



The effect of habitat and body size on the evolution of vocal displays in Thraupidae (tanagers), the largest family of songbirds

NICHOLAS A. MASON* and KEVIN J. BURNS

Department of Biology, San Diego State University, 5500 Campanile Dr., San Diego, CA 92182, USA

Received 28 August 2014; revised 17 October 2014; accepted for publication 19 October 2014

Animals rely on auditory cues to relay important information between individuals regarding territoriality, mating status, and individual condition. The efficacy of acoustic signals can depend on many factors, including the transmitter, the receiver, and the signalling environment. In the present study, we evaluate the effect of body size and habitat on the evolution of learned vocal displays across the tanagers (Aves: Thraupidae), a group that comprises nearly 10% of all songbird species. We find that body size affects tanager vocalizations, such that nine out of ten song characters and scores from two principal component axes were correlated with mass. More specifically, larger tanagers tended to produce slower-paced, lower-pitched vocal displays within narrower bandwidths. In contrast, habitat was correlated with only three out of ten song characters, and only one of these characters corroborated the directional predictions of the acoustic adaptation hypothesis. Thus, morphological characters, such as body mass, may play a more important role than variation among signalling environments in the evolution of avian vocal displays. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **114**, 538–551.

ADDITIONAL KEYWORDS: acoustic adaptation hypothesis – bird song – evolutionary constraint – oscines – sensory drive.

INTRODUCTION

Auditory signals are used profusely among animals to convey important information between individuals. Mate choice, territoriality, parent–offspring interactions, and kin recognition are a few of many processes that involve acoustic signalling in animals (Bradbury & Vehrencamp, 2011). However, auditory communication is only effective when sounds successfully reach their intended audience – the source, the receiver, and the environment through which the signal is transmitted all contribute to this transfer of information (Endler, 1992). Bird songs are used as auditory displays during the breeding season to elicit courtship and defend territories from rival conspecifics (Catchpole & Slater, 2008). The vocal displays of

oscine songbirds are learned, whereas suboscine vocal displays are mostly unlearned and are controlled genetically (Touchton, Seddon & Tobias, 2014). However, both oscine and suboscine vocal displays are targets of sexual selection (Tobias *et al.*, 2011; 2012). Thus, avian vocal displays are complex behaviours that are subject to multiple evolutionary pressures, including natural selection, sexual selection, and cultural transmission, implying rapid rates of evolution (Andersson, 1994; Blomberg, Garland & Ives, 2003; Kroodsma, 2005).

Bird songs are often projected over long distances and are thus affected by the acoustic properties of their signalling environment and the physical processes of attenuation and degradation (Morton, 1975; Linskens *et al.*, 1976; Wiley & Richards, 1978; Richards & Wiley, 1980). Attenuation is the continuing decrease of signal intensity, or the energy per unit surface, as propagation distance increases (Forrest, 1994). Degradation is the accumulation of structural changes that the signal experiences as it travels

*Corresponding author. Current address: Department of Ecology and Evolutionary Biology, Cornell University, 215 Tower Rd., Ithaca, NY, 14853, USA.
E-mail: nam232@cornell.edu

through space (Morton, 1986), which may consist of temporal rearrangements by echoes and reverberations or alterations by refraction and scattering through obstacles. All sounds degrade and attenuate as the distance from their source increases; however, higher frequencies experience greater levels of atmospheric and vegetational absorption, reverberation, and scattering than lower frequencies (Marten & Marler, 1977). Furthermore, lower frequency sounds have longer wavelengths that allow them to diffract around obstacles more easily than higher frequency sounds (Wiley & Richards, 1978). As a corollary, habitats with greater vegetation density should favour acoustic signals with lower frequencies for long-distance propagation as they experience proportionally less degradation and attenuation (Aylor, 1972). Furthermore, dense foliage vitiates both amplitude and frequency modulations, while atmospheric pressures, such as wind and thermal effects, only affect amplitude modulations (Bradbury & Vehrencamp, 2011). The earliest evidence of these phenomena came from experiments that examined the propagation of recorded bird songs or synthesized sounds in natural environments (Aylor, 1972; Morton, 1975; Marten & Marler, 1977; Wiley & Richards, 1978; Hansen, 1979).

The 'Acoustic Adaptation Hypothesis' (hereafter AAH; Morton, 1975; Hansen, 1979) postulates that aforementioned differences in vegetative structure among habitats should impose differing selective pressures on acoustic signals for optimal transmittance from signaler to receiver (reviewed by Boncoraglio & Saino, 2007). Collectively, the AAH predicts that songs with lower minimum, peak, and maximum frequencies, narrower bandwidths, fewer

frequency modulations, longer notes, and longer inter-note intervals should be favored in habitats with dense vegetational structure rather than open, herbaceous coverage (Morton, 1975; Table 1). The AAH is based on the assumption that bird song is selected for maximum distance propagation and that other selective pressures are equal between open and closed habitats, including eavesdropping by predators and parasites (Zuk *et al.*, 1996), metabolic costs of singing (Oberweger & Goller, 2001), morphological constraints (Wallschläger, 1980; Podos & Nowicki, 2004), and sexual selection (Searcy & Andersson, 1986; Byers, 2006). Most studies regarding the AAH have focused on either intraspecific variation among populations (e.g., Shy, 1984; Ruegg *et al.*, 2006; Lijtmaer & Tubaro, 2007; Derryberry, 2009; Kirschel, Blumstein & Smith, 2009), or comparisons between pairs or groups of closely related species (e.g., Tobias *et al.*, 2010; Weir, Wheatcroft & Price, 2012). Despite numerous intraspecific assessments of the AAH and a few interspecific studies (e.g., Badyaev & Leaf, 1997; Bertelli & Tubaro, 2002; Farnsworth & Lovette, 2008), there persists a relative paucity of broad-scale studies that extensively sample a monophyletic group to examine the relationship between vocal displays and the signalling environment.

In addition to variation among acoustic signalling environments, physical differences among signal propagators can affect vocal displays. Body mass is a particularly well-known correlate of many song features. Variation in body size can cause allometric changes in syrinx sizes, which in turn affects the range of fundamental frequencies that an organism can produce (Ryan & Brenowitz, 1985). Specifically, larger syrinxes tend to vibrate more slowly and

Table 1. Vocal characters used in this study, their descriptions, and predicted directional differences between open and closed habitats according to the Acoustic Adaptation Hypothesis. A '+' indicates that the character is predicted to be higher in 'closed' compared to 'open' habitats

Character	Description	Directionality
Average note length	Summed note duration divided by the number of notes in a song	+
Average pause length	Summed pause duration divided by the number of pauses in a song	+
Minimum frequency	Minimum fundamental frequency occurring in a song	-
Maximum frequency	Maximum fundamental frequency occurring in a song	-
Peak frequency	Fundamental frequency with the highest amplitude in the entire song	-
Average note bandwidth	The average frequency range of notes within a song	-
Song bandwidth	Difference between the maximum and minimum fundamental frequencies in a song	-
Frequency shift rate	Number of frequency sweeps that span 1 kHz in 20 msec divided by the song duration	-
Note rate	Number of notes in a song divided by the song duration	-
Trill rate	Number of notes per second in a trill. A minimum of five repeated notes within a second duration defined a trill	-

produce lower frequency sounds more effectively (Wallschläger, 1980). After sound is produced in the syrinx, variation in tracheal morphology as well as bill size and shape can affect frequency-related and structural components of avian vocalizations (Nowicki, 1987). Individuals actively reconfigure their vocal tract to act as a resonance filter and produce pure tones (Riede *et al.*, 2006). Larger-bodied birds with thicker bills are constrained in their ability to manipulate their vocal tract to match rapid changes in fundamental frequencies, and thus often sing within smaller frequency ranges (Podos, 2001). The influence of morphology on other aspects of avian vocal displays, such as note length, is not as well established. However, larger birds with larger syrinxes are thought to produce slower-paced songs overall (Podos, 2001), suggesting a possible positive correlation between body mass and note length, in addition to pause length. Taken together, these observations predict that larger birds will produce lower frequency, slower-paced songs within narrower bandwidths, highlighting the possible interplay between the evolution of body size, bill morphology, acoustic signalling environments, and vocal displays in birds (Slabbekoorn & Smith, 2002; Podos, Huber & Taft, 2004).

Here, we conduct the largest-scale assessment of the AAH and the effects of body mass on avian vocalizations to date. Specifically, we test whether different habitats and body sizes affects the evolution of vocal displays within tanagers (Thraupidae). Tanagers are the largest family of songbirds and comprise nearly 10% of all songbird species (Clements *et al.*, 2013). Although tanagers have a complicated taxonomic history, a recent multi-locus phylogeny indicates 371 species spread throughout the Neotropics define a monophyletic Thraupidae (Burns *et al.*, 2014). Species in the group span an impressive array of body sizes, habitat preferences, and vocal displays (Mason, Shultz & Burns, 2014; Fig. 1). For example, groups such as Neotropical seedeaters and seed-finches (Mason & Burns, 2013), warbling finches (Shultz & Burns, 2013), Darwin's finches (Burns, Hackett & Klein, 2002), and nectar-feeding honeycreepers (Burns, Hackett & Klein, 2003) are now considered tanagers. Furthermore, tanagers occur in 27 of the 29 terrestrial habitats of the Neotropics (Parker, Stotz & Fitzpatrick, 1996), inhabiting a range of environments from dense tropical rainforest to high-altitude grasslands. Tanagers also vary greatly in terms of body mass, ranging from 7–114 g (Dunning, 2007; Supporting Information, Fig. S1). Thus, tanagers provide an excellent opportunity to examine the effect of body size and habitat on avian vocalizations in an evolutionary context.

METHODS

TAXONOMIC SAMPLING

We used the most recent molecular phylogeny to delimit a monophyletic Thraupidae for taxonomic sampling (Burns *et al.*, 2014). To identify species for comparative analyses, we followed the species-level taxonomy of Clements *et al.* (2013). However, we also included *Sicalis luteiventris* and *Poospiza whittii* because they were included as full species in the phylogeny of Burns *et al.* (2014). Clements *et al.* (2013) treats these two taxa as subspecies of *Sicalis luteola* and *Poospiza nigrorufa* respectively, although other authorities have treated them as full species (Ridgely & Tudor, 1989; Sibley & Monroe, 1990).

SONG MEASUREMENTS

Recordings of tanager songs were downloaded from either the Macaulay Library (<http://macaulaylibrary.org/>) or the xeno-canto (<http://xeno-canto.org/>) online repositories. When possible, we sampled throughout the entire range of each species to account for intraspecific variation in song. We assumed that recordings from different localities or dates represented different individual males and avoided measuring multiple recordings of the same individual. To avoid pseudoreplication, we measured one representative vocalization per recording. In total, we measured vocalizations from 2737 individuals representing 321 species of tanagers (mean = 8.5, SE = 0.48 songs per taxon).

In addition to songs, tanagers produce a wide array of call notes (Ridgely & Tudor, 1989). Therefore, we followed the methods of Price, Friedman & Omland (2007) in defining 'songs' as any vocalization that included tonal elements, exceeded 0.5 s in duration, and was preceded and followed by intervals greater than 1 s. We excluded sections or entire recordings that included excessive background noise or were otherwise of poor quality. We followed written descriptions (Ridgely & Tudor, 1989; Isler & Isler, 1999) and recordists' notes to ensure that we measured songs of target, rather than background, species. Female song has not been reported in tanagers, except in rare instances of duetting (e.g. *Cypsnagra hirundinacea*); in these cases only male songs were measured.

Spectrograms were generated using RavenPro sound analysis software (version 1.4; Cornell Laboratory of Ornithology, Ithaca, NY). Within Raven, we used a Hann spectrogram window with 300 samples, a DFT size of 512 samples, a hop size of 3.4 ms, a sampling frequency of 44.1 kHz, and a time resolution of 11.6 ms. Measurements were taken by cross-referencing the spectrogram and waveform windows by eye to determine when vocalizations began and

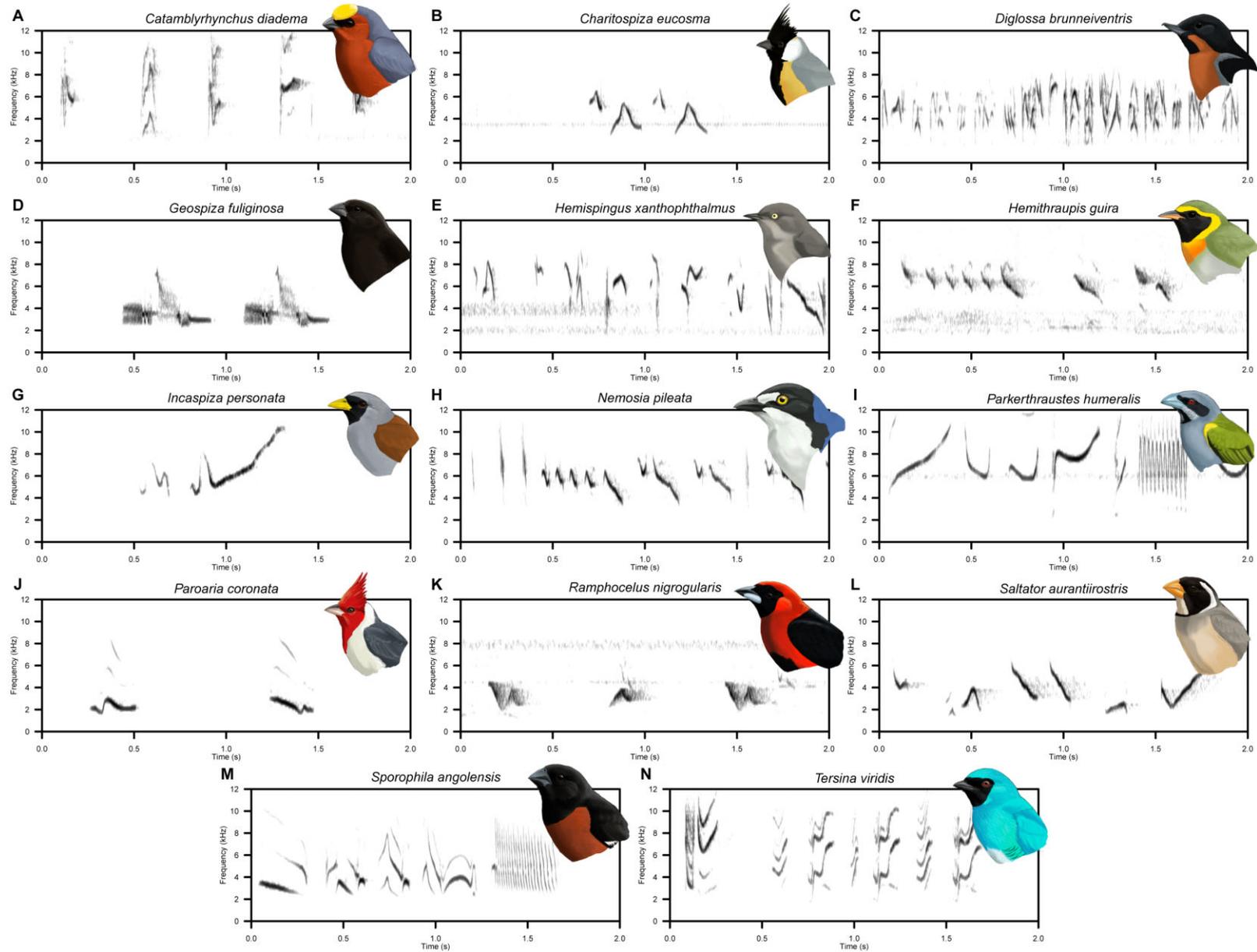


Figure 1. Spectrograms illustrating the diversity of vocalizations among tanagers. One representative species from each of 15 sub-families of Thraupidae is included. All spectrograms are on the same scale in terms of frequency and time, demonstrating the diversity in frequency and temporal components of thraupid songs. Darker shades of grey indicate higher decibel levels. Mary Margaret Ferraro drew each portrait.

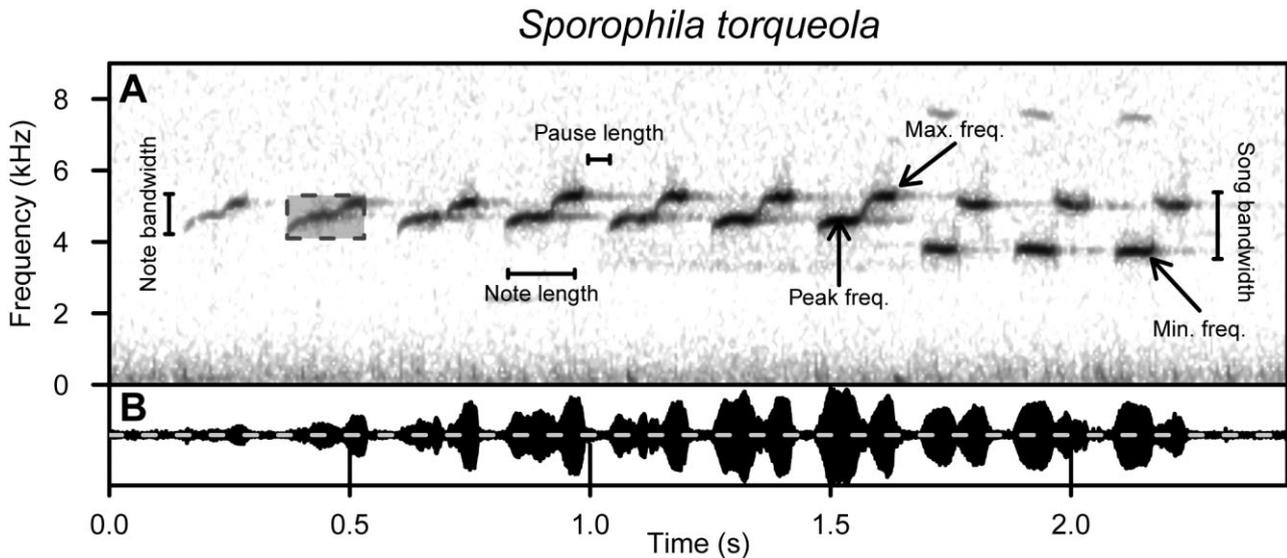


Figure 2. Spectrogram and oscillogram of *Sporophila torqueola*. A, Sample spectrogram illustrating measurements that were included in this study. The dotted grey box indicates how notes were measured using Raven, while the arrows and text refer to different song characters considered here. B, Sample oscillogram that was used in conjunction with spectrogram windows to determine the start and end point of vocalizations when taking raw measurements in Raven.

ended (Fig. 2). We choose this method over automated algorithms because variation among recordings, such as the presence of background noise or variation in overall volume or reverberation, reduces the accuracy of automated measurements. All measurements were either taken or verified by the same person (NAM) to ensure consistency across recordings. Raw measurements, including the start and end time as well as the minimum, maximum, and peak frequency of each note, were obtained within Raven (Fig. 2). We visualized spectrograms (Figs 1, 2) using the same parameters with the package *seewave* (Sueur, Aubin & Simonis, 2008). We wrote custom R scripts to extract ten temporal and frequency-related song characters (Table 1), which we averaged across individuals for each species. We measured only fundamental frequencies (i.e. first harmonic) and excluded overtones from all measurements (Mindlin & Laje, 2005). We also used a phylogenetic principal components analysis (PPCA; Revell, 2009) to reduce dimensionality among nine of the ten characters considered here (trill rate was excluded due to missing data among species that do not produce trills). The first two PPCA axes accounted for 62.9% and 26.9% of the total variation, respectively. The loadings of the first PPCA axis described an axis of variation in which more positive scores indicated larger frequency bandwidths, including lower minimum frequencies and higher maximum frequencies, and more rapid frequency changes (Table 2). The second PPCA axis described an axis of variation in which more positive

Table 2. Phylogenetic principal component analysis loadings for the first two axes using nine of the song characters included in this study. Trill rate was omitted due to excess missing data because many species do not sing trills. The first and second axes account for 63.0% and 26.9% of the total variation, respectively. The loadings of the first PPCA axis have been reversed to ease interpretation

Character	PC1	PC2
Average note length	0.02	-0.18
Average pause length	0.05	0.03
Minimum frequency	-0.67	0.73
Maximum frequency	0.70	0.68
Peak frequency	0.12	0.87
Average note bandwidth	0.78	0.01
Song bandwidth	0.99	-0.03
Frequency shift rate	0.57	-0.15
Note rate	0.03	-0.08

scores indicated higher maximum, minimum, and peak frequencies (Table 2).

BODY MASS MEASUREMENTS

We obtained body mass data from the CRC Handbook of Avian Masses (Dunning, 2007) for 305 of the 321 species for which we collected song data. We log transformed mass and all subsequent analyses were restricted to these 305 species. For most species, we used the average weight of both males and females.

For some species, data from both sexes were not available – in these instances, we used measurements from whichever sex was available.

HABITAT DESIGNATIONS

We used Parker *et al.* (1996) to assign species to different habitat types. Each species was assigned to a ‘closed’ (forest), ‘open’ (non-forest habitats, including grassland, marshland, and scrub), or ‘edge’ habitat group. Examples of habitat in the ‘edge’ group include montane evergreen forest edge, tropical lowland evergreen forest edge, and southern temperate forest edge, among others (Parker, III, Stotz, & Fitzpatrick, 1996). Many species occur in multiple habitats; thus, we focused on the primary habitat designation as indicated by Parker *et al.* (1996) and ignored intraspecific variation in habitat. In total, 168 species were assigned to ‘closed’, 31 species were assigned to ‘edge’, and 106 were assigned to ‘open’. Habitat designations for each species included in this study are available through the Supporting Information (Table S1).

COMPARATIVE ANALYSES

Using phylogenetic generalized least squares (PGLS; Grafen, 1989; Hansen & Martins, 1996; Martins & Hansen, 1997), we identified the best-fit model using the AIC_c criterion for each of the ten song characters and scores for the first two PPCA axes. We considered two models of character evolution, including Pagel’s model of character evolution (PG; Pagel, 1999), which describes a model of stochastic evolution wherein internal branches are multiplied by a parameter (λ) that reflects the level of phylogenetic signal present in a given character. We also evaluated Ornstein-Uhlenbeck (OU) models (Hansen, 1997; Butler & King, 2004), which describe a scenario of Brownian motion that is bounded by a global selective optimum (θ). In OU models, the strength of stabilizing selection is represented by the α parameter, which pulls the trajectory of Brownian motion towards θ . Both PG and OU models approximate Brownian motion when $\lambda = 1$ or $\alpha = 0$, respectively.

In total, we compared the performance of eight PGLS models via AIC_c scores for each song character. For both PG and OU branch length transformations, we tested the following models: (1) species separated into ‘closed’ and ‘open’ (wherein the ‘edge’ category was subsumed within the ‘open’ category) with mass as an additive effect; (2) species separated into ‘closed’ and ‘open’ with mass as an interaction effect; (3) species separated into either ‘closed’, ‘open’, or ‘edge’ and mass as an additive effect; and (4) species separated into either ‘closed’, ‘open’, or ‘edge’ and mass as

an interaction effect. For each analysis, we visually inspected the distribution of residuals of the best-fit model to ensure that they were normally distributed and subsequently log transformed average note length, average pause length, frequency shift rate and note rate (Freckleton, 2009). We also examined the distribution of phylogenetic residuals for any outliers and removed those species with studentized residuals ≥ 3 following the recommendations of Jones & Purvis (1997) and Garland, Harvey & Ives (1992).

Then, using the best-fit model with outliers removed, we ran 12 separate PGLS analyses with each song character or PPCA axis as a response variable and habitat and mass as predictor variables. We also consider results from any competing models that have a ΔAIC_c score smaller than seven (Burnham, Anderson & Huyvaert, 2011). To account for phylogenetic uncertainty and variation in branch length estimations, we ran each PGLS analysis over a set of 50 trees randomly sampled from a post-burn-in distribution of phylogenies from Burns *et al.* (2014) and extracted mean values for each statistic.

RESULTS

We identified best-fit and competing models for each of the 12 characters considered here via ΔAIC_c scores (Table 3). Six characters had a clearly favored model (all other models with $\Delta\text{AIC}_c > 7$), while the remaining six characters had multiple competing models. We found a correlation between body mass and ten out of 12 song characters (Table 4; Fig. 3. Average note length ($\beta = 0.26 \pm 0.1$, $P = 0.008$) and average pause length ($\beta = 0.04 \pm 0.01$, $P = 0.029$) were positively correlated with mass. In contrast, PC1 (bandwidth; $\beta = -1016.27 \pm 432.2$, $P = 0.02$), PC2 (frequency; $\beta = -2087.68 \pm 422.02$, $P < 0.001$), minimum frequency ($\beta = -845.37 \pm 227.32$, $P < 0.001$), maximum frequency ($\beta = -1582.38 \pm 377.75$, $P < 0.001$), peak frequency ($\beta = -1262.96 \pm 277.68$, $P < 0.001$), average note bandwidth ($\beta = -453.19 \pm 177.66$, $P = 0.011$), song bandwidth ($\beta = -682.67 \pm 333.59$, $P = 0.042$), frequency shift rate ($\beta = -0.47 \pm 0.11$, $P < 0.001$), and note rate ($\beta = -0.33 \pm 0.09$, $P = 0.008$) were all inversely correlated with mass. Taken together, these correlations imply that larger tanagers produce slower-paced vocal displays within smaller bandwidths at lower frequencies. Competing models were generally quite similar in terms of the directionality and magnitude of effect sizes (Supporting Information, Table S2). For simplicity, we will constrain our discussion to best-fit models that are largely congruent with competing models.

Among the ten song characters and two principal component axes that we considered, the broadest categorization, with solely forest and non-forest habitats,

Table 3. Comparison of model performance for eight different models when considering each song character using ΔAIC_C scores averaged across 50 randomly sampled phylogenies from the posterior distribution. Models with $\Delta\text{AIC}_C \leq 7$ are highlighted in bold. The best scoring model may have a ΔAIC_C scores greater than zero if it was not selected as the best-fit model for each of the 50 phylogenies. Models with ‘no edge’ have species in edge and open habitats lumped together, while these categories are separate in ‘edge separate’ models. ‘Additive’ models include mass as an additive effect, while ‘interaction’ models include mass as an interaction model

Character	Pagel's λ				OU			
	No edge		Edge separate		No edge		Edge separate	
	Additive	Interaction	Additive	Interaction	Additive	Interaction	Additive	Interaction
PC1 (bandwidth)	45.44	31.15	29.93	1.99	44.31	29.54	29.71	2.22
PC2 (frequency)	56.29	37.46	28.33	0.00	82.85	64.84	59.45	29.90
Average note length	0.29	4.02	2.11	8.76	9.19	12.93	11.81	17.80
Average pause length	13.21	19.48	20.50	32.28	0.32	5.11	7.48	17.89
Minimum frequency	44.49	31.26	26.03	0.00	113.43	99.25	95.25	67.21
Maximum frequency	52.29	35.41	29.11	1.51	56.04	39.25	36.11	7.84
Peak frequency	52.71	34.32	27.11	0.00	68.11	49.13	46.37	16.64
Average note bandwidth	34.08	22.91	23.03	0.00	52.2	40.19	41.30	17.05
Song bandwidth	44.04	30.35	29.17	1.83	42.11	28.29	28.16	1.88
Frequency shift rate	0.00	3.14	3.51	8.68	23.51	26.63	27.20	28.84
Note rate	0.00	2.86	2.06	7.07	11.29	13.40	13.60	17.26
Trill rate	17.42	10.92	12.40	0.00	31.41	25.04	23.55	10.86

best-fit four characters: average note length, average pause length, frequency shift rate and note rate (Table 4). A PGLS model that included edge in addition to open and closed habitats was the best-fit model for the remaining six characters (Table 4). Three out of ten song characters demonstrated significant differences between habitat types (Table 4; Fig. 3). In comparison to closed habitats, minimum frequency ($\beta = -1901.48 \pm 919.28$, $P = 0.04$) and peak frequency ($\beta = -2630.14 \pm 1076.58$, $P = 0.016$) were lower in open habitats. In contrast, frequency shift rate was higher in open habitats ($\beta = 0.25 \pm 0.1$, $P = 0.016$). The remaining seven characters demonstrated no significant differences among habitat types. Although interaction terms improved model performance for eight of twelve ten characters considered here, we observed no instances of a significant interaction effect between habitat type and mass among the best-fit models.

DISCUSSION

Our large-scale comparative study of tanager vocalizations expands upon the current understanding of the role that body size and habitat play in the evolution of acoustic signals. Our findings suggest that morphological characters, such as body size, may impact oscine vocalizations more than differences among acoustic signalling environments. We found that nine out of ten vocalization characters and scores

from two principal component axes were correlated with body mass, suggesting that larger tanagers sing slower-paced, lower-pitched songs within smaller bandwidths. In contrast, only four out of 12 vocal characters differed significantly between habitat types, and only one (frequency shift rate) followed the predictions of the AAH. Similarly, Wiley (1991) found that body size played a stronger role than habitat type in shaping the vocal displays of over 100 North American passerines. Badyaev & Leaf (1997) found a strong effect of habitat on temporal aspects of bird song, but not on frequency, whereas body mass was correlated with most vocal characters included in their study of *Phylloscopus* and *Hippolais* warblers. Thus, our study corroborates previous findings that interspecific differences in vocal displays may be more strongly influenced by variation in body mass than acoustics signalling environments.

THE EFFECT OF BODY SIZE ON SONGBIRD VOCALIZATIONS

Our findings are concordant with the widely accepted notion that body mass is negatively correlated with various measures of acoustic frequencies, particularly minimum, maximum, and peak frequencies (Wallschläger, 1980; Ryan & Brenowitz, 1985; Tubaro & Mahler, 1998). There is a well-studied functional relationship underlying this correlation: the frequency that a vibrating structure, in this case the

Table 4. Results from PGLS analyses averaged across 50 phylogenies that were randomly sampled from the posterior distribution. The number of competitive models (including the best-fit model) is indicated. Competitive models that were not the best-fit models are fully described in Table S1. The ‘best model’ column indicates whether a PGLS model with species assigned to a simplified habitat designation (habsimp; in which only ‘open’ (O) and ‘closed’ (C) categories are included) was preferred to the inclusion of an additional category for species in edge (E) habitats (habedge). Models with an asterisk include an interaction effect between habitat type and mass. The branch length transformation that was applied as part of the best model as well as the corresponding parameter (either Pagel’s λ or α). The effect size and its standard error are represented by β , while the statistical significance of each effect is indicated by the presence or absence of asterisks (*, **, and *** indicate $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively)

Character	# Competitive models	Best model	Branch length transformation	Parameter	Effect	$\beta \pm SE$	P
PC1 (bandwidth)	2	~habedge*Mass	PG	0.31	habedgeE	-2960.1 \pm 2754.7	0.284
					habedgeO	-1175.45 \pm 1895.14	0.536
					Mass	-1016.27 \pm 432.2	0.02*
					habedgeE:Mass	1099.13 \pm 860.74	0.203
					habedgeO:Mass	232.72 \pm 632.99	0.714
PC2 (frequency)	1	~habedge*Mass	PG	0.89	habedgeE	-1765.55 \pm 2356.99	0.456
					habedgeO	-3956.17 \pm 1626.67	0.016*
					Mass	-2087.68 \pm 422.02	< 0.001***
					habedgeE:Mass	729.19 \pm 736.45	0.325
					habedgeO:Mass	924.38 \pm 551.12	0.095
Average note length	3	~habsimp+Mass	PG	0.59	habsimpO	-0.01 \pm 0.09	0.919
					Mass	0.26 \pm 0.1	0.008**
Average pause length	2	~habsimp+Mass	OU	0.1	habsimpO	-0.02 \pm 0.02	0.593
					Mass	0.04 \pm 0.01	0.029*
Minimum frequency	1	~habedge*Mass	PG	0.69	habedgeE	844.22 \pm 1308.53	0.52
					habedgeO	-1901.48 \pm 919.28	0.04*
					Mass	-845.37 \pm 227.32	< 0.001***
					habedgeE:Mass	-232.31 \pm 408.61	0.571
					habedgeO:Mass	435.94 \pm 309.57	0.161
Maximum frequency	1	~habedge*Mass	PG	0.79	habedgeE	-2823.02 \pm 2151.12	0.191
					habedgeO	-2684.9 \pm 1502.28	0.077
					Mass	-1582.38 \pm 377.75	< 0.001***
					habedgeE:Mass	1013.73 \pm 671.76	0.133
					habedgeO:Mass	562.15 \pm 507.45	0.274
Peak frequency	1	~habedge*Mass	PG	0.88	habedgeE	-1322.39 \pm 1554.92	0.398
					habedgeO	-2630.14 \pm 1076.58	0.016*
					Mass	-1262.96 \pm 277.68	< 0.001***
					habedgeE:Mass	542.14 \pm 485.75	0.268
					habedgeO:Mass	645.97 \pm 364.53	0.078
Average note bandwidth	1	~habedge*Mass	PG	0.35	habedgeE	326.5 \pm 1115.37	0.77
					habedgeO	-489.77 \pm 770.95	0.528
					Mass	-453.19 \pm 177.66	0.011*
					habedgeE:Mass	0.47 \pm 348.54	0.982
					habedgeO:Mass	221.87 \pm 257.7	0.392
Song bandwidth	2	~habedge*Mass	PG	0.3	habedgeE	-2704 \pm 2130.91	0.206
					habedgeO	-774.25 \pm 1465.19	0.598
					Mass	-682.67 \pm 333.59	0.042*
					habedgeE:Mass	964.65 \pm 665.82	0.149
					habedgeO:Mass	120.29 \pm 489.31	0.806
Frequency shift rate	3	~habsimp+Mass	PG	0.31	habsimpO	0.25 \pm 0.1	0.016*
Note rate	3	~habsimp+Mass	PG	0.53	Mass	-0.47 \pm 0.11	< 0.001***
					habsimpO	0.02 \pm 0.09	0.831
Trill rate	1	~habedge*Mass	PG	0.82	Mass	-0.33 \pm 0.09	0.008**
					habedgeE	-41.45 \pm 72.67	0.57
					habedgeO	-66.82 \pm 56.54	0.241
					Mass	-27.22 \pm 17.52	0.124
					habedgeE:Mass	14.09 \pm 22.76	0.538
					habedgeO:Mass	22.91 \pm 19.71	0.249

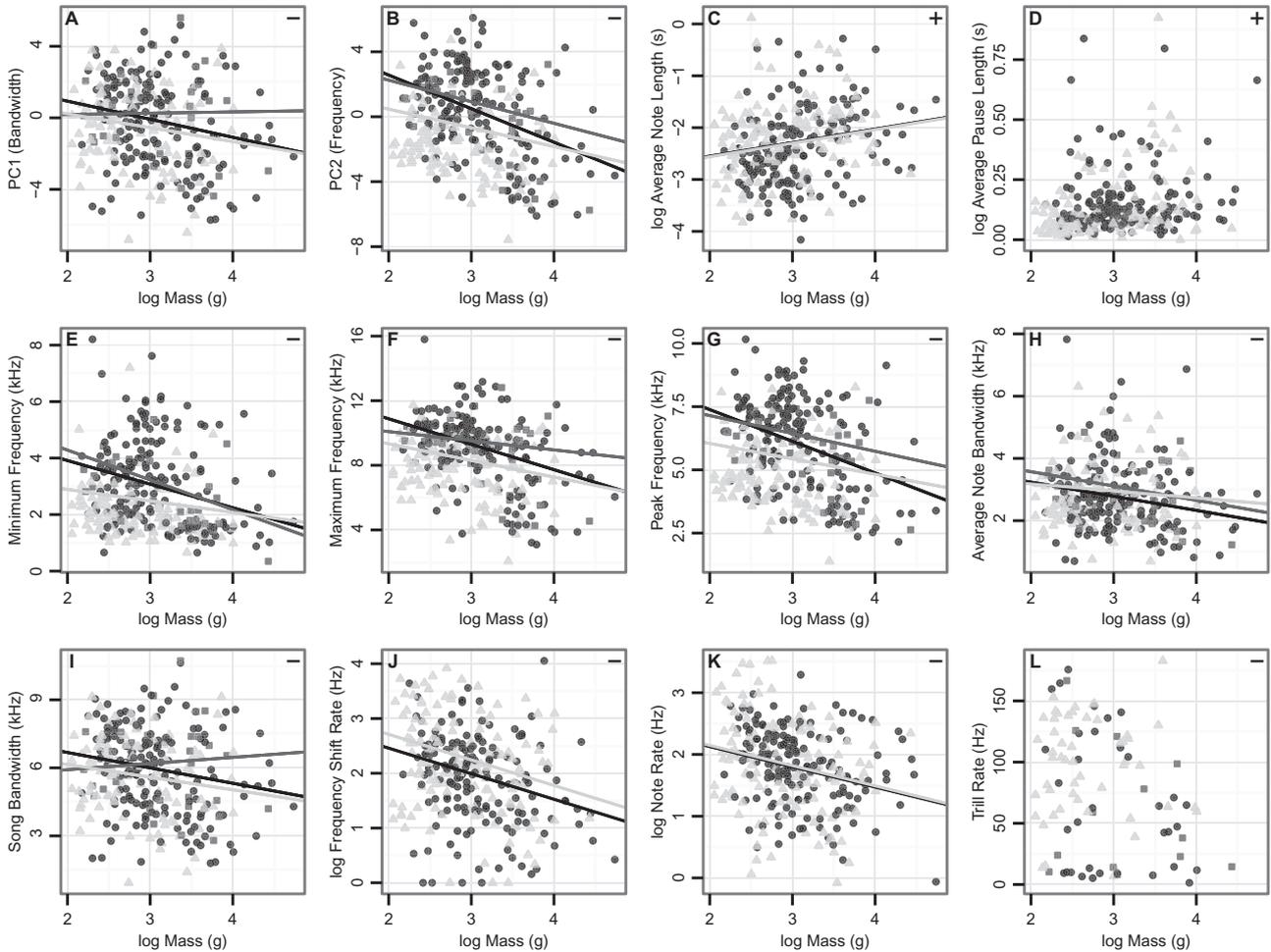


Figure 3. Scatterplot of ten vocalization characters and two principal components axes against log-transformed mass for 305 species of tanagers, except for trill rate, which includes 99 species. Black circles indicate taxa from closed habitats, dark grey squares indicate edge habitats, and light grey triangles indicate open habitats. The plus or minus sign in the upper-right hand corner of each panel indicates if the Acoustic Adaptation Hypothesis predicts the character to be larger or smaller in closed habitats (black circles), respectively. When a significant correlation between mass and a vocalization character is present, a line of best-fit that accounts for phylogenetic relatedness is drawn for each habitat type included. If the interaction term is included in the model of best fit, the best-fit lines have different slopes.

syrinx, can most efficiently produce is affected by the mass of the structure itself (Bowman, 1979; Wallschläger, 1980; Shy, 1983). Thus, larger tanagers possess more massive syrinxes that produce lower frequencies with greater efficacy.

In addition to acoustic frequencies, we found that body mass was correlated with average note bandwidths, song bandwidths, frequency shift rate, and temporal song features such as note length, pause length, and note rate. While consistent with the findings of previous studies on the effect of habitat and body mass on oscine songs (Ryan & Brenowitz, 1985; Wiley, 1991; Badyaev & Leaf, 1997), the functional relationships that underlie these correlations are less clear. In addition to body size, bill shape and size can

also influence various song parameters (reviewed in Podos & Nowicki, 2004). Recent findings suggest that bill depth and width are related to trill performance such that wider, deeper bills are constrained to produce slower trills in Medium Ground Finches (*Geospiza fortis*; Podos, 2001; Podos & Nowicki, 2004), Swamp Sparrows (*Melospiza georgiana*; Ballentine, 2006), and White-crowned Sparrows (*Zonotrichia leucophrys*; Derryberry, 2009). Bill size and shape can also influence other components of vocal displays, such as acoustic frequencies and bandwidths (Podos *et al.*, 2004; Huber & Podos, 2006; Derryberry *et al.*, 2012); however, these correlations have received mixed support from empirical studies (Palacios & Tubaro, 2000; Farnsworth & Lovette, 2005). There-

fore, the allometric relationship between body size, bill size, and bill shape could confound the correlations between mass and many of the song features presented here. Further studies that simultaneously consider both bill measurements and mass as independent variables may clarify whether morphological constraints imposed on vocal characters considered here are due to body size (i.e. syrinx size) or physiological constraints associated with larger, thicker bills.

THE EFFECT OF HABITAT ON SONGBIRD VOCALIZATIONS

Contrary to the evolutionary constraints that body size imposes on tanager vocalizations, our study suggests that acoustic signalling environments do not affect the majority of vocalization characters considered here. Only three out of ten vocal display characters demonstrated a statistically significant difference between habitat types. In addition, only one of these three characters followed the predictions of the AAH. Given the taxonomic breadth of our study (i.e., 10% of all songbirds) and our robust methodological framework, our findings suggest that acoustic differences between broad habitat categorizations (i.e., open vs. closed) do not impart strong selective pressures on the evolution of songbird vocalizations as predicted by the AAH. Although the AAH has a strong experimental underpinning (Endler, 1992), empirical evidence for the AAH within the sensory drive framework is undoubtedly mixed (reviewed in Ey & Fischer, 2009). Indeed, a meta-analysis conducted by Boncoraglio & Saino (2007) indicated that among studies of songbirds, only peak frequency consistently followed the directional predictions of the AAH. Despite an appreciable number of isolated studies that support the AAH, our study suggests that acoustic differences among open and closed environments do not cause predictable selective pressures on oscine vocalizations at larger taxonomic scales.

In concordance with the predictions of the AAH, we found that frequency shift rates are higher in non-forest than forest habitats. Rapid changes in frequency may be more difficult to perceive in habitats with denser vegetation, where increased obstruction and higher levels of background noise may reduce signal efficacy via low signal-to-noise ratios (Endler, 1992). In contrast, minimum and peak frequencies were lower in open habitats, which contradicts the predictions of the AAH. Previous studies have also uncovered conflicting evidence for the AAH in these and other characters. For example, maximum and peak frequencies were higher among New World doves in forest compared to non-forest habitat (Tubaro & Mahler, 1998), while Rufous-collared Spar-

rows sang faster trills in closed compared to open habitats (*Zonotrichia capensis*; Lijtmaer & Tubaro, 2007). Differences among microhabitats within broad habitat categorizations could account for some of the discrepancies among studies. For example, birds in forested habitats may sing from the tops of canopies with little vegetation, while in grasslands, birds may sing from within thick strands of scrubby vegetation. Thus, if either the signaler or the receiver of an acoustic signal occupies a microhabitat that differs in acoustic properties compared to other, nearby signalling environments, then the selective effects of signal propagation could be masked by broad categorizations of habitat.

ADDITIONAL SELECTIVE PRESSURES ON AVIAN VOCALIZATIONS

Avian vocalizations are influenced by many factors beyond habitat and morphology. Eavesdropping by unintended receivers, sexual selection, and cultural transmission are a few of many factors that also affect bird song evolution (Catchpole & Slater, 2008). Eavesdropping by predators and brood parasites may also influence acoustic signals (reviewed in Zuk *et al.*, 1996). Eavesdroppers that rely on auditory cues infer directionality from the result of the differences in phase, time of arrival, and amplitude between their ears (Marler, 1955). As a result, if eavesdroppers in closed habitats rely more on acoustic signalling than vision compared to open habitats, we might expect birds in forests to evolve higher frequency songs within narrower bandwidths to avoid detection by unintended receivers such as predators or brood parasites (Hale, 2004; Lima, 2009). While the AAH assumes that bird song is selected for maximum distance propagation, the cost of eavesdropping by predators and parasites might counteract the benefit of auditory signals reaching additional potential mates or rival conspecifics (Mougeot & Bretagnolle, 2000; Yasukawa *et al.*, 2009).

Sexual selection also influences the evolution of bird song (reviewed in Searcy & Andersson, 1986; Price, 1998). If mate choice varies between habitat types as a function of signal detectability and honesty (Schluter & Price, 1993), then the fitness benefits associated with sexual selection could overpower any selective pressures imposed by habitat. Sexual selection can also shape patterns of body size, especially sexual dimorphism (Fairbairn, 1997), and may indirectly affect evolutionary constraints on vocal displays. However, body size (and subsequently syrinx size) is likely under stronger developmental constraint than learned vocal behaviours (Frankino, 2005) such that interspecific differences in body mass may not be as strongly affected by sexual selection.

Thus, directional sexual selection is a potentially confounding factor that could result in either positive or negative support for the predictions of the AAH, depending on how mate choice for vocal characters and intrasexual competition vary among species and habitats.

The cultural transmission of learned songs from adult 'tutors' to young 'pupils' can also cause changes in avian vocalizations over time (Slater, 1986). If young birds preferentially learn songs that are less degraded by the environment, then cultural transmission could facilitate the development of acoustic adaptations (Hansen, 1979). Indeed, Peters, Derryberry & Nowicki (2012) recently found strong evidence that Swamp Sparrows (*Melospiza georgiana*) preferentially learn songs that are least perturbed by environmental degradation. If vocal learning increases the propensity to develop acoustic adaptations, then we may expect acoustic adaptations to be more prevalent among oscine than other birds that do not learn their songs. In contrast to these expectations, Boncoraglio & Saino (2007) found a weaker overall effect of habitat when considering oscines separately from all birds. Thus, the link between the cultural transmission of learned song and the development of acoustic adaptations remains unclear.

SUMMARY

Our study demonstrates that morphology has a strong impact on the evolution of vocal displays in a large, phenotypically diverse radiation of Neotropical songbirds, the tanagers. We find little evidence that differences among acoustic signalling environments have played an important role in shaping long-distance vocal displays in the evolutionary history of the tanagers. In contrast, body size appears to have played an important part in the evolution of thraupid songs. Future studies could expand upon the work presented here by considering the microhabitat (i.e., forest strata) where vocal displays take place or more specific categorizations of habitat beyond the broad-scale classification used here. Moreover, by simultaneously examining correlations between vocal displays and bill morphology in addition to body size, future studies could disentangle whether the strong correlations observed here are due to mechanical constraints associated with variation in bill size and shape or allometry.

ACKNOWLEDGEMENTS

We are very grateful towards M. Young and T. Bishop at the Macaulay Library for help with digitizing, accessing, and downloading recordings. We would like to thank A. Bernabe, D. Emmerson, J. L. Espinoza, H.

Macdonald, and C. Threlkeld for their assistance with collecting song data. We thank I. Lovette, R. Clark, P. Pryde, A. Shultz, P. Title, L. Klicka, S. Taylor, L. Campagna, P. Deane-Coe, Y. Kapetanakos, additional members of the Lovette Lab group, and three anonymous reviewers for valuable feedback on earlier versions of this manuscript. We are grateful towards B. Miner, who provided advice on statistical analyses. We thank M. Ferraro for drawing tanager portraits. This research was funded in part by the National Science Foundation (IBN-0217817, DEB-0315416, and DEB-1354006) and the National Geographic Society. For additional financial support, we are grateful to the CSU Sally Casanova Predoctoral Fellowship (NAM), the Crouch Scholarship for Avian Behavior (NAM), and the Mabel Meyers Memorial Scholarship (NAM).

REFERENCES

- Andersson M. 1994.** *Sexual selection*. Princeton: Princeton University Press.
- Aylor D. 1972.** Sound transmission through vegetation in relation to leaf area density, leaf width, and breadth of canopy. *The Journal of the Acoustical Society of America* **51**: 411–414.
- Badyaev AV, Leaf ES. 1997.** Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. *Auk* **114**: 40–46.
- Ballentine B. 2006.** Morphological adaptation influences the evolution of a mating signal. *Evolution* **60**: 1936–1944.
- Bertelli S, Tubaro P. 2002.** Body mass and habitat correlates of song structure in a primitive group of birds. *Biological Journal of the Linnean Society* **77**: 423–430.
- Blomberg S, Garland T Jr, Ives A. 2003.** Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.
- Boncoraglio G, Saino N. 2007.** Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Functional Ecology* **21**: 1–10.
- Bowman RI. 1979.** Adaptive morphology of song dialects in Darwin's finches. *Journal of Ornithology* **120**: 353–389.
- Bradbury JW, Vehrencamp SL. 2011.** *Principles of animal communication*. Sunderland: Sinauer Associates, Inc.
- Burnham KP, Anderson DR, Huyvaert KP. 2011.** AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* **65**: 23–35.
- Burns KJ, Hackett S, Klein NK. 2002.** Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. *Evolution* **56**: 1240–1252.
- Burns KJ, Hackett SJ, Klein NK. 2003.** Phylogenetic relationships of Neotropical honeycreepers and the evolution of feeding morphology. *Journal of Avian Biology* **34**: 360–370.
- Burns KJ, Shultz AJ, Title PO, Mason NA, Barker FJ, Klicka J, Lanyon SM, Lovette IJ. 2014.** Phylogenetics

- and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. *Molecular Phylogenetics and Evolution* **75**: 41–77.
- Butler M, King A. 2004.** Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *The American Naturalist* **164**: 683–695.
- Byers BE. 2006.** Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behavioral Ecology* **18**: 130–136.
- Catchpole CK, Slater PJB. 2008.** *Bird song: biological themes and variations*. Cambridge: Cambridge University Press.
- Clements JF, Schulenberg TS, Iliff MJ, Sullivan B, Wood CL, Roberson D. 2013.** *The Clements checklist of birds of the world: version 6.7*. Ithaca: Cornell University Press.
- Derryberry E. 2009.** Ecology shapes birdsong evolution: variation in morphology and habitat explains variation in white-crowned sparrow song. *American Naturalist* **174**: 24–33.
- Derryberry EP, Seddon N, Claramunt S, Tobias JA, Baker A, Aleixo A, Brumfield RT. 2012.** Correlated evolution of beak morphology and song in the Neotropical woodcreeper radiation. *Evolution* **66**: 2784–2797.
- Dunning JBJ. 2007.** *CRC handbook of avian body masses, 7th edn*. Boca Raton: CRC Press.
- Endler JA. 1992.** Signals, signal conditions, and the direction of evolution. *American Naturalist* **139**: S125–S153.
- Ey E, Fischer J. 2009.** The ‘acoustic adaptation hypothesis’ – a review of the evidence from birds, anurans and mammals. *Bioacoustics* **19**: 21–48.
- Fairbairn DJ. 1997.** Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**: 659–687.
- Farnsworth A, Lovette IJ. 2005.** Evolution of nocturnal flight calls in migrating wood-warblers: apparent lack of morphological constraints. *Journal of Avian Biology* **36**: 337–347.
- Farnsworth A, Lovette IJ. 2008.** Phylogenetic and ecological effects on interspecific variation in structurally simple avian vocalizations. *Biological Journal of the Linnean Society* **94**: 155–173.
- Forrest TG. 1994.** From sender to receiver – propagation and environmental-effects on acoustic-signals. *American Zoology* **34**: 644–654.
- Frankino WA. 2005.** Natural selection and developmental constraints in the evolution of allometries. *Science* **307**: 718–720.
- Freckleton RP. 2009.** The seven deadly sins of comparative analysis. *Journal of Evolutionary Biology* **22**: 1367–1375.
- Garland T, Harvey PH, Ives AR. 1992.** Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**: 18–32.
- Grafen A. 1989.** The phylogenetic regression. *Philosophical Transactions of the Royal Society B: Biological Sciences* **326**: 119–157.
- Hale A. 2004.** Predation risk associated with group singing in a Neotropical wood-quail. *The Wilson Bulletin* **116**: 167–171.
- Hansen P. 1979.** Vocal learning – its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Animal Behavior* **27**: 1270–1271.
- Hansen TF. 1997.** Stabilizing selection and the comparative analysis of adaptation. *Evolution* **51**: 1341–1351.
- Hansen TF, Martins EP. 1996.** Translating between microevolutionary process and macroevolutionary patterns: the correlation structure of interspecific data. *Evolution* **50**: 1404–1417.
- Huber SK, Podos J. 2006.** Beak morphology and song features covary in a population of Darwin’s finches (*Geospiza fortis*). *Biological Journal of the Linnean Society* **88**: 489–498.
- Isler M, Isler P. 1999.** *The tanagers*. Washington: Smithsonian.
- Jones KE, Purvis A. 1997.** An optimum body size for mammals? Comparative evidence from bats. *Functional Ecology* **11**: 751–756.
- Kirschel A, Blumstein D, Smith T. 2009.** Character displacement of song and morphology in African tinkerbirds. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 8256–8261.
- Kroodsma D. 2005.** *The singing life of birds*. Boston: Houghton Mifflin Harcourt.
- Lijtmaer DA, Tubaro PL. 2007.** A reversed pattern of association between song dialects and habitat in the rufous-collared sparrow. *The Condor* **109**: 658–667.
- Lima SL. 2009.** Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* **84**: 485–513.
- Linskens HF, Martens M, Hendriksen H, Roestenberg-Sinnige AM, Brouwers W, Van Der Staak A, Strik-Jansen AM. 1976.** The acoustic climate of plant communities. *Oecologia* **23**: 165–177.
- Marler P. 1955.** Characteristics of some animal calls. *Nature* **176**: 6–8.
- Marten K, Marler P. 1977.** Sound transmission and its significance for animal vocalization. I. *Temperate Habitats. Behavioral Ecology and Sociobiology* **2**: 271–290.
- Martins EP, Hansen TF. 1997.** Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* **149**: 646–667.
- Mason NA, Burns KJ. 2013.** Molecular phylogenetics of the Neotropical seedeaters and seed-finches (*Sporophila*, *Oryzoborus*, *Dolospingus*). *Ornitología Neotropical* **24**: 139–155.
- Mason NA, Shultz AJ, Burns KJ. 2014.** Elaborate visual and acoustic signals evolve independently in a large, phenotypically diverse radiation of songbirds. *Proceedings of the Royal Society of London, Series B Biological Sciences* **281**: 20140967.
- Mindlin GB, Laje R. 2005.** *The physics of birdsong*. New York: Springer.
- Morton E. 1975.** Ecological sources of selection on avian sounds. *The American Naturalist* **109**: 17–34.
- Morton ES. 1986.** Predictions from the ranging hypothesis for the evolution of long-distance signals in birds. *Behaviour* **99**: 65–86.

- Mougeot F, Bretagnolle V. 2000.** Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. *Animal Behaviour* **60**: 647–656.
- Nowicki S. 1987.** Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. *Nature* **325**: 53–55.
- Oberweger K, Goller F. 2001.** The metabolic cost of birdsong production. *Journal of Experimental Biology* **204**: 3379–3388.
- Pagel M. 1999.** Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.
- Palacios M, Tubaro P. 2000.** Does beak size affect acoustic frequencies in woodcreepers? *Condor* **102**: 553–560.
- Parker TA, III, Stotz DF, Fitzpatrick JW. 1996.** Ecological and distributional databases. In: Stotz DF, Fitzpatrick JW, Parker TA III, Moskovits DK, eds. *Neotropical birds: ecology and conservation*. Chicago: University of Chicago Press, 131–191.
- Peters S, Derryberry EP, Nowicki S. 2012.** Songbirds learn songs least degraded by environmental transmission. *Biology Letters* **8**: 736–739.
- Podos J. 2001.** Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* **409**: 185–188.
- Podos J, Huber S, Taft B. 2004.** Bird song: the interface of evolution and mechanism. *Annual Reviews of Ecology and Systematics* **35**: 55–87.
- Podos J, Nowicki S. 2004.** Beaks, adaptation, and vocal evolution in Darwin's finches. *Bioscience* **54**: 501–510.
- Price JJ, Friedman NR, Omland KE. 2007.** Song and plumage evolution in the New World orioles (*Icterus*) show similar lability and convergence in patterns. *Evolution* **61**: 850–863.
- Price T. 1998.** Sexual selection and natural selection in bird speciation. *Philosophical Transactions: Biological Sciences* **353**: 251–260.
- Revell LJ. 2009.** Size-correction and principal components for interspecific comparative studies. *Evolution* **63**: 3258–3268.
- Richards DG, Wiley RH. 1980.** Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *American Naturalist* **115**: 381–399.
- Ridgely RS, Tudor G. 1989.** *Field guide to the songbirds of South America: the passerines*. Austin: University of Texas Press.
- Riede T, Suthers RA, Fletcher NH, Blevins WE. 2006.** Songbirds tune their vocal tract to the fundamental frequency of their song. *Proceedings of the National Academy of Sciences of the United States of America* **103**: 5543–5548.
- Ruegg K, Slabbekoorn H, Clegg S, Smith TB. 2006.** Divergence in mating signals correlates with ecological variation in the migratory songbird, Swainson's thrush (*Catharus ustulatus*). *Molecular Ecology* **15**: 3147–3156.
- Ryan MJ, Brenowitz EA. 1985.** The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist* **126**: 87–100.
- Schluter D, Price T. 1993.** Honesty, perception and population divergence in sexually selected traits. *Proceedings of the Royal Society of London, Series B Biological Sciences* **253**: 117–122.
- Searcy WA, Andersson M. 1986.** Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics* **17**: 507–533.
- Shultz AJ, Burns KJ. 2013.** Plumage evolution in relation to light environment in a novel clade of Neotropical tanagers. *Molecular Phylogenetics and Evolution* **66**: 112–125.
- Shy E. 1983.** The relation of geographical variation in song to habitat characteristics and body size in North American tanagers (Thraupinae: *Piranga*). *Behavioral Ecology and Sociobiology* **12**: 71–76.
- Shy E. 1984.** Habitat shift and geographical variation in North American tanagers (Thraupinae: *Piranga*). *Oecologia* **63**: 281–285.
- Sibley DA, Monroe BL Jr. 1990.** *Distribution and Taxonomy of the Birds of the World*. New Haven: Yale University Press.
- Slabbekoorn H, Smith T. 2002.** Bird song, ecology and speciation. *Philosophical Transactions: Biological Sciences* **357**: 493–503.
- Slater PJ. 1986.** The cultural transmission of bird song. *Trends in Ecology and Evolution* **1**: 94–97.
- Sueur J, Aubin T, Simonis C. 2008.** Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics* **18**: 213–226.
- Tobias J, Aben J, Brumfield R, Derryberry E, Halfwerk W, Slabbekoorn H, Seddon N. 2010.** Song divergence by sensory drive in Amazonian birds. *Evolution* **64**: 2820–2839.
- Tobias JA, Brawn JD, Brumfield R, Derryberry EP, Kirschel AN, Seddon N. 2012.** The importance of subsong birds as study systems in ecology and evolution. *Ornitologia Neotropical* **23**: 259–272.
- Tobias JA, Gamarra-Toledo V, García-Olaechea D, Pulgarín PC, Seddon N. 2011.** Year-round resource defence and the evolution of male and female song in subsong birds: social armaments are mutual ornaments. *Journal of Evolutionary Biology* **24**: 2118–2138.
- Touchton JM, Seddon N, Tobias JA. 2014.** Captive rearing experiments confirm song development without learning in a tracheophone subsong bird. *PLoS ONE* **9**: e95746.
- Tubaro P, Mahler B. 1998.** Acoustic frequencies and body mass in New World doves. *The Condor* **100**: 54–61.
- Wallschläger D. 1980.** Correlation of song frequency and body weight in passerine birds. *Cellular and Molecular Life Sciences* **36**: 412–412.
- Weir JT, Wheatcroft DJ, Price TD. 2012.** The role of ecological constraint in driving the evolution of avian song frequency across a latitudinal gradient. *Evolution* **66**: 2773–2783.
- Wiley RH. 1991.** Associations of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist* **138**: 973–993.
- Wiley RH, Richards DG. 1978.** Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* **3**: 69–94.

- Yasukawa K, Enstrom DA, Parker PG, Jones TC. 2009.** Epaulet color and sexual selection in the red-winged blackbird: a field experiment. *The Condor* **111**: 740–751.
- Zuk M, Bryant MJ, Kolluru GR, Mirmovitch V. 1996.** Trade-offs in parasitology, evolution and behavior. *Parasitology Today* **12**: 46–47.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Histogram of masses for 305 species of tanagers considered in this study.

Table S1. Habitat designations for each of the 305 species of tanagers analyzed in this study.

Table S2. Results from phylogenetic generalized least squares analyses of competing models ($\Delta\text{AIC}_C < 7$) that were not the best-fit model for each character considered. Results are averaged over 50 trees sampled from the posterior distribution. The ΔAIC_C column indicates the difference in model performance between each competing model and the best-fit model for that character (Table 4). The 'model' column indicates whether a PGLS model with species assigned to a simplified habitat designation (habsimp; in which only 'open' (O) and 'closed' (C) categories are included) was preferred to the inclusion of an additional category for species in edge (E) habitats (habedge). Models that include an asterisk include an interaction effect between habitat type and mass. The branch length transformation that was applied as part of the best-fit model is indicated alongside the corresponding parameter (either Pagel's λ or α). The effect size and its standard error are represented by β , while the statistical significance of each effect is indicated by the presence or absence of asterisks (*, **, and ***) indicate $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively).