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CORRELATED EVOLUTION OF BEAK MORPHOLOGY AND SONG IN THE NEOTROPICAL WOODCREEPER RADIATION

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Mating signals may diversify as a byproduct of morphological adaptation to different foraging niches, potentially driving speciation. Although many studies have focused on the direct influence of ecological and sexual selection on signal divergence, the role of indirect mechanisms remains poorly understood. Using phenotypic and molecular datasets, we explored the interplay between morphological and vocal evolution in an avian radiation characterized by dramatic beak variation, the Neotropical woodcreepers (Dendrocolaptinae). We found evidence of a trade-off between the rate of repetition of song syllables and frequency bandwidth: slow paced songs had either narrow or wide frequency bandwidths, and bandwidth decreased as song pace increased. This bounded phenotypic space for song structure supports the hypothesis that passerine birds face a motor constraint during song production. Diversification of acoustic characters within this bounded space was correlated with diversification of beak morphology. In particular, species with larger beaks produced slower songs with narrower frequency bandwidths, suggesting that ecological selection on beak morphology influences the diversification of woodcreeper songs. Because songs in turn mediate mate choice and species recognition in birds, these results indicate a broader role for ecology in avian diversification.

KEY WORDS: Ecological adaptation, magic traits, mechanical constraints, phylogenetic comparative analyses, signal evolution, suboscine birds, vocal performance.

Speciation often entails the divergence of signals used in species recognition and mate choice (Fisher 1930; Dobzhansky 1937, 1940; Mayr 1963; Coyne and Orr 2004), and the evolutionary importance of signal divergence has been demonstrated empirically in many taxa (e.g., *Drosophila*: Coyne and Orr 1989, birds: Grant and Grant 1997, frogs and insects: Gerhardt and Huber 2002, crickets: Shaw and Parsons 2002). Understanding the forces underlying signal evolution is thus an important aspect of understanding the process of species diversification. Ecological factors, such as those that affect signal transmission (Morton 1975) and

production (Podos and Nowicki 2004b), appear to be important drivers of signal evolution. A wealth of evidence across a diversity of taxa suggests that habitat-dependent selection on signal transmission shapes signal evolution (Morton 1975; Wiley and Richards 1978; Ryan et al. 1990; Wiley 1991; Boughman 2002; Slabbekoorn and Smith 2002b; Leal and Fleishman 2004; Seddon 2005; Cummings 2007; Derryberry 2009). There is also increasing evidence of indirect effects via ecological selection on traits related to signal production. Such traits have been referred to as “magic traits” (Gavrilets 2004) when they affect the production

of mating signals because divergent ecological selection can give rise indirectly to nonrandom mating.

Signals are often produced by functional systems that evolved in other contexts (Tinbergen 1952) and that therefore may be subject to other sources of selection. For example, courting displays in waterfowl include many motor patterns, such as wing flapping, swimming, and changes in head posture, that involve the use of structures associated with other important functions such as feeding, preening, flight, and aquatic locomotion (e.g., Dane et al. 1959). Thus, one important route of signal evolution is as a byproduct of selection on the functional systems used to produce signals (Nowicki et al. 1992; Podos and Hendry 2006). Much of the evidence for an indirect effect of ecological selection on signals comes from studies on bird song (Podos 2001; Ballentine 2006; Huber and Podos 2006; Badyaev et al. 2008). The link between ecological selection and signal evolution is particularly clear in birds (Podos 2001), as the organ used to forage—the beak—can also be used to modulate the resonance properties of the vocal tract during sound production (Westneat et al. 1993). The avian beak is therefore often forwarded as one of the best examples of a “magic trait” linking ecological divergence to reproductive isolation (Pfennig and Pfennig 2010; Servedio et al. 2011).

In many bird species, beak size and shape are under strong selection in the context of foraging and food manipulation (Grant 1968, 1972; Freed et al. 1987; Smith 1990; Grant 2003; Grenier and Greenberg 2005; Herrel et al. 2005a). This selection can drive rapid changes in beak morphology via simple genetic mechanisms (Mallarino et al. 2011). Because the beak can also be used in coordination with vocal tract movements during sound production (Westneat et al. 1993; Suthers et al. 1999; Hoese et al. 2000; Goller et al. 2004; Podos et al. 2004b), ecological selection pressures on beak structures may have a significant effect on the trajectory of signal evolution. However, the mechanistic link between beaks and songs mainly has been studied in one family of passerine birds (Emberizidae) (Podos 2001; Podos and Nowicki 2004a; Podos et al. 2004b; Ballentine 2006; Huber and Podos 2006; Derryberry 2009). The few studies outside of emberizids (Anatidae: Hausberger et al. 1991, Furnariidae: Palacios and Tubaro 2000, Thamnophilidae: Seddon 2005) suggest that this mechanistic link may be more widespread but its generality remains unclear.

Like all functional systems, the specific physical structures used to produce signals face intrinsic and extrinsic limitations (Wainwright et al. 1982; Nowicki et al. 1992). The morphology or physiology of the structure as well as physical and biomechanical limitations can place constraints on the range of signal output (Nowicki et al. 1992; Lambrechts 1996; Patek and Oakley 2003). For example, the production of acoustic signals in vertebrates is constrained by limitations on the vocal apparatus. One

taxonomically widespread constraint is a trade-off between the rate at which sounds are produced and the frequency bandwidth of those sounds, as described in more than 40 species of oscines (Passeri; reviewed in Podos et al. 2009) including a large number of wood warblers (Parulidae; Cardoso and Hu 2011), one species of seabird (Stercorariidae; Janicke et al. 2008) and in Neotropical singing mice (Cricetidae; Pasch et al. 2011). This trade-off is a triangular distribution such that more slowly produced sounds may have narrow or wide frequency bandwidths whereas more rapidly produced sounds are limited to narrower bandwidths. The mechanism underlying this trade-off likely varies among species given the diversity of physical structures used in production of vocalizations. In oscines, the triangular trade-off may emerge as the result of constraints on modifying the resonant properties of the vocal tract (Westneat et al. 1993; Riede et al. 2006). One means of vocal tract modification is to modulate beak gape while singing (Nowicki 1987; Westneat et al. 1993; Hoese et al. 2000; Beckers et al. 2003) to track the fundamental frequency produced by the syrinx (Nowicki 1987; Nowicki and Marler 1988). Birds open their beak more widely during production of high frequencies and less widely during production of low frequencies (Westneat et al. 1993; Hoese et al. 2000). Because of limits on how rapidly and widely a bird can open its beak (Westneat et al. 1993; Hoese et al. 2000), this motor constraint can result in a triangular trade-off between the rate of note production and frequency bandwidth (Podos 1997; Podos and Nowicki 2004b).

The upper boundary of this triangular acoustic space estimates a performance limit and deviation from this limit may be an indicator of how well songs are performed relative to the motor constraint (hereafter, “vocal performance”) (Podos 2001; Ballentine et al. 2004). In birds, one hypothesis is that beak size may influence how well individuals can perform this trade-off (Nowicki et al. 1992; Podos and Nowicki 2004a,b) and this hypothesis has been examined most intensively in Darwin’s finches (Podos 2001; Huber and Podos 2006; Herrel et al. 2008). In this small radiation, species with larger beaks have a higher force application potential in jaw musculature or an ability to crack larger, harder seeds (Herrel et al. 2005a,b). Biomechanical and muscle-architecture adaptations for high force application necessarily lead to reduced maximal velocities of beak movement, largely independent of overall body size (Herrel et al. 2005a). Finches with larger beaks are less able to move their beak rapidly and widely and tend to produce slower songs with narrower frequency bandwidths (Podos 2001; Podos and Nowicki 2004b).

Despite many previous studies of biomechanical limitations on song production and their evolutionary consequences (Ryan and Brenowitz 1985; Nowicki 1987; Nowicki et al. 1992; Westneat et al. 1993; Suthers and Goller 1997; Podos 2001; Podos et al. 2004a), many significant gaps remain in our understanding. For example, although physical and biomechanical constraints on

vocal production are clearly widespread, we have a poor grasp of the broader relevance of morphological adaptation as a driver of vocal evolution because previous studies have focused either on single species or small radiations, and have been limited by the lack of well-resolved molecular phylogenies. In addition, most research in this area has been conducted on songbirds (oscines), which tend to learn their songs. This makes the influence of cultural processes on vocal evolution difficult to tease apart from the potential impact of morphological and ecological adaptation (Seddon 2005), and suggests that the conclusions of previous studies may only apply to song-learning birds (approximately 40% of all avian species). Thus, to answer a range of questions, there is a clear need for robust phylogenetic comparative studies to investigate the influence of morphological adaptation on signal design in the absence of vocal learning.

Woodcreepers (Aves: Furnariidae: Dendrocolaptinae) are suited to this approach for two main reasons. First, they are tracheophone suboscine passerines (Sibley and Monroe 1990; Irestedt et al. 2002; Remsen et al. 2011), and therefore song learning appears to be limited or absent (Seddon 2005; Seddon and Tobias 2007; Tobias and Seddon 2009). As such, all woodcreepers produce simple, stereotyped songs (Fig. 1), making them amenable to standardized acoustic analysis. Second, they rapidly open and close their beak while singing, suggesting that beak gape modulation plays a role in song production (J. A. Tobias, N., Seddon, and A., Aleixo, pers. obs.). In addition, woodcreepers exhibit extreme diversity in morphological characters associated with feeding and locomotion (Raikow 1994; Tubaro et al. 2002; Marantz et al. 2003; Claramunt 2010); in particular, their beaks range from small and straight (e.g., *Certhiasomus*) to long and down curved (e.g., *Campylorhampus* “scythebills”) (Fig. 1), suggesting that biomechanical limitations vary across the clade.

Using a well-resolved molecular phylogeny of the woodcreepers (Derryberry et al. 2011), we tested the vocal tract constraint hypothesis (Podos 1997). If this constraint is an important factor in song diversification and evolution in suboscines, then woodcreeper songs should occupy a bounded acoustic space of frequency bandwidth as a function of the rate of note production. We also tested the hypothesis that there is a biomechanical limit on performance of this motor constraint related to beak size (Podos 2001). We predicted a negative relationship between beak size and ability to perform the trade-off between frequency bandwidth and pace. Although we do not know whether beak size scales with adaptations for high force potential in suboscines, there is some evidence of strengthening of woodcreeper skulls associated with larger beaks as adaptations for dealing with large prey (Feduccia 1973). Further, beak size does appear to explain significant variation in song structure among some suboscine species. In antbirds (Thamnophilidae), temporal patterning varies significantly with beak size: birds with broad beaks produce slower paced songs

(Seddon 2005). Meanwhile, in woodcreepers, beak length correlates with song frequency: birds with long beaks produce lower pitched songs (Palacios and Tubaro 2000). However, no study of suboscine song has examined the specific prediction that beak size explains variation in the ability of birds to perform the trade-off between the rate of note production and frequency bandwidth (i.e., vocal performance). By addressing these specific predictions using the same approach as taken in studies of oscine species, we hope not only to evaluate the ultimate effect of mechanical limitations on suboscine song production, but also to shed light on the relative impact of these limitations across all passerines.

Materials and Methods

STUDY SPECIES

Woodcreepers are small to medium-sized (13–36 cm) insectivorous passerine birds occurring in forest and woodland throughout Central and South America. They are currently thought to comprise 13 genera, 52 species, and well over 250 distinct subspecies (Marantz et al. 2003; Remsen et al. 2011). Although dendrocolaptids sensu lato have long been considered part of a monophyletic lineage with furnariids (Furnariinae) based on a shared unique syrinx structure (Müller 1878; Ames 1971), they have tended to be treated as separate families on the basis of differences in external morphology relating to habitat, locomotion, and foraging (e.g., Hellmayr 1925; Vaurie 1971). However, recent phylogenetic studies have confirmed that woodcreepers are a clade embedded within Furnariidae (Irestedt et al. 2009; Moyle et al. 2009; Derryberry et al. 2011).

We followed the classification of Marantz et al. (2003) modified according to more recent studies (Claramunt et al. 2010; Derryberry et al. 2010; Remsen et al. 2011). We included three datasets within this study: vocal, morphological, and genetic. Our vocal dataset comprised 98 woodcreeper taxa, including all 52 species currently recognized and 46 subspecies with distinctive vocalizations. Of the 98 operational taxonomic units (OTUs) for which we had vocal data, we had morphological and genetic data for 61 OTUs; these samples included 51 of the 52 recognized species as well as 10 distinct subspecies.

SONG DATA

Many species of woodcreepers have a wide vocal repertoire including calls and so-called loudsongs. A “loudsong” is a consistently patterned, multiple-note vocalization typically repeated at regular intervals (Willis 1967) (see Fig. 1 for examples). The function of these signals has not been determined empirically, but they are likely to mediate territory defense and mate attraction, in common with other tracheophone suboscine birds (see Tobias et al. 2011). As this suggests they are functionally equivalent to

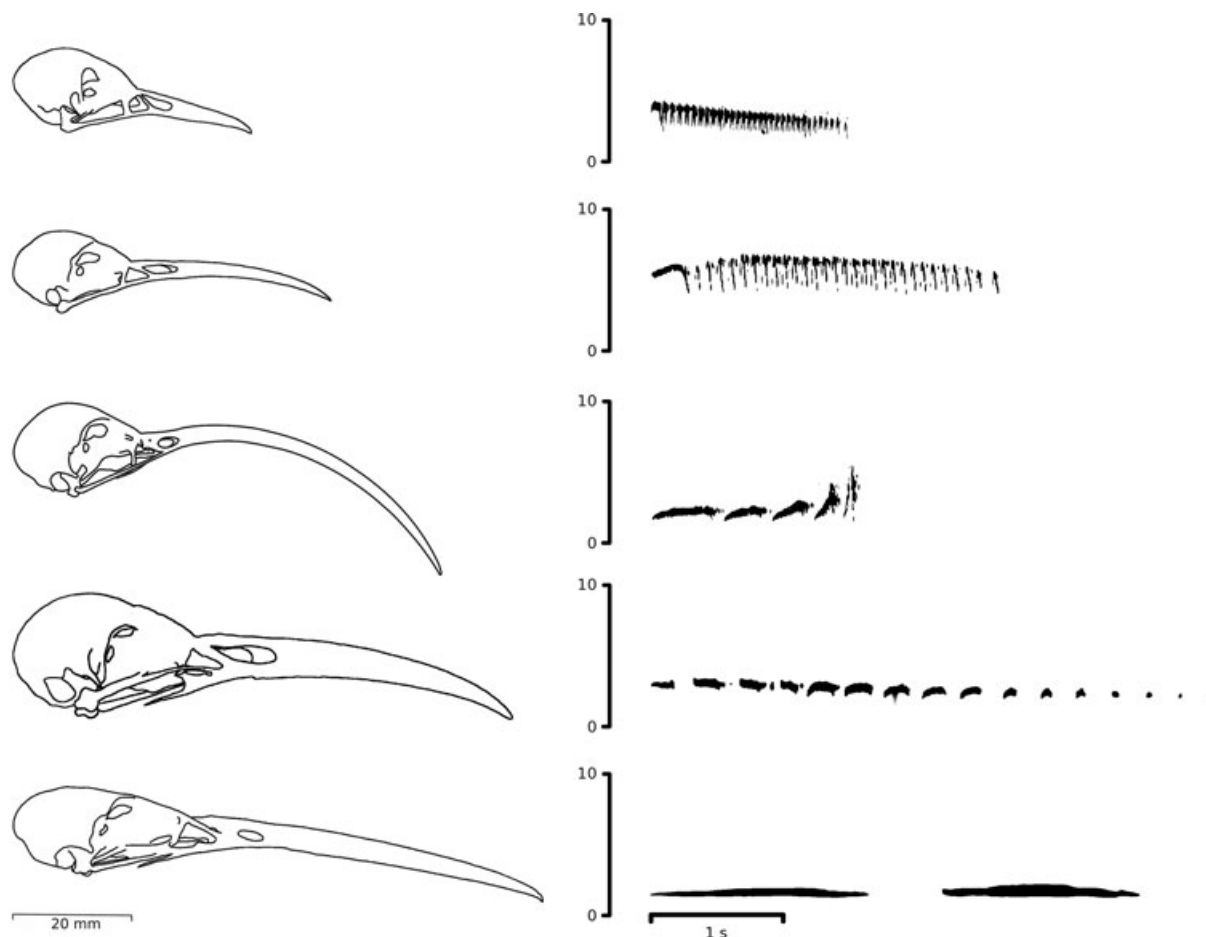


Figure 1. Outlines of bill profiles and sound spectrograms of typical loudsongs produced by five species representing variation in bill and song structure in Dendrocolaptinae, (top to bottom) *Certhiasomus stictolaemus*, *Lepidocolaptes albolineatus*, *Campylorhamphus trochilirostris*, *Xiphocolaptes promeropyrhynchus*, and *Nasica longirostris*.

the song of oscine species, we refer to them hereafter as “songs.” Few woodcreeper species have songs with more than three note types, and these note types often grade into one another. Therefore, woodcreeper songs can be characterized as one continuous trill, or songs in which notes are repeated in rapid succession.

Measurements were taken on songs from 550 individuals of 98 OTUs within the Dendrocolaptinae. Recordings came from the Macaulay Library of Natural Sounds, from the open-access online sound archive xeno-canto (www.xeno-canto.org), commercially available CD/DVDs, and the private audio collections of Neotropical ornithologists (see Table S1).

We scanned broadband spectrograms of recordings by eye in ADOBE AUDITION and extracted the highest quality song (highest signal-to-noise ratio with no overlap with background noise or songs of other bird species). We sampled one song per recording (individual) and at least three different individuals per taxon where possible (mean \pm standard deviation song cuts/individuals per taxon: 6.72 ± 4.4 , range: 1–19). All song cuts were saved as 44.1 kHz single-channel wav files.

We analyzed songs using the MATLAB signal processing toolbox (Mathworks, Natick, MA). All cuts were filtered using a 10th-order highpass Butterworth filter (cut-off frequency = 400 Hz) and broadband spectrograms were generated (window = Hann, bandwidth = 256 Hz, Fast Fourier Transform = 1024, overlap = 0.875). Spectrograms were visualized with a custom graphical user interface and manually segmented using on-screen cursors to record the sample number at note onset and offset. A note was defined as a continuous trace on the spectrogram; rapid trill phrases were classed as a single note if the individual notes could not be distinguished from one another or the background noise. Because our aim was to assess mechanical constraints on specific features of song, for this study, we extracted four standard core song variables from each segmented cut using a custom MATLAB script code: (1) number of notes in the entire song (note number, N), (2) interval between the onset of the first note of the song and the offset of the final note of the song (song duration, D), (3) upper frequency bound of the highest pitched note in the song (maximum song frequency, MaxF), and (4) lower frequency bound of

the lowest pitched note in the song (minimum song frequency, MinF).

From these features, we calculated the rate of note production (*N/D*, hereafter pace) and frequency bandwidth (MaxF–MinF). Our calculation of pace does not capture the changes in pace often observed in woodcreeper songs. For example, some species change the rate of note production within a song, either speeding up or slowing down in pace or both (see Fig. 1). However, as our aim was to assess the relationship between the rate of note production and frequency bandwidth for the entire song, we calculated one overall measure of pace. The loss of information in assessing the overall measure of pace is minimal compared to the scale of pace variation among species. If pace is measured at the beginning, middle, and end of each song, and we calculate the absolute change in number of notes per second, then, on average, species' songs change by 1.22 notes per second from the beginning to the middle of the song (range = 0.60–2.43) and by 1.12 notes per second from the middle to the end of the song (range = 0.86–1.19). In comparison, the overall range in average song pace among species is from 1.48 to 23.13 notes per second. Thus, even the largest change in pace of 2.43 notes per second is small relative to the differences in pace we find among species. We log-transformed all song variables prior to statistical analyses, so that they met parametric assumptions of normality and homogeneity of variance.

MORPHOLOGICAL DATA

We obtained morphological measures for 61 OTUs from museum specimens (Table S2). To capture morphological variation potentially associated with mechanical constraints on song production, we measured three linear variables that represent beak size: beak length, measured from the anterior border of the nostril to tip of the beak, and beak width and depth (vertically) at the level of the anterior border of nostrils. We did not include measurements of body size, as it is not thought to define the trade-off between the rate of note production and frequency bandwidth although it may set other limits on sound output, such as limits on fundamental frequency, as it should scale with syrinx size. The same person (S. Claramunt) took all measurements with a Mitutoyo Digimatic Point Caliper. As an overall measure of beak size, we multiplied beak length, depth, and width, which approximates to beak volume. We then used the logarithm of beak size in all analyses.

MOLECULAR DATA

We sampled molecular data from 61 OTUs for which we had morphological measurements. This sampling captured 51 of the 52 species in the subfamily Dendrocolaptinae (Table S3). Vouchered tissue was not available for *Lepidocolaptes squamatus*.

We used sequence data from three mitochondrial and three nuclear genes to reconstruct the phylogeny. Two of the nu-

clear genes, exons of the *recombination activating genes* RAG-1 (2904bp) and RAG-2 (1152bp), were sequenced previously for one individual per genus and obtained from Moyle et al. (2009). For the additional 35 OTUs, we amplified and sequenced three mitochondrial genes and one nuclear intron: *NADH dehydrogenase subunit 3* (ND3; 351 bp), *cytochrome oxidase subunit 2* (CO2; 684 bp), *NADH dehydrogenase subunit 2* (ND2; 1041 bp), and *β-fibrinogen intron 7* (Bf7; approximately 840 bp).

Using the Qiagen DNeasy kit (QIAGEN Inc., USA), genomic DNA was extracted from 25 mg of pectoral muscle following the manufacturer's protocol. Amplifications were performed using the polymerase chain reaction (PCR). Primers used for amplification and sequencing were L10755/H11151 (Chesser 1999) for ND3, NF3COII/SCTRCOII (Sanín et al. 2009; Claramunt et al. 2010) for CO2, FIB-BI7U/B17L (Prychitko and Moore 1997) and FIBI7–397U/439L (Chesser 2004) for Bf7, and H6313/L5758 (Johnson and Sorenson 1998), L5215 (Hackett 1996), and H5766 (Brumfield et al. 2007) for ND2. RAG-1 and RAG-2 genes were amplified and sequenced using multiple primer pairs (Groth and Barrowclough 1999; Barker et al. 2002, 2004).

In a 20 µl total volume, PCR amplifications contained approximately 60 ng of genomic template DNA, 50 mM KCl, 10 mM Tris-HCl, 1.5 mM MgCl, 0.5 mM dNTPs, 0.75 µM of each external primer, and 0.08 U Promega *Taq*. The thermocycling program consisted of an initial denaturing step (94°C for 2 min) followed by 35 cycles of 94°C for 1 min, a 30 sec annealing step (ND3, 46°C; CO2, 55°C; Bf7, 55°C; ND2, 50°C), and a 72°C extension step for 1 min. The program ended with a final 72°C extension step for 3 min. We purified PCR products using PEG precipitation, eluted in 12.5 µl 10 mM Tris, and sequenced using the ABI Prism cycle sequencing protocol (Applied Biosystems Inc.) modified for $1/4 - 1/2$ reactions (depending on the length of the gene). Sequencing reactions were purified using Sephadex® G-50 and 400-µl 96-well filter plates. Cycle-sequencing products were visualized on an ABI 3100 Genetic Analyzer.

We edited sequences using Sequencher 4.6 (Gene Codes Corporation, Ann Arbor, MI) and aligned sequences manually using Mesquite version 2.6 (Maddison and Maddison 2009). The final alignment included 6954 base pairs. Protein-coding sequences were translated into amino acids to confirm that there were no stop codons or anomalous residues. All new sequences were deposited in GenBank (Table S3).

PHYLOGENETIC INFERENCE

In previous analyses (Derryberry et al. 2011), we identified a fully partitioned dataset (a different partition for each codon position of each coding gene (15) and the nuclear intron) as the optimal partitioning regime. We also identified the GTR+Γ+I model as the best model for the majority of the partitions, and the HKY+Γ+I model as the best model for the first and second

codon positions of RAG1 and all three codon positions of RAG2. We estimated an ultrametric phylogeny in a Bayesian framework in the program BEAST version 1.5.2 (Drummond and Rambaut 2007) under an uncorrelated lognormal model (UCLD) (Drummond et al. 2006). We unlinked substitution model, rate heterogeneity, and base frequencies across partitions. We used a Yule prior for tree shape and the default priors for the substitution model and relaxed clock parameters. A UPGMA tree was used as the starting tree. No restrictions were placed on the topology.

To optimize the MCMC operators, we performed incrementally longer runs and adjusted the scale factors for the operators as suggested by the BEAST output. Once scale factors stabilized, we ran analyses for a total of 140 million generations across 10 independent runs. Using Tracer 1.5 (Drummond and Rambaut 2007), we determined that replicate analyses converged, and all parameters met benchmark effective sample size values (> 200). We identified and discarded the burnin. Converged runs were combined in LogCombiner (Drummond and Rambaut 2007) and used to estimate the posterior distributions of topologies and the maximum clade credibility (MCC) tree. The Bayesian analysis yielded a well-resolved molecular phylogeny for Dendrocolapinae appropriate for use in phylogenetic comparative analyses (Fig. S1).

PHYLOGENETIC COMPARATIVE ANALYSES OF CONSTRAINTS ON SONG PRODUCTION

All phylogenetic comparative analyses were conducted in *R* (R-Development-Core-Team 2008) using the Ape (Paradis et al. 2004) and Geiger (Harmon et al. 2008) libraries as well as code written by R. P. Freckleton (Freckleton et al. 2002). We used the MCC tree as our phylogenetic hypothesis. The sample size in each analysis reflects the number of OTUs for which we had the appropriate data.

RELATIONSHIP BETWEEN PACE AND FREQUENCY BANDWIDTH

We plotted frequency bandwidth as a function of pace for all individuals ($n = 550$; Table S1). To understand the extent to which woodcreeper taxa have diverged within this acoustic space, we ran a series of discriminant function analyses. We categorized songs based on genus and on clade as defined below. Most species had too few song exemplars to run this analysis based on species identification. We defined four clades within woodcreepers: clade 1: *Lepidocolaptes*, *Drymornis*, *Drymotoxeres*, *Campylorhamphus*, and *Dendroplex*; clade 2: *Xiphorhynchus*; clade 3: *Xiphocolaptes*, *Hylexetastes*, *Dendrocolaptes*, *Dendrexetastes*, and *Nasica*; and clade 4: *Dendrocincla*, *Sittasomus*, *Deconychura*, and *Certhiasomus*. The only species not included in any of these clades was *Glyphorhynchus spirurus*. We asked whether pace and bandwidth could discriminate among different genera. In other words, do

genera occupy unique areas of the acoustic space defined by pace and bandwidth? We asked this question with and without considering the clade identity of each genus.

Because the vocal tract constraint hypothesis predicts a triangular rather than a linear relationship between the rate of note production and song bandwidth, we calculated an upper bound regression. We used a standard approach for estimating upper bounds for triangular distributions between two variables (Blackburn et al. 1992; Podos 1997) to evaluate the relationship between pace and maximal bandwidth. We binned pace into 2-Hz increments (0–2 Hz, 2–4 Hz ... 28–30 Hz). Within each bin, we chose the song with the maximum bandwidth. We then calculated a linear regression using these maximum values ($n = 15$). It was not possible to assess the statistical significance of this upper bound regression as some species represented more than one point. However, we were able to compare statistically the slopes and intercepts of the woodcreeper and emberizid upper bound regressions using an analysis of covariance (ANCOVA).

The upper bound regression represents the realized extreme for pace and bandwidth production in the woodcreeper clade. The distance of a song from this upper bound can therefore be considered an indicator of relative song performance (Ballentine et al. 2004). We measured the minimum (orthogonal) distance of each song from the upper bound regression and refer to this measure as “vocal deviation” following Podos (2001). Higher values of vocal deviation reflect low song performance and lower values reflect high performance.

MORPHOLOGICAL CONSTRAINTS ON SONG PERFORMANCE

We tested the prediction that beak size limits vocal activity such that birds with larger beaks will tend to produce songs with high vocal deviation (low performance) whereas birds with smaller beaks will tend to produce high-performance songs (Podos 2001). We used the generalized least squares phylogenetic comparative method (PGLS) as described in Freckleton (2002) to analyze the relationship between bill size and song performance. This modified generalized least squares (GLS) approach simultaneously estimates and uses λ to adjust the phylogenetic correction to reflect trait lability. Beak size was the independent variable and vocal deviation was the dependent variable. For this analysis, we used the average vocal deviation for each OTU for which we also had morphological measurements (Table S4). We used maximum-likelihood functions in the Geiger library to estimate ancestral states for both vocal deviation and beak size to visualize how these traits have changed over time relative to one another. We also assessed the relationship between each beak dimension (Table S2) and song pace, frequency bandwidth, and vocal deviation (Table S4) to better understand how variation in beak shape may affect song production in woodcreepers.

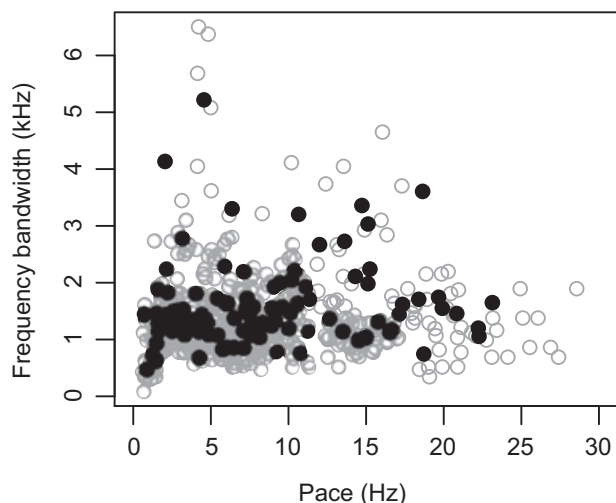


Figure 2. Relationship between song pace and frequency bandwidth for all woodcreeper songs ($n = 552$; open circle) and for an average song for each OTU ($n = 98$; closed circle). Note the triangular distribution, such that the highest values of frequency bandwidth decrease with increasing song pace.

Results

RELATIONSHIP BETWEEN TRILL RATE AND FREQUENCY BANDWIDTH

We found a triangular relationship between frequency bandwidth and pace: slow paced songs had either narrow or wide frequency bandwidths, and bandwidth decreased as song pace increased. This relationship was apparent when examining both all songs in our sample and the mean values of pace and bandwidth for each OTU (Fig. 2). Such a triangular relationship supports the hypothesis of a motor constraint on song production (Podos 1997; Podos and Hendry 2006).

We calculated an upper bound regression with a negative slope ($y = -0.0997x + 4.6$) and a moderate R^2 value (0.44). We compared the woodcreeper upper bound regression to that of the emberizids, which also has a negative slope ($y = -0.124x + 7.55$) and a high R^2 value (0.894) (Podos 1997). The higher R^2 value of the emberizid upper bound indicates that the data points used to calculate this line were less scattered. When we compared the upper bound regression lines for woodcreepers and emberizids, we found a significant difference in intercept (ANCOVA: $F = 36.65$, $P < 0.0001$) but no statistical difference in slope (ANCOVA: $F = 0.50$, $P = 0.49$). These results suggest that the two lines are parallel, but the woodcreeper performance limit is significantly lower than that of the emberizids (Fig. 3).

We also found some evidence of divergence of woodcreeper songs within this triangular acoustic space (Fig. 4). Results from a discriminate function analysis using only pace and bandwidth misclassified 77% of songs to genus. However, when this analysis was run within each clade, we found evidence that closely related

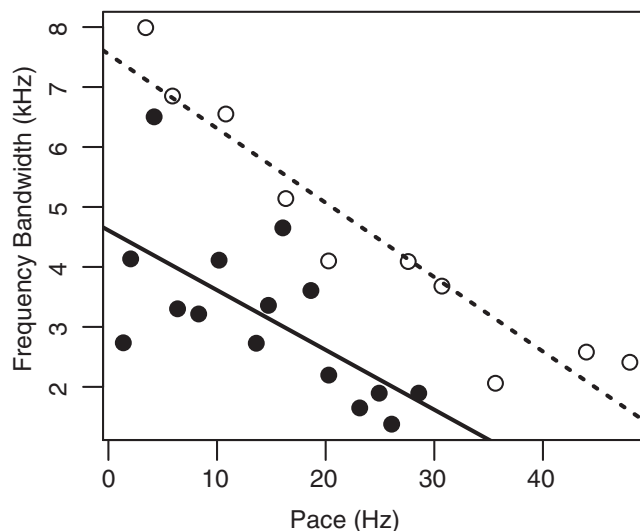


Figure 3. Comparison of the upper bound regression for woodcreeper songs (closed circles and solid line) and for emberizid songs (open circles and dashed line).

genera have diverged. This pattern is most apparent in clades 3 (e.g., *Xiphocolaptes*) and 4 (e.g., *Dendrocolaptes*). In clade 3, only 13% of songs were misclassified to genus and in clade 4, 34% of songs were misclassified. In other words, closely related genera within these clades can be accurately distinguished based only on bandwidth and pace information. In clade 1 (e.g., *Lepidocolaptes*), 50% of songs were misclassified, suggesting less divergence among taxa within this clade despite the fact that this clade appears to occupy most of the acoustic space (Fig. 4). The remaining clades (*Xiphorhynchus* and *Glyphorhynchus*) contained only one genus each and so we did not include these genera in the analysis. It is interesting to note that beak curvature, a notable feature in woodcreepers, does not appear to explain overall distribution of songs within the triangular acoustic space. The top left plot in Figure 4 includes all woodcreepers with curved bills, and their songs are scattered throughout the plot. For example, species of *Campylorhamphus*, which show the most extreme bill curvatures, show values of pace and frequency similar to the straight-billed species of *Dendroplex* and *Xiphorhynchus*. Species of two genera with clearly decurved bills, *Lepidocolaptes* and *Drymornis*, attain combinations of values very close to the hypothesized trade-off limit.

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As predicted, we found a positive relationship between beak size and vocal deviation across species (PGLS: $N = 61$, $R^2 = 0.18$, $F = 10.49$, $P = 0.002$; Fig. 5). Species with large beaks produce songs with high vocal deviation (low performance). In contrast, species with small beaks produce songs with low vocal deviation

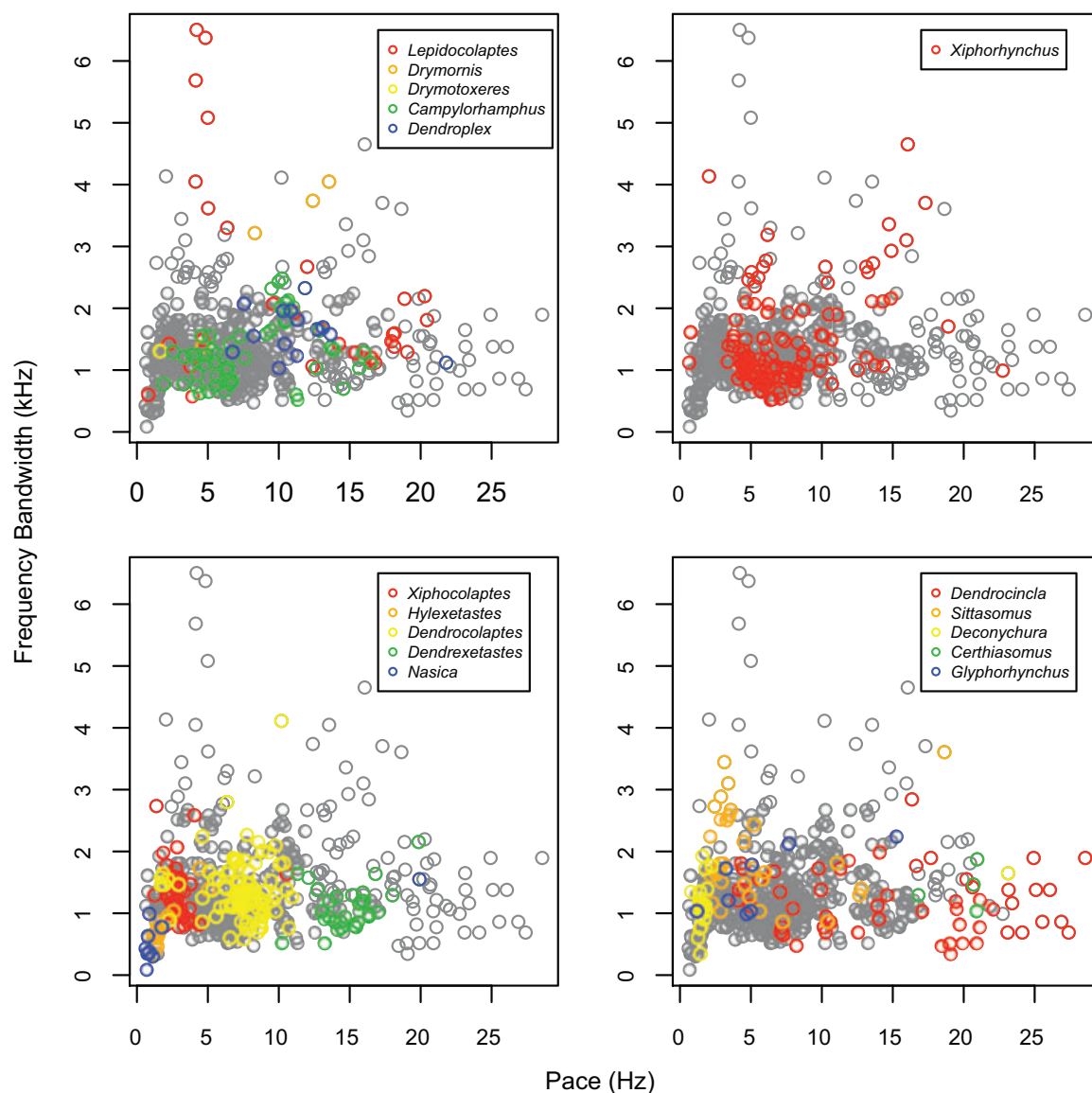


Figure 4. Scatterplots of song pace by frequency bandwidth describing variation within and among major woodcreeper clades. Each plot compares variation within a major clade and each genus in that clade is represented by a different color (see key within plots).

(high performance). Given the statistically significant relationship between beak volume and vocal deviation, we can conclude that vocal performance has evolved in close association with beak size. This result is illustrated in the ancestral state reconstructions for beak volume and vocal deviation (Fig. 6).

When we evaluated relationships (controlling for phylogeny) between each beak dimension and pace, frequency bandwidth, and vocal deviation (Table 1 and Fig. S2), we found overall weak relationships between each beak dimension and pace and stronger, significant associations with frequency bandwidth. Beak width and depth were weakly associated with vocal deviation, but we found a strong, significant relationship between beak length and vocal deviation.

Discussion

Our results suggest that the proximate features of signal production influence the evolution and diversification of woodcreeper songs. We found evidence that woodcreeper songs have diversified within a bounded acoustic space such that slow songs are produced at a range of frequency bandwidths but as song pace increases, maximal values of frequency bandwidth decrease. This pattern of song variation is consistent with the vocal tract constraint hypothesis (Podos 1997). We also found a positive relationship between beak size and ability to perform the trade-off between frequency bandwidth and pace: species with large beaks tend to produce low-performance songs, whereas species with small beaks tend to produce high-performance songs. The

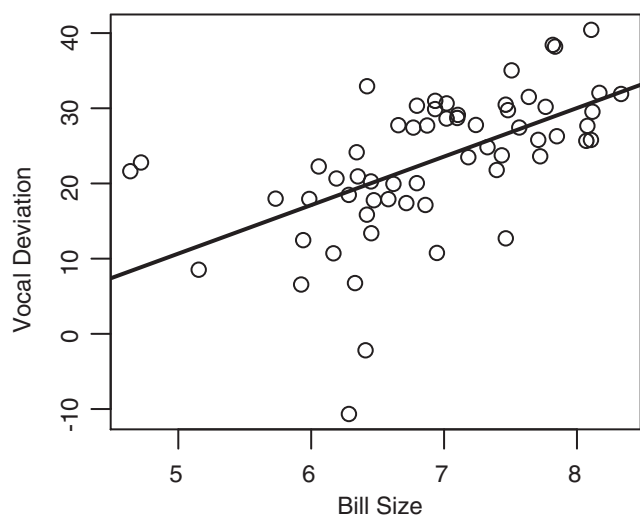


Figure 5. Vocal deviation (inverse of vocal performance) as a function of beak size. Solid line indicates best fit accounting for phylogenetic relatedness.

evolution of performance is associated closely with the evolution of beak size over time. These results support the hypothesis that there is a biomechanical limit on performance related to beak size (Podos 2001). Altogether, our findings suggest that limitations on signal production may play an important role in the evolution of vocal signals in woodcreepers. Because divergence in these vocal signals is in part a byproduct of ecological selection on beak morphology, our results have important implications for the role of ecology in suboscine diversification.

Our findings extend current knowledge about the role of constraints on vocal evolution in several ways. Both hypotheses addressed here were formulated based on mechanical trade-offs described in oscine species (Westneat et al. 1993; Hoesé et al. 2000; Podos et al. 2004b). Extensive research based on these hypotheses has led to strong evidence that song evolution in oscines is shaped by proximate features of song production (Podos and Nowicki 2004b). By comparison, no study of suboscine song has examined the specific predictions that (1) there is a trade-off between song pace and frequency bandwidth and (2) that beak size explains variation in the ability of birds to perform this trade-off (i.e., vocal performance).

Although we demonstrate that suboscine vocalizations occupy a bounded acoustic space, this acoustic space is not identical to that occupied by oscines. The triangular trade-off between bandwidth and trill rate is evident both within and among 34 species of songbirds (Passeriformes: Emberizidae) (Podos 1997). Although we found a similar trade-off among woodcreeper genera, within genera songs were highly clumped in acoustic space and did not exhibit a triangular distribution (Fig. 4). In addition, emberizid songs span a larger vocal space in both bandwidth and pace (Fig. 3). There are at least three potential reasons why

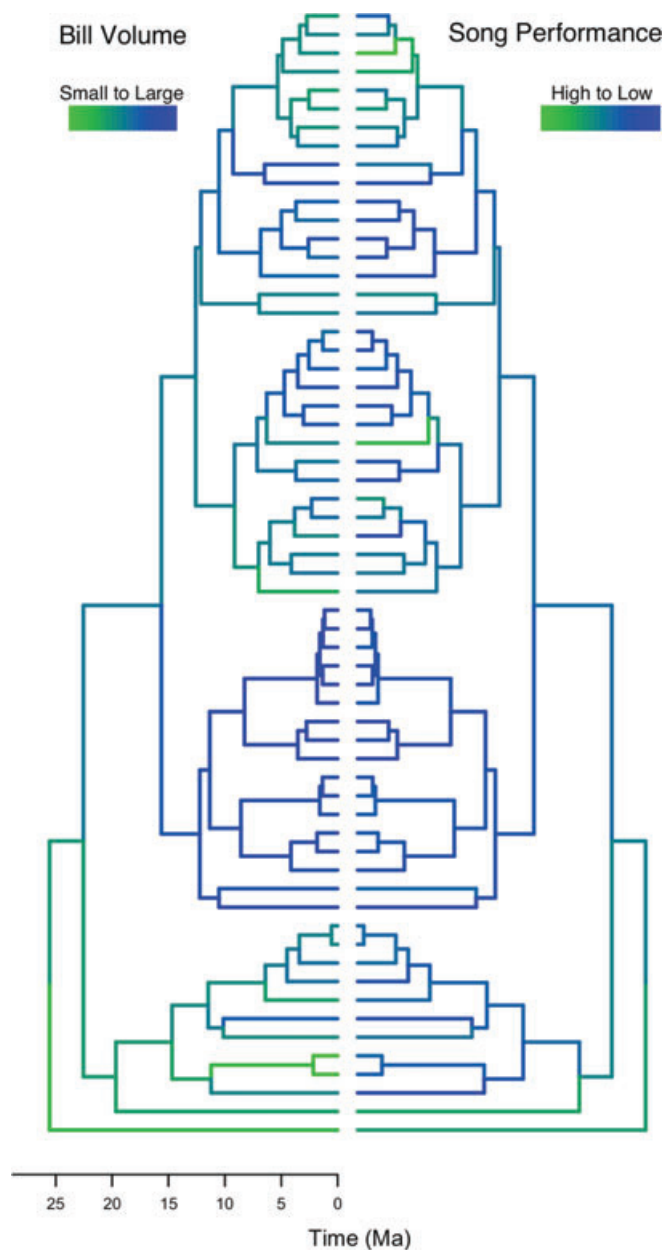


Figure 6. Estimates of ancestral states for beak size and vocal performance mapped onto the Dendrocolaptinae phylogeny. Species names are indicated in Figure S1.

the acoustic spaces of emberizids and woodcreepers do not overlap completely. One reason could be due to differences in body size. As mentioned before, body size is thought to scale with syrinx size, and thus, body size may place additional limits on sound production. Woodcreepers tend to be larger than emberizids (woodcreepers: 13–169 g (Marantz et al. 2003), emberizids: 9–54g (Rising et al. 2011)), which may explain why they occupy a smaller vocal space. Woodcreeper songs may also be more clumped in acoustic space because they develop with no or only minimal learning and tend to be much less variable than oscine

Table 1. Results of PGLS models fitted between each beak dimension and pace, frequency bandwidth, and vocal deviation.

Dependent variable	Independent variable	<i>F</i> -value	<i>R</i> ²	<i>P</i> -value
Pace	Bill depth	0.56	0.01	0.46
	Bill width	0.58	0.01	0.45
	Bill length	1.12	0.02	0.29
Frequency bandwidth	Bill depth	8.15	0.14	0.006
	Bill width	6.88	0.12	0.01
	Bill length	6.24	0.11	0.015
Vocal deviation	Bill depth	1.97	0.04	0.16
	Bill width	2.64	0.05	0.11
	Bill length	7.63	0.13	0.008

songs, resulting in a smaller acoustic space. A third possibility is that other sources of selection influence diversification within this phenotypic space. Forests (i.e., dense vegetation) are the primary habitat of all species of woodcreepers (Stotz et al. 1996), whereas many emberizid species occupy much more open habitats (Rising et al. 2011). High frequencies and fast paced songs do not transmit as well in closed habitats (Morton 1975; Tobias et al. 2010), and this form of selection (i.e., acoustic adaptation) may further constrain the acoustic space occupied by woodcreeper songs.

Despite differences in how these two clades occupy the acoustic space described by song pace and bandwidth, variation within this space can be explained by variation in beak size in both oscines, including swamp sparrows (Ballentine 2006) and Darwin's finches (Podos 2001; Huber and Podos 2006), and in suboscines (this study). The relatively tight coevolution of beak size and vocal performance among woodcreeper species suggests that diversification in beak size has influenced the diversification of song structure by correlated evolution. Although the exact mechanisms driving the trade-off between frequency and pace, and the performance of this trade-off, have not been determined for suboscines, our results suggest that these trade-offs exist and ultimately affect song diversification. Moreover, although the upper bound on the realized performance constraint in emberizids is much higher than that of woodcreepers, the two lines are almost parallel (Fig. 3), suggesting that a similar mechanism may underlie trade-offs in both clades. In the emberizids, it is thought that the triangular trade-off emerges because there is a limit on the rate at which a bird can open and close its beak depending on how widely the beak is opened (Westneat et al. 1993; Podos 1997). To test this hypothesis in woodcreepers would require mapping—or even experimental manipulation—of beak movement during song, similar to experiments conducted on oscines (Westneat et al. 1993; Suthers 1997; Hoese et al. 2000).

Our results also indicate that, like some oscine species, woodcreepers face a biomechanical limit on song performance such that species with larger beaks sing lower performance songs than species with smaller beaks. In Darwin's finches, a trade-off between force and velocity is thought to drive the correlation between beak size and performance (Podos 2001; Herrel et al. 2005a, 2008). Species with larger beaks require higher bite force to crack larger seeds; however, with greater force, beak movement becomes more limited. Does a similar mechanism operate in woodcreepers who use their beaks for catching invertebrates rather than manipulating seeds? There are several lines of evidence supporting the need for strong force application in woodcreepers. Strong-billed woodcreepers (*Xiphocolaptes*, *Hylexetastes*, *Dendrocolaptes*, *Dendrexetastes*, and *Nasica*), some of whom have beaks with the largest volume (Figs. 1 and 6), show greater ossification of the rostrum, more solidly constructed skulls, and deep and broad muscle attachments, which suggests that those beaks can exert and tolerate greater forces (Feduccia 1973). Strong-billed woodcreepers also typically eat large invertebrates and even some small vertebrates. Strong forces may be needed to subdue prey and crush exoskeletons. For several species of woodcreepers (i.e., *Campylorhamphus*), their beaks are larger not because they are wider (as in Darwin's finches) but because they are longer. And, indeed, we found evidence suggesting that bill length is the best predictor of vocal performance in woodcreepers. We also found that bill length is a good predictor of frequency bandwidth (Table 1). These results align with the results of a previous study on woodcreeper song structure, which found a significant relationship between bill length and acoustic frequency (Palacios and Tubaro 2000). As discussed by Palacios and Tubaro (2000), a relationship between bill length and frequency is consistent with the idea that the suprasyringeal vocal tract has resonating properties (Nowicki 1987) and that longer beaks add proportionally more to the length of the vocal tract, thus reducing its resonating frequency (Podos and Nowicki 2004a).

But what explains the relationship between bill length and the trade-off between song rate and frequency? Long beaks may need extra muscle mass to maintain comparable biting force at the tip of the beak (e.g., the lever effect). Thus, similar to oscines, woodcreepers with larger beaks might be more limited in their ability to open and close their beaks widely and rapidly because massive beaks and muscles are more difficult to move quickly. Another possibility is that a morphological character associated with bill length explains variation in both frequency and temporal characteristics of woodcreeper song. Indeed, Palacios and Tubaro (2000) found a significant and positive correlation between beak length and body mass. Because body mass scales with the size of the syringeal membrane, the vibrating frequency of which determines the acoustic frequency of a vocalization (Nowicki and Marler 1988), variation among species in body mass might explain

variation in acoustic frequency. Body mass may also constrain the maximum note repetition rate if woodcreepers use minibreaths during song production similar to some oscines and nonoscines (Wild et al. 1998; Suthers 2001). The maximum rate of minibreaths is dependent on the mass of the abdominal-thoracic cavity walls that must oscillate at the respiratory frequency, such that an increase in body mass decreases the maximum note repetition rate (Suthers 2001).

A recent surge of research on suboscine birds has revealed that many of the same processes driving the evolution of song in oscines are also important in suboscines, including direct adaptation of song structure to the signaling environment (reviewed in Slabbekoorn and Smith 2002a; Seddon 2005; Tobias et al. 2010), natural selection on species recognition (Seddon 2005; Seddon and Tobias 2010), and sexual selection (Tobias and Seddon 2009; Tobias et al. 2011). In addition, studies have shown that tracheophone suboscine songs are similar to oscine songs in that they function in mate attraction and territory defense (Tobias et al. 2011), and that very minor song divergence can mediate species recognition and potentially reproductive isolation (Seddon and Tobias 2007, 2010). Here, we present evidence indicating that suboscine song evolution is also constrained by the complex motor patterns involved in the production of sound, as was first demonstrated in oscines. However, although the general form of biomechanical constraint appears to be similar between these two widely separated branches of the passerine tree, we have shown that contrasts (e.g., the size of the performance acoustic space, position of the upper bound regression, and exact nature of relationship between beak size and performance) are also apparent. These findings highlight the need for further research into the proximate mechanisms involved in sound production in suboscines, as the similarities and differences between clades will generate new and testable hypotheses about how biomechanical limitations influence traits used in animal communication.

In summary, our results show that the songs of a major Neotropical bird radiation have diversified within the bounded acoustic space of bandwidth by pace and that a significant amount of this diversification in song structure is explained by variation in beak shape. We hypothesize that strong ecological selection during the adaptation of woodcreepers to different habitats and foraging niches promotes divergence in beak morphology among species, and that this leads, indirectly, to acoustic divergence in songs. Our results add weight to previous studies proposing a link between beak size and song structure in suboscines (Palacios and Tubaro 2000; Seddon 2005), suggesting that correlated evolution via biomechanical constraints may be widespread in birds. This is consistent with the idea that beak morphology serves as a “magic trait” not only in some oscine clades but across the entire passerine radiation (> 5000 species), and that “magic traits” themselves are relatively widespread (Servedio et al. 2011). Nonetheless, we

still have much to learn about the extent to which ecological selection on beak morphology has had a pleiotropic effect on the diversification of song, and the extent to which song divergence in turn influences reproductive isolation in suboscine clades. Further studies of the causes and consequences of suboscine song evolution are required.

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Supporting Information

The following supporting information is available for this article:

- Figure S1.** Bayesian estimate of phylogenetic relationships among species of woodcreepers (Passeriformes: Furnariidae: Dendrocolaptinae) as inferred from a partitioned analysis of three mitochondrial and three nuclear genes.
- Figure S2.** Song pace, frequency bandwidth, and vocal deviation as a function of each dimension of beak size.
- Table S1.** Catalogue numbers, locality information, and data for vocal samples.
- Table S2.** Specimen numbers, locality information, and beak measurements for samples included in morphological analyses.
- Table S3.** Accession numbers and locality information for samples included in the Dendrocolaptinae phylogeny.
- Table S4.** Song data for OTUs included in analyses of morphological constraints on song performance.

Supporting Information may be found in the online version of this article.

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