Title: Melodic Display as a Signal of Remote Targeting Ability: A Comparative Analysis of the Correlated Evolution of Locomotion and Vocalization in Primates

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ABSTRACT

The presence of musical behavior in several phylogenetically distinct taxa in the animal kingdom and throughout every society in the human species is one of the greatest unsolved mysteries in biology. I have incorporated knowledge of human musical universals into a measurable working (rhythm absent) definition of melody: essentially variation and repetition of (tonal) intervals. I hypothesized that repetition and variation in melody have evolved as honest signals of underlying quality of precision and range (respectively) of distance gauging abilities. I predicted that melodic display would be positively correlated with remote targeting behaviors such as projectile locomotion (jumping, brachiation, or arm-swinging). Quantitative locomotor distributions and spectrographic vocal repertoires of primates were collected and the spectrogram analysis program, *Gramparse*, was used to split, match, and score each vocalization type. Four linear least squares regression models of (percent) projectile locomotion vs melodic score (as measured by the number of repeated interval groups per vocalization) were run on both species level data and the corresponding phylogenetically controlled independent contrasts with and without control from additional behavioral and environmental variables. Percent projectile locomotion was statistically significant at the 0.01 level but failed to explain more than 20% of the variance in melodic display. This work is an important first step in both investigating possible selection pressures in a currently neglected corner of music origins research and, more generally, quantifying the formerly qualitative task of assessing musicality.

The origins of music is one of the most perplexing mysteries in biology. Music is highly pervasive and, apparently, independently evolved in numerous taxa. There also appears to be strong evidence for specialized neurological circuitry for musical processing in both humans and other animals. And yet, from Darwin's "mating call theory" (Darwin 1871) on, scientists have struggled with a way to structure compelling adaptationist solutions and most have conceded that the mystery remains unsolved or that existing solutions are highly problematic.

Music universals, definitions, and origins

The primary difficulty in investigating the evolution of music is that all problems--universals, definitions, and origins—are inextricably linked and each must be solved simultaneously (Mache 2000). Developing a list of human universals dictates a definition that, in turn, only expands and complicates the problem zoologically.

Nettl (Nettl 1983; Nettl 2000) has described traits common to every human musical "utterance" and (less strictly) to every human musical system. A rough structure-only version of these universal traits includes: rhythm, repetition, variation, tone and interval. Several other authors have elevated, one of these traits, repetition as the "obvious universal" (Mache 2000) or a core "scaffolding" (Bregman 1990) component of music. With these criteria, we can construct a somewhat crude and anthropocentric definition of music that does little more than enumerate these common unique traits and emphasizes music's redundancy.

Defining music in such a way captures all human forms, but also encompasses the vocal displays of many other animals. Birds, bats, whales, dolphins, and several primates must all now be included in our list of musical organisms. Although this increase in the scope of the problem simultaneously increases its difficulty to individual researchers by demanding a more multidisciplinary investigation, it may also decrease its difficulty by reducing possible common selective pressures. That is, assuming the existence of global pressures selecting for musical behavior in independent lineages, we should expect the list of common candidate behavioral and environmental characteristics to shrink as we add species.

So what is it that these extremely different animals have in common? Many mainstream theories have suggested the commonalities such as monogamy (Darwin 1871; Miller 2000) , territoriality and group bonding (Roederer 1984). These commonalities, however, are not universally present. Globally common characteristics can be elucidated only with vague experimental terms. Some have speculated on a correlation between music and a remote-targeting "ballistic" (Calvin 1983; Calvin 1989) or spatial-navigation "floating" (Cross 2001) locomotor behavior. Most explanations, however, have not shown a linkage between these specific features of environment or behavior and specific acoustic features of their musical displays (Miller 2000).

Hagen and Bryant (Hagen and Bryant 2003) have suggested that a core acoustic feature of (human) music, rhythm, is tied to an ancestral coalitional social behavior via a costly signaling mechanism. Although the task of linking environment with acoustic features is commendable, their theory is limited to only one (rhythm) of several important characteristics of musical structure. It does not address the equally important (frequency-domain) intervallic component of music, and does not explain the essential (timing-independent) repetition component. If we are to explain the origins of music, we must include interval and repetition in our definition and explain what environmental selection pressures might engender these features.

Interval repetition and precision distance gauging

How is vocalizing a repetition of intervals adaptive? What might this signal to mates, coalitions and enemies? One possible answer utilizes the fact that an animal perceives a melodic frequency interval as an excitation of follicles along or at the two ends of an actual physical distance of cochlear membrane (Johnston 1989). This fact, coupled with the idea that repeated measures in any metric (distance in this case) is the only way to estimate precision of that measurement, suggests that interval repetition in song could be a way to remotely and efficiently communicate precision in distance gauging ability (Table 1). The idea that higher precision in musical display may provide a selective advantage is not new as some have shown with black-capped Chickadees (Weisman and Ratcliffe 2004). There is also support from cognitive studies that precision in *judging* the relative distances between pitch takes place in same area of the brain (Schmithorst and Holland 2003) as where remote targeting does. But entirely new, in this paper, is the idea of linking musical display with a specific underlying cognitive ability (distance gauging) and a corresponding, readily measurable, naturally selected phenotype. Specifically, I hypothesize that selection pressures (such as falling and drowning) against inaccuracy in remote targeting (Table 1) have influenced the evolution of underlying distance gauging pre-motor abilities and the corresponding vocal interval repetition signaling displays (melody).

Interval variation and distance gauging range

Where does this leave tone, rhythm and variation? Tone probably has deeper and independent adaptive roots than what is within the scope of what I am suggesting here. But because tone is a prerequisite for interval I will consequently continue to use it in my definition of melody. Rhythm and, more generally, timing (along with the associated time-domain variation), are probably related to the proposed adaptations but are also not nearly as phylogenetically unique and scientifically neglected as its distant cousin melody. Thus we are left to explain this (supra-intervallic) variation in the frequency-domain.

To continue the distance-gauging hypothesis, I propose that absolute frequency variation, independent of the tone variation required to construct an interval, functions to exhibit a *range* of distance gauging ability. An exclusively arboreal primate who frequently crosses canopy gaps would quickly fall to his death if he could only gauge and successfully jump one fixed distance. A dynamic, flexible range of distance gauging ability is required for the constantly changing distances of remote targets.

Another possibility is that a larger number of variants of interval length and position corresponds to a higher dimensional environment. Animals that spend more of their time traveling in the vertical axis of three-dimensional space may experience even greater selective pressure for distance gauging abilities just by virtue of the fact that there are more distances upwards and downwards to gauge. For example, we might expect that an animal that travels through open air or water, as opposed to a two-dimensional plane, would require more sophisticated and adaptable scene analysis capabilities. This increased dimensionality complication, in addition to the complications of an additional field of force (gravity) acting on an organism in this new dimension, makes for spatially challenging locomotion. This idea of a connection between music and spatial abilities has been demonstrated in cognitive studies (Graziano and others 1999; Rauscher and Zupan 2000).

In either case, it is clear that there are enough logical reasons to hypothesize that selection pressures might be acting against memorized or static targeting and projectile locomotion (Table 1) in a way similar its selection against imprecision. Intervallic variation in melodic display (Table 1) may serve as a signal of the ability to improvisationally adapt to constantly changing spatial relationships in higher dimensional environments.

Accordingly, a narrower definition of a music that will allow us to answer this subset of the problem without getting distracted or misled by investigation into the origins of rhythm, is in order. I propose a working definition of melody as variation and repetition of (tonal) intervals (Table 1). These two quantities are measurable and quantifiable, and can be readily compared to other behaviors and environmental attributes for species and among individuals.

Here, I examine the evolutionary relationship between projectile locomotion and melodic vocalization and test for a correlated evolution of these two traits. The results suggest a significant but noisy relationship.

MATERIALS AND METHODS

A test case is examined in the primate order. Primates exhibit an enormous range of both locomotor and vocal behavior. Additionally, their songs are some of the most scientifically neglected of musical species. Quantitative locomotion and vocalization data were collected and analyzed for 37 species of primates.

Data Extraction and Cleaning

Environmental and behavioral factors. Because musical behavior most likely has several influences it was important to control for environmental factors that could influence surrounding acoustics or known behavioral characteristics which might influence motivations for vocalization. Habitat data for each species (wooded, arboreal) were collected from Nunn & van Schaik (2001). Territoriality for each species was ascertained from (Wich and Nunn 2002). For all three variables I used the original binary coded values.

Locomotion repertoire collection. The primate locomotion literature in Web of Science Citation Index was searched using the search string: <genus> AND (Leap* OR brach* OR jump* OR locomot*). Only studies with quantitative measures (predominantly locomotor bout count distributions) of each of the locomotor types (Table 2) in a species' repertoire were included. Bout count percentage distributions (rather than leap distance or bout time) were chosen because of greater availability of this type of measurement. Priority was put into finding locomotor distributions for species for which full spectrographic vocal repertoire was available. As the first acceptable study for each species was found, the search for subsequent studies on that species ended. If, however, multiple values were inadvertently discovered in other studies (with multiple species), both distributions were recorded. Only species that had both published full quantitative locomotor repertoires as well as spectrographic vocal repertoires were used.

The distribution of locomotor frequencies was categorized following the definitions in Table 2. If a study had both travel and foraging (and sometimes feeding) locomotor distributions, and a total wasn't already present, the two (or three) distributions were averaged using the number of bouts as a weight. Similarly, distributions from multiple studies (or sites within studies) on the same species were aggregated using a bout-weighted average. In all of these cases, if bout counts were not available, a simple average was performed.

Finally, I established a continuous quantitative index to represent of the amount of distanced targeting required in a species' environment by totaling the amount of projectile locomotion [%PLR]. The equation is as follows:

$$\%PLR = \%\ Leaping + \%\ Jumping + \%\ Brachiation + (0.5 * \%\ Armswinging)$$

Where each percentage reflects the number of observed bouts of each locomotion type over the total number of locomotor bouts observed during non-stationary activity. The justification for a partial inclusion of armswinging and for its categorization as a less targeting demanding form of locomotion than brachiation is due to the frequent use of prehensile tail in most armswinging new world monkeys and due to the lack of a projectile component.

Vocalization repertoire collection. Although the most direct way of studying vocalizations would be to analyze original audio recordings I just used published spectrograms. Analyzing spectrograms, offers several advantages. 1) repertoires are already systematically categorized and neatly organized 2) access is readily available (if the original authors are unavailable, the published results are often easily obtainable) and 3) analysis of spectrograms is easily verifiable visually.

The majority of complete vocal repertoires were located through the only current meta-analysis on primate vocalizations (McComb and Semple 2005). The remaining 13 of 37 studies were found in the Web of Science Citation Index via the search string: *<genus> AND (vocal* OR call OR calls OR acoustic* OR sing* OR song* OR melod* OR music*)* .

Because the number of species available for study was already so limited, there was no attempt to exclude vocalizations or studies on the basis of young age or imbalanced sex. Acceptable studies had to have published at least three spectrographically represented vocalization types.

Spectrograms were categorized into vocalization types provided by the author on the basis of 1) presence of a unique category and corresponding name or 2) presence of unique acoustic features (with some exceptions to this order of priorities). Like a previous study (McComb and Semple 2005), I excluded one unit vocalizations (Figure 2) as separate types if there was a longer series type available. Similarly, mixed unit types were excluded if both types were otherwise defined (McComb and Semple 2005). If multiple spectrograms were available for one vocalization type, they were noted and later concatenated into one spectrogram. This was to allow for the possibility of measuring non-adjacent repetition.

Five of the articles were available in electronic format. I captured the spectrograms from these using Acrobat Reader's graphics select tool at a zoom of 150%. I scanned the remaining paper bound articles at 300dpi as grayscale 8bit depth bitmaps.

Photoshop 6.0 was used to clean each spectrogram. Each spectrographic image was rotated, to level the axes, and then cropped out of the grid. Annotative markings, labels, tic marks, arrows, hash marks, gridlines, or textural background markings were removed. Additionally I removed obvious or otherwise indicated background noise from the plots. Similarly, easily distinguishable duets were separated into separate solo spectrograms and often times into separate acoustically distinct vocalization types entirely. Using duet separation, however, was a last resort to using unaltered isolated and non-overlapping spectrograms.

In some cases it was necessary to use a Gaussian blur to homogenize grainy plots and prevent over-splitting of the spectrogram during analysis. The spectrograms' existing range of grayscale values were systematically stretched (up to a subjectively determined threshold of approximately 200/255) to help homogenize the brightness and ensure that all spectrograms had white backgrounds. This was an important step to allow for uniform spectrogram splitting in the analysis steps.

After each spectrogram was cropped and cleaned, it was saved as an indexed 256 gray-scale, non-dithered, non-matted, normal row-order, non-interlaced "gif" file. I then systematically resized the height to = log(1+frequency)*100 using Imagemagic's batch convert function. These resized files were then converted to portable grayscale pixmap [pgm] format (essentially a matrix of grayscale values in ASCII text format).

Recoding, aggregation and statistics used

Parsing spectrograms. The R package *Gramparse* (Schruth, in prep) was used on the extracted and cleaned spectrogram matrices. The program works by cutting a spectrogram into vocalization subunits at low amplitude breakpoints (Figure 2a). The units are then taken pair-wise and various parameters (such as total amplitude, relative frequency range, absolute midpoint frequency, and duration) of each unit are used to select candidates for matching. Candidate unit matrix pairs within parametric range were subtracted from each other and divided by the total amplitude of the shorter duration unit. Detailed specifications for the package are available in another paper (forthcoming).

Units that were too narrow or short (less than three pixels wide or tall) were excluded as outliers. Units that were not sloped enough (range of the per column mean frequency values less than a 0.25 of the relative frequency range of the unit) or were too chaotic (average difference between adjacent frequency means is greater than 1.75 times the average per column frequency range) were thrown out because they did not meet the melody definitional requirements of interval and tone (respectively). If the units fell within double the width, 2.5 times the total amplitude, 1.3 of the relative frequency range of the longer unit, and 1.3 of the absolute frequency midpoint, then the units were subtracted. Unit pairs whose subtracted and amplitude adjusted difference was less than 1 (more than 50% overlap) were considered a pair and thus members of the same repetition group. The adjacency matrix of pairs and non pairs, a mathematical graph (Figure 2b), was subsequently analyzed. Plots of the parsed spectrograms and melody graphs are available on line at http://students.washington.edu/dschruth/acoustics/data/primates/ .

Selection of melody statistic. Several statistical measurements of the repetition graphs are possible to measure using *Gramparse*: number of tonal and intervallic repetition groups [nTIRGs], average repetition group size, average saturation of repetition group, and average frequency precision per group. In previous unpublished pilot work on non-primate musical species, I determined that nTIRGs was the best measure of subjective measures of melody. Unlike many other summary statistics that account for repetition of (in this case) tonal intervallic units, nTIRGs also takes variation into account. This one statistic was chosen for its empirically and logically determined embodiment of the core features of melodic display.

Aggregating melody scores. After each of the vocalizations were read in to the program and individually scored for nTIRGs, they were normalized by their representation of the energy of the entire spectrogram. Thus if a vocalization had a high nTIRGs, but only for a small fraction of the total energy of the spectrogram, then the score was proportionately down weighted. For example: An nTIRG score of five for repetition groups that only represent 1/5th of the energy of the vocalization will only get a weighted score of one. The scores were then averaged for each species (giving a species level score [avg(nTIRGs)]) and used in subsequent analysis described below.

Analysis

Both of the following comparative methods used linear least squares regression analysis. Both a simple model:

$$log(avg(nTIRGs)) \sim log(\%PLR)$$

and a full model

$$log(avg(nTIRGs)) \sim log(\%PLR) + wooded + arboreal + territorial$$

were investigated. The null hypothesis in all four cases was that the independent variables do not explain a significant amount of variance in the dependent variable. The alternative hypothesis was that the %PLR parameter is greater than 0: that there is a positive correlation between projectile locomotion and melodic display in primate vocalizations. The significance of the %PLR parameter was determined using a one sided t-test. The significance of the other variables in the model was established with a two-sided t-test. In the full model, the additional environmental terms are present to test for significance of the locomotion variable while controlling for environment.

Prior to analysis data were transformed using a log(x + c) for x as both avg(nTIRGs) and %LRA and the constant c is a correction to avoid zeros in the log transformations. I used the value of c = 1/6 recommended by Mosteller and Tukey (1977). Other appropriate transformations like square root for Poisson distributed counts (in the case of avg(nTIRGs)) and square root (x + 3/8) binomially 0/1 constrained proportions (in the case of %LRA) were explored but failed to stabilize the variance as well as log(x+1/6).

Non-phylogenetic regression. To assess the relationship between targeted locomotion and melodic display, regardless of the phylogeny, standard linear regressions were performed on both the full and simple models. If we assume that evolution has occurred entirely through biological channels (rather than cultural ones) then these species level values are not independent. However, because certainty as to the exact mechanism of evolution exists, an analysis that doesn't take phylogeny into account is justified.

Phylogenetic (independent contrasts) regression. To assess the evolutionary relationship between targeted locomotion and melodic display while controlling for non-independence of species, I used the independent contrasts method (Felsenstein 1985) to control for effects of phylogenetic inertia. This was accomplished using Purvis' composite phylogeny of the primates

(Purvis 1995) and the *Pendek* package for R (Purvis, in prep). The contrasts were calculated by recursively subtracting the available species level variables for sister taxon pairs at internal nodes in the phylogenetic tree. These contrast differences, unlike the species level data, are independent of each other even when a strictly biological mechanism is assumed.

RESULTS

The analysis resulted in a positive correlation between melodic display and projectile locomotion for the 37 species of primates. Plots of the regressions show this positive trend in both the original species level data and in the contrasts (Figures 3 & 4). All results for parameter estimates of %PLR were significantly positively correlated at the .01 level. This result was supported using phylogenetic methods or not, and with or without control via additional environmental variables. (Tables 2 & 3)

The results hold with a Bonferonni correction for the selection of one of the many possible melody statistics, (dividing the p-value by the number of possible melodic scores).

Although %PLR was significant in every model tested in this experiment, it failed to explain much of the variance. R^2 (adjusted R^2) values for the simple non-phylogenetic model was 0.40 (0.38), for the full non-phylogenetic model was 0.61 (0.54). For the phylogenetic models: 0.17 (0.15) for simple and .28 (0.15) for the full.

It is also important to note, is that none of the control factors territoriality, arboreal, wooded, appear to be significant in determining melodic display. This may however be due to the fact that they are binary variables without much statistical leverage.

DISCUSSION

The results of this study confirmed a correlation between melodic display and projectile locomotion. Both Hylobates and Tarsius, the two genera independently acknowledged as musical in previous work, scored very highly in both %PLR (over 50%) and ave(nTIRGs) and average vocalization scored greater than one type of repeated interval. The fact that the previously determined musical species also score high nTIRGs is an informal validation of Gramparse and the nTIRGs statistic. These high score, both for locomotion and melody, for tarsiers and gibbons was expected and came as no surprise.

Confirmation of the distance gauging / remote targeting theory on the opposite end of the distributions, however, was surprising. The absence of melody in any of the non-projectile locomoting primates confirmed the hypothesis even further than acrobatic and melodically sophisticated species in the high scoring ends of the distributions. None of the ground animals scored over 0.2 avg(nTIRGs). This tight clustering at the origin of the locomotion vs melody plots represent the most important corroborating finding of this paper: namely that ground primates don't vocalize melodically.

In between these two extremes a strong positively correlated trend was observed that appeared to be independent of the apparently outlying musical species. This too is a surprising confirmation of the theory.

Of the possible confounding variables investigated in this study, territoriality and wooded are both nearly significant (.05) in the non-phylogenetic model, but all ultimately fail to be significant in either of the full models. Future work should include the potentially highly significant effects of mating system on melodic display behavior.

Exceptions

The current work, however, also has its share of problems. As I have noted, the model did a poor job of explaining much of the variance of the melody statistic. This may result from a poor and unconfirmed choice of a projectile locomotion statistic. The melodic statistic used in this study (nTIRGs), despite its strong theoretical and logical justification for adoption, likewise has yet to be systematically confirmed as matching subjective notions of what is melodic.

Also problematic is the current state of *Gramparse*. As it is currently written the tool does a poor job of cutting, often times over and under cutting, and it doesn't detect trills. More computationally problematic is the fact that it cannot collapse harmonics into a single tone. These deficiencies create problems with scoring repetition (in the first case) and with detecting tone and interval (in the second). Additionally, all three of these, complicate the ability to measure precision, another important statistic test in this study. The low R^2 values should improve for runs on future datasets as the program is developed. Much of the unexplained R^2, however, is likely due to the many sources and levels of measurement error and may not improve despite future improvements in the program.

In this study, only 37 species (representing roughly only 15% of the total number of primate species) had appropriate vocalization and locomotion information. Worse yet, only 3 of the 4 musical non-human genera could be used. Callicebus was under-represented with one species (and surprisingly did not score very high melodically or in percent projectile locomotion) Indri was completely unavailable for this study due to lack of a current quantitative locomotor study. Tarsiers were also underrepresented with only spectrum providing a minimal three (song-only) spectrograms. Similarly, the two Hylobates species, agilis and lar, had song-only vocalizations available. The apparent outlier effect of these three species may be explained in part by this biased spectrographic sampling. Although it could be argued that the enormously disproportionate amount of acoustic energy spent on songs justifies the lack of other “close” calls, complete repertoires are needed to give more accurate scores. Also disappointing was a lack of any Langurs in the study. There is qualitative evidence that Langurs are a hidden trove of melodically and locomotively high scoring primates.

Even if these deficiencies are overcome, it is unlikely to improve R^2 to the point of explaining most of the variation in a melodic display statistic, given the current model. Additional control variables (such as threat, location and mating system) must be tested and referential linguistic sources of variation should be investigated, as vocal communication is most likely multi-channeled.

The main quandary, at least apparently, is that of where humans, arguably the most musical of primates and animals, are also very much on the ground.. It was mentioned before, however, that humans’ unique use of tools, especially ballistic ones, might have had something to do with the evolution of music. An important next step will be to confirm this connection between remote targeting (in this case, in the form of throwing) and melodic ability.

Agreement/disagreement with previous work:

There may be some conflict with previous studies that have shown repetition to be a key part of referential communication (Templeton), but these different layers of vocal communication need not be in conflict with each other. A single call can have referential, aesthetic, emotive meaning as signaled by (most likely) different acoustic features. For example, the number of repeats may signal the size of a predator, the precision of the repeats the size (distance) gauging skill of the caller, and the relative tonality may signal the amount of fear.

Theoretical implications & practical applications:

This relationship between melody and remote targeting / distance gauging may prove to be a relationship that applies to all animals. I suspect that flying animals--birds & bats, followed by leaping & swinging arboreal animals (primates, squirrels, & tree frogs, and then surface targeting water mammals)--will have the highest correlations. The severity of negative consequences of incorrectly judging the distance of a remote target should correlate highly with the amount of melody in a species' repertoire.

Future comparative work should not only investigate other species outside of the primate order but should study the individual level variation in ballistics and melody in humans. These studies along with the aforementioned--more quantitative locomotion studies, more published vocal repertories, complete repertories for musical primates (not just songs) and individual level studies for individual species--should all be undertaken.

One of the main advantages of using this melodic scoring method is that it allows us to specify musicality (without ever defining a black and white threshold between music and non-music) on a gradual scale. We can compare "more or less" but not "whether or not". However, we might be tempted to define music as greater than one ave(nTIRGs) per unit of study or greater than one TIRG per vocalization.

Conclusions:

I have shown that the variation of repeated (tonal) intervals, as measured by the number of repeat groupings of tonal intervals, is a good indicator of musical display and that, independent of rhythm, this melody score matches previously published determinations of musical species. Tarsisus and Hylobates scoring high melodically further back this up.

Secondly, I have demonstrated that there is a correlation between remote targeting, in the form of the projectile locomotion of primates, and this melody statistic. Models with phylogenetically controlled independent contrasts and other control factors remain significant.

The aim of the current paper isn't nearly as ambitious as trying to solve everything with regards to the origins of music, but it does make an attempt to lay out the initial groundwork for a testable framework which might serve as a starting point for repeatable, objective and theoretically sound future research in the area.

References used in Table 3

Voc: (Baldwin and Baldwin 1976; Bermejo and Omedes 1999; Buchanan 1978; Casamitjana 2002; Charles-Dominique 1977; Cherry and others 1987; Cleveland and Snowdon 1982; Fernandes 1991; Fontaine 1981; Gittins 1984; Gosset and others 2003; Green 1975; Grimm 1967; Macedonia 1993; Mackinnon 1974; MacLanahan and Green 1975; Masataka 1982; Moody and Menzel 1976; Newman 1985; Nietsch and Niemitz 1987; Palombit 1992; Pereira and others 1988; Pola and Snowdon 1975; Raemaekers and others 1984; Range and Fischer 2004; Robinson 1979; Robinson 1984; Schulze and Meier 1995; Stanger and Macedonia 1994; Struhsaker 1967; Struhsaker 1975; Tenaza and others 1988; Zimmermann 1985a; Zimmermann 1985b)

Loc: (Cannon and Leighton 1994; Cant 1988; Cant and others 2001; Chatani 2003; Crompton 1983; Curtis and Feistner 1994; Dagosto 1989; Dagosto 1995; Davison 1982; Defler 1999; Doran 1993; Fleagle and Mittermeier 1980; Garber 1984; Garber 1991; Gebo 1987; Gebo 1992; Gittins 1983; Hunt 1991; Johnson and Shapiro 1998; Johnston 1980; MacKinnon and MacKinnon 1980; McGraw 1998; Porter 2004; Rosenberger and Stafford 1994; Stafford and others 1994; Sugardjito 1982; Sugardjito 1986; Susman 1984; Susman and others 1980; Thorpe and Crompton 2005; Walker 1979; Walker 1996; Walker 2005; Walker and Ayres 1996; Youlatos 1998; Youlatos 1999a; Youlatos 1999b)

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TABLE 1: Conceptual Definitions

projectile locomotion	Locomotor behavior which involves projecting or impelling of the body (or an object) forward through space toward a remote target (e.g. Jumping, Brachiating)
remote targeting	The actual physical act of aiming and landing an object or body at a remote target. Most commonly manifested as projectile locomotion.
distance gauging	The cognitive ability to precisely and accurately compare and record distances perceived through various sensory input.
melodic display	Solo and vocally produced acoustic patterning which contains both variation and repetition of tonal and intervallic fundamental units (as distinguished from displays involving harmony and rhythm)

TABLE 2: Airborne Locomotor Definitions

leap	includes: jump, leap, vertical cling leap, boundleap
brachiate	armswinging without a prehinsile tail (apes only)
armswing	includes: armswing, suspension*, tension, cantelivering, tail-arm Brachiation

* (for combined locomotor and positional studies)

Non-Airborne Locomotion

walk, run, terrestrial bound

climb, ascent, descent, clamber, scansorial, verticalbound

bridging, hoist , foliage crossing , pronograde suspend

hop

TABLE 3: Raw Data, Species Included, and Data Sources

		Locomotion			Environment			Vocalization				
Genus	Species	Bouts	Percent Projectile Locomotion [%PLR]	Locomotion Repertoire Source	Wooded	Arboreal	Territorial	Vocal Count This Study	Vocal Count McComb & Semple	Probability of Repeated Intervals	Avg No. Repetition Groups per Vocalization [avg(nTIRGs)]	Vocalization Repe
Alouatta	palliata	5162	5.4%	Gebo 1992, Johnson & Shapiro 1998	1	1	0	20	22	7.7%	0.23	Baldwin & Baldwin 19
Arctocebus	calabarensis	NA	0.0%	Walker 1979	1	1	NA	3	2	3.0%	0.00	Charles-Dominique 1
Cacajao	calvus	325	27.4%	Walker 1996	1	1	0	12	NA	12.6%	0.10	Fontaine 1981
Callicebus	moloch	325	17.9%	Youlatos 1999	1	1	1	12	11	32.3%	0.41	Robinson 1979
Callimico	goeldii	2108	50.1%	Porter 2004,Rosenberger & Stafford 1994	1	1	NA	30	28	14.0%	0.16	Masataka 1982
Cebuella	pygmaea	701	24.6%	Youlatos 1999	1	1	NA	26	16	32.5%	0.24	Pola & Snowdon 197
Cebus	olivaceus	550	22.6%	Youlatos 1998	1	1	0	11	11	31.3%	0.06	Robinson 1984
Cercocebus	atys	466	1.1%	McGraw 1998	NA	NA	NA	20	18	13.0%	0.01	Range & Fischer 200
Chiropotes	satanas	>4031	24.7%	Walker 2005, Walker 1996, Fleagle & Mittermeier 1980	1	1	1	4	NA	4.2%	0.03	Fernandes 1991
Cercopithecus	aethiops	NA	1.9%	Isbell et al. 1998	0	0	1	26	25	5.6%	0.06	Strushaker 1967
Daubentonia	madagascariensis	3600	7.0%	Curtis & Feistner 1994	1	1	NA	9	9	13.0%	0.07	Stranger & Macedoni
Eulemur	macaco	525	31.0%	Gebo 1987	1	1	1	12	13	8.0%	0.28	Gosset et al. 2003
Galagoides	demidoff	2163	40.0%	Gebo 1987	1	1	1	9	NA	30.2%	0.05	Charles-Dominique 1
Galago	senegalensis	7615	57.7%	Crompton 1983, Gebo 1987	1	1	1	18	18	39.1%	0.54	Zimmermann 1985a
Hylobates	agilis	585	82.4%	Cannon & Leighton 1994, Gittins 1983, Hunt 1991	1	0	0	9	NA	82.9%	0.96	Gittins 1984
Hylobates	lar	211	60.7%	Hunt 1991	1	1	1	8	NA	85.5%	1.29	Raemaekers 1984
Lagothrix	lagotricha	5458	10.5%	Cant et al. 2001,Defler 1999	1	1	1	6	6	14.9%	0.09	Casamitjana 2002
Lemur	catta	642	22.0%	Gebo 1987	NA	NA	NA	29	22	23.9%	0.15	Macedonia 1993
Leontopithecus	rosalia	4833	18.0%	Rosenberger & Stafford 1994,Stafford et al. 1994	1	1	0	21	16	41.7%	0.39	MacLanahan & Green
Loris	tardigradus	2496	0.0%	Gebo 1987	1	0	1	7	NA	7.7%	0.01	Schulze & Meier 199
Macaca	fascicularis	>1463	8.9%	Cannon 1994,Cant 1988	1	1	1	17	17	1.0%	0.00	Palmobit 1992
Macaca	fuscata	858	7.6%	Chatani 2003	1	1	NA	42	41	10.2%	0.09	Green 1975
Macaca	nemestrina	NA	0.0%	Johnston 1980	1	1	0	25	16	7.7%	0.13	Grimm 1967
Microcebus	murinus	2149	38.0%	Gebo 1987	1	0	0	3	NA	63.3%	0.40	Cherry 1987
Nycticebus	coucang	605	0.0%	Gebo 1987	1	0	0	8	NA	4.4%	0.34	Zimmermann 1985b
Pan	paniscus	4461	24.1%	Doran 1993,Susman 1984,Susman et al. 1980	1	1	1	16	38	37.5%	0.30	Bermejo & Omedes 1
Perodicticus	potto	645	0.0%	Gebo 1987	1	0	NA	5	5	1.8%	0.00	Charles-Dominique 1
Pithecia	monachus	449	28.6%	Youlatos 1999	1	1	0	9	NA	36.5%	0.10	Buchanan 1978
Pithecia	pithecia	6273	43.1%	Walker 2005,Walker 1996	1	1	NA	13	NA	24.3%	0.52	Buchanan 1978
Pongo	pygmaeus	13412	21.1%	Thorpe & Crompton 2005,Sugardjito	1	0	1	6	10	16.5%	0.32	MacKinnon 1974
Procolobus	badius	6415	23.9%	Gebo & Chapman 1995,McGraw 1998	1	1	1	8	17	14.8%	0.08	Strushaker 1975
Rhinopithecus	roxellana	NA	16.8%	Davidson 1982	1	1	NA	16	NA	1.3%	0.06	Tenaza 1988
Saguinus	fuscicollis	4218	35.2%	Garber 1991,Porter 2004	1	1	1	20	16	33.6%	0.12	Moody & Menzel 197
Saguinus	oedipus	535	54.8%	Garber 1984	1	1	0	29	33	22.6%	0.12	Cleavland & Snowdo
Saimiri	sciureus	>569	26.8%	Fleagle & Mittermeier 1980,Youlatos 1999	NA	NA	NA	28	21	19.0%	0.21	Newman 1985
Tarsius	spectrum	NA	63.0%	MacKinnon & MacKinnon 1980	NA	NA	NA	4	NA	95.0%	1.90	Nietsh 1987
Varecia	variegata	>4550	33.2%	Dagosto 1989,Dagosto 1995,Gebo 1987	NA	NA	NA	14	13	18.6%	0.40	Pereira et al. 1988

TABLE 4: Results of Simple Linear Regression Model: *Vocalization [log(avg(nTIRGs))] ~ Locomotion*

	Nonphylogenetic (species level)				Phylogenetic (independent contrasts)			
Term	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)[$]**	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)[$]**
Intercept	-0.444	0.131	-3.387	0.002 **	-	-	-	-
Locomotion [log(%ALR)]	0.533	0.110	4.861	<0.001	1.077	0.395	2.730	0.005 **

[$] One-tailed Pr(>t) test for locomotion factor only

TABLE 5: Results of Full Linear Regression Model: *Vocalization [log(avg(nTIRGs))] ~ Locomotion + Control*

	Nonphylogenetic (species level)				Phylogenetic (independent contrasts)			
Term	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)$^{\$}$**	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)$^{\$}$**
Intercept	-1.425	0.415	-3.433	0.002 **	-	-	-	-
Locomotion [log(%ALR)]	0.360	0.111	3.255	0.002 **	1.058	0.425	2.489	0.010
Control [wooded]	0.427	0.380	1.124	0.273	0.459	1.062	0.433	0.669
Control [arboreal]	0.331	0.182	1.825	0.082	-0.033	0.228	-0.144	0.887
Control [territorial]	0.281	0.142	1.977	0.061	0.450	0.994	0.453	0.655

[$] One-tailed Pr(>t) test for locomotion factor only

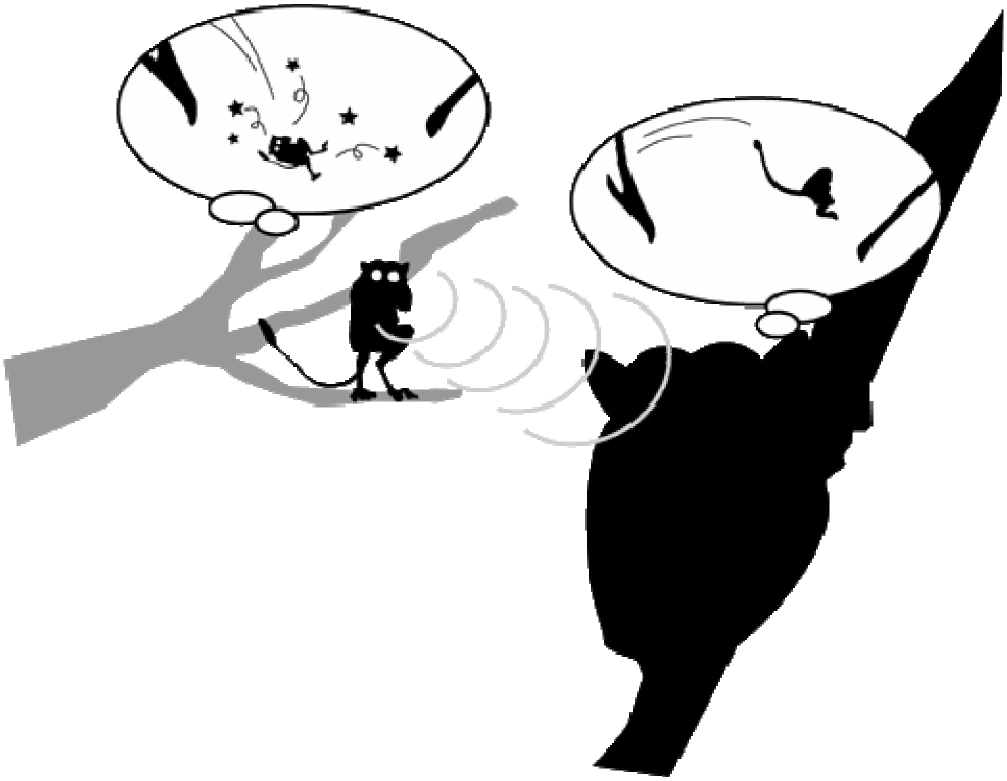

Figure 1.

Tarsisus spectrum vocalizing to a potential mate, coalition partner, or enemy who is scrutinizing the call for both improviziational quality and precision of repeated intervals. The listener envisions possible outcomes of an actual locomotor bout. The vocalizing tarsier can quickly and easily vocalize the underlying pre-motor distance gauging abilities required for remote targeting and in this case projectile locomotion.

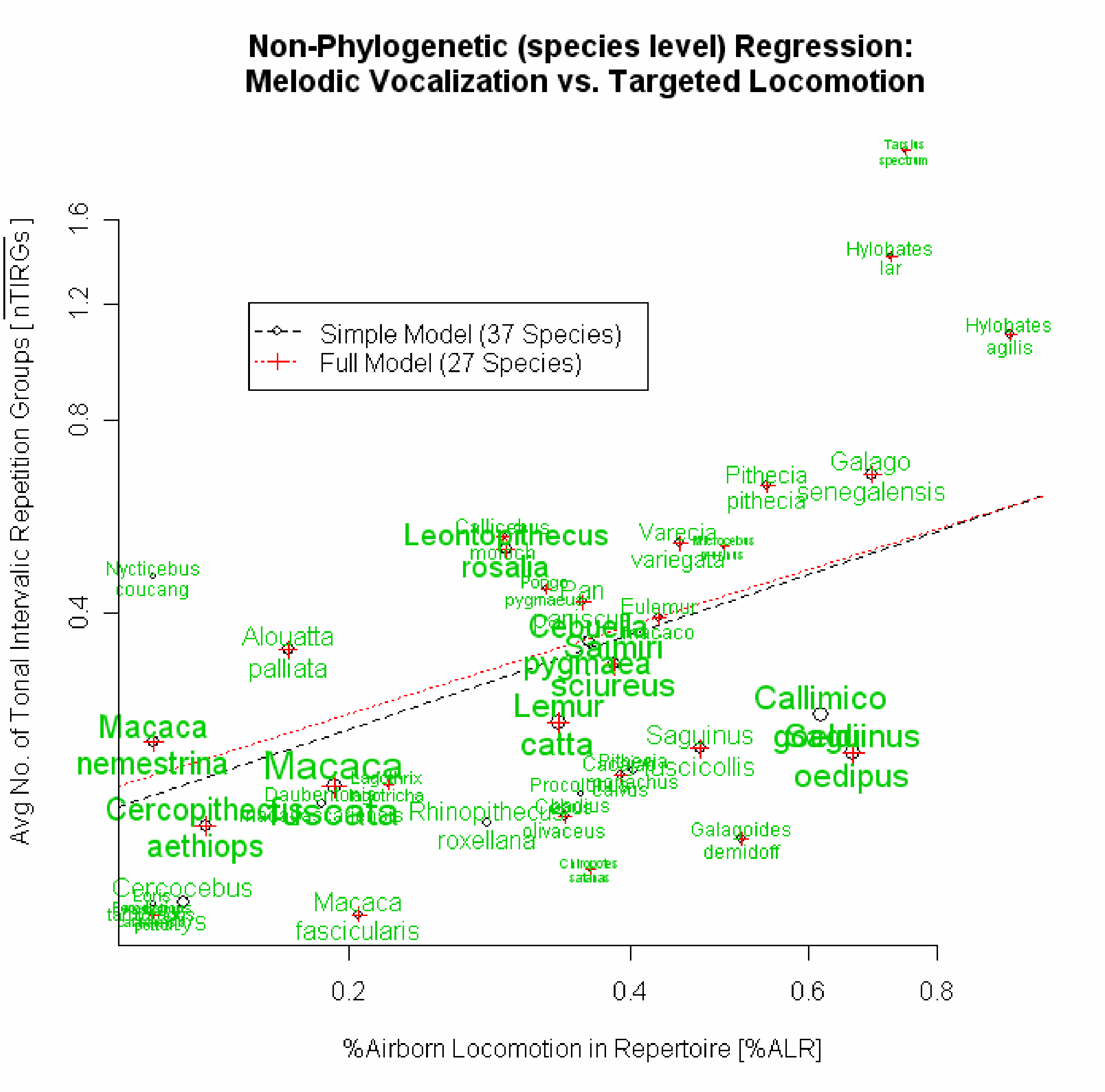

Figure 2.

Raw species level data collected from our 37 primate species. Each point represents (at least) one locomotor and one spectrographic study. In the full model only 27 species have enough data to remain as part of the regression. Both regression lines are significant in both cases at the .01 level, confirming the connection between melodic display and remote targeting behavior. Text size corresponds to the relative number of vocalizations available for use in estimating the ave(nTIRGs) score.

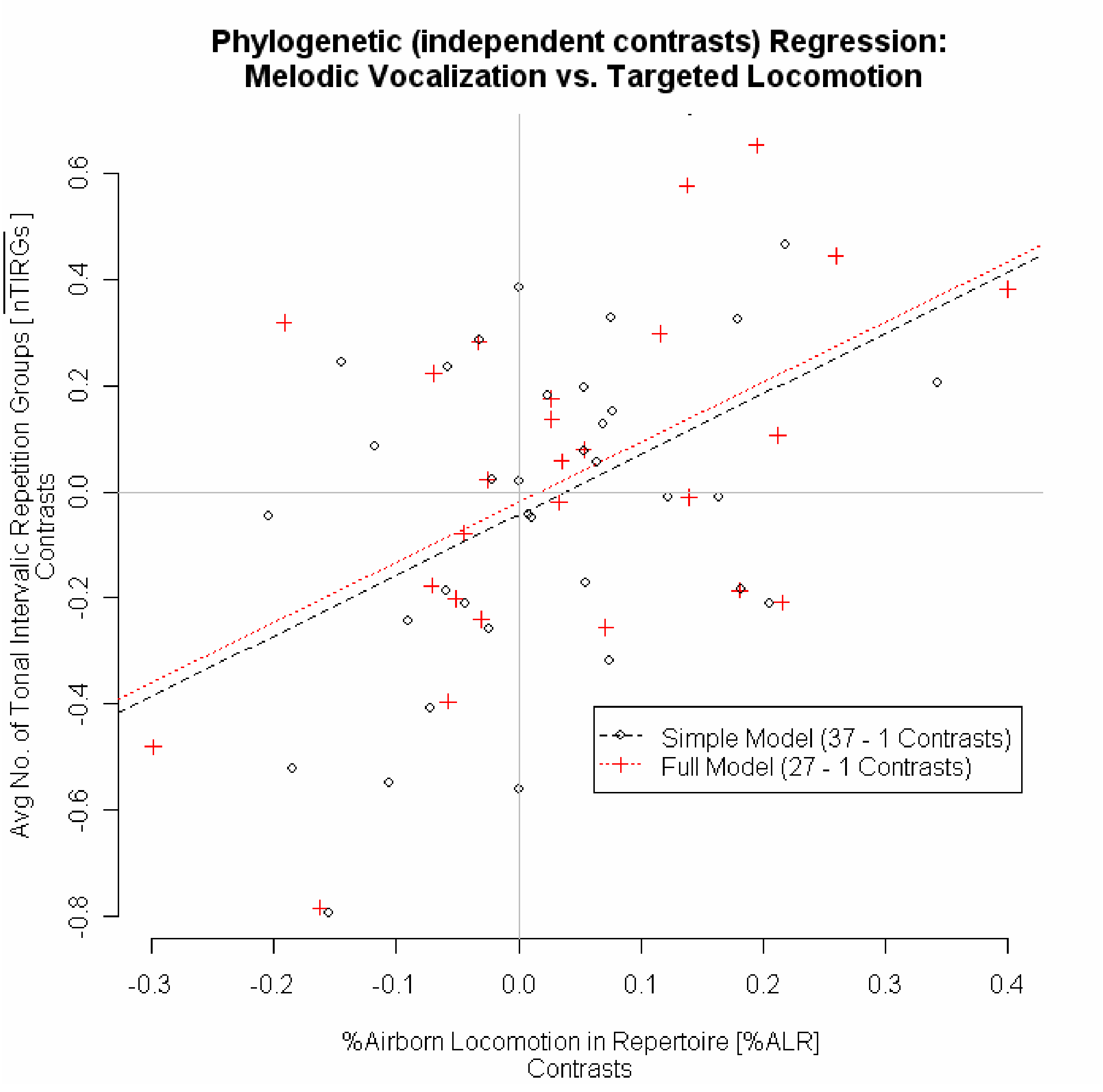

Figure 3.

Independent contrasts of the previous points in Figure 2. Sister branch values are subtracted from each other to determine relative change between closely related taxa to prevent biased of phylogenetic inertia. The number of points, therefore, corresponds to the N-1 internal nodes in Purvis' phylogenetic tree. Both egression lines are, again, significant at the .01 level.