; characterized by its duration, pitch, intensity (or loudness) and timbre (or quality); [ ] c**omplex tones** can be described as a sum of simple tones with harmonically related frequencies
interval	the difference between two (successively sounding) tones. The ratio between two sonic frequencies	distance, or difference in pitch, between two tones;	the relationship between two pitches; the “distance” [a spatial metonymy] between and upper and lower pitch;	***music***: the difference in pitch between two notes; 2a: a space between objects, units, points or states; **2b**: difference in pitch between two tones	the difference between two pitches; [ ] ***melodic***: if it refers to successively sounding tones; [ ] **scientific**: the ratio between two sonic frequencies
rhythm	a regular recurrence or pattern in time--a movement marked By the regulated succession of strong and weak elements, or of opposite or different conditions	[ ] undulation of a progression, marked by the rise and fall of stress and duration; arrangement of accented and unaccented and of long and short sounds; usually follows some pattern	the pattern of movement in Time; governs all aspects of musical movement as ordered In time (as opposed to aspects of musical sound conceived as pitch and timbre)	a regular, repeated pattern of sounds or movements [or events]; **1a:** an ordered recurrent alternation of strong and weak elements in the flow of sound and silence	regular recurrence or pattern in time [a cyclical periodicity or frequency]; regulated succession of strong and weak elements or of opposite or different conditions; timing of events [ ] of musical sounds and silences
repetition	restatement [over time], such as the restatement of an utterance, phrase, or theme.	the rapid repeating of a note or chord	the restatement of a musical idea or section of a work; principal elements in the the perception of form	The act of repeating something; something that is done or said again; **1a**: the act or instance of repeating	(***music***): restatement; [lies along a spectrum from irregular to periodic sounds]; establishes motifs and hooks; serves as an identifying factor for listeners;
transposition	moving a (collection of) note(s) up or down in pitch by a constant interval	the changing of the key of a composition; transposing scales	the rewriting or performance of music at a pitch other than the original one; raising or lowering each pitch of the original music by precisely the same interval; changing of the key of the original;	***transpose***: to change position or order or to a different form, using it in a different place or situation; **music**: to write or perform in a different key;	(***music***):operation of moving notes up or down in pitch by a constant interval; shifting of a melody, a harmonic progression or an entire musical piece to another key, while maintaining the same tone structure
syllable(s)	a unit of organization for a sequence of speech sounds. Typically made up of a syllable nucleus (most often a vowel) with optional initial and final margins (typically, consonants).	**_syllabic*_**: One [exhalation of] air in which each syllable has its [own] note	**_syllabic*_**: Characterized by the singing of only one note for each syllable; applicable to any type of vocal music and one of the three principal categories of style in Gregorian chant.	any one of the parts into which A word is naturally divided when it is pronounced; **1**: a unit of spoken language that is next bigger than a speech sound and consists of one or more vowel sounds alone; **3**: the smallest conceivable expression or unit of something	a unit of organization for a sequence of speech sounds; typically made up of a syllable nucleus (a vowel) with optional initial and final margins (consonants); considered the phonological building blocs of words.

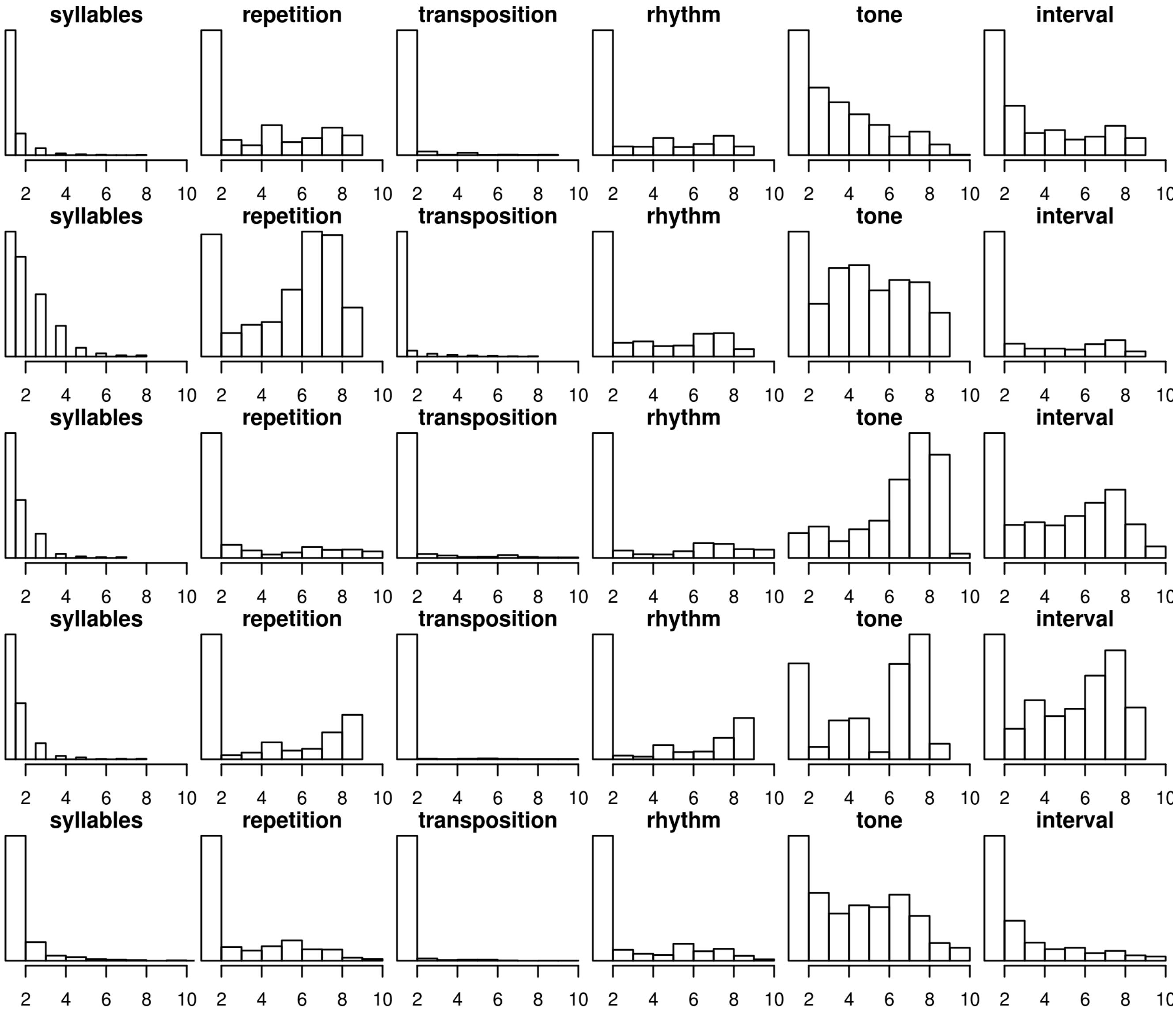
***** while “syllabic” was the closest word to “syllable” that we could find in these music focused texts, in contrast, our definition allows for within unit frequency changes

Table S2. Vocalization study variables along with spectrographic figure information and ARDI scores for top scoring vocalizations.

Author	Year	Family	Genus	Species	Individuals	Sexes	Ages	Setting	Vocalizations	Spectrograms	Figures	Name	ARDI
Baldwin	1976	Atelidae	Alouatta	palliata	155?	both	all	wild	17	29	2p1,2p2,2p3	Heh	2.34
Ybarra	1986	Atelidae	Alouatta	seniculus	15	male	adult	wild	4	9	4	Aouuo	1.56
Casamitjana	2002	Atelidae	Lagothrix	lagotricha	26	both	all	captive	6	15	1a,1b,1c	Screams	1.48
Masataka	1982	Callitrichidae	Callimico	goeldii	9	both	all	captured	30	40	4G4	Agonistic.Calls	1.29
Pola	1975	Callitrichidae	Cebuella	pygmaea	13	both	all	captive	26	30	5,6,7	J.Call	1.94
MacLanahan	1977	Callitrichidae	Leontopithecus	rosalia	13	both	all	zoo	21	23	7	Long.Call.Duet	4.21
Moody	1976	Callitrichidae	Saguinus	fuscicollis	9	both	all	captive	19	25	1b2	Long.Call	2.59
Cleveland	1982	Callitrichidae	Saguinus	oedipus	11	both	all	captive	36	36	3A	Twitter	2.55
Robinson	1979	Cebidae	Callicebus	moloch	0	both	all	wild	12	17	2f	Chirrup.Panting.Pumping	2.64
Gros-Louis	2008	Cebidae	Cebus	capucinus	17	both	all	wild	35	35	3d	Loud.Trill	2.11
Robinson	1984	Cebidae	Cebus	olivaceus	3	both	all	wild	11	14	2Vb	U.Trills	2.27
Newman	1985	Cebidae	Saimiri	sciureus	17	both	all	wild	27	39	5b	Purr	2.65
Range	2004	Cercopithecidae	Cercocebus	atys	31	both	adult	wild	24	27	6	Copulation.Call	3.19
Struhsaker	1967	Cercopithecidae	Cercopithecus	aethiops	4	both	all	wild	26	34	16.3c	Woof.Woof	1.82
Ouattara	2009	Cercopithecidae	Cercopithecus	campbelli	3	male	adult	wild	6	6	1.e	Krak.Oo	0.38
Bouchet	2012	Cercopithecidae	Cercopithecus	neglectus	23	both	all	captive	10	24	1.9.ma	Boom+.Khaf+	1.64
Schel	2012	Cercopithecidae	Colobus	guereza	12	male	adult	wild	3	3	1.a	Leopard.Roars	1.89
Palombit	1992	Cercopithecidae	Macaca	fascicularis	17	both	adult	wild	16	17	1C	Alarm.1	1.32
Green	1975	Cercopithecidae	Macaca	fuscata	0	both	all	wild	42	42	9c	Geckered.Screech	3.26
Grimm	1967	Cercopithecidae	Macaca	nemestrina	35	both	all	captive	25	32	III1b	Vibrato.Growl	1.62
Hohmann	1989	Cercopithecidae	Macaca	radiata	120	both	all	sanctuary	26	45	3f	Copulation.Call	2.02
Hohmann	1985	Cercopithecidae	Macaca	silenus	0	both	all	sanctuary	20	29	12A	Twit	1.70
Fischer	2002	Cercopithecidae	Macaca	sylvanus	92	both	adult	wild	17	17	2a	Modulated.Tonal.Screams	2.88
Kudo	1987	Cercopithecidae	Mandrillus	sphinx	300+	both	all	wild	6	6	1b	Crowing	1.72
Ey	2008	Cercopithecidae	Papio	anubis	~45	both	all	wild	3	9	1.2c,1c	Loud.Call.Bout	1.35
Struhsaker	1975	Cercopithecidae	Procolobus	badius	30+	both	all	wild	14	48	17A,17F,17M,17N,17V,17Z	Copulation.Quavers	2.24
Tenaza	1988	Cercopithecidae	Rhinopithecus	roxellana	8	both	adult	zoo	17	17	2N	Grunts	2.82
Aich	1990	Cercopithecidae	Theropithecus	gelada	29	both	noinfants	zoo	22	26	II.9		1.63
Cherry	1987	Cheirogaleidae	Microcebus	murinus	51	both	all	captive	3	3	1b	Twitter	2.07
Stanger	1994	Daubentoniidae	Daubentonia	madagascariensis	4	both	all	captured	10	35	1c	Whimpers	1.15
Zimmermann	1985	Galagidae	Galago	senegalensis	26	both	all	captive	19	22	3a	Low.Excitement.Call	2.50
Charles-Dominique	1977	Galagidae	Galagoides	demidoff	28	both	all	wild	10	12	68D	Gathering.Call	2.13
Harcourt	1993	Hominidae	Gorilla	gorilla	25	both	all	wild	17	44	2m1,2m2	Whimpers	1.84
Bermejo	1999	Hominidae	Pan	paniscus	68	both	all	wild	29	57	19	Hooting	2.58
Crockford	2005	Hominidae	Pan	troglodytes	16	both	adult	wild	5	8	1e,1f	Pant.Hoot.Drum	2.46
Mackinnon	1974	Hominidae	Pongo	pygmaeus	346	both	all	wild	6	12	32,33	Long.Call	3.12
Gittins	1984	Hylobatidae	Hylobates	agilis	30+	both	all	wild	9	24	30.3a – 30.3l	Great.Calls	3.31
Geissmann	2000	Hylobatidae	Hylobates	concolor	NA	both	noinfants	zoos	2	5	7b	Great.Call.Duet	3.56
Raemaekers	1984	Hylobatidae	Hylobates	lar	NA	both	all	wild	10	30	15a,15b,15c,15d	Quaver.Interlude	3.52
Geissmann	2000	Hylobatidae	Hylobates	leucogenys	NA	both	noinfants	zoos	3	5	5b	Male.Short.Phrases	3.86
Clarke	2006	Hylobatidae	Hylobates	pileatus	51	both	all	wild	7	7	2	Great.Call.Duet	4.48
Geissmann	2000	Hylobatidae	Hylobates	syndactylus	6	both	adult	zoos	11	26	5.1,5.2,5.3,5.4,5.5,5.6	Great.Call.Sequence	4.60
Maretti	2010	Indriidae	Indri	indri	28	both	all	wild	12	24	1j	Song	3.68
Fichtel	2011	Indriidae	Propithecus	verreauxi	10	both	adult	captive	3	3	1.b.2	Roaring.Bark	0.94
Gamba	2007	Lemuridae	Eulemur	coronatus	37	both	all	zoos	10	10	3k	Scream	0.52
Gosset	2003	Lemuridae	Eulemur	macaco	8	both	noinfants	captive	13	13	3	Clucking	1.79
Macedonia	1993	Lemuridae	Lemur	catta	27.5	both	adult	captive	29	62	4m1	Clicks	2.30
Pereira	1988	Lemuridae	Varecia	variegata	7	both	all	captive	14	17	6b	Pulsed.Squawk.Wail	2.52
Mendez-Cardenas	2009	Lepilemuridae	Lepilemur	edwardsi	21	both	adult	wild	6	11	3.6,4.1c	Duet	2.30
Charles-Dominique	1977	Lorisidae	Arctocebus	calabarensis	0	both	all	wild	3	8	72B,72C,72D,72E	Two.Phase.Groan	1.54
Schulze	1995	Lorisidae	Loris	tardigradus	79	both	adult	captive	5	5	5c	Chitter	1.06
Zimmermann	1985	Lorisidae	Nycticebus	coucang	9	both	all	captive	8	22	2h	Grunts	1.80
Charles-Dominique	1977	Lorisidae	Perodicticus	potto	9	both	all	wild	5	10	72B,72C,72D,72E	Two.Phase.Groan	1.47
Fontaine	1981	Pitheciidae	Cacajao	calvus	11	both	all	zoo	11	17	6N	Purr	1.62
Fernandes	1991	Pitheciidae	Chiropotes	satanas	17	both	all	captive	4	4	4D	Infant.Call	1.47
Buchanan	1978	Pitheciidae	Pithecia	monachus	22	both	noinfants	captive	9	22	17c,17d	Hee.Hee	1.85
Buchanan	1978	Pitheciidae	Pithecia	pithecia	25	both	all	captive	12	47	12l	Soft.Growl	3.52
Nietsch	2003	Tarsiidae	Tarsius	spectrum	22	both	noinfants	both	16	18	9.2a	Duet.Song	6.05
Rehakova-Petru	2012	Tarsiidae	Tarsius	syrichta	25	both	all	wild	10	10	2e	Trill	2.34



Supplemental Figure 1. Pairs of feature scores plotted against other feature scores as pairs. Ethnomusicologically universal acoustic music factor scores on 829 different primate calls are plotted in pairs of one factor against another. *Repetition* and *transposition* have strong associations with each other as do *tone* and *interval*.



Supplemental Figure 2. Histograms of feature scores by different scorers.
Acoustic feature scores from 829 primate species are plotted as histograms where each row above is a different scorer and each column is a different feature. Although feature scores for *transposition* and *syllable* and *rhythm* were not terribly inconsistent, the other three suffered from a lack of uniformity especially in the middle of the distribution.

Chapter 3 - Precision limb landing locomotion and the origins of primate morphological traits

Abstract

Arboreal living is thought to have driven the evolution of vision improvements associated with the origins of the primate order from the late Cretaceous up through the Eocene. We explore the possibility that rapid, high-risk, arboreal grasp-landed locomotion could be both an initial and continued force in *euprimate* cranio-visual evolution. Quantitative observations of locomotor behavior on 130 extant primate species was used to both reconstruct locomotor activity budgets of ancestral primates as well as to better understand the evolution of a most salient feature of the euprimate cranium, anteriorly convergent ocular apertures. The phylogenetic mean of locomotor mode frequencies was used to estimate ancient locomotor patterns. Fractional estimates of two rapid and high-risk locomotor mode spectrum behaviors were “leaping” at nearly one-third (for basal euprimates) and “swinging” at one-fourth (for basal hominoids). Although swinging and diet were less significant, phylogenetically controlled regressions highlight leaping ahead of color vision, group size, and activity period as significantly associated factors possibly driving the evolution of orbital convergence [OC]. Thus, OC appears to serve a multiplicity of purposes, as evidenced by the result that OC was simultaneously positively correlated with the conflicting traits of nocturnality and color vision. It is possible that the many plausible, competing influences on anterior OC were separately realized because of a relaxed requirement for lateral facing orbits—perhaps due to overall predation reduction. Less speculatively, these results support a gradual and sequential evolutionary accretion of the key defining morphological traits of the primate order (grasping, leaping legs, and OC) as driven by temporally disparate ecological shifts.

Introduction

Primates are typified by long hindlegs and clawless grasping appendages as well as cranial morphology related to both omnivorous diet and binocular focus on the frontal visual field at the expense of both the olfactory apparatus (Cartmill, 2002; Fleagle, 1999; Jolly, 1985) and input from the rear visual field. While our knowledge of early primates is biased by harder fossils such as teeth and skulls, these cranial visual changes toward large eyes, post-orbital bar, and convergent orbits are often cited as the most distinguishing and conspicuous in primates (Ross and Martin, 2007; Silcox and López-Torres, 2017). There are many ecological scenarios that could have brought about these distinct changes: terminal branch feeding (Sussman, 1991), active fine-branch locomotion (Martin 1979), arboreality (Jones, 1916; Smith, 1924), hand emancipation (Jones 1916), distance judgment (Clark, 1959), snake detection (Isbell, 2006), visual predation (Cartmill, 1972), nocturnal leaping (Crompton, 1995), and grasp-leap locomotion (Szalay and Dagosto, 1988). The last three theories focusing on advantages of reaching and grasping in euprimate and anthropoid origins serve as our primary theoretical foundation for exploration and testing.

It is important to distinguish theories on the origins of *primates,* or how stem primates originally diverged from mammals, from theories on the origins of *euprimates* (or primates of modern aspect) (Silcox and López-Torres, 2017). Primate origins theories primarily use fossil evidence to piece together how primates evolved from mammals. Euprimate origins theories explore how the common ancestor of all living primates (i.e. crown clade) evolved from the common ancestor of these extinct fossil primate lineages (i.e. stem groups). As our dataset is comprised of extant primates, we focus here primarily on the latter of these. All primate origins theories, however, are considered in order to better reconstruct a broad contextual chronology. Also important to note is that several of these hypothetical influences could have together shaped primates (e.g. into euprimates) via a gradual, “serial accretion” of the components in their mosaic suite of hallmark traits (Cartmill, 2012; Silcox et al., 2007). A compelling theory should, ideally, explain most, if not all, of these unique arboreal specializations of early euprimates (Szalay and Dagosto, 1988).

One of the most compelling of these, the grasp-leap locomotion theory, posits that lemuriform-like “rapid successive leaping and landing with a habitual grasp” best explains the “protoeuprimate form-function complex” (Szalay and Dagosto, 1988). While grasp-leap theory is highly explanatory of initial primate evolution, it only considers skeletal evidence of leaping as an influence on visual improvements as compared with Plesiadapiform stem-primates (Szalay and Dagosto, 1988). Grasp-leap theory, for example, does not address any continued evolution in anthropoids. There are many other ways in which OC, which enables stereoscopic vision and visual acuity upon the center of the visual field, could have been adaptive beyond leaping. An exceptional level of hand-eye coordination, for example, is argued to be the “fundamental adaptation” of primates (Ross and Martin, 2007).

Uncertainty in grasp placement comprises another highly compelling problem relevant to the evolution of plesiadapiform-like stem primates into euprimates. OC is theorized to help improve foraging, climbing, and leaping along and between terminal branches in alleviation of the constant visual demands of arboreal locomotion (Crompton, 1995). This visual complexity deciphering based theory, whose stereoscopic solution has been described as “camouflage breaking” (Isbell, 2006) or “camouflage countering” (Heesy, 2008), emphasizes the visual confusion, or crypsis, when tasked with distinguishing a diverse array of possible targets in the fine-branch niche (Crompton, 1995). While ambitious in scope, Crompton’s theory, like many others discussed here, focuses mainly on early Paleocene stem primates, and may be less applicable for later OC changes in the crown group that makes up euprimates.

One of the other more recently well-developed explanations, the visual predation hypothesis (Cartmill, 1972), presents an alternative to these more substrate-based theories: that OC evolved to enhance primate predation on insects in the terminal branch milieu (Cartmill, 1972). Visual predation [VP] is thought to have selected for orbital aperture convergence upon the mid-sagittal plane (defined by Cartmill 1970), enabling stereoscopic vision and visual acuity in the center of the visual field. The theory is inspired by observations that there are many non-primates that climb sans grasping and the observation that predators usually have convergent orbits (Ross and Martin, 2007; Silcox and López-Torres, 2017). Furthermore, high OC can act, paradoxically, to *reduce* depth perception due to reduced parallax, as the eyes are too close together for stereoscopic vision to be useful, and, in most primates, this range doesn't exceed more than a meter in target distance (Cartmill, 2012). Thus, any compelling explanation of OC should explore selection pressures for focus on close-range targets.

Anthropoid origins is another contested area where theories have tended to extrapolate upon primate origins theories, for example, invoking a "reduction of orthogenetic evolutionary trends pervading the Primate order" (Clark, 1959). OC is so pronounced in anthropoids, that it has been described as a "complete" forward rotation (Clark, 1959). Modern theories on possible selection pressures on these extreme degrees of OC include venomous snakes (Isbell, 2006) or as a side effect of reduction in relative orbit diameter resulting from a shift to diurnality (Cartmill, 1970). This compelling OC as side-effect null hypothesis is thought to occur because increasing body (and skull) size has a negative allometry with orbit size (Cartmill, 2002; Ross, 1995). After controlling for this allometric effect, lorises, tarsiers, and anthropoids have the largest OC (Kay et al., 1997) which runs somewhat counter to most leaping based theories. Anthropoids are thought to leap less, not more, than their predecessors (Kay et al., 1997), and lorises tend not to leap at all. Beyond this default understanding, no adaptive explanation has been satisfactorily proposed or supported for OC in anthropoids. It is possible that continued reduction in posterior threats (Schruth, 2015) —perhaps due to predation-deterring increases in body and group size—could provide such an adaptive explanation.

As an extension and combination of the three modern grasp-locomotion theories on primate origins discussed above, we argue that rapid, inter-substrate locomotion in-general, both hind-limb aerial *and* suspensory forms, could have influenced the evolution of many hallmark primate characteristics. Specifically, we entertain the notion that leaping behavior initiated a co-evolution with many other skeletal changes observed in early *euprimates* and further hypothesize that swinging continued this selection pressure on cranial changes in *Hominoidea*. More frontally focused vision may have enabled close-range acuity for adjusting *position of a grasp* to ensure safe limb-landing during rapid and precarious arboreal locomotor bouts. Put another way, primates evolved long hindlimbs to rapidly *leap* from source supports—then subsequently needed to evolve convergent orbits (and associated vision improvements) to help them *land* these leaps on uncertain destination substrate. A logical extension of this two-fold hypothesis is that brachiation could have continued to drive further vision changes, more recently, in the early evolution of hominoids. These two precision landed-grasp forms of locomotion could have both been selected against by gravitationally exigent forces of natural selection via lethal falls. We have thus encapsulated them as a unified concept as gravitationally time-sensitive “precision limb landing” locomotion.

There are several easily testable predictions derived from this precision limb landing hypothesis. First, early primates should have used their distinctly elongated femoral and tarsal bones for frequent leaping, as these lever arms are suggestive of facilitating long leaps (Martin, 1979). Second, basal hominoids should have used their long arms and increased OC for frequent swinging and accurate hand-eye coordination—if we can assume this form of locomotion also had some degree of positional uncertainty in substrate targets. Third, there should be an association between frequencies of locomotion involving precision limb placement and stereoscopic vision enabling OC—due to alleviation of high-impact grasp-landing. Lastly, other influences (e.g. fruit and arboreality) should have less significant influences than our locomotion-based predictors.

We collected original data from the primary literature on primate positional behavior and collapsed many of the more specific positional modes into two primary forms of precision limb landed locomotion: leaping and swinging. This consolidation provides a convenient short-hand for both discussion and analysis. For example, many statistical and visualization tools often require univariate inputs, specifically when performing an independent contrasts analysis. We used these data from extant primates to estimate ancestral leaping and swinging frequencies for the Primate order and the hominoid super-family, respectively. A regression that controls for shared ancestry, allometry, and various socio-ecological variables, is used to elucidate the co-evolutionary association between locomotor form and OC. These results lend the most support to the two grasping—and especially the two leaping—based theories of primate origins. The precision limb-landing theory is strongly supported for leaping, but only very weakly supported for swinging.

Materials and Methods

Locomotion

We collected quantitative data from the primary literature on primate positional behavior with an emphasis, specifically, on quantitative estimates of leaping. The online searches used ISI Web of Knowledge and Google scholar, initially using broad search terms such as “locomot* position* primate*.” Additional, more specific, searches were subsequently made for genera that were not found in the initial search.

The resulting data came from 75 journals articles, 8 meeting abstracts, 9 books chapters, and 7 theses or dissertations published before 2015. While we strove for completeness, this online search technique likely over-represents newer studies over older published data. Preference was also given to complete repertoire, catalog-style studies over those that focused on ontogeny or experimental manipulation. The primary exclusion criterion from the current project, however, was simply a lack of a quantitative estimate for leaping.

The many reported locomotor modes were parsed into fewer, broader locomotion categories. Although as many locomotor modes as possible were collected and recorded, only 16 categories resembling leaping and swinging were factored into subsequent analyses considered here. As a result, effects of other continuous-contact modes of locomotion (e.g. bipedal, quadrupedal, and climb) were not highlighted here. Estimates for the same species over multiple studies (or observation sites) were averaged, resulting in estimates for 130 total unique species (representing 54 genera).

Most studies quantified the number of discrete movements, or “bouts,” of recorded locomotor movements within each species’ repertoire. In these cases, we simply divided the number of observed bouts for each type of locomotion by the total number of bouts (across all types) to obtain percentages for the species. In other cases, only the percentage was reported and thus was used as reported. For some species whose daily motion may not have inspired quantitative study so that no observation counts or estimates were available, a proxy description (e.g. “strictly terrestrial”) could be used to justify using a zero percent value for leaping and swinging.

We amassed percentages for each species. For example, leaping percentages ranged from 0% for *Gorilla gorilla* to 81% for *Indri indri*. The distributions of locomotor frequencies were then further aggregated into the following two main behavioral-spectrum categories for subsequent analysis. The first category is *swing* and includes *brachiate, semi-brachiate, arm-swing, tension, suspensory,* and *torso-orthograde.* The second is *leap* which includes *leap, vertical cling leap, bound leap, jump, drop, leap/drop, and airborne* (Fig. 1). If a study split locomotor bouts across different field sites or classified them functionally (e.g. travel vs. foraging), we weighed the locomotion percentages by bout counts and then averaged them. The tables of locomotion percentages and source study information are archived online[1].

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[1] ProQuest Dissertations & Theses https://www.proquest.com/products-services/dissertations/

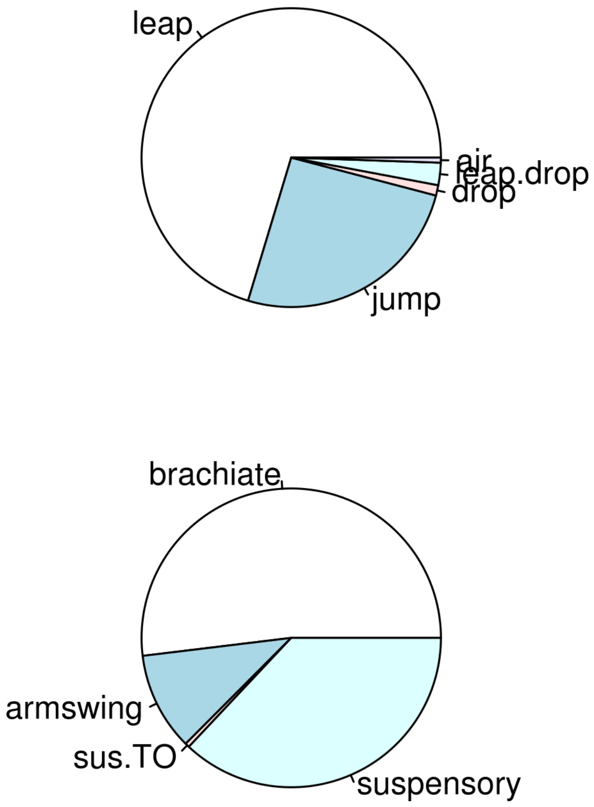

Figure 1. **Locomotion categories – leap and swing locomotion sub-composition** Leaping (top), as it is used in this paper, is actually composed of several other (less common) possible forms of locomotion: jump, drop, leap/drop, and "air". Swinging (bottom) is similarly composed of brachiation, suspensory, armswing, and suspensory (torso-orthograde).

Orbital Convergence

Orbital aperture convergence is perhaps the most visually salient and taxonomically distinguishing morphological feature of primates relating to their origins and evolution. We collected these values as measured by two primary studies (Heesy, 2003; Ross, 1995). Measures of orbit orientation were collected by Ross (1995) on 88 species using a dihedral goniometer (Cartmill, 1970) and by Heesy (2003) on 93 species using a MicroScribe 3DX coordinate data stylus. Though different tools were used, the measurements of OC had a strong correlation (|Spearman's rho|= 0.966, $p < 0.001$, $n = 41$) (Heesy, 2003). In both studies, the measurements were taken on primate crania on loan from various museums in the United States. The values used in subsequent analyses were obtained by averaging together the OC values from these two studies. Case-wise deletion effects were inevitable after including control variables. These missing control variable values resulted in dropping many species from analysis, resulting in 46 species included in the final regression model.

Control Variables

We also collected variables on trichromatic vision, activity pattern, and environmental variables (including rain, temperature, latitude, and region) from a prior study (Wheeler et al., 2011). Many of these (e.g. rain and temperature) serve as proxy indicators of the prevalence of snakes (Wheeler et al., 2011). We additionally included other control variables such as physiology (claws, prehensile tail), diet (fruit, insects), behavior (nocturnality, daily path length) and group size (Lehmann et al., 2007; Rowe and Meyers, 2017; Wheeler et al., 2011).

Statistical Methods

Estimation of ancestral locomotion: We calculated leap and swing percentages on extant primates in order to estimate ancestral bout frequencies. This was accomplished by performing a branch length weighted (or “phylogenetic”) mean calculation following published methods (Paradis et al., 2004). Although the main focus was in estimating the root phylogenetic mean, we also interpolated the internal node values as inferred from a residual log-likelihood equation using an algorithm known as Restricted Maximum Likelihood [REML] with kappa = 0.52, for visualization purposes (Fig. 2). We used a RAxML phylogram based on a 61199 bp concatenation of 69 nuclear and ten mitochondrial genes (Springer et al., 2012) for branch lengths in our phylogenetic mean calculation and figures.

Phylogenetic regression analysis: We used phylogenetic regression to assess the evolutionary association of leaping with vision changes in the primate cranium (specifically orbital convergence). Generally speaking, this method provides for tests of associations between evolved traits in extant species in a phylogenetic tree while controlling for their shared lineage. The specific method is phylogenetic generalized least squares (PGLS). In PGLS, the parameters of the evolutionary model—lambda, delta, and kappa—are typically co-estimated with the regression parameters.

Variables included in the final regression analysis (Table 1) were determined by searching combinations of variables for optimal values of R^2 (the coefficient of determination) and AIC (a relative measure of goodness of fit). Phylogenetic regression analysis of this dataset co-estimated the following parameter values: lambda=0.7, delta= 3.0, and kappa =2.7 (Orme et al., 2012) for use in reconstructing the internal node values. We used the same nuclear and mitochondrial phylogram as mentioned above (Springer et al., 2012) in order to control for non-independence due to shared lineage (Felsenstein, 1973). Analysis of variance (ANOVA) was performed to assess the contribution of each of these variables in explaining the variance of the overall model.

Results

The breakdown of leaping-spectrum behavior (including jumps and drops) and suspensory swinging spectrum behavior (including brachiation and other suspensory locomotion) were largely represented by their namesake (Fig. 1) so that our shorthand labels of these two categories were fairly representative of the original author-determined descriptions. The analysis[2] resulted in an estimate of 31% leaping-spectrum behavior for ancestral euprimates (Fig. 2a). Swinging-spectrum behavior was 26% for ancestral hominoidea (Fig. 2b). We previously reported estimates for ancestral leaping that were 21% higher using a smaller subset of this dataset (Schruth, 2014). The smaller estimate for the current study is also due to the inclusion of a non-leaping, outgroup species, *Tupaia minor*, in the phylogenetic consensus tree.

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[2] System=*R*; package=*ape*; version=3.0.5; function=*ace*; method=*REML*; model=*BM*

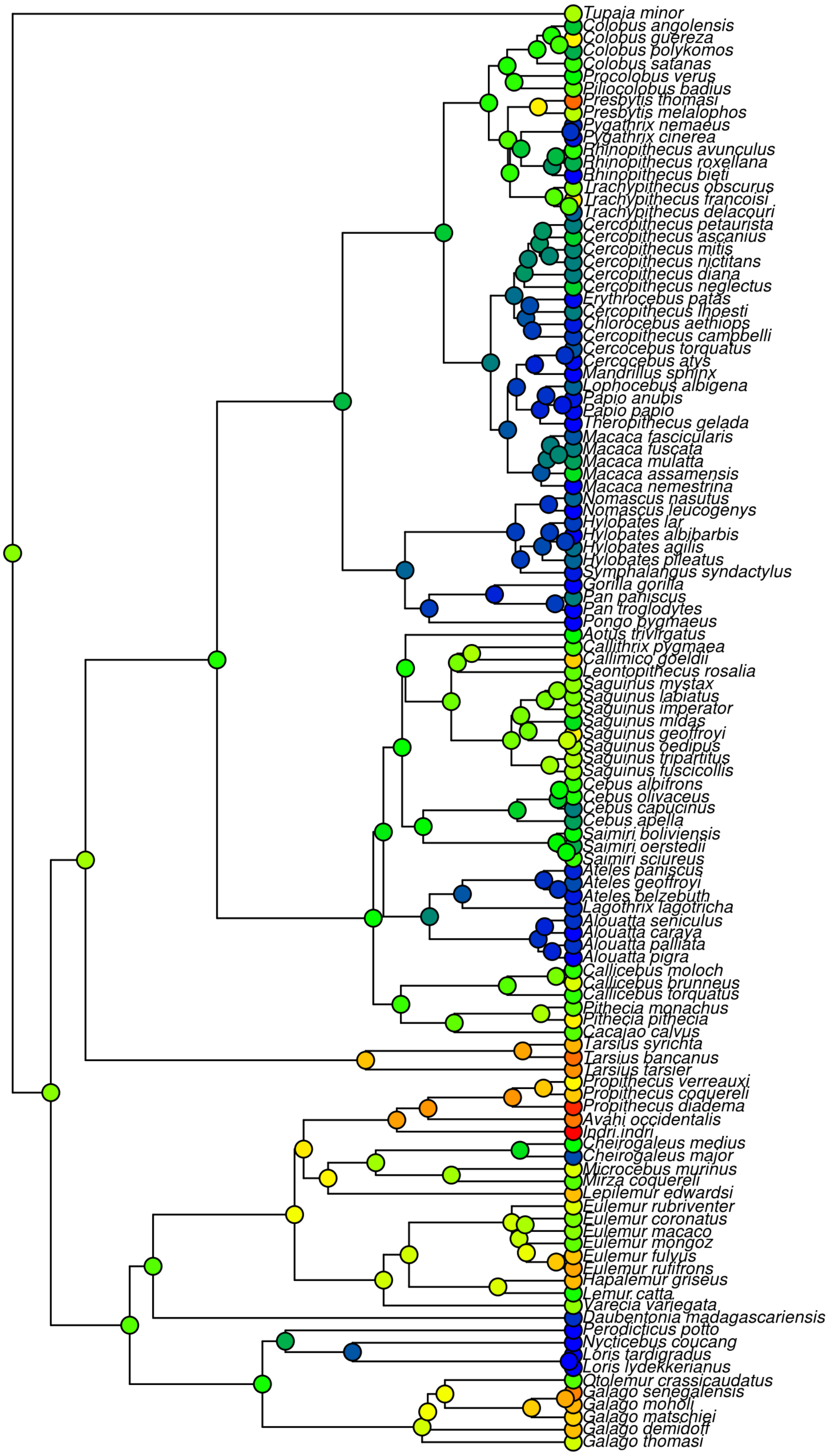

Figure 2a. Ancestral character estimation tree^2 of the Primate order Colors range between blue (no leaping), to green (some leaping), to yellow (moderate leaping), to orange (predominantly leaping), to red (mostly leaping). It is likely that Lorises, blue clade at the bottom, lost or substantially reduced their levels of leaping from a more frequent leaping ancestor.

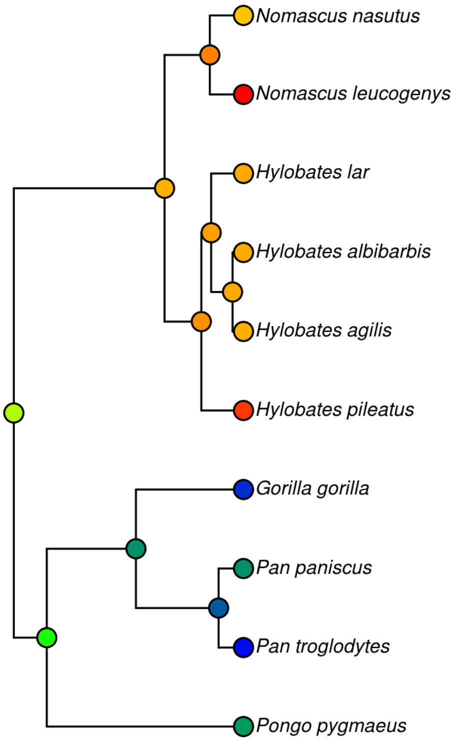

Figure. 2b. **Ancestral Character Estimation[2] tree of swinging percentages for the Hominoidea superfamily**
Colors range from blue (nearly zero swinging) to green some swinging (10-20%) to orange mostly swinging (>40%) and red (nearly all swinging). The ancestral ape was likely somewhere above modern day orangutans in the middle–around 40% torso-orthograde suspensory locomotion.

The PGLS regression[3] (df= 38, R^2 = 0.58) found locomotion and vision related variables to be significant predictors of orbital convergence (Tables 1 and 2) after controlling for physiology such as body mass (Fig S1). Controls such as nocturnality (+3.3 deg) and body weight (+0.16 per Kg) had strong positive associations with OC ($p < 0.05$). Trichromatic vision (+14 degrees), and group size (+0.25 deg. per indiv.) had even more significant positive relationships with OC ($p < 0.01$). Also, while leaping (+0.11 deg. per %) had the most significant positive association with OC ($p < 0.001$), swinging (+.06 deg. per %) and frugivory (+7 deg.) had weak, albeit positive, associations ($p > 0.2$). Daily path length traveled (-1.9 deg. per km) was the only strongly negatively associated ($p < 0.05$) variable.

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[3] system=*R*; package=*caper*; version=0.5; function=*pgls*; method=*lambda,kappa,delta='ML'*

Table 1. **Parameter estimates for predictors phylogenetically regressed on orbital convergence**

Variable	Estimate	Std. Err.	*t*-value	Pr(>|*t*|)	
mass (Kg)	0.16	0.07	2.32	0.0255	*
trichromatic vision?	14.29	5.04	2.84	0.0073	**
daily path length (Km)	-1.87	0.86	-2.17	0.0362	*
frugivorous diet?	7.08	5.22	1.36	0.1832	
group size	0.25	0.08	2.93	0.0057	**
nocturnal?	3.27	1.55	2.11	0.0416	*
swinging %	5.99	10.84	0.55	0.5838	
leaping %	10.59	2.92	3.63	0.0008	***

Table 2. **Analysis of Variance for predictors phylogenetically regressed on orbital convergence**

Variable	Df	Sum Sq	Mean Sq	*F*-value	Pr(>*F*)	
mass, Kg	1	3.96E+11	3.96E+11	12.51	0.0011	**
CVt	1	1.24E+11	1.24E+11	3.90	0.0555	.
fruit	1	5.64E+10	5.64E+10	1.78	0.1899	
DPL, km	1	5.64E+11	5.64E+11	17.81	0.0001	***
group size	1	5.24E+10	5.24E+10	1.65	0.2061	
nocturnal	1	1.14E+09	1.14E+09	0.04	0.8506	
swing, %	1	5.37E+10	5.37E+10	1.70	0.2006	
leap, %	1	4.16E+11	4.16E+11	13.15	0.0008	***
Residuals	38	1.20E+12	3.17E+10			

These results are largely consistent with previous results (Wheeler et al., 2011) that found body mass and daily path length to be the most significant variables associated with OC (see Table 2). In contrast to our finding of nocturnal and large group species having higher OC, however, their analysis found a weak positive correlation with diurnality in the Ross dataset (Wheeler et al., 2011) and did not find any significant effect of group size in either. This discrepancy in findings regarding activity period could be due to our controlling for frugivory which could mask the effects of diurnality.

While the *arboreal* and *wooded* indicators combined explained less than 5% of the variation in OC, the two quantitative measures of locomotor frequencies together explained nearly a quarter of it. This higher coefficient of determination suggests that leaping-spectrum locomotion could serve well as a proxy or mediating variable for a more general arboreal selection pressure—better, for example, than our binary *arboreal* complexity measure we have relied on previously (see Chapter 2).

Discussion

Primates’ claw-less grasping hands, long hind legs, convergent orbits, and enlarged brains echo a neuroanatomy specialized for sense of vision over smell (Cartmill, 2002; Silcox et al., 2007). These arboreal specializations seem to have evolved, ultimately, as a result of helping them avoid, rather than engage in head-on encounters with, predators (Crompton, 1995; Isbell, 2005). However, it is unclear when these morphological changes happened evolutionarily in the sequence of other possible ecologically driven evolutionary shifts of the late Cretaceous and early Cenozoic. Also unclear is the relative contribution of individual ecological forces, posited by various origins theories, on the euprimate morphotype. A compelling explanation should be “multifactorial”—minimally addressing a combination of vision, diet, and locomotion through a fine branch habitat (Crompton, 1995).

This study endeavored to test several interrelated core influences on the origins and evolution of the hallmark traits of extant primates, such as orbital convergence, to determine the relative influence of each and to what extent, if any, leaping played. Key influences on vision changes include diet, social, and habitat factors. Diet and foraging related factors include terminal branch florivory and insectivory. Social factors range from forest communication strategies to selection for group member recognition. Habitat manifests as an evolutionary influence by enabling arboreal locomotion to avoid more terrestrial specialized predators, for example. These ecological factors are all interrelated, but habitat, in particular, is inextricably interconnected with locomotion and predation in primates—as successful predation avoidance would rarely be possible without proficiency in locomoting up into and between the terminal branches of such arboreal refuges.

Arboreal life’s complex three-dimensional topology, requisite climbing, and frequent distance judgments have been theorized to be responsible for the unique suite of traits ascribed to primates (Clark, 1959; Jones, 1916; Smith, 1924). This “arboreal theory” attributes primate morphology as direct consequence of life in the trees (Howells, 1947). More specifically, primates inhabiting three-dimensional arboreal habitats may have evolved orbital convergence [OC], and stereoscopic vision, for more accurate leaping behavior (Collins, 1921). While leaping through such habitats is indisputably “precarious” (Szalay and Dagosto, 1988), we now know that binocular vision, for example, can evolve through other flight-related means (e.g. felids, raptors, and megachiropterans have OC) (Allman, 1977; Pettigrew, 1986) and that it is by no means an inevitable effect of arboreality (e.g. rodents, sloths, squirrels, and hyraxes do not have OC) (Cartmill, 1972; Heesy, 2009). To more finely distinguish between arboreality and leaping, we used percentage of precision limb landed locomotor bouts (e.g. leaping), as a proxy for risk of harmful falls, in order to test an extension of grasp-leap theory (as applied also to suspensory swinging-spectrum behaviors). The strongly positive association of leaping-spectrum behavior and strongly negative association of daily path length with OC was consistent with inter-substrate leaping driving the evolution of cranial changes in primates. We suggest that these two theories are quite complimentary and that grasp-leap lies on a more proximate end of the spectrum of more ultimate arboreal-based theories, where a measure of the former could serve as a decent proxy or mediator for the other. Further, our continuous locomotion measure seems to statistically mask the effect of our more simplistic binary arboreal variable, arguably supporting the notion that such active locomotion utilizes the arboreal environment in a uniquely primate, predator-avoiding way.

Subsistence in the form of terminal-branch foraging likely drove the very first defining shifts in primates, eventually favoring dental despecialization, claw loss, and grasping improvements (Silcox et al., 2007). Predation upon insects in the “fine-branch milieu” via VP (Cartmill, 1972) was possibly a second core selective influence following arboreal grasping and perhaps preceding (Heesy, 2009) dietary dependence on flowering plants (Cartmill, 2012, 1972). Indeed, fossil teeth of early primates suggest an omnivorous diet including insects as well as fruit (Silcox and López-Torres, 2017). Insectivory was not a significant factor, in our model of euprimate evolution, and was excluded from the final model, though we cannot, using only extant data, rule out VP as in important influence on early primate evolution. Frugivory, however, may have acted to evolve primates, toward a modern euprimate morphotype, concurrently with angiosperm co-radiation (Rasmussen, 1990; Sussman, 1991) during the Eocene (Silcox and López-Torres, 2017). While others have found OC to correlate with frugivorous diet (Heesy, 2003), in our own analysis, frugivory was not a highly significant variable (behind most other controls reported here). This coupled with the fact that frugivrory has a somewhat uncertain directional effect suggests it is likely not the most influential factor driving OC in euprimates.

There are many ways organisms can avoid predation including out-growing, mobbing, evading, fleeing, freezing, and self-protection via spines or armor (Morse, 1976). Predation's influence on primates, both initially inhabiting as well as moving amongst arboreal substrate while fleeing, was a highly plausible factor shaping the evolution of primate morphology. Unfortunately, it is also a factor that is notoriously difficult to measure (Stanford 2001). In counteraction to terrestrial threats from mammalian carnivores such as mesomychnids (Van Valkenburgh, 1999), predation avoidance via active arboreal locomotion likely trumped any other single primate originating adaptive shift (Crompton and Sellers, 2007). After an initial transition to arboreality, a concomitant radiation with large-gape, constricting snakes likely introduced an additional predatory selection pressure driving even further orbital convergence, for snake detection [SD] (Isbell 2006). Selection for orbital convergence would have been strong if these terminal branch predators were abundant and leaping was frequent. Although no snake-specific proxy variables were significant here or in an independent analysis (Wheeler et al., 2011), many of the other significant variables discussed here indirectly suggest not ruling out serpentine predation as possibly being an important pressure. Primates (e.g. *Microcebus murinus*) are known to use leaping as a primary means of avoiding predators (Legreneur et al., 2012), and snakes have long been theorized to be an evolutionary influence for the past 200 million years (Silcox and López-Torres, 2017). Thus, we conclude here that reach-grasp theory does not need to be mutually exclusive of snake-predation based theories despite the inconclusive evidence relating reaching and grasping with stereoscopic vision (Watt and Bradshaw, 2000).

In mammalian brains, binocular visual stimuli are integrated in overlapping central visual fields which are known to correlate with degree of orbital convergence and visual brain structures (Barton, 2004). In primates (as well as megachiropterans and dermopterans), contra-lateral orbital field information from *both* eyes is projected through the uniquely configured optic chiasma. Primates are further singular, however, in that they segregate these inputs as specialized and non-redundant right and left sides in the superior colliculus of the tectum in the brainstem (Preuss, 2007), which is thought to aide in rapid and accurate sensory motor targeting (Allman, 1977). In the higher brain, central ganglion cells project to each side of the visual cortex from both retina to both parvo- and magno- cellular layers of the lateral geniculate nucleus, but OC correlates more significantly in parvo-cellular (p=0.01), for acute discrimination, than in magno-cellular (p=0.1), for movement discrimination (Barton, 2004). This observation has been used to support SD over grasp-leap (Isbell 2006), but it is still possible that both pathways were important in primate evolution. For example, this neural bias for parvo- over magno- cellular layers could be stronger for more recent evolutionary events, such as SD in anthropoids, but weaker and more degraded for more ancient adaptations, such as grasp-leap in basal euprimates. The closeness of significance levels of the Barton study, and the small sample sizes in both studies (Barton, 2004; Watt and Bradshaw, 2000) (n=10 and n=11 respectively), contraindicates wholesale rejection of grasp-leap theory.

In the present study, the two most significant variance-explaining locomotion related factors of leaping and daily path length are consistent with hypotheses invoking these leaping-driven changes (ANOVA, p<0.001). Frequent leapers that use gap-spanning leaps to avoid long path lengths (e.g. down, between, and back up into adjacent trees for example) would save time and energy during foraging or evasion (Crompton et al., 1993). Uncertainty in landing, due to either emergency leaps away from arboreally-specialized predators (e.g. constricting snakes) or due to environmental uncertainty in branch position (e.g. due to wind) (Miller et al., 2009) could have further actuated the convergence of early euprimates' orbits. While we did not look at substrate effects, a previous study also found arboreal substrate as having a significant effect on OC (Heesy, 2003) although this was later contradicted (Heesy, 2008). Our results are consistent with fossil evidence in that early primates did at least "some leaping" (Silcox and López-Torres, 2017) albeit not the "super leaps" of modern day tarsiers (Rosenberger and Preuschoft, 2012).

Swinging, surprisingly, was not a significantly positive (pglm, *p*=0.58) nor a significant variance-explaining variable (ANOVA, *p*=0.2). It is possible this is due to the small sample of species that perform this relatively rare form of locomotion. As swinging lies on the opposite end of a free limb-landing spectrum than leaping, a less pronounced evolutionary signature of its effect on OC is expected. Brachiation and other forms of suspensory locomotion should be more predictable (entailing less risk) when along the same branch, in the same tree, and often with the same substrate orientation. Nonetheless, given this preliminary test on the limited sample size of bi-manual suspensory primates, it appears that our generalized precision limb-landing theory (an extrapolation of grasp-leap) is not fully supported in this extended way.

Activity period related vision changes (toward tricromatic vision for Haplorines) was the second most significant variance-explaining factor (ANOVA, *p*=0.056) leading to higher OC behind locomotion related factors of leaping and DPL. Previous researchers have found nocturnality to be highly predictive of OC (Walker 1987; Heesy, 2008; Allman, 1977; Kay, and Cartmill, 1977). And while it has strong value for inclusion in models—activity period and trichromatic vision were #2 and #3 factors overall by AIC (Wheeler et al., 2011)—its directionality here is uncertain. Our nocturnality factor (likely a Prosimian confounded effect), however, was only marginally significant and, interestingly, contradicts previous findings (Wheeler et al., 2011). Both the effect size and significance color vision, however, are higher than nocturnality (see Table 1). These influences are independent of locomotion and could have more to do with improvements upon central visual field maximization for both detailed frugivorous (nearly significant) and nocturnal foraging. Despite the fact that nocturnal visual grasping was likely instrumental in early primate evolution (Cartmill, 1972; Crompton, 1995; Heesy, 2008), nocturnal leaping theory (Crompton, 1995) was not as strongly supported by our extant primate dataset (ANOVA, *p*=0.85). While nocturnality may not have played a major role in OC euprimate evolution, its positive association with OC (PGLM, *p*=0.04) suggests we should not reject either of these nocturnal grasping-based theories. The seeming contradiction of both color vision and nocturnality being significant, suggests that orbital convergence could be a somewhat convergent phenomenon in later euprimates. That is, part of the reason primate orbital convergence has such confusing origins, is that there exists a multiplicity of forces positively incentivizing their anterior position and few negative, defensive reasons for keeping them in a more archaic, lateral position.

Primate body mass was ancestrally rather small (less than a kilogram) (Silcox and López-Torres, 2017) with some estimates as smaller than modern tree shrews at 15g (Gebo, 2013). In this study, body mass was also the most significant variance explaining variable of any other control (ANOVA, *p*=0.001). This high significance of body mass has been described as the “strongest evidence of something other than snakes” driving OC (Wheeler et al., 2011). It is not immediately obvious why this might be the case, but it is possible that predation plays a role as apex predators (e.g. many felines and raptors) are known to have highly convergent orbits (Cartmill, 1972; Pettigrew, 1986; Wheeler et al., 2011). Surviving radiations of primates increased in body mass and consequently reduced predation threats (Isbell, 2005). This increase in size was evidently not driven, for example, by increased leopard predation (Zuberbühler and Jenny, 2002). As mentioned previously, a reasonable null hypothesis suggests that allometrically smaller orbits relaxed constraints on continued orbital convergence in diurnally enlarged anthropoids. Similarly, it is thought that body mass increases associated with suspensory locomotion and a shift toward terrestriality could drive OC (Isbell, 2006). It is possible, alternatively, that these changes are related to shifts toward a high calorie diet and increases in group size. This form of predator deterrent, gross mass dominance, could have further allowed for converging orbits due to a relaxed need for a defensive view of attacks from behind.

Group size was the second most significantly positively correlated factor with OC. Primate vision improvements towards information processing at finer levels of detail could have evolved for better reading of facial social cues (Joffe and Dunbar, 1997) or group member recognition in large group-living terrestrial primates such as macaques and geladas (Lehmann et al., 2007). It is possible that these changes toward larger group membership continued to select for convergent orbits in anthropoids as they became more terrestrial and visually social[4]. The added group-size benefits of vigilance, deterrence, and safety in numbers during attacks could have compounded this effect. It is important to point out that while the directionality of the correlation of group size with OC was highly significant, group size seems to be less certain as a significant control variable (ANOVA, $p=0.2$) and consequently, speculations above should be assessed with skepticism.

Taken together, the neuro-ocular-motor vision system improvements in primates could have evolved in response to pressures for leaping—perhaps away from co-radiating snakes—to topologically uncertain landing sites on remote substrate. These pressures were perhaps further compounded by environmental perturbation such as wind. The more remote and uncertain the landing substrate, and the longer the leaps, the stronger the evolutionary effect would be. This conclusion is compatible with nearly all of the other theories of primate origins. The snake detection theory is difficult to test as we didn’t have direct data on predation rates, but it is consistent with possibly driving leaping in the first place. Arboreal complexity, as discussed in more detail below, presents another difficult to test case, but results here are entirely consistent and fully compatible

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[4] Increased anthropoid OC could have also co-evolved with anti-parasitic social grooming, as could have been necessitated by the prolonged periods of inter-personal contact during infant-carrying.

with it. Furthermore, we point out the importance of recognizing masking effects of locomotion variables on arboreality indicators and suggest perhaps using one as a proxy for the other.

Although logic similar to that used above for leaping could apply to rapid suspensory (e.g. ricochetal brachiation) locomotion, the findings on the smaller swinging subset of primate locomotion data do not provide strong support for it driving further orbital convergence. While the effect of this improvised response (to predation or substrate perturbation) is less pronounced for larger primates, the effect on smaller early primates could have been much stronger. While our proposed adaptation—arboreally driven hand-eye coordination improvements in visual landing tasks (Cartmill, 1970; Ross and Martin, 2007; Smith, 1924)—is supported by our locomotion data, the OC associations with frequent leaping, observed here, could originate from another source of reduction in posterior predation—that of general body mass increases, as mentioned above.

A project of such ambitious scope as this may inevitably entail a multitude of defects. For example, leaping distance or velocity might have been more directly useful for testing this hypothesis involving risks of misjudged limb-landing; however, virtually no such studies exist. Although previous studies have successfully reconstructed ancestral primate behavior (Griffin et al., 2012; Opie et al., 2012), additional limitations and biases remain in estimating behavior using modern data and phylogenetic trees. Some paleoprimatologists echo concerns that modern primate data shouldn’t be used in reconstruction at all, that they are “irrelevant” due to parallel evolutionary phenomena such as those that manifest according to Cope’s rule (Silcox and López-Torres, 2017). Moreover, it is difficult to say if some of these findings aren’t merely an artifact of the simplistic binary nature of several of the control variables compared with the near-continuous measures of locomotion.

Our main rebuttal to these concerns is our depth and breadth of data. We were able to leverage a plethora of species as data points and scores of ecological variables as controls. Ecological controls abound here while they are rarely available in paleontological study (Soligo and

Smaers, 2016). Each of the different evolutionary influences discussed above can be modeled and controlled for using extant primate data in ways that are not otherwise possible. Nonetheless, future studies could improve upon our present test of an extended grasp-leap theory by including even more controls and detailed data such as comparative precision in grasp *rotational* abilities. Despite these imperfections, this new quantitative locomotion data should continue to be useful for future quantitative studies into primate origins.

Orbital convergence is a hallmark trait of euprimates—as all extant primates have a some amount of it and to a higher degree, per body mass, than any other mammalian order. All other primate characteristics, such as grasping and leaping, point towards this—that is, OC follows from the others—as they are part of an integrated complex (Ross and Martin, 2007). As mentioned above, OC was likely the last of these defining characteristics to evolve 55-50 million years ago when the crown clade came into modern aspect. But as a continuous, spectrum trait, OC continued to evolve into the various modern forms, alongside an increase in body size and shift to a diurnal diet as seen in anthropoids.

Admittedly, the high degree of binocular field overlap, associated with aperture OC, does not necessarily guarantee stereoscopic vision. Furthermore, binocular field overlap certainly has other (more ocularly redundant) uses, ranging from increased light sensitivity to enhanced contrast discrimination (utilized most notably by nocturnal strepsirrhines) (Heesy, 2009). But all of the logical arguments above, combined with the leaping frequency driven modeling reported here, support the idea that primates could have evolved OC and binocularity for (non-redundant, disparity-based) stereoscopic fine-tuning during the landing phase of high-speed, high-impact leaps.

We have attempted to formulate and test a hypothesis focusing on landing, or the *late phase* of a leaping locomotor bout, in order to properly address the paradoxical concerns of OC acting to reduce parallax (Cartmill, 1972). We'd like to point out, however, that under our hypothesis, while leap landing may have, as a side effect, acted to *reduce* (OC-based) *parallax*, improved landing of higher impact leaps—assuming one-leap-ahead landing target previews—could act to further lengthen these leaps and thereby serve to *increase* (motion-based) *parallax*. Future leaping focused locomotion studies should include length of these leaping bouts, as well as mid-leap visual field orientation data, in order to help resolve this issue.

Leap-landing is likely a highly influential factor in primate evolution—as well as a defining behavior. As an evolutionary influence, its status should be considered intimately entangled with many of the others above, for example as a more proximate factor than the more ultimate but interdependent factor of arboreal complexity. It manifests as lying flanked between tree trunk originated predation threats and terminal branch associated fall risks. This core dilemma, to stay at a dead-end terminal branch and face death by arboreal predation versus deciding to *safely* leap to another tree, all while avoiding terrestrial threats below, could likely be the single most pivotal evolutionary turning point in shaping the most distinctive trait of any order of non-apex predators on earth.

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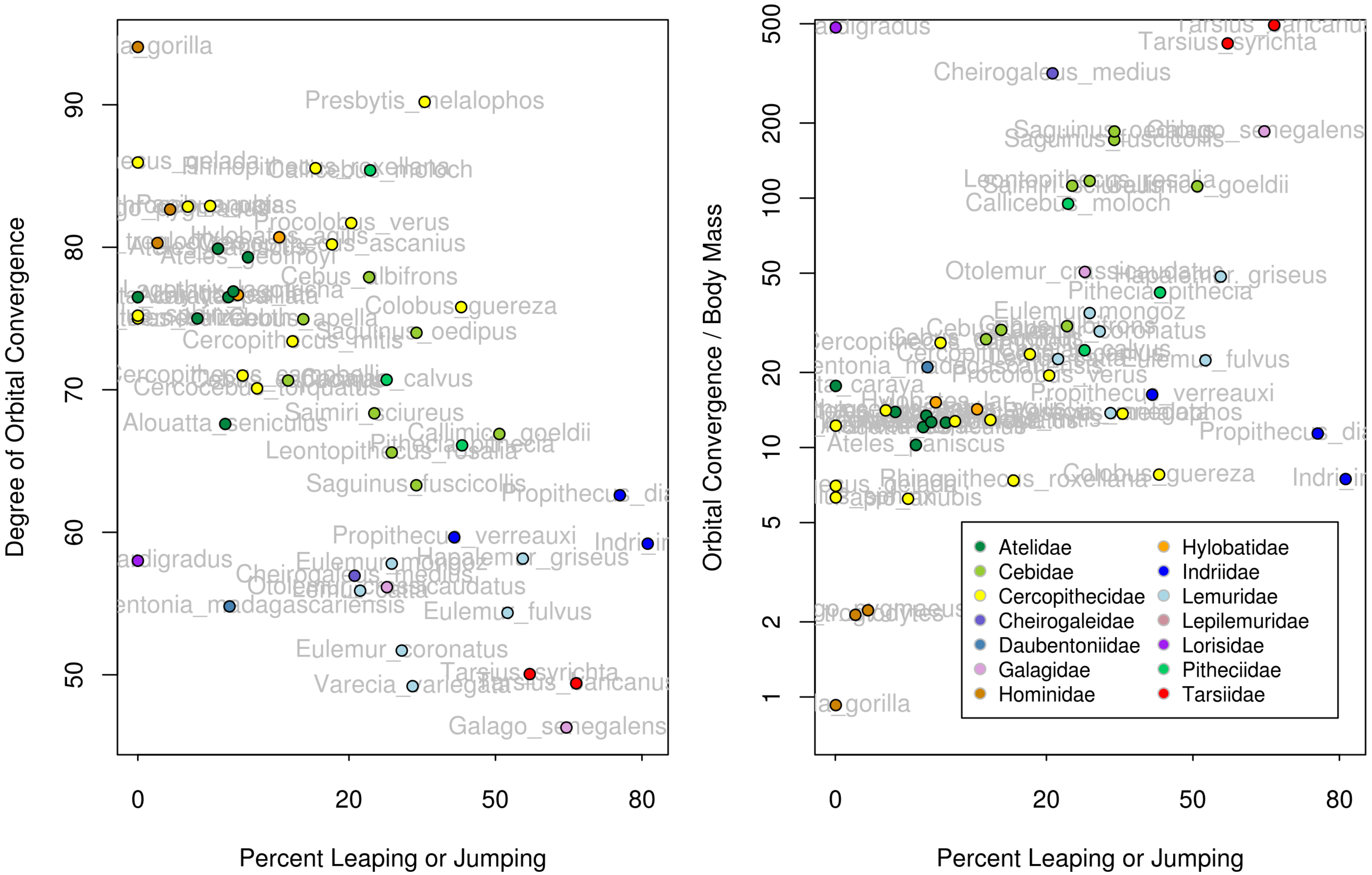

Supplemental Figure 1. Leaping percentage as a function of orbital convergence and mass
Scatter plots of leaping-spectrum behavior percentages versus orbital convergence [OC] **left** are plotted above for all primate species. After controlling for body mass (OC/mass **right**), we see a positive, albeit allometric, relationship with leaping. Loris tardigradus is an outlier in the upper left of **right**.

Supplemental Table 1. OC, control variables, and aerial locomotor percentages per species.

Genus species	OC	Cvt	DPL (km)	mass (Kg)	fruit	group	nocturnal	swing %	leap %
Alouatta caraya	76.5	TRUE	0.48	5.38	FALSE	14.6	FALSE	0%	0%
Alouatta palliata	76.5	TRUE	0.39	6.24	FALSE	13.1	FALSE	7%	4%
Alouatta seniculus	67.6	TRUE	0.55	6.09	FALSE	7.9	FALSE	6%	4%
Ateles belzebuth	75.0	FALSE	2.30	8.07	TRUE	14.5	FALSE	48%	2%
Ateles geoffroyi	79.3	FALSE	1.68	7.54	TRUE	42.0	FALSE	29%	6%
Ateles paniscus	79.9	FALSE	2.70	8.78	TRUE	20.0	FALSE	36%	3%
Cacajao calvus	70.7	FALSE	3.75	3.17	TRUE	39.0	FALSE	0%	27%
Callicebus moloch	85.4	FALSE	0.62	0.99	TRUE	4.5	FALSE	0%	24%
Callimico goeldii	66.9	FALSE	2.00	0.48	TRUE	6.9	FALSE	2%	51%
Cebus albifrons	77.9	FALSE	1.85	2.74	TRUE	25.0	FALSE	0%	24%
Cebus apella	75.0	FALSE	2.00	3.09	TRUE	7.9	FALSE	2%	13%
Cebus capucinus	70.7	FALSE	2.00	3.11	TRUE	18.2	FALSE	2%	11%
Cercocebus torquatus	70.1	TRUE	2.33	7.49	FALSE	26.9	FALSE	0%	7%
Cercopithecus ascanius	80.2	TRUE	1.59	3.31	FALSE	15.0	FALSE	0%	17%
Cercopithecus campbelli	71.0	TRUE	1.69	3.60	FALSE	9.0	FALSE	0%	5%
Cercopithecus mitis	73.4	TRUE	1.33	6.03	FALSE	20.7	FALSE	0%	11%
Cheirogaleus medius	57.0	FALSE	0.87	0.28	FALSE	1.0	FALSE	11%	21%
Colobus guereza	75.8	TRUE	0.54	11.35	FALSE	7.6	FALSE	0%	43%
Daubentonia madagascariensis	54.8	FALSE	2.95	2.56	FALSE	1.0	FALSE	0%	4%
Erythrocebus patas	82.9	TRUE	3.43	9.45	FALSE	31.3	FALSE	0%	1%
Eulemur coronatus	51.7	NA	0.91	1.18	FALSE	9.5	FALSE	2%	30%
Eulemur fulvus	54.4	FALSE	0.14	NA	FALSE	12.0	TRUE	3%	53%
Eulemur mongoz	57.8	FALSE	0.61	1.49	FALSE	2.9	TRUE	4%	28%
Galago senegalensis	46.3	FALSE	2.10	0.21	TRUE	3.5	FALSE	1%	65%
Gorilla gorilla	94.1	TRUE	0.70	124.68	FALSE	6.0	FALSE	4%	0%
Hapalemur griseus	58.2	FALSE	0.43	0.95	FALSE	3.1	FALSE	7%	56%
Hylobates agilis	80.7	TRUE	1.22	5.85	TRUE	4.2	FALSE	65%	9%
Hylobates lar	76.7	TRUE	1.49	5.62	TRUE	3.2	FALSE	66%	5%
Indri indri	59.2	FALSE	0.25	6.34	FALSE	3.1	FALSE	0%	81%
Lagothrix lagotricha	76.9	FALSE	1.00	7.15	TRUE	33.0	FALSE	30%	4%
Lemur catta	55.9	FALSE	0.95	2.21	FALSE	16.5	FALSE	4%	22%
Leontopithecus rosalia	65.6	FALSE	1.44	0.61	TRUE	4.5	FALSE	5%	28%
Loris tardigradus	58.0	FALSE	1.35	0.19	FALSE	1.0	TRUE	30%	0%
Macaca nemestrina	75.0	TRUE	2.00	7.58	FALSE	22.6	FALSE	0%	0%
Mandrillus sphinx	75.2	TRUE	3.00	22.25	FALSE	13.9	FALSE	0%	0%
Otolemur crassicaudatus	56.2	FALSE	1.25	1.15	TRUE	3.5	FALSE	0%	27%
Pan troglodytes	80.3	TRUE	3.05	44.97	FALSE	50.0	FALSE	1%	0%
Papio anubis	82.9	TRUE	3.80	17.83	FALSE	43.0	FALSE	0%	3%
Pithecia pithecia	66.1	FALSE	1.88	1.76	TRUE	3.0	FALSE	0%	43%
Pongo pygmaeus	82.7	TRUE	0.50	56.95	TRUE	1.0	FALSE	14%	1%
Presbytis melalophos	90.2	TRUE	0.88	6.53	FALSE	14.0	FALSE	3%	35%
Procolobus verus	81.7	TRUE	1.21	4.45	FALSE	8.5	FALSE	0%	20%
Propithecus diadema	62.6	FALSE	0.99	6.10	FALSE	6.0	FALSE	1%	76%
Propithecus verreauxi	59.7	FALSE	0.85	3.50	FALSE	6.3	FALSE	8%	41%
Rhinopithecus roxellana	85.6	TRUE	2.10	14.75	FALSE	65.0	FALSE	4%	14%
Saguinus fuscicollis	63.3	FALSE	1.32	0.35	TRUE	6.0	FALSE	0%	33%
Saguinus oedipus	74.0	FALSE	1.37	0.41	TRUE	7.1	FALSE	0%	33%
Saimiri sciureus	68.4	FALSE	1.50	0.79	TRUE	34.9	FALSE	1%	25%
Tarsius bancanus	49.4	FALSE	1.80	0.12	FALSE	1.0	TRUE	0%	67%
Tarsius syrichta	50.1	FALSE	1.12	0.13	FALSE	1.0	TRUE	0%	58%
Theropithecus gelada	86.0	TRUE	2.50	15.35	FALSE	10.0	FALSE	0%	0%
Varecia variegata	49.2	FALSE	2.31	3.49	FALSE	2.8	FALSE	8%	32%

OC measures are averaged from Ross 1995 & Cartmill 1970, Cvt and DPL are from Wheeler 2011, body mass is an average across sex from (Lehmann et. al. 2007), and leaping and swinging percentages were calculated using the values from the “Locomotion sources” listed above. Other controls were collected from various reference texts including (Rowe & Meyers 2017). Abbreviation key: OC=orbital convergence, CVt=color vision (trichromatic), DPL=daily path length

Chapter 4 - The Co-evolution of Elaborate Vocal Displays and Precision Landing Locomotion in Primates

Abstract

The complex ecological niche of arboreality, via associated locomotion through it, may have provided the selective context for spatial-cognitive evolution in primates. We suggest that elaborate vocal displays (i.e. singing) subsequently evolved to signal these underlying spatial proficiencies. We test this using data on vocal elaborateness and forms of spatially demanding locomotion from 51 non-human primate species. Vocal elaborateness was assessed by a recently developed “acoustic reappearance diversity index” and for locomotion we used leaping and swinging frequencies. We were able to demonstrate a positive association between aerial spectrum locomotion, such as brachiation and jumping and leaping, with elaborate vocalizations, such as songs, duets, and great calls. We used phylogenetically controlled regression analysis on a merged dataset which included these measures of both vocalization and locomotion as well as other socio-ecological controls such as social monogamy and habitat. While we reconfirm that monogamy had a significant positive association with musical behavior in primates, forest dwelling (a proxy for habitat acoustics) was not significant after controlling for shared ancestry. The results fail to reject our hypothesis that elaborate vocal displays could have co-evolved with spatially demanding locomotion as signals of spatial abilities.

Introduction

Elaborate acoustic display behavior is universal across human societies (Nettl, 2000), and it has also evolved in many animals, including other primates, cetaceans, and aves (Fitch, 2006; McDermott and Hauser, 2005). Biologists have sought to understand the origins and adaptive function of this “most mysterious trait” since Darwin (Darwin, 1871). Elaborate acoustic display behavior has since been proposed to function in various ways, such as language acquisition (Patel, 2008) and mother-infant bonding (Dissanayake, 2000; Trehub and Trainor, 1998), sexual selection (Darwin, 1871; Miller, 2000), territoriality (Cooney and Cockburn, 1995), emotionally regulatory group bonding (Dissanayake, 2009; Roederer, 1984; Snowdon et al., 2012), coalition signaling (Hagen and Bryant, 2003), and the null case of no obvious direct function (Feenders, 2008; Pinker, 1997). In non-human primates, elaborate vocalizations are associated with monogamy (Haimoff, 1986; Tilson and Tenaza, 1976), but it is unclear what these displays might signal *within* a breeding pair. Although many theories have been proposed to explain elaborate acoustic display behavior, its ultimate function remains “most mysterious.”

Elaborate acoustic display behavior (in the form of human music) is comprised of several structural features, including tone, interval, rhythm, repetition, transposition, and variation (Brown and Jordania, 2013; Nettl, 1983), and different musical features might reflect different types of signaling advantages. For example, tone, can improve signal propagation in dense forests (Haimoff, 1986; Hansen, 1979; Mitani and Stuht, 1998), where many perching songbirds and display calling primates live. Intervalic changes in fundamental frequency are similarly thought to help with long distance communication (Hansen, 1979; Mitani and Stuht, 1998; Morton, 1975). While rhythm may function to signal general timing abilities for complex locomotion (Bispham, 2006; Calvin, 1983), variation, both within and across calls, on the other hand, may reliably signal general learning abilities (Boogert et al., 2011; Farrell et al., 2012; Moore et al., 2011). By contrast, there has been less evolutionary analysis of reappearance—repetition and transposition of musical units such as bird song syllables or human musical notes. To gain deeper insights into the origins of elaborate acoustic display behavior, we act upon the methodological suggestions of others in measuring specific features of these displays across different species for comparative analysis (Bispham, 2006; Fitch, 2006; Mache, 2000; Miller, 2000).

We propose a new explanation for the evolution of elaborate acoustic display behavior by considering relations between acoustic cognition and spatial and motor cognition. Research on amusia (difficulty perceiving pitch and recognizing music) indicates that it may be associated with deficits in spatial proficiency (Williamson et al., 2011). Further, human brain imaging studies show that music perception occurs in some of the same cortical areas (Schmithorst and Holland, 2003) as spatial visualization (Harris and Miniussi, 2003) and magnitude comparison (Dehaene et al., 2003), and that music processing shares neural circuitry with spatial abilities (Douglas and Bilkey, 2007; Janata and Grafton, 2003; Williamson et al., 2011). Recent studies in birds have shown similar overlapping neural circuitry (Feenders, 2008) as well as co-evolution of song complexity, length, and repertoire size with motor circuitry (Moore et al., 2011), spatial learning ability (Farrell et al., 2012), and detour reaching (Boogert et al., 2011). Together, these studies indicate common neural circuitry could underlie the processing of visual spatial information and spatial motor control. And while some have since questioned these connections (Nunes-Silva et al., 2016), the above findings are curious enough to justify further investigation into the possibility of elaborate acoustical display behaviors co-evolving with other traits that utilize these abilities.

We hypothesize that the morbidity and mortality from falling during rapid locomotion through spatially challenging arboreal niches selected for accurate perception of spatial relationships, and precision in execution of the locomotion required to successfully navigate these spaces. Precise, complex acoustic displays could serve as reliable indicators, or honest signals[1] of these capacities, indicating an individual's neurocognition for adaptable spatio-temporal proficiencies. Conspicuous acoustic signals of spatio-temporal precision could advertise an animal's genetic quality and phenotypic condition. Such advertisements can have positive individual-level ramifications such as mate attraction, parental investment, improvement in social standing, and deterrence of territorial rivals (Cooney and Cockburn, 1995; Darwin, 1871; Dissanayake, 2000; Miller, 2000). This spatial-cognitive signaling hypothesis predicts that vocalizations will evolve to be more elaborate among species that face greater spatial-cognitive challenges.

Non-human primates are an ideal taxon for study as they share many similarities with humans, show high variation in both locomotor (Gebo, 2013) and vocal behavior (Hammerschmidt and Fischer, 2019), and their vocalizations develop with little social input (Geissmann, 1993; Hammerschmidt et al., 2001). Using transformations of quantitative data available from the primate behavioral repertoire literature, we were able to test this hypothesis via phylogenetically controlled regression analysis. The regression results support our proposed "dimensional precision" signaling hypothesis (Schruth and Templeton, 2014) by showing that high-risk forms of locomotion (e.g. leaping and swinging) strongly associate with singing behavior. Furthermore, while we re-confirm previous findings that socially monogamous primates do have more elaborate display calls, the effect of wooded habitat on call elaborateness was no longer significant ($p < 0.05$) after controlling for locomotion and phylogeny. We discuss these results and their implications with respect to human music and evolution of more complex aspects of early hominine evolution.

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1 This signaling system could evolve via a) direct selection for *choice* [of song qualities] and b) indirect selection on the [genetically] correlated traits (Brooks et al., 2010) of singing and leaping.

Methods

Vocal, locomotor, and ecological data were collected on extant non-human primates from the primary literature. We compiled vocalization and locomotion behavior of primates at two different resolutions: fine-scale continuous, for 51 overlapping species representing over half of the 61 genera and 15 out of the 16 families, as well as categorical descriptions for hundreds of primate species. Observations of these two behaviors of interest, vocal elaborateness of acoustic syllables and aerial-spectrum locomotion, where most limbs become detached from substrate, were tabulated and re-factored into continuous variables, so as to elucidate their relationship at higher resolution than the independently collected ordinal call-category dataset alone would allow (see Fig. 1). Full methods for vocalization and locomotion data collection and index development can be found in the previous two chapters. Here, we provide an abbreviated version of the data processing and methodologies.

Vocalization data collection was carried out by searching for vocal repertoire studies using ISI Web of Knowledge and Google Scholar. Spectrograms (plots of acoustic energy over time and frequency) were cropped out of these primary research articles. Five trained observers blindly scored randomly ordered spectrograms along six different acoustic aspects of human music universals: tone, interval, rhythm, repetition, transposition, and syllable count. A total of 832 vocalizations representing 58 species were scored. These six scored variables were then averaged across scorers resulting in a single (832 by six) table of mean feature scores.

We statistically explored this table of mean scores using principal components analysis [PCA]. The PCA helped to inform a reduction of the original six variables down to just three: repetition, transposition and syllable count. We further reduced these three acoustic features into a single continuous index using the following equation: syllable count × (repetition + transposition). This index is simply an expectation, or average, of the number of distinctly reappearing units within a call. This "acoustic reappearance diversity index" [ARDI] was consistent with call names including "song" or "musical" and contexts of "display." ARDI is simple, elegant, and highly sensitive in helping to identify minimally musical vocal utterances (Schruth et al., 2019)[2]. As the final composite elaborateness measure for each species, we selected the most (max) elaborate vocalization, because many species (e.g. *Indri indri*) only have a single elaborate (e.g. "display") call in their repertoire. Thus, our elaborateness measure reflects a species' upper extreme of vocal display proficiency—that is, its best performance rather than its average performance.

Locomotion data was collected in a fashion similar to vocalization data, using ISI Web of Knowledge and Google Scholar, but searching for the terms "position" or "locomot*" in the titles or abstracts of primary research articles. Studies had to have some form of quantification of leaping to be included. Overall, from 99 studies, 210 observational records were split into 16 locomotor categories (or "modes") and averaged across species—resulting in 130 records for individual species. Full details of the collection and refactoring work is described in Chapter 3.

We focused on two broad locomotor categories for subsequent analysis. The first is *swinging* and includes the subcategories of *brachiate, semi-brachiate, arm-swing, tension, suspensory,* and *torso-orthograde*. The second is *leaping* and includes the subcategories *leap, vertical cling leap, bound leap, jump, drop, leap/drop,* and *airborne*. Although we measured and analyzed leaping and swinging as separate factors, we discuss them together under the terms *aerial-spectrum*[3] and *precision limb landed* locomotion (Chapter 3). We coined these terms to more efficiently discuss putative influences of these locomotor modes that involve detached, multiple free-limb, risky or "precarious" ballistic movement through the air. Aerial-spectrum locomotion can be an especially risky, spatio-temporally demanding behavior, where miscalculations of distance (Wilson, 1975, p. 515), timing, angle, or effort

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[2] see also Chapter 2

[3] Aerial spectrum locomotion includes both leap-spectrum and swing-spectrum locomotion and is calculated here using the simple addition of the two percentages.

can result in lethal falls or serious injury (Szalay and Dagosto, 1988).

The subset of these locomotion records that had spectrographic vocalization data for corresponding species were retained (from *n*=101 to *n*=51). Many species (*n*=14) had questionable inclusion status: six non-zero, but infrequent, leapers and eight species without any bout counts. Six species for which we had spectrographic data did not have published quantitative locomotion estimates. *Macaca nemestrina, M. radiata, M. silenus, M. sylvanus*, *Cercopithecus neglectus*, and *Mandrillus sphinx* were determined to potentially have a non-negligible, but yet to be published, amount of jumping in their locomotor repertoire. Each of these species was removed from the final locomotion versus vocalization comparative analysis leaving 51 species (from 38 genera) and 725 vocalization types (from 1107 spectrograms). Of these species, eight lacked bout count information: five jumpers (*Indri indri*, *Tarsius spectrum*, *Hylobates leucogenys*, and *Rhinopithecus roxellana*) and three non-jumpers (*Cercopithecus aethiops*, *Gorilla gorilla*, and *Theropithecus gelada*). Despite lacking bout counts, studies for these species provided quantitative estimates of aerial-spectrum locomotion and were retained in the comparative analysis.

Environmental and behavioral data were included in the model, in addition to our core locomotion predictors of *swinging*, *leaping*, and *climbing*, to assess their relative influence on the structure of elaborate acoustical display signals. We reduced the originally sizable array of possible control variables (Chapman and Lefebvre, 1990; Fleagle, 1999; Fuentes, 1998; Jolly, 1985; Lindenfors, 2002; Rowe and Meyers, 2017; Soligo and Müller, 1999; Swindler, 1998) to just six that were hypothesized to have most influenced the evolution of acoustical display: habitat (*wooded* vs. open landscape), elevation (*arboreal* vs. terrestrial), social system (*territorial* vs. non-territorial), group size, activity period (*nocturnal* vs diurnal or cathemeral) and mating system (*monogamy* vs. non-monogamy). We had also considered several other variables such as those related to diet, activity period, body mass, and non-locomotion related attachment physiology (*claws* or *prehensile* tail) as other possibly influential factors. A combination of R^2 and AIC values helped to further reduce the model to eliminate variables of *claws*, *climbing*, *prehensile* tail, and the non fruit dietary indicators.

We limited the *arboreal* category to primates species that were considered strictly arboreal (*n*=38), thus some species that were sometimes or often *arboreal* were categorized as non-arboreal (e.g. *Pongo pygmaeus*). Similarly, we coded three primate species, *Cercopithecus aethiops, Papio anubis,* and *Theropithecus gelada* as living in open habitats even though the grassland dwelling *C. aethiops* can be partially arboreal. The continuous *group size* variable was split into categories (solitary, 2-6, 7-20, 21-40, 41-85) where natural breaks occurred along an non-monotonically increasing trend. We followed previous literature (Fuentes, 1998) in assigning species to mating system categories; we included the species as monogamous if there was any hint of it—even in marginal cases such as “pair-bonded” or “two-adult” groups. Other control variables (such as territoriality, group size, nocturnality, weight, presence of a prehensile tail or claws, various dietary indicators, and other forms of locomotion) were also considered and eliminated according to R^2 and AIC values.

Score transformations for regression: We transformed several of the key locomotion predictor variables (Fig. S1) to satisfy the normality assumptions of linear regression. We transformed each of the locomotion percentages (with the exception of climbing) by taking the arcsine of their square root. These transformations helped to stabilize the residual variance of the regressions. Untransformed data and regression lines, however, are available in Figure S2.

Phylogenetic regression: For the all of the following comparative methods, we used regression analysis to assess the effect of each of the socio-ecological factors on vocal reappearance diversity. We investigated both a full model (including habitat, arboreality, territoriality, group size, monogamy, and locomotion measures) and compared these with a set of reduced models (assessing each of these factors individually). We determined the significance of the locomotion parameters, and the other control variables, using two tailed *t*-tests. For both techniques, we used a composite phylogeny of the primates

(Springer 2012).

To assess the relationship between aerial locomotion and acoustic display, while controlling for phylogeny, we performed regressions on both the full and reduced models with the *pgls* function in the *caper* R-package (Orme et al., 2012) where all scaling factors (kappa, delta, and lambda) were determined automatically by built-in maximum-likelihood routines. We also performed phylogenetically independent contrasts to assess the relationship between aerial forms of locomotion and reappearance diversity using the *pic* function in the *ape* R-package (Paradis, 2012).

Results

We found a significant positive relationship between elaborate (high acoustic reappearance diversity) vocalizations, and aerial-spectrum locomotion (PGLM[4] and PIC[5], n=51, $P < 0.01$; Figs. 1a, 1d, 3, 4, and Table 2). This relationship was confirmed with the categorical data: singing primates also tend to be swingers and leapers (Table 1). Further confirmation of the association between the two continuous measures and the categorical measures is visually demonstrated in Fig. 1. This relationship was robust whether or not the analysis controlled for phylogeny or additional socio-ecological variables (Table 2). The association between these continuous measures is demonstrated in Fig. 2, Fig. S2, and Fig. S3 and their contrasts in Fig. S4. Of all the socio-ecological variables, after controlling for phylogeny, only monogamy was significantly related to high acoustic reappearance diversity calls (PGLM[1] and PIC[2], n=51, $P < 0.05$; Table 2), confirming earlier reports (Haimoff, 1986).

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[4] system:*R*; package:*caper*; version:1.0.1; function:*pgls*; params:*lambda,kappa,delta='ML'*
[5] system:*R*; package:*ape*; version:5.3; function:*pic*; params:scaled=*F*

Table 1. Vocal categories vs locomotion categories cross-tabulation counts

	Vocalization Type					
Locomotion Type	none	loud call	long call	chorus	duet / song	**Total**
vertical cling and leap	2	10	14	1	6	**33**
true brachiation	0	0	0	0	11	**11**
O.W. semibrachiation	14	19	4	1	1	**39**
N.W. semibrachiation	3	1	8	4	0	**16**
branch run and walk	38	31	41	1	9	**120**
quadrumanous	0	0	1	0	0	**1**
slow climb	3	1	3	0	0	**7**
knuckle walk	0	2	1	0	0	**3**
ground run and walk	1	27	2	0	0	**30**
Total	**61**	**91**	**74**	**7**	**27**	**260**

Numbers indicate counts of species in each categorical combination (*n*=260 species). Categories are arranged in increasing complexity, with “duet / song” being the most elaborate vocalization, and “vertical cling and leap” having highest degree of limb free locomotion. We list each species in the highest category for which it was reported. Vocalization descriptions were unavailable for 61 species (n/a). Semibrachiating monkeys are subdivided into Old World (O.W.) and New World (N.W.), the later having the benefit of prehensile tails. A chi-squared[6] test of this matrix is highly significant (*p* < 0.0001) suggesting a very non-random allocation of species amongst the vocal/locomotor categorical combinations. The complete absence of musical primates that live on the ground (Brown and Jordania 2013) likely drives the significance of this effect.

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[6] I had originally complied data, from the primary literature, to construct a very similar (also categorical) version this table in 2001, but did not perform the chi-squared test on it until 2019. While highly significant, it does not control for phylogeny, nor does it lend it-self to controlling for other confounding socio-ecological variables. While the main justification for this multi-decade long investigation started with this simple table, its inability to control for confounders served as the primary motivation for the bulk of the rest of the work underlying both my masters thesis and this dissertation. These subsequent efforts include the development of *ARDI* which can serve both as an outcome variable in socio-ecologically controlled phylogenetic regression as well as serving as a companion to my continuous locomotion percentage variables in phylogenetic independent contrasts.

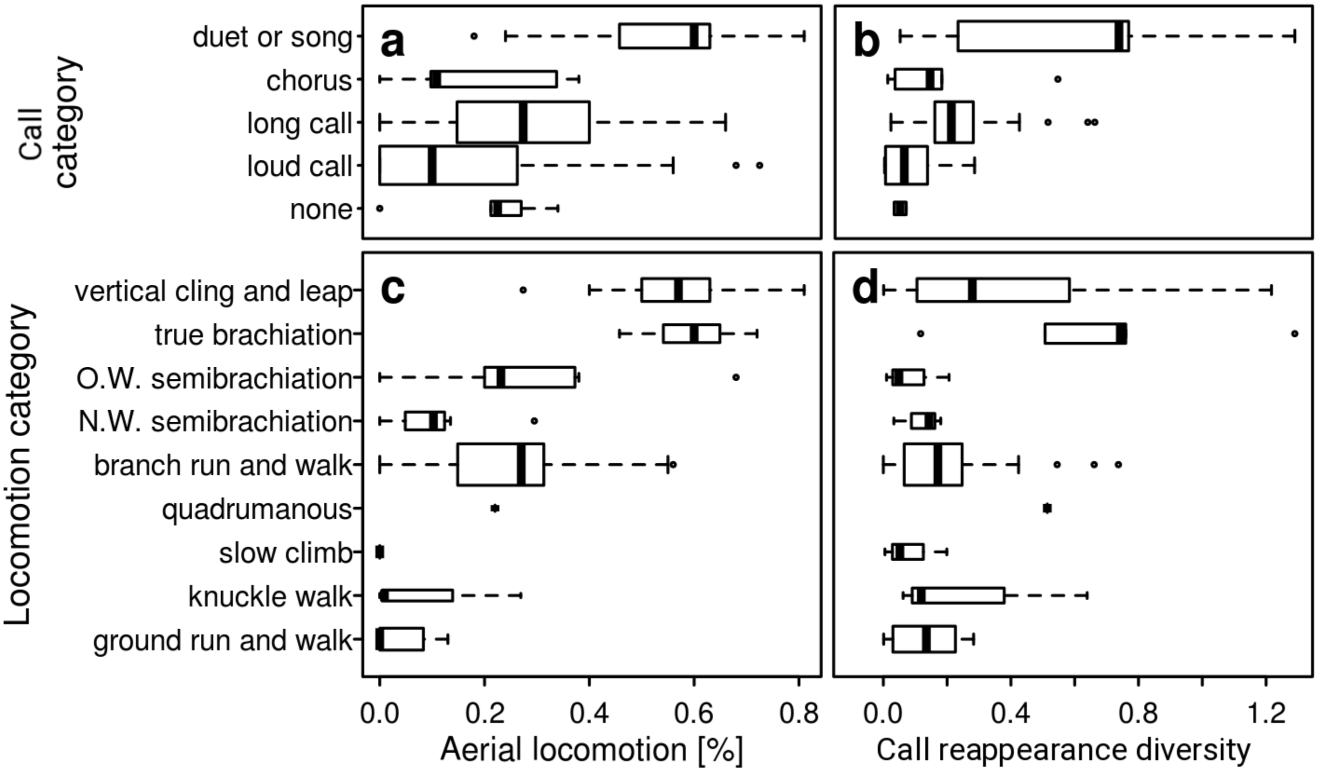

Figure 1. Boxplots of locomotor and call categories vs aerial*-spectrum and Acoustic
Categorical descriptions from the literature (y-axes) are plotted against our continuous scores (x-axes) for both locomotion and vocalization. Panels (b and c) indicate the relationship between our continuous scores and categories used by previous researchers. Panels (a and d) demonstrate the association between locomotion and display vocalizations. Aerial-spectrum locomotion categories had significant positive association with continuous reappearance diversity scores (Mann-Whitney U test, n=57, U=144, P=0.001) and continuous aerial-spectrum locomotion scores had significant positive association with the "duet or song" category (Mann-Whitney U test, n=102, U=160, P < 0.0001). Box plots indicate medians and interquartile range, with whiskers indicating confidence intervals and box thickness corresponding to the relative sample size of each category.

Table 2. Phylogenetic regression and independent contrast results of locomotion and control variables on ARDI

	a. IC bivariate				b. PGLM bivariate				c. PGLM multivariate			
	est.	std.err.	*t*-value	Pr(>|*t*|)	est.	*t*-value	Pr(>|*t*|)	R^2	est.	std.err.	*t*-value	Pr(>|*t*|)
wooded	1.21	0.87	1.39	0.172	0.423	0.895	0.3744	0.014	0.348	0.807	0.432	0.6688
arboreal	0.02	0.40	0.05	0.958	0.044	0.144	0.8860	0.000	-0.482	0.396	-1.219	0.2310
territorial	-0.02	0.37	-0.05	0.961	0.161	0.591	0.5569	0.006	-0.287	0.313	-0.918	0.3651
group size	-0.01	0.01	-1.06	0.296	-0.005	-0.865	0.3908	0.013	0.009	0.007	1.167	0.2511
monogamy	0.78	0.38	2.02	0.050 *	1.188	4.529	0.0000 *	0.265	0.687	0.328	2.092	0.0437 *
nocturnal	-0.24	0.55	-0.44	0.664	-0.018	-0.032	0.9745	0.000	0.444	0.354	1.255	0.2177
fruit	0.51	0.44	1.16	0.254	0.712	2.318	0.0240 *	0.086	0.438	0.266	1.651	0.1076 .
insect	-0.12	0.47	-0.25	0.806	0.109	0.278	0.7822	0.001				
mammals	0.31	0.58	0.52	0.604	0.166	0.304	0.7623	0.002				
mass, Kg	0.00	0.02	0.18	0.855	-0.005	-0.774	0.4423	0.010	0.006	0.007	0.861	0.3951
claws					0.003	0.019	0.9853	0.000				
climb, %	-2.06	1.27	-1.62	0.112	-0.021	-1.701	0.0967	0.067				
swing, %	0.44	0.79	0.56	0.576	1.027	2.166	0.0357 *	0.096	1.363	0.553	2.463	0.0188 *
leap, %	1.13	0.61	1.86	0.071 .	0.803	1.963	0.0560 .	0.081	1.533	0.493	3.109	0.0037 **

Bivariate (**a** and **b**) as well as multivariate (**c**) phylogenetically controlled models using both independent contrasts (*n*=42) and phylogenetic generalized linear modeling [PGLM] of various controls and locomotion estimates on the acoustic reappearance diversity scores. The R^2 value for the full PGLM model[1] was 0.43 (adjusted R^2 = 0.27). Missing rows reflect removal of a variable from the multivariate model (**c**) due to low R^2 or prohibitively missing data (**a**). It is interesting to note that, while *arboreality* individually has a positive association in the reduced models, adding *locomotion* (and *wooded*) seems to reverse the direction of association to negative. Also leaping and swinging spectrum behaviors are significantly positively associated with ARDI scores except when using independent contrasts. Independent contrasts has more severe penalties for close relatedness of phylogenetic clades, suggesting that a gibbon, genus-specific, effect is likely driving the significance of swinging in the PGLM models is instead more effectively controlled for under IC.

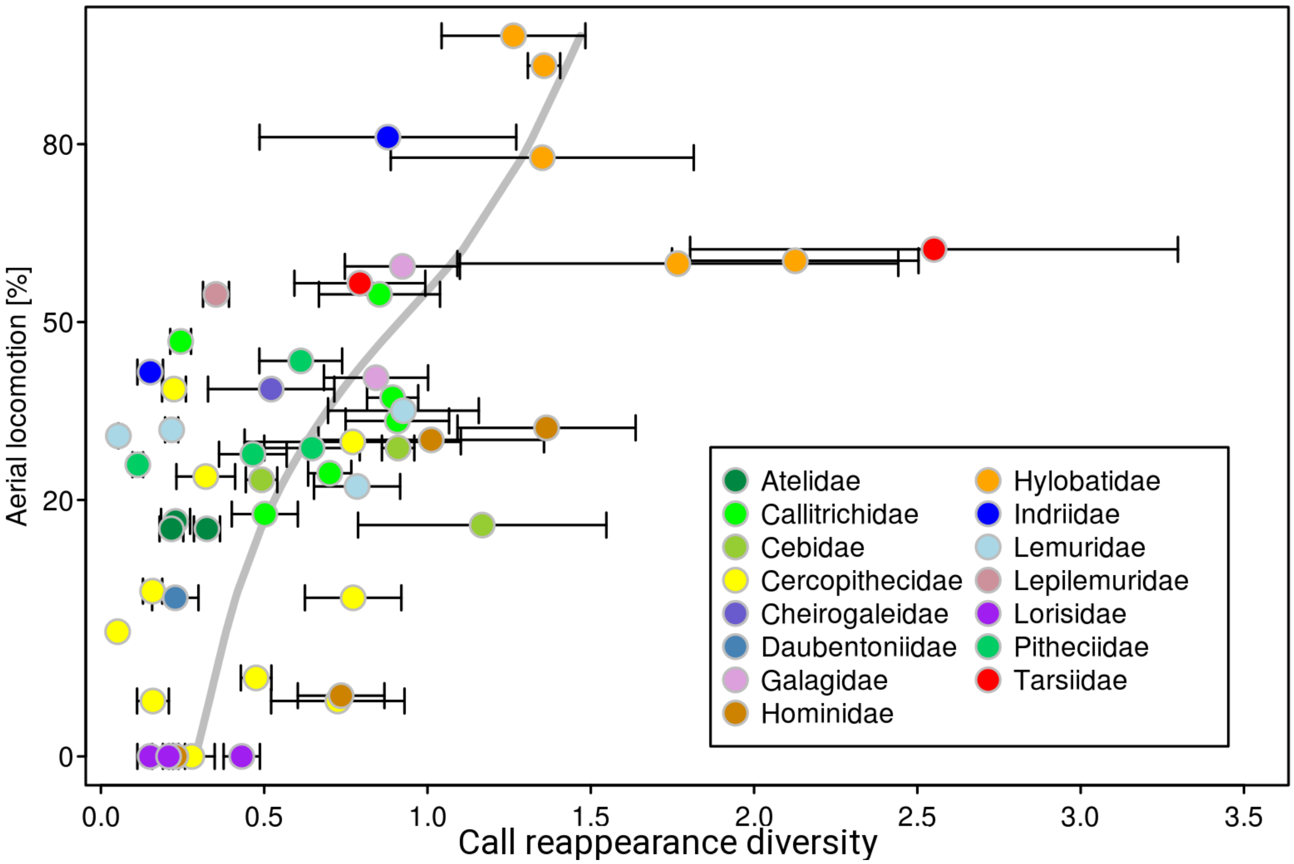

Figure 2. Continuous measure scatterplot: aerial (leap+swing) vs reappearance diversity
Max (±SE) reappearance diversity scores from manual spectrographic scoring are shown against estimated "aerial-spectrum" locomotion (leaping + swinging) percentages for each species (*n*=51). The standard error for each reappearance diversity score was estimated via bootstrap by taking the standard deviation of the max estimates for 10,000 different samplings (with replacement) of all vocalization-level reappearance diversity scores for each species. A smooth spline (gray line) was fit to the data (using 3 degrees of freedom). Points are colored according to taxonomic family membership.

Discussion

Our analysis reveals a strong contrast in levels of vocal acoustic display behavior between aerial-spectrum arboreal locomotors and more terrestrial primates (Fig. 2). Although some of the most acrobatic locomoting genera (e.g. *Hylobates*, *Tarsius*, and *Indri*) were previously known to sing, the relatively high vocal reappearance diversity measures for the frequently jumping Galagidae and Callitrichidae further confirm the relationship between locomotion and acoustic display behavior (Fig.

2). The lack of singing amongst non-aerial spectrum locomoting primates was even more striking: their vocal reappearance diversity scores showed no overlap with those of the most aerial species. Terrestrial primates (e.g. *Papio*, *Theropithecus*, *Gorilla*, and most *Macaca*) did not produce notably elaborate vocalizations. Importantly, vocal reappearance diversity tracked aerial-spectrum locomotion rather than habitat or elevation: for example, all four strictly arboreal, yet non-jumping Lorisidae species had quite low acoustic reappearance diversity. Further, highly vocal genera such as *Allouatta*, exhibit somewhat monomorphous, unvaried, and low reappearance diversity howls, and, as predicted, rarely jump or brachiate. Thus, high levels of vocal activity alone did not confound our observed association of display calls with precarious aerial-spectrum locomotion.

While we have demonstrated a strong and controlled correlation between aerial spectrum locomotion and elaborate vocalizations, we must further consider that more monogamous mating systems also play a strong role in this possibly three-way co-evolution. We see a significant effect for not only monogamous[7] groups but also those groups that tend to have a relatively small group size of two to six individuals. It is possible that primate species that perform best in small intimate groups, such as gibbons, callitrichids, and indrii, tend to also require many years of learning complex survival-enhancing locomotion. Thus, it seems that many of the observations of other researchers, regarding the importance of parental and group learning effects on the evolution of song, may be confounded by the main reason for this extended parental care. That is, the extended parental investment of primates may exist to facilitate learning precarious arboreal subsistence strategies that typically involve high-risk locomotion, which, in some of these species, has entailed the learning of sophisticated calls used to *signal* the underlying cognitive circuitry that could underlie both behaviors.

It is important to point out that, while significant in previous analyses (Chapter 2), wooded

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[7] Mate choice leading to these prolonged social associations confers deferred direct benefits ranging from collaboration on home range defense to collective infant care (Brooks et al., 2010).

habitat was not significant in this phylogenetically controlled analysis run. Also, while our continuous locomotion variable could be partially masking these more simple, binary wooded and arboreality variables, most of the reduction in significance appears to primarily originate from adding phylogenetic control. Thus, terrestriality is likely to be highly confounded with just a few closely related taxa in the entire primate tree and therefore represents far fewer independent data points. A larger dataset will likely re-vindicate the adaptive influence of habitat acoustics on elaborate call evolution. However, for now, it appears that a more arboreal *complexity* oriented theory, one that is mediated by, or manifests through, more acrobatic locomotion, holds as strongest in predicting elaborate display behavior in primates.

The association between aerial locomotion and elaborate acoustic display we have demonstrated for primates could also apply to other animal groups. For example, many non-flying birds produce rather simple vocalizations, whereas more aerial and branch-landing species such as songbirds (Passeriformes) and hummingbirds (Trochilidae) sing more elaborate songs and have more specialized neural circuitry for learning and producing these vocalizations (Catchpole and Slater, 1995). Problematic exceptions to our hypothesis likely exist in other lesser known taxa such as Chiropterans, Cetaceans, and Arthropods. Many bats are similarly acrobatic and also produce relatively elaborate, yet non-display, echo-locative vocalizations. Cetaceans are known for producing elaborate vocalizations and although they do not fly, they could face similar multidimensional, spatio-temporal demands for precisely estimating their dives in relation to swimming speed and air reserves to avoid drowning. Indeed, of the thousands of singing species, nearly all appear to locomote along trajectories through three-dimensional space, with the obvious exception of *Homo sapiens* who locomotes on a two-dimensional surface (Brown and Jordania, 2013).

So what does this hypothesis suggest about humans, the most musically elaborate of all species? Much like language, human music is rather unique—none of the primate species we have reviewed here produces calls that are as sophisticated as human music. This singularity may correspondingly result from similarly unique evolutionary and cultural processes. It is also possible, however, that hominid acoustic display behavior was subject to evolutionary pressures similar to what we have reported here[8] for non-human primates (Mithen, 2006, p. 126). A variety of environmental spatio-temporal pressures, specifically, could have selected for neural circuitry that underlies the successful execution of both multi-dimensional vocal patterning and trajectory-cognizant locomotion. Humans are no less ballistic than gibbons, but whereas gibbons throw themselves from tree to tree, humans throw rocks and other projectiles for hunting and warfare (Calvin, 1983). These and other human behaviors (e.g. bipedal locomotion, tool use, spatially-complex foraging) that rely heavily on spatio-temporal perception and motor control indicate the extraordinary degree of human spatial cognition, which could in turn be efficiently signaled through singing and drumming. Thus, the specific primate-order-level association demonstrated here—between elaborate singing and aerial locomotion—could exemplify a more general pattern for all animals (including humans) to evolve elaborate acoustic displays that advertise their neural competencies[9] for spatio-temporally demanding behaviors.

The observed connections above between locomotor ability and vocal display should not come as a surprise as all human cultures are also known to have some form of dancing. The two art forms, in humans, are for the most part not usually disassociated from one another (Nettl 1983) and typically manifest as a combined vocal and motor display. In some cultures, in fact, the word music also implies dance. While the leaping and swinging behaviors studied here are not typically necessarily used as a part of display or even for the purposes of play, we feel that they reflect proficiencies for the same underlying motor control and coordination-related cognition. We have noted that combined vocal and locomotor displays, especially high risk arboreal ones, are fairly rare in primates. Gibbons are the only

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[8] especially with regards to our findings surrounding small, intimate groups

[9] Obviously there are still issues to work out in applying this theory to the songs of arthropods.

genera who regularly perform both forms of display simultaneously, although callitrichids could arguably form an additional example. In light of the recent archaeological finding of *Ardi*[10]—a habitually arboreal fossil hominine, that continued to practice palmigrade, above-branch, quadrupedal clambering (Lovejoy et al., 2009)—it seems likely that other primitive arboreal hominoid-associated behaviors persisted into early hominines. Such behaviors, perhaps including social monogamy or even duetting behavior, could have have continued to manifest in humans in the form of a combined locomotor and vocal display system. It has not escaped our attention that our song-to-music bridging ARDI formulation, in combination with the paleolithic revelations of *Ardi*, will continue to provide illuminating insights into the multi-million year, fossil-poor miocene gap, separating humans from the rest of the primate order.

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[10] Ardipithecus ramidus (ARA-VP-6/500) is a near-complete fossil skeleton discovered in Eastern Africa dated as having lived 4.4 million years ago.

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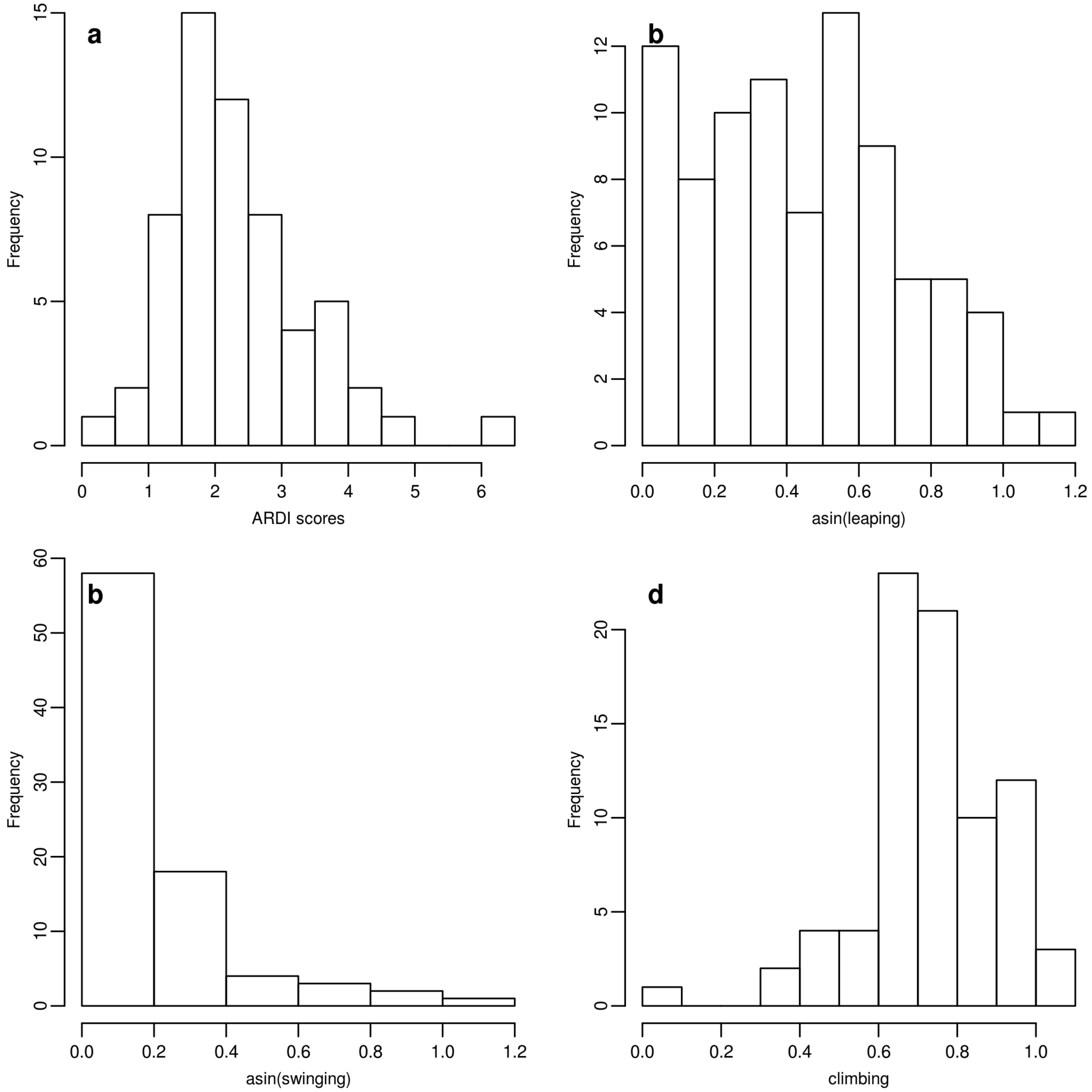
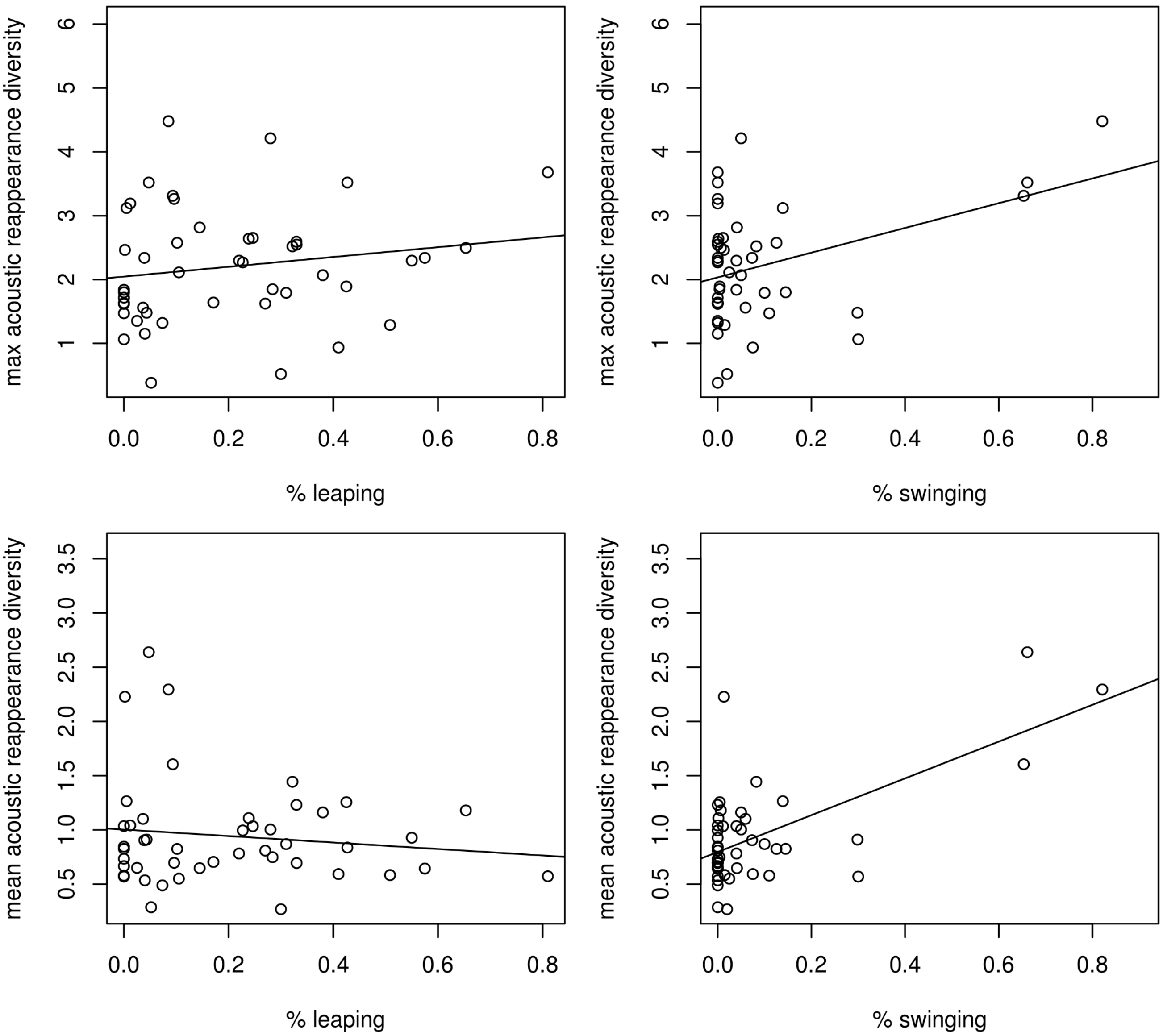
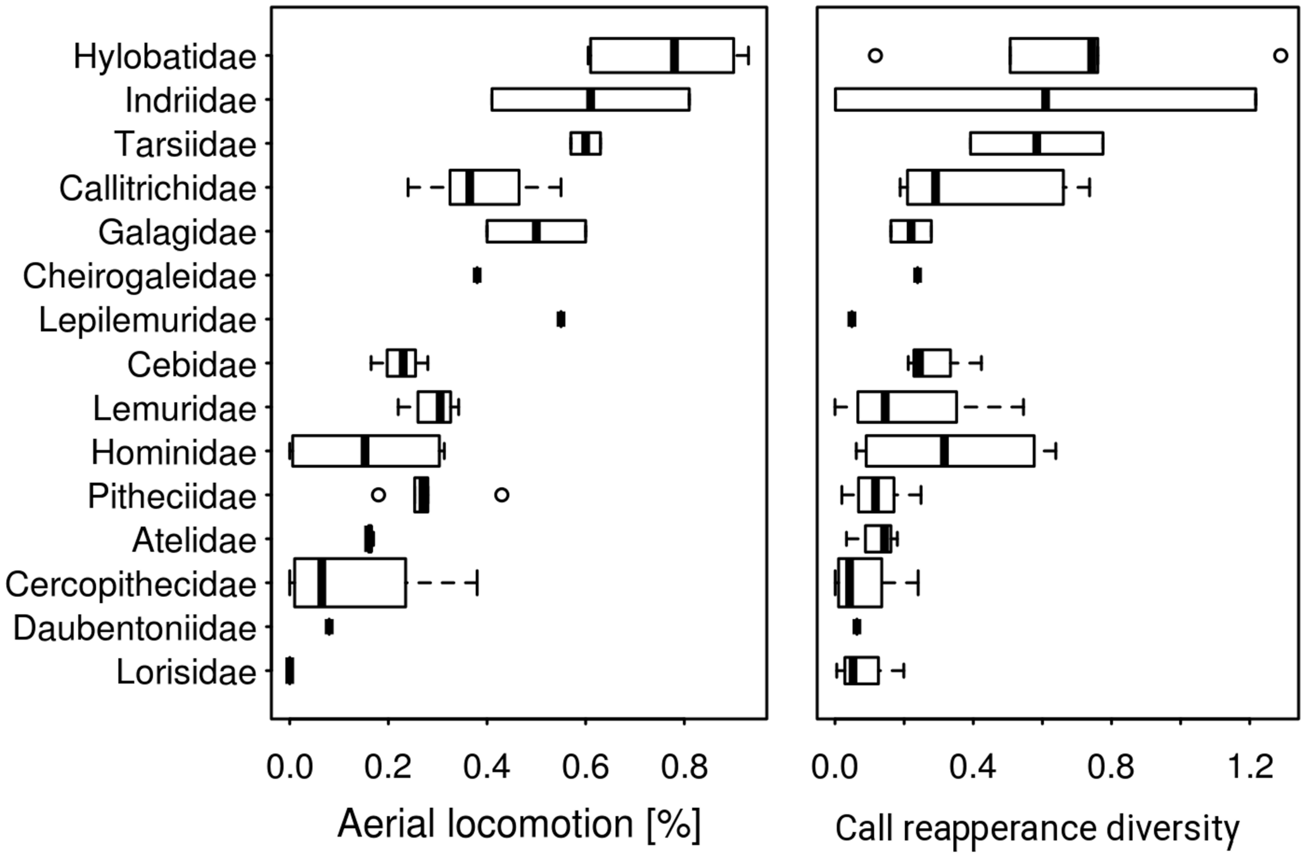


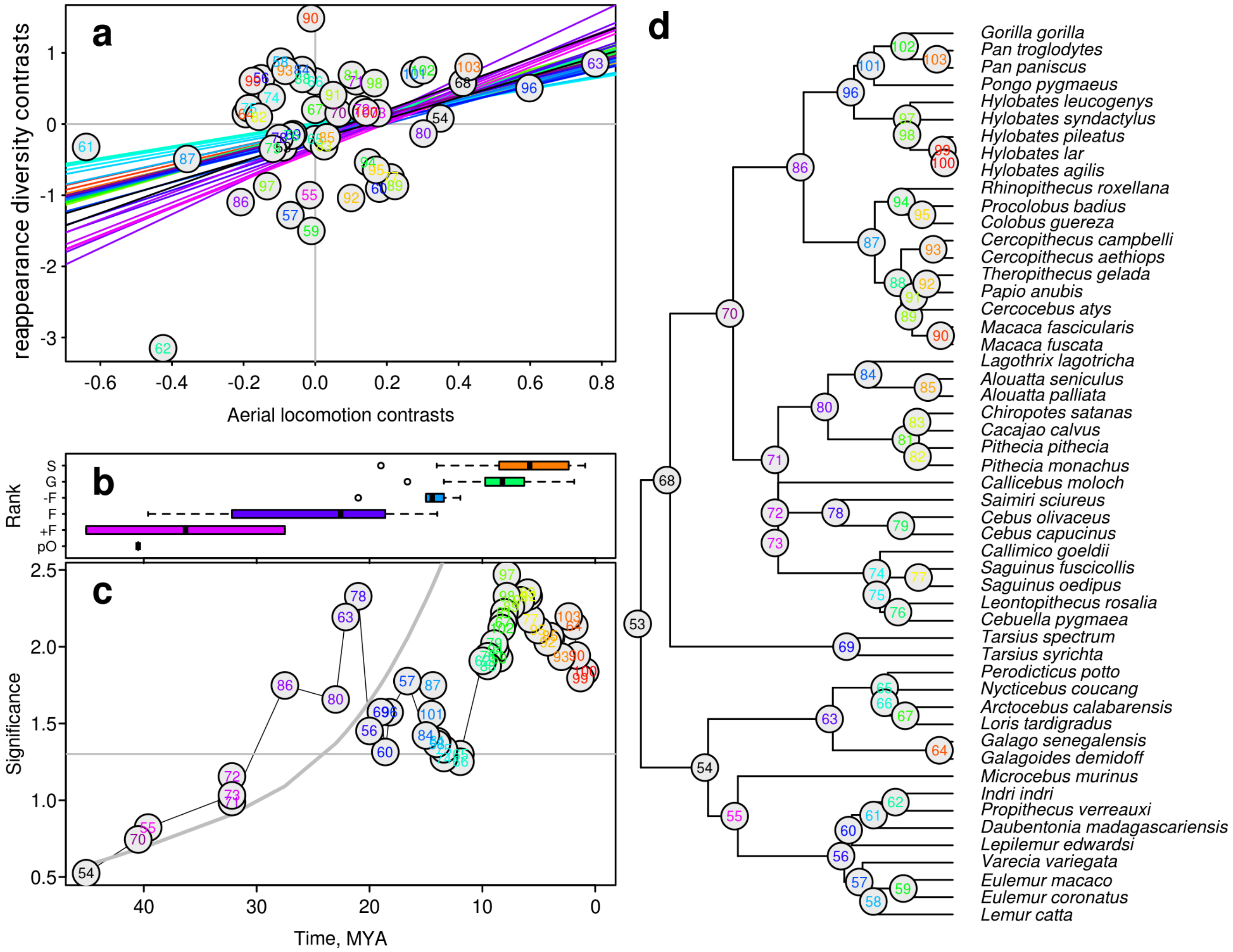
Supplemental Figure 1. Histograms of continuous variable distributions and transformations
While we did not transform our main ARDI outcome variable, or climbing (including scrambling), we did transform swinging and leaping variables by applying the arcsine of the square-root of percentages. These changes helped to normalize the variable distributions and, in-turn, improve the normality of the residuals of subsequent regression analysis.



Supplemental Figure 2. Scatterplots of leap and swing percentages versus max and mean ARDI Max and mean reappearance diversity scores from manual spectrographic scoring are plotted untransformed against leaping and swinging locomotion percentages for each species (*n*=46). Simple linear regression lines were fit to the data for each locomotion type independently. The p-values for these regression lines are 0.25 for leaping and less than 0.001 for swinging on max(ARDI) and 0.4 for leaping and less than 0.0001 for swinging on mean(ARDI). The negative associating regression line for leaping regressed on mean(ARDI) is concerning only when analyzed in isolation and without considering the typical rarity of display calls.



Supplemental Figure 3. Boxplots of ARDI scores for each primate family
The (**a**) percentage of aerial-spectrum locomotion scores (*n*=102) and (**b**) acoustic reappearance diversity scores (*n*=51) partitioned by taxonomic family. Boxplots show medians and quartiles, with whiskers signifying the range of points still within several standard deviations from the median. Families are decreasingly ordered by average of their locomotion and reappearance diversity scores



Supplemental Figure 4. Regressions on phylogenetic contrasts with successive tree pruning Elaborate vocal displays and acrobatic locomotion appear to have co-evolved at every taxonomic rank of the primate tree. Contrasts (pair-wise subtractions between both variables' values at adjacent nodes) and their regression lines, plotted in a progressively rank-trimmed fashion (trimming the tree node-by-node from right to left) showing the most recent species level divergence (**a**). Colors for each rank trim (**b**) correspond to a particular internal phylogenetic divergence at which all contrasts younger than it are excluded from the linear regression. Each time a terminal branch is trimmed a new regression on remaining points results in a new significance level (**c**). Trimmings at the family and super family level have the highest significance. These nodes are correspondingly colored in the phylogenetic tree (**d**). Lower than expected p-values and correspondingly higher "significance", given the decreasing number of datapoints at each successive trimming, at earlier times and higher taxonomic ranks, in the last 10 to 20 million years, as depicted in (c), could suggest that these two traits are co-evolving very slowly, perhaps taking as long as 5 million years for elaborate acoustic display behavior to catch up with changes in locomotion or habitat. This raises the interesting, albeit unlikely, possibility that the entire history of hominine musically could exist due to phylogenetic inertia alone.

Supplemental Table 1 Vocalization, locomotion, and control data used in the analyses

		ARDI		socioecology						physiology			A.P.	diet			locomotion	
genus	**species**	**mean**	**max**	**wooded**	**arboreal**	**territorial**	**monogamy**	**group**	**range**	**mass**	**claws**	**prehensile**	**nocturnal**	**fruit**	**insect**	**mammals**	**leap %**	**swing %**
Alouatta	palliata	0.91	0.39	TRUE	TRUE	FALSE	FALSE	12.0	0.4	6.2	0	TRUE	FALSE	FALSE	FALSE	FALSE	4%	7%
Alouatta	seniculus	1.10	0.20	TRUE	TRUE	FALSE	FALSE	8.9	0.6	6.1	0	TRUE	FALSE	FALSE	FALSE	FALSE	4%	6%
Lagothrix	lagotricha	0.91	0.14	TRUE	TRUE	TRUE	FALSE	33.0	1.3	7.2	0	TRUE	FALSE	TRUE	FALSE	FALSE	4%	30%
Callimico	goeldii	0.58	0.14	TRUE	TRUE	TRUE	TRUE	7.7	NA	0.5	4	FALSE	FALSE	TRUE	TRUE	FALSE	51%	2%
Cebuella	pygmaea	0.89	0.09	TRUE	TRUE	TRUE	TRUE	5.7	NA	0.1	4	FALSE	FALSE	TRUE	TRUE	FALSE	28%	0%
Leontopithecus	rosalia	1.00	1.11	TRUE	TRUE	TRUE	TRUE	4.7	NA	0.6	4	FALSE	FALSE	TRUE	TRUE	FALSE	28%	5%
Saguinus	fuscicollis	1.23	0.17	TRUE	TRUE	TRUE	TRUE	5.0	1.3	0.4	4	FALSE	FALSE	TRUE	TRUE	FALSE	33%	0%
Saguinus	oedipus	0.70	0.30	TRUE	TRUE	TRUE	TRUE	7.4	2.1	0.4	4	FALSE	FALSE	TRUE	TRUE	FALSE	33%	0%
Cebus	capucinus	0.55	0.30	TRUE	FALSE	FALSE	FALSE	17.5	2.0	3.1	0	TRUE	FALSE	TRUE	TRUE	FALSE	11%	2%
Cebus	olivaceus	1.00	0.37	TRUE	TRUE	FALSE	FALSE	17.4	2.3	2.9	0	TRUE	FALSE	TRUE	TRUE	FALSE	23%	0%
Saimiri	sciureus	1.03	0.14	TRUE	TRUE	TRUE	FALSE	42.0	1.5	0.8	0	TRUE	FALSE	TRUE	TRUE	FALSE	25%	1%
Cercocebus	atys	1.04	0.61	TRUE	FALSE	FALSE	FALSE	50.0	NA	8.6	0	FALSE	FALSE	FALSE	FALSE	FALSE	2%	0%
Cercopithecus	aethiops	1.05	0.05	FALSE	FALSE	TRUE	FALSE	19.7	1.0	4.2	0	FALSE	FALSE	FALSE	FALSE	FALSE	1%	0%
Cercopithecus	campbelli	0.29	0.04	TRUE	TRUE	TRUE	FALSE	9.0	NA	3.6	0	FALSE	FALSE	FALSE	FALSE	FALSE	5%	0%
Cercopithecus	neglectus	0.70	0.31	TRUE	FALSE	FALSE	FALSE	5.0	NA	5.7	0	FALSE	FALSE	FALSE	FALSE	FALSE	17%	0%
Macaca	fascicularis	0.49	0.16	TRUE	FALSE	FALSE	FALSE	82.5	1.9	4.5	0	FALSE	FALSE	FALSE	FALSE	FALSE	7%	0%
Macaca	fuscata	0.70	0.68	TRUE	FALSE	FALSE	FALSE	36.5	NA	9.5	0	FALSE	FALSE	FALSE	FALSE	FALSE	10%	0%
Macaca	nemestrina	0.73	0.05	TRUE	FALSE	FALSE	FALSE	35.0	2.0	7.6	0	FALSE	FALSE	FALSE	FALSE	FALSE	0%	0%
Macaca	radiata	0.80	0.17	TRUE	FALSE	FALSE	FALSE	24.9	NA	5.3	0	FALSE	FALSE	FALSE	FALSE	FALSE	NA	NA
Macaca	silenus	0.86	0.12	TRUE	TRUE	TRUE	FALSE	26.5	NA	7.5	0	FALSE	FALSE	FALSE	FALSE	FALSE	NA	NA
Macaca	sylvanus	1.42	0.42	TRUE	FALSE	TRUE	FALSE	18.3	NA	13.5	0	FALSE	FALSE	FALSE	FALSE	FALSE	NA	NA
Mandrillus	sphinx	0.85	0.33	TRUE	FALSE	FALSE	FALSE	13.9	NA	22.3	0	FALSE	FALSE	FALSE	FALSE	FALSE	0%	0%
Papio	anubis	0.65	0.47	FALSE	FALSE	FALSE	FALSE	58.8	NA	17.8	0	FALSE	FALSE	FALSE	FALSE	FALSE	3%	0%
Theropithecus	gelada	0.67	0.20	FALSE	FALSE	TRUE	FALSE	60.0	2.5	15.4	0	FALSE	FALSE	FALSE	FALSE	FALSE	0%	0%
Colobus	guereza	1.26	0.38	TRUE	TRUE	TRUE	FALSE	9.0	0.5	11.4	0	FALSE	FALSE	FALSE	FALSE	FALSE	43%	0%
Procolobus	badius	0.79	0.45	TRUE	TRUE	TRUE	FALSE	42.5	0.6	8.5	0	FALSE	FALSE	FALSE	FALSE	FALSE	28%	0%
Rhinopithecus	roxellana	0.65	0.89	TRUE	TRUE	TRUE	FALSE	85.0	NA	14.8	0	FALSE	FALSE	FALSE	FALSE	FALSE	14%	4%
Microcebus	murinus	1.16	0.53	TRUE	TRUE	FALSE	FALSE	1.0	NA	0.1	0	FALSE	FALSE	FALSE	FALSE	FALSE	38%	5%
Daubentonia	madagascariensis	0.54	0.13	TRUE	FALSE	TRUE	FALSE	50.0	NA	2.6	4	FALSE	FALSE	FALSE	TRUE	FALSE	4%	0%
Galago	senegalensis	1.18	0.32	TRUE	TRUE	TRUE	FALSE	2.0	NA	0.2	1	FALSE	FALSE	TRUE	TRUE	TRUE	65%	1%
Galagoides	demidoff	1.27	0.17	TRUE	TRUE	TRUE	FALSE	1.5	NA	0.1	1	FALSE	FALSE	TRUE	TRUE	TRUE	55%	0%
Gorilla	gorilla	1.04	0.09	TRUE	FALSE	FALSE	FALSE	8.5	0.7	124.7	0	FALSE	FALSE	FALSE	FALSE	FALSE	0%	4%
Pan	paniscus	0.83	0.26	TRUE	FALSE	TRUE	FALSE	27.8	NA	39.1	0	FALSE	FALSE	TRUE	FALSE	FALSE	10%	13%
Pan	troglodytes	2.23	0.06	TRUE	FALSE	TRUE	FALSE	49.8	3.9	45.0	0	FALSE	FALSE	FALSE	FALSE	TRUE	0%	1%
Pongo	pygmaeus	1.26	0.65	TRUE	FALSE	FALSE	FALSE	1.4	0.5	57.0	0	FALSE	FALSE	TRUE	TRUE	TRUE	1%	14%
Hylobates	agilis	1.60	0.51	TRUE	TRUE	TRUE	TRUE	4.4	1.2	5.9	0	FALSE	FALSE	TRUE	FALSE	FALSE	9%	65%
Hylobates	concolor	3.56	0.00	TRUE	TRUE	TRUE	TRUE	NA	NA	7.7	0	FALSE	FALSE	TRUE	FALSE	FALSE	NA	NA
Hylobates	lar	2.64	0.15	TRUE	TRUE	TRUE	TRUE	3.4	1.5	5.6	0	FALSE	FALSE	TRUE	FALSE	FALSE	5%	66%
Hylobates	leucogenys	3.60	0.14	TRUE	TRUE	TRUE	TRUE	3.8	NA	7.4	0	FALSE	FALSE	TRUE	FALSE	FALSE	0%	91%
Hylobates	pileatus	2.29	0.77	TRUE	TRUE	TRUE	TRUE	4.0	NA	5.5	0	FALSE	FALSE	TRUE	FALSE	FALSE	9%	82%
Hylobates	syndactylus	1.12	1.48	TRUE	TRUE	TRUE	TRUE	4.0	0.9	11.3	0	FALSE	FALSE	TRUE	FALSE	FALSE	0%	59%
Indri	indri	0.57	1.49	TRUE	TRUE	TRUE	TRUE	4.3	0.3	6.3	1	FALSE	FALSE	FALSE	FALSE	FALSE	81%	0%
Propithecus	verreauxi	0.59	0.21	TRUE	TRUE	TRUE	TRUE	5.1	0.9	3.5	1	FALSE	FALSE	FALSE	FALSE	FALSE	41%	8%
Eulemur	coronatus	0.27	0.08	TRUE	TRUE	TRUE	FALSE	8.4	NA	1.2	1	FALSE	FALSE	FALSE	FALSE	FALSE	30%	2%
Eulemur	macaco	0.87	0.15	TRUE	TRUE	TRUE	FALSE	8.4	NA	1.8	1	FALSE	TRUE	FALSE	FALSE	FALSE	31%	10%
Varecia	variegata	1.44	0.13	TRUE	TRUE	TRUE	TRUE	5.3	NA	3.5	1	FALSE	FALSE	FALSE	FALSE	FALSE	32%	8%
Lemur	catta	0.78	0.34	TRUE	FALSE	TRUE	FALSE	12.2	1.0	2.2	1	FALSE	FALSE	FALSE	FALSE	FALSE	22%	4%
Lepilemur	edwardsi	0.93	0.54	TRUE	TRUE	TRUE	FALSE	1.0	NA	0.9	1	FALSE	FALSE	FALSE	FALSE	FALSE	55%	0%
Loris	tardigradus	0.57	0.19	TRUE	TRUE	TRUE	FALSE	1.0	NA	0.2	1	FALSE	TRUE	FALSE	TRUE	FALSE	0%	30%
Nycticebus	coucang	0.83	0.21	TRUE	TRUE	TRUE	FALSE	1.0	NA	0.7	1	FALSE	TRUE	FALSE	TRUE	FALSE	0%	15%
Arctocebus	calabarensis	0.94	0.31	TRUE	TRUE	TRUE	FALSE	1.0	NA	0.3	1	FALSE	TRUE	FALSE	TRUE	FALSE	NA	NA
Perodicticus	potto	0.58	0.44	TRUE	TRUE	TRUE	FALSE	1.0	NA	1.1	1	FALSE	TRUE	FALSE	TRUE	FALSE	0%	11%
Callicebus	moloch	1.11	0.50	TRUE	TRUE	TRUE	TRUE	4.5	0.6	1.0	1	FALSE	FALSE	TRUE	TRUE	FALSE	24%	0%
Cacajao	calvus	0.81	0.13	TRUE	TRUE	FALSE	FALSE	30.0	NA	3.2	0	FALSE	FALSE	TRUE	FALSE	FALSE	27%	0%
Chiropotes	satanas	1.12	0.19	TRUE	TRUE	TRUE	FALSE	19.0	2.5	2.9	0	FALSE	FALSE	TRUE	FALSE	FALSE	NA	NA
Pithecia	monachus	0.75	0.30	TRUE	TRUE	TRUE	TRUE	4.0	NA	2.4	0	FALSE	FALSE	TRUE	FALSE	FALSE	28%	0%
Pithecia	pithecia	0.84	1.18	TRUE	TRUE	TRUE	TRUE	2.7	NA	1.8	0	FALSE	FALSE	TRUE	FALSE	FALSE	43%	0%
Tarsius	spectrum	1.84	1.51	TRUE	TRUE	TRUE	TRUE	2.5	NA	0.1	2	FALSE	TRUE	FALSE	TRUE	FALSE	NA	NA
Tarsius	syrichta	0.64	0.57	TRUE	TRUE	TRUE	FALSE	1.0	NA	0.1	2	FALSE	TRUE	FALSE	TRUE	FALSE	58%	0%

Chapter 5 - Acoustic utterance universals, a syllabically discrepant definition, and ocular-motor signaling origins

Abstract

Darwin considered music to be the most mysterious behavior with which we are endowed and the best example of sexual selection in humans (Darwin, 1871). This dissertation attempted to help solve this mystery by applying principles of behavioral ecology and signaling theory to a broad base of data and theories developed in ethnomusicology and biomusicology, as well as from the primate locomotion, vocalization, and origins literature. I have provided a new and compelling theory in the form of the spatio-motor signaling hypothesis presented in the previous chapter. This theory posits that spatio-visual cognitive evolution in primates was largely driven by an increasing requirement for active locomotion, especially in the form of leaping, between the terminal branches of floral entities. These elaborate vocal communication systems likely evolved, initially, to both stay in contact and assert identity across these distances, and, eventually, to signal the spatially discriminating cognition and ocular sensory-motor proficiencies required to land such leaps.

Primate origins theories re-purposed: arboreal, acoustic, and social adaptations

Primates are an order of mammals originating 50 to 80 million years ago. Due to their success in radiating across the globe, primates diversified substantially as they adapted to a wide array of ecosystems (Fleagle, 1999). Consequently they have a correspondingly vast array of locomotor and vocalization behaviors (Delgado, 2006; Gebo, 2013), which make them not only fascinating to study but also convenient to model quantitatively (Wich and Nunn, 2002). They originated as a strictly arboreal clade, adept at using arboreal substrate to avoid predators (Crompton et al., 1993), and endowed with distinct features such as largely clawless[1] grasping appendages, relatively long leaping legs, and unusually convergent eyes that may have helped them in landing these embracing appendages on complex substrate (Szalay and Dagosto, 1988).

It is also possible that primates evolved a more embracing grasp friendly morphology, such as nails[1], to facilitate infants riding more comfortably upon their parents, rather than having them parked alone, to avoid infant predation exposure (Ross, 2001). As a result, they have developed a more permanently mobile predation avoidance and subsistence strategy while venturing between terminal branches to forage arboreal territories. Such a locomotively dispersed lifestyle likely required them to evolve corresponding communication systems for transmitting information across forest substrate to conspecifics, relying predominantly upon sound rather than vision or smell, over these long, often visually-occluded, distances (Catchpole and Slater, 1995). Simple location, identity, and food foraging calls were likely the first kind to emerge (Fig. S1). The acoustic adaptation hypothesis [AAH], predicts tonal and highly intervallic calls in more dense substrate as is found in forests in which many primates evolved (Hansen, 1979; Morton, 1975). While my study had mixed results regarding the influence of forest habitat on the elaborate calling of euprimates, this could still be a selection pressure, earlier, in the evolution from mammals to primates (from 100 to 68 MYA) despite its weaker signal in this

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[1] an important exception includes callitrichids who have re-evolved claw-like nails.

euprimate aspect limited analyses (see Chapters 2 and 4).

Social theories, such as those relating to signaling by groups (Brown, 2000; Hagen and Bryant, 2003) and potential mates (Darwin, 1871; Miller, 2000), were also minimally tested via monogamy and group size variables that additionally served as instrumental controls for my main co-evolutionary test on locomotion. Here I found a strong effect for social monogamy which suggests that mate choice, and perhaps sexual selection[2], were core mechanisms governing the emergence of song like calls throughout the course of euprimate evolution. The group effects which I found to be significant (those with 2-6 individuals), were quite confounded with my social monogamy variable. I found this group size effect to occur independently of the many obvious candidate species who are both monogamous and musical such as Indri, most gibbons, and some tarsiers. That is, I discovered many more genera of musical primates that also happened to be socially monogamous (e.g. some lemurs), as well as those that are polyandrous but live in small family sized groups such as callitrichids. This three-way signaling relationship is further constrained by habitat and feeds back into the evolution of arboreal and leaping conducive morphology (Fig. 1)

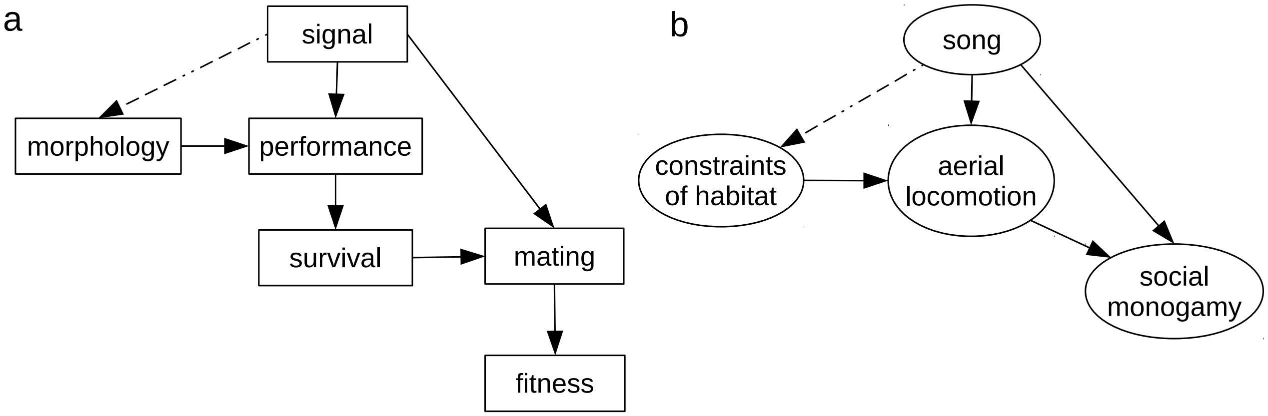

Figure 1 a) Graph theoretic signaling model and b) preliminary ecological causal model of song The above flow diagram (**a**) illustrates the indirect feedback effect (dashed arrow) of a signal on morphology evolution based on its impact on performance (redrawn from Irschick et al., 2015, p. 50). An analogous causal diagram (**b**) of song's indirect effect (dashed arrow) on morphological solutions to habitat constraints via influencing how proficient aerial locomotion can be signaled to potential mates.

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[2] plus “indirect selection” acting on genetically correlated [vocal and motor] traits (Brooks et al., 2010)

Spatio-motor signaling origins of elaborate acoustic display

I have previously reported a significant association between "airborne" locomotion and the average number of tonally intervallic repeated syllabic groups [nTIRGs] in a phylogenetically controlled analysis (Schruth, 2006 unpublished masters thesis). I have since modified terminology, reduced sources of bias, and looked more systematically at other possible connections between musical components of calls and their ecological influences (see Fig. S2). And despite these modifications—a re-branding of the locomotion of interest as "aerial-spectrum," removing *tone* from the more recent "ARDI" formulation[3], and impartializing my perspective with more exploratory statistical tools such as PCA and causal modeling—my core results, from last decade, remain significant.

My masters' thesis approach improved upon my earlier proposals which suggested that music evolved as "*communication*" of spatial intelligence (Schruth, 2001) and focused specifically on "*signal*[s] of remote targeting ability" (Schruth, 2006). The current work has shifted attention backwards in time towards early primates, instead of humans, focused on song, rather than music, and zeroed in on (substrate) surface landing, rather than remote targeting. Similar to other researchers, I have run in to difficulties in modeling exactly *what* elaborate acoustic display indicates or signals about these performers. My cognitive focus has recently morphed away from the higher-brain (esp. parietal lobe) dimensional processing toward more ancient cortical levels (esp. basal ganglia and brain stem) governing sensory input comparisons relevant for fine control of the small muscles (Sachs, 2007).

While I have targeted my theories on signals of cognition required for comparing orbital input discrepancies, others have focused on the "tonal gymnastics" (Nettl, 1983, p. 33) of music or the multi-modality of art as indicators of physical, "hands-on" competence (Dissanayake, 2000a) or motor control (Pinker, 1997). Such coordination is likely required for rotating forelimbs in the grasp-landing

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[3] See chapter 2 for details on the development of the acoustic reappearance diversity index [ARDI].

of primates. While a high degree of orbital convergence [OC] facilitates generation of a single, stereoscopic image from disparate inputs of overlapping visual fields in primates, as is likely required for successfully landing these high-impact leaps, it is further accentuated via *motor-based control* over ocular orbits *within* these apertures. Furthermore, while *short* range depth perception for the late-stage of a leaping bout is important (Chapter 3), fine-tuning of ocular rectus muscles for focusing, with precision, on *distant* targets could be as well. This caveat, to the main point of the current rendition of my spatial-based signaling theses, arguably preserves the theory's relevance to the many species of singing aves and cetaceans, both typically with laterally oriented orbits, who must precisely focus on and land at distant surface locales, which they target from extreme distance or depth.

Theoretical contributions

This research has several major specific contributions in addition to the main theory, outlined above. First, I have contributed to the biomusicology literature by introducing an acoustic musical elaborateness index, ARDI (see Chapter 2). ARDI cues in on diverse and reappearing syllables as core components of elaborate songs and interfaces well with the within-song "pattern matching" (Roederer, 1984) and call unit discrepancies that are required for both learning and producing calls. Second, I have contributed to the primate origins literature by introducing two new theories for orbital aperture convergence [OC] as well as providing both modern and ancient quantitative leaping estimates. Third, I have contributed to the music and song origins literature by both introducing a new theory for the evolution of elaborate acoustic display and comparing it to the established social and ecological theories of music and song evolution. Along these lines, arguably the most important contribution of the current work lies in gathering this evidence across several disciplines for the purpose of assessing various competing selection pressures and using *controlled modeling* techniques. Chiefly, this involves controlling for phylogeny, to compare my theory with others *without* over inflating my effective sample-size due to high relatedness of adjacent terminal nodes in the primate tree. I found evidence that successful appendage landing on arboreal substrate, as proxied by leaping percentage, could relate to both visual-sensory evolution, as proxied by OC, and acoustic signaling, as measured by ARDI─all after controlling for diet, activity period, habitat, mating system, and shared ancestry.

Implications for human music

A convenient distinction, often used in behavioral ecology, proposes that the traits of organisms can be explained by ultimate or proximate causes (Mayr, 1976). Here I have focused on evolutionary explanations of musicality along the deep history of the primate order. It is interesting to speculate if this historically relevant, singing-like behavior is also still currently adaptive, and if its presence in a more modern human setting can be explained. There exist four possible types of evolutionary causal explanations of traits (and corresponding examples of extreme cases where just one of these explanations applies). **I**) naturally selected [NS] genotypes that are still maintained (Winterhalder and Smith, 1993) or traits that otherwise enhance modern reproductive success, i.e. traits with "current utility" (Bateson and Laland, 2013) or "adaptive significance" (Nesse, 2013); **II**) mechanistically functional phenotypes that have (non-NS) proximate utility (e.g. exaptations); **III**) non-genetic and non-adaptive functionality retained due to developmental constraints (e.g. ontogenetic by-products or dysfunctions); and **IV**) traits that were formerly NS favored but are not currently enhancing (e.g. vestigial traits perpetuated through phylogenetic inertia[4]).

It is uncertain if the various classes of elaborate musical display considered in this project

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[4] I would argue that the "musical sequence" of *Macaca fuscata* or the "pant-hoots" of *Pan troglodytes* are prime examples of vestigial traits that have persisted as terrestrial artifacts of more arboreal signals used in these species' distant evolutionary past. They perhaps both originate from a common catarrhine ancestor whose vocalizations resembled a gibbon great call or tarsier estrus whistle or duet.

embody all of these “non-mutually exclusive” and “equally legitimate” categories (Mayr, 1976; Nesse, 2013). The development of ARDI (Chapter 2) helps to explain how acoustic call structure could have mechanistic functionality (**II**) ranging from manipulating receiver interest to propagating through dense vegetation (notably irrelevant for modern music). More recently, ARDI scores suggest primates may modify or develop (**III**) aspects of their calls as they mature into adults (Schruth and Templeton, 2019). I have also argued for the ultimate functions of location, identity, and perhaps also display signals (Fig. 2; Chapter 4) as manifesting as [NS] adaptations (**IV**). While my phylogenetic analyses do not directly address “current utility” or “[modern] adaptive significance” (**I**), I nonetheless attempt an understanding by outlining the chronology leading up to it.

I have explored the likelihood that primates first utilized vocalizations, in disconnected and visually occluded substrate, as location calls while foraging (Slater, 2000). As increasingly acrobatic, gap-spanning locomotion enabled expanded territories, these calls may have encoded additional layers of sophistication─functioning both as unique acoustic identifiers and perhaps also as signals (Fig S1) of spatio-motor proficiency. As groups became less solitary, individuals might have innovated further levels of complexity to their calls to *accentuate* their identity (Beecher, 2017). In hominines, acoustic signaling behavior could have been further shaped by scavenging (Mithen, 2006, p. 132) or by ballistic hunting (Calvin, 1983), as addressed previously (see Chapter 4). While other primates that have become terrestrial may possess atrophied vocal signals, I discourage thinking that musical behavior is correspondingly vestigial in humans, as it is practiced with great enthusiasm in all societies and appears to benefit the performers, at least reproductively. Thus, as I have explained, ultimately, that song evolved as an *adaptation* and that music is likely currently (reproductively) *adaptive,* it is unlikely that this spectrum trait (when viewed along the ARDI continuum) should be relegated as unbalanced toward proximate causal explanations or unfairly denigrated by arguments invoking dysfunction or side-effect.

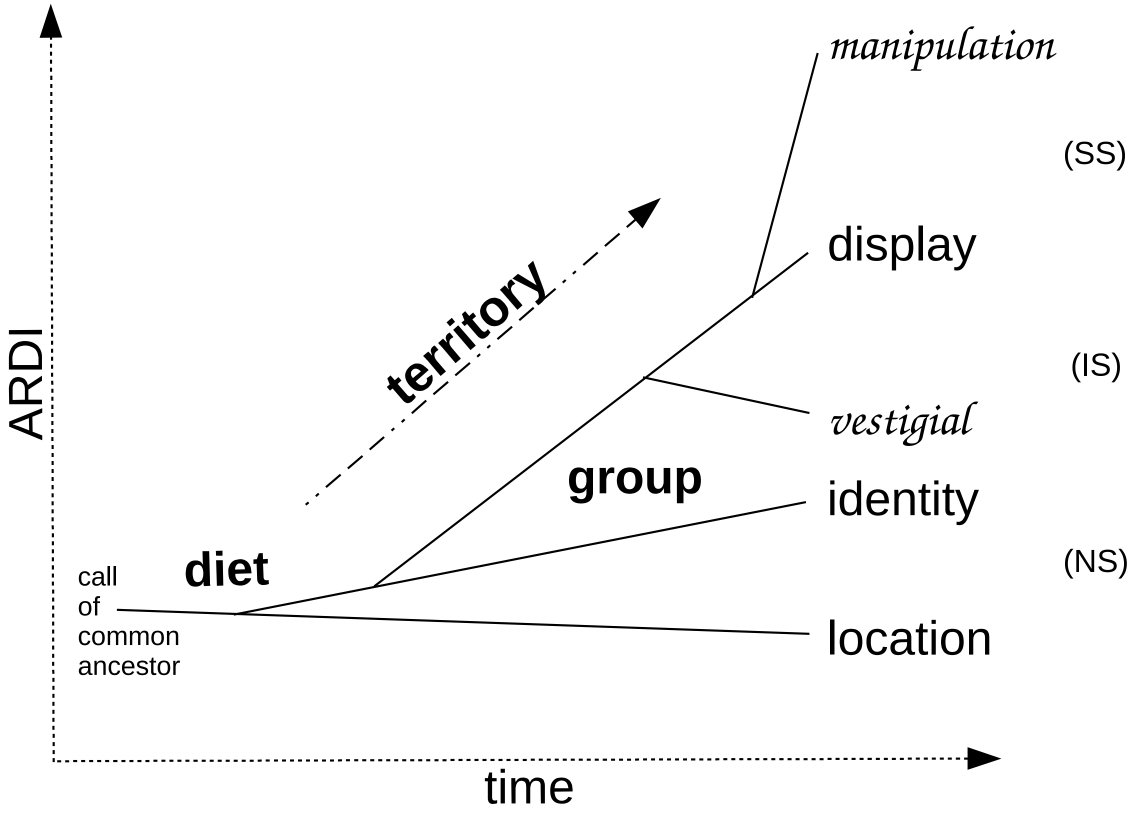

Figure 2. **Chronology and ARDI of various ecological and functional drivers of song**
A diagram illustrating a possible evolutionary progression of increasingly elaborate (higher ARDI) vocalizations, over time from a common ancestor. Calls range from simpler location whistles or trills (via natural selection [NS]) to more complex identity and display based signals (via indirect or sexual selection: [IS or SS]). While manipulation and dysfunction can occur at an upper extremes of ARDI, lower scores may reflect vestigial calling behavior due to reduced maintenance of selection pressures.

An interesting reconsideration, however, in this debate on music being adaptive or not, parallels the debates in primate origins regarding which selective influences were most profound for early morphological evolution. As mentioned, some of the apparent conflict and contradictions in resolving primate origins can be distilled down to a time-frame specifying issue in confusing primate origins with euprimate origins (Cartmill, 2012; Silcox and López-Torres, 2017). As I concluded in Chapter 3, leaping and landing could have largely driven *euprimate* origins (Szalay and Dagosto, 1988), but this does not rule out the possibility that camouflage decrypting (Crompton, 1995) and nocturnal insectivory (Cartmill, 1970) could have previously driven *primate* origins. Its increasingly apparent that a similar confusion is plaguing debates surrounding the origins of music. In Chapter 4, I explored the idea that the cognitive and visio-spatial improvements associated with leap landing behavior could have driven the evolution of initial primate song-like signaling. These traits, though adaptive, were also likely co-opted as exaptations (Gould and Vrba, 1982) from more simple tonal and intervallic location and food foraging calls. Modern music, on the other hand, while perhaps initially co-opted from the simpler songs of our primate ancestors, has likely been rendered into an exaptation, as current survival and reproductive benefits are unclear in many spheres of modern society. And, arguably, with every re-defining of such complex and mosaic traits, and with each new gradualistic evolutionary tweak, a new corresponding evolutionary influence─and thus possibility for understanding these traits as exaptations─is realized. (Reeve and Sherman, 1993).

A more cynical take on this line of proximate causal re-purposing considers, contrary to my reasoning above, the idea that music survives in the modern day as a possibly dysfunctional byproduct of former function. That is, the music of western society could exploit our biased sensitivities with elaborate auditory input which, in the not-too-distant past, could have been evolutionarily useful (Charlton et al., 2012; Ryan, 1998). In other words, they are no longer useful for us, but are used anyway to manipulate a response in receivers against their best interests. Automated and remotely disseminated recordings, for example, can manipulate listeners' moods, behaviors, and habits (Dunham, 2011). Many instances of live performances as a healthy and non-exploitative part of modern music making and honest signaling, however, abound and are undeniably directly, albeit perhaps only modestly, adaptive for these performers. Thus, modern western civilization could run the full gamut of possible uses and abuses of music as display including deception and manipulation.

In any aspects of modern western life, our cultural evolution has undeniably out-stripped our biological evolution. Much more work needs to be done, in general, for improving understanding of and innovating solutions for this disconnect between technology, culture, and biology. Modern medicine, for example, has recently recognized music as a form of therapeutic intervention, which can be administered to alleviate, among other symptoms, the possible effects of this biological disconnect. It's reasonable that prescribing elaborate audio tracks to depressed or disaffected patients (Aalbers et al., 2017) could serve to simulate communal participation in music making, despite it having little directly relevant survival benefit to listeners. While there exists a myriad of ways in which music has been used as treatment for more common medical conditions (Standley, 1995) ranging from depression to stress (Aiyer and Kuppuswamy, 2003), more recently, it has been shown to help both patients diagnosed with schizophrenia (Costa and Negreiros-Vianna, 2011) and with breastfeeding mothers (Keith et al., 2012; Vianna et al., 2011). This very last connection arguably lends support to the more proximately and socially oriented theories of music origins including those suggesting emotional coordination, conjoinment promotion, and infant attachment benefits (Dissanayake, 2000b). Thus, while many of us currently practice music in a fashion vastly dissociated from its socio-reproductive and maternal-developmental roots, there are plenty of ways in which we may strive to remind ourselves of these roots and to reclaim more traditionally intimate, family[5], and infant focused, musical settings.

Future directions

In every cycle of the scientific method, the test of hypotheses seems to open up a pandora's box of new possible lines of research rather than to completely resolve the existing threads of inquiry. The present case is no exception. This research has shown that there is, indeed, a strong association of high-risk arboreal locomotion on the evolution of both primate morphological features, acoustic display behaviors, and likely the cognitive evolution of primates. However, the picture is far from clear and

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[5] Pianist Franz Schubert, interestingly, advocated for revitalizing the spirit of local community in the form of family home gatherings, which encouraged active participation in music making. He would personally orchestrate many of these so-called s*chubertiades*, often infusing popular poetry of the time.

unresolved questions remain. For example, when and why did the features of rhythm and harmony become more prevalent during the (tens of) millions of years of transition from primate song to human music? More narrowly, at what point, if at all, did music cease to be an evolutionary adaptation in modernity? More broadly, if precision limb landing in complex arboreal environments has driven the need to signal musical proficiencies in primates and aves, what analogous behavior necessitated this signaling in cetaceans, an order that lacks grasping limbs? How can findings from primate visual evolution research help us resolve the convergence of musical behaviors observed in phylogenetically disparate taxa beyond our own order? Does the greater significance of using binocular vision for acute color and pattern discrimination over using it stereoscopically for visually guided reaching (Chapter 3) mean that grasp-landing is not an important part of the evolutionary story of elaborate vocal display? We cannot fully answer these questions conclusively currently, but the enigma is intriguing. Obviously, there is much data yet to be collected and many research results still to be compiled and interpreted.

I have been rather forthright about the many shortcomings of my initial research design as detailed in this work. The process of defining music and song, using a univariate index, was challenged by even coming to consensus on the multitude of possible selections and definitions of the feature themselves. Subjective biases are an inescapable aspect of any intellectual venture, as sometimes innocent enough seeming assumptions, be they definitional or algorithmic[6], can end up planting seeds of self-sabotage before analyses even begin. As mentioned regarding my main outcome variable, while I measured duets in the same way as solo calls, future work might consider disentangling such tandem output. Replicates of each call and from different locations could also be obtained to assist in variance estimates of ARDI. Future work could additionally refocus more towards *human* music origins by

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6 I developed a software tool the *melody* r-package, not used for this project, that "automatically" parses spectrograms and scores them for repetition, transposition, tone, interval, and rhythm, and syllable count. (version 0.4.7 archived at https://cran.r-project.org/src/contrib/Archive/melody/). I used others' visual assessments, rather than my coded feature assessment functions, to avoid possible bias.

looking at the important co-evolutionary connections with language (Beecher, 2017; Mithen, 2006; Patel, 2008; Pinker, 1997) or by building an elaborateness index from statistical human universals (Schwartz et al., 2003), rather than the utterance-level used here. Additional improvements could include resolving if ARDI should be considered more of a performance *index* rather than an honest *signal* as well as determining the degree of variation, cost, and receiver interactivity (Enquist et al., 2010). Influences of each stage of the mate-choice cycle, could also be assessed (Brooks et al., 2010).

New studies could also refine measurements of locomotion, for example, by using distance rather than frequency of leaps. Many of my control variables[7], as mentioned in previous chapters, could also could be converted from binary to more ordinal gradation variables. I have also suggested that depth perception in primates could have evolved to accommodate uncertainty in substrate position and orientation during landing, which logically suggests future research should more carefully observe the last second in positional and rotational adjustments of such landed grasps. Another complex factor, in the evolution of primates that has heretofore been highly neglected, is in considering what effect infant carrying behavior has on other complex behaviors (e.g. weight and stability in leaping behavior) and the interrelated issues of development and learning of these behaviors.

Throughout this research, I have illustrated and stressed the importance of considering as many controlling influences as possible, such as substrate, predation, and phylogeny. Unfortunately, much of the research encountered seems to under-recognize the multi-factorial and multi-causal nature of the evolutionary processes involved in such complex behaviors (Crompton, 1995). The current work, of course, is not entirely devoid of imperfections in modeling either: many possible statistical issues remain such as model over-fitting, estimation instability due to dataset singularity, and extensive intra-specific variation in highly labile behavioral traits (Powell et al., 2017). The methods share drawbacks

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[7] other issues include disentangling *monogamy* from duetting and *territorial* from scent marking

of any naturalistic experiment where data are limited[8] and replicate[9] datasets are difficult if not impossible to collect. Another major, non-algorithmic issue, concerns the lack of *intra*-species data, which would be necessary to confirm the intra-species *variation* and corresponding *maintenance* of this putative co-evolutionary signaling-based relationship (of ARDI with aerial spectrum locomotion).

On the other hand, there are plenty of reasons to be optimistic about the merits of this research as it stands. While over-fitting can be problematic, it can also be construed as being as theoretically inclusive as possible. Many of the new findings presented in this work, such as reduced predation relaxing lateral constraints on OC, would not be possible without looking at so many of the possible evolutionary influences simultaneously (such as nocturnality and color vision). This highly controlled approach also supports the revitalized recognition of the importance of habitat over social effects in driving advances in primate cognition (Powell et al., 2017). In vindication of the spatio-motor signaling hypothesis, I note that studies on primate cognition are increasingly finding evidence for selection on spatial memory (Powell et al., 2017), for example. Importantly, while I have avoided the term “intelligence” throughout this work, I’d like to recognize that much of what happens during primate evolution, towards the human form, is enhancing the capacity and capabilities of the central nervous system (Jolly, 1985). The picture that emerges is one of complex arboreal habitats, driving the evolution of larger brains, for increasingly complex locomotion, foraging, and signaling behaviors.

Along these lines, the great mystery surrounding music could be due in part to its inherent behavioral complexity. It uses organs that overlap with several of our senses, involves control of many small muscle groups acting in a coordinated fashion, and requires the training of feedback loops between these systems using neural circuits throughout much of the brain. I have argued here that the additional sensory-motor processing and feedback overlap with the visual system will be crucial to

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[8] with the associated temptations of multiple-testing and *p*-hacking

[9] While I expect to see this same pattern of association upon subsequent sampling, the inferences from this collection of species already covers most primate families and all genera considered to be musical.

further understanding this signaling puzzle. The neurobiology of primates has been largely outside the scope of the present work, but should be an important part of future research. Numerous questions remain regarding this proposed input discrepancy processing overlap─that between left and right visual fields and that which takes place in comparing acoustic units over time. Which of these, for example, takes place in lower versus higher cortical areas? How much of this is involuntary versus conscious? Resolving these types of issues will prove useful for further validation of my dimensional precision based, spatio-motor signaling hypothesis.

What I have presented here is a preliminary proof of concept of the slow, interdependent evolution of precarious arboreal locomotion and elaborate vocalization behavior in primates. While I have made every effort to ensure the quality of input datasets, soundness of logic, and appropriateness as well as robustness of statistical analyses, my work comprises only an initial effort to tackle these very interdisciplinary questions surrounding rather complex and diversely manifesting traits and interconnecting influences (see Fig. S2). I hope my findings prove to be both interesting and useful for other researchers in many of the related fields that serve as my foundations.

Lastly, I must draw my readers' attention to the fact that primate populations are shrinking across the globe at an alarming rate due to deforestation, hunting, and the pet trade. As their fragile habitats disappear, so do the primate species, many of whom do not thrive and often die in captivity. When these species disappear, so do the opportunities to capture their behavior for future generations to learn about and enjoy. There are hundreds of species of primates and only a small fraction of them have recorded and characterized vocal repertoires. When forests and their primate inhabitants disappear, we will no longer hear these elaborate and long-distance acoustic calls. All those who have even remote interests in this work or affections for primates should explore ways to get involved, for example by shifting their diets away from habitat destructive plantation products and learning as much as possible from local zoos and sanctuaries, to improve the prospects for these unique and beautiful creatures.

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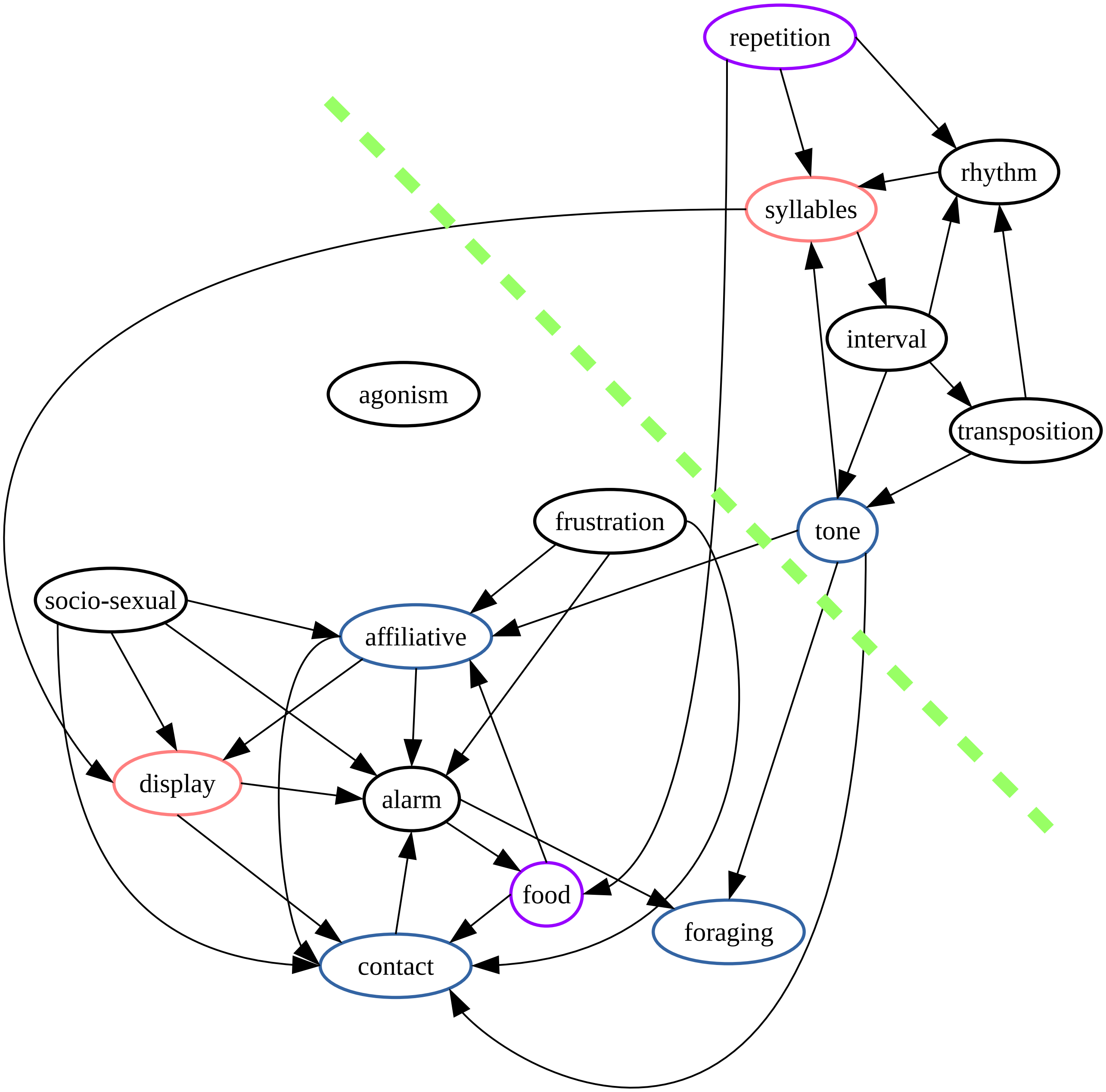
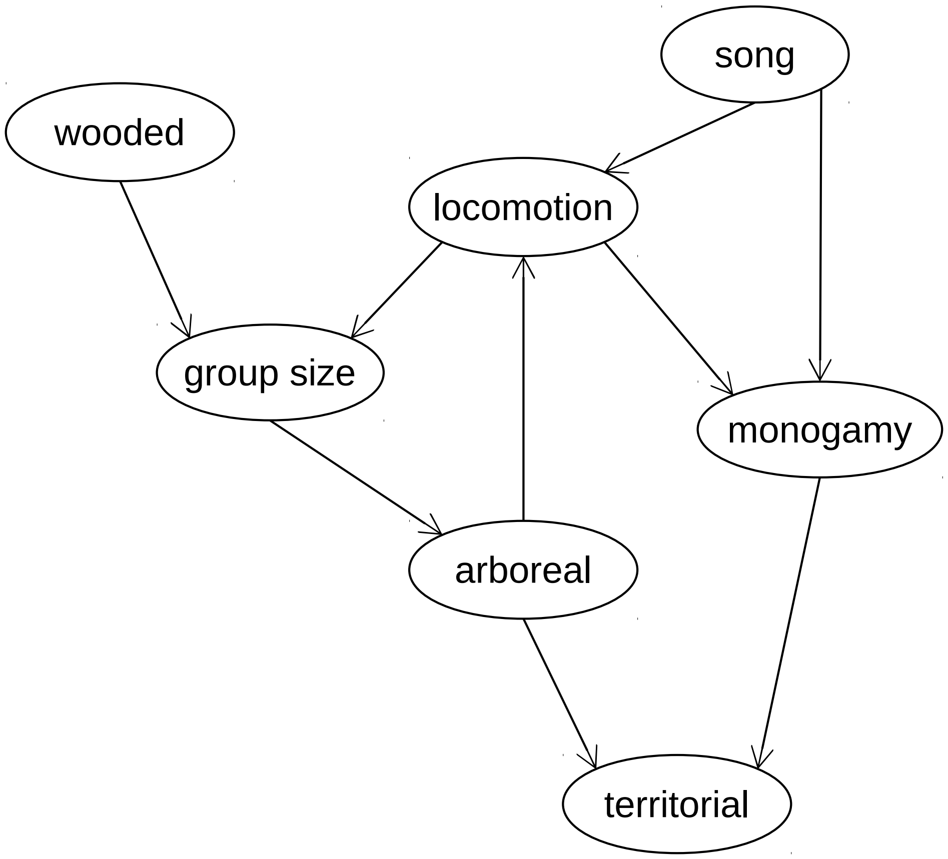


Supplemental Figure 1. Preliminary causal model of call contexts and song components
Exploratory graph of the possibly causal relationships between the 504 annotated vocalization subset of acoustic feature scores (upper right of dashed line) and their various contexts (lower left of dashed line). In confirmation of the acoustic adaptation hypothesis, *repetition* of *tonal* calls may have been useful for maintaining *contact* after separation over large distances during foraging (blue and purple ovals) across forest elements. The singularity of connectivity of *syllable count* with *display* suggests it could be an important aspect driving elaborate calls (pink ovals) in confirmation of ARDI's syllable-centric formulation.



Supplemental Figure 2. Preliminary causal model of ARDI and socio-ecological controls.

A preliminary graph depicting possible relationships between song (as measured by ARDI), locomotion (as measured by leaping and swinging spectrum behaviors), and other socio-ecological control variables.

Vita

David Schruth is a Pacific Northwest native, and he has spent the entirety of his academic career at the University of Washington. In addition to majoring in Anthropology, he minored in Music and Philosophy. Outside of school, he ran cross country and competed in the non-jumping distance events in track. He is an outdoors enthusiast, a commuter cyclist, and a perennially proficient climber of things both igneous and arboreal. As for music, he is a classically trained guitarist and amateur song writer. On numerous road trips throughout the state of Washington, he fell in love with its spectacular snow-covered volcanoes, its diversely reappearing seasonal weather cycles, and its tremendous ecosystemic diversity. After several breaks from graduate school to obtain hands-on experience with databases, statistics, and ecology he returned to his graduate program to transform his Masters thesis into a PhD dissertation. In 2019, he will receive a Doctor of Philosophy in Anthropology from the University of Washington.