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Singing Behavior and Geographic Variation in the Songs of the Veery (Catharus Fuscescens) Across the Appalachian Mountains

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SINGING BEHAVIOR AND GEOGRAPHIC VARIATION IN THE SONGS OF THE VEERY (*CATHARUS FUSCESCENS*) ACROSS THE APPALACHIAN MOUNTAINS

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SINGING BEHAVIOR AND GEOGRAPHIC VARIATION IN THE SONGS OF THE
VEERY (CATHARUS FUSCESCENS) ACROSS THE APPAPACHIAN MOUNTAINS

COURTNEY L. BRENNAN

ABSTRACT

The Veery (*Catharus fuscescens*) is a common Neotropical migrant thrush whose breeding distribution spans the northern United States and southern Canada and continues south through the high elevations of the Appalachian Mountains. Despite its wide distribution, many aspects of Veery biology are largely unknown, including a clear characterization of song and knowledge of geographic song variation. I describe the song structure, repertoire size, and patterns of song delivery in the songs of the Veery and describe geographic song variation across four regions along the Appalachian Mountains. Visual analysis of song spectrogram images of territorial males revealed that Veeries' repertoire ranges from one to six different song types, which is larger than what was previously described in the literature. Spectrogram analysis suggested that Veeries present song types in predictable patterns, and patterns of song presentation can change depending on repertoire size. Veeries also presented their songs in an oscillating frequency pattern regardless of repertoire size, a previously undocumented feature of their singing behavior. Random coefficient models show significant variation infrequency and temporal features of the Veery song within each sample area and across the Appalachian Mountains.

The interconnectedness of developmental and behavioral processes such as song learning, natal and breeding dispersal, and varying levels of gene flow among populations may be influencing the geographic frequency shifts found in Veery songs across this more isolated portion of the breeding range.

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SONG STRUCTURE AND SINGING BEHAVIOR OF THE VEERY (*CATHARUS FUSCESCENS*)

INTRODUCTION

Birds (Class: Aves) rank as one of the most diverse tetrapod classes that exist today, and currently there are nearly 10,000 extant species of birds that fall into nearly 30 taxonomic orders found across the globe (Gill 2007). Although there is an incredible diversity of birds, over half all of the described species (~5,700) are classified in a single order, Passeriformes, making it one of the largest and most diverse terrestrial vertebrate orders. Members of the Order Passeriformes are often referred to as passerines, perching birds, and more generally, songbirds. Within the order of passerine birds there are two clades recognized as suborders: Passeri (the oscines) and Tyranni (the suboscines). Oscines birds include the most recognizable and familiar songbirds, including sparrows, warblers, and thrushes. There are about 4,000 oscines, and many of these birds are known for their elaborate and melodious songs. Oscine birds are able to produce such complex and melodious sounds because of the elaborate musculature associated with the syrinx, where sound production originates (Gill 2007). Oscine birds have up to seven pairs of syringeal muscles that can be precisely controlled to create complex vocalizations, whereas suboscine birds have only two pairs of syringeal muscles. As a result, suboscines often have very simple and single-note vocalizations. Oscine and suboscine birds also differ in song acquisition pathways; suboscines have the details of their songs innately encoded in their DNA (Catchpole and Slater 1995), while oscine birds are guided by innate frameworks of their songs and must learn their species' songs in a multi-phase social and developmental process (Bell et al. 1998).

The enchanting songs that birds produce have intrigued the artistic and scientific alike. Bird songs have been the subject of many poems and prose throughout history (Catchpole and Slater 1995), and songs and other vocalizations that birds produce have been the focus of a wealth of research spanning across many scientific disciplines from ethology and neurobiology to ecology and conservation biology (Kroodsma 2007).

This study focuses the melodious and complex vocalizations of the Veery (*Catharus fuscescens*), a small oscine thrush. Veery vocalizations and singing behavior have been the focus of several studies, although many aspects of the Veery as a species remain poorly understood (Bevier 2005). An early study by Dilger (1956) focused on how some sympatric members of *Catharus* use vocalizations and non-vocal behaviors to discriminate conspecifics from heterospecifics to avoid hybridization. Playback experiments by Weary et al. (1987) demonstrated how Veeries use song structure to recognize and discriminate between intruding conspecifics and established neighbors and how territorial responses of male Veeries is influenced by sung frequency ranges of intruders (Weary et al. 1991). Belinsky et al. (2012) discovered Veeries engage in dusk chorus singing as a consequence of increased acoustic competition during morning choruses, and a new study by Schmidt and Belinsky (2013) found that Veeries alter their dusk singing behavior in the presence of predators.

Although some aspects of Veery singing behavior have been investigated, a clear and basic description of Veery song structure is lacking. Understanding the structure and variation of the Veery song will further our understanding of how birds use song to communicate in various contextual and motivational situations.

Song as a form of communication plays an important role in the ecology, evolution, and behavior in songbirds (Barker 2008; Catchpole and Slater 1995; Catchpole 1981). Song is used primarily for mate attraction and territory defense (Aweida 1995; Krebs et al 1978), and song may also communicate species identity (Emlen 1972; MacNally 1985), individual identity (Weary et al 1986; Vargas-Castro et al 2012), and breeding status (Stacier 2006), as well as other information about the singer. Song quality may be an honest signal of male size, strength, or motivation, and females have evolved the ability to finely discriminate song quantity and quality of male songs (Catchpole and Slater 1995). Although birds can employ several modes of communication (including olfaction [Caspers et al. 2013]), acoustic communication is the most versatile compared to the other channels.

The elaborate diversity of plumages and display behaviors seen across birds implies the importance of visual communication, but visual cues can be an unsatisfactory mode of communication across long distances and for communicating in densely vegetated habitats (Catchpole and Slater 1995; Dilger 1956). Songs, on the other hand, can be produced softly or loudly to communicate information across short and long distances, and sound can move ‘through’ objects making the transmission of information possible in habitats where visibility is low.

Songbirds can possess large repertoires composed of many different song types, and which song a bird sings and the order in which song repertoires are presented may have various contextual and circumstantial implications (Price and Crawford 2013; Stacier et al 2006). Investigating the basic song structure and song delivery behavior in a songbird species is the foundation needed to further understand the behavioral and motivational contexts of song communication.

Females use the features of a male’s song, such as repertoire size, vigor of singing, and quality of songs as a rubric to assess a prospective mate’s overall quality. Because song plays such an important role in communication and mate selection in birds, it is subject to elaboration through sexual selection (Gill 2007).

The elaborate and distinctive song of the Veery has been described in early field guides as a sadly sweet and ghostly song unlike any other eastern bird (Hausman 1946), yet this species and its song are understudied. The Veery is a common thrush that breeds in young deciduous and mixed woods in southern Canada and the northeastern United States, continuing south through the higher elevations of the Appalachian Mountains (Fig. 1). Despite the Veery’s wide distribution, this species is poorly studied in many regards (Bevier et al. 2005). Currently the Veery has four or five described subspecies (Ripley 1964; Phillips 1991; Dickinson 2003) that are based on subtle variations in plumage and range distribution. These described subspecies are not strongly supported and a more critical evaluation of each subspecies is needed (Bevier et al. 2005). There is also a lack of understanding of other basic features of Veery biology, such as hatchling and fledgling growth and development, energy and nutritional requirements of adults, and habitat selection and timing of broodiness (Bevier et al 2005). Another aspect of Veery biology that warrants more investigation is the overall structure of Veery song and repertoire size, where disagreement exists in the current literature possibly because song varies across the species' geographic range.

The typical song of the male Veery (females do not sing) is a three part song. Beginning the song in a short, up slurred introductory 'A' note, followed by the 'B' phrase, typically comprised of two high-frequency, duplicate syllables. The song ends with the 'C' phrase, which is typically comprised of two lower-frequency duplicate syllables (Fig. 2). Veery dawn chorus begins approximately 50 minutes before sunrise (Wright, 1913) and as a consequence of acoustic competition during morning chorus (Belinksy et al. 2012), Veeries are especially active singers at dusk and will continue to sing up to 30 minutes after sunset (Dilger, 1956).

Weary et al. (1986) suggested that the Veery repertoire consists of one to five song types that are structurally similar, whereas an earlier paper by Borror (1964) reported two song types with additional phrases for each song. Hartshorne (1956) described two distinct song types that were not repeated more than a few times before the introduction of the next song type. In this study I clarify the structure and repertoire size of the Veery song, as well as describe additional characteristics of Veery song by analyzing song structure and delivery behavior in Veeries across their breeding range in the Appalachian Mountains.

STUDY SITE AND METHODS

During late May through June 2012 I recorded male Veery vocalizations in four locations along the Appalachian Mountains: eastern North Carolina, central West Virginia, north-central Pennsylvania, and southern Vermont (Fig. 1). Veery songs were recorded in damp, deciduous, and brushy habitats along forested roads and trails or in areas that were recently logged, resulting in patches of young, mixed woods appropriate for breeding Veeries. This habitat type was similar across all sample states. Weather conditions were fairly consistent throughout the recording season, with temperatures ranging from 13-25°C with partly cloudy to clear skies and little to no wind. Recordings were not made during adverse conditions that diminished Veery song bouts such as unseasonably cold, windy, and rainy weather.

In this study I recorded spontaneously singing, unbanded Veeries during both dawn and dusk choruses: morning recordings were conducted from 0430-0930 hours EST, evening recordings were conducted from 1800- 2130 hours. No playback was used. In order to avoid recording the same individual twice, each sampling area was visited only once. I moved at least 500 m from one sampling area to the next to avoid recording the same individual from the same territory, which is thought to be less than half this size (Weary et al. 1991). Vocalizations were recorded as digital .wav files 48 kHz and a 24-bit depth with a Nagra ARES BB+ recording unit with Sennheiser ME 67 shotgun microphone.

Rivers and Kroodsma's (2000) investigation into singing behavior of the Veery's congener, the Hermit Thrush (*Catharus guttatus*), found that Hermit Thrushes cycle through their entire song repertoire in approximately 20 consecutive songs. Due to the close relationship between the congeneric Hermit Thrush and Veery, I attempted to record at least 30 consecutive songs from each individual Veery to capture the full repertoire of each focal individual.

Appropriate habitat conditions were scouted and individual males were located by ear from forested roads and trails and then pursued on foot. Each focal male's singing was recorded while I moved closer to the individual to obtain as clear a recording as possible. Each Veery was recorded for at least 5 minutes or as long as the bird would allow before the focal bird stopped singing, used only contact calls for five minutes, or flew away.

The typical advertising song of the Veery has an overall descending sound and consists of three parts (Fig. 2). The song begins with an up slurred introductory 'A' note, followed by the 'B' phrase which typically consists of two high frequency duplicate syllables, and the song ends with the 'C' phrase, typically comprised of two lower frequency duplicate syllables. The introductory 'A' note of the Veery song is not an important feature for song recognition (MacNally et al. 1985), therefore song diversity analysis focused on the 'B' and 'C' syllables and phrases and the introductory 'A' note was largely ignored.

Visual analysis of spectrograms were used to investigate song diversity, repertoire sizes, and song delivery behavior of individuals whose single recording captured more than 30 consecutive songs. Spectrogram images were generated using the bioacoustics programs Raven Pro 1.4 and 1.5 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Each sound file was band pass filtered with a lower frequency limit of 500 Hz and an upper limit of 24,000 Hz to optimize the song image quality of Veeries songs, which are sung within approximately 6,500 – 1,500 Hz range.

Each discrete, individual vocalization within a song was considered a syllable. Phrases describe the pairs or triplet sets of syllables that share identical shape and frequency range (Fig. 2). A frequency shift of at least 500 Hz from one syllable to the next was considered a phrase change. Song spectrogram images for an individual Veery were visually analyzed and each phrase and syllable was labeled. Because the introductory note in the Veery song is not an important feature for song recognition (MacNally et al. 1985), the introductory note was not labeled and was ignored for the song typing analysis. If a specific combination of identical phrases and syllables was repeated at least three times in a singing bout that exceeds 30 consecutive songs, it was considered a ‘song type’. Several atypical songs were recorded that matched other songs within a focal bird’s repertoire, but were missing the ending of the song. These were scored as aborted versions of an already recognized song type, and included in the analysis. I did not encounter a song type that appeared only once or twice in a singing bout that was completely unique.

The spectrogram images of a Veery’s songs were grouped together based on similarities in the number of phrases and syllables, as well as the shape of syllables, providing groups of distinct song types for each individual Veery. The number of different song types the Veery sang in a singing bout was considered its repertoire size.

I investigated song delivery behavior by arbitrarily numbering song types in each individual’s repertoire and noted which song type was delivered throughout its singing bout. I also noted the overall peak frequency of each song in these singing bouts. Peak frequency describes the frequency of the peak energy visible on each song spectrogram image.

To verify the repeatability of the song typing results, four naïve biology students were asked to duplicate my song typing methods using spectrogram images of entire song bouts from two randomly selected Veeries from each sampled state (total of eight Veeries per student). The students were given a brief explanation of the overall structure of Veery song, and using the song typing protocol above, independently assigned song types to the entire singing bout for each of the eight individual Veeries.

RESULTS

Sampling efforts resulted in a total of 3,088 songs recorded from 109 individual Veeries across the Appalachian sampling range (VT: n= 750 songs from 30 individuals; PA: n= 523 songs from 24 individuals; WV: n= 952 songs from 26 individuals; NC: 863 songs from 29 individuals). Fifty-four individual Veery recordings (NC n= 11; WV n= 17; PA n= 10; VT n= 16) met the requirement of at least 30 consecutive songs and were of high enough quality to be visually analyzed. Statistical analysis was performed using SPSS 19 (IBM SPSS Statistics for Windows, Version 19.0. IMB Corp., Armonk, NY, USA).

Using the song typing protocol above, I described 22 distinct song types across 54 analyzed Veeries (Table 1). The naïve student's results of duplicating the song typing protocol for eight randomly selected Veeries were 100% identical to my results.

Songs types varied in the number of phrases and syllables sung, with a range of 1-3 phrases per song ($\bar{x}$ = 2.72, SD= 0.83) and a range of 2-7 syllables per song ($\bar{x}$ = 4.55, SD= 1.34). Although I found substantial song type diversity among the analyzed Veeries, more than half of all the total song types analyzed were ‘BBCC’ songs. Most of the analyzed Veeries (48 out of 54, 88%) included at least one ‘BBCC’ song type in their repertoire. Only four song types (‘BBCC’, ‘BBB’, ‘BBC’, and ‘BCC’) (Table 1) were sung across all four states, while other song types were geographically isolated, and some song types were sung by only one individual Veery. Visual analysis of spectrogram images revealed diversity in syllable morphology across individuals. An example of syllable diversity is shown in Figure 3, which shows individual variation in syllable morphology in four ‘BBCC’ song types sung by four different Veeries.

Each individual whose recordings met the song limit criteria were also used to describe the repertoire sizes of Veeries. Analyses suggested that a Veeries repertoires ranges from one to six song types, with the modal repertoire size being three songs (Figure 4). Repertoire size was normally distributed within each state, as well as across all sample states ($\bar{x}$ = 3; SD= .903; Skewness= .47; Kurtosis= 1.56). Repertoire size was not correlated to the number of songs sampled per bird (ANOVA: $F_{(2, 51)=}$ 0.99, p= 0. 38), with the number of songs sampled per bird as the dependent variable and repertoire size as the predictor variable in the analysis. Also, average repertoire size was not influenced by the time of day in which the singing was recorded (Morning recordings: n= 28 individuals, $\bar{x}$ repertoire size= 2.92, SD= 0.76; Evening recordings: n=26 individuals, $\bar{x}$ repertoire= 2.96, SD= 0.96).

Once song types and repertoire size were described for each Veery, I arbitrarily numbered the most frequently sung song type in an individual singing bout as ‘song one’, the next most sung song type was labeled ‘song two’, and so on for each song type in a repertoire. For many Veeries the most frequently sung song type was the typical ‘BBCC’ song type, therefore I labeled all ‘BBCC’ song types (or the more frequently sung ‘BBCC’ song type if more than one version was present in the repertoire) as ‘song one’. Once an individual’s song types were numbered I recorded the order in which they were originally sung and noted which song type was presented throughout the entire singing bout to investigate the way in which Veeries showcase their song repertoires.

Veeries present their song repertoires in patterns, and the structure of that pattern can vary depending on the size of an individual’s song repertoire. For example, Veeries that have a two-song repertoire tend to repeat one song type (which is usually the typical ‘BBCC’ song type) several times in a row before presenting the second song type (e.g., 1 1 1 1 1 1 2 1 1 1 1 2 1 1 1 1 2…) This pattern can be more structured, where the focal song is sung a specific number of times before introducing the second song type (e.g., 1 1 1 2, 1 1 1 2, 1 1 1 2…), or both songs types can be sung evenly back and forth (e.g., 1 1, 2 2, 1 1, 2 2, 1 1…) Veeries with three-song repertoires can have a similar pattern structure, where a focal song type is repeated several times before alternating between the other two song types (e.g., 1 1 1 2, 1 1 1 3, 1 1 1 2, 1 1 1 3…). This pattern can be more structured as well, and some Veeries with a three-song repertoire present each song type one after another without repeating any song type before the entire repertoire has been presented (e.g., 1 2 3, 1 2 3, 1 2 3…). Veeries that sing a four-song repertoire tend to not repeat any one song type more than once or twice in a row, rather they present each song type one right after the other without repeating any song type before the whole repertoire has been presented (e.g., 1 2 3 4, 1 2 3 4, 1 2 3 4…), or they present their repertoires in a pattern that features one or two song types more than once before the whole repertoire has been presented (e.g., 1 2 1 2 3 4, 1 2 1 2 3 4, 1 2 1 2 3 4…). I recorded a single Veery that sang a five-song repertoire and one Veery that sang a six-song repertoire. These two individuals presented their song repertoire in loose patterns that are similarly structured to Veeries with a four-song repertoire. The individual Veery with a five-song repertoire presented four out of the five song types in a regular pattern and would replace one song type in the pattern with the fifth song type every two or three cycles (e.g., 1 2 3 4, 1 2 3 4, 1 2 3 5, 1 2 3 4, 1 2 3 4, 1 2 3 5…). The Veery with the six-song repertoire did not present its repertoire in a clear pattern like Veeries with smaller repertoires, although there was minimal repeating of one song type more than once in a row, and some song types were always presented in sequence (e.g., song type 1 was always followed by either song type 5 or song type 3, and song type 6 always preceded song type 1). Each of the 54 analyzed singing bouts was described as either 'alternating' or repetitious'. Veeries that repeated any song type three or more times in a row was labeled as 'repetitious' while Veeries that did not repeat any song type more than twice in a row were described as 'alternating'. Overall the distribution of song delivery patterns was uniform across the each sample state (Table 2).

I also measured the overall peak frequency of each song throughout each individual's singing bout. Veeries present their songs in oscillating peak frequency patterns, a previously undescribed feature of Veery song behavior. Peak frequencies of each song ranged from 4.0 to 6.5 kHz, and sequential songs were presented in predictable peak frequency patterns that gradually oscillated between the highest peak frequency and the lowest peak frequency. This oscillating pattern of peak frequencies was seen regardless of repertoire size.. Each song type was sung within a particular peak frequency range, and the frequency range for each song type presented was fairly consistent throughout the singing bout (Fig. 5). Peak frequencies of two consecutive songs were never the same (regardless of song type). Since Veeries present their song types in patterns, indicating the peak frequency of each consecutive song revealed the complex way in which Veeries present their song repertoires: repertoires are presented in a song type pattern as well as an oscillating peak frequency pattern (Fig 5)

DISCUSSION

Visual analysis of Veery song spectrograms revealed variation in song type diversity, variation in syllable morphology, and patterns in song delivery that have not been previously documented. A basic repertoire size of one to five songs has been described in the literature (Weary et al. 1987; Borror 1964; Hartshorne 1956), underestimating the true repertoire size that I describe here. The Veery's repertoire range of one to six song types falls within the ranges of other North American thrushes. The Veery's sister species, Bicknell's Thrush (*Catharus bicknelli*) (Voelker et al. 2013), has a comparable repertoire size (Ball 2000), the Hermit Thrush has a repertoire range of six to twelve song types (Rivers and Kroodsma 2000), and the closely related Swainson's

Thrush (*Catharus ustulatus*) has a song repertoire ranging from three to seven types (Mack & Wong 2000).

Variation in song repertoire size has been linked to many aspects of avian biology. Repertoire size has been positively correlated with territory size or better quality territories (Howard 1974; Aweida 1995) and repertoire size has also been described as a tool in mate attraction (Catchpole 1980) and territory security (Krebs et al. 1978). A larger repertoire of songs may be an honest signal of fitness to perspective females, if repertoire size reflects the amount of time a male can devote to singing (Krebs 1977). Larger repertoire sizes may also be advantageous for males engaging in territorial encounters where discrimination between neighbors and intruders can be made by recognition of repertoires and song sharing (Hughes et al. 2007). Weary et al. (1987) investigated neighbor-stranger discrimination by song in the Veery and found in several trials that males responded to playbacks of strangers after hearing only one or two songs, suggesting that Veeries can discriminate between strangers and neighbors based on within song features, i.e., syllable morphology, rather than repertoire size. The role repertoire size plays in mate attraction and territory acquisition for the Veery is unknown.

The typical advertising song of the Veery is a three part song: an introductory note followed by a two-syllable B phrase, ending with a two-syllable C phrase. Veeries create different song types by adding or subtracting phrases and/or syllables from the typical 'BBCC' song structure. Although there are a variety of song types described (22 visually distinct song types from 54 individuals), the overwhelmingly common song type found across all recorded Veeries was the typical 'BBCC' song type. Most (88% of total recorded individuals) of the sampled Veeries included at least one 'BBCC' song type in its repertoire, and the ‘BBCC’ song type was usually the most frequently sung song type across all singing bouts and was also the most commonly repeated song type within singing bouts.

Species recognition is a clear and important function of bird song (Catchpole & Slater 1995), and this particular fucntional aspect of song is especially important for the Veery because of poor visibility in breeding habitats (Dilger 1956) and the overlap in breeding ranges the Veery shares with closely related species like the Wood Thrush and its congeners: Bicknell’s, Swainson’s and Hermit thrushes. To minimize the occurences of species misidentification, each species typically possess stereotyped and unvarying songs within a population (Emlen 1972) that communicates species identifcation. As an oscine bird, Veeries develop song through a process of song learning that includes an initial sensory or instructional phase where young birds listen to and commit tutor songs to memory, followed by the motor or production phrase where memorized songs are practiced and crystallized (Bell et al 1998). Innate templates of proper song strucutre aid in the song learning process (Gill 2007). The typical ‘BBCC’ song type could be considered the genetically innate template song of the Veery, which may explain the pervasive use of this one song type. Diversity in song types could be reflection of learning or inventing variations of the ‘BBCC’ template, based on the way Veeries create different song types by adding or subtracting phrases and/or syllables from the typical ‘BBCC’ song structure.

Although common song types like the ‘BBCC’ song of the Veery may communicate species identity, another important function of song is to communicate the individual identity of the singer. Studies have shown other thrush species use song as a tool for individual identification. Clay-colored Thrushes (*Turdus grayi*) sing syllables that are largely unique to the individual (Vargas-Castro et al. 2012). In Bicknell's Thrush, individuals convey their identity by singing distinct song types (Ball 2000). Veeries sing a variety of song types that are structurally similar (e.g., most Veeries sang a 'BBCC' song), but visual analysis of spectrogram images showed that the syllable morphology within similarly structured songs varied from individual to individual (Fig 3). The high variation in syllable morphology found in Veeries may be a signal used for individual identification, which Veeries could employ for kin and neighbor-neighbor recognition (Vargas-Castro et al. 2012).

The variation in syllable morphology may be a consequence of song learning in Veeries. There is little information on song development in the Veery (Bevier et al. 2005), but song learning has been studied in hand reared Wood Thrushes.Whitey and Miller (1987) hand-reared Wood Thrushes and exposed young males to 16 tutor recordings: four natural, unaltered songs and four frequency-altered variants for each natural song. Four out of the five young Wood Thrushes copied songs heard from the tutor. These Wood Thrushes did not prefer to copy one song type over another, they did not selectively copy songs in a way that would develop a highily contrasting repertoire, and two of the five Wood thurshes created several versions of one song type and ignored other song types. The fifth Wood Thrush developed phrases that did not resemble any of the tutor's songs or songs recorded from the population from which the bird was taken. All of the Wood Thrushes in this study failed to develop exact copies of the tutor songs, rather they sang songs that contained similar elements to their tutors and invented their own syllable details. Although more reaserach is needed in this area for the Veery, individual varaition in the morphology of syllables seen in the Veery songs may be a consequence of song learning and development.

Visual analysis of consecutively sung songs in a singing bout revealed patterns in the way Veeries present the song types in their repertoire. Some patterns of singing included prolonged repetition of one song type before introducing a different song type, while other individuals presented songs in an alternating fashion, i.e., constantly switched song types in a pattern throughout the singing bout without repeating a particular song type more than once in a row. The way in which birds present their repertoires may vary in context and circumstance (Rivers & Kroodsma 2000; Price et al. 2013), and singing behavior may be used as a signal of breeding status. Stacier et al. (2006) found that unpaired American Redstarts (*Setophaga ruticilla*) sang at higher rates and tended to repeat one song type throughout a singing bout or “Repeat Mode”, whereas paired males tended to sing in “Serial Mode”, where two or three song types were sung in an alternating fashion. In unpaired American Redstarts, repeating one song type in a singing bout could be a signal for mate attraction, while the Serial Mode of singing (sung more often by paired males) may be a signal for conspecific males and used in territory defense.

Veeries with smaller repertoires (1-3 song types) presented songs in a variety of patterns, ranging from song patterns that feature one repeated song type (usually the BBCC song type) more than other song types (e.g., 1 1 1 1 1 2 1 1 1 1 3 1 1 1 1 1 1 2…), to patterns that featured all song types equally (e.g., 1 2 3, 1 2 3, 1 2 3…) Veeries with larger repertoires (4-5 song types) tended to present songs in patterns with minimal repeating of any one song type. There was no clear pattern in song type delivery in the individual Veery that sang a six-song repertoire, as compared to individuals with smaller song repertoires. Dobson (1977) investigated singing patterns in Swainson's Thrush and speculated that the 'errors' in the delivery order of song types in individuals with larger repertoires (as opposed to individuals with smaller repertoires delivered in ridged, predictable patterns) could be a consequence of having more songs to remember, and possibly due to the structural similarities of song types. It could be speculated that larger song repertoires are more challenging to remember and present in a set pattern, and the Veery with the six-song repertoire, like the Swainson's Thrush with a seven-song repertoire, consequently sang its song in an unclear pattern.

The ways in which Veeries present their repertoires (i.e., individuals with similar repertoire sizes that have different song delivery patterns) may reflect contextual differences in the message the songs are communicating and the intended recipient of the signal (Price and Crawford 2013; Stacier et al. 2006). I could not test the contextual circumstances in singing patterns in this study because the Veeries I recorded were not banded or examined for pairing status. However, no Veery switched the pattern of song presentation during their recorded singing bout. Additionally, Veeries in NC were recorded up to three weeks earlier than Veeries in VT and this presumably covers different parts of the breeding season. Since singing patterns did not vary from state to state (Table 2) there was no evidence that singing pattern indicates breeding status. Recording singing bouts and monitoring of breeding behavior in a focal population of Veeries throughout a breeding season could reveal if Veeries change the way in which they present their song repertoires based on breeding status and would shed light on the context that song patterns have in Veery interaction.

Regardless of repertoire size and pattern of song delivery, Veeries presented their songs in an oscillating frequency pattern. This fluctuation of singing songs at high and low frequencies ranges may be a tool used in mate attraction, where showcasing each male's ability to sing at a variety of different frequencies could be a reflection of male fitness.

Ballentine et al. (2004) investigated the influence of vocal performance of male Swamp Sparrows (*Melospiza georgiana*) and showed that females respond more to males with high-performance singing (songs with higher trill rates and frequency bandwidths). It is thought that female Swamp Sparrows prefer males that can sing more complex songs that reach towards song production limits (i.e., the physiological constraints of song production). Veeries may showcase vocal control and precision by singing multiple song types at varying frequencies to attract females, who may find this feature of song production a sign of higher fitness.

Songs contain a variety of information about the singer, such as territory location and breeding status, and each message may have optimal transmission requirements (Emlen 1972). The way in which Veeries present their repertoires (i.e. in various song type patterns and oscillating peak frequencies) may be related to whom the singer is attempting to send a signal to, whether it is a rival male or a perspective mate.

During the song typing analysis, song images did not include a frequency axis, therefore I did not take the overall peak frequency of each song into account as a feature that defines a song type, rather I grouped songs together based on structural similarities of phrases and syllables. Veeries can sing structurally identical song types in varying frequency ranges, and it is unknown if Veeries use frequency range to define a song type;

therefore there I may have underestimated the repertoire size of the recorded Veeries. For example, I described an individual Veery from VT as having a one-song repertoire. This individual Veery sang one structurally identical song type throughout a sixty-five-song singing bout, but presented this one song type at three oscillating frequency ranges with different peak frequencies (4.5, 5.0, and 5.5 kHz; Fig. 6). It is unknown if songs sung at different frequencies convey different messages. The function of presenting consecutive song in oscillating frequencies needs further investigation.

I found Veery song stucture and singing behavior to be more complex and variable than previously described in the literaure. Veeries have a song reperoire ranging from one to six song types, and Veeries deliver their song repertoires in various song type patterns and present songs in oscillating frequency patterns. Further investagtion into the singing behavior of Veeries is needed to understand the significance of repertoire size variability and the contextual function of singing patterns and oscillating frequencies of Veery song delivery.

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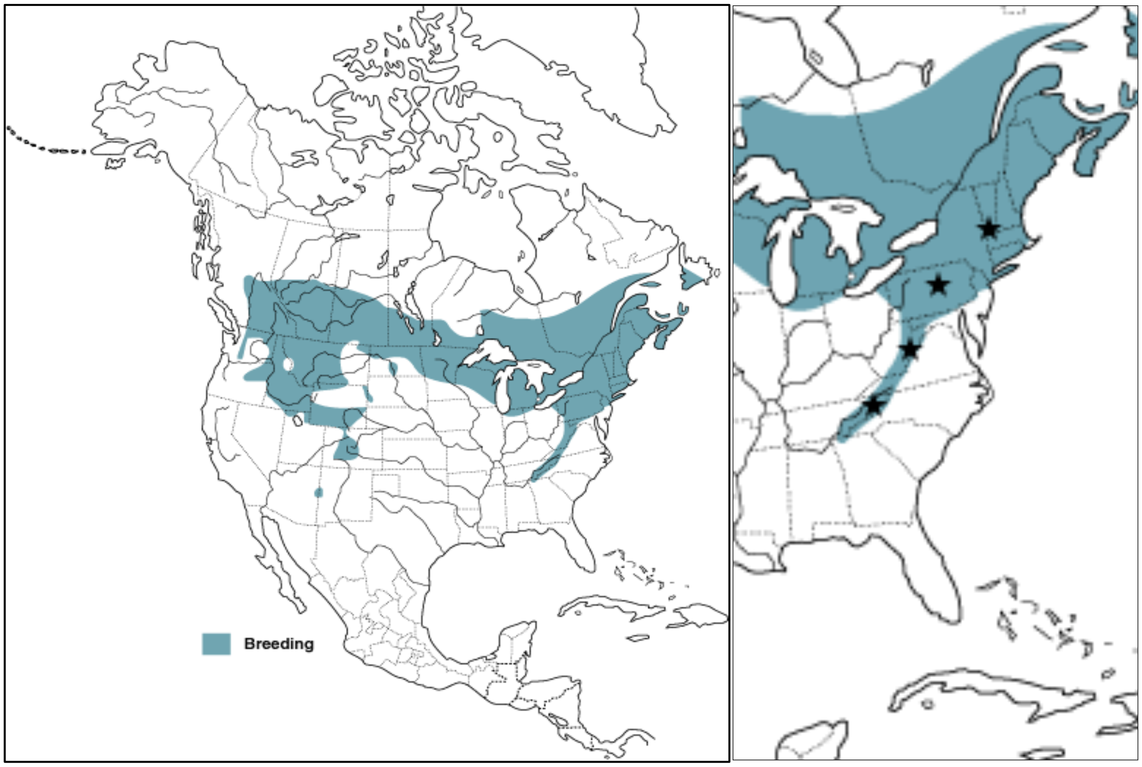

Figure 1

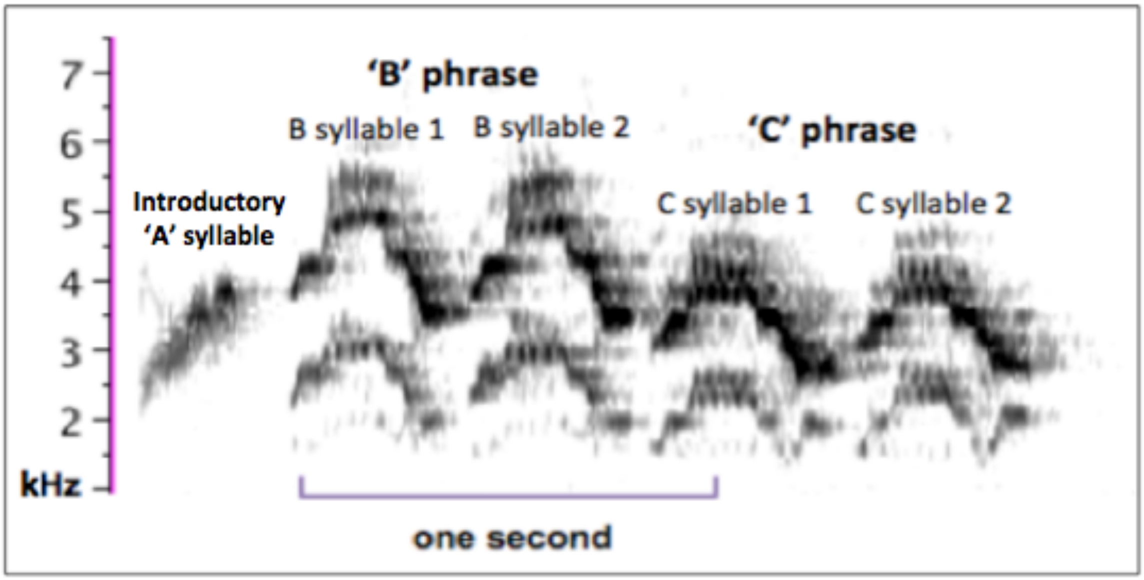
7
6
5
4
3
2
kHz
'B' phrase
B syllable 1
B syllable 2
'C' phrase
Introductory
'A' syllable
C syllable 1
C syllable 2
one second

Figure 2

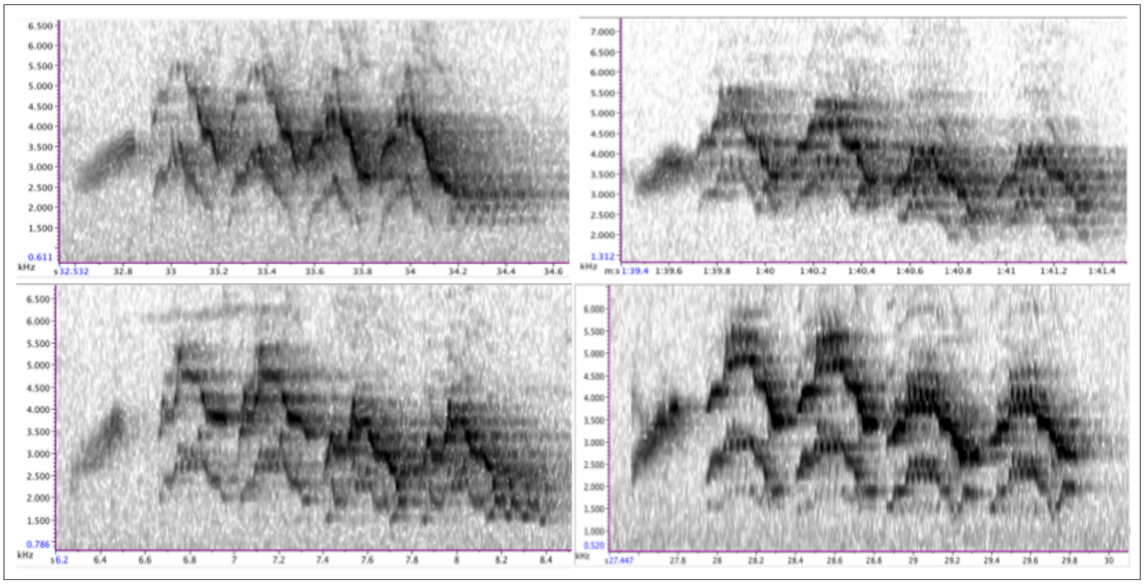

Figure 3

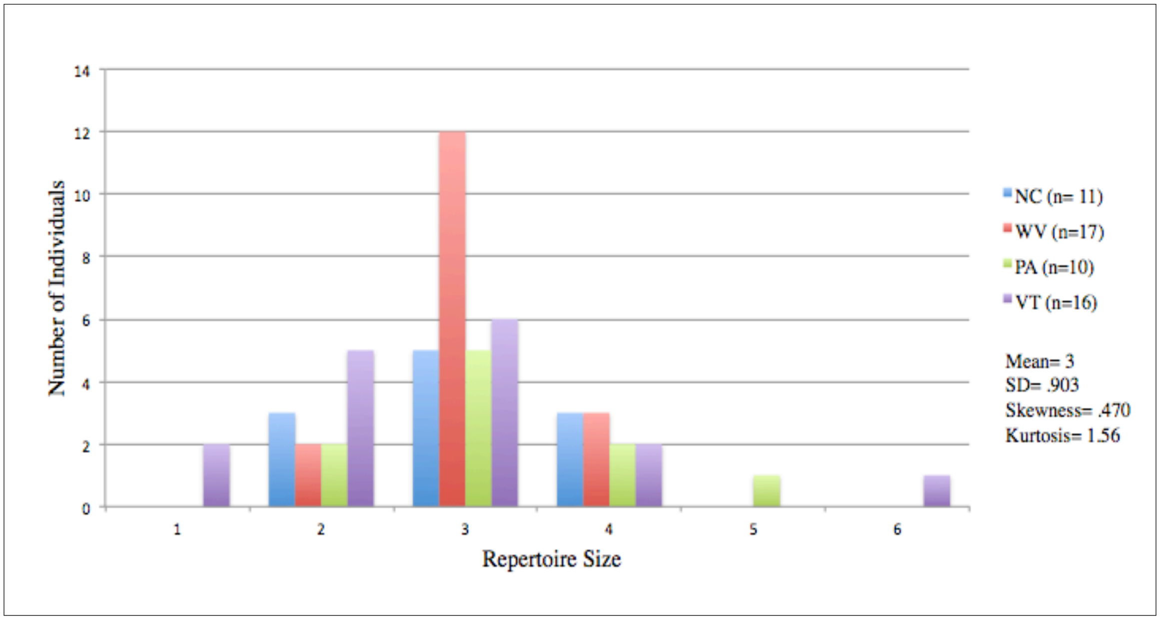
14
12
10
8
6
4
2
0
Number of Individuals
1
2
3
4
5
6
Repertoire Size
NC (n= 11)
WV (n=17)
PA (n=10)
VT (n=16)
Mean= 3
SD= .903
Skewness= .470
Kurtosis= 1.56

Figure 4

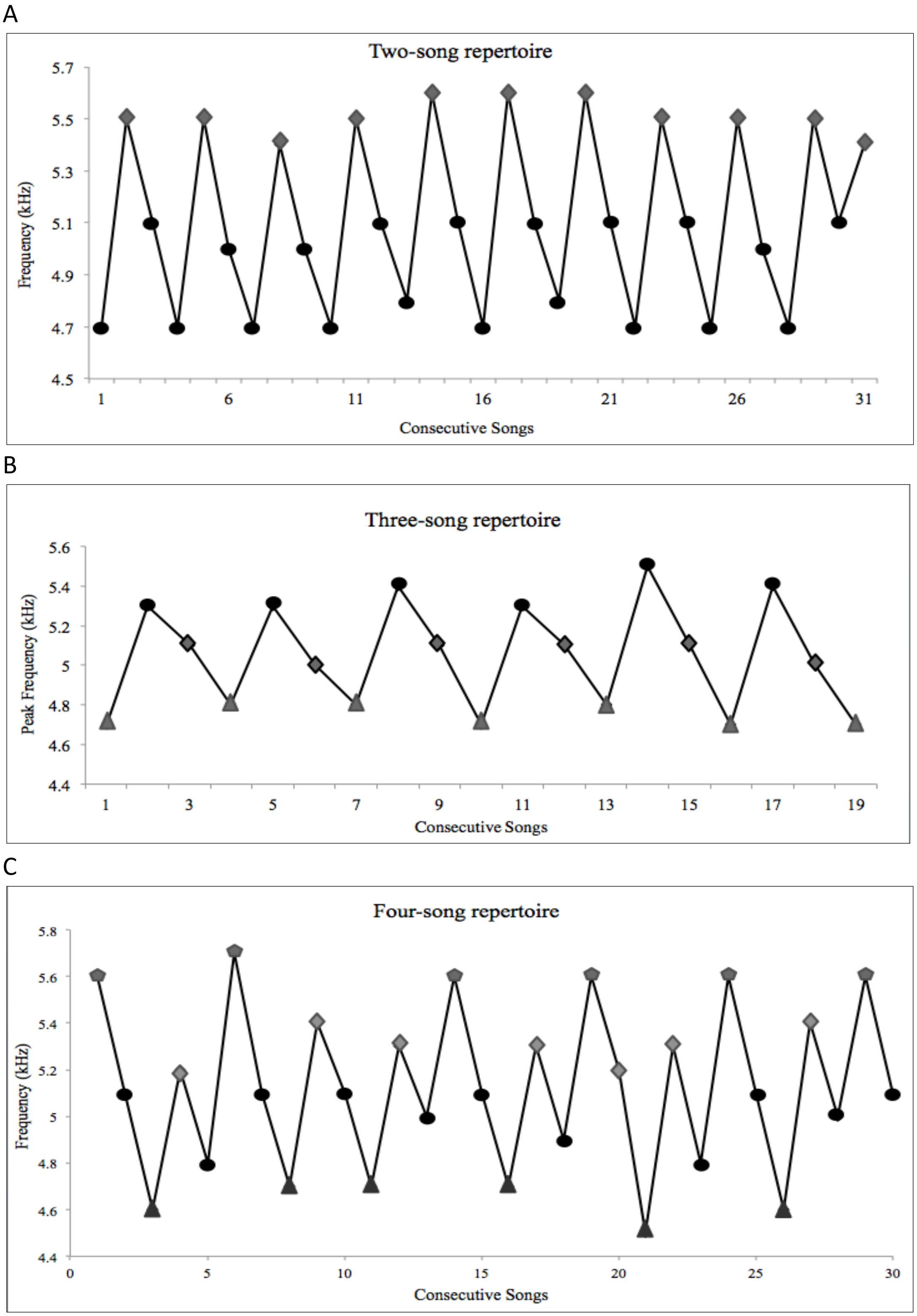
A
Two-song repertoire
Frequency (kHz)
5.7
5.5
5.3
5.1
4.9
4.7
4.5
1
6
11
16
21
26
31
Consecutive Songs
B
Three-song repertoire
Peak Frequency (kHz)
5.6
5.4
5.2
5
4.8
4.6
4.4
1
3
5
7
9
11
13
15
17
19
Consecutive Songs
C
Four-song repertoire
Frequency (kHz)
5.8
5.6
5.4
5.2
5
4.8
4.6
4.4
0
5
10
15
20
25
30
Consecutive Songs

Figure 5

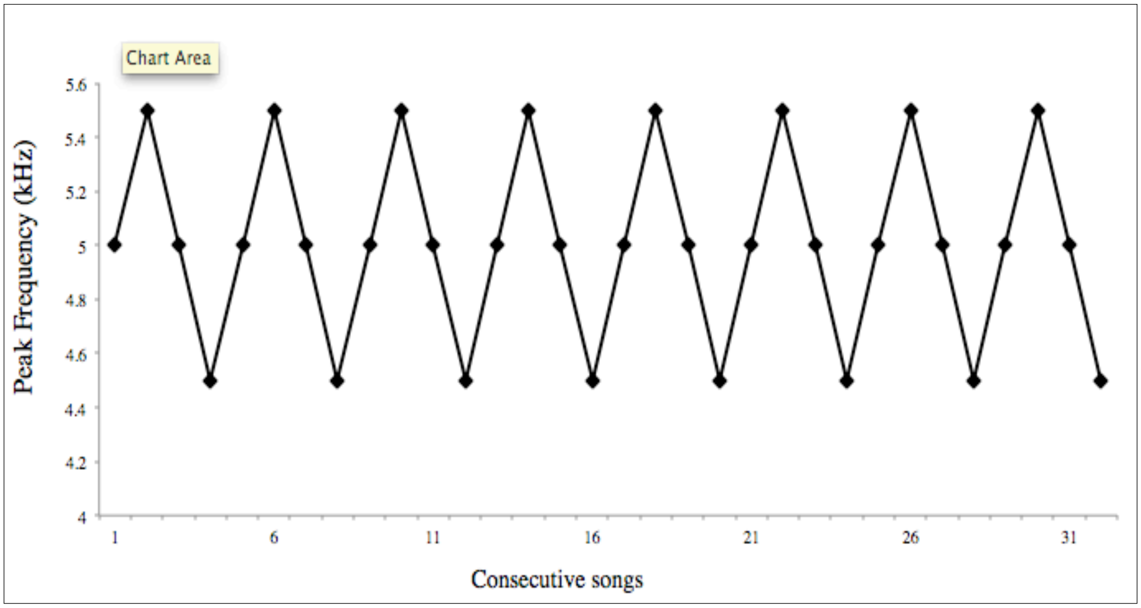
Chart Area
Peak Frequency (kHz)
5.6
5.4
5.2
5
4.8
4.6
4.4
4.2
4
1
6
11
16
21
26
31
Consecutive songs

Figure 6

Table 1. Twenty song types were recorded across all individuals sampled in the Appalachians. The three most common song types are highlighted, and all song type frequencies are shown here.

	NC	**WV**	**PA**	**VT**	**Overall #**	
# of individuals	n=11	n=17	n=10	n=16	54	**% of Total Songs**
ALL SONG TYPES	N= 491	N= 852	N= 477	N= 827	2647	
BBCC	314	414	84	552	1364	51%
BBB	3	85	26	102	216	8%
BBC	24	81	87	30	222	8%
BCC	8	65	49	36	158	6%
BBCCC	36	21	56	0	113	4%
BBBCCC	0	85	12	0	97	4%
BBBB	0	67	10	0	77	3%
BBCDD	9	11	0	56	76	3%
BCD	0	0	73	0	73	3%
BCCD	22	0	13	28	63	2%
BBCCD	29	0	0	14	43	2%
BBBCC	0	0	46	0	46	2%
BCCC	30	0	9	0	39	1%
ATYPICAL	0	0	17	0	17	0.6%
BCCDD	6	0	0	8	14	0.5%
BB	0	0	0	15	15	0.5%
BBBBCCC	0	11	0	0	11	0.4%
BCDD	0	0	0	8	8	0.3%
BBCCDD	0	7	0	0	7	0.2%
BCCDDD	5	0	0	0	5	0.1%
BBCCDDD	5	0	0	0	5	0.1%
BBBBB	0	5	0	0	5	0.1%

Table 2. Analyzed singing bouts were described as either ‘alternate’ or repetitious’. Singing bouts where one song type was repeated three or more times in a row was labeled ‘repetitious’. Singing bouts that had minimal repeating of any song type were labeled as ‘alternate’. Overall, Veeries recorded from each state sang more alternate singing patterns than repetitious singing patterns.

Singing Pattern Type	State	Percent
NC	NC n=11	%
Alternate	8	72.7
Repetitious	3	27.2
WV	WV n=17	%
Alternate	13	76
Repetitious	4	23
PA	PA n=10	%
Alternate	8	80
Repetitious	2	20
VT	VT n=16	%
Alternate	10	62.5
Repetitious	6	37.5
Overall	Overall n=54	%
Alternate	39	72.2

CHAPTER II

GEOGRAPHIC VARIATION IN THE SONGS OF THE VEERY (*CATHARUS FUSCESCENS*) ACROSS THE APPALACHIAN MOUNTAINS

INTRODUCTION

Song divergence across populations of birds has been recognized as a precursor to sexual isolation that could potentially lead to speciation (Ruegg et al. 2006). Because song has such an important role in avian communication and population dynamics, geographic variation in song has been a growing topic of research. A wealth of studies focused on song variation in many species, especially in the White-crowned Sparrow (*Zonotrichia leucophrys*), have suggested geographic song variation and dialect systems across populations may play a role in assortative mating (Nottebohm 1970), female mate choice (Baptista and Morton 1988), male and female dispersal (Baker and Mewaldt 1978; Petrinovich et al 1981), acoustic adaptation to habitat structure (Morton 1975) and gene flow between populations (Baker et al. 1982, Zink and Barrowclough 1984).

The ontogeny of song and its influence on song variation at individual, population, and geographic scales is a current and often conflicting topic of research with a long history in ornithology (Marova et al. 2010). Geographic variation in bird song found in many species may simply be an artifact of cultural transmission of acquiring and learning song (Jenkins 1977; Catchpole and Slater 1995) from conspecifics (paternal or neighboring) during song development. Regional dialects of shared song elements with a population (Harris and Lemon 1972) may form and persist due to beneficial social adaptations that allow individuals to effectively interact within conspecifics (Catchpole and Slater 1995), such as song matching between neighbors (Jenkins 1977) and copying songs of older, dominant males (Payne 1981).

Oscines (Order Passeriformes: Suborder Passeri) typically have vocal organs developed in such a way to produce diverse and complex songs, and the songs and repertoire sizes of the roughly 4,000 different species of oscine birds can vary dramatically in size and complexity (Slater and Catchpole 1995). For example, the Ovenbird (*Seiurus aurocapillus*) song repertoire includes only one simple song (Falls 1978), while the repertoire size of the Brown Thrasher (*Toxostoma rufum*) includes upwards of 2,000 different songs (Kroodsma and Parker 1977). Unlike suboscine birds that innately produce their species' song (see Chapter One for further discussion), oscines learn their species' song in a multi-phase process guided by genetically encoded frameworks and social interaction that results in the eventual production of songs that can be recognized by conspecifics (Gill 2007).

Although the song learning and development processes may vary from species to species, in general, oscines learn songs in two steps. First, young birds must recognize and commit conspecific songs to memory. This stage of learning occurs within 10-50 days of age in some species (Marler 1970), although studies have shown that this sensitive period of song learning can last up to 100-150 days of age and even well into the next breeding season in some species (Marler 1997). Later in development, perhaps weeks to months following exposure to and memorization of tutor songs (Marler 1997), young birds will begin to produce ‘plastic songs’, which are attempts to produce memorized conspecific songs. This process is similar to the babbling of babies in human vocal development. Young birds practice singing memorized songs until the songs match the conspecific model. Plastic songs are then crystallized and incorporated into the individual’s adult song repertoire (Nottebohm 1991). Again, song development and timing of each learning phase varies from species to species, and there is evidence that song learning may not be limited to nestling songbirds (Slater 1983, Marler and Peters 1987). But overall it is thought that the songs experienced by nestling birds may have an influence on singing behavior later in life (Marler 1997) and is subject to change because acquiring song is a learning process.

In this study I investigate regional and geographic variation in the typical advertising song of the Veery (*Catharus fuscescens*) across a continuous portion of the breeding range. The Veery is a member of the Family Turdidae (the thrushes), within the oscine songbirds. In general, the Veery is a poorly understood species (Bevier et al. 2005), and little is known about the genetic and behavioral (song) variation in their populations. Veeries are a common Neotropical migrant thrush that breeds in secondary growth and woodland habitats spanning from southeastern British Columbia and south into the southeastern Rocky Mountains, across southern Canada and south into the northeastern United States, continuing through the higher elevations of the Appalachian Mountains from western Maryland to northern Georgia (Bevier et al. 2005) (Figure 1). This study investigates frequency and temporal variation in the songs of the Veery across the

Appalachian Mountains, a continuous portion of the breeding range with isolated southern populations.

Five thrush species inhabit the Appalachian Mountains during the breeding season. In the northeastern section of the Appalachian Mountains the breeding range of the Veery, Gray-cheecked Thrush (*Catharus minimus*), Hermit Thrush (*Catharus guttatus*), Swainson's Thrush (*Catharus ustulatus*), and Wood Thrush (*Hylocichla mustelina*) are sympatric. Noon (1981) observed that in northeastern Appalachia, the five thrush species distribute breeding territories in distinct, yet overlapping, elevation gradients thought to be caused by heightened interspecific and intraspecific competition for habitat and resources. The breeding ranges of these thrush species reach their southern limit in the northeastern portion of the mountain range, and only the Wood Thrush and the Veery breed in high elevations of the southernmost Appalachians. The reduced interspecific competition Wood Thrushes and Veeries in southern Appalachian experience causes an ecological release and Veeries will breed in a wider range of elevations than more northern populations. Along with the ecological release Veeries experience in southern Appalachia, Morse (1971) found that Wood Thrushes and Veeries tend to show minimal hostile behaviors in shared habitats.

Veeries that breed in southern Appalachia are restricted to appropriate habitats found only in high elevations, and therefore dispersal may be limited for southern Veeries when compared to Veeries that inhabit northern Appalachia, where elevations decline and appropriate habitat is more broadly available. Varying levels of interspecific competition as well as variation in dispersal opportunities across the Appalachian Mountain range make this an interesting system to investigate song variation. Song variation has been described in two congeners, the Hermit Thrush (Rivers and Kroodsma 2000; Roach et al 2012) and Swainson's Thrush (Ruegg et al. 2006), and although not explicitly studied in the Veery, song variation is expected.

In this study I tested the hypothesis that the songs of the Veery show geographic variation by investigating three questions: (1) Does the typical ('BBCC') advertising song of the Veery vary within each sampled region, (2) Does the typical advertising song of the Veery vary across the four samples regions, and (3) Does elevation and/or time of day in which a Veery sings have an effect on song variation?

STUDY SITE AND METHODS

To test for geographic variation in the songs of the Veery, recordings of male vocalizations (females do not sing) were made during late May through June 2012 in four locations along the Appalachian Mountains: eastern North Carolina, central West Virginia, north-central Pennsylvania, and southern Vermont (Fig. 1). Veery songs were recorded as digital .wav files at 48 kHz and a 24-bit depth with a Nagra ARES BB+ recording unit with Sennheiser ME 67 shotgun microphone. In this study I recorded spontaneously singing, unbanded Veeries during both dawn and dusk choruses. Morning recordings were conducted from 0430-0930 hours EST, and evening recordings were conducted from 1800- 2130 hours. To avoid recording the same individual twice, each sampling area was visited only once. Veery territories are thought to have a radius of approximately 250 m (Weary et al. 1991), therefore I moved at least 500 m from one sampling area to the next to avoid recording the same individual from the same territory. Weather conditions were fairly consistent throughout the recording season, with high temperatures ranging from 13-25°C with partly cloudy to clear skies and little to no wind. Due to the decrease in singing activity, recordings were not made during adverse conditions such as unseasonably cold, windy, and rainy weather.

Veeries breed and defend territories in damp, deciduous, and brushy habitats along forested roads and trails or areas that were recently logged. Appropriate breeding habitats were scouted and individual Veeries were located by ear from forested roads and trails and then pursued on foot. Each focal male's singing was recorded while I moved closer to the individual until I was as close as possible to the focal Veery, approximately within 3 m of each singer. Each Veery was recorded for at least five minutes or as long as the bird would allow before the singing bout ended. Based on the recording protocol of Rivers and Kroodsma's (2000) investigation into the singing behavior of the Veery's congener, Hermit Thrush, which cycles through their entire repertoire in approximately 20 songs, I attempted to record at least 30 consecutive songs from each individual Veery to capture the full song repertoire of each focal individual. A general habitat and weather description, as well as time of day information were documented with every recorded Veery. Geographic coordinates were noted for every Veery recorded using a Garmin etrex 20, and Google Earth (Google Inc. [2013] Version 7.1.1.1888 [Software]. Available from kh.google.com) was used to determine the elevation of each recording location.

The typical advertising song of the Veery has an overall descending sound and consists of three parts (Fig. 2). The song begins with an upslurred introductory 'A' note, followed by the 'B' phrase, which typically consists of two high frequency duplicate syllables. The song ends with the 'C' phrase typically comprised of two lower frequency duplicate syllables. The introductory 'A' note of the Veery song is not an important feature for song recognition (MacNally et al. 1985), and preliminary analysis showed little variation in the introductory note, within or across states (Table 1); therefore the introductory note was largely ignored in this study, and descriptions of song types (e.g., ‘BBCC’) will not include the ‘A’ introductory note separately, but the note will be included in the whole song measurements (e.g., song length). Although Veeries present song repertoires ranging from 1-6 song types (see Chapter One for further discussion), only the typical ‘BBCC” song type was analyzed for geographic variation because the ‘BBCC’ structured song is the most commonly presented song type sung across Veeries. Eliminating song type variation found in Veery repertoires allowed the analyses to focus on the geographic variation in the acoustic features of a common, widespread song.

To investigate geographic variation in Veery song I measured the following song variables for each ‘BBCC’ song: highest frequency (HF) (Hz), lowest frequency (LF) (Hz), change in frequency (ΔF) (Hz), and song length (ΔT) (sec) (Table 2). These basic acoustic features of song structure have been analyzed in many studies investigating geographic variation (Ribot et al. 2009; Bond and Diamond 2004; Austen and Handford 1991). Song feature measurements were made on each complete song, and within each song each B and C phrase was measured separately. This song measuring protocol resulted in twelve measurements per song (Figure 3; Table 2). Spectrogram images of recorded songs were generated and all song measurements were made using the bioacoustics programs Raven Pro 1.4 and 1.5 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). The songs of the Veery are sung within a frequency range of approximately 6,500 – 1,500 Hz. To optimize song image quality of Veery songs all sound files were band pass filtered with a lower frequency limit of 500 Hz and an upper frequency limit of 24,000 Hz.

Statistical analyses were performed using the programs SPSS 19 (IBM SPSS Statistics for Windows, Version 19.0. IMB Corp., Armonk, NY, USA) and the statistical package HLM 7 (Scientific Software International, Inc., Skokie, IL). Due to the nested nature of the data (i.e., variation in songs can be observed within a single bird's repertoire, among localities within a single state, and across a continuous range), I constructed a three-level (HLM-3) uncentered random coefficient model to test for variation in each of the measured acoustic features between and within each state.

For each measured song feature, a HLM-3 null model was conducted. Intra class correlations were calculated for each null model to assess the amount of unexplained variance between level-2 and level-3. Below is an example of the modeling process for one of the 12 song variables measured: whole song, lowest frequency (WSLF). The output variable for the HLM-3 model is WSLF, and there are no predictor variables in the model, creating a null model for WSLF. Null model level-1 results showed whether or not average WSLF intercepts were different from zero (i.e., is the average WSLF for songs within a bird different from zero), and level-2 intercept results showed if average WSLF for each bird differed from zero (i.e., if the WSLF for each bird was averaged for each bird, is the average of those averages different from zero). The null model also tests whether birds show variance in those intercepts (level-1) and whether states show variance in those intercepts (level-2). If there was significant intercept variability in the null model, the next step was to run a new model that included level-2 predictor variables (elevation and day vs. night). These results showed whether the slopes of the predictor variables are significant (i.e., whether the predictor variables had an effect), as well as whether or not the slopes of the predictor variables had significant variance across states. This modeling process was repeated for each song variable measured.

The song features that were measured (Table 2) represent the first level in the model (Level-1). For each Level-1 equation, one of the twelve song features (Table 2) measured was the output variable. The song data are nested within individual Veeries, which represent the second level of the model (Level-2). In each random coefficient model, the Level-2 equation incorporated predictor variables (1) time of day (day vs. night singing) and (2) elevation. Each singing bout was coded as either day or night (day=1, night=0) to create the time of day data. Because the focal interest was in investigating how the elevational differences between sample states effect Veery songs, the predictor variables were not centered; therefore the models are essentially exploratory tests using raw data. The disadvantage of conducting uncentered models is that more error is associated with the raw data and I am ignoring potential correlations between data from levels 1 and 2. The sample state in which the birds (and their songs) originated from represents the 3rd Level of the model (Level-3). State identification was the unifying factor that maintained the hierarchical structure of each model tested. Random coefficient modeling allows testing for within state song variation while simultaneously testing for across state variation, and random coefficient models are designed to deal with the violation of independence of observation, the assumption that data from similar contexts (i.e. birds from the same state) are more similar than data from different contexts.

Each acoustic variable that was measured (Table 2) was analyzed separately in a random coefficient model to test for geographic variation in each song feature within and across states (using the standard 0.05 significance criterion). For each of the twelve song variables measured, four separate models were conducted: (1) Null model- no predictor variables included, (2) elevation predictor included, (3) time of day predictor included, and (4) both elevation and time of day predictors included- resulting in a total of 48 models tested. Geographic variation in the measured acoustic features was followed up by ANOVA and Tukey's post-hoc analyses.

RESULTS

A total of 3,088 songs were recorded from 109 individual Veeries across the Appalachian sampling range (NC: 863 songs from 29 individuals; WV: n= 952 songs from 26 individuals; PA: n= 523 songs from 24 individuals; VT: n= 750 songs from 30 individuals). The typical 'BBCC' song type was the most commonly sung song type across the sample states and constituted 50% of the total songs recorded (1,558 out of 3,088 songs), and 87% (95 out of 109) of all recorded Veeries contained at least one 'BBCC' structured song type in their repertoire.

The twelve frequency and temporal characteristics (Fig. 3, Table 2) described above were measured on 1,525 'BBCC' songs sung by 83 individual Veeries (NC: 505 songs from 23 individuals; WV: 381 songs from 21 individuals; PA: 168 song from 15 individuals; VT: 471 songs from 24 individuals). The number of songs measured per bird ranged from 4 to 59 songs, with an average of 18.4 songs per bird (mode= 15 songs, median= 15 songs) (Table 3).

Intraclass correlations were calculated for each HLM-3 null model and I found 1-35% of the variation detected in the measured song features resides between sample states while 65-99% of the variance detected resides within each same state (Tables 6a-6c). Elevation data for each bird and the time of day in which the Veeries sang (day vs. night) were included in subsequent models to test if these predictor variables had a significant effect within states and if the effect of the predictor variables varied across sample states.

Results showed significant variation in each measured song features within each state based on uncentered random coefficient models. Each frequency and temporal feature of whole 'BBCC' songs as well as the 'B and C phrases' were significantly different ($p < 0.001$) within each sample state. These results were consistent for null models as well as models that incorporated elevation and time of singing data (Table 5).

Uncentered random coefficient models show significant geographic variation ($p = <0.05$) in some of the measured frequency and temporal features of the Veery song (Tables 6a-6c, rightmost column) across the Appalachian Mountains. HLM-3 null models showed low frequency ranges and change in frequency ranges of whole songs, B phrases and C phrases, as well as C phrase length and high frequency ranges vary significantly across sample states. High frequency ranges and length of song/phrase did not vary significantly across states for whole songs and B phrases (Tables 6a-6c).

Elevation and time of day data were included into subsequent models as predictor variables to test for possible effects on geographic song variation. Every model output included a value of residual or unexplained variance between states. Calculating an R^2 value using residual variance values from null models to models including elevation and time of day data assessed if these predictor variables had an effect on song feature variation. Weak R^2 values ranging from -0.01- 0.13 (Tables 6a-6c) showed that elevation and time of singing were weak predictor variables to help explain the variation found in

Veery song features and overall these predictor variables did not have a significant effect within each state, and also the effect of these variables did not vary significantly across sample states [Although in three models- whole song length + ELEV+TOD, C phrase length +ELEV + TOD, and whole song change in frequency + ELEV+TOD- the effect of elevation across states was significant (Table 6a & 6b)].

Although overall elevation and time of day in which a Veery sings does not fully explain the geographic variation found in Veery song features and in general did not have a significant effect within or across states, including these predictor variables influenced the results in many models. For example, low frequency ranges and change in frequency ranges were significantly different across states for whole songs, B, and C phrases- however, including elevation and time of day predictors in the models resulted in insignificant p values for variance across states for whole song and B phrase low frequency ranges, and insignificant p values for B and C phrase change in frequency ranges, even though elevation and time of today did not have a significant effect within or across states. These results imply that although elevation differences across the sample areas and the time of day in which a Veery sings may not have a significant effect on the geographic variation in Veery song, these variables may be involved in an unknown confounding factor influencing song variation that was not measured in this study.

To more fully understand the significant geographic variation in frequency and temporal features of the Veery song, random coefficient models were followed up with ANOVA and Tukey's HSD post-hoc analyses using pooled state data for each measured song feature. Elevation and time of day variation was ignored in these analyses since the random coefficient models showed that time of day and elevation did not have a significant effect with in or across states and only reduced unexplained variance by 1-10%. ANOVA results were consistent with HLM-3 null model results, except in the case of change in frequency of the B phrase and length of C phrase (Table 4). Tukey's HSD post-hoc results showed that in many cases significant HLM-3 results were driven by one state (i.e. one group of Veeries). Specifically, Veeries from NC (and WV Veeries in some models) deviated sufficiently from the frequency ranges sung by Veeries in the other sampled states, whose similar frequency ranges overlap (Table 4). Although there is overlap in frequency ranges, an overall south-to-north shift in frequency ranges was observed, albeit statistically non-significant.

DISCUSSION

Using random coefficient modeling I investigated geographic variation in basic temporal and frequency characteristics (Fig. 3) of the typical advertising song of the Veery (Fig. 2) within and across four regions of the Appalachian Mountains. I found significant variation in song characteristics within each sample state as well as across states. I found that elevation and time of day in which a Veery sings only reduced unexplained variance in the random coefficient models by about 1-10%, and these predictor variables do not have a varying effect within or across states (with the exception of three analyses: whole song-song length, C phrase- phrase length, and possibly whole song-change in frequency, see Tables 6a & 6b). ANOVA tests and Tukey's HSD post-hoc analyses were conducted to observe overall trends in pooled state data and to more fully understand the significant variation in frequency and temporal features of the Veery song found in the random coefficient models.

The regional (within-state) and large-scale (across-state) variation in frequency and temporal features of the typical 'BBCC' songs of the Veery (Table 4) across the Appalachian Mountains could be a consequence of the interconnectedness of many developmental and behavioral processes such as song learning and development (Marler 1997; Kroodsma et al. 1997), plasticity in song production (Marler 1997), natal and breeding dispersal (Greenwood & Harvey 1982; Noon 1981), and varying levels of gene flow among populations (the southern Appalachian population belongs to the *C.f. pulichorum* subspecies [Phillips 1991]).

All measured frequency and temporal features of the typical Veery song vary significantly within populations on a regional scale (i.e., within-state) (Table 5); meaning that within each sample state, individual Veeries present their songs in a wide range of frequencies and song lengths. Veeries and other songbirds use song as a tool to communicate a variety of information about the singer (Catchpole and Slater 1995). One important function of song is to communicate individual identity to conspecifics (Weary et al 1986; Vargas-Castro et al 2012). Veeries use song to communicate individual identity and other information by singing diverse song repertoires in oscillating song type and frequency patterns (See Chapter One for further discussion). Veeries present consecutive songs in diverse oscillating frequency patterns, and Veeries tend to sing each song type in their repertoire at a particular peak frequency (e.g., one Veery will sing the 'BBCC' song at 3.5 kHz peak frequency, while another will sing at 4.0 kHz peak frequency). Variation in frequency and temporal features of the typical 'BBCC' songs within a population may be a result of Veeries presenting their ‘BBCC’ songs in a wide variety of frequencies that contrast from individual to individual, perhaps as a tool for individual identification.

Geographic variation in the advertising song of the Veery across the Appalachian Mountains was more complex. Random coefficient models (including models controlling for elevation and time of singing bout differences) show significant geographic variation ($p < 0.05$) in many measured features of the Veery song (Table 6) across the Appalachian Mountains. ANOVA and Tukey’s HSD post-hoc results revealed what appears to be an overall south-to-north shift in frequency ranges across the Appalachian Mountains. High frequency ranges and change in frequency ranges appear to gradually increase from south to north (Fig. 5) and generally the low frequency ranges Veeries sang decreased from south to north. Tukey’s HSD post-hoc analyses revealed North Carolina Veeries, and in some cases West Virginia Veeries, are driving the significant results in high frequency and change in frequency HLM-3 models. For example, frequency ranges sung by North Carolina and West Virginia Veeries are significantly different from each other and PA, and VT Veeries, which have overlapping low frequency ranges that are not significantly different (Fig. 4). This trend is seen in the results for low frequency ranges for whole song, B Phrase, and C phrase models. As seen for low frequency ranges, Veeries from North Carolina were significantly different from the three other sample states in change in frequency range, and again there is an overall increase in frequency ranges sung from south to north, although the ranges sang by Veeries from WV, PA, and VT overlapped and are not significantly different.

However, the overall frequency shifts from south to north may still have implications of geographic cultural shifts in song. The sampling areas in this study encompassed a unique portion of the Veery breeding distribution all within a continuous mountain range. Veeries songs were recorded at the southernmost limit of Veery breeding distribution where appropriate habitats are limited to the high elevations of the Appalachian Mountains. The breeding range continues north through the Appalachian Mountains, with the lowest habitat elevations gradually decreasing as latitude increases. As a consequence of decreasing elevation, appropriate breeding habitat is more broadly available across the landscape as the Veery breeding range expands across southern Canada and northern United States (Fig 1). My sample sites included two regions where breeding habitat is restricted to high elevations (NC and WV) and two regions where appropriate breeding habitat is more broadly available across the landscape (PA and VT). The availability of suitable habitats may influence natal and breeding dispersal, especially in southern Appalachia where appropriate habitat is restricted.

Natal and breeding dispersal are important components of population dynamics that favors range expansion and reduce intraspecific competition (Forschle et al. 2010). Although there is little information available concerning the natal and breeding dispersal of Veeries (Bevier et al. 2005), the differences in habitat availability across the Appalachian Mountains, coupled with the tendency for passerine birds to show high breeding site fidelity (Forschle et al 2010; Ahlering and Faaborg 2006) may broadly influence on Veery song variation over many generations.

Returning to the same breeding grounds has the benefits of local knowledge and adaptation to an area for optimum resource exploitation, and some bird species will return to the same breeding area even if successful breeding was not achieved in the previous year (Ahlering and Faaborg 2006), demonstrating how critical local knowledge for an area may be for survival. Because appropriate habitat is restricted to high elevations the southern Appalachians, Veeries in this portion of the breeding range may have limited dispersal and may be more isolated from the more broadly distributed Veeries from northern Appalachian and beyond (Figure 1). Spatial behaviors such as dispersal and nest site fidelity coupled with song development may influence geographic song differentiation (Kroodsma 1999).

When, and from whom, a young bird learns to sing, and their influence on song variation at individual, population, and geographic scales is a current topic of research with a long history in ornithology (Kroodsma 2007). In general, song variation across groups of songbirds is thought to arise as groups of songbird species learn and imitate the songs of nearby conspecifics, leading to structural differences in songs between groups (Marova 2010). These structural differences in song are also attributed to song development, a process largely unknown for the Veery (Bevier et al 2005). It is unknown if Veeries learn their songs within the first summer during natal dispersal similar to the White-crowned sparrow (Baptista and Morton 1988; Marova 2010) or if Veery song development is similar to that of young Chaffinch males who can continue song learning up to the next breeding season (Marova 2010). One study investigating natal site fidelity of the Veery in New Jersey found that out of 142 banded individuals only 14 returned the following year to their natal site (Suthers 1987). Although this one study cannot definitively describe the nature of natal site fidelity in the Veery, further understanding of when song learning and development occurs as well as more rigorous investigation into site fidelity in Veeries would lead to a broader understanding of the geographic variation found in frequency related features of Veery songs as a result of song learning.

Geographic frequency range shifts found in Veery song may be a consequence of song development, differences in dispersal range options, and high breeding site fidelity across the Appalachian Mountains. Significantly distinct frequency ranges sung by North Carolina Veeries and the overlap in frequency ranges of the three more northern populations of Veeries may be a consequence of restricted gene flow between northern and southern populations.

The basic features of bird song such as tonal quality, frequency, and rhythmic qualities indicative of a species' song may have strong genetic control (Jenkins 1977), unlike features of song that may be influenced more by learning and auditory feedback, such as song-type variation and song-delivery patterns. The geographic variation in frequency features of Veery song therefore may be the consequence of philopatry, leading to genetic variation among populations over generations.

The breeding ranges of two (out of the four or five) described subspecies of the Veery are found within the Appalachian Mountain range: the more northern *C.f. fuscescens* (Stephens 1817) and southern *C.f. pulichorum* (Phillips 1991). The breeding range of *C.f. fuscescens* spans from Ontario east to New Brunswick and Nova Scotia south to Pennsylvania, while the breeding distribution of *C.f. pulichorum* is restricted to the southern Appalachian Mountains from West Virginia to Maryland south to Georgia and North Carolina (Bevier et al. 2005). Although the validity of *C.f. pulichorum* needs further review and a critical evaluation of all described subspecies of the Veery requires further exploration (Bevier et al. 2005), it is noteworthy to consider that geographic variation in Veery song across the Appalachian Mountains may be due to variation in gene flow among these populations.

The regional and geographic variation in frequency and temporal features of the typical songs of the Veery found within and across the Appalachian Mountains may be a consequence of the culmination of song ontogeny and variation in natal and breeding dispersal opportunities within the mountain range creating broad cultural shifts in song frequency ranges. Further exploration into Veery song development, natal and breeding dispersal, and exchange of gene flow among subspecies *C. f. pulichorum* and *C. f. fuscescens* is needed to fully understand the variation in song across the Appalachian Mountains.

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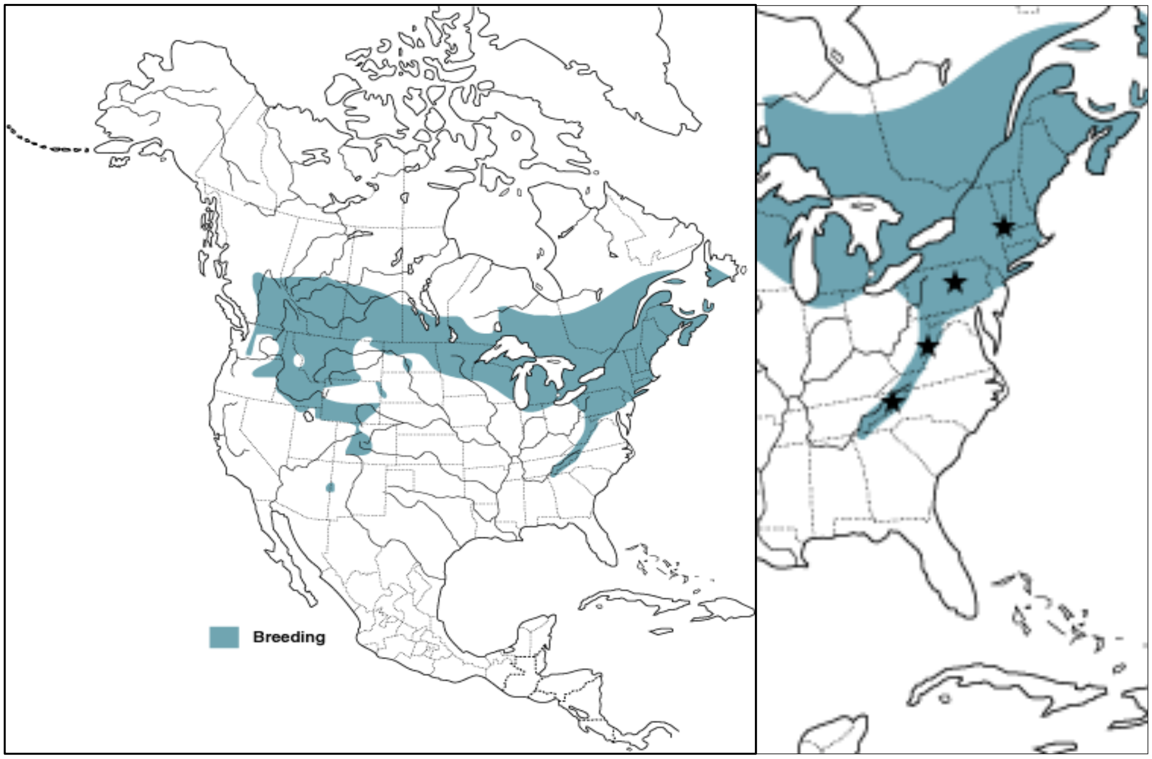


Figure 1

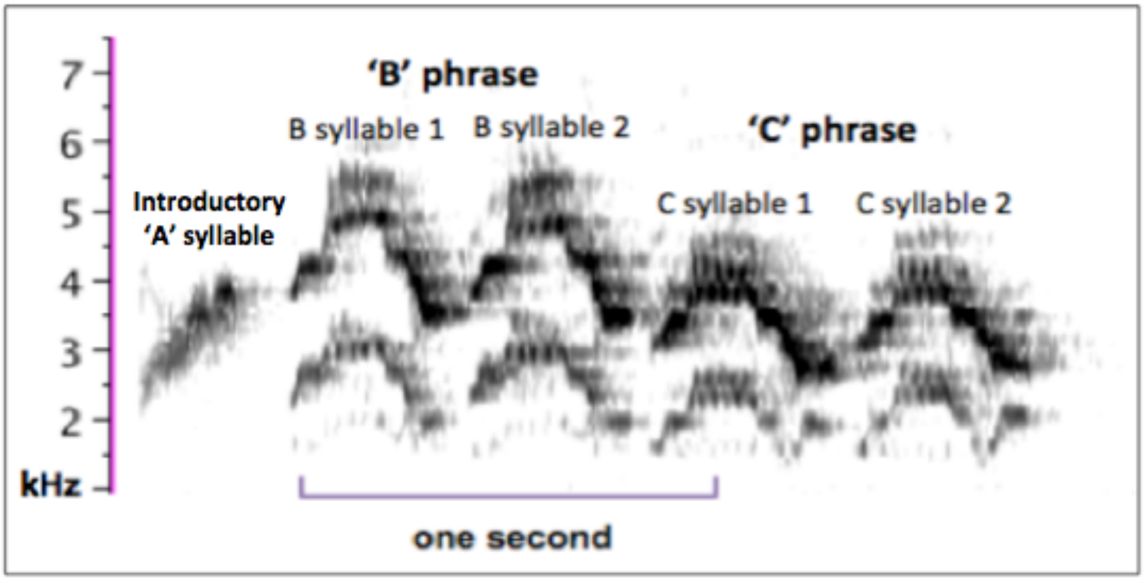
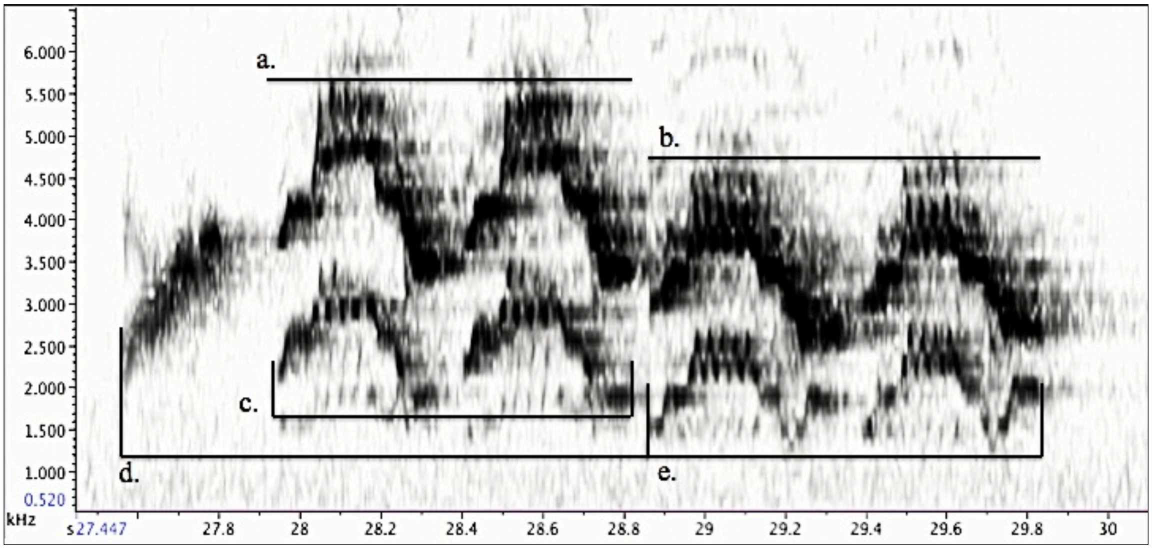

'B' phrase
B syllable 1
B syllable 2
'C' phrase
Introductory
'A' syllable
C syllable 1
C syllable 2
7
6
5
4
3
2
kHz
one second

Figure 2


a.
b.
c.
d.
e.
6.000
5.500
5.000
4.500
4.000
3.500
3.000
2.500
2.000
1.500
1.000
0.520
kHz
s 27.447
27.8
28
28.2
28.4
28.6
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29
29.2
29.4
29.6
29.8
30

Figure 3

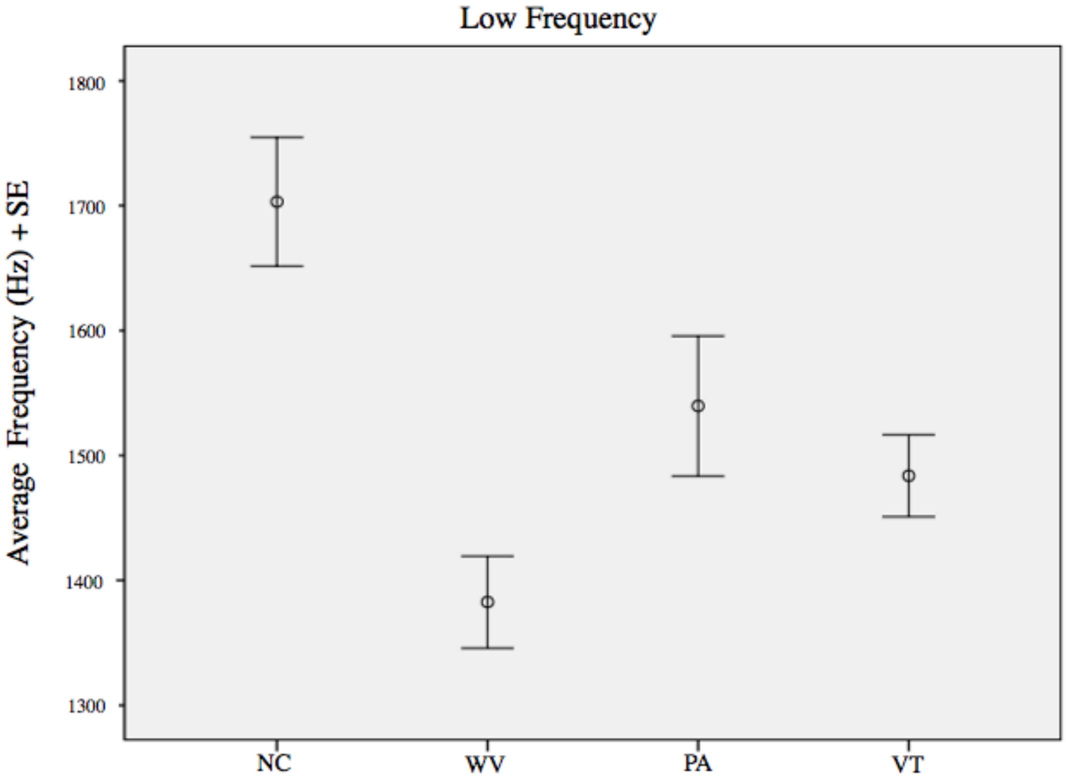
Low Frequency
Average Frequency (Hz) + SE
1800
1700
1600
1500
1400
1300
NC
WV
PA
VT

Figure 4

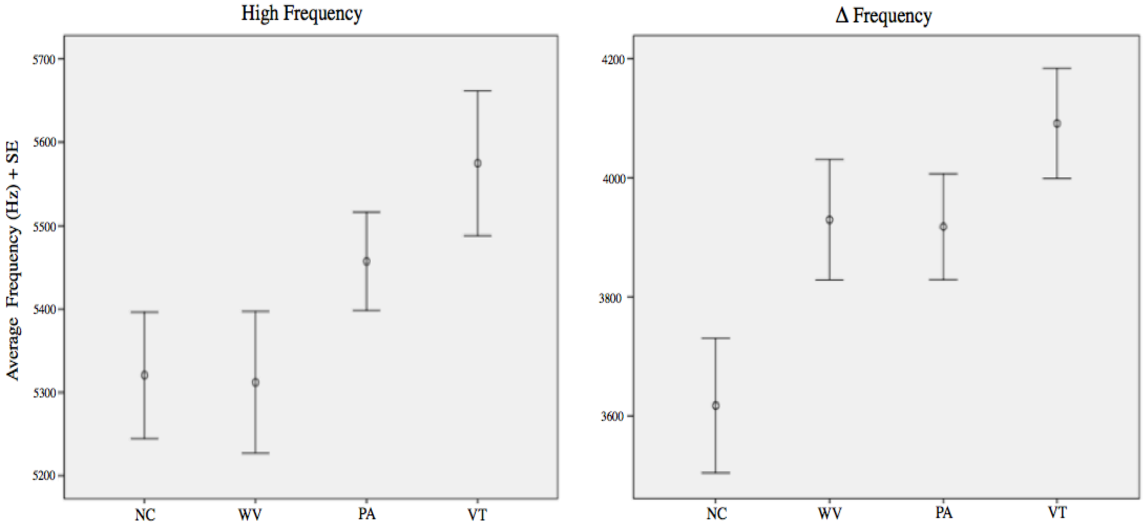
High Frequency
Δ Frequency
Average Frequency (Hz) + SE
5700
5600
5500
5400
5300
5200
4200
4000
3800
3600
NC
WV
PA
VT
NC
WV
PA
VT

Figure 5

Table 1. Results of ANOVA testing for differences in frequency and temporal characteristics in the introductory note of the Veery song. Differences were assessed across regions by comparing pooled state data. Differences were not significant.

Song Feature Measured	**F $_{(3,28)}$**	**p**
Minimum Frequency (Hz)	1.23	0.317
Maximum Frequency (Hz)	2.21	0.11
Δ Frequency (Hz)	1.97	0.142
Syllable Duration (sec)	0.057	0.982

Table 2. For each BBCC song, twelve measurements were made. Below shows the breakdown of each measurement and its associated code.

Measured song features & codes	**Low Frequency (Hz)**	**High Frequency (Hz)**	**Δ Frequency (Hz)**	**Song / Phrase length (sec)**
Whole Song	WSLF	WSHF	WSDF	WSDT
B Phrase	BSLF	BSHF	BSDF	BSDT
C Phrase	CSLF	CSHF	CSDF	CSDT

Table 3. State by state breakdown of raw data accumulated from recording efforts across the Appalachian Mountains. Shown are the total number of Veeries and songs recorded overall, as well as the total number of Veeries and BBCC songs analyzed for geographic variation.

Overall data collected	NC	WV	PA	VT	TOTAL
individuals recorded	*n*= 29	*n*= 26	*n*= 24	*n*= 30	109
Total songs recorded	863	952	523	750	3088
BBCC data analyzed					
individuals	*n*= 23	*n*= 21	*n*= 15	*n*= 24	83
BBCC songs	505	381	168	471	1525
Mean songs per bird	21.9	18.1	11.2	19.6	18.4
Range of songs per bird	7 to 54	6 to 37	4 to 20	5 to 59	4 to 59

Table 4. Geographical comparison (mean ± SE) of the frequency (minimum, maximum, and change) and temporal features (whole song duration, B phrase duration, C phrase duration) measured for each 'BBCC' Veery song type. Statistics show results of ANOVA tests using each state's pooled data; significant results ($p<0.05$) are in bold. Superscripts show results from Tukey's HSD post-hoc analyses. Similar superscripts denote which states have overlapping frequency and song/phrase length ranges that are not significantly different.

Measure	**NC (*n*=505)**	**WV (*n*=381)**	**PA (*n*=168)**	**VT (*n*=471)**	**Significance** F $_{(3, 79)}$	 p
Frequency (Hz)						
Whole Song						
Low	1680 ± 299^{A}	1359 ± 214^{B}	1511 ± 260^{A,C}	1491 ± 202^{B,C}	9.79	**≤ 0.000**
High	5311 ± 466^{A}	5307 ± 441^{A,B}	5512 ± 367^{A,B}	5538 ± 478^{B}	2.59	0.058
Δ	3630 ± 616^{A}	3948 ± 520^{B,C}	4000 ± 439^{A,B,C}	4046 ± 522^{B,C}	4.15	**0.009**
B Phrase						
Low	1983 ± 368^{A}	1670 ± 285^{B}	1840 ± 299^{A}	1916 ± 252^{A}	7.53	**≤ 0.000**
High	5314 ± 463^{A}	5298 ± 449^{A}	5516 ± 370^{A}	5509 ± 446^{A}	2.17	0.980
Δ	3331 ± 657^{A}	3618 ± 563^{B}	3675 ± ^{474A,B}	3593 ± 539^{A,B}	2.39	0.075
C Phrase						
Low	1719 ± 303^{A}	1397 ± 219^{B}	1537 ± 260^{A,C}	1496 ± 206^{B,C}	9.31	**≤ 0.000**
High	4034 ± 350^{A}	4290 ± 427^{B}	4505 ± 332^{B}	4545 ± 420^{B}	13.09	**≤ 0.000**
Δ	2314 ± 496^{A}	2893 ± 509^{B}	2968 ± 408^{B}	3048 ± 468^{B}	16.69	**≤ 0.000**
Time (s)						
Whole song	2.0 ± 0.2^{A}	2.1 ± 0.2^{A}	2.0 ± 0.2^{A}	2.0 ± 0.2^{A}	1.35	0.262
B phrase	0.8 ± 0.1^{A}	0.8 ± 0.1^{A}	0.8 ± 0.1^{A}	0.8 ± 0.1^{A}	0.358	0.783
C phrase	0.8 ±0.1^{A,C}	0.9 ± 0.1^{B,C}	0.9 ± 0.1^{C}	0.9 ± 0.1^{C}	2.53	0.063

Table 5. Results of the within-state song variation for each measured feature of the Veery song. Shown here are the variance components from the Level-1 regression equations from each song variable random coefficient null model that did not include elevation or time of day data. * denotes p = <0.001. Models not shown here that did include the predictor variables also showed a p= ≤0.001 for within-state variation.

Within-State Song Variation				
Intercept, r0 random effect, level-1	**Low Frequency (Hz)**	**High Frequency (Hz)**	**Δ Frequency (Hz)**	**Song length (sec)**
Whole Song	38507.48*	121926.16*	204481.45*	0.0277*
B Phrase	60282.57*	117164.36*	245483.79*	0.0091*
C Phrase	40568.01*	81098.72*	146511.13*	0.0086*

Table 6a. Coefficients for each ‘whole song’ measurement from HLM-3 analyses. Shown below are the results from two models: (1) null models and (2) models including both predictor variables (elevation and day vs. night). Intraclass correlations were calculated for each null model and ΔR^2 values were calculated to assess elevation and day vs. night as level-2 (L2) predictors. Significant p values (<0.05) are in bold.

Whole Song	**Coefficient**	**SE**	**T ratio**	**p**	**Parameter variance across states**	**p**
Low Frequency (Hz) (ICC= 0.24)						
Intercept (null model)	1526.48	59.11	25.83	<0.001	11995.19	**<0.001**
Intercept	1731.24	186.30	9.29	0.003	52228.15	0.08
Day/Night	-2.28	46.52	-0.05	0.964	113.25	>.500
Elevation	-0.21	0.15	-1.37	0.264	0.06	0.215
ΔR^2 including L2 variables= 0.06						
High Frequency (Hz)(ICC= 0.03)						
Intercept (null model)	5406.00	11.94	452.73	<0.001	4095.57	**0.089**
Intercept	5680.13	107.59	52.79	<0.001	268.70	0.091
Day/Night	-89.93	81.03	-1.11	0.348	1.74	>.500
Elevation	-0.23	0.09	-2.49	0.089	0.00	0.111
ΔR^2 including L2 variables= 0.04						
Δ Frequency (Hz) (ICC= 0.10)						
Intercept (null model)	3906.70	92.40	42.28	<0.001	23912.15	**0.003**
Intercept	4174.62	148.75	28.07	<0.001	3146.39	**0.036**
Day/Night	-92.79	107.22	-0.87	0.45	98.17	>.500
Elevation	-0.24	0.16	-1.50	0.231	0.02	**0.049**
ΔR^2 including L2 variables= -0.01						
Song Length (sec) (ICC= 0.03)						
Intercept (null model)	2.00	0.02	91.58	<0.001	0.00	0.153
Intercept	1.91	0.06	30.61	<0.001	0.00	**0.029**
Day/Night	0.07	0.04	1.76	0.176	0.00	>.500
Elevation	0.00	0.00	1.00	0.392	0.00	**0.024**
ΔR^2 including L2 variables= 0.11						

Table 6b. Coefficients for each 'B phrase' measurement from HLM-3 analyses. Shown below are the results from two models: (1) null models and (2) models including both predictor variables (elevation and day vs. night). Intraclass correlations were calculated for each null model and ΔR^2 values were calculated to assess elevation and day vs. night as level-2 (L2) predictors. Significant p values (<0.05) are in bold.

B Phrase	**Coefficient**	**SE**	**T ratio**	**p**	**Parameter variance across states**	**p**
Low Frequency (Hz) (ICC= 0.18)						
Intercept (null model)	1864.10	63.05	29.57	<0.001	12826.94	**<0.001**
Intercept	1940.78	92.59	20.96	<0.001	4369.53	0.163
Day/Night	22.83	58.70	0.39	0.723	232.50	>.500
Elevation	-0.12	0.14	-0.85	0.458	0.03	0.186
ΔR^2 including L2 variables= 0.02						
High Frequency (Hz)(ICC= 0.01)						
Intercept (null model)	5420.16	43.59	124.34	<0.001	1609.27	0.173
Intercept	5622.86	105.39	53.35	<0.001	216.17	0.115
Day/Night	-63.86	79.45	-0.80	0.48	166.88	>.500
Elevation	-0.19	0.09	-2.14	0.122	0.00	0.126
ΔR^2 including L2 variables= 0.04						
Δ Frequency (Hz) (ICC= 0.05)						
Intercept (null model)	3555.66	80.26	44.30	<0.001	13430.54	**0.037**
Intercept	3695.28	161.48	22.88	<0.001	3327.17	0.058
Day/Night	-78.79	116.06	-0.68	0.546	73.22	>.500
Elevation	-0.10	0.18	-0.56	0.613	0.03	0.056
ΔR^2 including L2 variables= 0.01						
Phrase Length (sec) (ICC= 0.00)						
Intercept (null model)	0.80	0.01	76.08	<0.001	0.00	>.500
Intercept	0.78	0.03	26.76	<0.001	0.00	0.098
Day/Night	0.01	0.02	0.60	0.59	0.00	>.500
Elevation	0.00	0.00	0.75	0.507	0.00	0.105
ΔR^2 including L2 variables= 0.00						

Table 6c. Coefficients for each 'C phrase' measurement from HLM-3 analyses. Shown below are the results from two models: (1) null models and (2) models including both predictor variables (elevation and day vs. night). Intraclass correlations were calculated for each null model and ΔR^2 values were calculated to assess elevation and day vs. night as level-2 (L2) predictors. Significant p values (<0.05) are in bold.

C Phrase	**Coefficient**	**SE**	**T ratio**	**p**	**Parameter variance across states**	**p**
Low Frequency (Hz) (ICC= 0.24)						
Intercept (null model)	1554.42	61.17	25.41	<0.001	12884.33	**<0.001**
Intercept	1814.49	226.16	8.02	0.004	104526.55	**0.046**
Day/Night	-12.54	47.02	-0.27	0.807	24.75	>.500
Elevation	-0.25	0.17	-1.47	0.238	0.02	0.177
Δ R2 including L2 variables= 0.08						
High Frequency (Hz)(ICC= 0.28)						
Intercept (null model)	4345.00	95.62	45.44	<0.001	32242.47	**<0.001**
Intercept	4593.87	100.62	45.66	<0.001	1474.20	0.106
Day/Night	17.49	72.42	0.24	0.825	1585.78	>.500
Elevation	-0.28	0.11	-2.53	0.085	0.01	0.101
Δ R2 including L2 variables= -0.03						
Δ Frequency (Hz) (ICC= 0.35)						
Intercept (null model)	2790.89	146.71	19.02	<0.001	78521.10	**<0.001**
Intercept	2411.74	448.04	5.38	0.013	441449.41	0.052
Day/Night	21.61	96.86	0.22	0.838	5643.43	>.500
Elevation	0.31	0.32	0.96	0.408	0.07	0.163
Δ R2 including L2 variables= 0.08						
Phrase Length (sec) (ICC= 0.10)						
Intercept (null model)	0.87	0.02	51.57	<0.001	0.00	**0.016**
Intercept	0.78	0.03	23.21	<0.001	0.00	**0.01**
Day/Night	0.05	0.02	2.57	0.083	0.00	>.500
Elevation	0.00	0.00	1.67	0.194	0.00	**0.006**
Δ R2including L2 variables= 0.13						

Table 7. Pearson correlations comparing the two predictor variables, elevation and time of singing (day vs. night), to all measured song features. Results show a negative correlation between elevation and high frequency as well as change in frequency in whole song and C phrase and a positive correlation between day vs. night and C phrase length, although random coefficient modeling showed that overall elevation and time of singing did not have a significant effect across states and only reduced the unexplained variance by 1-10%.

**. Correlation is significant at the 0.01 level (2-tailed). *. Correlation is significant at the 0.05 level (2-tailed).

Pearson Correlations	Elevation	Day/Night	WSLF	WSHF	WS Change	WS Song Length	BSLF	BSHF	BS Change	BS Phrase Length	CSLF	CSHF	CS Change	CS Phrase Length
Elevation	1	-.291**	0.136	-.256*	-.262*	0.014	-0.037	-.235*	-0.146	0.073	0.189	-.496**	-.449**	0.054
Day/Night	-.291**	1	-0.121	-0.049	0.019	0.196	-0.017	-0.027	-0.01	-0.015	-0.153	0.168	0.197	.306**
WSLF	0.136	-0.121	1	-.254*	-.668**	-0.138	.805**	-.275*	-.632**	0.165	.978**	-.306**	-.713**	-.257*
WSHF	-.256*	-0.049	-.254*	1	.889**	0.155	-.236*	.989**	.830**	0.113	-.279*	.603**	.572**	-0.001
WS Change	-.262*	0.019	-.668**	.889**	1	0.184	-.563**	.891**	.937**	0.009	-.677**	.609**	.777**	0.12
WSSongLength	0.014	0.196	-0.138	0.155	0.184	1	-0.107	0.144	0.16	.677**	-0.105	0.174	0.177	.737**
BSLF	-0.037	-0.017	.805**	-.236*	-.563**	-0.107	1	-.262*	-.729**	0.064	.740**	-.326**	-.607**	-0.197
BSHF	-.235*	-0.027	-.275*	.989**	.891**	0.144	-.262*	1	.852**	0.121	-.297**	.591**	.572**	0.007
BSChange	-0.146	-0.01	-.632**	.830**	.937**	0.16	-.729**	.852**	1	0.051	-.612**	.597**	.735**	0.112
BSPhraseLength	0.073	-0.015	0.165	0.113	0.009	.677**	0.064	0.121	0.051	1	0.207	-0.067	-0.152	0.192
CSLF	0.189	-0.153	.978**	-.279*	-.677**	-0.105	.740**	-.297**	-.612**	0.207	1	-.325**	-.738**	-.256*
CSHF	-.496**	0.168	-.306**	.603**	.609**	0.174	-.326**	.591**	.597**	-0.067	-.325**	1	.879**	.279*
CSChange	-.449**	0.197	-.713**	.572**	.777**	0.177	-.607**	.572**	.735**	-0.152	-.738**	.879**	1	.328**
CSPhraseLength	0.054	.306**	-.257*	-0.001	0.12	.737**	-0.197	0.007	0.112	0.192	-.256*	.279*	.328**	1