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Cite this article: van der Kamp AAW, Ottenburghs J. 2026 Cotinga communication constrained: body size and lekking behaviour influence cotinga song (Aves: Cotingidae). *Proc. R. Soc. B* **293**: 20253150.
https://doi.org/10.1098/rspb.2025.3150

Received: 8 December 2025
Accepted: 25 February 2026

Subject Category:
Evolution

Subject Areas:
behaviour, evolution, taxonomy and systematics

Keywords:
acoustic adaptation, bioacoustics, bird song, frequency, morphological constraint, lek, mating system

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8390226.

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Cotinga communication constrained: body size and lekking behaviour influence cotinga song (Aves: Cotingidae)

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Bird vocalizations can be influenced by different ecological and evolutionary factors. For example, the ‘morphological constraint’ hypothesis predicts a negative correlation between body size and song frequency, while the ‘acoustic adaptation’ hypothesis predicts that organisms in dense habitats sing lower-frequency songs compared with organisms inhabiting more open areas. However, little is known about how song structure is influenced under different lek mating systems. Here, we used 61 cotinga (Aves: Cotingidae) species to investigate fundamental relationships between morphology, ecology and mating system by compiling a dataset on song, morphological and environmental traits as well as different lek mating systems. We found that both peak frequency and frequency range correlate negatively with body size. Moreover, our results suggest a positive (albeit marginally significant) correlation between lek presence and frequency range. Our results thus support the ‘morphological constraint’ hypothesis, while environmental factors barely influence cotinga songs. These findings suggest that cotinga species are vocally constrained by body size, probably because of the limitation on the sound-producing organs, while evolution might have favoured a broad frequency song in avian lek mating systems.

1. Introduction

Acoustic signals play a dominant communication role in birds [1]. There is a wide diversity in bird vocalizations, which can be used to warn others of potential dangers, defend territories and attract mates [2,3]. Sexual selection can promote more elaborate vocalizations [4–6], and divergence in vocalization structure can reduce interbreeding between populations, which may lead to speciation [2,7]. Therefore, understanding the drivers of song divergence is fundamental to our understanding of avian speciation [8].

In birds, vocal development can be influenced by the structure of the birds’ brains, and whether the bird’s song is innate or learnt [4,9]. However, morphological features can also influence their song. For example, body size is known to constrain vocalizations throughout the animal kingdom (e.g. in insects, fish, reptiles, amphibians, birds and mammals) [1,10,11]. The ‘morphological constraint’ hypothesis predicts a negative correlation between body size and song frequency [12,13]. In general, larger birds tend to sing lower-frequency songs [8,12,13], produce narrower bandwidths [14] and sing with a slower song pace compared with smaller birds [15,16]. These patterns are probably caused by the morphological limitation in the birds’ sound-producing structures, including the syrinx and the rest of the vocal tract [13,16–18].

Apart from body size, environmental factors such as habitat cover, annual precipitation, temperature and elevation may also affect sound production [4,8]. The 'acoustic adaptation' hypothesis predicts that organisms in dense habitats tend to produce lower-frequency songs compared with organisms in more open areas [19]. This is because low-frequency sounds are less affected by vegetation and therefore offer better signal detectability [8,20]. By contrast, high-frequency sounds are more susceptible to attenuation, scattering and reverberation, which lower signal transmission and detectability in dense environments [10]. Despite this theoretical framework, limited support exists for the 'acoustic adaptation' hypothesis, where empirical large-scale studies have found mixed results [11,14,15,21,22]. Similar to habitat cover, annual precipitation and humidity can affect song transmission owing to the environmental noise of rainfall and because of the link between precipitation and thermoregulation in birds [16,23]. Therefore, we predict that birds in areas with high precipitation sing lower-frequency songs. In addition, vocalizations can be indirectly influenced by elevation [4] because elevation relates to differences in habitat structure, climate and species diversity [24,25]. For that reason, elevation can be used as a proxy for broader environmental variation. It is expected that birds in lower elevations sing with a lower-frequency song compared with species inhabiting locations in higher altitudes, owing to the lower atmospheric density in higher-altitude areas [4].

In addition, morphological traits and environmental factors might interact in complex ways. Body size is fundamental in an organism's ability to maintain homeostasis and thermoregulation. Environmental temperature can strongly influence body size and consequently affect vocalizations [16]. It is predicted that birds in colder areas (such as at higher elevations) have a bigger body size and, therefore, sing lower-frequency songs. Additionally, according to Bergmann's rule, body size is expected to increase with latitude [26–29]. For these reasons, average temperature and latitudinal position need to be considered while studying the relationship between body size and vocalization [16,26].

Besides morphological and environmental characteristics, mating systems might also be correlated with vocalization traits. Birds have a wide variety of mating systems, with some species showing monogamous pair-bonding, where both sexes build the nest and share incubation and feeding duties, while other species are polygamous. Males of some polygamous bird species display for females at clustered display sites called leks [30]. Males of lekking species tend to have visual ornamentations and courtship displays that are often accompanied by song [31]. For example, in birds-of-paradise, both song and dance behaviours and ornamention characteristics tend to evolve unconstrained rather than being subjected to evolutionary trade-offs [32] (but see Badyaev *et al.* [33] for a trade-off in finches). It is expected that lekking species with more elaborate displays also have elaborate songs and striking visual traits, and that evolution has favoured more elaborate songs in lekking bird species, compared with non-lekking species.

To date, the influence of physical traits and environmental factors on song structure has been extensively examined in both oscine [14,16] and suboscine [2,4,8,15] bird families, as well as global analyses of passerines [11,34]. Moreover, the evolutionary relationship between mating systems and song structure has been studied with mixed results [35–38]. However, the effect of lekking behaviour on song structure has been, to our knowledge, unexplored. By incorporating information on mating systems while testing for the 'morphological constraint' and 'acoustic adaptation' hypotheses, we may provide a more comprehensive understanding of how morphology, environment and mating systems jointly shape vocal evolution.

Here, we investigate the influence of morphology, ecology and mating system on bird songs by focusing on a monophyletic family with a great diversity in songs, body sizes, habitats and mating systems. The cotingas (Aves: Cotingidae) comprise a family of neotropical suboscine birds. Most cotinga species, being suboscine passerine birds, have an innate song, except for two *Procnias* species [39,40]. Therefore, vocal divergence patterns are barely complicated by cultural evolution [8]. Cotingidae have a great array of vocalizations, including some of the loudest vocalizations among birds (e.g. *Procnias* and *Lipaugus* sp.) [41]. This vocal diversity is paired with a diverse syringeal morphology within the cotinga family [42]. Moreover, cotingas show a wide variety of morphological, ecological and mating systems [43] that might influence their song. First, cotingas show a wide range of body sizes, ranging from 29.5 to 450 g [44,45]. Second, cotingas occupy a wide variety of ecological niches across a wide range of latitudes, from Mexico to the south of Chile. This distribution also includes a wide range of elevations owing to the presence of the Andes in the habitats of many cotinga species, and a broad spectrum of temperature and precipitation conditions [46]. Third, cotingas have a wide variety of mating systems, with group-living territorial species (*Querula purpurata*), socially monogamous species (*Ampelion*, *Phytotoma* and *Pipreola* sp.), concentrated lekking species (e.g. *Rupicola* sp.) and dispersed lekking species (e.g. *Phoenicircus* and *Procnias* sp.) [43]. All in all, the wide variety of body sizes, ecological niches and mating systems makes cotingas an ideal suboscine family in which to study the influence of morphology, ecology and mating systems on song characteristics.

Specifically, we compiled a dataset of cotinga song, morphological, geographical and ecological traits, and mating systems to test (i) the 'morphological constraint' hypothesis, where we predict a negative correlation between body size and song frequency, bandwidth and song pace, because of the larger sound-producing structures in bigger birds [2,12,15]; and (ii) the 'acoustic adaptation' hypothesis, where we predict that species in closed habitats produce lower frequencies in songs because low-frequency songs propagate better in closed vegetations compared with high-frequency songs [10,19]. Finally, we predict that (iii) bird species with a lek mating system produce a wider range of frequencies and a higher song pace compared with non-lekking species because of the strong male–male competition within lekking species [47] that might favour more elaborate songs compared with non-lekking species.

2. Material and methods

We sourced songs from the xeno-canto database (https://xeno-canto.org/) and the Macaulay Library at Cornell Lab of Ornithology (https://www.macaulaylibrary.org) (June 2025), representing 61 of 66 cotinga species, from all 24 genera. We excluded the

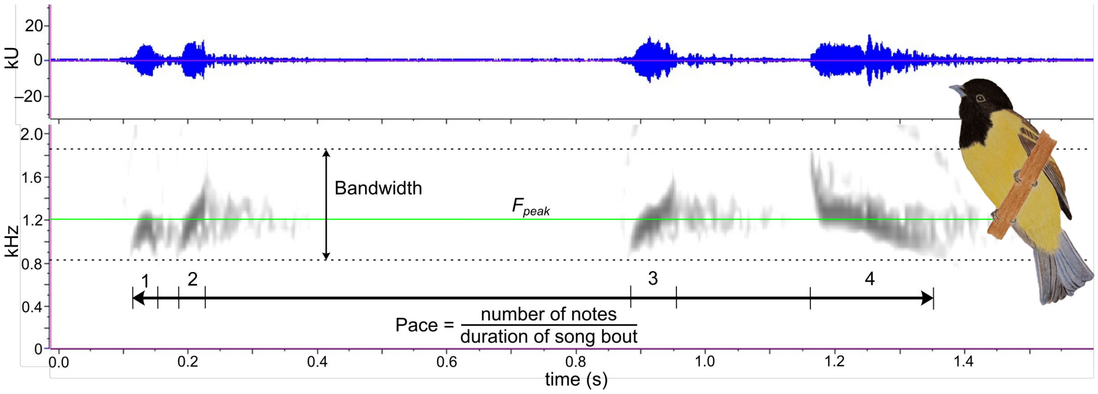

Figure 1. Song bout of a Hooded berryeater (*Carpornis cucullata*; xeno-canto accession number: XC349680) with a waveform in amplitude (kU) and spectrogram in frequency (kHz) over time (s). The bandwidth, peak frequency (F_{peak}; green line) and song pace are displayed in the spectrogram. Brackets on the horizontal duration line denote the start and end of the four different notes in this song bout. The illustration of a male Hooded berryeater is for illustrative purposes only. See electronic supplementary material, S4, for image attributions. Edited with Inkscape v.1.4.2.

species *Carpodectes antoniae*, *Carpodectes nitidus*, *Phibalura boliviana*, *Cotinga cotinga* and *Co. maculata* from our analyses as no usable songs were available for these species. Only adult male songs were selected. Although the exclusion of female vocalization cannot be guaranteed for all species, especially in species with similar vocalizations between the sexes, we minimized the risk of female song inclusion by selecting recordings with explicitly stated sex of the bird from the recorders. Moreover, the bird songs were selected based on previous descriptions from Kirwan *et al.* [48] and Winkler *et al.* [49] and they include advertisement and agonistic songs. Using similar references, we excluded other types of vocalizations, such as calls. In addition, only recordings with suitable signal-to-noise levels were used to reduce potential errors or biases by manually selecting high-quality recordings available for each species with minimal background noise and a clearly distinguishable cotinga vocalization. We followed the IOC World Birds Names v.15.1 [50] for the scientific names of the cotinga species.

Following Hay *et al.* [16], we analysed from each recording a single song bout from an individual song to ensure sample independence. A song bout was defined as a continuous vocalization including tonal notes from an individual bird that was separated from another song bout of the same individual by a gap of >1 s. Hereby, a note was defined as a continuously produced sound, appearing as a continuous trace on a spectrogram, bounded by a break (>1 ms) before and after the sound. We assumed recordings from different geographic coordinates (threshold 0.0001° ≈ 10.5 m) to be of a different individual [16]. Raven Pro v. 1.6.5 (Cornell Laboratory of Ornithology) was used to make Hann spectrograms with the default settings of Raven Pro 1.6.5 [51] (50% contrast and brightness and a window size of 512 samples) of 514 individuals from 61 cotinga species (1–20 recordings per species; mean = 8.43; median = 4; electronic supplementary material, S1).

Following previous studies [16,31], three acoustic variables for each song bout were selected to capture a general overview of the cotinga species' song and because these acoustic variables have been used in previous studies testing the 'morphological constraint' and 'acoustic adaptation' hypotheses [4,11,16]: (i) bandwidth, the range between the lower frequency of the lowest pitched note and the higher frequency of the highest pitched note within a song bout; (ii) peak frequency, a frequency measure from where the highest portion of energy is released within the song bout [21], measured with the '*peak frequency*' function of Raven Pro v. 1.6.5; and (iii) song pace, the number of notes within a song bout divided by the total time duration of a song bout (figure 1; electronic supplementary material, S1). Song pace is therefore determined by the number of notes and the duration of a song bout. It is of note that song pace might be underestimated for species that have long breaks (>1 s) within their song. Therefore, caution needs to be taken when interpreting results with this variable. We did not include minimum and maximum frequencies as separate variables, given that these variables were used to calculate the bandwidth and because we already use the peak frequency as a frequency measurement.

The distribution maps from BirdLife International (https://datazone.birdlife.org/) and the environmental and elevation data with a 1 km^2 resolution from WorldClim 2 [52] were used to obtain the mean value for three bioclimatic variables for each cotinga species with the 'raster' package [53]. The bioclimatic variables in this study include (i) annual precipitation (mm), (ii) average year-round temperature (°C) and (iii) average elevation (m). Annual precipitation and average year-round temperature were already averaged over the years 1970–2000 before obtaining the mean value for each cotinga species.

For each species, we also obtained the habitat cover, centroid latitude and longitude from the AVONET database [44]. Habitat cover was categorized into (0) dense habitats (n = 52), where species primarily inhabit the lower and middle storey of forests, or dense thickets or dense shrubland, and (i) semi-open habitats (n = 9), where species primarily live in open shrubland, scattered bushes, parklands, low dry or deciduous forest or thorn forests [44]. Note that none of the cotinga species is categorized in open habitats (coded as '2' in Tobias *et al.* [44]). The databases from Tobias *et al.* [44] and Dunning [45,54] were used to obtain body mass values for each species (figure 2). If available, we only used male body mass, as we only consider male song, and because of the sexual size dimorphism within the cotinga family [42,48]. Among the 61 cotinga species in this study, male body size data were available for 25 species. For 30 species, only the average body size across both sexes was available and therefore used. For three species, the sex of the measured individuals was unknown, and for three other species, only female body size was available (electronic supplementary material, S2). The predictor variables average elevation, average temperature, annual precipitation and body size were $\log_{10}$-transformed to normalize the data (electronic supplementary material, S2).

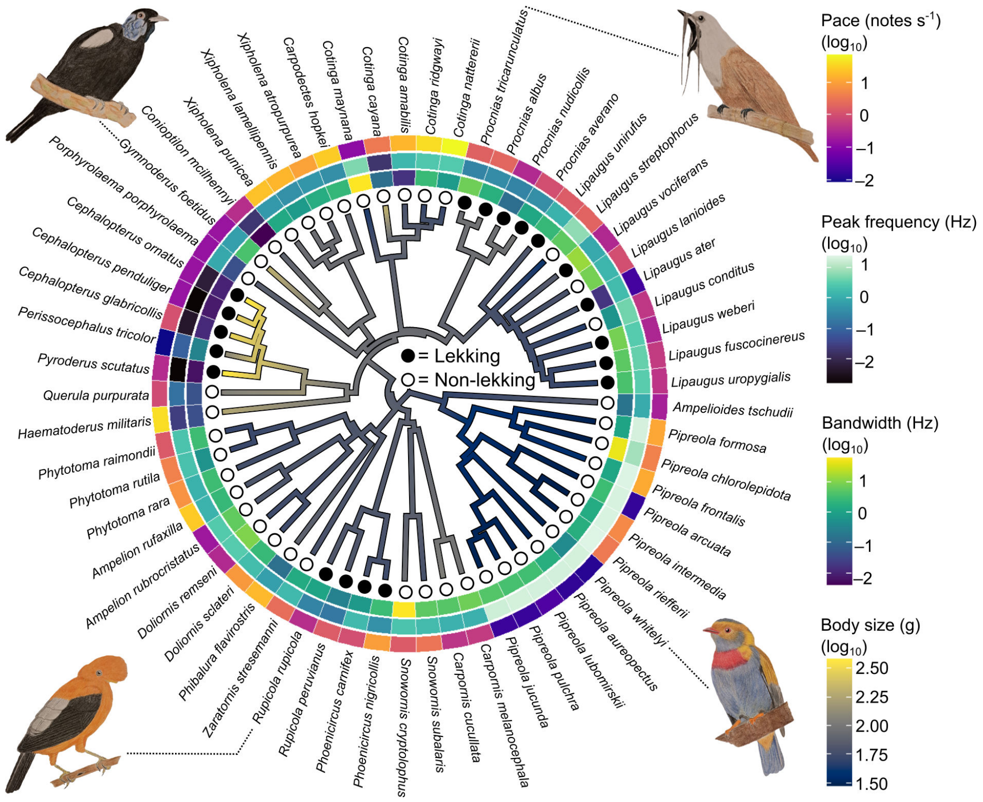

Figure 2. Phylogeny of 61 Cotingidae species from Harvey *et al.* [55] coloured by body size in grams (log$_{10}$-transformed). Dots at the tip labels are coloured according to lekking (black) and non-lekking (white) species. The heatmap shows (from outer to inner circle) the log$_{10}$-transformed average values for song pace, peak frequency and bandwidth per species. Illustrations are included for illustrative purposes only. Image attributions can be found in electronic supplementary material, S4. Edited with Inkscape v.1.4.2.

Based on mating system descriptions from Kirwan *et al.* [48], Anderson *et al.* [56] and Winkler *et al.* [49], we categorized cotinga species into lekking (n = 19) and non-lekking (n = 42) species, which were added to the dataset as a binary variable (1 = lekking, 0 = non-lekking; figure 2; electronic supplementary material, S2). For the main analyses, we did not distinguish between 'classical' lekking species, where males come together in clustered display sites or cooperate together to perform for females (n = 6), and 'exploded' lekking species, where males are more dispersed and in auditory rather than visual contact (n = 13) [47,56].

The phylogenetic tree was obtained from Harvey *et al.* [55] (electronic supplementary material, S3). This phylogeny was estimated using data from 2389 genomic regions. We trimmed the tree to the 61 cotinga species for which we obtained song measurements using the '*keep.tip*' function from the package 'ape' [57] (electronic supplementary material, S3). The '*contMaps*' function from the package 'phytools' [58] was used to colour the branches in the phylogeny according to the body size. To visualize the phylogenetic relationships over song traits, we used the 'ggtree' package [59] to create a heatmap around the tree (figure 2).

(a) Statistical analysis

The use of recording data may introduce spatial biases because more recordings tend to be made in more accessible areas. Therefore, before statistical analysis, we calculated for each species the average value for our three song variables (bandwidth, peak frequency and song pace). Subsequently, we log$_{10}$-transformed the song variables because logarithmic scales represent the perception of birds and to meet the parametric assumption of normality and homogeneity of variance [15,16,60]. Moreover, all predictor variables (habitat cover, body size, elevation, precipitation, centroid latitude, centroid longitude and lek presence) were checked for collinearity by testing the variation inflation factors (VIFs), using the '*vif*' function from the 'car' package [61]. The average temperature appeared to be collinear with average elevation (VIF > 5; electronic supplementary material, S5). Additionally, we calculated pairwise Pearson correlation coefficients between all predictor variables, which confirmed the high collinearity between elevation and average temperature (electronic supplementary material, figure S1). As elevation is associated with multiple environmental gradients such as temperature, precipitation and wind, and because the average temperature is a more straightforward environmental variable, we decided to use average temperature in our model. However, to test for potential differences between average elevation and average temperature, we performed additional analyses with average elevation instead of average temperature (electronic supplementary material, S6, S7). All other predictor variables showed no collinearity between each other (VIFs < 5; electronic supplementary material, S5).

We performed separate phylogenetic generalized least squares (PGLS) regressions using the package 'caper' [62], with the three song variables as response variables to determine the influence of the predictor variables on song within the cotinga family, while accounting for non-independence owing to phylogenetic relationships. We used Pagel's lambda (λ) in each regression to evaluate the phylogenetic signal and to correct for the phylogenetic signal intensity in the regression model using

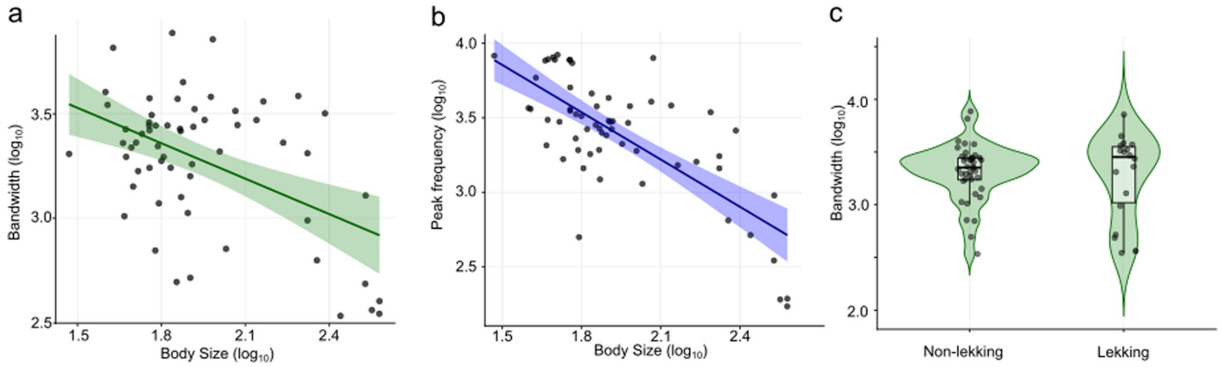

Figure 3. Significant ($p < 0.05$) correlations from the PGLS regressions (table 1). Black dots represent single Cotingidae species. The 95% confidence intervals (a,b) and violin plot with mean and interquartile ranges (c) are coloured according to the predictor variable in the PGLS (bandwidth (green) and peak frequency (blue)). Edited with Inkscape v.1.4.2.

the '*phylosig*' function from the 'phytools' package. The trait values are phylogenetically independent when $\lambda = 0$, while $\lambda = 1$ indicates a strong phylogenetic signal consistent with the Brownian motion model, suggesting that the vocal trait difference accumulates randomly over time [63]. We also performed additional PGLS analyses excluding the six 'classical' lekking species (*Rupicola peruvianus*, *R. rupicola*, *Perissocephalus tricolor*, *Pyroderus scutatus*, *Lipaugus ater* and *L. fuscocinereus*) to test whether 'exploded' lekking species alone explain the observed patterns and to ensure that these six species do not drive the main results. Similarly, separate analyses excluding the three species with only female body size data (*Lipaugus conditus*, *Cephalopterus ornatus* and *Haematoderus militaris*) were performed to ensure that these three species do not influence correlations, given the strong sexual size dimorphism within the Cotingidae family [42,48].

To confirm the results from our PGLS analysis, we also assessed the relationship between vocal traits and the predictor variables with Bayesian regression models using Stan (BRMS). We used the package 'brms' [64] with a Gaussian response distribution. All continuous predictor variables were standardized using Z-score transformation (mean = 0 and s.d. = 1) for direct effect size comparison. Phylogenetic non-independence was modelled via a correlation matrix using the '*vcv*' function from the 'ape' package [57]. We ran our models with four independent Markov Chain Monte Carlo chains and with 4000 iterations for each chain. In addition, for each chain, 2000 warm-up iterations were run. An effect was considered significant when the 95% credible intervals of the effect size did not overlap zero [16].

Finally, to further explore causal associations between song, morphological and environmental traits and mating systems, we performed a phylogenetic path analysis (PPA) using the package 'phylopath' [65]. A PPA allowed us to investigate our three hypotheses ('morphological constraint', 'acoustic adaptation' and 'acoustic lek' hypotheses), by testing interactions among the vocal, morphological, environmental and lek mating system variables within a single model, instead of performing separate models as in the PGLS and BRMS. Several PPA models were performed using the 61 cotinga species, and models were compared using a corrected C-statistic information criterion (CIC_c). All statistical analyses were conducted using R v. 4.4.1 [66].

3. Results

Species from the Cotingidae family showed a wide variety of songs. Average bandwidth values ranged from 341.38 (*Gymnoderus foetidus*) to 7694.74 Hz (*Cotinga maynana*). Peak frequency values varied from 172.27 to 8341.44 Hz and were lowest in *Cephalopterus glabricollis* and the highest in *Pipreola intermedia*. In addition, *P. scutatus* and other *Cephalopterus* species showed narrow average frequency ranges and low peak frequency values (figure 2). Song pace was fastest in *Cotinga ridgwayi* (20.27 notes s^{-1}) and slowest in *P. tricolor* (0.28 notes s^{-1}), although several *Pipreola* species also showed low song pace (0.32–8.63 notes s^{-1}; figure 2).

The three song variables as response variables showed diverse phylogenetic signal values according to our PGLS models, when testing the relationship between morphological, environmental and mating systems on Cotingidae song traits. Peak frequency and pace had a high phylogenetic signal ($\lambda = 0.618$ and 1.000, respectively; table 1). However, the low Pagel's lambda value for bandwidth ($\lambda = 0.000$) suggests that this trait is more phylogenetically independent (table 1; electronic supplementary material, S6).

Multiple significant relationships were revealed by the PGLS models. Cotinga species with a bigger body size sang with a narrower frequency range ($\beta_{st} = -0.8211$; $p \leq 0.0001$; $\lambda = 0.000$; table 1; figure 3a) and at a lower frequency ($\beta_{st} = -0.7770$; $p \leq 0.0001$; $\lambda = 0.618$; table 1; figure 3b) compared to species with a smaller body size. We did not find any significant effects of the predictor variables habitat cover, average temperature, annual precipitation, centroid latitude and centroid longitude on any of the song variables. In contrast, lekking behaviour in cotinga species was significantly positively correlated with bandwidth ($\beta_{st} = 0.2738$; $p = 0.0142$; $\lambda = 0.000$; table 1; figure 3c), suggesting that lekking birds sing with a wider range of frequencies compared to non-lekking birds. While the violin plot displays a large variation in bandwidth across both lekking and non-lekking groups (figure 3c), the PGLS confirms a significant positive correlation. Song pace as a response variable was not influenced by any of the predictor variables. The additional PGLS models without the six 'classical' lekking species showed similar results (electronic supplementary material, S6). In addition, the results of the PGLS models excluding the three species where only female body mass is known were similar (electronic supplementary material, S6). Finally, the additional PGLS

Table 1. Results of the multiple phylogenetic generalized least square (PGLS) model for three song variables (bandwidth, peak frequency and song pace) as response variables in 61 Cotingidae species. β_{st} is the estimated value and s.e. stands for standard error. Significant *p*-values ($p < 0.05$) are highlighted in bold. The table layout is obtained from Porzio *et al.* [4]. Full model results can be found in electronic supplementary material, S6.

Bandwidth	β_{st}	s.e.	*t*-value	*p*-value
(intercept)	5.4043	0.9292	5.8160	**<0.0001**
habitat cover	−0.1563	0.1252	−1.2489	0.2172
body size	−0.8211	0.1844	−4.4523	**<0.0001**
temperature	−0.0845	0.4189	−0.2017	0.8410
precipitation	−0.1949	0.2016	−0.9670	0.3379
latitude	−0.0010	0.0050	−0.1986	0.8433
longitude	−0.0022	0.0041	−0.5327	0.5965
lek presence	0.2738	0.1079	2.5372	**0.0142**
	$\lambda = 0.000$	$R^2_{adj} = 0.285$		

peak frequency	β_{st}	s.e.	*t*-value	*p*-value
(intercept)	6.0156	0.8300	7.2479	**<0.0001**
habitat cover	−0.1605	0.1081	−1.4846	0.1436
body size	−0.7770	0.1749	−4.4428	**<0.0001**
temperature	−0.6802	0.3814	−1.7835	0.0802
precipitation	−0.0686	0.1502	−0.4570	0.6495
latitude	0.0051	0.0039	1.3225	0.1917
longitude	−0.0009	0.0033	−0.2803	0.7803
lek presence	0.0085	0.1016	0.0833	0.9339
	$\lambda = 0.618$	$R^2_{adj} = 0.308$		

pace	β_{st}	s.e.	*t*-value	*p*-value
(intercept)	1.5514	1.4703	1.0551	0.2962
habitat cover	0.1484	0.1919	0.7734	0.4427
body size	−0.4161	0.3454	−1.2046	0.2337
temperature	−0.8562	0.7198	−1.1894	0.2396
precipitation	0.1498	0.2137	0.7012	0.4863
latitude	0.0048	0.0060	0.7983	0.4283
longitude	−0.0048	0.0047	−1.0266	0.3093
lek presence	−0.2269	0.1964	−1.1553	0.2532
	$\lambda = 1.000$	$R^2_{adj} = 0.073$		

where we used the average elevation instead of average temperature revealed no correlations between the response variables and average elevation (electronic supplementary material, S6).

The BRMS analysis partially supported the PGLS results because body size was negatively correlated with both bandwidth and peak frequency (figure 4; electronic supplementary material, S7). However, the correlation between bandwidth and lek presence found in the PGLS was no longer significantly supported in the BRMS (β = 0.09; 95% CI = −0.04 to 0.21), although the 95% CI slightly overlapped with zero, suggesting a marginally significant correlation between bandwidth and lek type (figure 4). No additional significant correlations were found in our BRMS compared with the correlations found in the PGLS. The model diagnostics confirmed that the BRMS estimates were stable ($\hat{R}$ = 1.00; effective sample sizes were large; electronic supplementary material, S7). Additional models using average elevation instead of average temperature, and models excluding the three species without information on male body mass showed similar results (electronic supplementary material, S7). However, the BRMS excluding the six 'classical' lekking species found a significant correlation between lek type and bandwidth (β = 0.12; 95% CI = 0.02 to 0.22) (electronic supplementary material, S7).

The best-supported PPA showed similar results compared to the PGLS (electronic supplementary material, S8). Lek presence was positively associated with a broader bandwidth, and body size was negatively associated with both bandwidth and peak frequency (figure 5). Moreover, body size had a positive association with lek presence. Additionally, the environmental variables did not correlate with any of the song variables. However, some environmental variables did correlate with each other. For example, centroid latitude and longitude were positively associated with average temperature, whereas average

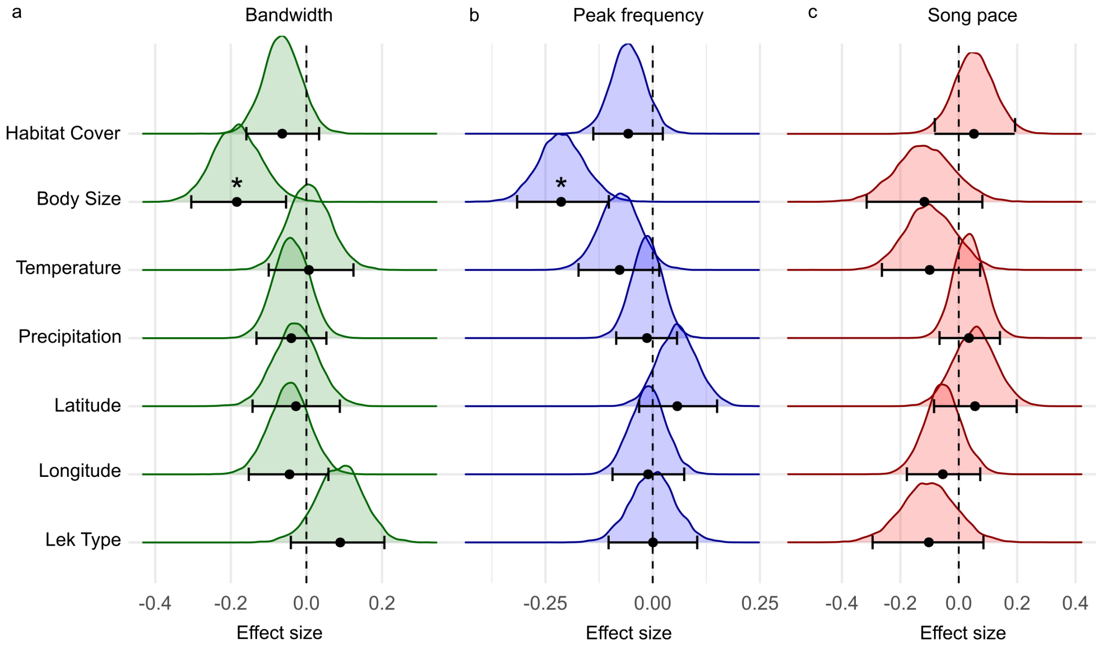

Figure 4. Results of the Bayesian regression models using Stan (BRMS) displaying posterior probability densities for multiple morphological, environmental and mating systems predictor variables of three song variables (bandwidth (a), peak frequency (b) and song pace (c)) across 61 Cotingidae species. The predictor variables have been scaled for effect size comparison. Black dots and bars represent the mean and 95% credible intervals, respectively. Significant correlations are indicated with a black asterisk (*) above the mean. Edited with Inkscape v.1.3.2.

precipitation was correlated with centroid latitude and habitat cover (figure 5; electronic supplementary material, figure S1). Finally, habitat cover was negatively associated with average temperature (figure 5). Models excluding the six 'classical' lekking species and the three species with only female body mass values showed similar results (electronic supplementary material, S8).

4. Discussion

(a) 'Morphological constraints' hypothesis

We studied the influence of morphology, ecology and lek mating system on Cotingidae songs and found strong evidence that song within the Cotingidae family is mainly constrained by body size. Specifically, body size is negatively associated with peak frequency and bandwidth according to our PGLS, BRMS and PPA analyses. Smaller Cotingidae species sing higher-frequency songs with a broader bandwidth compared with bigger species. This pattern indicates that bigger species sing at a narrower bandwidth owing to a greater reduction in their higher frequency compared with their lower frequency. The negative correlation between body size with both peak frequency and bandwidth was predicted by the 'morphological constraint' hypothesis and aligns with previous studies testing the relationship between body size and song characteristics in suboscines ([4,8,14,15], but see Friis *et al.* [69] for an opposite pattern in oscines). Taken together, our findings suggest that larger cotingas with longer and wider vocal tracts are vocally constrained and therefore cannot produce higher-frequency songs and broad ranges of frequencies compared with smaller Cotingidae species.

An alternative reason why larger cotingas do not produce high-frequency songs may be because high-frequency songs in general transfer less efficiently in dense areas compared with low-frequency songs. A large body size can therefore not be a constraint but an advantage in the production of low-frequency songs, especially in 'exploded' lekking species where efficient sound production over long distances is an advantage for males to attract females. Supporting this, a positive correlation between body size and lek presence was detected in our PPA, suggesting that lekking cotingas have a higher body mass compared with non-lekking cotingas. Evidently, the lekking species *Ce. glabricollis and P. scutatus* sing two of the lowest-frequency songs within the Cotingidae family (average peak frequencies of 172.27 and 191.54 Hz, respectively), and even within passerines [11]. Moreover, these species show the highest male body sizes within the Cotingidae family along with other species of the Cephalopterinae subfamily (>300 g; figure 2). These low-frequency songs may therefore be linked to specific morphological adaptations associated with big body size. For example, *C. ornatus* has a unique pendulous oesophageal vocal sac to produce low resonating sounds [11,70]. Therefore, cotinga species with high body masses may have a benefit in having a big body to optimize their song-detectability range.

Although non-significant, song pace tends to decrease with body size. As predicted, larger Cotingidae species sing with slower song paces compared with smaller species, consistent with previous studies [14–16]. The generally larger syrinxes and longer vocal tracts in larger birds might result in a limited speed modulation while singing compared with smaller birds. Moreover, the respiratory and muscular systems of larger birds might function at slower timescales compared with those of smaller birds. Furthermore, because larger birds have greater oxygen demands and typically take fewer breaths per unit of time compared with smaller birds [71], larger birds may be physically limited in their ability to produce rapid, high-paced songs.

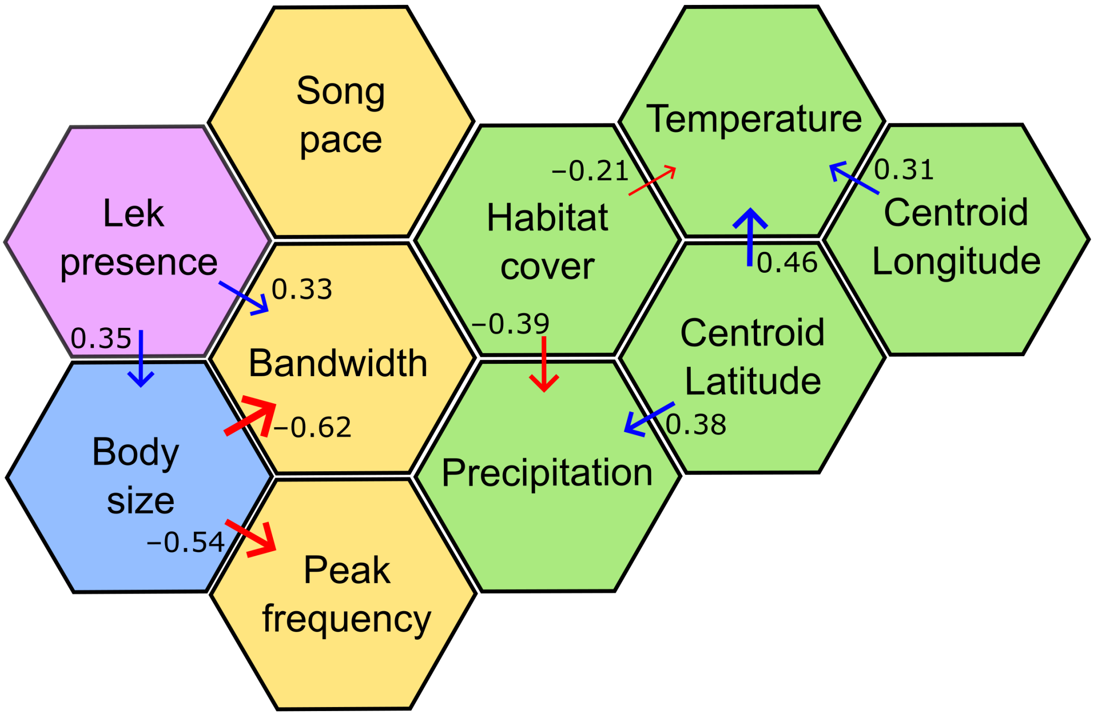

Figure 5. Schematic overview of the best-fitting model for the phylogenetic path analysis (PPA). Arrows represent significant paths between the three song variables and the predictor variables, including correlations between predictor variables. Arrow colour and width represent the direction (blue = positive; red = negative) and size of the regression coefficient, respectively. Regression coefficient values are also displayed next to the corresponding arrows. Hexagons are coloured according to the three hypotheses (purple = 'acoustic lek' hypothesis; blue = 'morphological constraint' hypothesis; green = 'acoustic adaptation' hypothesis). Figure adjusted from Odom *et al.* [67] and Liedtke *et al.* [68]. Full model results can be found in electronic supplementary material, S8. Edited with Inkscape v.1.4.2.

(b) 'Acoustic adaptation' hypothesis

We did not find support for the 'acoustic adaptation' hypothesis within the Cotingidae family. Although the environmental variables did correlate with each other, none of the environmental variables, including average elevation, affected Cotingidae song according to our PGLS, BRMS and PPA analyses. Empirical studies on the 'acoustic adaptation' hypothesis have shown mixed results, with some supporting evidence in antbirds (Thamnophilidae) [8] and tinamous (Tinamidae) [13]. Nevertheless, most studies found no support for the 'acoustic adaptation' hypothesis [10,11,16].

A reason for the absence of significant effects of song and habitat cover within the Cotingidae family might be explained by the fact that none of the cotinga species inhabits a fully open terrain, and that this variable only had two classes (namely dense and semi-open habitats). Potentially, a more detailed habitat scale (e.g. tree cover) might uncover a correlation between habitat cover and certain song features. Alternatively, some species may select specific microhabitats during perch-singing [8] with different properties from those captured by the habitat cover characterization of Tobias *et al.* [44] [11]. In addition, individuals might adjust their frequency to local microhabitat conditions [11,72,73]. The influence of microhabitats could be studied with phylogenetically corrected mixed models that account for inter- and intraspecific variation. Overall, these confounding factors might thus explain the lack of evidence for the 'acoustic adaptation' hypothesis within Cotingidae species.

(c) 'Acoustic lek' hypothesis

Cotingidae species have a wide variety of mating systems. As predicted, lekking species seem to perform songs with a broader bandwidth compared with non-lekking species according to our PGLS and PPA, suggesting that Cotingidae species with lekking systems sing with a broader frequency range compared with non-lekking species. Lekking species are known to have a strong male–male competition [47], and sexual selection may have favoured the evolution of broad frequency range songs in lekking birds. Female choice in lekking species might therefore be influenced not only by plumage ornamentation [32] and courtship dance displays [74] but also by songs with broad frequency ranges. Therefore, males in lek mating systems may signal over different sensory modalities [31,75].

Notably, the significant correlation between bandwidth and lek presence detected in the PGLS and PPA analyses was not strongly supported by the BRMS model (figure 4; electronic supplementary material, S7). However, when 'classical' lekking species were excluded from the analysis, the BRMS model recovered a significant association between lek presence and bandwidth (electronic supplementary material, S7). This result suggests that the observed relationship between lek presence and bandwidth is primarily driven by 'exploded' lekking species. The variety in average bandwidth values between all lekking cotinga species might explain why a more marginally significant correlation was found in the BRMS including all lekking cotinga species. Nevertheless, the three analytical methods (PGLS, BRMS and PPA) do suggest an interesting association between lek presence and a wider bandwidth that aligns with similar patterns in other taxa. Previous studies on the effect of mating systems and song found that polygynous species had a longer and more complex song compared with monogamous

Troglodytidae species [38]. Read & Weary [37] found that polygyny is associated with lower song rates, but more syllables per song across the species in the superfamilies Tyrannoidea, Corvoidea, Fringilloidea, Sylvioidea and Turdoidea. Although marginally significant, a correlation between lekking behaviour and frequency range has, to our knowledge, not been previously described.

Surprisingly, no effect was found between lek presence and song pace. We predicted a positive correlation between these two variables as sexual selection might favour more complex songs with a higher pace. The lack of a correlation between lek presence and song pace might be confounded by our song pace calculations. When calculating the song pace, we only included the number of notes, without information on the diversity of the notes within a song. Moreover, our song bout definition might underestimate song pace for species that take long breaks (>1 s) within their song, which could have influenced our results. Alternatively, song pace might be overshadowed by other signals in lekking males, such as bright-coloured plumages, ornamentations or mechanical sounds [43,76,77]. These alternative signals might be more important in female choice within the Cotingidae family, with song pace playing a more negligible role, explaining why we did not find a correlation between song pace and lek presence.

Although we focused only on the vocal sounds in our analysis, some cotinga species can generate mechanical wing sounds, especially during lekking behaviour [48]. Future studies could include mechanical sound production in the analysis while studying vocalization in lekking birds. Besides body size, other morphological variables could also be considered in future studies. For example, beak size and sexual size dimorphism are known to influence bird song [11,15,78], although beak size is often correlated with body size [16]. Similar to morphological variables, other environmental variables such as background noise and canopy height could be considered in future studies. For instance, Kirschel *et al.* [3] found that green hylia (*Hylia prasina*) sing at lower frequencies to presumably avoid masking by lower-frequency insect sounds. Additionally, canopy height can influence acoustic richness during lekking displays in birds-of-paradise, with higher acoustic richness in canopy leks compared with lekking vocalizations from the ground [32]. Finally, studies covering multiple bird families with lekking species (e.g. manakins and birds-of-paradise) may prove to be interesting in clarifying whether vocalization characteristics are associated with lekking behaviour in general. Nevertheless, the findings in our study may contribute to a better understanding of how morphology, ecology and mating systems influence avian songs.

5. Conclusion

In conclusion, we found convincing evidence for the ‘morphological constraint’ hypothesis, suggesting that bigger birds experience size-related constraints, probably owing to their bigger sound-producing structures. By contrast, little evidence was found for the ‘acoustic adaptation’ hypothesis. Finally, our results suggest that cotinga species with a lek mating system sing broader-frequency songs compared with non-lekking species, probably owing to the strong male–male competition in lek mating systems, although this relationship reflected a more marginal correlation in a Bayesian framework and the correlation between lek presence and bandwidth seems to mainly apply to ‘exploded’ lekking cotinga species. Overall, our study revealed interesting relationships between morphological, environmental and mating system traits and highlighted the potential importance of considering mating systems while studying the evolution of avian songs.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Supplementary material and R code are provided for the reproducibility of the study on Zenodo [79].

Supplementary material is available online [80].

Declaration of AI use. The authors declare their use of Grammarly v.1.2.132.1587 (accessible via: Grammarly.com) to improve grammar and spelling of the manuscript and ChatGPT 4.0 (accessible via: Chatgpt.com) to generate and improve R codes/scripts. Generative AI content was reviewed and edited as needed. An overview of the user prompts and model outputs from ChatGPT 4.0 can be found in supplementary material S9.

Authors’ contributions. A.A.W.v.d.K.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; J.O.: methodology, visualization, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. No funding has been received for this article.

Acknowledgements. We thank Nadja Meister and Sara Karvo for their feedback on the figures in the manuscript as well as Anders F. Opdal for discussion about the phylogenetic path analysis. Also, special thanks to the three anonymous reviewers for their insightful and constructive feedback, which helped to improve the manuscript.

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