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**PROCEEDINGS**

Editors

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# From Olfactory Sensory Reliance to Musical Signals of Vision, Space, and Motion

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## Abstract

Humans make complex music, but animals also make complex sounds that resemble our music. Underlying features, such as repetition, transposition, and melismatic syllables, are ubiquitous and can be assessed in various combinations as continuous measures of musicality. Such continuous indexing allows us to bridge the gap between human music and the calls of primates and other animals. I compared levels of musical output using both, acoustic (syllable) reappearance diversity index (ARDI; scores for primates) and song counts of other species that sing. I surveyed many different ecological variables thought to influence such vocalizations, including mass, age, call contexts, mating system, group size, arboreality, predation, and locomotion. Most of these factors seem to influence musical output. In primates, members of small, mixed-sex groups produce these calls, with higher scoring calls trending with age. Body mass correlated with high song output across all taxa. I also compared primate brain volumes to ARDI scores. Areas for visual, spatial, and motor processing are associated positively, whereas areas for smell are associated negatively. These results suggest animals vocalize musically for numerous interdependent reasons. First, signalers use discrete syllables to compensate for the loss of communication via sense of smell and vision. Second, animals showcase spectrally discrete quality in their calls to spatially dispersed conspecifics who can orient themselves using such signals. Third, many animals appear to use dramatic intervallic features to showcase spatial motive emplacement abilities. Lastly, I highlight additional analysis which suggests shifts to terrestriality can render such calls either vestigial, as in monkeys, or ornamental, as in apes.

## Introduction

Music is a complex acoustic phenomenon produced principally by a single species, namely humans. However, many other species pro-

duce sounds (e.g., song-like calls and music-like note progressions), which overlap considerably with the acoustic features fundamentally present in most human societies (Darwin, 1871). For many years, the definition of musicality has been deeply confounded with originating context (Schruth et al., 2021). But a small but robust subset of key features of human music includes repetition, transposition, and syllabic diversity. Tone, interval, and rhythm can also be found to varying degrees in the calls of non-human primates (Schruth et al., 2021).

## Musical Signaling as ARDI

When these acoustic components are analyzed via exploratory statistical methods, they yield a possibly zoologically applicable index of musicality, useful for comparing the origins of this phenomenon across species. Equipped with this newly developed acoustic (syllable) reappearance diversity index (ARDI) of musicality (Schruth et al., 2021), a statistically tractable investigation into possible functional correlates in other variables is improved.

## Motive Emplacement and PIANO

I hypothesized the existence of two interconnected mechanisms driving the evolution of musical signaling amongst conspecifics. First, musical signaling appears to function in compensating for olfactory signals in a way that enables *listeners* to identify, locate, and orient towards their own kind (Schruth, 2021b; Schruth et al., 2021). Specifically, I hypothesized that brain structures medially adjacent to the lateral temporal lobe, including paralimbic and insular regions, facilitate orientation among ‘acoustic neighbor[hood]s’. (PIANO) that are con-

strained by limited opportunities for chemical signaling (Schruth, 2021c). Secondly, musical signals may also function in *callers* as indicators of micro-athletic capacities for spatio-motive emplacement (Schruth, 2021b). I define motive emplacement here as the ability of an organism to both identify arbitrary targets in space and time and to accurately place themselves (e.g., limbs or mouths) at these specific and narrowly delineated spatial and temporal targets (e.g., substrates, surfaces, prey, fruit). Such precision control of small muscles is not only used in visually resolving small focal-targets but may be signaled by precise auditory displays.

I endeavored to compare various levels of musical display output of species with aspects of their unique ecological settings. Typical factors influencing vocalization, such as morphology (e.g., mass, age, sex, and dimorphism), immediate behavioral contexts (e.g., contact, foraging, and display), as well as more habitual ones (e.g., sex ratio, group size, mating system, diurnality, arboreality, territoriality, predation, and acrobatic locomotion), were considered.

## Data

In birds, I used counts of songs ( $s_{ai} = 633$ ) and calls ( $c_a = 1781$ ) alongside habitat and behavioral covariates for ( $n_a = 584$ ) North American avian species (*All About Birds*, 2015). In primates, I used ARDI scores as determined by 5 blind scorers on 1024 spectrograms for ( $c_p = 832$ ) calls of ( $n_p = 59$ ) species corresponding to nearly all taxonomic families in the order (Schruth et al., 2021). I also compared brain component ( $k_b = 42$ ) volumes (Matano et al., 1985) and leaping and swinging locomotion (Schruth, 2021a) with ARDI scores. ARDI was developed using PCA on the above-mentioned 6 features prevalent in human music utterances (Schruth et al., 2021). In humans, I used the indexes of melodic and rhythmic tension from the Natural History of Song database (Mehr et al., 2016) and compared these with subsistence behaviors of ( $n_h = 339$ ) human hunter gatherer societies (Binford, 1962).

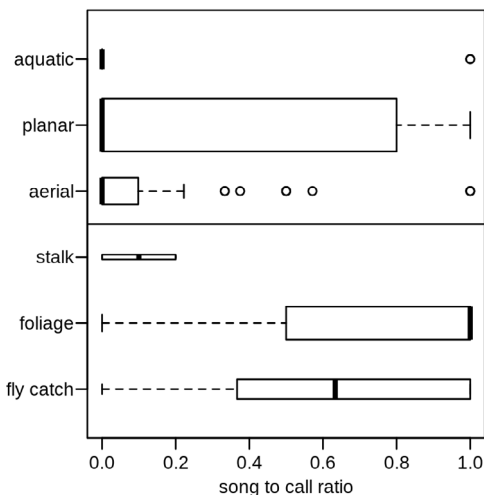
## Methods

I used scores for 6 structural acoustics for features (tone, interval, rhythm, repetition, transposition, and syllable count) that are highly prevalent in the music of human societies. Five students were trained on spectrographic examples from bird calls that exhibited these 6 features. Scorers were blind to taxonomic information, and the 832 vocalizations were randomized for individual scoring sessions. Principal components analysis (Dunteman, 1989) informed variable reduction (Jolliffe, 1972) guided formulation of ARDI from three (transposition, repetition, and syllable count) of the 6 features. ARDI measures the average reappearance (repetition + transposition) of these unique acoustic vocal units (Schruth et al., 2021). I used these resultant ARDI scores from the vocalizations of non-human primates – alongside measures of musical tension in humans, and raw song (to call) count (ratios) in birds – as measures of musical output. I was able to interrogate, via linear regression (R Core Team, 2018), the array of candidate predictors of morphology, behavior, and habitat. I also used a causal modeling PC algorithm (Kalisch, 2012) and phylogenetically controlled multivariate regression (Orme, 2013) on the ARDI scores for primate calls.

## Results

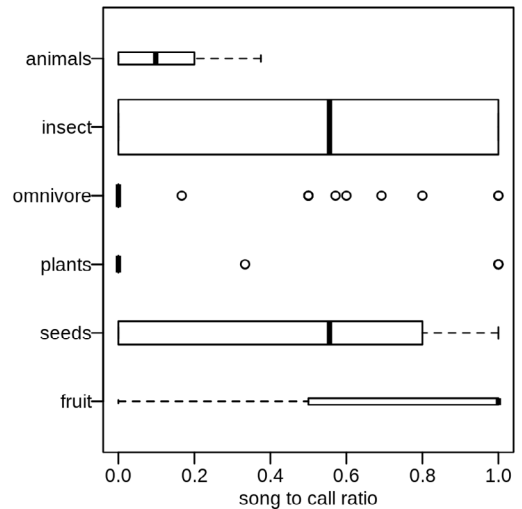
Many of the above factors were found to have at least a moderate influence on complex vocal signaling behavior across species. Most of these factors had positive associations except for group size (mixed), sex (neutral), and predation (negative). In birds, habitat had a surprisingly weak pattern of association with musical output, as measured by song-to-call ratios (Figure 1). However, targeting small dietary items (e.g., flies, seeds, and berries) had much stronger associations with this ratio of song-to-call output (Figure 2). In primates, males had only slightly less musical output than females (Schruth, 2022), and territorial display calls outperformed foraging and socio-sexual calls (Figure 3). Gibbons typify this general pattern as musical members of small, family-sized groups

(Schruth et al., 2019) that experience reduced predation (Schruth & Jordania, 2020) and tend to make more musical vocalizations. Causal modeling revealed that shorter tonal calls were associated with intra-group foraging, while longer, more elaborate syllabic displays were associated with territoriality (Figure 4). Juveniles had the lowest scoring calls, possibly reflecting that infants benefit from tutoring during maternal attachment (Schruth & Dissanayake, 2022) and that primates separately recoup the musicality of their calls upon maturation into self-sufficient adults (Figure 5). Neurologically (Figure 6), primate species with reduced olfactory neural capacities vocalize with higher musicality (Schruth, 2022). Spatial areas had positive correlations with musical calls, suggesting an orientation function (Schruth, 2021b). Visual areas (e.g., visual cortex and LGN) were strongly correlated with musical calling (Figure 6) in primates, suggestive of a more locomotion related evolutionary persistence (Schruth, 2021b). Motor areas associated strongly with large changes in frequency such as interval and transposition, suggesting a more general motor signaling functionality. Leaping (e.g., leap/drop) and swinging (e.g., brachiation) locomotion were strongly correlated with musical output. Lastly, humans that hunt land animals exhibited more musical ‘tension’ (Figure 7).

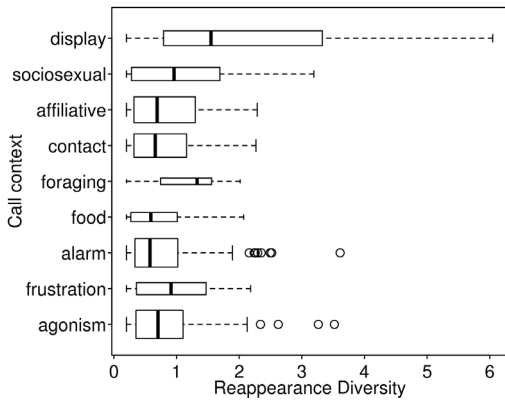


**Figure 1. North American bird behavior and song count. The above behaviors of birds are divided**

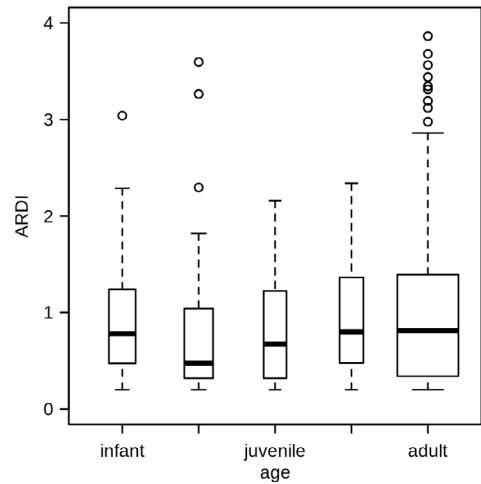
**into habitat and unusual forms of locomotion. The top three – aquatic (dabbling, surface diving), planar (ground foraging, bark foraging, or probing), and aerial (aerial diving, aerial foraging, hovering, soaring) – show that habitat dimensionality alone may not necessarily drive differences in song production by themselves. The bottom three forms of unusual locomotion – stalking, foliage glean-ing, and fly catching – show that targeting small or moving dietary items could play a much more influential role in determining song-to-call ratio than habitat itself.**



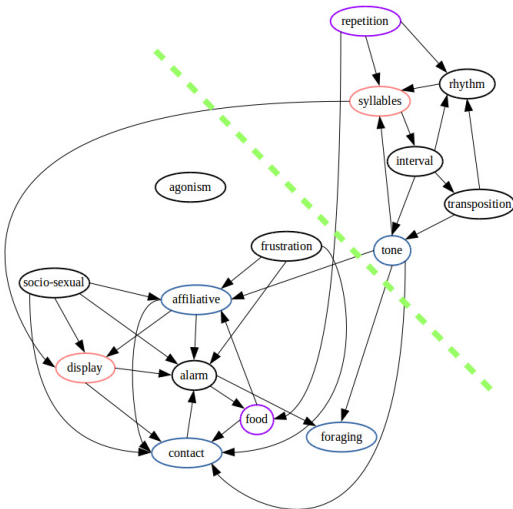
**Figure 2. North American bird diet versus song count. Dietary targets of birds, including animals (mammals, birds, carrion, small animals), plants (including nectar), and omnivory, do not associate strongly with a higher song-to-call ratio. Eaters of relatively smaller food items such as fruit, seeds, and insects, have strikingly higher song-to-call ratios. Although there were no data available on branch targeting, it undoubtedly would have a strong effect, analogous to the effect of rapid arboreal locomotion of primates.**



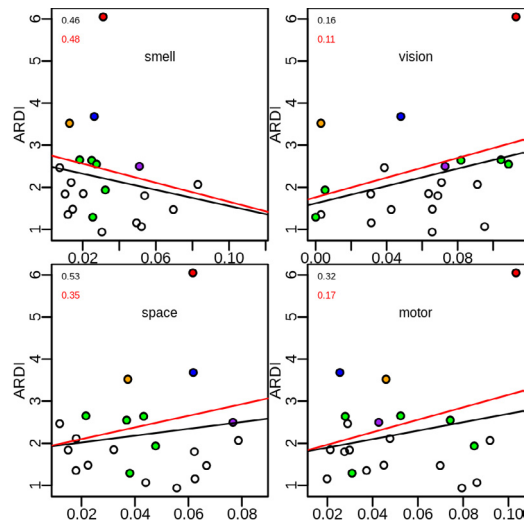
**Figure 3. ARDI versus primate call contexts for 502 calls.** A survey of primate vocalizations and their calling contexts revealed that display (and territorial) calls have higher ARDI scores. Socio-sexual and foraging contexts also had higher than average ARDI scores. These suggest that musical signals may assist in within-group foraging, as well as extra-group mate solicitations and range defense. (Figure from Schruth et al., 2019).



**Figure 5. ARDI versus age categories for primate species.** Primates experience a significant drop in ARDI scores after weaning but improve again upon reproductive maturity. Infant and locational call contexts such as “exploration” suggest the roots of musicality begin with maternal tutoring. The recovery of musicality towards mates, in more mature calls, may reflect adult exaptation of infant-generated maternal contact calls (Miani, 2015). This parabolic trend, from tutored infants towards independent musical maturity, could reflect the re-appropriation of spatial capabilities – from contact with a single maternal food source to function in social buffering of arboreal foraging ranges.



**Figure 4. Context graph of musical components in primate calls.** The PC causal-modeling algorithm was used to generate the above exploratory graph ( $p < .01$ ) of related call contexts (lower left) and musical content (upper right). Syllable diversity associated with display contexts while tone associated most strongly with affiliative contact-calling in foraging contexts. Repetition also associated with food-calling contexts (Figure from Schruth, 2019).



**Figure 6. ARDI vs smell, space, visual, and motor brain parts.** Inspection of volumetric fractions (x-axes) of the cerebellar complex of primate compo-



nents reveals reduced smell in favor of other spatio-temporal faculties, such as visual, spatial, and motoric centers. Smell parts included lobus piri-formis, bulbus olfactorius, and bulbus olfactorius accessorius. Visual parts included tractus opticus, area striata, visual cortex, corpus geniculatum laterale [LGN]. Spatial parts included the schizo-cortex and hippocampus. Motor parts included the thalamus and mesencephalon. Black (and red) trend lines reflect regression of species weighed equally (or double for “musical” species).

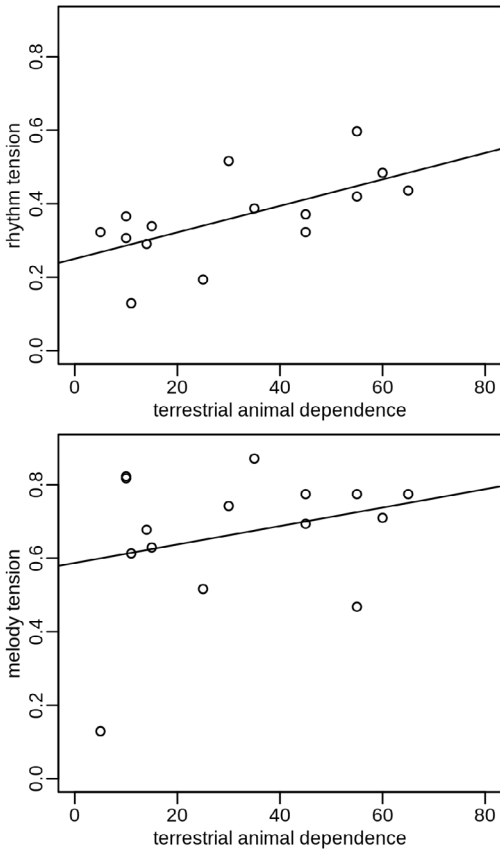


Figure 7. Hunter-gatherer hunting vs two musical indexes. Human hunter-gathers have varying degrees of dependence upon hunting for nutritional needs. These percentages, from the Binford database, appear along the x-axis. Two measures of musical tension, rhythmic (top) and melodic (bottom), were matched to 15 overlapping societies with hunting estimates. Both trend lines exhibit significantly non-zero slopes, reflecting a positive relationship between musicality and (predominantly ballistic) hunting.

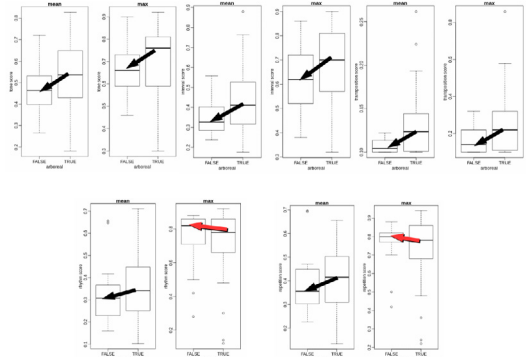


Figure 8. Mean and max musical features versus terrestriality. In primates, all musical feature scores drop (~10%) upon arboreal descent, suggesting most music-like behavior declines through a process of terrestrial vestigialization. Max rhythm and repetition (red arrows) are exceptions, however, suggesting a more ornamental function in terrestrial forms.

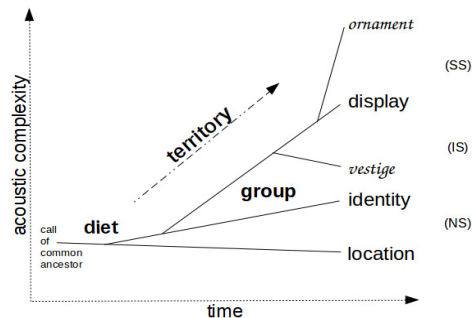


Figure 9. Signal function versus ARDI over evolutionary time. Musical calls are typically thought to function in communicating location, identity, and display qualities to mates and neighbors. But these various functions change according to the level of acoustic complexity and evolutionary time point. Aboriginal calls were likely much less territorial and functioned to retain contact between mother and infant or to coordinate foraging within a small but dispersed group (natural selection [NS], lower right). These orientation and navigation functional predictions of the PIANO hypothesis were partially borne out in this analysis (Figure 6) as spectral features were most strongly correlated with spatial areas. As primates matured and evolved, their calls became increasingly exhibitional to both attract mates and defend home ranges (sexual selection [SS], upper right). The predictions of the motive emplacement hypothesis were corroborated here

(Figure 6) as intervallic features associated most strongly with motor brain areas. (Figure from Schruth, 2019)

## Conclusion

Animals appear to have initially evolved complex vocalizations to compensate for a loss of olfaction in more chemically dilute environments (Schruth, 2021c). This compensation may have manifested as articulation and discretization of distinct syllabic acoustic structures. Secondly, animals appear to use musical calls to remain in acoustic contact and spatially orient with conspecifics during foraging and ranging in visually occluded environments (Schruth et al., 2021). This second ecological pressure appears to favor spectral elements in calls to compensate for visual occlusion. Effective anti-predation tactics, in many vocally active species, could have not only required higher proficiency in evasive locomotion and associated precision in spatio-motive landing, but also emboldened an expansion of such intra-group contact calls into more externally facing territorial displays (Schruth, 2021a). This third ecological pressure, influencing the co-evolutionary interplay of motor-eye coordination with musical-acoustic output, appears to have augmented the production of intervallic features (transposition and interval) of calls. In extrapolation, a combination of these functions may manifest in the form of parabolic projectile motion as used in leap landing (Schruth, 2022). These trajectories appear to also possibly apply to flying birds as they may to free-falling leaps of primates, ballistic throws of human hunters, and (e.g., polynya) ocean surface landing of air-breathing marine swimmers. Lastly, in terrestrial species exhibiting musical behavior, spectrally elaborate music may persist as merely vestigial whereas rhythmic displays could be under more ornamental selection (Schruth, 2022).

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