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RESEARCH ARTICLE

Geographic variation in songs of the Common Yellowthroat

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ABSTRACT

The Common Yellowthroat (*Geothlypis trichas*) exhibits widespread geographic variation in plumage, morphology, migratory behavior, and song. In addition, researchers recently found evidence that the Common Yellowthroat has three genetically distinct groups across its North American range: eastern, western, and southwestern. These groups are more genetically similar to other *Geothlypis* species than to each other, which suggests relatively long-term isolation. I hypothesized that geographic variation in song behavior should reflect these genetic differences. To test this hypothesis, I examined spatial patterns of variation in both note types and acoustic characteristics of song. Consistent with the hypothesis, I found significant differences among the three groups, particularly in frequency measures, internote duration, notes per phrase, and note elaborateness. Within the eastern and western groups, I also found significant song differences among historically recognized subspecies. When comparing western and eastern subspecies, I found different latitudinal trends, even though subspecies found at similar latitudes that exhibit similar migratory behavior might be expected to have similar song characteristics. Two possible explanations for this lack of convergence are (1) stochastic changes in song in isolated populations and (2) nonlatitudinal dissimilarities in habitat, including transmission properties or effects on morphological evolution, that drive song divergence. Without excluding other explanations, I found evidence of an effect of morphological divergence: Subspecies with larger bills sang songs with lower frequencies. Overall, the geographic variation in the songs of the Common Yellowthroat demonstrates that multiple evolutionary processes interact to shape birdsong, and that the importance of each of these processes and their interactions varies among populations.

Keywords: birdsong, evolution, *Geothlypis trichas*, geographic variation

Variación geográfica en los cantos de *Geothlypis trichas*

RESUMEN

Geothlypis trichas es una especie que exhibe amplia variación geográfica en su plumaje, morfología, comportamiento migratorio, y canto. Además, investigaciones recientes han encontrado evidencia de que *G. trichas* presenta tres grupos genéticamente distintos dentro de su rango territorial en Norte América: oriental, occidental, y suroccidental. Estos grupos son más similares a otras especies de *Geothlypis* que entre sí, lo que sugiere su aislamiento durante un plazo largo. Mi hipótesis fue que la variación geográfica del canto debería reflejar estas diferencias genéticas. Para probar esta hipótesis, examiné patrones espaciales de variación en tipos de notas, y en las características acústicas del canto. De conformidad con la hipótesis, encontré una variación significativa entre los tres grupos, específicamente en medidas de frecuencia, duración entre notas, notas por frase y complejidad de la nota. Dentro de los grupos occidental y oriental, también encontré diferencias significativas entre las canciones de las subspecies históricamente reconocidas. Al comparar las subspecies occidentales y orientales observé diferentes tendencias latitudinales, si bien podría esperarse que subspecies en latitudes similares que exhiben un comportamiento migratorio similar tengan canciones similares. Dos posibles explicaciones para esta falta de convergencia son los cambios estocásticos en el canto de las poblaciones aisladas y las disimilitudes del hábitat no relacionadas a la latitud, incluyendo propiedades o efectos de transmisión sobre la evolución morfológica, que alimentan tal divergencia de canto. Sin excluir otras explicaciones, encontré evidencia de un efecto de divergencia morfológica: subspecies con picos más grandes cantaban canciones con frecuencias más bajas. En conclusión, la variación geográfica de las canciones de *G. trichas* demuestra que múltiples procesos evolutivos interactúan para formar el canto de las aves y que la importancia de estos procesos y sus interacciones varía entre poblaciones.

Palabras clave: canto de aves, evolución, *Geothlypis trichas*, variación geográfica

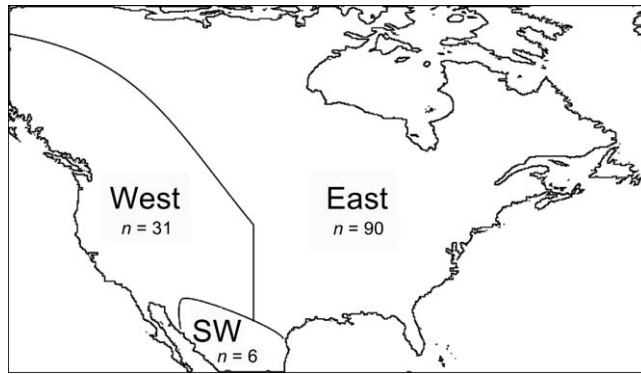


FIGURE 1. Map of boundaries for western, eastern, and southwestern individuals. The boundary between east and west followed Kelly and Hutto (2005): the 100° longitude line in the southern part of the range and the Rocky Mountains in the north. The southwestern boundary matched the northern edge of the range of *Geothlypis trichas chryseola*. Four additional Mexican subspecies are part of the southwestern group but were not included because of the unavailability of archived recordings for these subspecies.

INTRODUCTION

Geographic variation can reveal much about the evolutionary history of a species. Such variation results from mutation and dispersal and may be reinforced by isolation, drift, and selection (Endler 1977). The geographic variation of learned vocalizations, such as oscine birdsong, reflects both genetic and cultural changes that occur as populations expand into new environments (Lemon 1975, Mundinger 1983, Podos and Warren 2007). Not only do changes in birdsong reflect divergence, they can also enhance it, because song is an important signal for mate choice (Kroodsma and Byers 1991). Changes in song could reinforce genetic divergence at contact zones, because birds that do not recognize each other do not mate (Irwin 2000). In the present study, I tested hypotheses about the role of genetic differentiation and selection on the evolution of Common Yellowthroat (*Geothlypis trichas*) song by examining patterns of geographic variation.

There are three genetically distinct populations of Common Yellowthroats (Escalante et al. 2009): the eastern, western, and southwestern groups (Figure 1). Despite their similarities in appearance and behavior, the eastern and western groups are more genetically similar to other *Geothlypis* species than to each other. Specifically, the eastern group is more closely related to the Central American resident species *G. nelsoni* and *G. flavovellata*, whereas the western group is more closely related to *G. beldingi* of Baja California. The southwestern group appears to be more recently differentiated, and more closely related to eastern than to western *G. trichas*. Given the genetic differentiation (and correspondingly distinct

recent evolutionary histories) of the eastern, western, and southwestern groups, I hypothesized that they would have evolved distinct songs. Also, I predicted that the southwestern group would sing more similarly to the eastern group, given that the groups appear to share a more recent evolutionary history (Escalante et al. 2009).

What might have caused song differences between these groups? One explanation is that regional differences in song result from stochastic events (Podos and Warren 2007). Similar to genetic divergence associated with the process of allopatric speciation (Endler 1977), cultural divergence in song is often correlated with geographic separation (Slater 1989, Koetz et al. 2007). Such cultural divergence may arise via random changes introduced during song transmission between generations. As a result of this drift-like process, birds closer together often sing more similarly to each other than birds farther apart, with increasing divergence over space (Morton 1987). Eventually, isolated birds may sing so differently that they do not recognize conspecifics from other populations (Irwin 2000). I tested the hypothesis that song evolution is related to isolation-by-distance by testing the relationship between distance and song spectral characteristics and note-type repertoires within genetic groups.

In addition to drift, selective pressures may shape song, and these pressures may vary among populations that live in different environments (Mundinger 1983). I tested the effects of migration, bill morphology, and habitat variation on the variation of song within and among groups. In particular, I compared the results of these tests between eastern and western groups, to examine whether similar pressures have shaped song in these isolated groups and whether these patterns can elucidate some of the processes that have contributed to their genetic divergence.

Migration likely affects song evolution, because different migration schedules among individuals in a population can result in different breeding schedules and assortative mating (e.g., Bearhop et al. 2005). Furthermore, different schedules among metapopulations might reinforce the spatial isolation among them. If migration isolates metapopulations more quickly and this increased isolation decreases either the genetic or cultural transmission of songs (or both) among them, I predicted that song-type variation should be greater in migratory subspecies than in sedentary ones. Alternatively, if migrants disperse farther, on average, from their natal areas than sedentary birds (Paradis et al. 1998), migratory populations might be more panmictic than sedentary populations, which would be more isolated from each other over long distances. In this case, there should be less variation in the songs of migratory birds than in those of sedentary birds.

As well as affecting dispersal distances, migration is sometimes hypothesized to affect song elaborateness (Catchpole 1982, Read and Weary 1992, Spottiswoode

and Møller 2004, Cardoso et al. 2012). Birds farther from the equator experience shorter breeding seasons and, presumably, more intense sexual selection. If increased sexual selection results in more elaborate songs, the more northern migratory subspecies should consistently have more elaborate songs than sedentary ones.

Migration is not the only potential selective pressure on birdsong. Differences in sound transmission in different habitats may also influence song evolution. Sounds transmit differently among habitats that vary in structure, and the spectral qualities of local birdsong may be selected to optimize transmission in these areas, a process described as the “acoustic adaptation hypothesis” (Morton 1975, Wiley and Richards 1978, Boncoraglio and Saino 2007, Derryberry 2009). As predicted by this hypothesis, habitat structure (i.e. open, edge, or closed-canopy habitat) should affect the frequency of song; birds in open habitats should sing with broader bandwidths, higher frequencies, and longer repeated phrases than birds in closed, high-canopy habitats (Morton 1975).

The acoustic environment may influence the frequency or timing of songs, but these characteristics are also partially determined by the size of sound-producing organs, as a result of physical constraints on sound production (Podos 2001). The bill is an important part of sound production, and sound can be affected by bill and correlated gape size (Palacios and Tubaro 2000, Podos et al. 2004). Specifically, if bird size is a factor in the spectral qualities of song, I predicted that subspecies with larger bill dimensions would also sing lower-frequency songs with longer repeated phrases (Podos 2001).

The mechanisms described above are not mutually exclusive; one or more of them may have shaped Common Yellowthroat song evolution. Also, the mechanisms may have yielded different outcomes in the independent evolutionary trajectories of the eastern, western, and southwestern yellowthroat groups. Elucidating the possible causes of song divergence in these closely related genetic groups might reveal the interacting pressures that vary among populations, ultimately illustrating the complexity of evolutionary processes.

METHODS

Focal Species

The Common Yellowthroat is a small wood warbler that uses many different habitats, including cattails, marshes, bogs, agricultural and forest edges, and shrublands (Guzy and Ritchison 1999). It prefers breeding habitats with low canopy cover and dense low-level vegetation, because it nests and feeds low to the ground. The Common Yellowthroat is a generalist insectivore that feeds mainly by gleaning the leaves and twigs of shrubs.

The Common Yellowthroat currently has 13 described subspecies (Pyle 1997, Guzy and Ritchison 1999). These subspecies reflect geographic variation in song types (Borror 1967), plumage, size, and migratory behavior (Guzy and Ritchison 1999). Nine subspecies are represented in archived song recordings (Figure 2). Of the four southwestern subspecies, only *G. t. chryseola* have archived recordings.

Song Basics

The Common Yellowthroat has two forms of song, the flight song and the perch song (Borror 1967, Ritchison 1991, 1995, Guzy and Ritchison 1999). The perch song has been most commonly observed and recorded and is the focus of my analyses. Males sing the perch song throughout spring and summer, using it for mate attraction and territorial defense (Kroodsma and Byers 1991, Ritchison 1995). Each individual has a repertoire of one perch song, which is learned (Kroodsma et al. 1983) but does not change after crystallization (Borror 1967, Ritchison 1995). Local breeding groups may contain many song types, although shared types within a population are common. Song types extend for approximately 198–454 km (Borror 1967).

Components of song are variously named among species and researchers. I chose to use the same terms as Borror (1967), who referred to Common Yellowthroat song as being made of distinct, repeated “phrases” (Figure 3). In the common mnemonic for Common Yellowthroat song, “witchity-witchity-witchity,” each “witchity” is considered an individual phrase. The number of times an individual male repeats his phrase per song can vary; it is greater, on average, during the courtship phase of the breeding season (Ritchison 1995) and can change within a day and even within a bout of singing. Song length and the number of repeated phrases are therefore good measures of an individual’s context-dependent seasonal variability, but poor measures of between-individual variation. A better unit for exploring broad geographic variation is the structure of the phrase itself, because it is usually consistent within an individual’s songs but differs among birds (Borror 1967). The phrases are made up of two to six notes sung in a consistent order. “Notes” are defined as the discrete units within a phrase that are separated by silence. These notes are further described as having distinct “elements,” or individual frequency upsweeps and downsweeps. Notes may have as few as one or as many as five distinct elements (Borror 1967).

Song Data

I obtained archived recordings from three sources: the Cornell Lab of Ornithology Macaulay Library of Natural Sounds ($n = 57$ individuals), The Ohio State University Borror Laboratory of Bioacoustics ($n = 57$ individuals), and

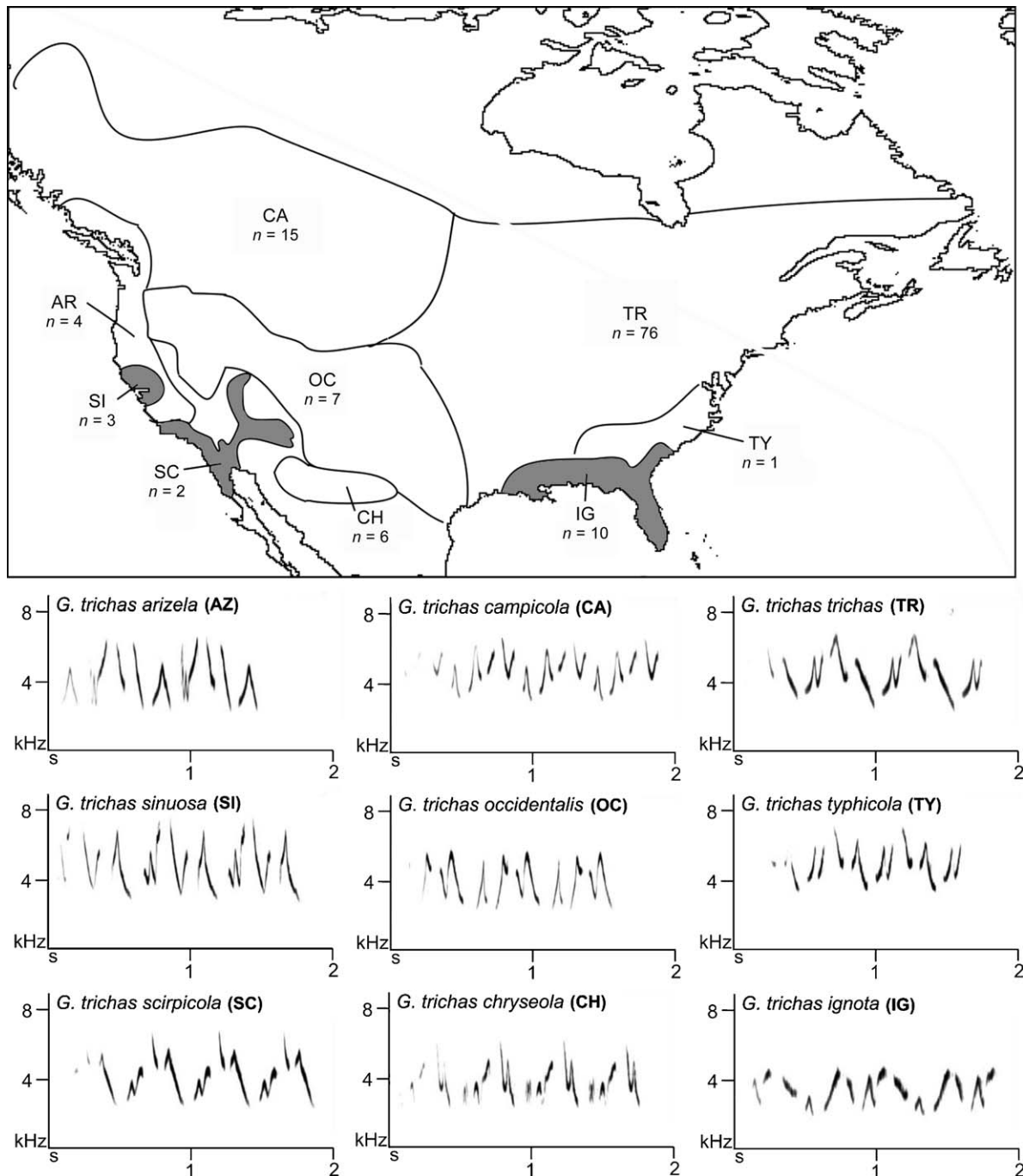


FIGURE 2. Map of approximate subspecies boundaries (based on Behle 1950, Borror 1967, Pyle 1997, Van Rossem 1930), demonstrating spatial relationships among subspecies, and representative sonograms. The archived recordings analyzed for this study represented 9 of the 13 described Common Yellowthroat subspecies, all found in the United States and Canada. Subspecies that are sedentary year-round are indicated with gray shading. Representative sonograms from each subspecies demonstrate variation in frequency, note composition, and syntax. Sonograms are arranged geographically. (This map does not represent local abundances; Common Yellowthroat abundances are often extremely patchy in the dry southwestern United States.)

xeno-canto.org ($n = 10$ individuals). I also included one of my own recordings of an individual from each of the following locations: Lackawanna County, Pennsylvania ($41^{\circ}33'51''\text{N}$, $75^{\circ}43'15''\text{W}$); Franklin County, Massachu-

setts ($42^{\circ}27'15''\text{N}$, $72^{\circ}28'27''\text{W}$); and Mobile County, Alabama ($30^{\circ}43'22''\text{N}$, $88^{\circ}1'48''\text{W}$). All three birds were recorded with a 44.1-kHz sampling rate, using a Sennheiser ME66 shotgun microphone and an M-Audio

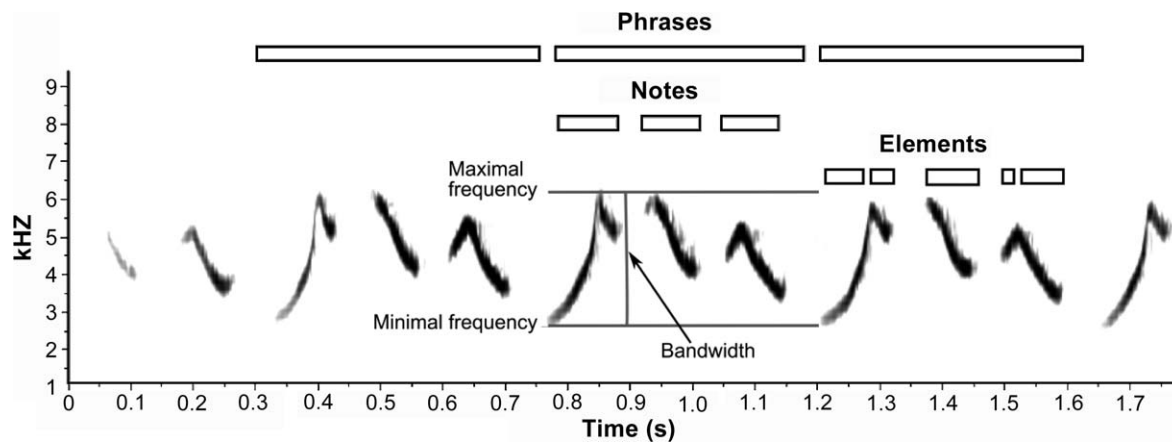


FIGURE 3. Representative sonogram demonstrating song nomenclature and measurements. Common Yellowthroat perch songs are repeated phrases made up of two to six notes, which vary in number of elements. In each song the maximal frequency, minimal frequency, phrase duration, bandwidth, note durations, and internote durations were measured from each sonogram. Raven Pro calculated peak frequencies, and I counted the number of notes per phrase and the number of elements per note.

Microtrack II digital recorder. The total number of individuals from all sources was 127 (124 archived, 3 personal recordings). I randomly selected one song per individual ($n = 127$ songs) by using a random number table to identify which song in the sequence of songs in the recording to measure. Although there is some variation among songs of an individual, most of this variation is in song duration and song volume (Ritchison 1995), which were not measured.

I randomly selected a single individual from each latitude and longitude (to the nearest degree) combination, to ensure independence of sampled songs. Latitude and longitude were obtained from field notes submitted by the recordist. If the recordist noted the latitude and longitude specifically, I used their information in the analysis. In other cases, only locations (e.g., towns, counties, state parks, road names, etc.) were mentioned, so latitude and longitude were estimated from Google Maps.

I classified *G. trichas* individuals as “eastern” or “western” using the 100°W longitude line to split eastern from western birds in the south, and the Rocky Mountains in the north (Kelly and Hutto 2005). Birds in the subspecies *G. t. chyrseola* were classified as southwestern (Escalante et al. 2009). There was a sampling bias in the archived data, favoring eastern birds ($n = 96$) over western ($n = 25$) or southwestern birds ($n = 6$). I classified individuals as members of a subspecies on the basis of maps and descriptions in Borror (1967) and Pyle (1997). The subspecies summaries of song characteristics are available in the [Supplementary Material](#). One individual was not assigned to any subspecies because of uncertainty, given that it was located on a border between *G. t. trichas* and *G. t. typhicola*. This unknown individual was included in analyses comparing genetic groups and was included in

the migratory analyses as migratory, but it was not included in the subspecies summaries in the [Supplementary Material](#).

The archived songs were recorded between 1929 and 2011. Although evolution likely affected populations during this period, the differences among populations are probably greater than the changes within them. First, regional song types appear to persist for a long time. For example, when I was exploring the archived recordings, I discovered that a song type originally recorded in 1963 in Lackawanna County, Pennsylvania, was still present in 2008, and a song type recorded in 1951 in Kern County, California, was still present in 2001. Second, to ensure that time was not a factor in the spatial analyses, I ran a constrained analysis (capscale in the “vegan” package in R; Oksanen et al. 2012) on eastern and western spectral song data (minimal frequency, maximal frequency, peak frequency, bandwidth, phrase duration, mean internote duration, and mean note duration) with recording year as the constrained factor. I tested whether time was a significant factor by using the “anova.cca (by terms)” function, which sequentially partials out variables to test their influence on the model. Time (recording year) was not a significant factor for eastern or western groups (Eastern_{time}: $F = 1.4$, $P = 0.16$, Western_{time}: $F = 0.48$, $P = 0.92$).

I collected data on the presence or absence of previously defined note types and on spectral characteristics. Specifically, I assessed the note types defined by Borror (1967), who identified 83 notes from the 411 songs he sampled. Most notes in my sample matched one of these note types, but I encountered 15 new note types, for a total of 80.

An individual blind to the predictions of the study measured the spectral characteristics of all songs with

Raven Pro version 1.4 (Cornell Lab of Ornithology, Ithaca, New York, USA). Common Yellowthroat songs have a few introductory notes of low amplitude, so in each song the first clearly visible phrase was measured. An individual's song can begin with any note of the phrase, so identifying a note as the beginning or end of a phrase is subjective. For consistency, I defined the beginning of a phrase as the note with the lowest beginning frequency. The following phrase measurements were made: maximal frequency (Hz), minimal frequency (Hz), peak frequency (or frequency in Hz at peak power, calculated by Raven Pro), and phrase duration (s). I defined "phrase duration" as the time between the beginning of the initial note and the beginning of its next occurrence. Using the measured maximal and minimal frequencies (Hz), I calculated the difference between them, the bandwidth. In addition, the durations of each note and internote intervals (silence) in the phrase were measured, and then I calculated the mean note duration (s) and mean internote duration (s) across the measured phrase. All frequency measurements were made on spectrograms with an FFT value of 1,024 (precision = 47 Hz), and all time measurements were made with an FFT value of 128 (precision = 1.3 ms). To estimate song elaborateness, I counted the number of notes per phrase and calculated the average number of elements per note (total elements per number of notes per phrase).

Statistical Analyses

To test whether song characteristics differed among groups, I ran a Type II analysis of variance (ANOVA) comparing eastern and western birds for each song variable ("car" package in R; Fox and Weisberg 2011). Because the southwestern birds comprised only six *G. t. chryseola*, I did not include them in the ANOVAs, but instead noted whether values of each variable were closer to those for eastern or western birds. To compare note-type distribution among the three genetically distinct groups, I used a chi-square test to determine whether the number of unique note types per group indicated differences in rates of song diversity or was more reflective of variation in sampling effort.

To examine the effects of isolation-by-distance on song patterns, I tested whether Euclidean distance predicted similarity of spectral characteristics and note types within the eastern and western groups separately. I used a Mantel test ("ecodist" package in R; Goslee and Urban 2007) that compared latitude and longitude with column-standardized (*z*-score) song characteristics and another that compared latitude and longitude with presence or absence of note types, all transformed into Euclidean distance matrices.

To test whether migration has a consistent effect on song evolution in the Common Yellowthroat, I separated individuals within the eastern and western groups into

migratory and sedentary groups (Figure 2). I computed rates of note-type sharing (unique notes per number of birds) in each migratory group within each region to compare rates of change. I also ran a two-way Type II ANOVA on notes per phrase and elements per note, testing the effects of genetic group (eastern vs. western), migratory behavior (migratory vs. sedentary), and the interaction between the two variables.

To test the role of habitat structure on song spectral characteristics, I used the subset of the Macaulay Library archives that included habitat descriptions, and personal recordings, for which the habitat was known. Forty Common Yellowthroats were recorded in nine habitat types. I classified the habitat types as low (marsh, fallow field, meadow, bog), middle (brush, riparian, edge), or high (forest, swamp) canopy types. Because of low sample sizes of habitat-documented western birds ($n = 9$, with 8 in the low classification), I was able to test for a relationship between songs and habitat only in eastern birds. I used Type II ANOVAs to test differences in minimal frequency, maximal frequency, peak frequency, bandwidth, and phrase duration.

To test whether bill morphology has affected song spectral characteristics, I tested for correlations between the subspecies mean culmen length (Pyle 1997) and the subspecies mean of all measured song characteristics. I computed Pearson's correlations for eastern and western groups separately.

All statistical tests were computed using R version 2.15.2. All reported values in the text, tables, and figures are means \pm SD. Because of the large number of analyses, I used a family-wise Bonferroni correction; the corrected level of significance for tests is 0.01. I made an exception for the level of significance of Pearson's correlations because sample sizes for correlations were so low ($n = 4$) that a P value < 0.01 was not possible; for these tests, I set the critical P value at 0.05. Additionally, I assessed the strength of the correlation even if the P value was not significant. Pearson r values > 0.50 were considered indicative of strong correlations (Cohen 1992).

RESULTS

Comparing Eastern, Western, and Individuals of *G. trichas chryseola*

Some song characteristics differed significantly between the eastern and western genetic groups. Specifically, western birds' songs had higher maximal frequencies, larger bandwidths, longer mean internote durations, and more elements per note than those of eastern birds (Table 1). All groups had similar peak frequencies, phrase durations, and average note durations. The songs of the southwestern *G. t. chryseola* were more similar to those of the western group, particularly in peak frequencies, phrase

TABLE 1. Western and eastern Common Yellowthroats differ in the spectral characteristics of song and in song-type elaborateness measures. The characteristics of the songs of the southwestern subspecies *Geothlypis trichas chryseola* are included for comparison. An “E” or “W” in the last column indicates whether the *G. t. chryseola* mean is more similar to eastern or western values, respectively. Significant values are in bold.

| Song characteristic | West (<i>n</i> = 31) | East (<i>n</i> = 90) | <i>F</i> | <i>P</i> | Southwest <i>G. t. chryseola</i> (<i>n</i> = 6) | |
|-----------------------------|-----------------------|-----------------------|----------|-------------------|--|---|
| Minimal frequency (Hz) | 2,325 ± 273 | 2,465 ± 383 | 2.96 | 0.088 | 2,130 ± 223 | E |
| Maximal frequency (Hz) | 6,886 ± 846 | 6,361 ± 769 | 8.86 | 0.004 | 6,344 ± 698 | E |
| Peak frequency (Hz) | 4,734 ± 650 | 4,475 ± 551 | 4.06 | 0.046 | 4,658 ± 771 | W |
| Bandwidth (Hz) | 4,562 ± 812 | 3,895 ± 590 | 21.4 | <0.0001 | 4,214 ± 634 | |
| Phrase duration (s) | 0.529 ± 0.080 | 0.537 ± 0.098 | 0.15 | 0.703 | 0.520 ± 0.050 | W |
| Mean note duration (s) | 0.120 ± 0.020 | 0.114 ± 0.023 | 1.43 | 0.235 | 0.111 ± 0.020 | W |
| Mean internote duration (s) | 0.064 ± 0.010 | 0.051 ± 0.009 | 30.8 | <0.0001 | 0.063 ± 0.010 | W |
| Mean notes per phrase | 2.92 ± 0.49 | 3.34 ± 0.87 | 5.47 | 0.021 | 3.00 ± 0 | W |
| Mean elements per note | 2.42 ± 0.51 | 1.96 ± 0.51 | 16.2 | <0.0001 | 2.83 ± 0.07 | W |

durations, mean note duration, mean internote duration, mean notes per phrase, and mean elements per note. Only minimal and maximal frequencies of southwestern songs were more similar to eastern birds than to western.

The three genetically distinct groups had broadly overlapping note types. Forty-five percent of note types were shared between at least two groups, and 9% were shared among all three groups. The number of unique note types per group did not differ from chance ($\chi^2 = 0.79$, *df* = 2, *P* = 0.68). However, five of six southwestern birds shared a particular note type that was not observed in the other groups, despite sharing 89% of their note-type repertoire with eastern and western birds. This note (Borror 1967: figure 42) was also the only note in the perch-song repertoire to show pronounced harmonic overtones.

Distance

In the east, birds that were closer to each other were more likely to share song characteristics (Mantel *r* = 0.15, *P* = 0.01) and note types (Mantel *r* = 0.13, *P* = 0.01) than birds that were farther apart. However, adjacent subspecies shared similar proportions of note types with each other compared with nonadjacent subspecies. Specifically, adjacent *G. t. ignota* and *G. t. trichas* shared 33% of their note-type repertoires, adjacent *G. t. trichas* and *G. t. campicola* shared 26%, and nonadjacent *G. t. ignota* and *G. t. campicola* shared 25%.

Unlike the eastern subspecies, western individuals that were closer together were not more likely to share song characteristics (Mantel *r* = 0.20, *P* = 0.03) or note types (Mantel *r* = 0.063, *P* = 0.24). An extreme example, *G. t. sinuosa*, the small sedentary subspecies of San Francisco Bay, California, did not share any note types with many nearby subspecies, including the surrounding subspecies *G. t. arizela*, the migratory subspecies *G. t. occidentalis*, and the southwestern subspecies *G. t. chryseola*. However, 83% of the note types of *G. t. sinuosa* were also in the repertoire of *G. t. campicola*, which also had two note types in common with *G. t. scirpicola*.

Migration

In both the east and west, there was more note-type variation (and less note-type sharing) in sedentary individuals. In the east, migratory birds (*n* = 96) sang 65 note types, and sedentary birds (*n* = 10) sang 31 note types. An average of 1.32 individuals sang each note in the migratory group’s repertoire, compared with 0.32 individuals per note in the sedentary group. In the west, migratory birds (*n* = 25) sang 38 note types (0.66 individuals per note type), and sedentary birds (*n* = 4) sang 10 note types (0.4 individuals per note type).

Migration effects were not consistent across genetic groups for the two measures of song elaborateness, notes per phrase and mean elements per note (Table 2). For both elaborateness characteristics, there was a significant interaction between the effects of genetic group and migratory behavior. In particular, migratory birds had fewer notes per phrase than sedentary birds in the east, and more in the west. Also, migratory birds had more elements per note than sedentary birds in the east, and fewer in the west.

Habitat: Acoustic Adaptation Hypothesis

There was no effect of habitat on the songs of eastern Common Yellowthroats. Minimal frequency ($F_{2,28} = 0.29$, *P* = 0.75), maximal frequency ($F_{2,28} = 0.39$, *P* = 0.68), peak frequencies ($F_{2,28} = 0.45$, *P* = 0.64), bandwidth ($F_{2,28} = 1.0$, *P* = 0.36), and phrase duration ($F_{2,28} = 0.35$, *P* = 0.71) were not significantly associated with canopy height.

Bill Morphology

Mean bill length was negatively correlated with mean minimal frequency, strongly and significantly in the east and strongly in the west (Table 3 and Figure 4). In the east, mean bill length was strongly negatively correlated with maximal frequency, peak frequency, and bandwidth and strongly positively correlated with phrase duration. In the west, mean bill length was strongly and significantly correlated with phrase duration and mean notes per

TABLE 2. Summary of differences in song elaborateness between eastern and western Common Yellowthroat groups that differ in migratory behavior. Significant values are in bold.

| | | | | Results of Type II ANOVA | | | | | |
|-------------------|-----------|-------------|-------------|--------------------------|----------------|--------------------|----------------|-------------|----------------|
| Summary | | | | Genetic group | | Migratory behavior | | Interaction | |
| | Behavior | West | East | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| Sample size | Migratory | 21 | 86 | | | | | | |
| | Sedentary | 4 | 10 | | | | | | |
| Notes per phrase | Migratory | 2.95 ± 0.50 | 3.16 ± 0.67 | 20.1 | < 0.001 | 35.3 | < 0.001 | 14.2 | < 0.001 |
| | Sedentary | 2.75 ± 0.50 | 4.90 ± 0.88 | | | | | | |
| Elements per note | Migratory | 2.34 ± 0.45 | 1.98 ± 0.52 | 16.5 | < 0.001 | 0.29 | 0.593 | 8.26 | 0.005 |
| | Sedentary | 2.83 ± 0.69 | 1.71 ± 0.36 | | | | | | |

phrase, and strongly correlated with peak frequency, mean internote duration, and mean elements per note.

DISCUSSION

I found support for the hypothesis that the songs of the genetically distinct groups of eastern and western Common Yellowthroats are diverging. They appear to have evolved in a way that could reinforce isolation among the groups and, therefore, perhaps promote eventual speciation. Common Yellowthroats use song bandwidth and internote duration to recognize conspecifics (Wunderle 1979), and the songs of eastern and western birds have diverged in both of these important species-recognition characteristics.

By contrast, the bandwidths and internote durations of *G. t. chryseola* were intermediate. Southwestern birds are genetically more similar to eastern birds (Escalante et al. 2009) but geographically—and, presumably, ecologically—more similar to western birds. Against the prediction that southwestern birds would be more similar to the eastern group with which they have more recently shared a common ancestor, *G. t. chryseola* birds actually sang more similarly to nearby western birds. This similarity suggests that the environment is an important influence on southwestern *G. t. chryseola* song.

The spectral characteristics of *G. t. chryseola* songs appear to have changed in comparison with those of eastern birds, and they have also incorporated an unusual harmonic note in their perch-song repertoire (Borror 1967: figure 42); harmonics are usually used only in flight songs (e.g., Guzy and Ritchison 1999). Despite the oddity of the note, five of the six representative individuals shared it. The popularity of a unique note type supports the hypothesized recency of this group (Escalante et al. 2009), which has had less time to culturally diversify since isolation and range expansion.

Distance

The relationship between distance and song spectral characteristics and note-type distribution differed between eastern and western Common Yellowthroats, suggesting different evolutionary histories. The observed gradient of eastern subspecies' singing behaviors supports Escalante et al.'s (2009) suggestion of a gradual range expansion and separation of sedentary and migratory subspecies, perhaps due to dissimilarities in the timing of breeding activities (e.g., Bearhop et al. 2005). Alternatively, the seemingly clinal pattern was mostly driven by how different the songs of the most southern subspecies, *G. t. ignota*, are. Supporting this alternative, Chapman (1907) found that individuals of different subspecies looked and behaved most differently at contact zones and suggested that although *G. t. ignota* and *G. t. trichas* were likely related, they had distinct origins and were not the result of range expansion. In the west, the sedentary *G. t. sinusosa* and *G. t. scirpicola* have small ranges and are similar in many acoustic measures to the other western subspecies. It is possible that they are more recently founded sedentary

TABLE 3. Pearson's correlations between mean subspecies bill length and mean subspecies song characteristics in the western and eastern Common Yellowthroat groups. Significant values are in bold.

| Song characteristic | West (n = 4) | | East (n = 4) | |
|-----------------------------|--------------|-------------|--------------|-------------|
| | r | P | r | P |
| Minimal frequency (Hz) | -0.93 | 0.07 | -0.97 | 0.03 |
| Maximal frequency (Hz) | -0.13 | 0.87 | -0.85 | 0.15 |
| Peak frequency (Hz) | -0.67 | 0.33 | -0.69 | 0.31 |
| Bandwidth (Hz) | 0.14 | 0.86 | -0.76 | 0.24 |
| Phrase duration (s) | -0.95 | 0.04 | 0.85 | 0.15 |
| Mean note duration (s) | 0.52 | 0.48 | 0.31 | 0.69 |
| Mean internote duration (s) | -0.62 | 0.38 | -0.10 | 0.89 |
| Mean notes per phrase | -0.99 | 0.01 | 0.19 | 0.81 |
| Mean elements per note | -0.86 | 0.14 | 0.22 | 0.78 |

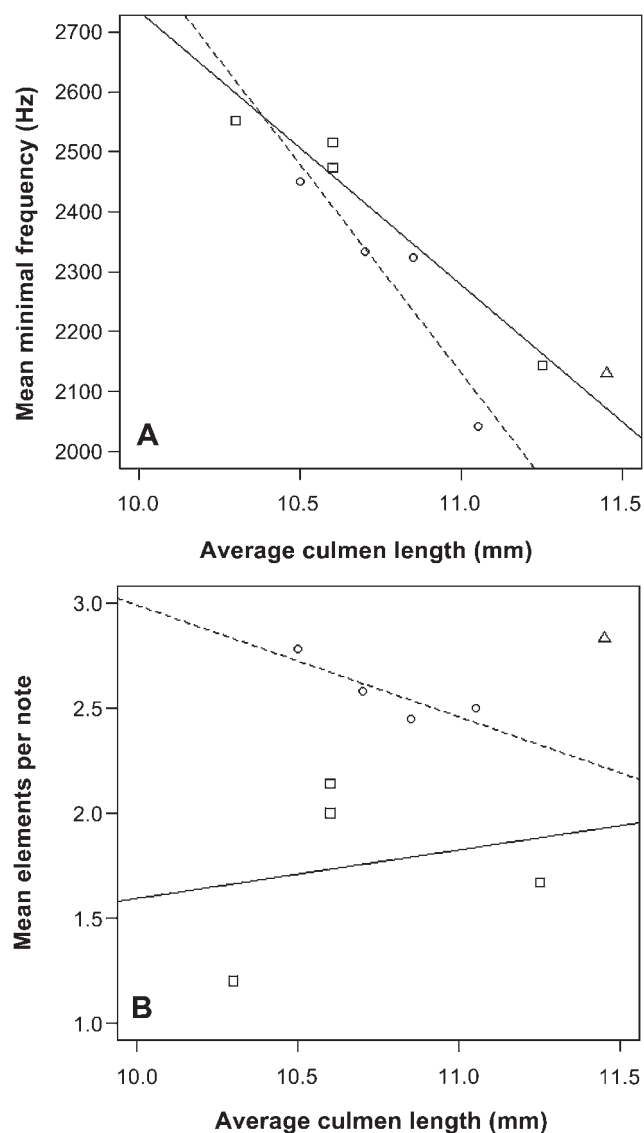


FIGURE 4. Plot and fitted regression lines demonstrating the strong correlations between mean bill length and minimal frequencies in both the east and west (A) and mean bill length and number of notes per phrase in the west (B). Eastern points are represented with a square and a solid line, whereas western points are represented by a circle and a dashed line.

populations that have broken off from contiguous migratory subspecies, rather than the direct descendants of sedentary groups that expanded into the current migratory subspecies.

Indeed, the patterns of note-type sharing hint at the relationships of other subspecies to *G. t. sinuosa*, which does not share any note types with the surrounding migratory *G. t. arizela*. However, most of the *G. t. sinuosa* note-type repertoire (83%) is also found in the long-distance migratory subspecies *G. t. campicola*. Perhaps this small sedentary population was founded when opportu-

nistic migrant *G. t. campicola* individuals settled in the seasonally mild San Francisco Bay area (Barron et al. 2003), forgoing long-distance migration in future generations. *Geothlypis t. sinuosa* migrate extremely short distances down the California coast to San Diego (Bent 1963), which may be evidence of recent migratory origins. Ultimately, further genetic studies within regions would elucidate the exact relationships among subspecies better than the hints provided by the song data.

Migration

The data supported the hypothesis that note-type variation should vary according to migratory behavior. Both eastern and western migrants had less song-type variation than sedentary birds, sharing note types more often, which supports the conclusion that sedentary populations are more isolated and migratory populations are more panmictic than sedentary ones, presumably because migratory populations have larger (on average) dispersal distances over time. This result does not contradict the finding (Borror 1967) that sedentary birds share more note types and song types within a neighborhood than migratory neighborhoods.

Some researchers have suggested that migration is a consistent force in song evolution, pushing birds toward more elaborate song repertoires (Catchpole 1982, Read and Weary 1992, Spottiswoode and Møller 2004, Cardoso et al. 2012). However, migratory Common Yellowthroats do not consistently show more elaborate song than their sedentary counterparts in the same region. The patterns observed do not have parallel directionality between regions and suggest stochastic changes, or unique selective pressures among subspecies that are unrelated to migration or latitudinal factors. They are not consistent with the hypothesis that migrants evolve more elaborate songs because of increased sexual selection.

Habitat

The acoustic adaptation hypothesis was not supported. Although Common Yellowthroats have territories that vary in canopy cover, they prefer habitat that has shrubby understory, where they spend much of their time. The understory of these territories may be similar in habitat structure, which would account for similarities in song characteristics among canopy heights. Alternatively, Common Yellowthroats may be able to counteract the effects of poor transmission properties by moving to the parts of their territories that have better acoustic transmission. Birds with high-canopy-cover territories often sing from the top of the canopy to improve transmission without altering their song structure (R. T. Bolus personal observation). Lastly, this analysis was also limited by the available data on habitat. This limitation emphasizes how

important it is for recordists to include habitat details for archived song recordings.

Bill Morphology

Different relationships between bill length and song characteristics in eastern and western subspecies revealed that birds within these regions are constrained by different aspects of performance. Eastern birds had the predicted relationship between the frequency and timing of phrases, in that larger subspecies had lower frequencies, smaller bandwidths, and slower, longer phrases. With the exception of minimal frequencies, the songs of western subspecies did not follow these predictions. Instead, larger western subspecies had more elaborate notes than smaller western subspecies, and the elaborateness of notes was strongly correlated with bill length, which suggests that western birds are singing notes as elaborate as is physically possible. There is a tradeoff between bandwidth and the rapid modulation of notes (Podos 1997), and western Common Yellowthroats appear to be singing songs that maximize modulation rather than bandwidth. Future studies could test whether these between-region differences in song performance are targets for sexual selection.

The fact that minimal frequencies are consistently and strongly correlated with bill length is evidence that acoustic ecology plays some role in song evolution. Common Yellowthroats prefer densely shrubby habitats (Guzy and Ritchison 1999) and often sing in the middle of shrubs, particularly when interacting with their mate or fighting with neighboring males (R. T. Bolus personal observation). Dense habitat structure attenuates sound and can affect the clarity of the signal (Morton 1975). Higher frequencies attenuate more than lower frequencies, so if Common Yellowthroat songs have evolved to maximize transmission, they should be as low-frequency as physically possible (Marten and Marler 1977). Supporting this prediction, Common Yellowthroat song in both the east and west is strongly correlated with bill morphology: Subspecies with the largest culmens have lower minimal frequencies. If bill length limits song frequency (Palacios and Tubaro 2000, Podos et al. 2004), the observed correlation suggests that each Common Yellowthroat sings as low as it possibly can.

In conclusion, the present data offer insights about the evolution of Common Yellowthroat song, illustrating that genetically different groups have evolved distinct songs, reflecting unique evolutionary histories and trajectories. As such, Common Yellowthroat song diversity reflects the species' evolutionary diversity.

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