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Body Mass and Beak Size Drives Acoustic Evolution in Manakins

Daniel Barboza Capella

danielbcapella@gmail.com

Universidade Federal de Santa Catarina

Selvino Neckel-Oliveira

Universidade Federal de Santa Catarina

Guilherme Renzo Rocha Brito

Universidade Federal de Santa Catarina

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Abstract

In this study we investigated the drivers of acoustic diversification in the advertisement calls of manakins (Pipridae), a Neotropical family of suboscine birds. We investigated how environment, morphological constraints, and sexually selected traits influenced spectral and temporal parameters in the advertisement calls of manakins. We analyzed 756 advertisement call recordings from 44 manakin species, and then used phylogenetic generalized least squares (PGLS) to test the influence of different drivers on these acoustic traits, along with generalized linear models (GLM) to test for Bergmann's rule. The results showed that body mass was positively related to call duration, consistent with the hypothesis that larger species have greater energy reserves for acoustic communication. Beak size was negatively related to call pace, as predicted by the biomechanical trade-off between force and speed in bill movement. Beak size also influenced peak frequency, with larger beaks producing lower peak frequencies. Lower average temperatures were directly related to call duration, suggesting energetic limitations on vocalization. No relationships were found between sexual dichromatism or display complexity and any call trait, although the smaller sample sizes for these analyses limit their conclusiveness. We also observed no evidence of Bergmann's rule acting on song variation. Significant phylogenetic signals were detected in peak frequency, frequency bandwidth, maximum frequency, and call duration, indicating that shared ancestry strongly influences these traits. We conclude that morphological constraints, particularly body mass and beak size, play important roles in shaping song differentiation in manakins, especially for call duration and pace. However, these drivers explain only a portion of the variation, with stochasticity likely accounting for much of the remaining song diversity. The lack of support for frequency allometry and sexual selection trade-offs highlights the complexity of acoustic evolution and the need for further study, particularly with larger datasets for sexually selected traits.

INTRODUCTION

Acoustic communication is a way to transmit information across individuals of the same species highly utilized in many groups of animals, specially birds, mammals, amphibians and insects (Stebbins, 1983). For birds, this form of communication is particularly important, being used for instance in territorial disputes, courtship displays, individual recognition, and to alert the presence of predators (Aubin et al., 2004; Vielliard, 2004; Catchpole & Slater, 2008). For this reason, efficiency in the transmission and reception of acoustic signals is essential for the survival and reproductive success of birds. Therefore, it is expected that natural selection, and other active evolutionary processes of niche construction, act to increase fitness of the signal sender (Endler, 1993; Slabbekoorn & Smith, 2002; Araújo et al., 2020).

Many studies have been made in order to understand how selection mechanisms act in the diversification of bird song, which assessed acoustic parameters of different species among monophyletic groups, and their relation with probable evolutionary drivers(Slabbekoorn & Smith, 2002). For example, Derrybery *et al.* (2018) found that ovenbirds (Furnariidae) song frequencies are highly related with body size and habitat characteristics, while temporal patterns are influenced by bill size.

Seddon (2005) found similar results among anteaters (Thamnophilidae), with the added effect of increased song differentiation among closely related species that live in sympatry, and Hay et al. (2024) demonstrated that in honeyeaters (Meliphagidae), body size has a much stronger influence on song. Finally, Marcolin *et al.* (2024) found that calls from parrots (Psittaciformes) are related both with body size and sexual dichromatism. From these results found in literature, we can list a variety of drivers capable of directing the evolution of acoustic signals, such as habitat characteristics, sexual selection, and morphological constraints on sound production. Although, the relative importance of each driver, and even their participation in acoustic signal evolution, varies greatly between different bird taxa (Podos, 1997; Laiolo & Rolando, 2003; Boncoraglio & Saino, 2007; Ligon et al., 2018; Marcolin et al., 2022).

According to the principles of the Acoustic Adaptation Hypothesis (AAH) (Chapuis, 1971; Morton, 1975), species can show adaptations in their acoustic signals in relation with the physical environment in which they occur. This hypothesis suggests that acoustic signal production will occur in a way that minimizes effects of sound attenuation and degradation, which can interfere with signal transmission. The intensity of these effects depends on the sound frequency of the signal and a diversity of environmental characteristics, such as temperature, humidity, vegetation density, and position of the sound source in relation to the ground (Larom et al., 1997; Brown & Handford, 2000; Snell-Rood, 2012; Escalona Sulbarán et al., 2019).

Most studies that aim to understand the effects of the AAH are more focused on differences in sound frequency according to the structure of the environment, comparing closed forest habitats with open areas (Boncoraglio & Saino, 2007). However, there are some studies that relate acoustic parameters with variation in temperature and humidity (Hay et al., 2024), although these relations are often non-linear and much more complex (Snell-Rood, 2012).

Acoustic signals are highly used in mating contexts, and are thus susceptible to sexual selection pressures (Slabbekoorn & Smith, 2002). When two or more characters are simultaneously under influence of sexual selection pressures, it is common to observe that an increase in resources to one of these characters can result in a decrease in resources for the other (Gilliard, 1956; Shutler, 2010). This is known as the transference hypothesis, and in birds it can occur as a trade-off between acoustic and visual signals, such as coloration and mating displays (Gomes et al., 2017; Marcolin et al., 2022).

As an alternative to the transfer hypothesis, sexual selection may lead to a concomitant increase in resource allocation to more than one trait. In interspecific analyses, not only costs but also benefits of resource allocation to different traits will be unequal, and the absence of allocation trade-offs becomes even more evident when resource distribution among species does not follow a normal curve (Shutler, 2010). It is also possible that sexual selection acts on multiple traits holistically, as a single mating phenotype, as has been demonstrated in Birds-of-paradise (Ligon et al., 2018), a group that shares many parallels with manakins in their lek mating displays. Finally, sexual selection may act by reinforcing

deterministic evolutionary patterns, such as those driven by physiological or environmental pressures, or diverge toward less predictable evolutionary pathways (Friis et al., 2021).

Acoustic signals in birds are physiologically limited by organs and structures in the vocal tract (Fletcher, 2004; Seddon, 2005; Torres et al., 2017; Derryberry et al., 2018). The lower range of frequencies that can be produced by a bird are limited by the thickness of the vocal tract, which is directly related to the body mass of the individual. Thus, larger species commonly produce sounds in lower frequencies than smaller species (Fletcher, 2004). Bill size can also be related to acoustic parameters (Seddon, 2005; Derryberry et al., 2018). As the last part of the vocal tract, sound frequencies can be filtered and limited by the bill in a similar way as for body size (Palacios & Tubaro, 2000). Besides frequencies, bill size can be related to how many distinct notes can be produced in a set amount of time. The reason is that larger bills usually have larger muscles associated with it, and are therefore subject to a biomechanical tradeoff between force and velocity when opening and closing (Herrel et al., 2009).

Bergmann's rule states that animals living in colder climates should have a larger body size compared to animals of the same species, or of closely related species, living in warmer climates (Bergmann, 1847; Salewski & Watt, 2017). Since body mass can affect acoustic signals, that is another way in which the habitat could indirectly modify bird songs, which has been shown to be probably the case with the song of honeyeaters (Hay et al., 2024). Traits that show indirect evolution due to adaptive selection in other traits are called "magic traits" (Thibert-Plante & Gavrilets, 2013; Derryberry et al., 2018).

The Pipridae family, commonly known as manakins, consists of a Neotropical group of small, mostly frugivorous Suboscine birds (Kirwan & Green, 2011). Currently, 55 species in 17 genera are recognized within the family (Gill et al., 2025), forming a well-established monophyletic group (Prum, 1997; Mckay et al., 2010; Ohlson et al., 2013; Leite et al., 2021). They are particularly known for their vibrant colors and elaborate lek mating displays, often involving coordinated dances among several males.

Although they are Suboscines, they possess highly complex syringeal musculature and form a highly vocal group (Prum, 1992). This group represents an excellent model for studying acoustic evolution for several reasons. They exhibit high diversity in sounds, colors, and courtship displays, as well as pronounced sexual dichromatism, which is related to sexual selection (Doucet et al., 2007; Kirwan & Green, 2011; Lindsay et al., 2015). Species within the group are highly resident and exhibit high habitat specificity, meaning that environmental influences are likely to affect different populations of the same species in similar ways (Anciães & Peterson, 2009; Villegas et al., 2021). They have been extensively studied in terms of phylogeny, natural history, and behavior (Prum, 1992, 1997; Kirwan & Green, 2011; Leite et al., 2021), providing a solid foundation for the present study.

Among the known acoustic repertoires of manakins, an advertisement call has been identified (Sick, 1997; Kirwan & Green, 2011). This call is homologous among species and present in most of them, and its primary function is to attract females prior to the performance of display behaviors. Due to the homologous nature of this call, allowing interspecific comparisons, and its sexually selected context, it was chosen for analysis in the present study.

The objective of this study is to identify how potential drivers of acoustic diversification influence the bioacoustics of Pipridae. The hypotheses tested are as follows: 1) Acoustic parameters should be influenced by habitat, following the principles of the AAH (Morton, 1975). In the case of manakins, which all occur in forest environments, the main environmental influences are expected to be temperature and humidity in the areas inhabited by the species. However, no directional prediction is made regarding these relationships due to their complex nature. 2) Sexually selected traits, such as sexual dichromatism and the complexity of courtship displays, are expected to be negatively related to vocal complexity parameters (e.g., duration and frequency bandwidth), according to the transference hypothesis (Gilliard, 1956). 3) Call frequency parameters should show a negative allometric relationship with body size (Fletcher, 2004). 4) Beak size should be negatively related to the number of notes produced per second in acoustic signals, due to the biomechanical trade-off between force and speed (Herrel et al., 2009). It should also negatively influence signal frequencies, although to a lesser degree than body size.

METHODS

Song data

We obtained the advertisement calls of 44 species of manakins from the online citizen-science repositories Xeno-canto (https://xeno-canto.org/) and Wikiaves (https://www.wikiaves.com.br/). We aimed to cover as much of the range of each species in our sampling to account for regional variability. To avoid pseudoreplication we sampled no more than one recording from the same location at the same date and we randomly extracted one call from each recording, so that we could consider each call sample to represent a different individual. We obtained 756 call recordings this way.

To minimize the effects of differences in recording settings and equipment we standardized our samples (Zollinger et al., 2012) with a high pass filter of 140 Hz and a normalization to 0 dB using the software Audacity version 2.4.2 (2021). Spectrograms were generated with a Blackman FFT window size 1024 and 90% overlap for further analysis using Raven Pro version 1.6.4 (2014). We measured spectral and temporal parameters of the calls (Fig. 1). Those parameters were maximum frequency of the first harmonic (FMax), minimum call frequency (FMin), frequency bandwidth (Ban), Peak frequency (FDom), call duration (Dur), and number of notes (NNot). From the latter two parameters we calculated call pace, as the average number of notes per second (Pace = NNot / Dur). The same researcher took all measures to make up for cognitive bias. We calculated mean values for each variable, and thus we considered each species as a single sampling unit for statistical analysis. Spectral parameters and call duration were log transformed prior to analysis (Cardoso, 2013).

Morphological data

We took all the morphological traits from the AVONET database (Tobias et al., 2022). We used total body mass as a proxy for body size (Rising & Somers, 1989), and considered all four beak size traits present in

the database (beak length from tip to base through the culmen, beak length from tip to nostrils, beak width and beak depth).

Bioclimatic data

We obtained bioclimatic variables from the coordinates of each sample from the Worldclim database (Hijmans et al., 2005). We used maximum average temperature and minimum average temperature as possible predictors of bird song variation, which can be either by direct influence on sound production, or as an aftereffect of morphological variation. As an alternative, we also calculated Pearson correlation coefficients between all 19 bioclimatic variables, excluding those that had > 90 correlation with annual mean temperature (Bio01) and annual mean precipitation (Bio 12). We then reduced all remaining bioclimatic variation into a first axis of a Principal Components Analysis (PCA) (Derryberry et al., 2018). This axis explained 53% of all variation and was related to annual temperature and precipitation stability.

Sexual selection traits

We used two sexually selected traits to assess possible tradeoffs with the advertisement calls. Those traits were sexual dichromatism and courtship display complexity. We took all data of these traits from the literature. Sexual dichromatism measures were taken as the distances in perceptual color space between homologous plumage patches in males and females (Doucet et al., 2007), while display complexity was measured as values related to repertoire size, arena organization, and presence of cooperating males (Lindsay et al., 2015). Of the 45 Manakin species considered in this study, we obtained sexual dichromatism data for 37 of them and display complexity data for 10 in the aforementioned literature.

Phylogeny

We used the most recently published phylogeny of the manakins (Leite et al., 2021) to calibrate the statistical analysis (Fig. 2). The phylogeny selected was the maximum likelihood tree using the concatenated UCE for 95% of the data set. Taxonomic nomenclature was the same used in the aforementioned publication, with the exception of the genus Pseudopipra instead of Dixiphia (Kirwan et al., 2016).

Statistical analysis

We used phylogenetic generalized least squares (PGLS) to test how different drivers could explain the variation in acoustic parameters. For each acoustic parameter, we started with models containing all drivers that could potentially alter bird calls, and then dropped the least significant driver in the model until only one remained. For the models including sexual dichromatism and mating display complexity, we dropped terms until all drivers remaining were also included in the full 44 species analyses.

Alternatively, we also fitted models using the first axis of the bioclimatic PCA, instead of individual bioclimatic variables. We did this considering three different branch length transformations in the phylogeny: Brownian evolution and maximum likelihood estimates for Pagel's λ and delta (Pagel, 1997, 1999). We also used Moran's autocorrelation index (I) to estimate phylogenetic signal in all song traits (Pavoine et al., 2008), as well as Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999).

To account for Bergmann's rule in call variation, we fitted generalized linear models (GLM) of spectral parameters of all individual recordings instead of using the means for each species. In these models we verified changes in maximum, minimum and peak frequency, as well as call duration, in relation to latitude, minimum, and maximum annual temperatures of the coordinates from where the recordings were taken, including the species as a covariate.

For all models we selected the best fit using Akaike Information Criterion corrected for sample size (AICc). Upon selection, model fits were validated by checking the residuals dispersion and line fit in a Q-Q plot.

RESULTS

We analyzed 756 call samples from 44 species of manakins. The number of samples per species varied from 49 for *Antilophia galeata* to just one for *Corapipo leucorrhoa*. The number of samples per species was dependent on availability on bioacoustic repositories, which means that rarer and less studied species ended up with fewer samples. The distribution of samples per species is shown in Fig. 3.

The values of AICc for every fitted model can be visualized in the supplementary material. Additionally, the best fitted PGLS model for every song trait within the 45 species dataset, along with their respective R^2 and p-values, are shown in Table 1. Among the best fitted PGLS models for the 37 species with data on sexual dichromatism, and for the 10 species with data on display complexity, none showed any significant relation. Of all the PGLS models, four of them showed significant relations ($p < 0.5$). Peak frequency was related with beak length and beak width ($R^2 = 0.1$); song pace was related to beak length in a model that considered mass and beak depth ($R^2 = 0.16$); and call duration had two significant models involving body mass, one with beak length ($R^2 = 0.39$), and the other with bioclim variable 06, which represents the minimum temperature of the coldest month ($R^2 = 0.19$). This latter model was obtained when we ran the analyses excluding bill size variables, for which we had no prior hypothesis to direct cause and effects related to call duration. Graphical representations of these models are shown in Fig. 4.

Table 1
Best fit PGLS model for every song trait in analyses involving 44 species of manakins. Bio 05 represents the maximum average temperature of the warmest month, while Bio 06 is the minimum average temperature of the coldest month. Significant p-values (< 0.05) are marked (*).

Maximum frequency	**Drivers**	**Adjusted R^2**	**p-value**
	Bio 06	**0.0563**	**0.07**
Minimum frequency	Bio 05	0.0335	0.13
Frequency bandwidth	Beak length culmen	0.0424	0.11
Peak frequency	Beak width + beak depth	0.1035	0.04*
Call duration	Body mass + beak length culmen	0.3895	< 0.001*
Number of notes	Body mass	0.0611	0.06
Pace	Body mass + beak width + beak depth	0.1651	0.02*

We found no relation between sexual dichromatism or mating display complexity with any of the call traits we analyzed. Although, sexual dichromatism was present in significant models for maximum frequency, call duration and pace, while mating display complexity was part of a significant model for pace. These models can be seen in the supplementary material. We found no relation between song spectral parameters and latitude, minimum and maximum annual temperature across all species when individual samples were fitted in a GLM.

We found significant phylogenetic signal within four song parameters, peak frequency, frequency bandwidth, maximum frequency and call duration (Table 2). Peak frequency and frequency bandwidth had the strongest signals which were significant across all indexes analyzed. While maximum frequency had significant values of both I and K, and call duration was significant only for I. For these four parameters, we present phylogenetics correlograms and Local Moran's I value plots (Figs. 5 and 6).

Table 2
Moran's autocorrelation Index (I), Blomberg's K and Pagel's λ for different song traits among 44 species of manakins. Highlighted in red are results that showed significant p-values (< 0.05) and thus represent call traits with phylogenetic signal.

Maximum frequency	**I**	**K**	**K.star**	**λ**
	0,0279464	**0,4423351**	**0,5178328**	**0,7139800**
Minimum frequency	-0,0148820	0,4075467	0,4457367	0,0000542
Frequency bandwidth	0,0285035	0,3678598	0,4347955	0,5153382
Peak frequency	0,0217710	0,4934390	0,5429586	0,7971416
Call duration	0,0161318	0,2917219	0,3403413	0,0000488
Number of notes	-0,0164571	0,2228817	0,2587153	0,0000701
Pace	-0,0167494	0,2667464	0,2973391	0,0000796

DISCUSSION

Contrary to what's expected from Fletcher (2004), no allometric relationship between frequency and body size was observed in species of the family Pipridae. The absence of such relationships has also been documented in birds of the family Turdidae (Torres et al., 2017). In both Turdidae and Pipridae, there is limited overall variation in body size among species compared to other bird groups. Consequently, allometric pressures may be masked by vocal plasticity (Patel et al., 2010) coupled with the influence of distinct evolutionary drivers. The considerable morphological diversity in the syrinx of Pipridae (Prum, 1992), which is not directly associated with species size, is another factor that could explain the absence of allometric relationships. This latter factor also demonstrates the lack of universality in Fletcher's (2004) hypothesis, given that the author employed proportionality between body size and vocal tract thickness to explain vocal allometry.

Although body size was not related to song frequencies, we found it to be positively related to song duration, a finding consistent with the hypothesis that the proportion of energy allocated to communication relative to total available energy is constant across species (Brown et al., 2004; Gillooly & Ophir, 2010). Thus, larger species, which consequently possess greater energy reserves, would use more energy in absolute terms for acoustic communication. This greater expenditure is ultimately reflected in sound amplitude, which could not be measured in this study, and call duration.

The inverse relationship between beak size and call pace was found as predicted and in accordance with what has been reported for other groups (Seddon, 2005; Mason & Burns, 2015; Derryberry et al., 2018). This relationship was expected due to a biomechanical trade-off between the force and speed of bill opening and closing (Herrel et al., 2009), preventing larger bills from producing a greater number of distinct notes within a given time interval. Considering that beak sizes typically experience natural selection pressures according to food preferences and availability (Gibbs & Grant, 1987), these acoustic

variations may be an indirect reflection of such adaptations, another example of "magic trait" evolution (Thibert-Plante & Gavrilets, 2013). Indirect effects might explain the relation we found between beak size and call duration, which was the model with the most predictive power among all song parameters.

We also found beak size to be significantly related to peak frequency, as has also been found in woodcreepers (Palacios & Tubaro, 2000), even though beak size differences are much smaller in manakins. As the bill is the last part of the vocal tract, it has no influence on generating the fundamental frequencies of the song. Instead, it acts more by amplifying and/or filtering certain frequencies within harmonics (Nowicki, 1987). In this case, we observed larger beaks often produce sounds with lower peak frequency, which may be more related to the harmonic amplification of these frequencies.

Bioclimatic variable 06, which represents minimum temperature of the coldest month, was directly related to call duration. This could once again be related with energetic limitations because higher temperature, in this case coupled with higher climate stability, provides more available energy for vocalization (Gillooly & Ophir, 2010). Besides that, no other song parameter showed any relations with bioclimatic variables, and we observed no evidence of Bergmann's rule acting on song variation. It is also important to highlight that climatic variation often occurs over the course of a day, potentially resulting in adaptation to the timing of vocalization (Larom et al., 1997), which was not assessed in this study.

Of all acoustic parameters analyzed here, none were related to sexual dichromatism or mating display complexity. Similar results have been observed in the genus *Oriolus* (MATYSIOKOVÁ et al., 2017), in the families Trogonidae and Thraupidae (MASON; SHULTZ; BURNS, 2014; ORNELAS; GONZÁLEZ; ESPINOSA DE LOS MONTEROS, 2009), and in the family Estrildidae (GOMES et al., 2017), with the latter study also incorporating mating display data. As the dataset for these models was much smaller, specially for the ones involving mating display complexity, the results here should be taken more as an exploratory study, considering its limitations.

Although coloration patterns in manakins involve high energetic costs and are implicated in sexual selection contexts (DOUCET; MENNILL; HILL, 2007), no relationships were found between these patterns and any aspect of the acoustic signals studied. This may occur if the molt period, during which dimorphic coloration is acquired, takes place outside the species' breeding season. However, the few studies containing such information often show contrasting results (KIRWAN; GREEN, 2011). For instance, in *Pipra filicauda*, molt periods were observed prior to the reproductive period (HEINDL, 2002), whereas in *Chiroxiphia caudata*, these periods were observed occurring simultaneously (BUGONI et al., 2002).

Finally, the presence of phylogenetic signals in most frequency parameters, and in call duration, show that these are highly influenced by shared ancestry, especially in shorter evolutionary times. Also, these findings, along with the low coefficient of determination for most drivers, indicate that stochasticity explains much of the song variation in manakins. Similar results have also been found in many other studies with different bird groups, indicating that non-deterministic processes may be the main factors

of bird song evolution (Slabbekoorn & Smith, 2002; Boncoraglio & Saino, 2007; Irwin et al., 2008; Derryberry et al., 2018; Marcolin et al., 2022).

CONCLUSION

The allometric constants of frequency were analyzed following the model proposed by Fletcher (2004), along with the influences of morphological attributes, environmental factors, and sexual selection on various acoustic parameters in species of the family Pipridae. No support was found for any of the frequency allometry hypotheses put forward by Fletcher (2004), but we found evidence of an allometric relationship between peak frequency and beak size, which should be further analyzed in future studies. There was also no evidence of relationships between investment in different sexually selected traits, specifically between acoustic frequency parameters and the complexity of mating displays among the species included in this analysis. Relationships were found between temporal and spectral aspects of vocalizations and both morphological variation and bioclimatic variation across the 44 species studied, although they did not seem to be under influence of Bergmann's rule.

These results show that there are morphological constraints shaping song differentiation in manakins, especially in relation to call duration and pace. We observed that body mass and beak size are very important drivers for these song parameters, although they do not explain all the variation, and most of them must be still related to stochastic evolution.

Declarations

Declarations

This project was funded by the Coordenação de Aperfeiçoamento de Pessoal do Nível Superior (CAPES). All data and codes are available at https://doi.org/10.5281/zenodo.23348843. D.B.C. proposed the study, collected and analyzed data, and wrote the manuscript. S.N. and G.R.R.B. supervised the study and reviewed the manuscript. We declare no conflicts of interest.

CONFLICT OF INTERESTS

We declare no conflict of interests.

Author Contribution

D.B.C. proposed the study, collected and analyzed data, and wrote the manuscript. S.N. and G.R.R.B. supervised the study and reviewed the manuscript.

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Data Availability

All data and codes are available in zenodo.org at https://doi.org/10.5281/zenodo.23348843

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Figures

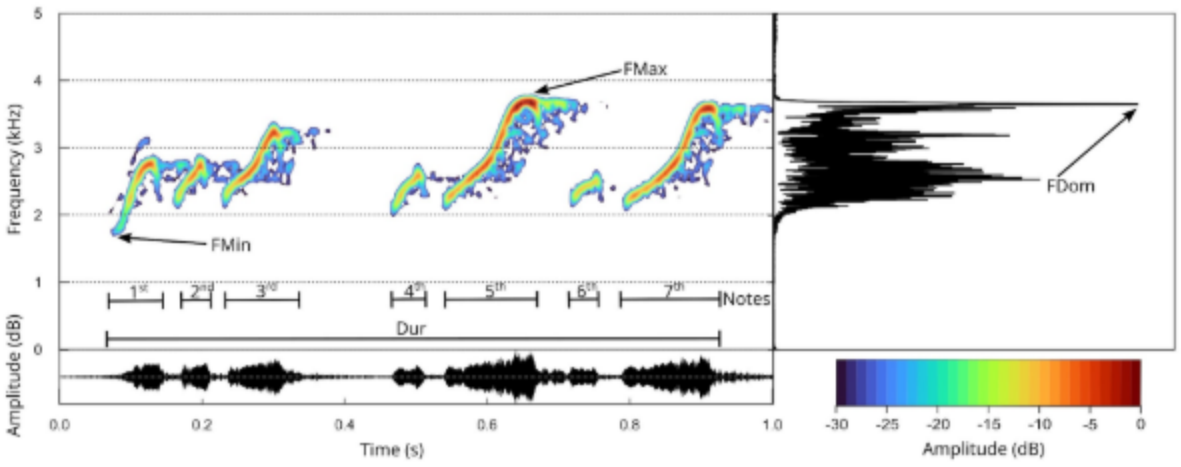


Figure 1

Spectrogram of *Antilophia galeata* showing acoustic parameters that were extracted for this study: Peak frequency (FDom), maximum frequency (FMax), minimum frequency (FMin), Duration (Dur) and number of notes.

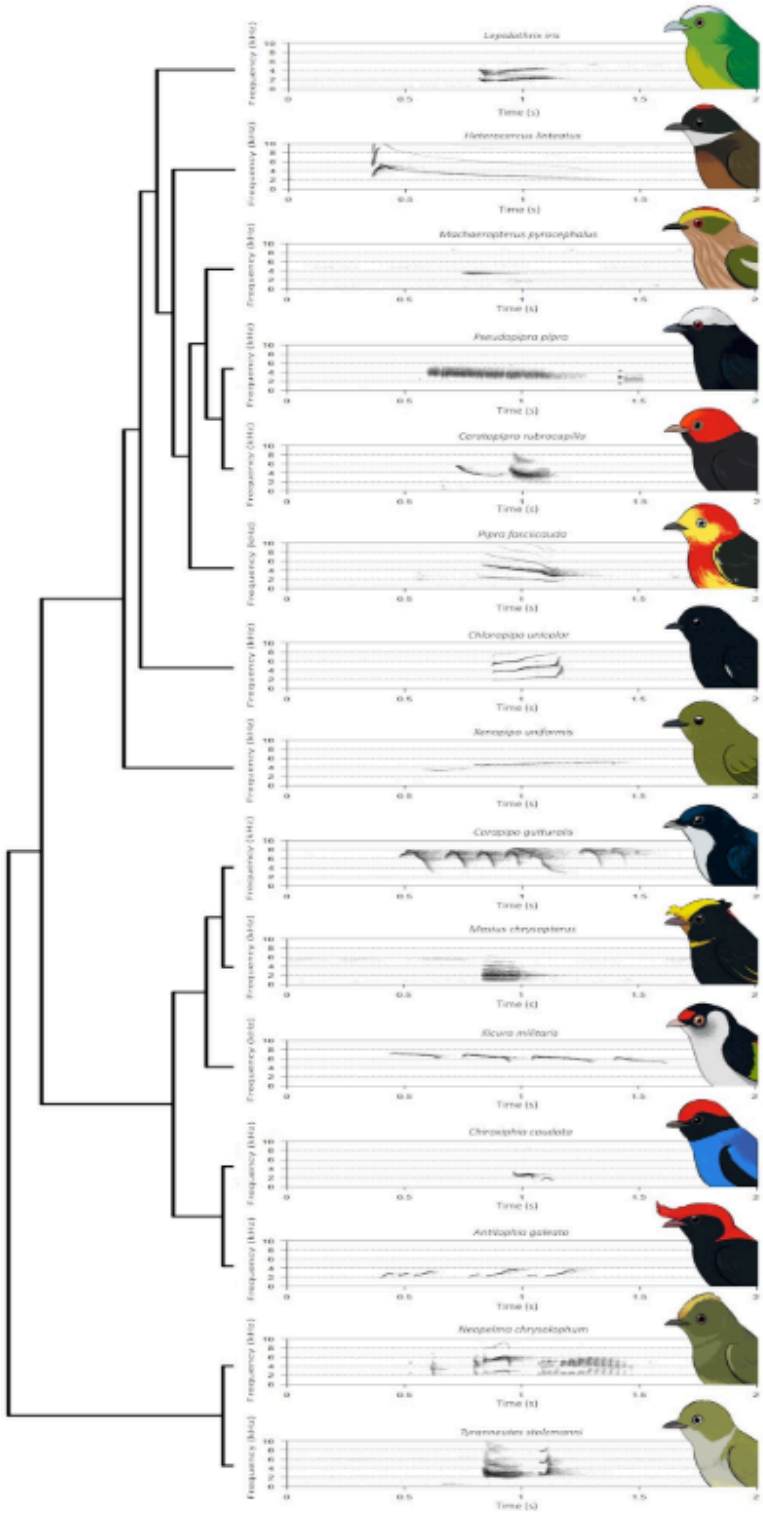


Figure 2

Phylogeny of manakins, showing the males for one species of each genera present in this study and the spectrograms of their respective calls.

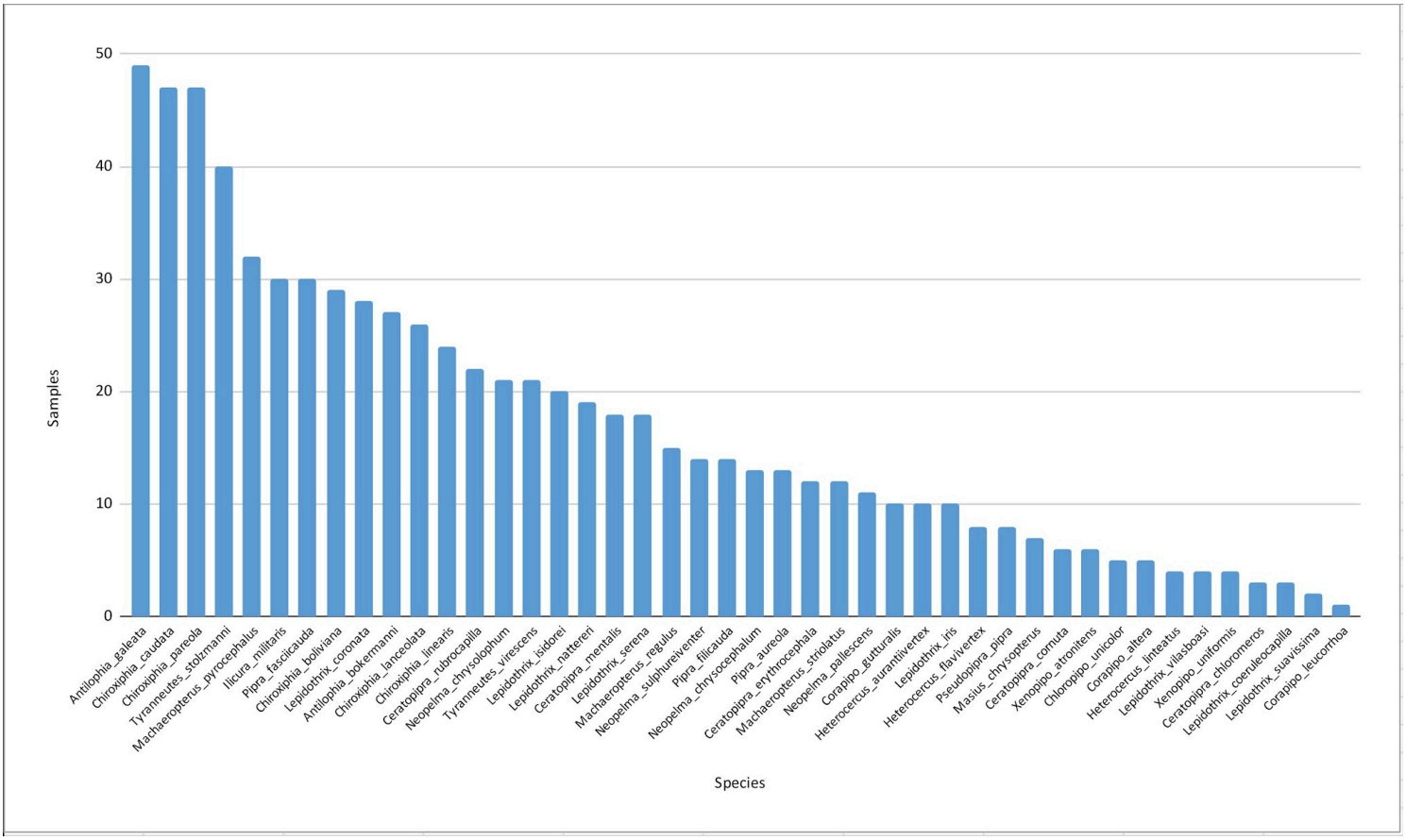


Figure 3

Number of call samples analyzed for each of 44 species of manakis present in the study.

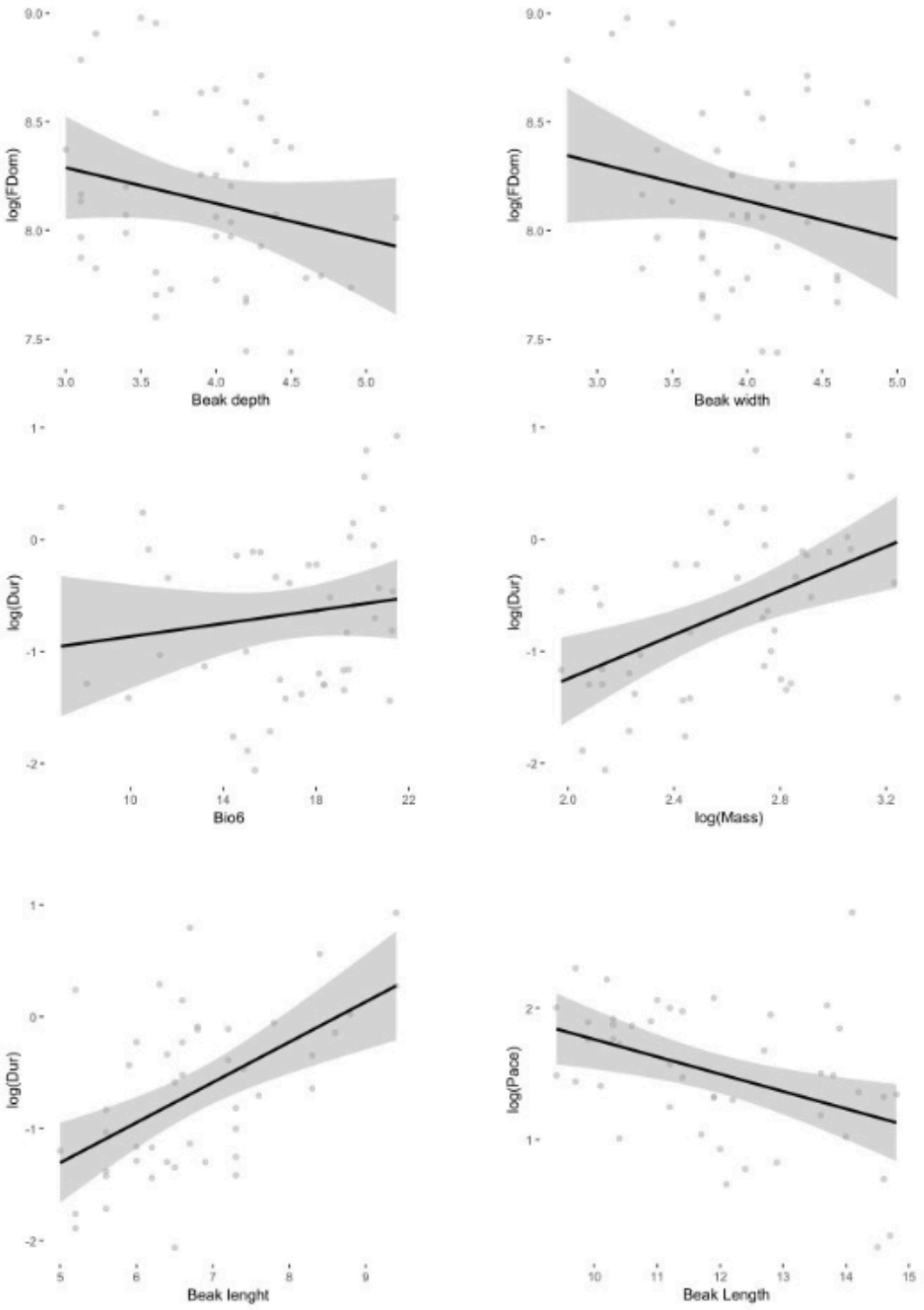


Figure 4

Significant correlation between three song traits and potential drivers of song evolution in 44 species of manakins. Song traits are peak frequency (FDom), Call duration (Dur) and Call pace. The lines represent PGLS models adjusted for the data.

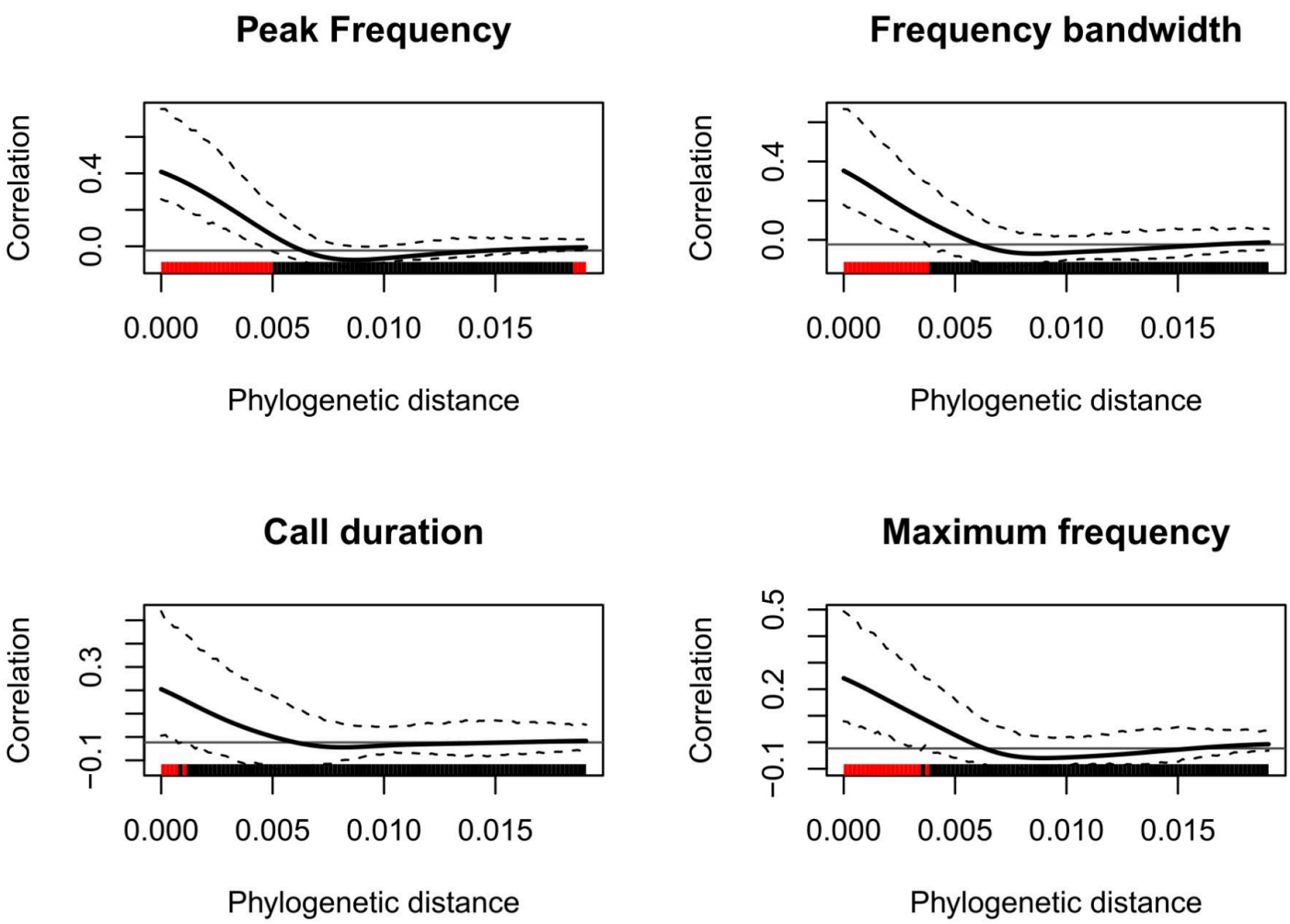


Figure 5

Phylogenetic correlograms for four song traits across 44 species of manakins. The line represents trait correlation between species along phylogenetic distances. The red bar indicates significant positive correlation.

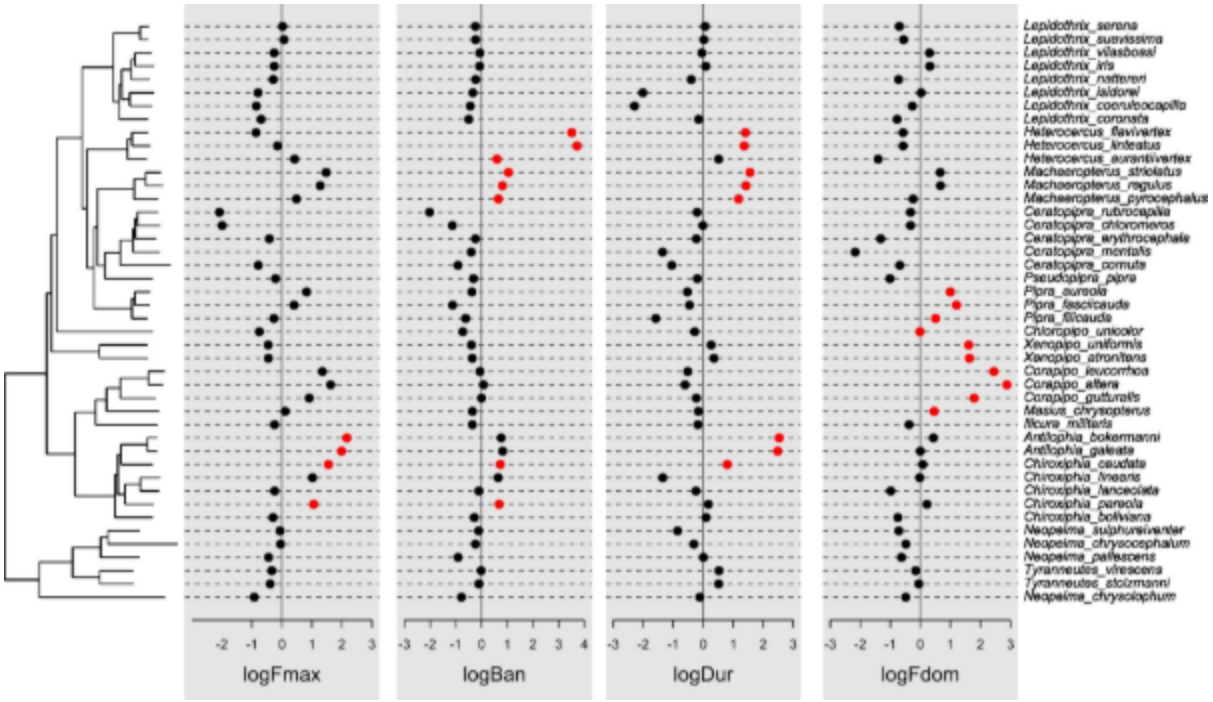


Figure 6

Local Moran's (I) values of different song traits plotted against phylogenetic relations of 44 species of manakins. Song traits are maximum frequency (Fmax), frequency bandwidth (Ban), call duration (Dur) and peak frequency (Fdom). Red dots indicate significant values of I, which indicate the presence of phylogenetic signal in the trait for the respective species.