PATTERNS OF SONG VARIATION IN A MIGRATORY POPULATION OF PINE WARBLERS

Behavioral Implications in a Changing Climate

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"There is much more to be said of this song than mere description. Its charm gains much from the setting in which it is heard:

a bright December day in the pineries of the deep South,

a faint tang of wood smoke in the cool air,

the almost imperceptible whispering of a breeze in the canopy of shining needles

- then the pure tones of a pine warbler from far overhead bring

true enchantment

to the listener."

– Griscom & Sprunt (1957)

Abstract

As our climate continues to change, the range of suitable habitats for many species will be in flux, which along with changes in many biotic and abiotic factors will bring about changes in migratory behavior. This has already been seen for many species of birds, which have begun migrating shorter distances and even halting migration entirely as necessary resources become available year-round. Behavioral differences between migratory and non-migratory populations of birds have been observed for some species, particularly in song repertoire size and sharing. As a way to predict how vocal behavior and patterns will change as a result of climate change, comparisons can be made between populations of pine warblers, a wood-warbler unique for the presence of migratory behavioral plasticity, with migratory populations in the northern United States and Canada, and non-migratory populations in the southern United States. Due to the absence of previous studies on pine warbler song behavior, the patterns and variation across populations was assessed to provide good baseline data with which to make future comparisons. In the assessment of two migratory populations of pine warblers in northern Michigan, I found birds to possess relatively small repertoires, singing an average of three songs each. These songs could be categorized as "first" and "second" category songs, with characteristics similar to other wood-warblers. However, the use of these songs differed dramatically from what was expected, as birds sang both first and second category songs throughout the day, showing quite unique behavior for a wood-warbler. In an analysis of song variation across a population, I found that neighbors were not significantly more likely to share songs than non-neighbors. In a comparison of note repetition rates with frequency ranges, I found a very tightly clumped distribution, falling quite close to a theoretical vocal performance limit. Though the small repertoire size and low levels of song sharing observed in this population agree with predictions about migratory songbirds, the use of first and second category songs as well as vocal performance show interesting differences from other wood-warblers that would benefit from further study. The observations collected in this study will help greatly in the study of behavioral differences in migratory and non-migratory populations, and could give great insight into the potentially far-reaching behavioral consequences of climate change.

Contents

1 Introduction

1.1 Climate change and global biodiversity

Humans are altering the planet in a number of ways, adding billions of tons of heat-trapping gases to the atmosphere each year (International Panel on Climate Change [IPCC] 2007). The worldwide climate change that has occurred as a result has played a huge role in altering global biodiversity by changing the abundance, distribution, and phenology of many different plants and animals (Walther *et al.* 2002). Phenology refers to cyclical biological events, such as flowering, fruiting, breeding, and migration, which react to climatic conditions. Over the past century, average global temperatures have risen by 0.74 ºC and are projected to continue to rise between 2.4 and 6.4 ºC in the next century (IPCC 2007). Temperatures have increased more rapidly since 1976 than at any point throughout the last millennium, bringing changes in precipitation patterns, including increases in mid- to high latitudes and decreases in tropical and subtropical latitudes (Walther *et al.* 2002). Climate, driven primarily by temperature and precipitation, has significantly changed in many areas, contributing to changes that we see in the abundance, distribution, and phenology of many plants and animals. As a result, many plant and animal ranges are in flux, and will continue to change as the climate continues to change.

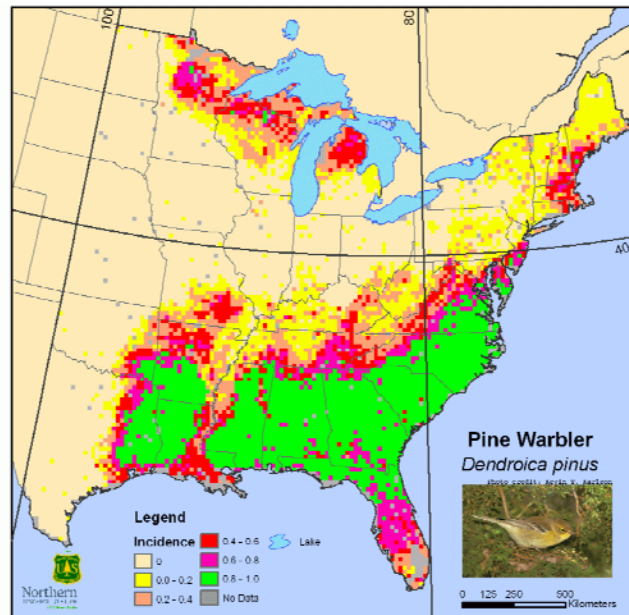## 1.2 The effects of climate change on migration

Migratory animals, particularly migratory birds, provide some of the best examples of climate driven changes in phenology. Many species are struggling to adapt to these changes and have experienced population decreases (Leech & Crick 2007, Saino *et al.* 2011). Many birds have experienced shifts in breeding and migration times as biotic and abiotic cues driving the timing of these events have chaged, which in many cases have had detrimental ecological consequences (Both & Marvelde 2007). Many birds show significant decreases in the amount of time spent in winter ranges, especially short distance migrants (Visser *et al.* 2009). Bird migration habits change as the ranges of plants and animals upon which they depend change as well. In some cases, migration distance decreases as species begin to satisfy ecological requirements in new locations. For example, some birds have begun wintering at more northern latitudes that have recently warmed enough to support them (La Sorte & Thompson 2007, Visser *et al.* 2009). In extreme cases, if food and water sources become available reliably throughout the entire year, some migration may stop entirely (Moore 2011, Pulido & Berthold 2010). Some species with

recently established non-migratory, year-round populations in areas previously only inhabited as stop-over sites are: Canada geese in the Midwest United States (Moore 2011); monarch butterflies in Hawai'i (Moore 2011); white storks in Spain (Moore 2011); and cranes in Western Europe (Prange 2010). It is thought that as climates continue to change, more and more species will follow this trend, trading in migratory habits for a more sedentary lifestyle. Changes in such influential behavior are bound to cause a cascade of changes in the ecology of a species.

To get an idea of how behaviors may change in the future as a result of climates influence, we can compare the behaviors of migratory and non-migratory populations that exist today. In our study, we assess the typical singing behavior and patterns of variation across previously unstudied migratory populations of pine warblers, *Dendroica pinus*. This is done with the end goal of comparing these migratory populations in northern Michigan to non-migratory populations in the southeast United States.

1.3   The pine warbler - *Dendroica pinus*

The pine warbler, *Dendroica pinus*, is a wood-warbler common in the pine forests of eastern North America. The pine warbler is unusual among songbirds, and unique among warblers, in that it has distinct and geographically separated populations of both migratory and non-migratory birds. This geographically influenced behavioral plasticity can be seen well in its range (Figure 1, Matthews *et al*. 2007-ongoing).

Figure 1 – Pine warbler range in eastern North America. Distinctly separated migratory populations in the northern US and non-migratory populations present year-round in the southern US are shown. Taken from Matthews *et al.* (2007-ongoing).

Dendroica pinus consists of four subspecies (Rodewald *et al*. 1999): *D. p. pinus* breeds in southeast Canada and the northeast United States, migrating to the southeast United States as far south as Florida, sometimes even making it to Mexico, Central America, and the West Indies; *D. p. florida* is a permanent resident of Florida; *D. p. achrustera* is a permanent resident of the Bahamas; and *D. p. chrysoleuca* is a permanent resident of the

Dominican Republic. *D. p. pinus* is one of the earliest wood-warblers to migrate in spring and one of the latest to migrate in fall (Rodewald *et al.* 1999). This relatively hardiness is perhaps related to the partially migratory nature of the species. Climate change models predict the distribution of pine warblers to move north as a result of climate change (Figure 2, Matthews *et al.* 2007-ongoing), making an eventual changes in migratory behavior seem likely.
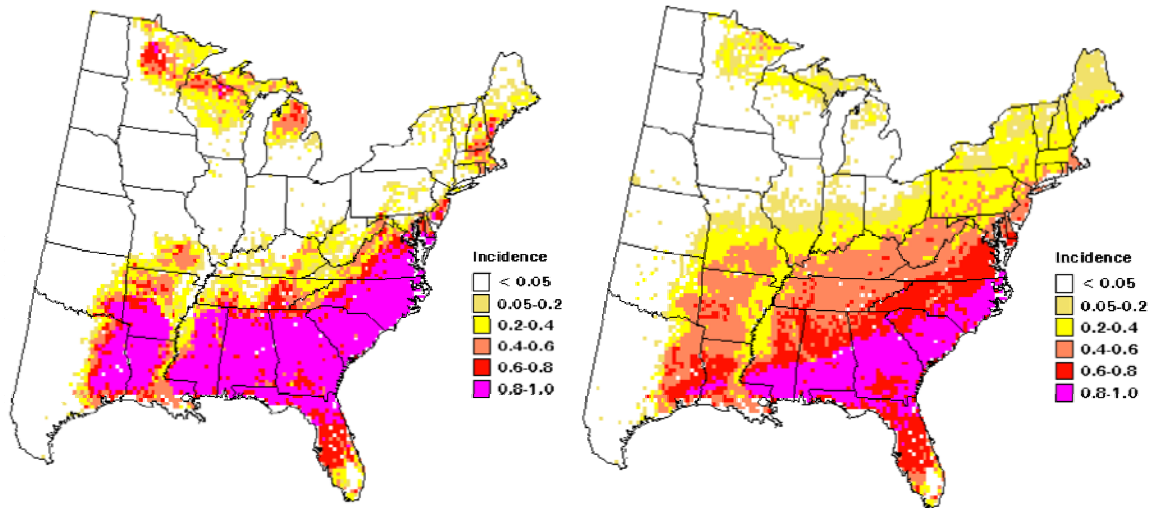

Figure 2 – Current (left) and future (right) pine warbler distributions as predicted by the average of three high emissions climate change models. Taken from Matthews *et al*. 2007-ongoing.

The song of the pine warbler is a sweet sounding trill, sung with a crescendo and decrescendo at the beginning and end, respectively. In this way the song is different from that of the chipping sparrow, a bird with which it is often confused. The notes have a softer tone to them than those of the chipping sparrow, whose notes are rather sharp and staccato, and is often shorter in length. The pine warbler is sexually dimorphic in coloration: males possess a distinctive bright yellow color while females are a much duller gray-brown faded yellow. They are insectivorous, feeding primarily on the larvae of the order *Lepidoptera*, though they will sometime eat fruit and seeds during the fall and winter (Rodewald *et al.* 1999). It is estimated that migratory pine warblers in northeastern US and southern Canada build nests around late April and May, shortly after forming pairs, and young remain in the nest predominately in June in northern populations, and fledglings can be expected as late as August (Rodewald *et al.* 1999). These breeding events happen earlier in the year in southern, sedentary populations, forming pairs and nests as early as mid February (Burleigh 1927), though mid to late March is more common, with fledglings as early as April. They will breed in many different kinds of upland pine (*Pinus* spp.) and occur in many types of pine-hardwood forests. They are seldom found in deciduous forests with only small areas of pine trees, but this is not uncommon during migration (Rodewald *et al.* 1999).

1.4   Vocal Interactions

Bird song is thought to serve two main functions in birds of temperate regions: attracting a mate and establishing and defending a territory (Catchpole & Slater 2008). Bird song can work to both attract and stimulate females, and is thought to be a good indication of male condition or quality. As a result, songs can serve to intimidate potential male threats while at the same time attracting females. In birds that have multiple different songs, as many songbirds do, different singing patterns and organizations can be used to convey different meanings, such as in the chestnut-sided warbler (Byers 1996). Some birds have very simple songs, consisting of a single note or trill, whereas other birds have very long, complex songs made up of a wide variety of whistles, chirps, and trills. Some birds only have one song, which they repeat over and over again, while others have the ability to sing a multitude of different songs, forming a song repertoire. In some birds, such as the brown thrasher, a single bird's repertoire can consist of over 1500 songs (Kroodsma & Parker 1977). In many species, the possession of a larger song repertoire is an indication of fitness. This could be related to benefits that accompany high versatility, which can reduce habituation in listening birds or prevent the singing bird to avoid exhaustion by frequently switching song types (Catchpole & Slater 2008). The vocal interactions within a species can be quite complex, no matter how many different songs a bird can sing. In species of birds that sing multiple songs, individual birds do not necessarily sing the same songs. In some cases, song types are shared between neighboring birds, with the amount of sharing decreasing with geographic separation (Griessmann & Naguib 2002, Handley & Nelson 2005). Song type matching, a type of interaction in which a bird sings back an identical or similar song in response to a neighbor's song, is widely considered a sign of low-level aggression, a way to show dominance and avoiding physical fights over territories (Searcy & Beecher 2009).

1.4.1 Wood-warbler song characteristics and singing modes

The Parulidae family, which contains the pine warbler and other species of New World wood-warblers, exhibits unique song behaviors (Spector 1992). Though wood-warblers tend to have relatively small repertoires sizes, incredibly complex interactions are made possible through the use of different singing modes. Some warblers possess two groups of song types: one consisting of a single "repeat song," sung with eventual variety for long periods of time, and one consisting of a group of "serial songs," which are sung together with immediate variety (American redstart, Lemon *et al.* 1987). When a bird sings with immediate variety, it will rarely repeat the same song type multiple times in a row, cycling through the various songs in its repertoire. When a bird

sings with eventual variety, it will repeat the same song type many times before switching to another song type found in its repertoire. Wood warblers show great consistency in the possession of two categories of songs, referred to as "first" and "second category" songs (Spector 1992). As Spector (1992) describes, first category songs are sung with eventual variety in large amounts by unmated males, throughout the day, but decline in use throughout the breeding season. These are thought to be associated with male-female interactions, as these songs are given most often in the company of females, similar to the repeat songs described earlier. In contrast, second category songs are often sung with immediate variety during dawn singing bouts and at low light levels, during which first category songs are often absent (Spector 1992). Second category songs become more common late in the breeding season, and are thought to be mainly concerned with male-male interactions, similar to the serial songs described earlier. For birds possessing multiple songs in their repertoires, second category songs are often more complex (Spector 1992).

1.4.2 Differences between migratory and non-migratory populations

Many differences between migratory and non-migratory populations have been shown, especially in vocal interactions. As migration strategies become more likely to change, these differences will become more relevant. It is thought that non-migratory populations of birds that remain in one place all year have vocal interactions of a greater complexity (Ewert & Kroodsma 1994). More specifically, non-migratory populations are thought to display a larger degree of song sharing between neighbors as well as possess larger song repertoires. The many differences between migratory and sedentary populations in the amount of song sharing observed has been strongly correlated with migratory behavior (Handley & Nelson 2005). This correlation has been shown in a number of studies, (white-crowned sparrow, Nelson *et al.* 2001; rufous bristlebird, Rogers 2004) but particularly well in a study done on rufous-sided towhees (Ewert & Kroodsma 1994). Population processes stemming from sedentary behavior, in which birds stay in one place all year and therefore have a longer time to form territorial relationships with surrounding neighbors, could give rise to more songs shared between neighbors and larger song repertoires. In sedentary populations, territories may switch possession less frequently, leading to the formation of more stable neighborhoods. Since the pine warbler lives in both migratory and non-migratory populations, it provides the perfect candidate with which to test this idea that migratory behavior influences song patterns and variation.

2 Methods

To assess the relationship between long-term residency and vocal behavior, recordings were made of pine warblers in mixed pine-deciduous forest along the eastern shore of Douglas Lake, a lake in the northern part of Michigan's lower peninsula between Cheboygan and Pellston, as well as on Sugar Island, on the border between Michigan's upper peninsula and Canada. I collected recordings during the dawn chorus, lasting from about a half hour before to a half hour after sunrise, as well as throughout the day, so as to obtain the most complete song repertoire for each individual. Over the course of the collection period (June 28 - July 30, 2011), the sun rose progressively later in the morning, shifting from about 6:00 AM at the end of June to about 6:30 AM at the end of July. I used a Marantz Portable Solid State Recorder, model PMD670, and a Sennheiser shotgun microphone to make digital recordings, which I then transferred to a portable computer. To account for the effects of weather on the songs and recordings, temperature and other weather characteristics were recorded for each set of song recordings.

2.1 Study Sites

The areas in which the birds were sampled consisted of a mixed pine-deciduous forest dominated by eastern white pine, *Pinus strobus,* and red pine, *Pinus resinosa,* while also containing paper birch, *Betula papyrifera*, northern red oak, *Quercus rubra*, big-toothed aspen, *Populus gradidentata*, and red maple, *Acer rubrum*. I sampled at various sites on University of Michigan Biological Station (UMBS) property, including UMBS Campus, Pine Point, the Gorge, and the Chase S. Osborn Preserve on Sugar Island. All maps were made with Google Maps (Google, Mountain View, CA) and ArcMap (Esri, Redlands, CA), using a Garmin GPS 60.

Figure 3 - A map of Michigan showing UMBS at Douglas Lake and Sugar Island. Map taken from Google Maps (Google, Mountain View, CA)
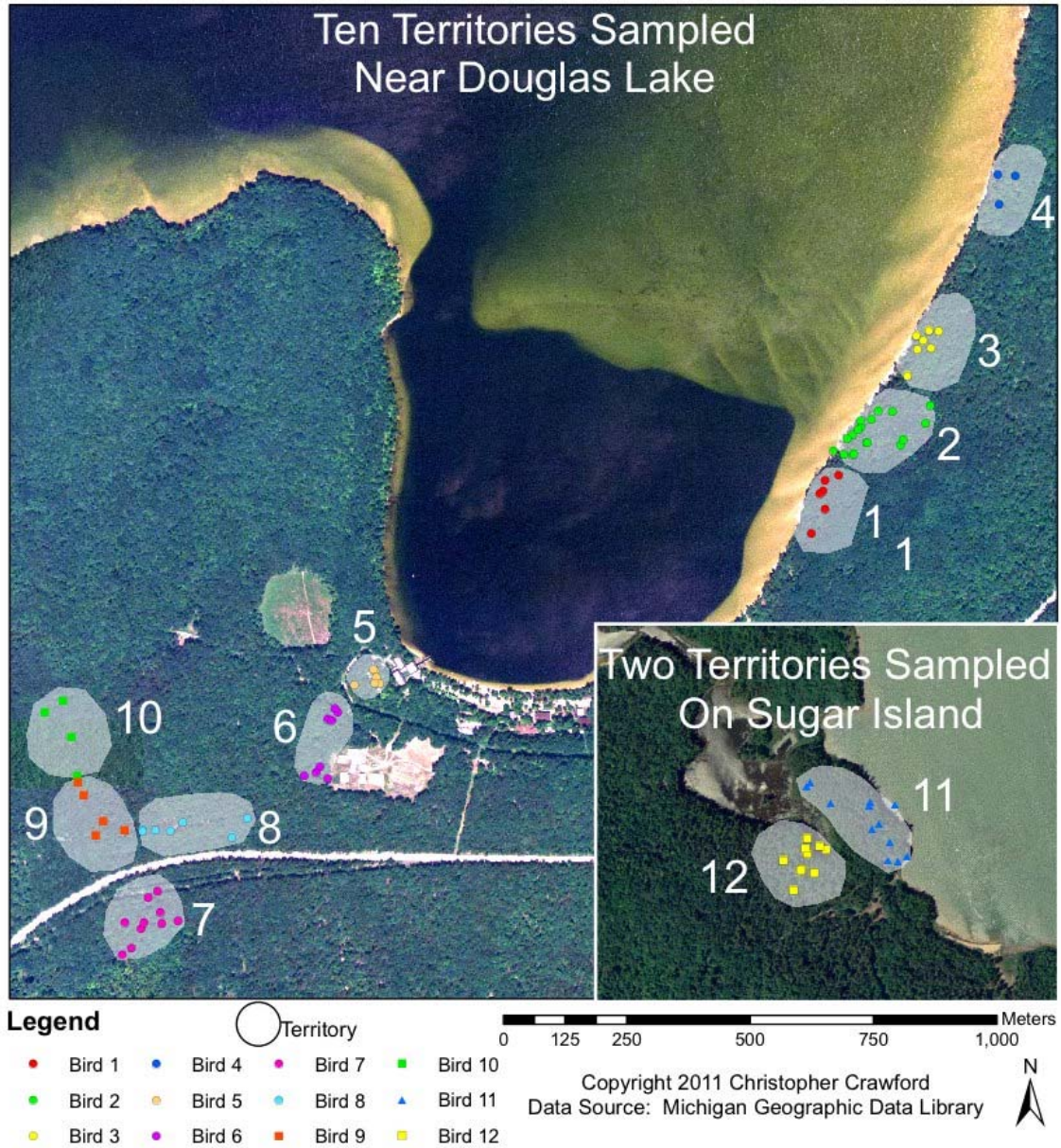
Figure 4 - Pine warbler territories sampled at Douglas Lake and Sugar Island (bottom right) in this study. Each territory is represented as a white area surrounding colored points, which each represent recordings or sightings of the corresponding bird whose identifying number is shown next to each territory.

2.2 Song Analysis

All songs were analyzed and compared using RavenPro 1.4 (Lab of Ornithology, Cornell Univ., Ithaca, NY), with much of the interpretation following examples from the literature. To perform the bulk of the statistical analyses, I used IBM SPSS (IBM, Armonk, NY). I also used the statistics program R (R Foundation for Statistical Computing, Vienna, Austria) for additional

computations. All means were compared using one-way ANOVA or independent *t*-tests when the data were normally distributed and Mann-Whitney U tests when not normally distributed. All p-values reported are two-tailed. After the recording process, I first separated each bird's library of recorded songs into groups based on similarity of the shape and sound of the songs, giving me an initial idea of each individual's song repertoire size. After this preliminary sorting, I used RavenPro 1.4 to take various measurements that allowed me to judge the accuracy of these groupings. To aid in the identification and comparison of these song types, I measured note repetition rate (notes per second, Hz), note length (s), minimum frequency (Hz), maximum frequency (Hz), and frequency range, the difference between maximum and minimum frequency (Hz). In order to measure the frequency range of each song type, I used methods similar to those explained by Podos (1997) in his study of performance constraints in species of Emberizidae (Figure 5).

To maintain consistency, I took measurements using a random sample of five songs for each song type from each bird's library of recordings. For song types with less than five recordings, we measured all recordings available. After the initial sorting of each bird's recordings into distinct songs, I pooled all of the songs and formed seven groups that showed some similarities in shape, sound, and characteristics such as note repetition rate. Some of the songs showed completely unique shapes and sounds and were therefore not included in any of the groups. However, these first groups of similar songs were based merely on my own visual and auditory perception, and a more rigorous statistical analysis was required. In order to test whether or not these groups of seemingly similar songs showed statistical significance, I performed principal components analyses, as explained by James & McCulloch (1990) in IBM SPSS (IBM, Armonk, NY). I performed a separate principal components analysis for each of the seven song groupings, based on the five variables measured in Raven: note repetition rate, note length, minimum frequency, maximum frequency, and frequency range. This analysis is widely used to reduce the dimensions of a data set into a smaller number of uncorrelated and abstract variables, known as principal components. In the case of my data, the majority of the variation in the data set could be explained using one or two of these principal components.
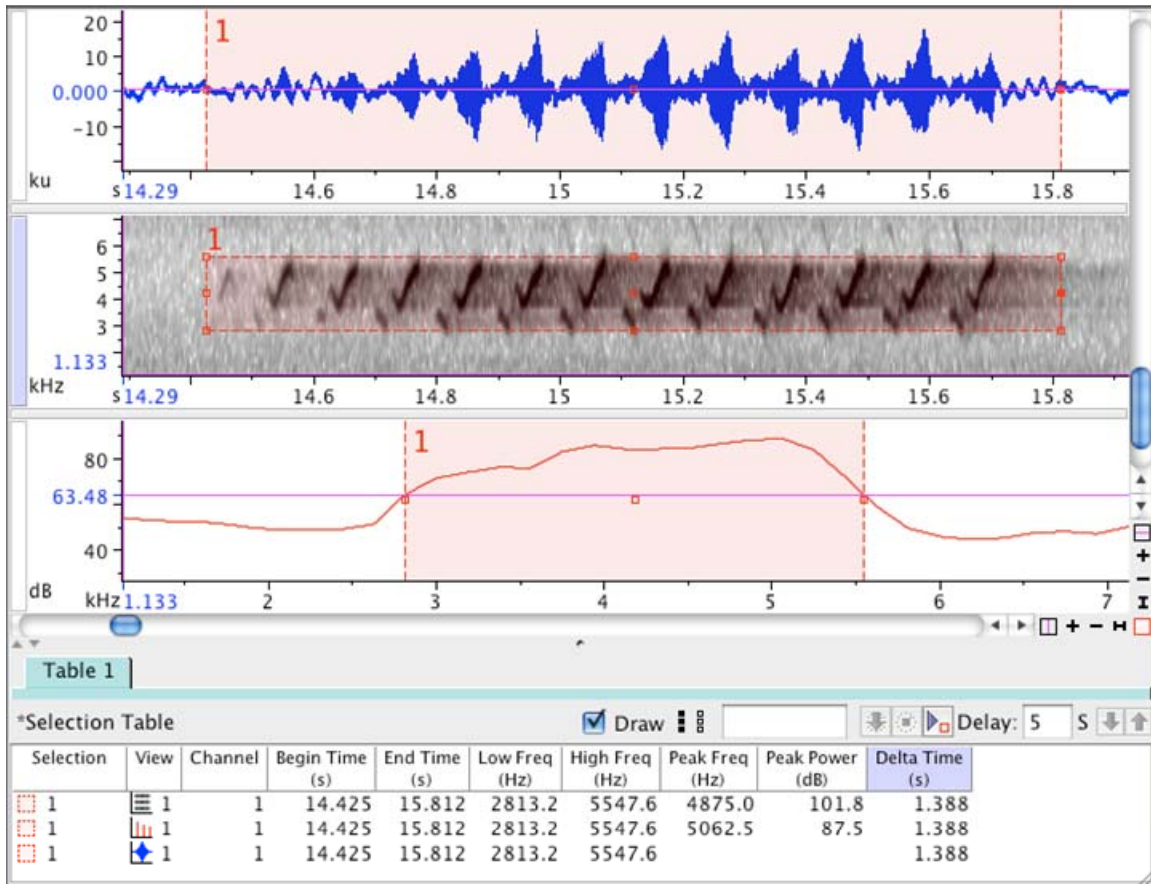
Figure 5 - An example of a typical song analysis. This includes three views (from top to bottom): waveform, spectrogram, and selection spectrum views. The waveform view (top) shows sound amplitude over time (s). The spectrogram view (middle) shows sound frequency (kHz) over time (s). Darker areas represent frequencies with higher intensity. The selection spectrum view (bottom) shows signal power (dB relative to an arbitrary value of 1 dB) in terms of frequency (kHz). The frequency range of each song type was determined as the difference between the lowest and highest frequencies with amplitudes higher than -24 dB relative to the peak power of the signal, a method adapted to RavenPro 1.4 from Podos (1997). I chose the -24 dB criterion in an effort to make the analysis as consistent as possible. In general, the -24 dB limit served to exclude background noise while including almost the entire signal. See the RavenPro 1.4 users manual (Charif *et al.* 2010) for further explanation of various views.

If the analysis could explain the majority of the variation in the data using only one of these principal components (as it could for three of the seven groups of similar song types), the statistical similarity between song types could be determined using independent t-tests and one-way ANOVA tests. If the analysis used two principal components to explain variation, the similarity between songs sung by different birds could be determined by simply plotting these two values on a scatter plot and looking for clustering of points. I used the R package "ellipse" (Murdoch & Chow 2007) to make these scatter plots, one for each of the original seven groups of songs, along with 95% confidence ellipses around the cluster of points for each bird. I considered

two birds with overlapping confidence ellipses to have statistically similar song types and those whose ellipses did not overlap to be singing unique song types. Drawing from these analyses, I determined an index of repertoire sharing (RS) for each pair of birds, both neighboring and non-neighboring, in an effort to address the influence geographic proximity has on song sharing. To do this, I used the formula $RS = Z / ((X + Y) - Z)$, in which X and Y represent the number of songs identified each bird in a pair, birds *x* and *y*, and Z represents the number of songs shared by the two birds (Hultsch & Todt 1981). The index of repertoire sharing varies between 0, in which no songs are shared, and 1, in which all songs are shared. To assess the influence proximity has on song sharing, I compared the average repertoire sharing between neighboring and non-neighboring pairs of birds.

3 Results

3.1 Repertoire sizes and song characteristics

Repertoire sizes of the twelve pine warblers included in this study are shown in Figure 6. Pine warblers are shown to have repertoires of between one to five songs (mean ± standard deviation, 3 ± 0.389), differing from only one song as previously thought (Lemon *et al*. 1987). A regression analysis of the relationship between the number of songs recorded for each bird and the total number of song types identified showed a positive linear correlation (R-square = 0.531). However, it is interesting to note that while many of the birds with the fewest number of recordings also possess the smallest song repertoires, the bird with the fewest recordings (bird 3) possessed an average sized repertoire (*n* = 3). Some birds had the same repertoire size but a much large larger number of songs recorded (particularly bird 8).

	Individual birds sampled											
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
Identified song types (*n*)	4	5	3	3	1	4	4	3	3	1	1	4
Total songs sampled	189	290	135	24	66	169	116	157	36	25	50	95

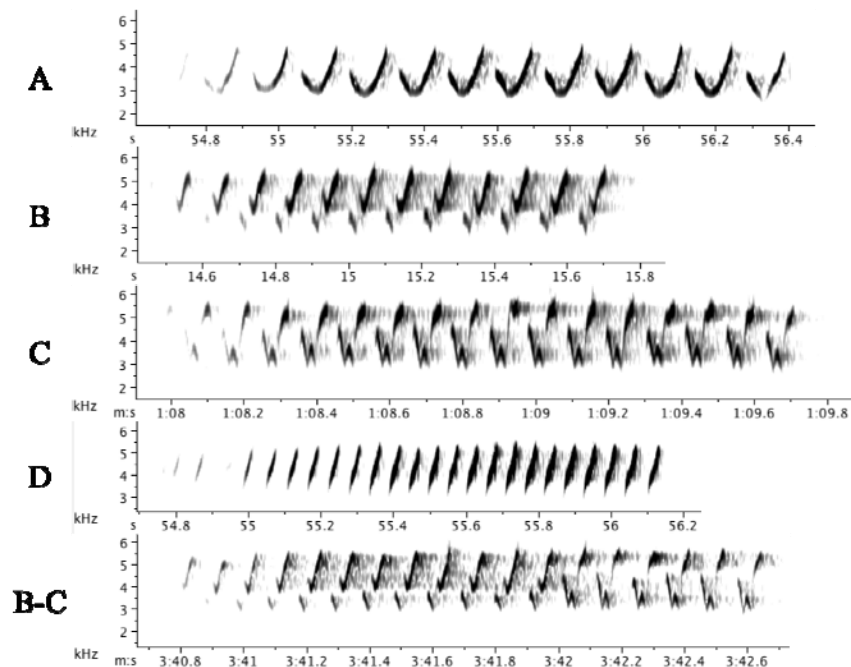**Figure 6 – Repertoire sizes for the twelve pine warblers studied.**

Figure 7 - A typical song repertoire (bird 1). Four types are shown (A-D), as well as a hybird type. This can consist of any of the types combined, but a combination of B and C is shown as an example.

3.1.1 Singing behavior

The pine warbler displays an energetic singing style, often flying from tree to tree, singing only a few songs at each perch before moving on. This is consistent with the descriptions provided by Griscom & Sprunt (1957). The birds would hop up and down branches in between songs, often foraging for larvae at the same time. Some birds were even observed singing while holding larvae in its beak, with no noticeable change in song tone or quality. In general, singing frequency decreased throughout any given day, most likely due to a decrease in activity related to higher temperatures in the late morning and afternoon. Over the course of the entire sampling period (June 30 – July 30), pine warbler singing activity decreased dramatically, probably related to the relative lateness in the breeding season.
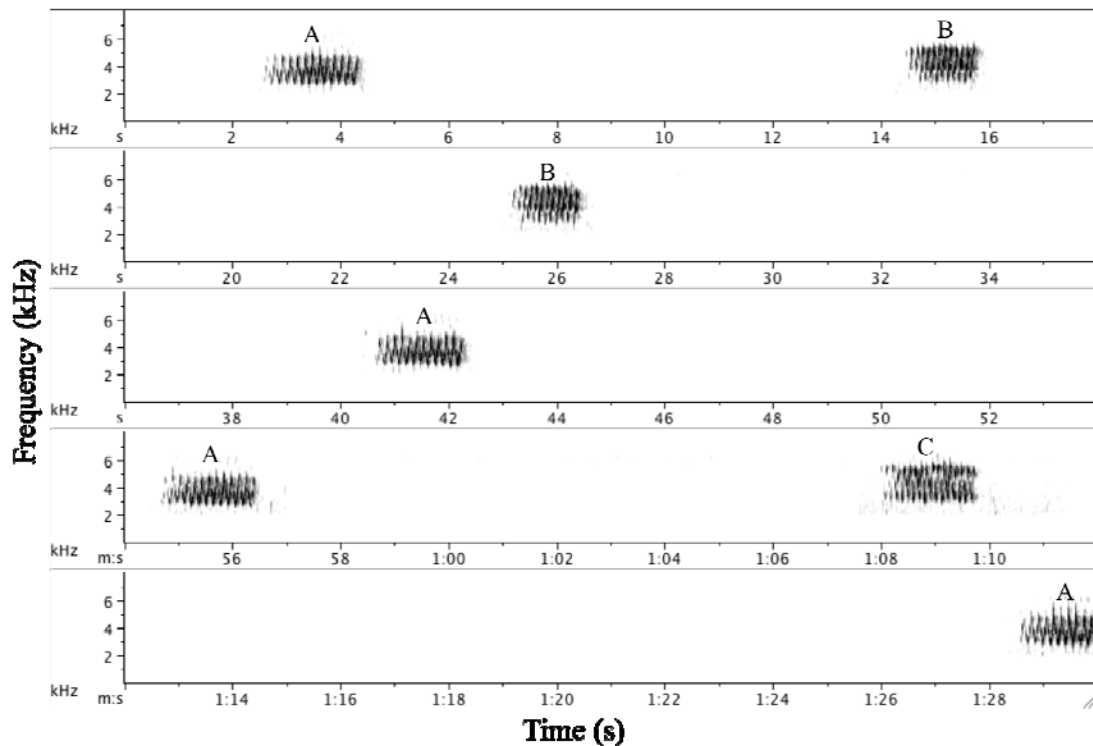

Figure 8 - A typical singing bout, recorded for bird 1, showing a continuous recording progressing from left to right. This shows immediate variety, in which the bird will rarely sing the same song multiple times in a row.

3.1.2 Singing Modes

A singing bout from bird 1 is shown in Figure 8, displaying typical singing behavior. As seen in this figure, the bird sings songs A, B, and C with immediate variety as a group. In contrast, it sings song type D with eventual variety, in long bouts. It is interesting to note that while each

bird sang mostly unique songs, every bird sang a simple song with a quick repetition rate and the slanted, slash-mark shape like type D shown in Figure 7. For birds with small repertoires similar to those observed in this study, it is uncommon to sing with immediate variety (Catchpole & Slater 2008; specific example: chaffinch, Slater 1983). When the descriptions of serial and repeat singing are taken with those of first and second category songs, the songs of the pine warbler appear to fall into similar categories. The simple, slanted song type, represented by type D in Figure 7, appears to have characteristics of first category songs, while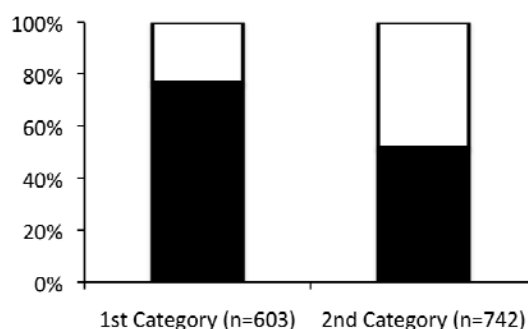 the other song types with more complex features show characteristics of second category songs. This song type was the most commonly

Figure 9 - The proportion of 1st and 2nd Category songs sung with eventual (in black) and immediate variety (in white). The total number of 1st and 2nd category songs recorded is shown on the horizontal axis.

heard of all the song types, and was heard throughout the day. For birds with the smallest repertoires, the lone song always had this shape. The total proportion of first and second category songs observed with immediate and eventual variety is shown in Figure 9. The proportion of first and second category songs over the course of a day shows that second category songs dominate singing in the early morning and late afternoon (Figure 10). During the bulk of the peak daylight hours, both category one and two songs are sung at about equal rates.
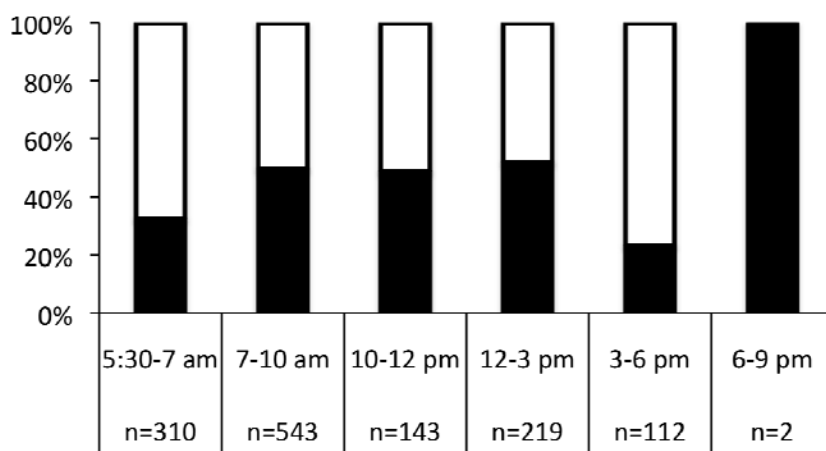
Figure 10 - The proportion of first (shown in black) and second (shown in white) category songs, recorded at different times throughout the day. The number of recordings taken at each part of the day is shown below each time label.

Figure 11 shows the proportion of first and second category songs sung with eventual and immediate variety, separated by each bird. This figure shows a higher degree of eventual variety

in song bouts of category one songs than in song bouts of category two songs. There are some exceptions to this trend, particularly in bird 2 and 8.
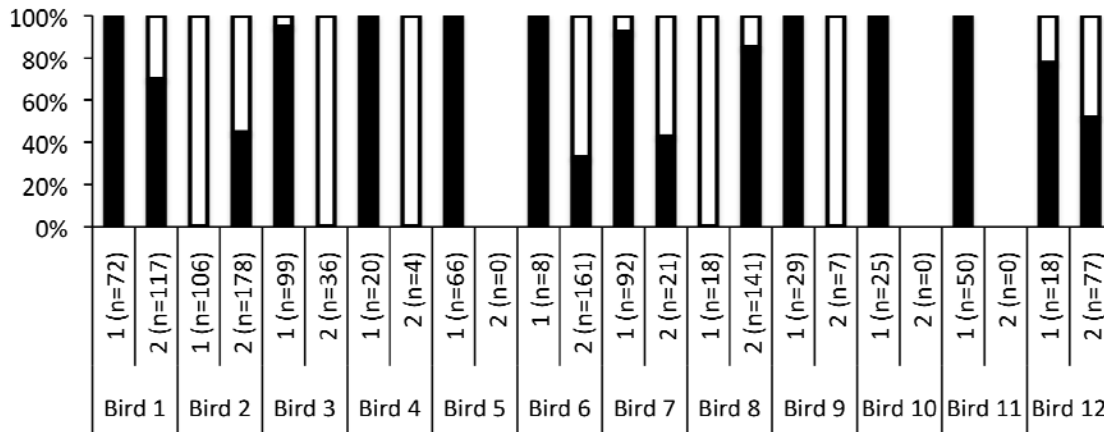

Figure 11 – The proportion of first and second category songs sung with eventual (shown in black) and immediate variety (shown in white), shown for each bird. First and second category songs are shown as 1 and 2, with the number of songs recorded for each category shown in parentheses.

3.1.3 Average song characteristics

The average song characteristics across all the birds sampled, as well as for two separate populations at Douglas Lake and Sugar Island are shown in Figure 12. The results of a Mann-Whitney U Test show no significant difference between any of the averages of the five measurements compared (note repetition rate, p=0.541; note length, p=0.791; minimum frequency, p=0.920; maximum frequency, p=0.269; and frequency range, p=0.219).

Measurement	All birds sampled n = 168 Mean ± Std. Deviation	UMBS - Douglas Lake Area n = 143 Mean ± Std. Deviation	Sugar Island n = 25 Mean ± Std. Deviation	Mann-Whitney U Test p
Note Repetition Rate (Hz)	14.87 ± 6.66	15.11 ± 7.00	13.49 ± 4.07	0.541
Note Length (s)	0.057 ± .042	0.057 ± .045	0.055 ± .022	0.791
Low Freq (Hz)	2,990 ± 322	2,993 ± 333	2,972 ± 251	0.920
High Freq (Hz)	5,325 ± 391	5,305 ± 381	5,442 ± 436	0.269
Delta Freq (Hz)	2,336 ± 451	2,312 ± 451	2,470 ± 432	0.219

Figure 12 – Average song characteristics for two populations of pine warblers, at Douglas Lake and Sugar Island. Results from a Mann-Whitney U test show no significant difference between the two.

3.2 Repertoire sharing

In total, we observed 25 distinct song types. Evaluations of song sharing between every possible pairing of birds are shown in Figure 13, showing indices of repertoire sharing below the diagonal

and total songs shared above the diagonal. Indices of repertoire sharing represent the ratio of shared to non-shared songs for any given pair of birds, which takes into account differences in repertoire size (Hultsch & Todt 1981). In assessing the effect proximity has on the amount of repertoire sharing between pairs of birds, we found no significant difference in average song sharing between neighbors and non-neighbors (Mann-Whitney U test, p=0.232; Figure 14). An example of a group of similar songs from different individuals that were tested for statistical similarity is shown in Figure 15 along with the scatter plot produced using a principal components analysis, shown in Figure 16. When we found two birds in our study to show repertoire sharing, it was never more than one song type that was shared. A total of 15 out of 66 possible pairs shared a song.

Number of songs shared

	1	2	3	4	5	6	7	8	9	10	11	12	n
1	X	1	0	0	0	0	0	1	0	1	0	1	4
2	0.125	X	1	1	1	0	0	0	0	0	0	0	5
3	0	0.14286	X	1	0	0	0	0	0	0	0	0	3
4	0	0.14286	0.2	X	1	0	0	0	0	0	0	0	3
5	0	0.2	0	0.33333	X	1	0	0	0	1	0	1	1
6	0	0	0	0	0.25	X	1	0	1	0	0	0	4
7	0	0	0	0	0	0.14286	X	0	0	0	0	0	4
8	0.16667	0	0	0	0	0	0	X	0	0	0	0	3
9	0	0	0	0	0	0.16667	0	0	X	0	0	0	3
10	0.25	0	0	0	1	0	0	0	0	X	1	0	1
11	0	0	0	0	0	0	0	0	0	1	X	0	1
12	0.14286	0	0	0	0.25	0	0	0	0	0	0	X	4

Index of repertoire sharing (RS)

Figure 13 – The number of songs shared between pairs of birds (above diagonal) and their corresponding indices of repertoire sharing (RS, below diagonal). The column on the far right shows the observed repertoire size for each bird. All shaded boxes represent pairs that exhibit song sharing. Boxes with bold borders represent pairs of birds that are considered neighbors. See Figure 4 for spatial representations of each bird's territory.
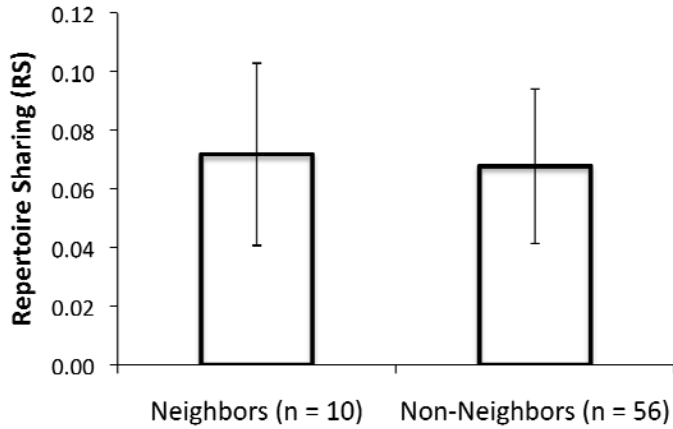
Figure 14 – Average repertoire sharing (RS) for neighboring and non-neighboring pairs of birds.
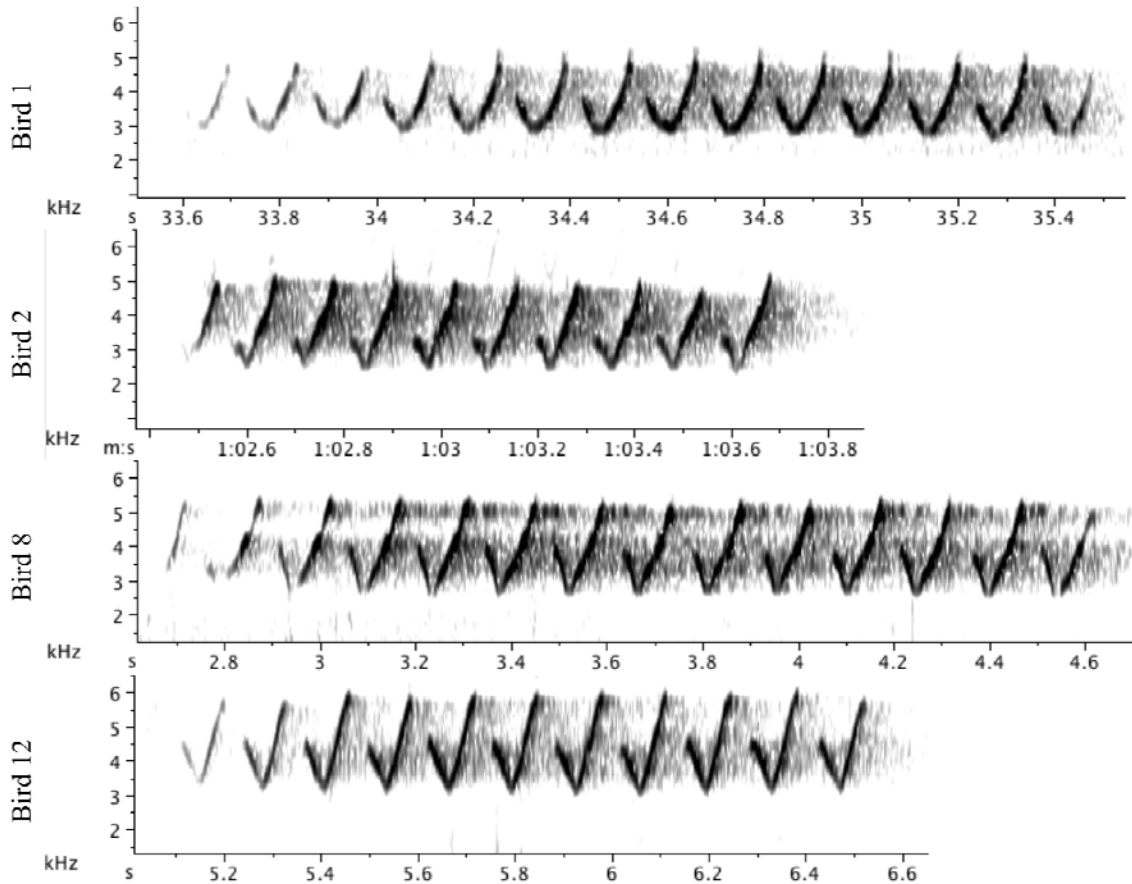

Figure 15 - An example of a group of similar songs, sung by birds 1, 2, 8, and 12, that were analyzed using a principal components analysis to assess the statistical significance of their similarities. These groupings were made based on visual and auditory similarities.
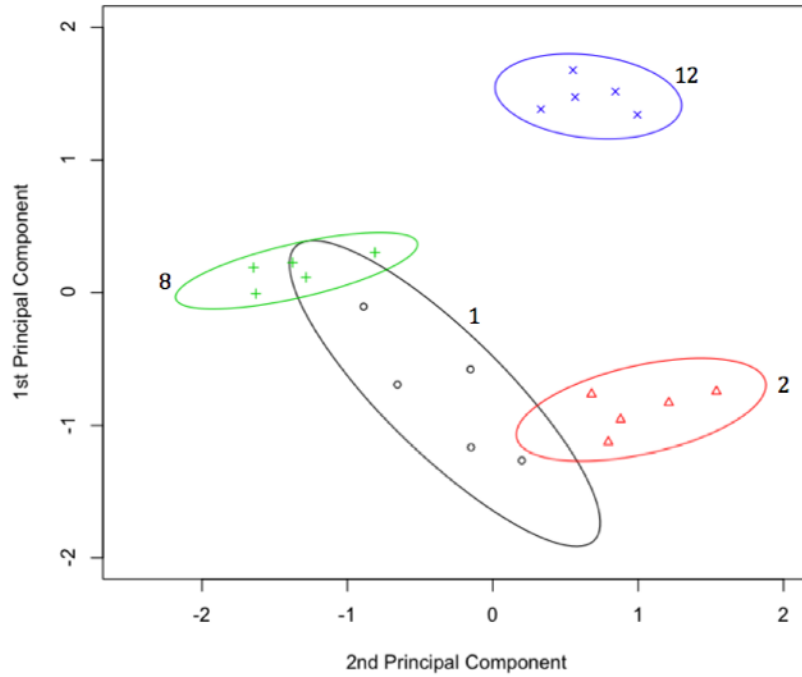
Figure 16 - A scatter plot showing songs by principal components of songs by birds 1, 2, 8, and 12. Around each bird's points is a 95% confidence ellipse, which was used for assessing statistical similarity between song types. Songs were considered shared between two birds if the corresponding 95% confidence ellipses overlapped.

3.3   Vocal performance constraints

When average note repetition rates (Hz) are plotted against average frequency ranges (Hz) for each pine warbler included in this study, a clear triangular distribution is shown (Figure 17). The distribution for pine warblers fits quite well into a similar distribution produced by Podos in his study of 34 species of trilling birds in the family Emberizidae (1997). The regression lines shown on each graph represent a theoretical physical limit on how quickly a bird can sing in a given frequency range (Podos 1997).
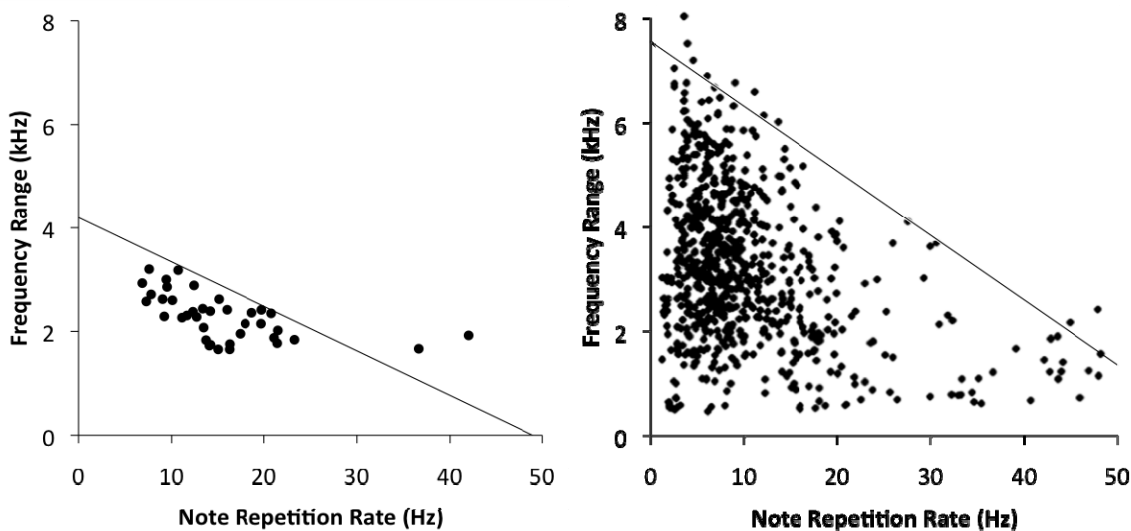

Figure 17 – Average note repetition rate (Hz) plotted against average frequency range (Hz) for each of the studied pine warbler's distinct songs (shown on the left). Shown on the right is a note repetition rate (Hz) against frequency range (Hz) plot for a 34 species of Emberizidae produced in a study done by Podos (1997). The lines (y = -0.0858x + 4.2 for pine warblers, y = -0.124x + 7.55 for Emberizidae) represent a fundamental performance constraint related to the physical production of sound in trilling songbirds.

4 Discussion

4.1   Typical singing behavior

The pine warbler is shown to have a relatively small repertoire, possessing an average of three songs. Larger repertoires have been shown to give greater reproductive success (red-winged blackbird, Yasukawa *et al.* 1980), but the mating strategy of the species may have an impact. Bell *et al.* (1997) found that polygynous male sedge warblers had both larger repertories and greater reproductive success than monogamous males, showing that perhaps large repertoires are only really beneficial in polygynous species, of which the red-winged blackbird is one. Repertoires of songs are more successful in territory defense than single songs (Krebs *et al.* 1978), but there is not much evidence for the benefits of increasing repertoire size, especially in monogamous species.

4.1.1 First and second category songs

I found that in comparing singing behaviors, such as immediate and eventual variety, also referred to as serial and repeat mode, the songs observed could be assigned to one of two categories of songs described by Spector (1992). Though first and second category songs were observed in singing bouts showing both immediate and eventual variety, the proportion of first category songs sung with eventual variety is much higher than that of second category songs (Figure 9), consistent with Spector's observations of other *Dendroica* species. However, unlike almost all other species described, the pine warbler sings both first and second category songs throughout the day. I found that even though a higher proportion of the songs recorded during the dawn chorus were second category songs, still more than 30% of the songs heard were first category songs (Figure 10). This contradicts the thought that second category songs dominate the dawn chorus, from which primary songs are absent. During the early morning through early afternoon, the amount of first and second category songs observed was about equal. This alternation of singing types during the day is quite unique. Also, the presence of first category songs so late in the breeding season contradicts behavior in other wood-warblers. In fact, first category songs seemed to become more common and second category songs less common as the breeding season progressed.

The songs placed in category 1 exhibit show many similarities with the descriptions provided by Spector (1992), including higher average minimum and maximum frequencies (mean ± standard

error; 3188 ± 34 Hz and 5448 ± 39 Hz respectively for first category songs versus 2888 ± 29 Hz and 5262 ± 40 Hz respectively for second category songs) and the simple structure mentioned before. However, in actual use of first category song, the pine warbler shows a strong departure from the rest of *Dendroica*. Because this study was conducted late in the season after breeding pairs were formed, the designation of the observed songs into the first and second categories used must be taken with caution. It is entirely possible that there were simply no recordings of any first category songs at all, and that all of the songs recorded fall into the second category. This could explain the unexpectedly high observation rate of first category songs so late in the breeding season.

When the total number of category one and two songs is shown for each bird, almost all of the birds show much higher eventual variety in category one songs than in category two songs. The two exceptions to this, bird 2 and bird 8, could be due to a variety of factors. Because of a noticeably lower level of consistency in song structure seen in the songs of bird 2, it is most likely that the bird was a young individual testing out its own vocal capabilities. Bird 2 possessed the largest song repertoire of all birds studied, which could be a sign of a younger bird testing out multiple songs before settling on a final repertoire. However, this could merely be a function of the higher number of recordings taken. The absence of eventual variety in first category songs could also be a function of the bird's younger age. The absence of eventual variety in the first category songs of bird 8 is most likely a function of the small number of recordings (n=18) of these songs.

4.2   Repertoire sharing

In my examination of the repertoire sharing between pairs of pine warblers, only 23% of the possible pairs of birds shared a song. Therefore it can be said that song sharing is not a common trait seen in pine warblers. After investigating the effect proximity has on song sharing between neighbors and non-neighbors, I found that two birds were no more likely to share a song in each others repertoires if they were neighbors than if they were not neighbors. These results could be due to a variety of things, but most likely it stems from how and when they learn the songs in their repertoires, which is linked to the migratory behavior of this species. The birds probably learn the songs in their repertoires before establishing territories in their breeding areas (Catchpole & Slater 2008). After arriving, these birds probably pay no attention to the songs of neighboring birds and settle in a relatively random fashion, as shown in the absence of a significant difference in repertoire sharing. Some birds such as the chaffinch (Lachlan & Slater

2003) actually show significantly higher sharing between non-neighbors than for neighbors. For these birds, it is more likely that they actively birds singing similar songs when settling (Catchpole & Slater 2008).

Interestingly, if a young bird learns songs for the first time where it fledged, presumably before migrating elsewhere to set up a territory, there is a possibility that levels of sharing observed in pairings of young and old birds would be elevated. Therefore, the relatively low levels of sharing seen in this population of pine warblers could be solely a function of the amount of young birds learning to sing for the first time in the area. A more detailed study assessing the proportion of fledglings and juveniles that return to the same area as adults could help judge the validity of this idea. In addition, a study comparing the levels of sharing between pairs of birds based on their ages could provide some interesting insight into this idea.

4.3   Vocal performance constraints

As shown in the plots of note repetition rate (Hz) against frequency range (Hz) in Figure 17, the distribution of song types for the pine warbler fits quite well into the distribution for 34 species of Emberizidae studied by Podos (1997). However, the pine warbler distribution shows some interesting differences, especially in the amount of variance in frequency range observed. For many of the species studied by Podos (1997), the frequency range at low note repetition rates shows much more variance, decreasing for higher note repetition rates. In contrast, the pine warbler shows a relatively narrow range of frequency ranges, clumping closely to each other and the theoretical performance limit. This limit is related to respiration and the physical structure of the vocal tract and limits on how quickly it can move. In trilling species, such as zebra finches (Wild *et al*. 1998), birds are known to take short "mini-breaths" in between trill syllables, and there are limits on how quickly this can be done. It is interesting that there is less of a performance gradient for pine warblers as there is for Emberizidae, where only some birds are singing as close to the limit as they can, with many others a wide range of distances from the limit (Podos 1997). There has been evidence that females base mate choice on how close a male sings to the vocal performance limit, particularly in a study performed on swamp sparrows by Ballentire *et al*. (2004). However, from the absence of a large gradient in performance quality, it might be possible that female selection based on how close a bird is singing to the theoretical vocal performance limit does not play a large role in mate selection.

The presence of two trill production techniques in pine warblers is shown by the gap between the main clump of points and the two points falling on the right side of the performance limit. In order to sing at very high note repetition rates, birds sing in short pulses without mini-breaths, as seen in a study conducted by Podos (1996) in which young birds were played trills with note repetition rates that had been increased artificially. When they attempted to sing the trills themselves, they often left gaps in which to breathe, giving the trill a pulsed pattern. This very same song structure is seen in the two sampled songs that fall to the right of the performance limit, one of which is shown in Figure 18. Though these songs were quite uncommon in our study, they present a very interesting look into trill production limits and vocal performance constraints.
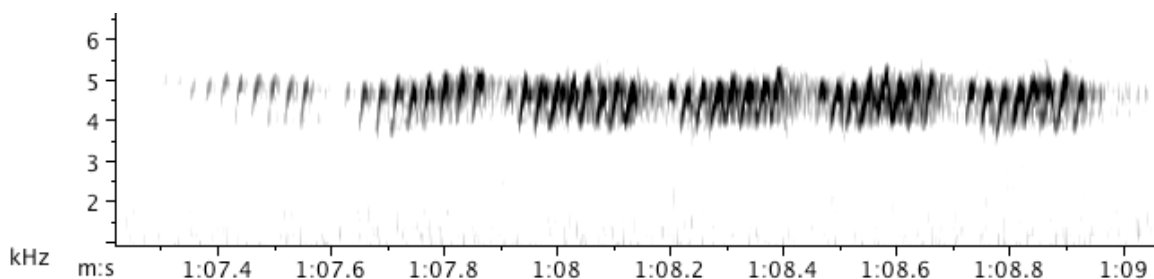

Figure 18 – A song sampled from bird 4, showing an alternative trill production technique, contrasting the typical technique using mini-breaths and producing an even trill. In order to sing with such a high repetition rate, the bird sings in short pulses while taking breaths in between instead of during.

5 Conclusions and Recommendations

This study has provided a good description of the typical singing behavior and variation in song patterns across a population of migratory pine warblers, which had not previously been done. Many of the singing characteristics of the pine warbler have been described for the first time here, including estimates of average repertoire size and the magnitude of song sharing between birds. I found birds to have an average of 3 songs in their repertoires, a value that could potentially rise to 4 or 5 with a larger number of recordings for each bird. Pine warblers sang with both immediate and eventual variety, and these songs could be separated into a "first" and "second" category, typical of other wood-warblers (Spector 1992). However, a few key differences existed between the first and second category songs observed in this study and the general trends described in the literature. For example, the pine warbler sang both first and second category songs at dawn and evening choruses, as well as throughout the day, a behavior not seen in other warblers. However, as this study was conducted late in the breeding season, songs may have been inappropriately designated, and a more complete study including data from the earliest part of the breeding season is highly recommended.

Small levels of song sharing were found for some pairs of birds, but limited to one song per pair. No significant difference was found in the amount of repertoire sharing between neighboring pairs and non-neighboring pairs of birds (Mann-Whitney U test, p=0.232). Further studies assessing the proportion of young birds returning to the same area after migration as well as comparing the levels of sharing between pairs of birds based on their ages could help to explain potential sources of song sharing.

Interestingly, the distribution of note repetition rate plotted against frequency range (Figure 17) falls in the same general distribution as 34 trilling songbird species in the Emberizidae family. However, the variation in frequency ranges at each note repetition rate is much less for pine warblers than much of Emberizidae, being tightly clumped near the performance threshold.

The absence of significant song sharing between neighbors, along with small repertoire sizes, follow predictions for migratory populations explained by Ewert & Kroodsma (1994). This initial survey of the song patterns and variation across a migratory population of pine warblers provides great baseline data with which to make future comparisons. Specifically, comparisons can be made to future populations that have experienced northern range movement as a result of

climate change to see how behaviors change. Also, comparisons can be made to future populations here in northern Michigan, as these populations may become sedentary as the climate continues to change and habitats become suitable year-round. Most importantly, comparisons can now be made with non-migratory populations of pine warblers in the southern United States to test the idea that non-migratory birds exhibit more song sharing and possess larger repertoires, and also as a way to assess the way singing behavior would change if migratory behavior in northern Michigan changes. This type of comparison would give great insight into the behavioral consequences of climate change, the results of which could then be applied to the great many migratory species that are being affected by climate change.

Acknowledgements

References

Ballentine, B., Hyman, J., & Nowicki, S. (2004). Vocal performance influences female response to male bird song: An experimental test. *Behavioral Ecology, 15*(1), 163-168.

Bell, B. D., Borowiec, M., McConkey, K. R. & Ranoszek, E. (1997). Settlement, breeding success and song repertoires of monogamous and polygynous sedge warblers (*Acrocephalus schoenobaenus). Die Vogelwarte, 39,* 87-94.

Both, C., & te Marvelde, L. (2007). Climate change and timing of avian breeding and migration throughout Europe. *Climate Research, 35*(1-2), 93-105.

Burleigh, T. D. (1927). Effect of an early spring on the resident breeding birds of Athens, Clarke Co., Georgia. Auk 44:429-431.

Byers, B. E. (1996). Messages encoded in the songs of chestnut-sided warblers. *Animal Behaviour, 52*, 691-705.

Catchpole, C. K., & Slater, P. J. B. (2008). *Bird song: Biological themes and variations* (2nd Ed.). The Pitt Building, Trumpington Street, Cambridge CB2 1RP, England; 40 W. 20th Street, New York, New York 10011-4211, USA: Cambridge University Press; Cambridge University Press.

Charif, R.A., Waack, A.M., & Strickman, L.M. (2010). *Raven Pro 1.4 User's Manual*. Cornell Lab of Ornithology, Ithaca, NY.

Ewert, D. N., & Kroodsma, D. E. (1994). Song sharing and repertoires among migratory and resident rufous-sided towhees. *Condor, 96*(1), 190-196.

Golawski, A., & Kasprzykowski, Z. (2010). The influence of weather on birds wintering in the farmlands of eastern poland. *Ornis Fennica, 87*(4), 153-159.

Griessmann, B., & Naguib, M. (2002). Song sharing in neighboring and non-neighboring thrush nightingales (luscinia luscinia) and its implications for communication RID C-2650-2009. *Ethology, 108*(5), 377-387.

Griscom, L., & Sprunt Jr., A. (1957). The Warblers of America. Devin-Adair, New York.

Handley, H. G., & Nelson, D. A. (2005). Ecological and phylogenetic effects on song sharing in songbirds. *Ethology, 111*(2), 221-238.

Hultsch, H., & Todt, D. (1981). Repertoire sharing and song-post distance in nightingales (luscinia-megarhynchos B). *Behavioral Ecology and Sociobiology, 8*(3), 183-188.

Intergovernmental Panel on Climate Change. (2007). In Solomon S. (Ed.), *Climate change 2007: The physical science basis: Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change.* Cambridge University Press.

James, F., & McCulloch, C. (1990). Multivariate-analysis in ecology and systematics – panacea or Pandora box. *Annual Review of Ecolgoy and Systematics, 21,* 129-166.

Krebs, J. R., Ashcroft, R. & Webber, M. (1978). Song repertoires and territory defence in the great tit. *Nature, 271*, 539-42.

Kroodsma, D. E., & Parker, L. D. (1977). Vocal virtuosity in brown thrasher. *Auk, 94*(4), 783-785.

La Sorte, F. A., & Thompson, F. R. III. (2007). Poleward shifts in winter ranges of North American birds RID A-2849-2009. *Ecology, 88(7)*, 1803-1812.

Lachlan, R. F. & Slater, P. J. B. (2003). Song learning in chaffinches: how accurate, and from where? *Anim. Behav.*, *65*, 957-69.

Leech, D. I., & Crick, H. Q. P. (2007). Influence of climate change on the abundance, distribution and phenology of woodland bird species in temperate regions. *Ibis, 149*, 128-145.

Lemon, R. E., Monette, S. & Roff, D. (1987). Song repertoires of American warblers (Parulinae): Honest Advertising or assessment? *Ethology*, 74, 265-84.

Matthews, S.N., L. R. Iverson, A.M. Prasad, A. M., and M.P. Peters. 2007-ongoing. A Climate Change Atlas for 147 Bird Species of the Eastern United States [database]. http://www.nrs.fs.fed.us/atlas/bird, Northern Research Station, USDA Forest Service, Delaware, Ohio.

Moore, T. T. (2011). Climate change and animal migration. *Environmental Law, 41*(393), 393.

Murdoch, D. <murdoch@stats.uwo.ca> & Chow E. D. (porting to R by Jesus M. Frias Celayeta <iosu@bureau.ucc.ie>) (2007). ellipse: Functions for drawing ellipses and ellipse-like confidence regions. R package version 0.3-5.

Nelson, D. A., Khanna, H., & Marler, P. (2001). Learning by instruction or selection: Implications for patterns of geographic variation in bird song. *Behaviour, 138*, 1137-1160.

Nowicki, S., & Marler, P. (1988). How do birds sing. *Music Perception, 5*(4), 391-426.

Podos, J. (1996). Motor constraints on vocal development in a songbird. *Animal Behaviour*, *51*, 1061-70.

Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, *5*, 537-51.

Prange, H. (2010). Migration and resting of the common crane grus grus and changes in four decades. [Zug und Rast des Kranichs Grus grus und die Veranderungen in vier Jahrzehnten] *Vogelwelt, 131*(2), 155-168.

Pulido, F., & Berthold, P. (2010). Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proceedings of the National Academy of Sciences of the United States of America, 107*(16), 7341-7346.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rodewald, P. G., Withgott, J. H., & Smith, K. G. (1999). Pine Warbler (*Dendroica pinus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/438doi:10.2173/bna.438

Rogers, D. (2004). Repertoire size, song sharing and type matching in the rufous bristlebird (dasyornis broadbenti). *Emu, 104*(1), 7-13.

Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Huppop, K., et al. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B-Biological Sciences, 278*(1707), 835-842.

Sample, B. E., R. J. Cooper, and R. C. Whitmore. 1993. Dietary shifts among songbirds in a diflubenzuron-treated forest. Condor 95:616624.

Searcy, W. A., & Beecher, M. D. (2009). Song as an aggressive signal in songbirds. *Animal Behaviour, 78*(6), 1281-1292.

Sibley, David A. *The Sibley Field Guide to Birds of Eastern North America*. New York: Alfred A. Knopf, 2003. Print

Slater, P. J. B. (1983). Sequences of song in chaffinches. *Animal Behaviour*, *31*, 272-81.

Spector, D. A. (1992). Wood-warbler song systems: A review of paruline singing behaviors. *Current Ornithology, 9*, 199-238.

Visser, M. E., Perdeck, A. C., van Balen, J. H., & Both, C. (2009). Climate change leads to decreasing bird migration distances. *Global Change Biology, 15*(8), 1859-1865.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., et al. (2002). Ecological responses to recent climate change. *Nature, 416*(6879), 389-395.

Wild, J. M., Goller, F. & Suthers, R. A. (1998). Inspiratory muscle activity during birdsong. *J. Neurobiol.*, *36*, 441-53.

Yasukawa, K., Blank, J. L. & Patterson, C. B. (1980). Song repertoires and sexual selection in the red-winged blackbird. *Behav. Ecol. Sociobiol., 7,* 233-8.

Appendices

Type 1

Variable	Principal Component	
	1	2
Frequency range (Hz)	0.942	0.061
Note Repetition Rate (Hz)	-0.940	-0.019
Note Length (s)	0.916	-0.113
Minimum Frequency (Hz)	-0.557	0.796
Maximum Frequency (Hz)	0.611	0.771
Eigen Value	3.293	1.245
Variance explained (%)	65.866	24.910

Type 2

Variable	Principal Component
	1
Frequency range (Hz)	0.991
Maximum Frequency (Hz)	0.981
Note Length (s)	0.979
Note Repetition Rate (Hz)	-0.978
Minimum Frequency (Hz)	-0.423
Eigen Value	4.038
Variance explained (%)	80.759

Type 3

Variable	Principal Component	
	1	2
Maximum Frequency (Hz)	0.954	0.286
Frequency range (Hz)	0.849	0.325
Minimum Frequency (Hz)	0.835	0.146
Note Length (s)	-0.775	0.525
Note Repetition Rate (Hz)	0.286	-0.922
Eigen Value	3.011	1.335
Variance explained (%)	60.212	26.702

Type 4

Variable	Principal Component
	1
Frequency range (Hz)	0.997
Note Repetition Rate (Hz)	-0.992
Maximum Frequency (Hz)	0.984
Note Length (s)	0.981
Minimum Frequency (Hz)	-0.944
Eigen Value	4.798
Variance explained (%)	95.964

Type 5

Variable	Principal Component	
	1	2
Minimum Frequency (Hz)	-0.990	-0.016
Frequency range (Hz)	0.960	0.220
Note Repetition Rate (Hz)	0.807	0.554
Maximum Frequency (Hz)	-0.615	0.556
Note Length (s)	0.561	-0.593
Eigen Value	3.246	1.016
Variance explained (%)	64.911	20.330

Type 6

Variable	Principal Component	
	1	2
Minimum Frequency (Hz)	0.955	-0.296
Maximum Frequency (Hz)	0.908	0.316
Frequency range (Hz)	-0.176	0.886
Note Repetition Rate (Hz)	0.215	0.704
Note Length (s)	-0.021	0.009
Eigen Value	1.813	1.468
Variance explained (%)	36.262	29.366

Type 7

Variables	Principal Component
	1
Frequency range (Hz)	0.971
Note Repetition Rate (Hz)	-0.933
Note Length (s)	0.924
Maximum Frequency (Hz)	0.920
Minimum Frequency (Hz)	-0.832
Eigen Value	4.205
Variance explained (%)	84.099

Figure A 1 – Eigenvalues from the principal components analyses performed for five variables measured in seven groupings of similar songs. Only principal components with eigenvalues greater than 1.0 are shown for each group. The weight of influence each variable had on the eigenvalues is shown in descending order, with the most influential variable in explaining variance shown at the top. The amount of variance in the data set that each eigenvalue explained is also shown.