

DOES BEAK SIZE AFFECT ACOUSTIC FREQUENCIES IN WOODCREEPERS?¹

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Abstract. We assessed the effect of beak morphology on the acoustic structure of woodcreeper (subfamily Dendrocolaptinae) songs using a comparative analysis of independent contrasts. For the song of each species, we measured the maximum and minimum frequencies, the bandwidth, and the emphasized frequency. Residuals of variation in beak length and acoustic frequencies after controlling for body size and phylogeny were calculated for each species and compared. We found a negative relationship between the residuals of acoustic frequencies and the residuals of beak length. This relationship was significant for emphasized frequency when we excluded two open-habitat species, Scimitar-billed Woodcreeper (*Dryornis bridgesii*) and Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*). This result is consistent with the hypothesis that the suprasyringeal vocal tract has resonating properties that affect the frequency spectrum of the song.

Key words: beak length, body size, Dendrocolaptinae, resonance, song structure, woodcreepers.

INTRODUCTION

Recent studies have shown that the suprasyringeal vocal tract can affect the frequency spectrum of avian vocalizations. Nowicki (1987) showed that some songbird species singing in an helium-enriched and nitrogen-depleted atmosphere had a harmonic structure normally absent, suggesting that vocal tract resonances filter out most of the spectral structure of the signal. In the Barnacle Goose (*Branta leucopsis*), those individuals that vocalize with their bills wide open emphasize higher frequencies (Hausberger et al. 1991). Westneat et al. (1993), in a study of White-throated Sparrows (*Zonotrichia albicollis*) and Swamp Sparrows (*Melospiza georgiana*), found that the acoustic frequencies of notes in a song have a positive correlation with beak gape in both species. In addition, in Song Sparrow (*Melospiza melodia*), changes in beak gape during vocal ontogeny appear to correspond with the development of tonal quality of song (Podos et al. 1995). One possible explanation for these observations is that changes in beak gape influence the tonal quality of song by dynamically modifying the vocal tract's reso-

nance properties (Nowicki 1987, Nowicki and Marler 1988, Gaunt and Nowicki 1998).

Based on this evidence, that the resonance of the vocal tract affects the spectral structure of song, we predicted that the acoustic frequencies contained in avian song will be negatively related to beak length across species, all other factors being equal. We tested this prediction using a comparative analysis of the spectral structure of the song in woodcreepers (Dendrocolaptinae). We chose to use this monophyletic group endemic to the Neotropics because bill length varies enormously, ranging from 12 mm in the genus *Glyphorhynchus* to 76 mm in the genus *Nasica*. In addition, there is a cladistic phylogeny for the group (Raikow 1994), and song recordings of almost all the species (Hardy et al. 1995). Several studies have demonstrated a negative relationship between acoustic frequencies and body size (Wallschläger 1980, Ryan and Brenowitz 1985, Tubaro and Mahler 1998); it is reasonable to assume that beak size correlates with body size and phylogeny as well. To study the relationship between beak morphology and the acoustic frequencies of song, it is important to remove the confounding effect of body size and phylogeny. Thus, we present the results of the analyses between the residuals of variation in bill length and acoustic frequencies after con-

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TABLE 1. Database used in the comparative analysis of the relationship between body mass and song frequencies. For acronyms see Methods.

Species	MAX (Hz)	MIN (Hz)	ENF (Hz)	BAND (Hz)	Body mass ^a (g)	Beak length ^b (mm)	Phylogenetic position ^c
Curve-billed Scythebill							
<i>Campylorhynchus procurvoides</i>	2,610	1,470	2,417	1,140	33.0	58.0	BBBBBBBBBIBC
Brown-billed Scythebill							
<i>Campylorhynchus pusillus</i>	3,050	1,100	2,265	1,950	39.6	50.0	BBBBBBBBBBJB
Red-billed Scythebill							
<i>Campylorhynchus trochilirostris</i>	3,090	1,670	2,569	1,420	39.1	57.0	BBBBBBBBBBJA
Long-tailed Woodcreeper							
<i>Deconychura longicauda</i>	4,680	1,990	3,839	2,690	23.8	23.0	BBBBBA
Spot-throated Woodcreeper							
<i>Deconychura stictolaema</i>	4,070	2,160	3,826	1,910	18.1	20.0	BBBA
Cinnamon-throated Woodcreeper							
<i>Dendrexetastes rufigula</i>	2,690	1,140	2,100	1,550	70.0	32.0	BBBBBBBBJA
Tawny-winged Woodcreeper							
<i>Dendrocincla anabatina</i>	3,700	1,470	2,735	2,230	37.4	25.3	BBBABB
Tyrannine Woodcreeper							
<i>Dendrocincla tyrannina</i>	3,090	1,710	2,182	1,380	60.2	31.5	BBBABA
Barred Woodcreeper							
<i>Dendrocolaptes certhia</i>	2,780	1,340	1,408	1,440	64.2	37.5	BBBBBBBBLBBBA
Concolor Woodcreeper							
<i>Dendrocolaptes concolor</i>	2,530	970	1,806	1,560	62.7	35.0	BBBBBBBBLBBBC
Hoffmann's Woodcreeper							
<i>Dendrocolaptes hoffmannsi</i>	2,370	1,510	1,947	860	89.0	12.0	BBBBBBBBLBBBB
Black-banded Woodcreeper							
<i>Dendrocolaptes picumnus</i>	2,130	840	1,643	1,290	73.8	38.0	BBBBBBBBLBBAB
Planalto Woodcreeper							
<i>Dendrocolaptes platyrostris</i>	2,900	1,510	2,106	1,390	61.9	35.7	BBBBBBBBLBBAA
Scimitar-billed Woodcreeper							
<i>Drymornis bridgesii</i>	4,480	970	3,522	3,510	80.0	62.8	BA
Wedge-billed Woodcreeper							
<i>Glyphorhynchus spirurus</i>	5,210	2,520	4,060	3,690	14.6	12.0	BBBBBBBA
Red-billed Woodcreeper							
<i>Hylexetastes perrotii</i>	2,560	1,400	2,030	1,160	114.0	37.0	BBBBBBBBLBA
Spot-crowned Woodcreeper							
<i>Lepidocolaptes affinis</i>	8,830	2,400	6,008	6,430	35.4	15.0	BBBBBBBKA
Lineated Woodcreeper							
<i>Lepidocolaptes albalineatus</i>	3,910	2,280	3,666	1,630	33.3	28.0	BBBBBBBBKBBBA
Narrow-billed Woodcreeper							
<i>Lepidocolaptes angustirostris</i>	3,380	1,100	3,080	2,280	31.3	31.0	BBBBBBBBBKBBBB
Lesser Woodcreeper							
<i>Lepidocolaptes fuscus</i>	3,990	1,420	3,052	2,570	21.8	21.5	BBBBBBBBBH

TABLE 1. Continued.

Species	MAX (Hz)	MIN (Hz)	ENF (Hz)	BAND (Hz)	Body mass ^a (g)	Beak length ^b (mm)	Phylogenetic position ^c
White-striped Woodcreeper							
<i>Lepidocolaptes leucogaster</i>	6,390	2,240	4,750	4,150	36.0	ND	BBBBBBBBBKBBBBBA
Scaled Woodcreeper							
<i>Lepidocolaptes squamatus</i>	3,460	2,320	3,356	1,140	27.0	26.7	BBBBBBBBBKBA
Long-billed Woodcreeper							
<i>Nasica longirostris</i>	1,830	1,340	1,713	490	92.0	76.0	BBA
Olivaceous Woodcreeper							
<i>Sittasomus griseicapillus</i>	4,970	1,670	3,508	3,300	14.3	17.0	BBBBBBA
White-throated Woodcreeper							
<i>Xiphocolaptes albicollis</i>	2,510	1,730	2,407	780	116.0	41.0	BBBBBBBBBLBABBB
Great Rufous Woodcreeper							
<i>Xiphocolaptes major</i>	3,500	1,100	2,417	2,400	155.0	58.0	BBBBBBBBBLBABBA
Strong-billed Woodcreeper							
<i>Xiphocolaptes promeropirhynchus</i>	5,220	2,000	3,052	3,220	136.0	52.0	BBBBBBBBBLBABA
Elegant Woodcreeper							
<i>Xiphorhynchus elegans</i>	4,070	1,550	1,970	2,520	34.1	30.0	BBBBBBBBBBB
Spotted Woodcreeper							
<i>Xiphorhynchus erythropygius</i>	2,930	1,710	2,583	1,220	46.8	ND	BBBBBBBBBLA
Dusky-billed Woodcreeper							
<i>Xiphorhynchus eytoni</i>	2,560	1,260	1,947	1,300	58.8	40.0	BBBBBBBBBCC
Ivory-billed Woodcreeper							
<i>Xiphorhynchus flavigaster</i>	3,300	1,630	2,583	1,670	47.2	ND	BBBBBBBBBD
Buff-throated Woodcreeper							
<i>Xiphorhynchus guttatus</i>	2,850	1,420	2,417	1,430	49.5	42.0	BBBBBBBBBG
Black-striped Woodcreeper							
<i>Xiphorhynchus lachrymosus</i>	2,320	1,260	1,643	1,060	56.4	39.7	BBBBBBBBBIAB
Striped Woodcreeper							
<i>Xiphorhynchus obsoletus</i>	5,330	1,590	3,508	3,740	39.0	25.0	BBBBBBBBBIIAA
Ocellated Woodcreeper							
<i>Xiphorhynchus ocellatus</i>	6,310	1,140	4,682	5,170	35.1	31.0	BBBBBBBBBIC
Chestnut-rumped Woodcreeper							
<i>Xiphorhynchus pardalotus</i>	5,330	1,830	3,660	3,500	40.4	33.0	BBBBBBBBBBF
Straight-billed Woodcreeper							
<i>Xiphorhynchus picus</i>	2,520	850	2,251	1,670	41.6	29.0	BBBBBBBBBA
Spix's Woodcreeper							
<i>Xiphorhynchus spixii</i>	4,310	1,380	2,030	2,930	31.2	32.5	BBBBBBBBBIB
Olive-backed Woodcreeper							
<i>Xiphorhynchus triangularis</i>	3,460	1,550	3,273	1,910	48.4	30.0	BBBBBBBBBBE

^a Based on Dunning 1993.^b ND: no data.^c After Raikow (1994), and according to the convention of Purvis and Rambaut (1995). This convention consists in looking at each node of the phylogeny and letter of its daughter branches. When this is done for each node in turn, each species has a unique code formed by the sequence of letters on the branches leading to it, starting from the root (last common ancestor of all the species).

trolling for the effect of body size and phylogeny.

METHODS

The present analyses of woodcreeper song were based on recordings published by Hardy et al. (1995) representing songs of 46 out of 50 species. Sonograms for the song of each recorded species were made with a Proaudio Spectrum 16 Sound Blaster (Media Vision, Fremont, California) and Canary v.1.2 software (Charif et al. 1995). On each sonogram we measured the following variables: maximum and minimum frequencies (MAX and MIN, respectively), bandwidth (BAND = MAX - MIN), and emphasized frequency (frequency with the highest amplitude in the song, ENF, see Table 1). All measurements were made by an assistant who knew neither the beak length nor the body mass of the species under study. Body mass data were obtained from Dunning (1993). Sources consulted for species' bill lengths were: von Ihering (1899), Dabbene (1912), Sneathlage (1914), Chapman (1917), Cory and Hellmayr (1925), Gyldenstolpe (1945a, 1945b), Esteban (1948), Wetmore (1972), Phelps and Meyer de Schauensee (1978), Fjelds  and Krabbe (1990), Dubs (1992), and Ridgely and Tudor (1994). Beak lengths of *Drymornis bridgesii* and *Lepidocolaptes squamatus* males were measured on study skins deposited at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia. We could not find information about the bill lengths of *Lepidocolaptes leucogaster*, *Xiphorhynchus erythropygius*, and *X. flavigaster*; therefore these species were deleted from some comparative tests, but still considered in the estimation of the relationship between body mass and acoustic frequencies of the song. Common names of species are given in Table 1.

We based our phylogenetic analysis on the cladistic hypothesis of Raikow (1994). This hypothesis is not based on the acoustic structure of the song, but on the morphological characters of 39 species of woodcreepers. We estimated the ancestral states of the characters using the punctuated model (Harvey and Purvis 1991) that assumes that changes occur only at the nodes of a tree. Details of the general procedure for estimating the ancestral character values are outlined in Felsenstein (1985). Finally, we made the nondirectional comparative tests using the independent contrasts method (Felsenstein 1985)

and the CAIC software v.2.0 (Purvis and Rambaut 1995).

Briefly, the independent contrasts method is based on the comparison between pairs of sister species. Each comparison produces a new variable termed a "contrast," which results from the difference between the values of the variable measured on the species within the pair. Contrasts may be standardized if divided by the square root of the length of the branches under comparison. These contrasts are considered independent among pairs of sister species, because they result from the evolutionary divergence that occurred after the origin of each pair. Homogeneity of variance of standardized contrasts was confirmed using the method proposed by Purvis and Rambaut (1995). Thus, any association between standardized contrasts belonging to different variables may be detected using a standard linear regression model adjusted to pass through zero (Grafen 1989, Garland et al. 1992). This is because the expected value in the dependent variable contrast must be zero when the independent variable contrast is zero. In computing comparative analyses, polytomies (i.e., points in the phylogeny with more than two derived branches simultaneously) were resolved by the method of Pagel (1992).

To assess the effect of beak length on acoustic frequencies of the song, it is important to control for all other sources of variation in the signal. In addition to body size, the habitat used by the species may affect the spectral structure of the song employed for long-range communication (Morton 1975, Wiley 1991). Although woodcreepers comprise a uniform group of mainly humid and montane forest species that forage on tree trunks well above the ground, two exceptions to this pattern are *Drymornis bridgesii* and *Lepidocolaptes angustirostris*, which live in arid lowland scrub and chaco-cerrado habitats (Ridgely and Tudor 1994, Parker et al. 1996). For this reason, we repeated the comparative analyses with and without these species included in the data matrix. All statistical tests were performed on the log-transformed values of the original variables.

RESULTS

Independent contrast analysis revealed that beak length correlates positively with body mass ($\beta = 0.45$, $F_{1,20} = 5.2$, $P < 0.03$). In addition, acoustic frequencies varied negatively with body

TABLE 2. Regressions of phylogenetically independent contrasts in acoustic frequencies with contrasts in body mass. All original variables were log-transformed. For acronyms see Methods.

Comparisons	β^a	<i>F</i>	<i>P</i>
Excluding <i>D. bridgesii</i> and <i>L. angustirostris</i> (df = 1, 22)			
MAX with body mass	-0.41	4.5	0.05
MIN with body mass	-0.40	4.3	0.05
BAND with body mass	-0.35	3.0	0.10
ENF with body mass	-0.54	8.9	0.01
Including <i>D. bridgesii</i> and <i>L. angustirostris</i> (df = 1, 24)			
MAX with body mass	-0.33	3.0	0.10
MIN with body mass	-0.32	2.8	0.11
BAND with body mass	-0.27	1.9	0.18
ENF with body mass	-0.44	5.9	0.02

^a Slope of the regression forced to pass through zero.

mass, although this relationship was significant for MAX, MIN, and ENF, but not for BAND (Table 2). The inclusion of both *D. bridgesii* and *L. angustirostris* in the analysis reduced the statistical significance of the regression slopes of MAX and MIN in relation to body mass, although the relationship between ENF and body mass was still significant (Table 2). To avoid the confounding effect of body mass differences in comparisons involving other variables, we calculated residuals of variation using the slope of the regression (forced to pass through zero) among their respective contrasts and body mass contrasts (Garland et al. 1992). Thus residuals of variation in acoustic frequencies were compared with residuals in beak length, but controlling again for phylogeny. We found a negative relationship between both sets of residuals. Notably, the slope of the regression between contrasts in ENF and beak length was negative and significant (Table 3). In other words, within each compared pair of forest species, the species with the longest beak had the lowest emphasized frequencies in its song. However, this relationship was not significant when *D. bridgesii* and *L. angustirostris* were included in the analysis (Table 3).

DISCUSSION

These data represent the first comparative study of the relationship between bill length and the spectrum of frequencies contained in the song of a diverse group of Neotropical passerines. Residuals of acoustic frequencies and beak length

TABLE 3. Regressions of phylogenetically independent contrasts in residuals of acoustic frequencies with contrasts in residuals of beak length. For acronyms see Methods.

Comparisons	β^a	<i>F</i>	<i>P</i>
Excluding <i>D. bridgesii</i> and <i>L. angustirostris</i> (df = 1, 20)			
MAX with beak length	-0.23	1.1	0.30
MIN with beak length	-0.30	2.0	0.17
BAND with beak length	-0.14	0.4	0.53
ENF with beak length	-0.42	4.4	0.05
Including <i>D. bridgesii</i> and <i>L. angustirostris</i> (df = 1, 22)			
MAX with beak length	-0.21	1.0	0.33
MIN with beak length	-0.32	2.5	0.13
BAND with beak length	-0.10	0.2	0.63
ENF with beak length	-0.39	4.0	0.06

^a Slope of the regression forced to pass through zero.

were negatively correlated, indicating that the longer the beak, the lower the acoustic frequencies of the song. This pattern is present within the group of woodcreepers living in humid forests, even after accounting for the effect of interspecific differences in body mass and phylogeny. When the species living in more xeric and open-country habitats were included in the analyses, the statistical significance of the relationship was lost. This lack of significance is mainly because the song of *D. bridgesii* contained higher frequencies than expected based on its body size and beak length. We think that such a pattern could be related to the specialized open-country and ground foraging habits of this primitive species. In general, studies of passerine species living in open habitats have shown that they have higher frequencies and wider bandwidths than their counterparts from more closed habitats (Morton 1975, Wiley 1991).

The existence of a negative relationship between residuals of beak length and emphasized frequency is compatible with the idea that the suprasyringeal vocal tract has resonating properties that affect the frequency spectrum of the song (Nowicki 1987, Nowicki and Marler 1988, Gaunt and Nowicki 1998). Length of the tube formed by the trachea and buccal cavities changes with beak aperture. If species use a similar bill gape at the tip, this implies that the angle between upper and lower mandibles is proportionally smaller for the species with a longer beak. In this way, a longer beak adds proportionately more to the length of the orotracheal

cavity compared to a short beak, reducing its resonating frequency.

It is interesting to note that, if species were not constrained in their angle of beak aperture, species with longer beaks could produce maximum frequencies as high as shorter-beak species. Moreover, they could produce wider bandwidth songs depending on the degree of change in beak aperture during singing. This is because for the same range of angular apertures of the beak at the base, longer-beaked species produce a wider variation in the length of the resonating tube. We found no evidence of longer-beaked species singing wider bandwidth songs than their shorter-beaked counterparts. In contrast, residuals of beak length correlated negatively with residuals of BAND, although this relationship was not significant. However, a correct test of this prediction requires the comparison of song bandwidth of video-recorded birds during singing, so as to assess their degree of beak aperture.

There are strong differences in beak curvature among woodcreepers ranging from the genus *Campylorhamphus* with its strongly decurved beak, to the genera *Sittasomus* or *Dendrocincla* with their straight beaks. Curvature of the beak could affect the relationships between song structure and beak length in at least two different ways. First, beak length usually is measured dorsally as the chord from the tip to the base (Baldwin et al. 1931). However, the acoustically effective length of a beak is the one which determines its resonance properties when modeled as a hollow tube. For a curved beak, this effective length is better estimated as a geometric arc because the use of chord length instead of its arc systematically underestimates the effective length of a curved beak relative to a straight one. Second, strongly curved beaks exhibit a reduced and more uniform gape rostral to the bend when the jaws are open (Olson and Feduccia 1980), thus affecting the effective length of the resonating tube as well as its properties as an impedance matching device.

Greenewalt (1968) compared the tracheal length of several bird species and their songs, and concluded that there was no relationship between them. Furthermore, he found no evidence for resonances and antiresonances in continuous modulated notes covering a wide range of frequencies. These observations indicate why classical models of sound production proposed that spectral properties were determined at the source

(i.e., oscillating membranes of the syrinx), with no appreciable effect of suprasyringeal tract (Brackenbury 1982, Gaunt and Gaunt 1985, Gaunt and Nowicki 1998).

More recent studies of birds singing in a less dense atmospheric condition largely composed of helium instead of nitrogen (i.e., "heliox" atmosphere) indicated that the suprasyringeal vocal tract could indeed affect the acoustic spectrum of the sound (Nowicki 1987). Because acoustic resonance depends on sound wavelength, which increases in a heliox atmosphere, the frequency of resonance of the vocal tract is shifted upwards. This change should be reflected in a concomitant drop in the amplitude of the fundamental frequency because it will now lie outside of the resonance peak of the vocal tract. In addition, the finding of the presence of any overtone could indicate that the vocal tract has filtered that band in the normal song. Nowicki (1987) found evidence for both phenomena in at least 10 species of songbirds. Another study in Budgerigars (*Melopsittacus undulatus*) showed no evidence of suprasyringeal tract resonance (Brittan-Powell et al. 1997), demonstrating that different species could use different mechanisms of sound production. Even within the same species, steady and modulated frequency notes may differ as to whether or not vocal tract resonances are involved in the sound production mechanism (Ballintijn and Ten Cate 1998).

Finally, it is important to note that information about within-individual, inter-individual, and geographical variation of songs also are required to assess whether song samples included in this study are representative of the species. However, Marantz (1992) suggests that variation in woodcreeper vocalizations parallels that of members of the related families Tyrannidae and Formicariidae in that advertising song varies little over large geographic distances, and generally lacks both dialects and repertoires. He also found a high degree of conservatism in the temporal structure of song among genera as well as within the genus *Dendrocolaptes*. Even for *Dendrocolaptes certhia*, a species showing geographical variation in song, differences are reflected in timing and note shape rather than overall frequency.

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