

VOCAL GEOGRAPHIC VARIATION IN MESOAMERICAN COMMON BUSH TANAGERS (*CHLOROSPINGUS OPHTHALMICUS*)

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ABSTRACT.—We studied patterns of geographic variation in the fine structural characteristics of the songs of five recognized subspecies of Common Bush Tanagers (*Chlorospingus ophthalmicus*) in Mesoamerica to examine whether songs vary with geography. Multivariate analyses (PCA and DFA), based on 11 fine structural characteristics of the songs provided similar results indicating that both *albifrons* and *regionalis* had unique songs significantly different from the rest of the subspecies. Conversely, *ophthalmicus*, *dwighti*, and *postocularis* had similar song characteristics, regardless of restricted gene flow and substantial morphological variation reported in previous studies. Our findings suggest there is a possible relationship between the length of isolation and variation in songs of *albifrons* and *regionalis*, whereas the lack of divergence in songs of *ophthalmicus*, *dwighti*, and *postocularis* suggests some of these forms have not diverged vocally, and vocal traits may be evolutionary conserved. Received 27 March 2012. Accepted 27 September 2012.

Key words: acoustic variation, *Chlorospingus ophthalmicus*, cloud forest, conserved vocal traits, geographic variation.

The study of geographic variation in morphological and genetic characters in birds, and the exploration of the possible causes of the variation, is a well-established area of research (e.g., Zink and Remsen 1986, Brumfield and Remsen 1996, Cicero and Johnson 2006). Similarly, behavioral characters such as bird songs show substantial geographic variation in acoustic features among and within taxa (Mundinger 1982). Variation in song attributes may arise from evolutionary processes such as: genetic or cultural mutations because of isolation (cultural and genetic drift; Baker 1996, Podos et al. 2004a), different mechanisms of sexual selection driven by female choice or male-male competition (reviewed by Podos et al. 2004a), and adaptive responses to local ecological conditions such as habitat structure (Slabbekoorn and Smith 2002, Tubaro and Lijtmaer 2006), given that environmental factors are known to influence variation in birdsong by constraining sound transmission (Tubaro and Segura 1995). Thus, variation in songs could occur as a response to different selection pressures or by neutral processes, and may provide insight into the factors driving the evolution of acoustic

signals (Shy 1983, Peters et al. 2000, Sosa-López et al. in press).

The Common Bush Tanager (*Chlorospingus ophthalmicus*) species complex is disjunctly distributed in fragmented cloud forest patches extending from southern Mexico to northwestern Argentina. Previous genetic and phenotypic studies have demonstrated restricted gene flow and substantial morphological variation between currently recognized subspecies (Isler and Isler 1987, Sánchez-González et al. 2007, Bonaccorso et al. 2008, Weir et al. 2008). This variation has resulted in recognition of 27 subspecies (Gill and Donsker 2012) with each subspecies primarily restricted to a single patch of cloud forest in the major mountain ranges of the Neotropics. This noticeable divergence between populations or subspecies is likely a result of a combination of the natural fragmented distribution of cloud forests along with paleoecological and colonization events (Peterson et al. 1992, García-Moreno et al. 2004, Sánchez-González et al. 2007, Bonaccorso et al. 2008, Weir et al. 2008). Populations of each area may have evolved in isolation and have unique combinations of genetic and morphological features (Bonaccorso et al. 2008, Weir et al. 2008). This long-term isolation has likely produced variation in most sets of attributes of the populations, including song (Koetz et al. 2007a, b).

The genetic and morphological divergence described is remarkable for Mesoamerican populations, where at least eight genetically distinct populations have been identified with a clear separation between taxa distributed to the west and east of the Isthmus of Tehuantepec (García-Moreno

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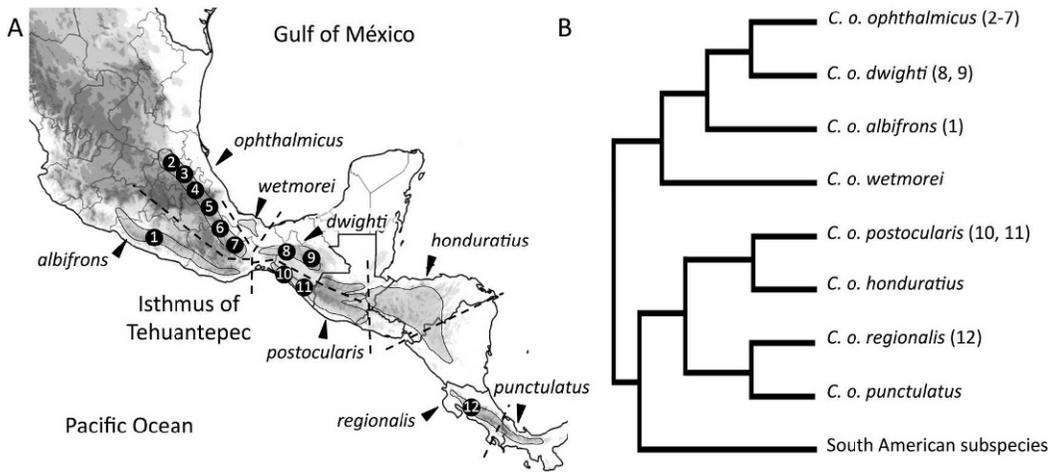


FIG. 1. Distribution and phylogenetic relationships of Common Bush Tanagers. (A) Recording locations in Mexico and Central America. The outlined areas indicate the distribution of Common Bush Tanagers in Mesoamerica, whereas dashed lines indicate subspecies boundaries. The subspecies *wetmorei*, *honduratus*, and *novicius* are not included in the analysis. (B) Generalized phylogeny of Middle American *C. ophthalmicus* modified from Weir et al. (2008) and Bonaccorso et al. (2008); localities with songs sampled for each taxon in parentheses.

et al. 2004, Bonaccorso et al. 2008, Weir et al. 2008; Fig. 1). Several studies suggest songs of Common Bush Tanagers show obvious variation among subspecies, but no study has been conducted to examine this variation (Isler and Isler 1987, Cadena et al. 2007; Fig. 2).

We explored the patterns of geographic variation in the fine structural characteristics of the song of five subspecies of Common Bush Tanagers from Mesoamerica, and discuss whether song variation resembles allopatric populations and patterns of genetic variation reported in previous studies (Bonaccorso et al. 2008, Weir et al. 2008). Analyses of song variation in long-isolated neotropical cloud forest bird populations are necessary to complement our understanding of the geographic patterns and speciation processes that have shaped the patterns of bird diversity (Alström and Ranft 2003).

METHODS

Study Species, Locations, and Recordings.—We analyzed songs of populations representing five of the eight subspecies of Common Bush Tanagers from Mesoamerica (Fig. 1A): *C. o. ophthalmicus* (mountains of the Atlantic Slope of Mexico from San Luis Potosí to Veracruz and Oaxaca); *C. o. albifrons* (Sierra Madre del Sur of the Pacific Slope from Guerrero to Oaxaca); *C. o. dwighti* (mountains of the Caribbean Slope of Chiapas, Mexico, and adjacent Guatemala); *C. o. postocularis*

(Pacific Slope of Chiapas, Mexico, and Guatemala); and *C. o. regionalis* (Nicaragua and Eastern Costa Rica), all of which have been previously described as genetically distinctive populations (Bonaccorso et al. 2008, Weir et al. 2008). The best supported phylogenetic hypothesis of the relationships in this species complex indicates the existence of three monophyletic groups corresponding to subspecies in South America, Central America, and Mexico, while those in South America are more closely related to those in Central America than to those in Mexico (Weir et al. 2008, Fig. 1B).

We included songs from 17 localities representing five of the eight recognized subspecies of Common Bush Tanagers in Mesoamerica. Individuals were recorded at 10 cloud-forest sites across Mexico in 2003, 2005, 2007, and 2010 (Fig. 1A; Appendix) using a Marantz PMD-430 tape recorder and an Audio-Technica AT835 microphone. We obtained recordings year-round during ground surveys of suitable habitat at each locality, usually from 0700 to 1100 and 1600 to 1800 hrs (CST). Previous observations suggest Common Bush Tanagers in Central and South America have a dawn chorus behavior, starting to sing shortly after first light (Isler and Isler 1987, Cadena et al. 2007). Our first recordings of the day were generally obtained between 10 min before sunrise and 45 min after sunrise. We believe we detected the full-spectrum of songs that the populations express throughout the day,

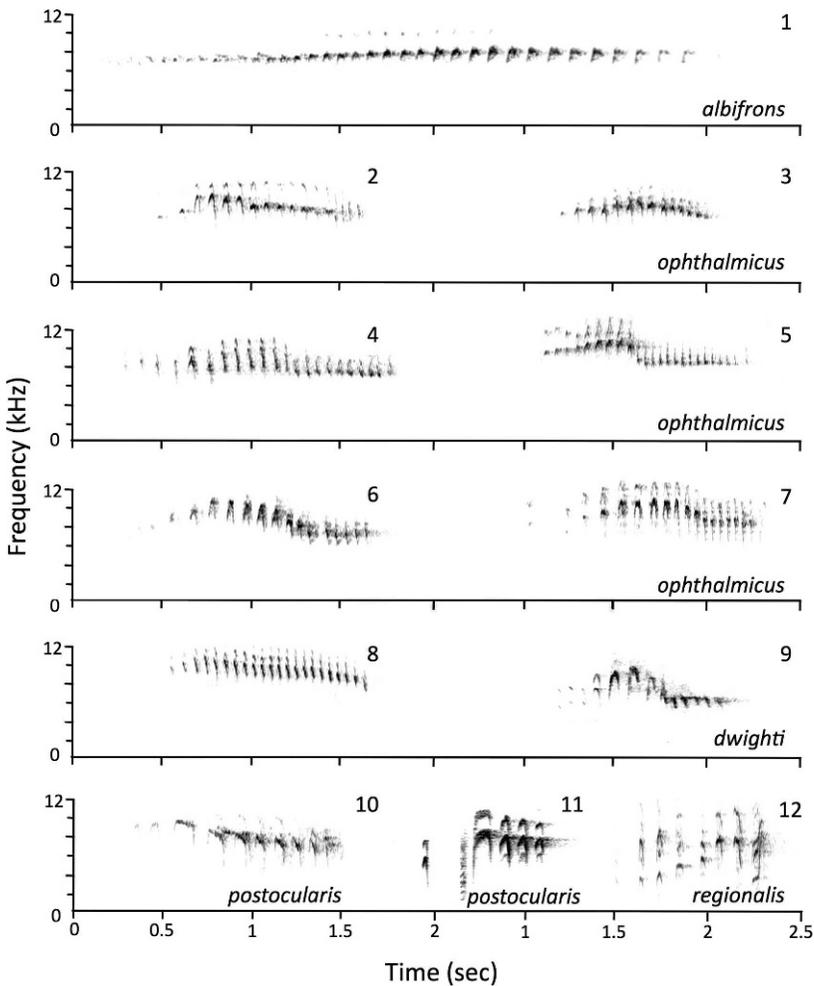


FIG. 2. Sound spectrograms showing the variation in songs of Common Bush Tanagers. A representative song is presented as a spectrogram for each recording locality. Numbers refer to localities in Figure 1.

including the dawn chorus. We prevented recording individuals on multiple occasions by moving 1–2 km in different directions each day. We also obtained recordings from seven localities archived in libraries of natural sounds and from private recording collections (Fig. 1A; Appendix). We only used library and private recordings made on different dates to avoid analyzing multiple recordings from the same individual.

Song Measures.—We digitized recordings (44.1 kHz, 16-bit) using CANARY, Version 1.2.4 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Spectrograms were also produced in CANARY (filter bandwidth 699.40 Hz, overlap 98.44%, FFT size 2040). We measured 11 acoustic variables (Fig. 3). A first set of variables focused

on general patterns of the song: (1) number of notes (NN), (2) song length (SL), (3) highest frequency (HF), (4) lowest frequency (LF), (5) frequency range (FR), and (6) rate of note delivery (SR; number of notes/song length). We then selected the note with the maximum relative amplitude in each song, and measured (7) time of the maximum relative amplitude (PT; number of seconds between song onset and moment of peak amplitude), (8) initial frequency of the note with the maximum relative amplitude (IFN), (9) middle frequency of the note with the maximum relative amplitude (the frequency at the mid-point duration of the note with the maximum relative amplitude, MFN), (10) final frequency of the note with the maximum relative amplitude

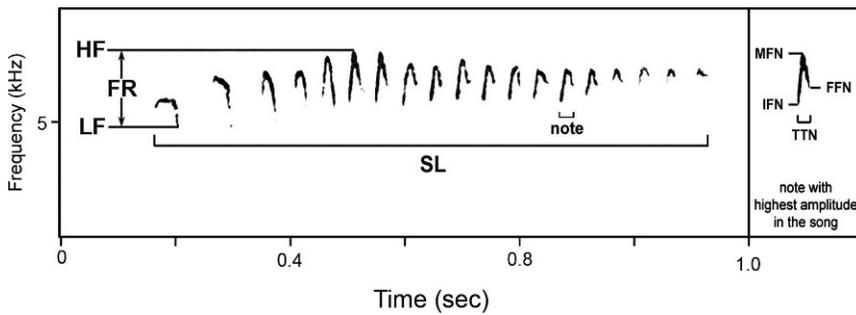


FIG. 3. Sample spectrogram of a Common Bush Tanager song showing the variables measured for the analyses. SL = song length; LF = lowest frequency; HF = highest frequency; FR = frequency range; IFN = initial frequency of the note with the maximum relative amplitude; MFN = middle frequency of the note with the maximum relative amplitude; FFN = final frequency of the note with the maximum relative amplitude; TTN = total duration of the note with the maximum relative amplitude.

(FFN), and (11) total duration of the note with the maximum relative amplitude (TTN). Studies of other *Chlorospingus* (*C. semifuscus*; Bohórquez and Stiles 2002) suggest males consistently sing more often than females. However, we analyzed all vocalizations together because of the absence of sexual dimorphism, the evidence that both males and females sing (Moynihan 1962), and the inability to distinguish between sexes by vocal or behavioral differences.

Statistical Analyses.—We measured multiple songs for each individual (range = 1–18; depending on the number of available songs for each individual) and used mean values for each variable across all recorded songs of a particular individual to avoid pseudoreplication. Continuous data were $\log(x + 1)$ transformed and discontinuous data were square-root $(x + 0.5)$ transformed to improve normality.

We assessed whether there are differences between songs of Common Bush Tanager populations and estimated overall song differences between subspecies by reducing the number of variables using a principal component analysis (PCA). We computed a multivariate analysis of variance (MANOVA) using factor scores from the PCA with eigenvalues > 1 as dependent variables, and subspecies as the independent variables. We computed a planned comparison *post-hoc* analysis between the five subspecies using the Bonferroni correction.

We performed a discriminant function analysis (DFA) based on acoustic measurements. Our objectives were to examine whether individuals could be discriminated by subspecies and to describe the variables explaining the variation. We

report the results of the cross-validation analysis, where each case is classified by the functions derived from all cases other than that case.

We calculated the variance-inflation factors (VIF) of the variables to estimate whether variables were highly correlated, because principal component and discriminant function analyses are affected by excessive multicollinearity between variables (Garson 2012a, b). VIF analysis indicated some variables were highly correlated (values > 4 would indicate an excess of correlation; Garson 2012c, data not shown). However, VIF does not indicate the variables that are highly correlated and we performed a pair-wise Pearson correlation analysis between all variables to identify pairs of variables with high correlation. We eliminated variables that were correlated in multiple instances with an index above 0.7, trying to eliminate as few variables as possible. Those variables were song length (SL), frequency range (FR), and final frequency of the note with maximum relative amplitude (FFN). We re-estimated the variance-inflation factors (VIF) for the remaining variables and none had values > 4 . Analyses were performed in PASW statistics 18.0 for Mac (SPSS Institute Inc., Chicago, IL, USA).

RESULTS

We analyzed 263 recordings of Common Bush Tanagers that met our criteria for inclusion in the analysis. These recordings corresponded to 93 individual birds (1–18 songs/bird), representing five of the eight subspecies in Mesoamerica (Fig. 1; Appendix). Individuals in Mexico sang persistently during the morning after sunrise and less frequently at sunset at all sites. Singing individuals were

TABLE 1. Principal component analysis of songs of Common Bush Tanagers. PCA rotated factor loadings are provided for each component.

Variables	Principal component ^a		
	I	II	III
Number of notes (NN)	0.254	0.875 ^b	-0.053
Highest frequency (HF)	0.455	-0.619	0.100
Lowest frequency (LF)	0.693	0.262	-0.105
Rate of note delivery (SR)	0.247	-0.052	-0.883 ^b
Time of the maximum relative amplitude (PT)	0.042	0.787 ^b	0.408
Initial frequency of the note with the maximum relative amplitude (IFN)	0.875 ^b	0.092	-0.196
Middle frequency of the note with the maximum relative amplitude (MFN)	0.869 ^b	-0.230	0.098
Total duration of the note with the maximum relative amplitude (TTN)	0.067	0.046	0.839 ^b
Eigenvalues	2.4	2.0	1.4
Percent of total variation	30.5	25.2	18.7

^a Principal component analysis was based on a correlation matrix, and factors were rotated using the method *Varimax*.

^b Variables explaining most of the variation in each component.

detected year-round, encompassing both the breeding (Mar–Jun, pers. obs.) and non-breeding seasons. Individuals were frequently observed in pairs during the peak of the breeding season, and in groups of 3–5 birds (presumably family groups) towards the end of the breeding season. Individuals were also observed in small numbers in mixed-species flocks throughout the year.

Common Bush Tanagers showed a complex pattern of spatial variation in song characteristics (Fig. 2). The PCA resulted in three principal components (PC) explaining 74.5% of the total variation (Table 1). Principal component I mainly explained variation in the initial frequency of the note with the maximum relative amplitude (IFN) and the middle frequency of the note with the maximum relative amplitude (MFN); PC II mainly explained variation in number of notes (NN) and time of the maximum relative amplitude (PT); and PC III mainly explained variation in rate of note delivery (SR) and total duration of the note with the maximum relative amplitude (TTN). Multiple analyses of variance revealed significant differences among subspecies (Wilks' Lambda = 28, df = 12, 227.8; $P < 0.001$). The first three principal components showed significant variation between subspecies ($F = 14.1$, $P < 0.001$; $F = 32.8$, $P < 0.001$; $F = 16.2$, $P < 0.001$; respectively); the comparison analysis of the five subspecies showed significant differences between *albifrons* and the rest of the subspecies in PC I, and *regionalis* and the rest of the subspecies in PC II (Fig. 4).

The discriminant function analysis (DFA) explained 91.3% of total variance with the first two canonical functions (Wilks' Lambda = 0.005, df = 32, $P < 0.001$; Table 2). The canonical discriminant function 1 mainly explained variation in the number of notes (NN) and the time of the maximum relative amplitude (PT); whereas canonical discriminant function 2 mainly explained variation in rate of note delivery (SR), lowest frequency (LF), and initial frequency (IFN) and total duration (TTN) of the note with the maximum relative amplitude. The first two canonical functions in multivariate space showed two defined groups, where *albifrons* is separated from all the other overlapping groups (Fig. 5). The cross-validation analysis correctly classified 64.5% of all songs and confirmed the observed pattern. The subspecies *albifrons* was the only category for which the analysis correctly classified 100% of the songs, having a larger number of notes (NN), and a longer time to the maximum relative amplitude (PT); none of the songs from the other groups was classified as *albifrons*. The discriminant function analysis also discriminated between *ophthalmicus* and *regionalis*, where *ophthalmicus* had a larger rate of note delivery and higher lowest frequency (Table 3); however, there was no clear classification pattern for the rest of the subspecies (Table 3).

DISCUSSION

We studied patterns of geographic variation in the songs of five Mesoamerican Common Bush Tanager subspecies in Mexico and Costa Rica. Our observations suggest that individuals from all

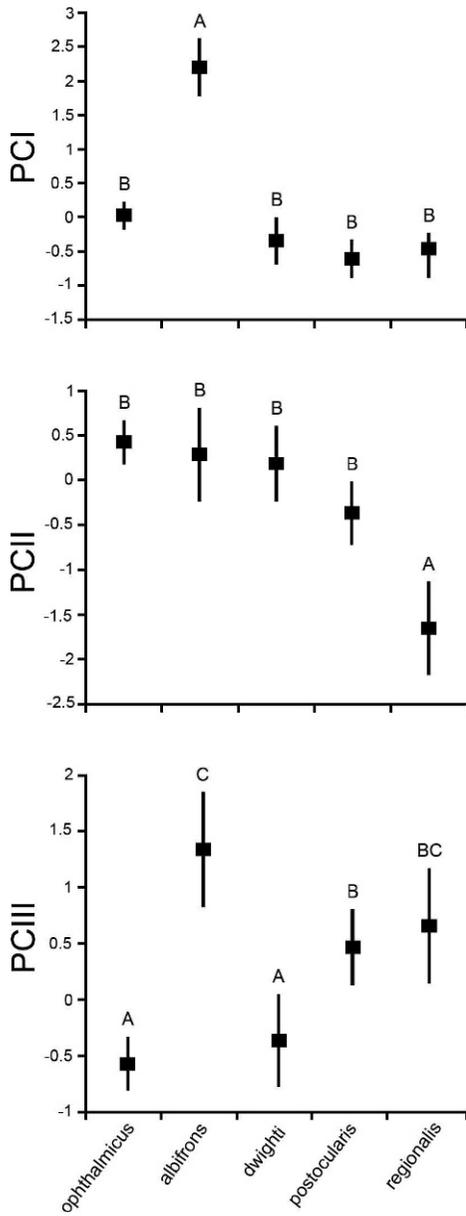


FIG. 4. Means of the first three principal components by subspecies of songs of Common Bush Tanagers. Columns sharing letters are not significantly different. Boxes show means and lines indicate the 95% confidence interval.

subspecies recorded in the field have a dawn chorus behavior (except for populations from Costa Rica, where recordings were gathered from libraries and private collections), singing right after sunrise. Individuals recorded in Mexico sang

TABLE 2. Correlations between discriminating variables and standardized canonical discriminant functions of songs of Common Bush Tanagers.

Variables	Canonical discriminant function	
	1	2
Number of notes (NN)	0.637 ^a	-0.035
Highest frequency (HF)	-0.149	0.196
Lowest frequency (LF)	0.412	0.456 ^a
Rate of note delivery (SR)	0.045	0.580 ^a
Time of the maximum relative amplitude (PT)	0.466 ^a	-0.375
Initial frequency of the note with the maximum relative amplitude (IFN)	0.208	0.439 ^a
Middle frequency of the note with the maximum relative amplitude (MFN)	0.131	0.282
Total duration of the note with the maximum relative amplitude (TTN)	-0.015	-0.405 ^a
Eigenvalues	3	1.9
Percent of total variation	55.2	36.1

^a Largest absolute correlations between each variable and any discriminant function.

all day long in contrast to Common Bush Tanagers from Central and South America (Isler and Isler 1987, Cadena et al. 2007). Our analyses of the fine structural characteristics of songs yielded similar results using two different approaches indicating that both *albifrons* and *regionalis* had unique songs significantly different from the rest of the subspecies. Conversely,

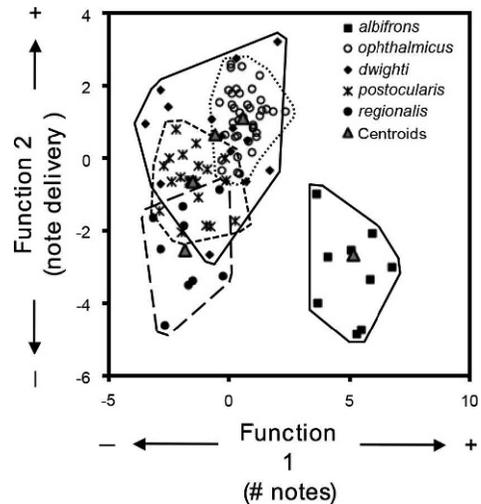


FIG. 5. Multidimensional representation of songs from five subspecies of Common Bush Tanagers. The first two canonical functions of the discriminant function analysis are shown (DFA).

TABLE 3. Predicted group classification from the discriminant function analysis of songs of Common Bush Tanagers. Values are the result of cross-validation analysis.

Subspecies	Number of songs classified into each subspecies					Total number of songs analyzed
	<i>albifrons</i>	<i>ophthalmicus</i>	<i>dwighti</i>	<i>postocularis</i>	<i>regionalis</i>	
<i>albifrons</i>	9	0	0	0	0	9
<i>ophthalmicus</i>	0	31	8	1	0	40
<i>dwighti</i>	0	9	1	3	1	14
<i>postocularis</i>	0	1	4	14	2	21
<i>regionalis</i>	0	0	1	3	5	9

ophthalmicus, *dwighti*, and *postocularis* shared similar song characteristics.

Previous studies reported that songs sung at dawn by Common Bush Tanagers from Costa Rica and South America have variable and distinctive traits, markedly distinct from vocalizations performed throughout the day (Isler and Isler 1987, Cadena et al. 2007). However, we found that songs detected immediately after sunrise (presumably dawn chorus songs) were similar to those songs recorded later during the day. This observation was based on visual analysis of hundreds of spectrograms; further studies are needed to understand whether Mexican populations of Common Bush Tanagers exhibit a structurally distinctive dawn song.

We found that both *albifrons* and *regionalis* have songs significantly different from each other, and from all other subspecies. The patterns of variation in songs of these subspecies reflect patterns of genetic divergence (García-Moreno et al. 2004, Bonaccorso et al. 2008, Weir et al. 2008). Genetic analyses suggest the subspecies *albifrons* inhabiting a group of mountains in the Sierra Madre del Sur has been isolated for a long period of time. Similar patterns of strong genetic differentiation have been reported in other taxa distributed within this area (e.g., Navarro-Sigüenza et al. 2008, Puebla-Olivares et al. 2008). Genetic analyses suggest the subspecies *regionalis*, in contrast, has diverged more recently (Bonaccorso et al. 2008, Weir et al. 2008; Fig. 1B). Our results, despite significant differences in song traits, showed that *regionalis* shared some vocal traits with *postocularis*, *dwighti*, and *ophthalmicus*. Thus, the congruence between genetic and vocal divergence in *albifrons* and *regionalis* suggests the extent of differentiation for multiple traits is related to the period of isolation (long vs. recent). Similar patterns of song divergence have been reported for isolated

South American populations of Common Bush Tanagers (Cadena et al. 2007). The relevance of vicariant isolation in the evolution of strong song divergence has also been documented in other montane birds (e.g., *Cistothorus* wrens, Kroodsma et al. 2001; *Prionodura* bowerbirds, Westcott and Kroon 2002; *Catharus gracilirostris*, Sánchez-Morales 2005; *Orthonyx chowchillas*, Koetz et al. 2007a). Under this scenario, novel acoustic traits could evolve by cultural drift, acoustic adaptation to habitat, natural selection, and/or sexual selection after an isolation event (Morton 1975, Wiley 1991, Grant and Grant 2002, Podos et al. 2004b).

The sister subspecies *ophthalmicus* and *dwighti* shared similar song features with the more distantly related subspecies *postocularis*, despite the limited gene flow between them (Bonaccorso et al. 2008, Weir et al. 2008; Fig. 1B). Patterns of vocal variation suggest these forms have not diverged vocally and the fine structural characteristics of songs are probably conserved. This may indicate the three subspecies possess songs or vocal traits that were sung by ancestral populations of Common Bush Tanagers (Podos 1997, Price and Lanyon 2002). Alternatively, cultural selection through acoustic adaptation to similar habitats in combination with the length of isolation between both *postocularis-dwighti* and *ophthalmicus*, suggest similar songs could be achieved through convergence (e.g., Morton 1975, Wiley 1991). The lack of data, however, does not allow drawing definitive conclusions, and song recordings from isolated and poorly sampled populations (i.e., *honduratus*, *punctulatus*, and *wetmorei*) are needed.

Whether South and North American populations of Common Bush Tanagers have different song traits is unknown. Common Bush Tanagers from Colombia have similar structural characteristics to the songs sung by birds from Mexico and

Central America. In general, songs start with a series of notes at a low rate of repetition, and then switch to an accelerated series of notes towards the end of the song (Fig. 2; see subspecies *flavopectus* and *nigriceps* from Colombia, figures 3–4 in Cadena et al. 2007). Despite similarity in song structure, songs of *flavopectus* and *nigriceps* are longer, and are sung at lower frequencies than songs of Common Bush Tanagers from Mexico and Central America (Cadena et al. 2007). These differences are more noticeable when comparing Mesoamerican populations with the subspecies *jacqueti* (Fig. 5 in Cadena et al. 2007), whose vocalization is a monotonic repetition of the same note, and lack the trills observed in *flavopectus* and *nigriceps*.

Spatial patterns of vocal variation in Mesoamerican Common Bush Tanagers are complex, and the framework of conditions in which geographic variation of song arises is intricate with some subspecies showing unique traits and others showing shared traits. Further research is needed to understand the mechanisms underlying vocal evolution of Mesoamerican Common Bush Tanagers.

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LITERATURE CITED

- ALSTRÖM, P. AND R. RANFFT. 2003. The use of sounds in avian systematics and the importance of bird sound archives. *Bulletin of the British Ornithologists Club* 123A:114–135.
- BAKER, M. C. 1996. Depauperate meme pool of vocal signals in an island population of Singing Honeyeaters. *Animal Behaviour* 51:853–858.
- BOHÓRQUEZ, C. I. AND F. G. STILES. 2002. The paradoxical social system of the Dusky Bush-Tanager (*Chlorospingus semifuscus*): lekking in a nine primaried-oscine? *Journal of Field Ornithology* 73:281–291.
- BONACCORSO, E., A. G. NAVARRO-SIGÜENZA, L. A. SÁNCHEZ-GONZÁLEZ, A. T. PETERSON, AND J. GARCÍA-MORENO. 2008. Genetic differentiation in the *Chlorospingus ophthalmicus* complex of Mexico and Central America. *Journal of Avian Biology* 39:311–321.
- BRUMFIELD, R. T. AND J. V. REMSEN JR. 1996. Geographic variation and species limits in *Cinnycerthia* wrens of the Andes. *Wilson Bulletin* 108:205–396.
- CADENA, C. D., S. CÓRDOBA-CÓRDOBA, G. A. LODOÑO, D. CALDERÓN-F., T. E. MARTIN, AND M. P. BAPTISTE. 2007. Nesting and singing behavior of Common Bush Tanagers (*Chlorospingus ophthalmicus*) in South America. *Ornitología Colombiana* 5:54–63.
- CICERO, C. AND N. D. JOHNSON. 2006. Diagnosability of subspecies: lessons from Sage Sparrows (*Amphispiza belli*) for analysis of geographic variation in birds. *Auk* 123:266–274.
- GARCÍA-MORENO, J., A. G. NAVARRO-SIGÜENZA, A. T. PETERSON, AND L. A. SÁNCHEZ-GONZÁLEZ. 2004. Genetic variation coincides with geographic structure in the Common Bush-Tanagers (*Chlorospingus ophthalmicus*) complex from Mexico. *Molecular Phylogenetics and Evolution* 33:186–196.
- GARSON, G. D. 2012a. Discriminant function analysis. Statistical Associates Publishers, Asheboro, North Carolina, USA.
- GARSON, G. D. 2012b. Factor analysis. Statistical Associates Publishers, Asheboro, North Carolina, USA.
- GARSON, G. D. 2012c. Multiple regressions. Statistical Associates Publishers, Asheboro, North Carolina, USA.
- GILL, F. AND D. DONSKER. 2012. IOC World Bird Names (Version 3.1). www.worldbirdnames.org
- GRANT, B. R. AND P. R. GRANT. 2002. Simulating secondary contact in allopatric speciation: an empirical test of premating isolation. *Biological Journal of the Linnean Society* 76:545–556.
- ISLER, M. L. AND P. R. ISLER. 1987. The tanagers: natural history, distribution and identification. Smithsonian Institution Press, Washington, D.C., USA.
- KOETZ, A. H., D. A. WESTCOTT, AND B. C. CONGDON. 2007a. Geographical variation in song frequency and structure: the effects of vicariant isolation, habitat type and body size. *Animal Behaviour* 74:1573–1583.
- KOETZ, A. H., D. A. WESTCOTT, AND B. C. CONGDON. 2007b. Spatial pattern of song element sharing and its implications for song learning in the Chowchilla, *Orthonyx spaldingii*. *Animal Behaviour* 74:1019–1028.
- KROODSMA, D. E., K. WILDA, V. SALAS, AND R. MURADIÁN. 2001. Song variation among *Cistothorus* wrens, with a focus on the Mérida Wren. *Condor* 103:855–861.
- MORTON, E. S. 1975. Ecological sources of selection on avian sounds. *American Naturalist* 109:17–34.
- MOYNIHAN, M. 1962. Display patterns of Tropical American “nine-primaried” songbirds. I. *Chlorospingus*. *Auk* 79:310–344.
- MUNDINGER, P. C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. Pages 147–208 in *Acoustic communication in birds* (D. E. Kroodsma and E. H. Miller, Editors). Volume 2. Academic Press, New York, USA.

- NAVARRO-SIGÜENZA, A. G., A. T. PETERSON, A. NYARI, G. GARCÍA-DERAS, AND J. GARCÍA-MORENO. 2008. Phylogeography of the *Buarremon* Brush-finch complex (Aves, Emberizidae) in Mesoamerica. *Molecular Phylogenetics and Evolution* 47:21–35.
- PETERS, S., W. A. SEARCY, M. D. BEECHER, AND S. NOWICKI. 2000. Geographic variation in the organization of Song Sparrow repertoires. *Auk* 117:936–942.
- PETERSON, A. T., P. ESCALANTE, AND A. NAVARRO. 1992. Genetic variation and differentiation in Mexican populations of Common Bush-Tanagers and Chestnut-capped Brush-Finches. *Condor* 94:244–253.
- PODOS, J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51:537–551.
- PODOS, J., S. K. HUBER, AND B. TAFT. 2004a. Bird song: The interface of evolution and mechanism. *Annual Review of Ecology, Evolution, and Systematics* 35:55–87.
- PODOS, J., J. A. SOUTHALL, AND M. R. ROSSI-SANTOS. 2004b. Vocal mechanics in Darwin's finches: correlation of beak gape and song frequency. *Journal of Experimental Biology* 207:607–19.
- PRICE, J. J. AND S. M. LANYON. 2002. Reconstructing the evolution of complex bird song in the Oropendolas. *Evolution* 56:1514–1529.
- PUEBLA-OLIVARES, F., E. BONACCORSO, A. ESPINOSA DE LOS MONTEROS, K. OMLAND, J. LLORENTE, A. T. PETERSON, AND A. G. NAVARRO-SIGÜENZA. 2008. Speciation in the Emerald Toucanet (*Aulacorhynchus prasinus*) complex. *Auk* 125:39–50.
- SÁNCHEZ-GONZÁLEZ, L. A., A. G. NAVARRO-SIGÜENZA, A. T. PETERSON, AND J. GARCÍA-MORENO. 2007. Taxonomy of *Chlorospingus ophthalmicus* in Mexico and northern Central America. *Bulletin of the British Ornithologists' Club* 127:34–49.
- SÁNCHEZ-MORALES, C. 2005. Influencia del hábitat y del aislamiento geográfico en la estructura del canto y morfología de cinco especies del género *Catharus* (Turdidae). Thesis. Universidad de Costa Rica, San José.
- SHY, E. 1983. The relation of geographic variation in song to habitat characteristics and body size in North American tanagers (Thraupidae: *Piranga*). *Behavioural Ecology and Sociobiology* 12:71–76.
- SLABBEKOORN, H. AND T. B. SMITH. 2002. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London, Series B* 357:493–503.
- SOSA-LÓPEZ, J. R., D. J. MENNILL, AND A. G. NAVARRO-SIGÜENZA. 2012. Geographic variation and the evolution of song in Mesoamerican Rufous-naped Wrens *Campylorhynchus rufinucha*. *Journal of Avian Biology*: In Press.
- TUBARO, P. L. AND D. A. LIJTMAR. 2006. Environmental correlates of song structure in forest grosbeaks and saltators. *Condor* 108:120–129.
- TUBARO, P. L. AND E. T. SEGURA. 1995. Geographic, ecological and subspecific variation in the song of the Rufous-browed Peppershrike (*Cycularhis gujanensis*). *Condor* 97:792–803.
- WEIR, J., E. BERMINGHAM, M. MILLER, J. KLICKA, AND M. GONZALEZ. 2008. Phylogeography of a morphologically diverse neotropical montane species, the Common Bush-Tanagers (*Chlorospingus ophthalmicus*). *Molecular Phylogenetics and Evolution* 47:650–664.
- WESTCOTT, D. A. AND F. J. KROON. 2002. Geographic song variation and its consequences in the Golden Bowerbird. *Condor* 104:750–760.
- WILEY, R. H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist* 138:973–993.
- ZINK, R. M. AND J. V. REMSEN JR. 1986. Evolutionary processes and patterns of geographic variation in birds. *Current Ornithology* 4:1–69.

APPENDIX. Locations, and number of individuals and songs recorded of Common Bush Tanagers. Acronyms show the institutions or persons that provided recordings. Institution acronyms are: LABIEXAL, Laboratorio de Bioacústica del Instituto de Ecología A.C., Xalapa, Veracruz; FMNH, Florida Museum of Natural History, University of Florida; BLB, Borror Laboratory of Bioacoustics; MLNS, Macaulay Library of Natural Sounds; and LS, personal collection of Luis Sandoval, Costa Rica.

	Localities and recordings dates	Subspecies	Birds ^a	Songs ^b
1	Leonardo Bravo, Guerrero, México (17° 30' N, 99° 30' W), April 2003	<i>albifrons</i>	9	11
2	Tlanchinol, Hidalgo, México (20° 3' N, 98° 35' W), June 2003	<i>ophthalmicus</i>	2	7
3	Pisaflores, Hidalgo, México (21° 11' N, 99° 0' W), June 2003	<i>ophthalmicus</i>	15	46
4	Huehuentla, Puebla, México (20° 6' N, 97° 35' W), June 2003	<i>ophthalmicus</i>	3	7
5	El Naranjal, Veracruz, México (18° 48' N, 96° 54' W), July 2003	<i>ophthalmicus</i>	8	25
6	Coatepec, Veracruz, México (19° 27' N, 96° 57' W), February 2003; Xalapa, Veracruz, México (19° 32' N, 96° 55' W), June 1997 (LABIEXAL)	<i>ophthalmicus</i>	5	25
7	Comaltepec, Oaxaca, México (17° 18' N, 96° 35' W), October 2003	<i>ophthalmicus</i>	7	18
8	Coapilla, Chiapas, México (17° 6' N, 92° 5' W), November 2003, June 2005, and December 2007	<i>dwighti</i>	9	14
9	Cerro el Huitepec, San Cristobal de las Casas, Chiapas, México (16° 41' N, 92° 35' W), January 2010; Lagos de Montebello, Chiapas, México (16° 22' N, 91° 51' W), May 1987 (FMNH)	<i>dwighti</i>	5	13
10	Reserva El Triunfo, Chiapas, México (15° 28' N, 92° 43' W), April 1993, April 1999, and April 2002 (LABIEXAL, MLNS)	<i>postocularis</i>	8	18
11	Volcán Tacaná, Chiapas, México (14° 54' N, 92° 12' W), August 2003 and June 2007	<i>postocularis</i>	13	52
12	Bosque del Niño, Grecia, Costa Rica (10° 9' N, 84° 14' W), April 2009 (LS); Parque Nacional Braulio Carrillo, San José, Costa Rica (10° 6' N, 83° 57' W) March 1983 and March 1989 (FMNH); Monteverde, Puntarenas, Costa Rica (10° 18' N, 84° 48' W), April 1989 and July 2009 (LS, FMNH); San Vito, Costa Rica (08° 49' N, 82° 57' W), February 1992 (BLB)	<i>regionalis</i>	9	27

^a Number of different individuals.

^b Number of songs analyzed.