Harnessing the power of citizen-science data to study the spatiotemporal patterns of birdsong

By
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Dissertation
Submitted to the Faculty of the
Graduate School of Vanderbilt University
in partial fulfillment of the requirements
for the degree of
DOCTOR OF PHILOSOPHY
in
Chemical and Physical Biology

May 8, 2020
Nashville, Tennessee

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ACKNOWLEDGMENTS

My most sincere and deepest appreciation goes to my mentor Dr. Nicole Creanza. Thank you for opening your lab to me without question and with lots of love. You have developed a lab in which both the scientist and science thrives! I have had the great pleasure of taking on your chippies project and have learned so much from your patient guidance in fields I had never explored before this experience. Your support has meant everything and gave me the opportunity to see my graduate career to the end. Thank you to all of those in the Creanza Lab. I have greatly benefitted from our crowdsourcing efforts as well as the intellectual discussions and critiques of each other's work. Most of all, I have enjoyed the many laughs and celebrations we have shared!

My network of women throughout this process has been paramount to my accomplishment. I am so grateful that I met Drs. Nora Foegeding and Megan Dumas that first year at Vanderbilt. You all have kept me strong both emotionally and physically with our lunch talks and workouts! Dr. Amanda Duran, thank you for being such a great hiking and birding partner! Nicole Sanchez, I found my kindred spirit in you; your presence always lights up the room and was a welcome surprise when I would get home from a long day. I miss our weekend escapades and cooking sessions; they were the balance I needed.

My greatest thanks go to my whole family for their love and support throughout this rollercoaster of a journey. They have all had a hand in my work in both getting to graduate school and finishing. Dad, I will never forget the many experiments that happened in your basement workshop, from testing concrete composition to figuring out what was wrong with "little Eddie". Mama, I will always hear your wise words, "don't borrow trouble". I cannot thank you enough for all of the hours you have spent editing my papers over the years. Amanda, you have been a role model throughout my life for what it means to be an incredibly strong and independent woman. You also taught me early on the importance of presentation; I have you to thank for teaching me how to make science posters and figures look great! Evan, thank you for letting me borrow your design and engineering skills and for being an example of how hard work can get you through anything! Finally, I want to thank my partner Kyle for supporting me through the ups and downs of this long process. I am so lucky to have the best "study partner" for life, and appreciate all of the time you have taken to think about and discuss my work with me. You have always been there when I needed you most and supported me in whichever direction I chose.

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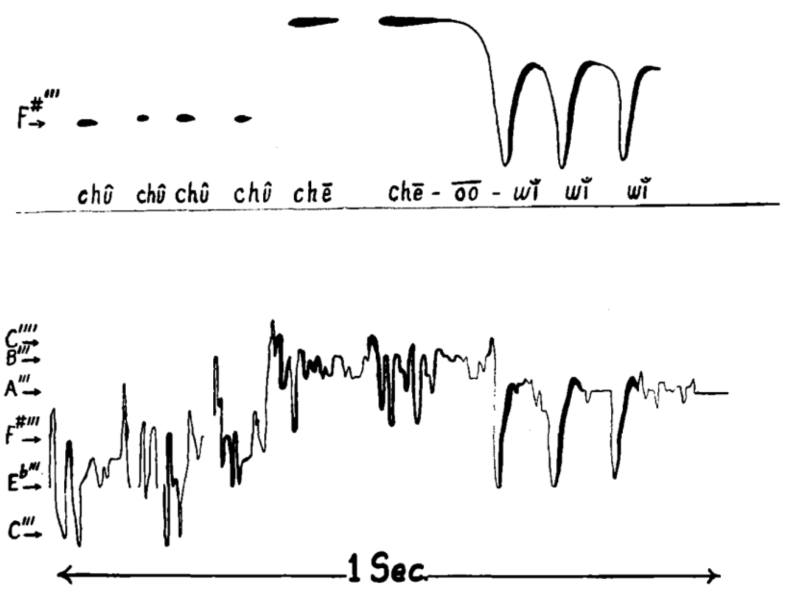
CHAPTER 1

INTRODUCTION

Throughout history, the serene sounds of nature have inspired artists, enthusiasts, and naturalists alike. And among all of nature's sounds, the diverse and often melodic songs of birds have captured the attention of many.

At first, most researchers used observation, description, and categorization to manually document the sounds produced by birds, but over the years, those who have studied birdsong have strived to better record and depict the unique sounds of the vast number of species. In 1889, Ludwig Koch created the first-known recording of a birdsong at the age of eight using a phonograph (Ranft, 2012). For the next several decades, others were borrowing and adapting methods from disciplines such as music and linguistics to describe birdsong, for example by attributing sounds of speech to the songs, termed syllabications (*i.e.* phonetic descriptions) (Cheney, 1891; Saunders, 1915, 1935). These methods provided useful descriptions of song and aided in species identification and basic interspecies comparisons. However, they were not precise enough to compare songs within a species or to objectively measure similarities and differences in songs. Researchers were eager to develop quantitative methods to measure birdsong to conduct comparative studies. Brand, in particular, invented a new method to quantitatively describe birdsong using existing scientific technology; he computed the frequency and timing of birdsongs using sound photographs on motion picture films (Brand, 1935). By using low-power microscopes to examine the acoustic track, which appears as light and dark lines perpendicular to the film strip, he could determine the pitch of the song based on the film rate and the number of lines recorded per second. The length of a song and syllables could also be determined. By improving on Saunders's method, which relied on the ear for pitch recorded on the left staff, duration and intensity drawn as lines with varying width, and syllabications written below, scientists could now accurately describe and visualize the songs as graphs of frequency versus time (Axtell, 1938; Brand, 1935; Saunders, 1915) (**Fig. 1.1**). This use of existing technology—microscopes and recording film—enabled previously impossible studies: with the use of a microscope to accurately determine from recordings the number of syllables in chipping sparrow songs, it was possible to demonstrate that the previously used method, trying to count by ear, was grossly inaccurate. For example, it was thought that chipping sparrows sung their syllables in multiples of 8, but this was not supported with more analytical methods (Brand & Axtell 1938). While Brand's new method did enable more detailed studies, these efforts were at the limits of the capabilities of the field and only barely began to provide ways to measure and compare recorded birdsong. Ultimately, this aspiration to quantitatively analyze birdsong was propelled by the engineering of new technology.



TEXT-FIG. 3.—Graphs of a single song of Kirtland's Warbler, showing comparative results from two methods of study. Upper figure, a graph as made by ear using Saunders's method; lower figure, a graph as made from analysis of sound track on film for the same song.

Figure 1.1 Early methods for drawing graphs of birdsong. Both visualizations are of a Kirkland's Warbler song. (Top) The song is depicted using Saunders's method in which the sound is drawn by ear with estimated pitch written to the left, syllabication written below, and intensity represented by line thickness. (Bottom) The same song is more accurately quantified and presented with scales of pitch and time that have been acquired from sound track on film. Figure from (Axtell, 1938).

It was not until the mid to late 1940s that the first machine was released that was capable of producing a written documentation of sound comparable to Saunders's or Brand's graphs (Koenig et al., 1946; Potter et al., 1947); the new visualization was first referred to as a "sound spectrograph". While the technology was developed during World War II by those at Bell Telephone Laboratories, it would later be made commercially available by Kay Electric company as a "Sona-Graph" machine in 1948 (Baker, 2001). As Bailey (1950) describes the machine, one must first have a recording of sounds (disk or magnetic tape), second, one must use an electrical filter for specific frequency bands, and lastly, the electric current is transferred into visible markings by a simultaneously rotating drum with facsimile paper, chemically induced ink, and a stylus. This results in a graph of the sound's frequency versus time in seconds, which has been called by various terms over the years, including sonagram, sonagraph, spectrograph, and spectrogram. The use of this technology was quickly adopted by ornithologists such as Bailey, Fish, and Borror (Bailey, 1950; Borror & Reese, 1953; Fish, 1953). Borror referred to the Kay Sona-Graph as a Vibrilizer, using it to create spectrograms of birdsongs and setting the expectation that these spectrograms would be valuable in intraspecific variation and behavioral studies (Borror & Reese, 1953). This method remained the primary tool for visualizing birdsong for decades, enabling an explosion of new applications and questions for ornithologists to explore.

Simultaneously, in the 1950s and into the 1960s, the variation of song within avian species was being noticed by many researchers (Marler., 1952; Marler & Tamura, 1962). The discovery of this intraspecies variation motivated the hypothesis that song was being learned. In 1954, Thorpe adopted the use of the spectrogram in his manuscript to provide evidence that song is indeed a learned trait (Thorpe, 1954). Recording and playback equipment alongside spectrograms continued to aid in answering further questions surrounding vocal learning. Specifically, the continued work by Thorpe, Marler, Nottebohm, and others often compared the recordings of a tutor's song to recordings of the learned song of a pupil, leading to increased understanding of innate song templates, song learning before song production, song matching, and time-sensitive learning periods (Marler & Tamura, 1964; Nottebohm, 1968b; Thorpe, 1954, 1958). Similarly, Konishi and others used spectrograms in their work to discover and explain the importance of auditory feedback—a bird hearing itself practice its song—on song learning (Konishi, 1965; Konishi, 1964; Nottebohm, 1968a). Importantly, the learned nature of song creates the possibility of mistakes in copying, also referred to as 'copy errors'. It is this simple inherent characteristic of vocal learning that enables song to evolve and shift within a species over space and time, explaining the noted dialects across well-defined geographic regions or variations over large geographic ranges (Baptista, 1975; Nottebohm, 1969).

Alongside this rich research on vocal learning, recording technology continued to advance, moving from reel-to-reel to cassette. Recording in the field became more and more accessible as did visualizing the increasing number of records. Particularly, in the 1980s and 1990s, cassette recorders were reduced in size and weight, eventually having the option of immediate playback (Hardy et al., 1988). With these recording devices, either shotgun microphones or microphones with parabolic reflectors were used to reduce ambient noise or amplify the song of interest (Catchpole & Slater, 2003). Together, these devices made fieldwork easier to conduct with the added beneficial result of increased recording quality. In addition, this time period saw rapid development in equipment to view real-time spectrograms on computer monitors and spectrogram analysis software (Catchpole, 1990; McGregor, 1989, 1991; Wilkinson, 1994). This growth in methods continued into the 2000s with the advent of digital recording and playback devices and even more software for improved quantitative analysis (Burt, 2001; Burt, 2000). As researchers continued to study song learning in the laboratory, much of the software developed was for model species such as the zebra finches and particular scenarios involving pupils and tutors in sound-controlled recording chambers. For instance, Sound Analysis Pro software was developed for this purpose and continues to be an invaluable resource in the field (Tchernichovski et al., 2000).

Leap forward to 2020, and now nearly everyone in the developed world has both a GPS and a recording device with them at all times—a smartphone. Thus, now enthusiasts are no longer observing birds and enjoying their songs only as a hobby but are also actively collecting and sharing valuable data in the form of sightings and recordings. The Cornell Lab of Ornithology, home to many of the early ornithologists conducting birdsong research and the Macaulay Library audiovisual database (www.macaulaylibrary.org), has capitalized on this resource. Specifically, they have gamified the sightings of birds, moving the records from hiker's pocket notebooks to electronic repositories by creating and promoting a citizen-science phone application, eBird (www.ebird.org) (Sullivan et al., 2009; Wood et al., 2011). Other databases of bioacoustic recordings, such as Xeno-canto (www.xeno-canto.org) (Vellinga & Planqué, 2015), also serve as a location for storing birdsong recordings. In the past two decades, these citizen-science databases of avian sightings and song recordings have gained considerable traction, experiencing remarkable growth in both usership and data collection (Sullivan et al., 2014; Vellinga & Planqué, 2015). Such databases foster the collaborative use of these recordings for conservation and research applications; in particular, the vast information gathered by birdwatchers around the world provides a much-needed broader scope to complement site-specific fieldwork.

However, just as the first technology to visualize and analyze spectrograms was driven by the need for better and easier methods of quantification, the current increase in digital recordings necessitates an increase in high-throughput methods of analysis for researchers. In the last ten years, a number of software programs or packages for bioacoustic analysis have surfaced or significantly improved (Araya-Salas & Smith-Vidaurre, 2017; Center for Conservation Bioacoustics, 2019.; Lachlan, 2007). Additionally, researchers are investigating ways to fully automate song annotation, but this often requires large amounts of data from recording chambers of the same individual bird (Adavanne et al., 2017; Daou et al., 2012; Mackevicius et al., 2019; Nicholson, 2016; Pearre et al., 2017; Sainburg et al., 2019; Wu et al., 2008). Thus, there is still a need in the community for open-source methods that are tailored specifically to analyzing recordings of varying qualities and from multiple species collected in nature by citizen scientists.

Together, this historical body of work demonstrates how technological advances improve data collection which subsequently necessitates new methods of analysis, creating a feedback loop that ultimately enables new scientific discoveries. As discussed above, most recently the availability of hand-held recording devices has driven the immense growth of citizen science repositories. While the repositories have the benefit of providing a well-distributed dataset, they also bring the challenge of analyzing recordings collected using devices of various quality, during different weather conditions, and with inconsistent methods. In order to take advantage of such resources, the field needed new methods to analyze recordings of numerous species at various recording qualities. Henceforth, we discuss our twofold approach: to satisfy this need for new software and to demonstrate the value of using citizen-science data to study birdsong. In Chapter 2, we describe Chipper, software developed to streamline the measurement and analysis of birdsongs from various species and of varied quality. In Chapter 3, we validate the workflow of using Chipper and citizen-science data to find subtle patterns in song previously revealed by fieldwork on a “little brown bird” of North America—the chipping sparrow. In Chapter 4, we use this same method to uncover long-range cultural structure in the chipping sparrow’s simple song. In Chapter 5, we explore the cultural evolution of the chipping sparrow song with particular interest in the distribution and evolution of syllable shapes.

In Chapter 2, we present Chipper, a Python-based software to semi-automate both the segmentation of acoustic signals and the subsequent analysis of their frequencies and durations. For avian recordings, we provide widgets to best determine appropriate thresholds for noise and syllable similarity, which aid in calculating note measurements and determining syntax. In addition, we generated a set of synthetic songs with various levels of background noise to test

Chipper's accuracy, repeatability, and reproducibility. Together, Chipper provides an effective way to quickly generate reproducible estimates of birdsong features. The cross-platform graphical user interface allows the user to adjust parameters and visualize the resulting spectrogram and signal segmentation, providing a simplified method for analyzing field recordings. Chipper streamlines the processing of audio recordings with multiple user-friendly tools and is optimized for multiple species and varying recording qualities. Ultimately, Chipper supports the use of citizen-science data and increases the feasibility of large-scale multi-species birdsong studies.

To demonstrate the applicability and value of citizen-science data and our complimentary analysis software Chipper, we examine the spatiotemporal patterns of the chipping sparrow song. The chipping sparrow was one of the earlier species in which the song was quantitatively examined and described (Borror, 1959; Marler & Isaac, 1960); it has since been studied further by Liu and Kroodsma (Liu & Kroodsma, 1999, 2006, 2007). With each individual chipping sparrow only singing one simple song of a single repeated syllable, it is a relatively easy system to study, since a single recording captures a bird's full repertoire. Additionally, the chipping sparrow range spans most of North and Central America with both a sedentary and migratory population. Together, these characteristics make the chipping sparrow an ideal species to study how song is being transmitted and ultimately changing over space and time.

Historically and still today, most studies of avian species entail fieldwork, in which birds at particular locations are often banded and observed for a season or even years. While song can now be documented and shared easily, behavioral observations are more difficult to record. Thus, song has begun to be studied in the absence of fieldwork, but behavioral studies still rely on site-specific observation. Therefore, how well citizen-science data can extend the results of in-depth field studies that hinge on detailed behavioral observations. In particular, it is worth investigating whether citizen-science data proves effective in predicting study species that have diel song patterns. As proof-of-principle, we test the prediction that diel patterns in birdsong observed in fieldwork can be detected range-wide using publicly contributed birdsong recordings. Specifically, in Chapter 3 we analyze all available chipping sparrow songs from Macaulay Library and Xeno-canto and test the prediction that the continent-spanning chipping sparrow recordings reflect the results of field-based research: chipping sparrows sing shorter songs with fewer syllables before sunrise (dawn song) than after sunrise (day song). With our analysis of citizen-science song recordings, we find support for this prediction, demonstrating that the results of a site-specific field study apply to chipping sparrows across their entire geographic range in North and Central America. Thus, we suggest that findings from public repositories can be used throughout the scientific process to detect whether daily song patterns exist in species even in the absence of prior fieldwork, which can then be used to inform cross-species hypotheses and facilitate future investigations into whether diel patterns in song are associated with differences in social behavior.

As the use of Chipper and citizen-science recordings successfully reproduced the field-based results of the diel patterns in chipping sparrow songs, we now turn to using these resources to find new patterns across the species' geographic range. Geographic variation has been widely studied in oscine songbirds, with particular attention paid to the interplay between variables associated with learned song and dispersal. While most field-based studies have focused on discrete dialects, we suggest that analyzing data from quickly growing citizen-science libraries could uncover geographic patterns in species previously thought to exhibit random variation in song. In Chapter 4, using citizen-science birdsong databases, we test whether chipping sparrow song is geographically structured on a continental scale. The chipping sparrow is a particularly well-suited species for such a study, since individuals have a simple song of one repeated syllable, have only the beginning of their first breeding season to adjust their song before crystallization, and have been shown to match their song to a nearby neighbor. Together, these properties might promote local enhancement of syllables; however, field studies have shown that local syllable diversity has been maintained over time. We analyze 820 individual recordings of the simple, yet diverse, song of chipping sparrows to assess whether long-range geographic patterns have formed despite this local song variation. We found significant correlation between song features and geographic distance, associated with longitude but not latitude: chipping sparrows in the Eastern United States and Canada sing at a slower rate (fewer, longer syllables) than the Western population. However, comparing syllable types in different regions, we found that all broad syllable categories were represented in both Eastern and Western United States/Canada. To better contextualize our findings, we re-evaluate available genetic sequences of chipping sparrows to test for genetic differentiation between the Eastern and Western populations in which we found song differences. Our results suggest that there are two culturally distinct sub-populations of migratory chipping sparrows that are genetically indistinguishable using mitochondrial DNA, motivating future studies on migration patterns and additional sequencing of nuclear DNA.

Our findings are an example of how behavioral traits, specifically learned song, can change over time and accumulate significant differences across geographic space. The change in behavior as information is transmitted through social interaction such as learning is an example of cultural evolution. While our initial findings involved broad song characteristics such as syllable durations and repetitions, we wanted to determine whether these changes manifested as larger structural changes in the syllables. In Chapter 5, we explore syllable shape further—how changes have accumulated over time—by examining the frequency of syllable shapes across the years of citizen-science data. Examining a syllable from each chipping sparrow recording, we categorized all syllables into six general categories with further division into 112 distinct syllable types. Following these syllable types over the course of six decades, we found that most syllable types are either very short-lived or very long-lived, with the long-lived syllables occurring much more frequently. To determine whether this trend toward common, long-lived syllables was a result of neutral cultural evolution or a selection pressure such as directional pressure or social conformity, we developed a model of song transmission for the chipping sparrow. Our preliminary results suggest chipping sparrows learn song with some directional pressure on tutor selection which may reflect a performance song feature. Moreover, our findings suggest chipping sparrows learn syllables with a low error rate, approximately 0.05%. Further model refinement is necessary before any final conclusions, including the incorporation of territory dispersal as well as directional selection on syllable types.

In Chapter 6, I challenge researchers to use citizen-science data and fieldwork together as complementary strategies: citizen-science can lead to better informed and thus less costly field studies, and field studies can guide researchers towards domains in which additional data could be illuminating. Specifically, I highlight examples in which this workflow could be applied to our findings, suggesting future field studies on chipping sparrow migration and song recognition. Additionally, I expand on how Chipper has enabled large-scale citizen-science studies beyond the chipping sparrow as well as served as a valuable teaching tool for seminar courses, allowing students to experience the entire research process. Throughout Chipper's development, one goal has been to maintain the project as open-source with the hope that others in the field will both benefit from the use of Chipper as well as contribute to its development. Towards this end, I suggest simple improvements to Chipper that would extend its applicability to additional song types as well as more advanced features that could be integrated. I contextualize these greater changes with the current challenges of song analysis in the field. Lastly, I present preliminary work on the employment of Chipper and citizen-science data to study a timely and important topic, the effects of urbanization on birdsong.

CHAPTER 2

CHIPPER: OPEN-SOURCE SOFTWARE FOR SEMI-AUTOMATED SEGMENTATION AND ANALYSIS OF BIRDSONG AND OTHER NATURAL SOUNDS

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A modified version was previously published as:
Searfoss, A.M., Pino, J.C., Creanza, N. (2020) Chipper: Open-source software for semi-automated segmentation and analysis of birdsong and other natural sounds. *Methods in Ecology and Evolution*, 11(4). https://doi.org/10.1111/2041-210X.13368

INTRODUCTION

Acoustic communication is one of the few natural behaviors that can be easily recorded, digitized, and studied (Catchpole & Slater, 2008; Cocroft & Rodríguez, 2005; Garland et al., 2017; Ryan & Guerra, 2014). Often, behavioral studies involve laboratory observations, which can lead to fundamental insights but may disrupt natural animal behavior (Fehér et al., 2009; Marler & Peters, 1977; Searcy, 1984). In addition, scientists can collect acoustic sounds in the wild without disturbing animals, eliminating potential influences of the laboratory environment on behavior but limiting the types of experiments possible (B. R. Grant & Grant, 1996; Robert F. Lachlan et al., 2018; Shizuka et al., 2016; Williams et al., 2013). Moreover, recordings can be pooled across sources—professionals and hobbyists, analog and digital, old and new—providing vast datasets that span many years and large geographic scales (Bolus, 2014; Roach & Phillmore, 2017). Thus, audio recordings are an advantageous resource for broad-scale animal behavior research.

Birdsong has been studied in ecology and evolution for decades (Marler & Tamura, 1964; Thorpe, 1958). Historically, field studies of birdsong have provided insights into mating and territory-defense behaviors, evolutionary events such as speciation and hybridization, and environmental adaptation (P. R. Grant & Grant, 1997; Mason et al., 2017; Nowicki & Searcy, 2004; Robinson et al., 2019; Slabbekoorn & Peet, 2003; Snyder & Creanza, 2019). These studies are often conducted with banded birds and direct recordings using parabolic microphones. Some song analysis software is well-suited to these studies, allowing users to visualize and manually select songs from their field recordings for analysis (Boersma & Weenink, 2019; Burt, 2001; Center for Conservation Bioacoustics, 2019; R. F. Lachlan, 2007). On the other hand, laboratory experiments often use individual sound-attenuating recording chambers. Such experiments have greatly extended our understanding of the neurobiology of learning and development (Tchernichovski et al., 2001). Alongside laboratory work, song analysis software has been developed to provide quantitative comparisons between individuals from a specific species, such as pupils and tutors in song-learning experiments (R. F. Lachlan, 2007; Tchernichovski et al., 2000). In sum, fieldwork and laboratory experiments, particularly when paired with software, have made large contributions in understanding acoustic communication.

Concurrently, portable audio recording devices have changed significantly over the last 50 years, moving from large reel-to-reel devices to handheld digital recorders and smartphones, which has made collecting natural recordings much easier (Sullivan et al., 2009; Vellinga & Planqué, 2015). This new technology has improved collection of both wild and laboratory recordings and led to an active worldwide community of citizen scientists who record and archive birdsong (Bonney et al., 2009; Silvertown, 2009; Sullivan et al., 2009; Wood et al., 2011). Although there are many scientific questions that can be answered using these expanding citizen-science datasets of birdsong or other natural sounds (e.g. Xeno-canto, eBird, Macaulay Library at the Cornell Lab of Ornithology), there is still a need for high-throughput and automated methods of song analysis that address the varying quality and multi-species nature of citizen-science recordings. One R package, WarbleR, has made progress by facilitating the retrieval and analysis of songs from the Xeno-canto repository (Araya-Salas & Smith-Vidaurre, 2017). Existing signal processing toolboxes in Python are neither optimized for natural recordings nor user-friendly for researchers unfamiliar with computer programming. To reduce and streamline the manual work involved in processing databases of natural recordings, we developed Chipper, an open-source Python-based (v3.6.2) software with a Kivy-based (v1.10.0) graphical user interface, to semi-automate the segmentation and analysis of acoustic signals.

Chipper facilitates syllable segmentation and subsequent analysis of frequency, duration, and syntax, improving efficiency in using citizen-science recordings and increasing the feasibility of multi-species studies. While primarily designed for birdsong, Chipper can also process other natural sounds, such as frog or insect vocalizations. Our software is open-source and user-friendly, allowing seamless integration into research and education. In particular, Chipper streamlines the song analysis process, eliminating the need to manually handle each song multiple times (**Fig. 2.1**). In addition, we created synthetic datasets of birdsong for testing acoustic software and conducted a thorough test of Chipper's accuracy, repeatability, and reproducibility.

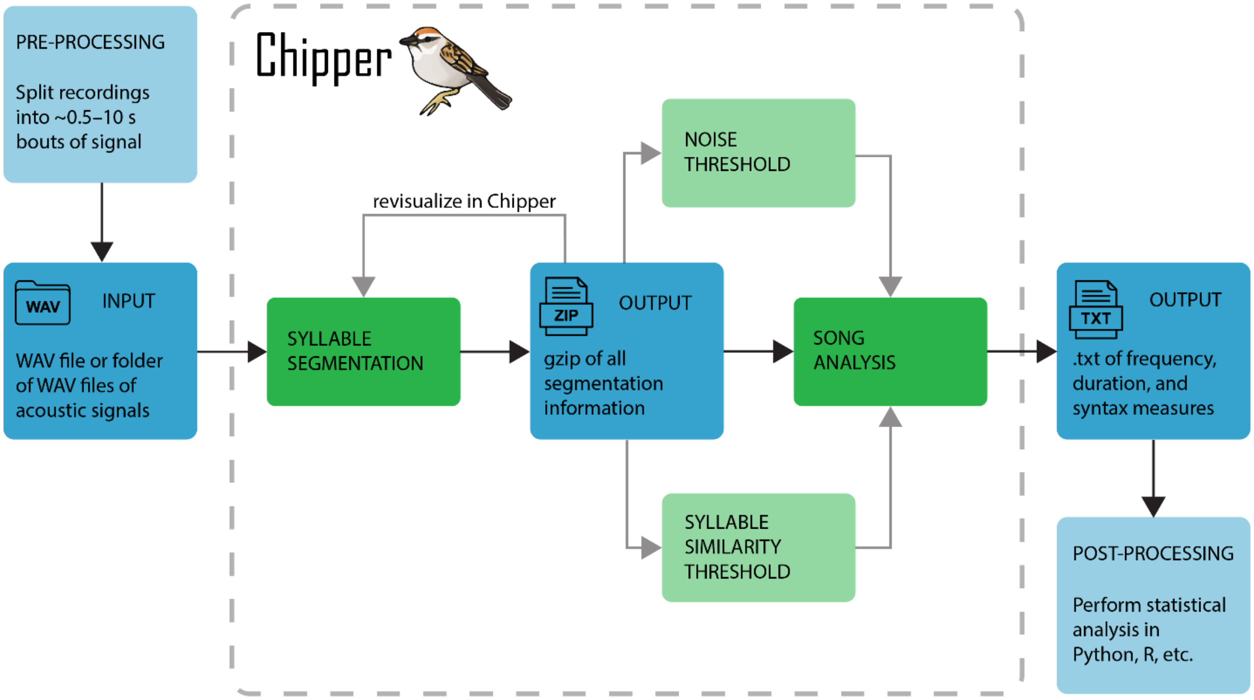


Figure 2.1 Chipper's streamlined process of segmenting and analyzing recordings. Blue steps indicate inputs and outputs; green steps indicate Chipper widgets. Navigate through Chipper as follows: 1) Split recordings into ~0.5–10 seconds of signal, often a bout of singing. 2) Gather bouts of acoustic signals (WAV files) to input into Chipper. 3) Load files and begin with the default syllable segmentation. Alter segmentation parameters, viewing how this changes the quality of the signal and the segmentation. 4) Segmentation results in zipped files with all necessary information. 5) Use widgets to determine the best thresholds for noise and syllable similarity. 6) Run song analysis using these thresholds. Measurements characterizing frequencies and durations for the song, syllables, and notes are calculated. 7) All measurements are output into two text files. 8) Perform statistical analysis on song measurements in Python, R, etc.

CHIPPER’S INTERFACE AND CAPABILITIES

Chipper is primarily designed to parse syllables from a bout of birdsong, but any sound recording can be processed. We suggest recordings <3MB or ~0.5–10 seconds, but the optimal value will differ between projects (based on sampling rate, syllable duration, computing resources, etc.). For long songs, we advise splitting the recording into multiple files before processing in Chipper. Therefore, users should first select and export song bouts (as WAV files) from in-house recordings or citizen-science data; we recommend Audacity for manual pre-processing and monitoR or Kaleidoscope Pro Analysis Software for semi-automated selection. Chipper guides the user through two main steps to extract information from WAV files of song bouts: syllable segmentation and song analysis (**Fig. 2.1**).

Syllable segmentation

On the Chipper landing page (**Fig. 2.2A**), the user can adjust the defaults for the automated segmentation. Next, a single WAV file or an entire folder of WAV files can be selected to begin segmentation. Chipper will then semi-automate the process of noise reduction and syllable parsing of each recorded bout of song. The syllable segmentation window (**Fig. 2.2B**) shows two images: the top image is the spectrogram of the file and the bottom shows a binary image calculated based on user-informed parameters, with onsets (short green lines) and offsets (tall green lines) depicting the automated syllable segmentation.

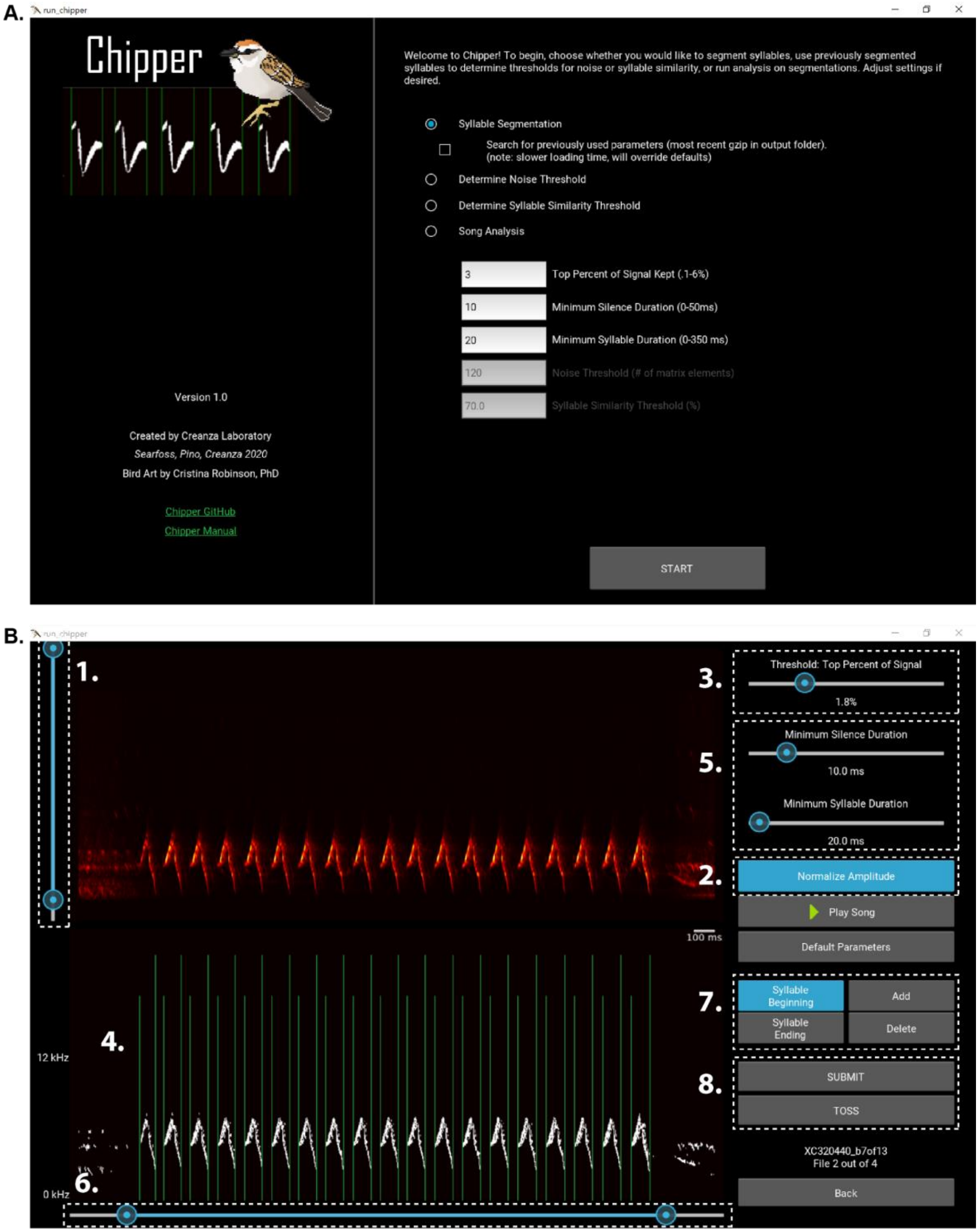
The user can adjust the segmentation parameters using the sliders. With each parameter adjustment, a new binary image and corresponding onsets and offsets are calculated in the following order (numbered as in **Fig. 2.2B**):

1. The spectrogram of the recording is created from the WAV file (method adapted from (Gardner & Magnasco, 2006)), and low- and high-frequency noise can be removed with high- and low-pass filters, respectively. Colors in the resulting spectrogram are rescaled based on the remaining signal.
2. Selecting “Normalize Amplitude” rescales the amplitude across the spectrogram.
3. The “Threshold: Top Percent of Signal”, *q*, is used to find the (100-*q*)th percentile of signal. Only signal above this percentile is retained and plotted in the binary image; all other signal is set to zero.

4. Syllable onsets (beginnings) and offsets (endings) are calculated by summing the columns of the spectrogram, creating a vector of total signal intensity over time. Then, an onset is defined as the position of the first element in the matrix where signal is present after silence and an offset as the position of the first element of the matrix with no signal after prolonged signal.
5. Two parameters act as constraints on the list of onsets and offsets—"Minimum Silence Duration" and "Minimum Syllable Duration". If the time between the offset of one syllable and the onset of the next syllable is less than or equal to the minimum silence duration, these boundaries are removed, combining the two syllables. Similarly, if the duration between an onset and offset of one syllable is less than the minimum syllable duration, the onset–offset pair is removed.
6. If any onsets or offsets are outside the time range of interest (determined by the slider below the binary image), they will be removed.
7. The user can manually add or delete onsets and offsets to adjust segmentation, such as adding a missing onset or offset or altering an incorrect placement due to noise.
8. Lastly, the user can submit the parameters, the final binary matrix, and syllable onsets and offsets. If a satisfactory segmentation was not reached, the file can be tossed.

Quantitative analysis

As syllable segmentation is completed for each song, Chipper generates an output file (gzip) containing all necessary information on the binary image, segmentation, and conversion factors for both time and frequency space. These output files can then be processed using Chipper's analysis tool. This portion of Chipper is fully automated; the window serves to show the number of files processed out of the total selected by the user. For each song being processed, Chipper produces multiple song, syllable, note, and syntax measurements (**Table 2.1**). Many of these outputs rely on the input parameters for noise and syllable similarity thresholds; thus, we recommend using our widgets in Chipper to determine appropriate thresholds for each species-specific set of songs studied.



Welcome to Chipper! To begin, choose whether you would like to segment syllables, use previously segmented syllables to determine thresholds for noise or syllable similarity, or run analysis on segmentations. Adjust settings if desired.

● Syllable Segmentation

☐ Search for previously used parameters (most recent gzip in output folder). (note: slower loading time, will override defaults)

○ Determine Noise Threshold

○ Determine Syllable Similarity Threshold

○ Song Analysis

3 Top Percent of Signal Kept (.1-6%)

10 Minimum Silence Duration (0-50ms)

20 Minimum Syllable Duration (0-350 ms)

120 Noise Threshold (# of matrix elements)

70.0 Syllable Similarity Threshold (%)

START

Version 1.0

Created by Creanza Laboratory

Searfoss, Pino, Creanza 2020

Bird Art by Cristina Robinson, PhD

Chipper GitHub

Chipper Manual

Threshold: Top Percent of Signal 1.8%

Minimum Silence Duration 10.0 ms

Minimum Syllable Duration 20.0 ms

XC320440_b7of13

File 2 out of 4

Figure 2.2 Chipper Interface. (A) Landing page of Chipper. Here the user can choose to segment songs, visualize the already segmented songs to choose thresholds for noise and syllable similarity, or run song analysis with default or user-defined thresholds. (B) Segmentation window with parameters labeled in the order that they are applied to the spectrogram and segmentation calculations (see *Syllable Segmentation* section). For images of other Chipper windows and more detailed instructions on the use of Chipper, see the manual at https://github.com/CreanzaLab/chipper/tree/master/docs.

Table 2.1 Chipper's output measurements

Measurement	Calculation
Song duration	(time of last syllable offset − time of first syllable onset)
Number of syllables	number of syllable onsets in a song
Syllable rate	(number of syllables)/(song duration)
Average syllable duration	mean(time of syllable offset − time of syllable onset)
Std. dev. of syllable duration	standard deviation(time of syllable offset − time of syllable onset)
Average silence duration	mean(time of syllable onset − time of previous syllable offset)
Std. dev. of silence duration	standard deviation(time of syllable onset − time of previous syllable offset)
Largest syllable duration	max(time of syllable offset − time of syllable onset)
Smallest syllable duration	min(time of syllable offset − time of syllable onset)
Largest silence duration	max(time of syllable onset − time of previous syllable offset)
Smallest silence duration	min(time of syllable onset − time of previous syllable offset)
Average syllable frequency range	mean(maximum frequency − minimum frequency for each syllable)
Std. dev. syllable frequency range	standard deviation(maximum frequency − minimum frequency for each syllable)
Average syllable lower frequency	mean(minimum frequency of each syllable)
Average syllable upper frequency	mean(maximum frequency of each syllable)
Largest syllable frequency range	max(maximum frequency − minimum frequency for each syllable)
Smallest syllable frequency range	min(maximum frequency − minimum frequency for each syllable)
Maximum syllable frequency	max(maximum frequency of each syllable)
Minimum syllable frequency	min(minimum frequency of each syllable)
Overall syllable frequency range	max(maximum frequency of each syllable) − min(minimum frequency of each syllable)
Syllable stereotypy	list of the mean(pairwise percent similarities) for each repeated syllable, where percent similarity is the maximum(cross-correlation between each pair of syllables)/maximum(autocorrelation of each of the compared syllables) × 100 Note: For the definition of repeated and unique syllables, see section *Determine threshold for syllable similarity*.
Mean syllable stereotypy	mean(stereotypy values for each repeated syllable)
Std. dev. syllable stereotypy	standard deviation(stereotypy values for each repeated syllable)
Syllable pattern	list of the syllables in the order that they are sung, where each unique syllable is assigned a number (i.e. the song syntax)
Number of unique syllables	number of unique values in syllable pattern
Degree of repetition	(number of syllable onsets in a song)/(number of unique syllables)
Degree of sequential repetition	(number of syllables that are followed by the same syllable)/(number of syllables - 1)
Number of notes	number of 4-connected elements of the spectrogram > than the noise threshold
Number of notes per syllable	(total number of notes)/(total number of syllables)
Average note duration	mean(time of note ending − time of note beginning)
Std. dev. of note duration	standard deviation(time of note ending − time of note beginning)
Largest note duration	max(time of note ending − time of note beginning)
Smallest note duration	min(time of note ending − time of note beginning)
Overall note frequency range	max(maximum frequency of each note) − min(minimum frequency of each note)
Average note frequency range	mean(maximum frequency − minimum frequency for each note)
Std. dev. note frequency range	standard deviation(maximum frequency − minimum frequency for each note)
Average note lower frequency	mean(minimum frequency of each note)
Average note upper frequency	mean(maximum frequency of each note)
Largest note frequency range	max(maximum frequency − minimum frequency for each note)
Smallest note frequency range	min(maximum frequency − minimum frequency for each note)
Maximum note frequency	max(maximum frequency of each note)
Minimum note frequency	min(minimum frequency of each note)

ADDITIONAL NOTE AND SYNTAX ANALYSES FOR BIRDSONG APPLICATION

For a subset of measurements provided by Chipper's analysis tool, the user can improve measurement accuracy by setting a noise threshold and syllable similarity threshold. The noise threshold affects any note-related and frequency-related calculations, since any signal smaller than the noise threshold is removed from the binary spectrogram. For example, low-frequency noise in a syllable that is not removed either in the segmentation process or by the noise threshold will affect multiple frequency measurements (minimum syllable frequency, average syllable frequency range, etc.). Any calculation that specifically uses the onsets and offsets, such as song, syllable, and silence durations, will not be affected by the noise threshold. The syllable similarity threshold only affects syntax-related calculations (number of unique syllables, syllable pattern, syllable stereotypy, etc.). Since it is useful to set these thresholds based on multiple songs, we have provided widgets to visualize these thresholds.

Determine threshold for noise

Chipper's quantitative analysis uses connectivity to classify signal within a syllable as either a note or noise. Specifically, any signal within the syllables (defined by onsets and offsets) in the binary image that is connected by an edge (not corner, i.e. 4-connected) and has an area greater than the user-specified threshold is labeled as an individual note, and any signal with an area less than or equal to the threshold is considered noise. Since signal connectivity is highly dependent on signal-to-noise ratio or amplitude, we provide a widget to determine the best threshold for a set of songs. In the noise threshold widget, the user selects a folder of multiple gzips (the output from syllable segmentation) as a representative subset of the songs being analyzed. For each song, the user can change the threshold to visualize areas being classified as notes (colored) versus noise (white) and then submit a threshold for that song. After going through the selected songs, a summary is provided including the average, minimum, and maximum thresholds selected for noise and, if enough songs are processed in the widget, a histogram. This information is provided to guide the user in choosing a single threshold that will be used in song analysis for the entire set of song files. We advise caution in using the output from note analysis for low-quality recordings: whereas high-quality recordings will have syllables in which signal is only disconnected at true notes, the degraded signal in low-quality recordings can lead to many false notes.

Determine threshold for syllable similarity

For each pair of syllables, a percent syllable similarity is calculated by sliding one syllable's binary matrix across another syllable's binary matrix and finding the maximum overlap (cross-correlation). This is then repeated for each syllable compared to itself, providing an autocorrelation for each syllable. We scale the maximum overlap between the two syllables by dividing by the maximum of the two syllables' autocorrelations; multiplied by 100, this results in a percent of the maximum possible overlap or percent syllable similarity for the syllable pair. Similar methods of spectrographic cross-correlation have been previously demonstrated as a useful method in determining syllable types (Clark et al., 1987). Applying the user-defined syllable similarity threshold to the resulting pairwise matrix, we establish the syntax for the recording by considering two syllables to be repeats of the same syllable if their similarity is greater than or equal to the user-specified threshold. If two syllables are considered to be the same type and the second one of those is considered the same as a third syllable, then the third syllable is classified as the same type as the first two. This prevents groups of similar syllables from being separated but also means that the first and third syllables could have a percent similarity below the threshold but still be considered the same type. Chipper's syllable similarity threshold widget guides the user in deciding an appropriate value. The binary song and the corresponding syllable onset and offset lines from syllable segmentation are plotted. Based on the threshold, the syntax is displayed in text as well as visually, with repeats of the same syllable shown in the same color. The user can change the threshold to see how this will change the syntax of the song, submitting the threshold when satisfied. When all of the sample songs have been processed, a summary will be displayed with the average, minimum, and maximum thresholds selected for syllable similarity and, if enough songs have been processed, a histogram. Once again, this information is provided to guide the user in choosing a threshold to process the entire set of song files of interest.

ASSESSING ACCURACY, REPEATABILITY, AND REPRODUCIBILITY

Generation of a standardized test set of synthetic birdsongs

We used the SciPy module in Python to generate 50 unique synthetic birdsongs (function ‘chirp’). Each song has 10 syllables in the following order: linearly constant, linearly increasing, linearly decreasing, quadratically increasing and concave, quadratically increasing and convex, quadratically decreasing and convex, quadratically increasing and concave, symmetric quadratic, logarithmically increasing, and logarithmically decreasing. For each song, a value was randomly chosen from a uniform distribution between 100 and 10,000. We then randomly selected a scaling factor for each syllable based on this value: specifically, a syllable amplitude scaling factor was randomly chosen from a uniform distribution of values 30% above or below the chosen song value, and this syllable scaling factor was then multiplied by the chirp output vector. The amplitude of each syllable was then altered to linearly increase to the maximum amplitude over the first 40% of the syllable duration and then linearly decrease to zero over the last 40% of the syllable duration; this smoothing both mimics natural signals and avoids discontinuities when performing the fast fourier transform on the waveform to produce the spectrogram. Lastly, the amplitude of each syllable was multiplied by an exponential decay function to mimic the natural decrease in signal intensity in bird sounds. Similarly, the starting frequency was randomly selected from a discrete, uniform distribution between 2,000–10,000 Hz; the ending frequency was then either the same as the starting frequency for flat syllables or randomly selected from the range of 2,000 Hz to starting frequency or from the range of the starting frequency to 10,000 Hz, depending on the shape of the syllable. The syllable durations and the durations of silence between each syllable were also randomly selected from 0.1–0.9 seconds and 0.01–0.5 seconds, respectively. Lastly, the beginning and ending of each generated song was padded with ~0.2 seconds of silence. Each song was saved as a WAV file, and all corresponding syllable and silence parameters were saved in a text file.

Next, different types of noise were added to each of the 50 synthetic songs. Using Audacity (menu option: Generate > Noise), two different tracks of white noise were created with an amplitude setting of 0.01 and 0.001 (on a scale of 0 to 1, where 1 is the loudest noise possible on a given track). Two tracks of natural noise were created by selecting sections of two different passive recordings collected in nature with a Wildlife Acoustics Song Meter 4 recorder that had minimal extraneous sounds (e.g. birds, crickets, car horns, etc.). Each of these noise tracks (white or natural) were added to the synthetic songs, creating 4 different noisy recording sets of 50 songs each (**Fig. 2.3**). The maximum amplitude of the noise and the signal for each song was calculated.

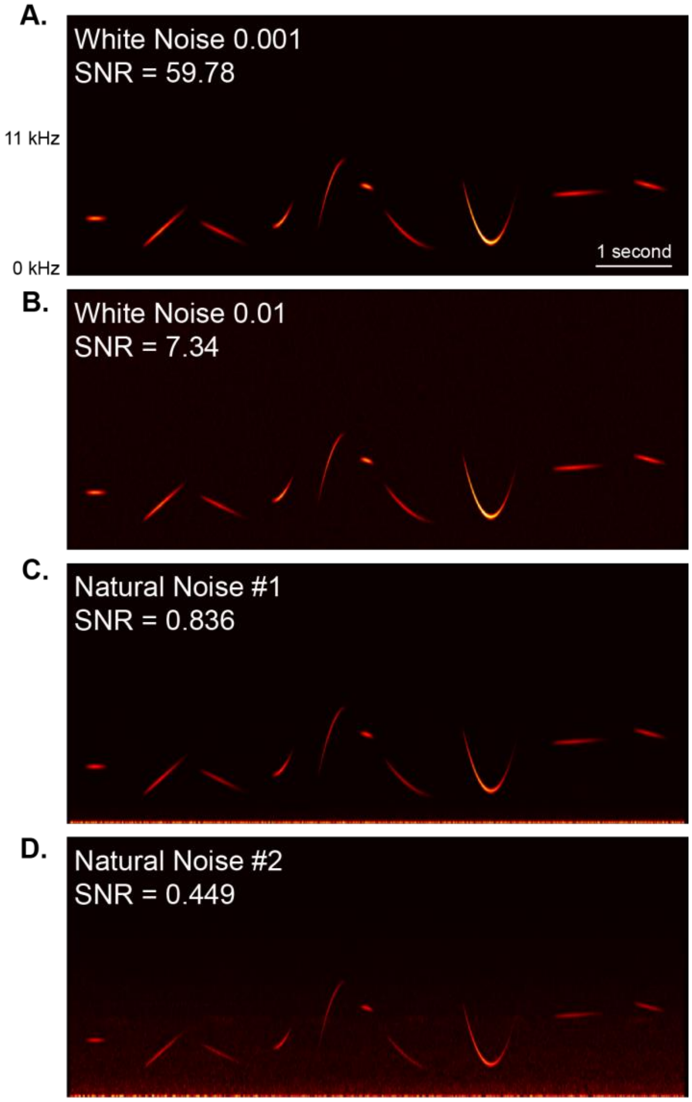


Figure 2.3 Example of a synthetic song with the four levels of added noise. (A) White noise with a low amplitude was added to the synthetic song. It is visually apparent that the signal-to-noise ratio (SNR) for this song is very high at 59.78. (B) A white noise track with a higher amplitude was added to the synthetic song, lowering the SNR for this song to 7.34. (C) The Natural Noise #1 track has most of its signal in the low-frequency range. As the noise track is similar in amplitude to the song's signal, the SNR drops to 0.836; however, Chipper's high-pass filter can remove most of this noise easily. (D) Similarly, Natural Noise #2 (SNR 0.449) has a significant amount of high amplitude noise in the low-frequency range. The high-pass filter can easily remove this band of noise, but there is still significant noise at higher frequencies occupied by the song. The synthetic song used for this example is on the project's GitHub (CreanzaLab/chipper) with the name SynSongs_amp100_30p_3.wav.

Assessing accuracy, repeatability, and reproducibility using synthetic birdsongs

All 250 synthetic songs (1 set without noise, 2 sets with natural noise, and 2 sets with white noise) were then processed in Chipper independently by two users. Both users kept the default thresholds for noise and syllable similarity in Chipper's analysis step (120 matrix elements and 70%, respectively). First, we compared the measurements from Chipper for the set of synthetic songs without added noise to the actual values used to create the songs (Figs. 2.4A and 2.5A). Since we created the syllables with amplitude linearly increasing over the first 40% of the syllable and decreasing over the last 40% to mimic real birdsongs, it was not surprising that the measured syllable durations are shorter than the "actual" values since the syllables begin and end at very low amplitude (Figs. 2.4A, second row). Similarly, the opposite effect occurs for average silence durations (Figs. 2.5A, first row). Our baseline measurements for bout duration and average syllable frequency range are close to the actual values used to generate the synthetic songs (**Fig. 2.4A**, first and third rows). Next, we compared the measurements from Chipper for the sets with noise to the measurements from Chipper for the set without noise. Specifically, we calculated a signal to noise ratio for each song using the maximum amplitude of the noise and the maximum amplitude of the signal that was documented when creating the synthetic songs. Then, we subtracted the Chipper measurements for the noisy files from the Chipper measurements for the set of songs without noise, which we used as baseline measurements (Figs. 2.4–2.5, Column B: Effect of Noise). For most measurements we assessed, the discrepancy between noisy files and files without noise began to increase when signal amplitude was approximately less than twice the amplitude of noise. Lastly, we tested the reproducibility and repeatability of Chipper measurements. The measurements from Chipper for all sets of synthetic songs were compared between users (Figs. 2.4–2.5, Column C: Reproducibility). Then the measurements from Chipper for all sets of synthetic songs were compared between the same user's first and second attempts at segmenting the songs in Chipper (Figs. 2.4–2.5, Column D: Repeatability).

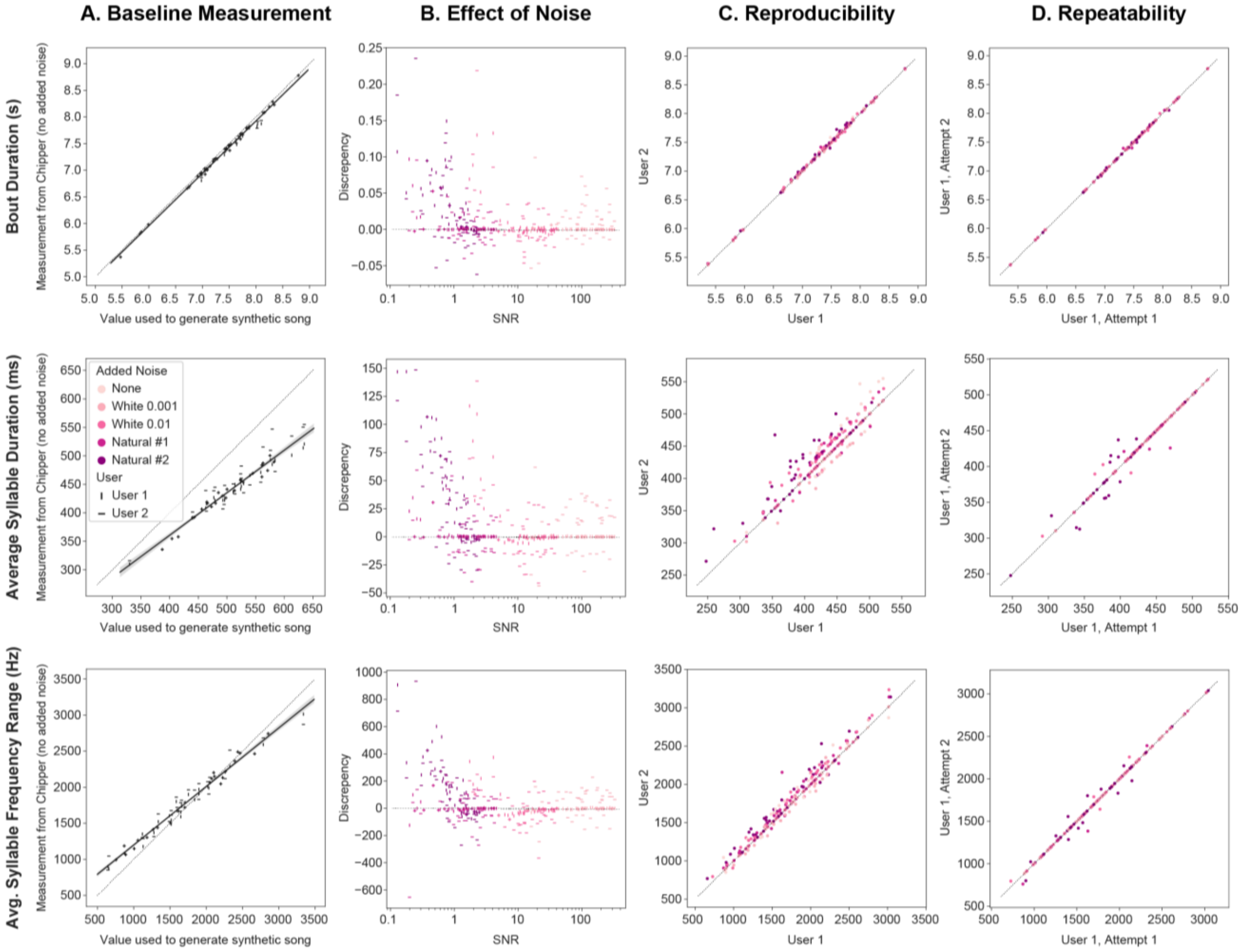


Figure 2.4 Accuracy, repeatability, and reproducibility of Chipper for key song features. (A) We compare the measurements from Chipper segmentation and subsequent analysis (*y*-axis) to the actual values (*x*-axis) used to generate the synthetic songs with no added noise. This provides a baseline for accuracy, as we expect measurements will not align with the line of unity (shown as dotted line) due to the method of creating synthetic songs. (B) We examine the effect of both white noise and natural noise on the segmentation and analysis of synthetic songs in Chipper. The discrepancy (*y*-axis) is the difference in the Chipper-measured song feature between synthetic songs with added noise and songs without noise. The signal-to-noise ratio (SNR) can be indicative of the possible accuracy; however, natural noise often has low-frequency noise that Chipper can reduce, providing a better accuracy than expected solely based on SNR. (C) To assess reproducibility, the measurements from segmentation and subsequent analysis conducted by two users is compared for synthetic songs of various noise levels. (D) To assess repeatability, the measurements from segmentation and subsequent analysis conducted twice by the same user are compared for all synthetic songs. These assessments are shown for three song features (rows): bout duration (seconds), average syllable duration (ms), and average syllable frequency range (Hz). Plots for additional song features can be found in Fig. 2.5.

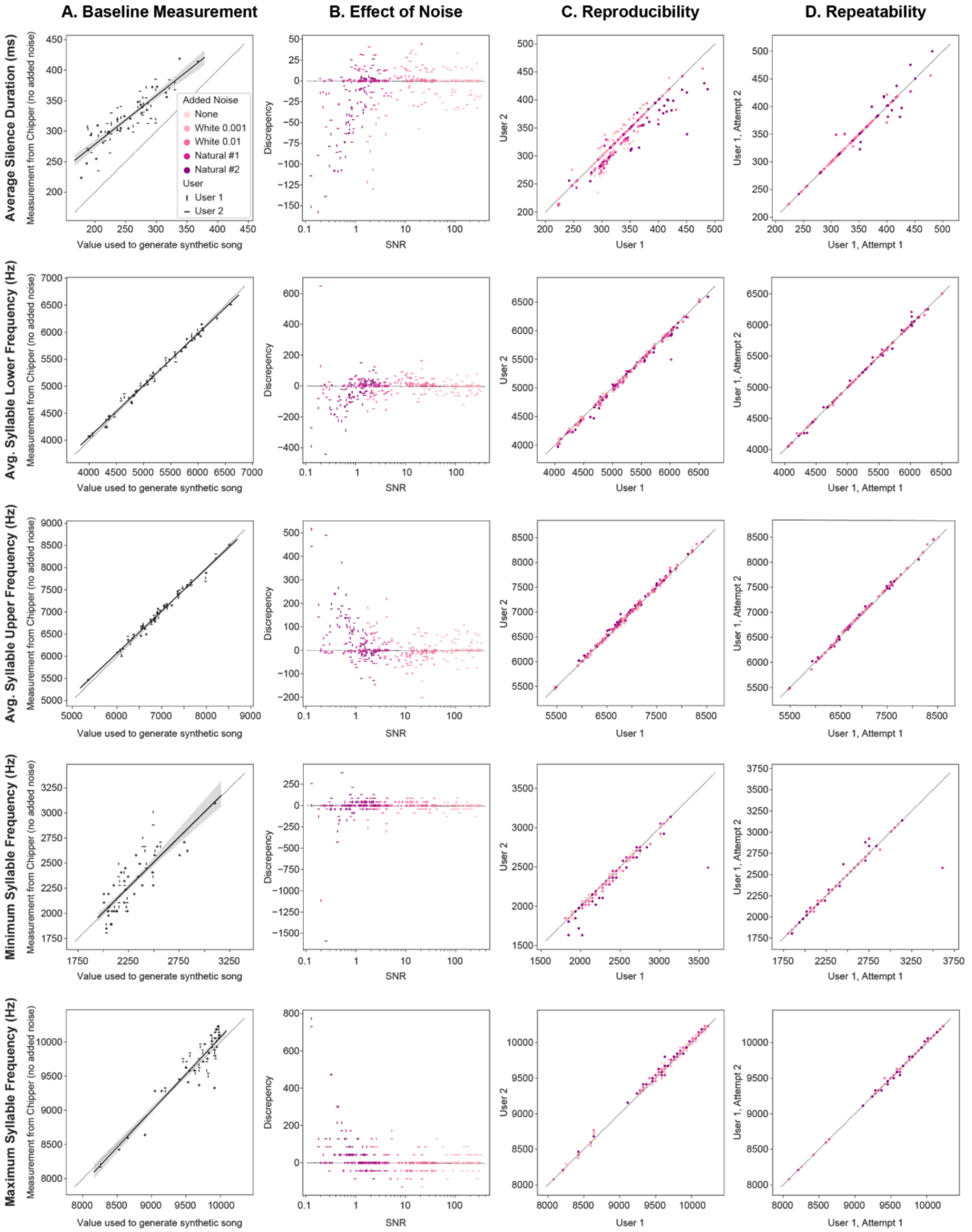


Figure 2.5 Accuracy, repeatability, and reproducibility of Chipper for additional song features. (A–D) See Fig. 2.4 for description of plots. Assessments are shown for five song features (rows): average silence duration (ms), average syllable lower frequency (Hz), average syllable upper frequency (Hz), minimum syllable frequency (Hz), and maximum syllable frequency (Hz).

CONCLUSIONS

With the ever-growing repositories of citizen-science recordings, a new software was needed to handle the various recording qualities and vast species coverage (**Fig. 2.6**). Thus, we developed Chipper as a free, open-source software to improve the workflow of audio signal processing with particular application to high-throughput analysis of citizen-science recordings. With its user-friendly graphical user interface, Chipper can be used by researchers, students in classrooms, and curious citizen-scientists alike. In testing Chipper, we found that it produced robust estimates of sound properties for a set of synthetic recordings, and these results were consistent within and between users and in the presence of natural and white noise (**Figs. 5–6**). We hope Chipper, in tandem with citizen-science data, can aid in large-scale spatiotemporal studies of acoustic signals, particularly global inter- and intra-species studies of birdsong. Chipper's song measurements could also prove valuable in studying the complex temporal variations associated with duets or coordinated singing. With open-source code on GitHub, we welcome users to extend and contribute to Chipper, tailoring it to additional projects and data types. In the future, as we continue to maintain and develop Chipper, we aim to add additional song measurements, such as syllable entropy, as well as functionality to accommodate longer recordings. Ultimately, using Python and Kivy, we have developed an application that facilitates audio processing of natural recordings, extending the utility of rapidly growing citizen-science databases and improving the workflow for current birdsong research in ecology and evolution.

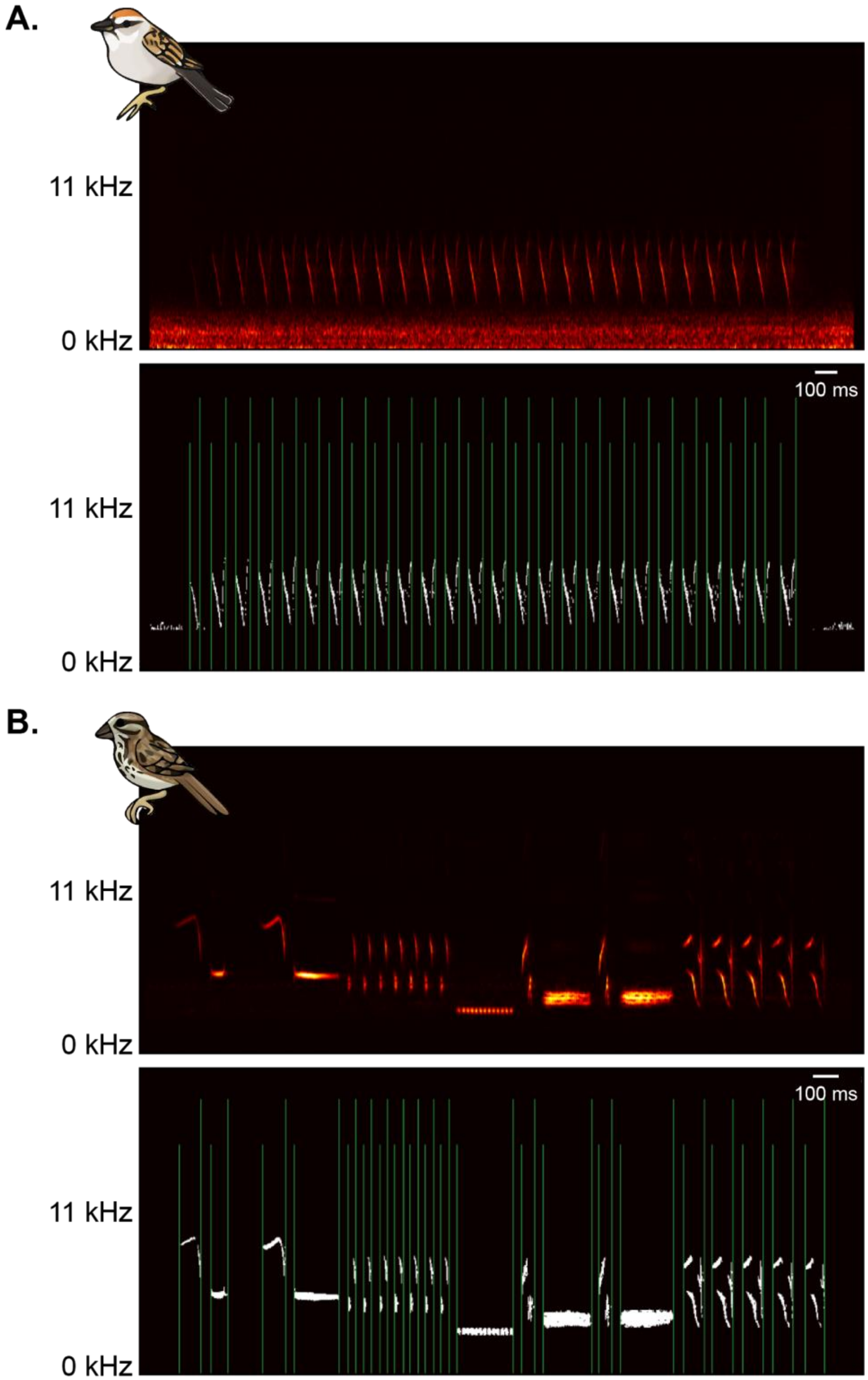


Figure 2.6 Chipper can segment songs of various qualities and from different species. Example song of (A) chipping sparrow and (B) song sparrow. The top images are the spectrograms when they are originally loaded into Chipper. The bottom images are the binary signal after parameters have been adjusted to optimize segmentation. The green lines show the syllable onsets (shorter lines) and offsets (taller lines).

MANUSCRIPT DATA AVAILABILITY AND ACKNOWLEDGMENTS

Chipper v1.0 can be downloaded for Mac, PC, and Linux at https://github.com/CreanzaLab/chipper/releases. The Chipper manual can be found in **Appendix A** or at https://github.com/CreanzaLab/chipper/tree/master/docs.

Code for Chipper and to create and analyze synthetic songs can be found at https://github.com/CreanzaLab/chipper. Chipper leverages several existing Python packages including SciPy (Jones et al., 2001), Pandas (McKinney, 2010), Matplotlib (Hunter, 2007), and NumPy (Oliphant, 2006; van der Walt et al., 2011). We also use the Python library Kivy v.1.10 for building the graphical user interface (Virbel et al., 2011).

The recordings used in this paper are freely available in the Xeno-canto repository: Jonathon Jongsma, XC320440, accessible at www.xeno-canto.org/320440; Chris Parrish, XC13690, accessible at www.xeno-canto.org/13690; Allen T. Chartier, XC16985, accessible at www.xeno-canto.org/16985.

The folder and file images used in **Fig. 2.1** are adapted from icons found at the Noun Project: tab file document icon by IYIKON, .WAV Folder by Linseed Studio, Audio by Ben Avery, zip file document icon by IYIKON, wax file document icon by IYIKON, and csv file document icon by IYIKON.

We thank the following students for testing Chipper during its development: Vanderbilt University BSCI 1512L Fall 2018 class, Vanderbilt University BSCI 3965 Spring 2019 class, Megan Mitchell, Nyssa Kantorek, Maria Sellers, and Emily Beach. In addition, we thank Megan Mitchell for editing the Chipper Manual and Dr. Cristina Robinson for the bird art used in this paper and in the Chipper logo.

CHAPTER 3

DETECTING DIEL PATTERNS IN CHIPPING SPARROW SONG USING CITIZEN-SCIENCE DATA

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A modified version has been submitted for publication:
Searfoss, A.M., Liu, W.-c., Creanza, N. (2020) Detecting diel patterns in chipping sparrow song using citizen-science data. *Journal of Field Ornithology*.

INTRODUCTION

For decades, ornithologists have been studying diel patterns in birdsong and in particular the phenomenon known as the "dawn chorus," the period of time when birds sing before sunrise (Staicer et al., 1996). This period of intense singing has been studied in several species, leading to a variety of hypotheses about the purpose of the dawn chorus: for example, it could play an important role in social interactions such as territory defense, mate attraction, extra-pair copulations, and mate guarding (Amrhein et al., 2002, 2004; Dalziell & Cockburn, 2008; Amrhein & Erne, 2006; Roth et al., 2009), or dawn could be an advantageous time to sing due to optimal conditions for acoustic transmission, low predation rates, or inefficient foraging (Berg et al., 2006; Brown & Handford, 2002; Dabelsteen & Mathevon, 2002; Santema et al., 2019; Thomas et al., 2002). Not only are individuals more likely to sing during this time, but some species (*Spizella pusilla*, *Poecile atricapillus*, *Parula americana*, *Dendroica magnolia*, *D. coronata*, *D. virens*, *D. fusca*) also show differences in song between dawn chorus and day singing, including changes in song type, complexity, duration, rate, and frequency (Foote et al., 2008; Morse, 1989; Zhang et al., 2016). Observations of these diel song differences have led to the hypothesis that song could serve distinct functions at different times of day; however, testing whether a species shows diel song patterns, and whether these patterns correspond with differences in song's function or intended audience, usually requires extensive fieldwork.

In parallel with researchers conducting fieldwork, the public has long contributed to natural sciences (Butcher et al., 1987; Miller-Rushing et al., 2012), but the way in which these efforts have been conducted has changed drastically over the years (Bonney et al., 2009; Irwin, 2018; Silvertown, 2009). With widespread access to the internet, multiple groups began to crowdsource and digitally archive data to drive and support large-scale scientific research and conservation efforts (*Citizen Science*, 2020, *Citizen Science*, 2020, *Citizen Science Projects*, 2020, *SciStarter*, n.d., *Zooniverse*, n.d.; Wood et al., 2011). With new digital recording technologies and a vast network of birders and ornithologists already avidly collecting data, citizen-science databases of bird sightings and song recordings quickly became a valued resource. Publicly accessible repositories such as Xeno-canto (www.xeno-canto.org) (Vellinga & Planqué, 2015), Macaulay Library (www.macaulaylibrary.org), and eBird (www.ebird.org) provide a user-friendly way for birders to store their own records as well as a rich dataset of natural behavior for research. Over the course of two decades, these citizen-science databases have seen remarkable growth in the number of users and recordings (Sullivan et al., 2014; Vellinga & Planqué, 2015). As stated by eBird, one goal of the databases is to "[complement] more rigorous ornithological research and monitoring programs, allowing scientists to generate new hypotheses and direct future research efforts based on large amounts of data" (Sullivan et al., 2009). Indeed, some research groups are now using these databases to evaluate large-scale patterns, such as species diversity and population distributions, and thus address questions regarding habitat, migration, and conservation (Callaghan & Gawlik, 2015; Gasc et al., 2013; Kelling et al., 2012; Lagoze, 2014; Sullivan et al., 2017; Velásquez-Tibatá et al., 2012), whereas others are using the sound recordings to study song evolution (Mason et al., 2014; Tobias et al., 2014; Weir & Wheatcroft, 2011) and song patterns (Benedetti et al., 2018).

Typically, citizen-science databases are used for large scale biodiversity, phenology, and conservation monitoring. Here we propose they can also be useful in studying animal behavior, and more specifically the diel patterns of avian vocalizations, which is often approached only with field studies. While field studies have limited geographic range, they provide researchers with the ability to monitor the interactions of individual birds and obtain crucial observational details, which is not possible with citizen-science efforts. In contrast, citizen science has the geographic and multi-species coverage needed for population-wide and phylogenetically controlled studies. Thus, we propose that pairing the analysis of large-scale databases of birdsong with findings from fieldwork can increase the efficiency and effectiveness of continent-wide, cross-species studies linking social behavior and diel song patterns.

In particular, in ornithology, the study of diel patterns in behavior is ripe for the integration of citizen-science analyses. As citizen-science recordings are most often accompanied by metadata including date, time, and location of recording, researchers can take advantage of these resources to further understand diel patterns in birdsong. First, for species that are understudied in the field, analysis of this broad-scale data could reveal which species' song patterns change over the course of the day, enabling researchers to make broader predictions about the geographic and phylogenetic distribution of diel song patterns and the behavioral differences that might accompany them. This information will not reveal the function for such diel patterns since behavioral data are rarely included in citizen reports, but it can be used to generate hypotheses and inform species-of-interest for more targeted field studies. Alternatively, for species that are known to exhibit diel patterns of behavior such as territory defense or mate attraction, citizen science could provide a way to easily test hypotheses of whether song differences align with such behavioral differences.

The chipping sparrow is an excellent focal species for demonstrating whether citizen-science data can reveal diel song patterns: first, its simple song consists of a single syllable repeated a variable number of times (Borror, 1959; Marler & Isaac, 1960), and second, a series of site-specific field experiments determined that individual chipping sparrows show a daily pattern of singing between dawn and morning that is associated with differing social interactions (Liu, 2001, 2004; Liu & Kroodsma, 2007). The presence or absence of neighboring males and females influenced the extent to which a chipping sparrow sang during the dawn chorus or during the day respectively (Liu, 2004), supporting the hypothesis that the dawn song appeared to be primarily used for territorial purposes and the day song primarily used for mate attraction (Liu, 2001). Lastly, a subsequent multi-year study of banded birds revealed significant diel song differences: the dawn song was shorter than the day song due to smaller number of repeated syllables (n=15 chipping sparrows) (Liu & Kroodsma, 2007).

Citizen-science data have been invaluable in expanding the scope of research studies of species diversity, global distribution, and migration patterns as well as the changes in all of these over time and in response to global changes (Both et al., 2010; Horns et al., 2018; Kelly et al., 2016; Lepczyk, 2005; Sohl, 2014; Sullivan et al., 2017; Taylor et al., 2014). However, citizen-science archives have not been leveraged in identifying diel patterns in birdsong. Here, we sought to test whether large-scale datasets can provide range-wide support for results from past field studies at a particular site, ultimately providing evidence that citizen-science data can be a valuable resource for studies of diel patterns in song even without accompanying fieldwork. Specifically, we use citizen-science data from across the chipping sparrow's entire range to evaluate differences between dawn and day song. We aim for this study to serve as an example of the utility that large publicly available datasets offer to the biological phenomenon of cross-species diel patterns. Importantly, although citizen-science databases will not eliminate the need for rigorous field studies, analyzing these databases provides an efficient and accurate workflow, prompting more complex hypotheses and informing experimental design of future cross-species and behavioral studies.

METHODS

Compiling citizen-science chipping sparrow recordings

We gathered chipping sparrow recordings from public repositories of citizen-science data: the Macaulay Library at the Cornell Lab of Ornithology (www.macaulaylibrary.org) and Xeno-Canto (www.xeno-canto.org). We also compiled the annotated metadata: time, date (day, month, and year), latitude, and longitude of the recording. Recording files without the necessary metadata for statistical analysis were discarded. All recordings collected in the same year and same latitude and longitude were visually compared in Audacity (audacity.sourceforge.net) to determine if they were the same bird: since chipping sparrows have only one syllable in their repertoire, we could confidently classify recordings with different syllables as songs from different birds. If there were multiple recordings that appeared to correspond to a single bird, the least noisy recording was kept or one was selected at random. This elimination of similar recordings (from the same year and location) was conducted to reduce the chance of bias from multiple recordings of the same bird at the risk of removing unique recordings of different individuals that sang very similar songs. Ultimately, our dataset consists of 319 unique recordings (see **Appendix B** for database, recordist, and license) that had the metadata necessary for categorizing into before sunrise, morning, and afternoon (**Fig. 3.1**): latitude, longitude, month, year, day and time.

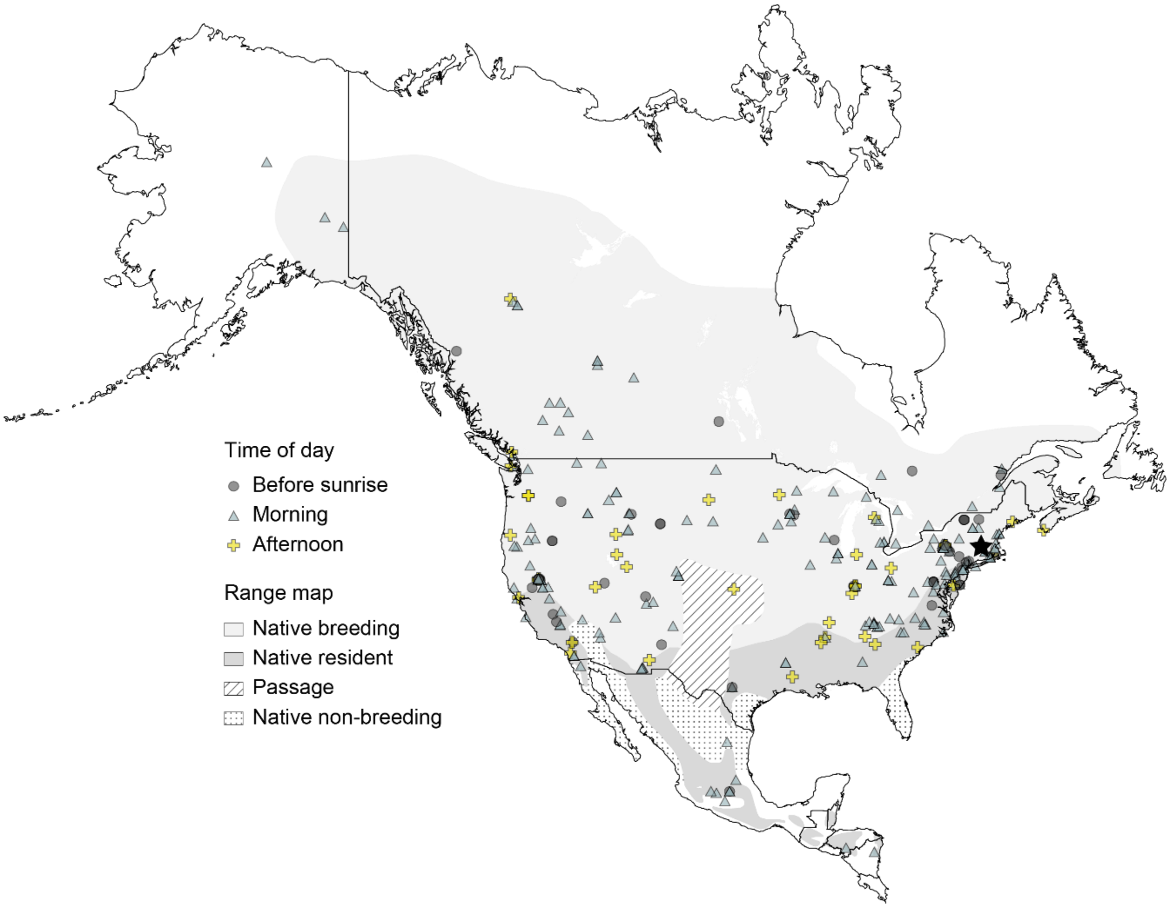

Figure 3.1 Geographic distribution of citizen-science recordings of chipping sparrows. The locations (latitudes and longitudes) of the 319 citizen-science song recordings are plotted. The color of the points corresponds to the time-of-day category. The range map shows native breeding (light gray), native resident (dark gray), passage (striped), and native non-breeding (dots) (adapted from BirdLife International and Handbook of the Birds of the World (2018) Bird species distribution maps of the world. Version 2018.1. Available at http://datazone.birdlife.org/species/requestdis.); country outlines are from Esri, DeLorme Publishing Company, Inc. A black star indicates the location of the field study of chipping sparrow song during dawn and day (Liu & Kroodsma, 2007) (field sites in and around Amherst, Massachusetts).

Next, each recording was opened in Audacity and, if the recording included more than one bout of singing, the highest quality song (preferably one without interfering sounds from birds, humans, other animals, etc.) was chosen from each recording. If all songs in the recording were of approximately equal quality, one was chosen of intermediate length. This procedure was conducted without knowledge of the time of day of recording. The chosen song was then exported in WAV format sampled at 44,100 Hz. We extracted song features of interest—song duration, total number of syllables, mean syllable duration, and mean inter-syllable silence—using Chipper, software we developed in Python for signal processing, noise reduction, and syllable segmentation of birdsong. (Full code and documentation is available on GitHub; for Chipper see https://github.com/CreanzaLab/chipper and for all statsitical analyses see https://github.com/CreanzaLab/chipping_sparrows_time_of_day). Specifically, within our software, a Gaussian-windowed spectrogram (based on code from (Gardner & Magnasco, 2006)) is produced from the WAV file and binarized according to a default signal threshold: in the processed spectrogram, signal above this threshold is set to 1 and signal below this threshold is set to 0. The songs are then automatically parsed into syllable segments based on when signal begins (onset) and ends (offset). Next, the user can adjust this segmentation by using a high-pass filter to remove low-frequency noise, changing the amount of signal kept in the binary matrix, and adjusting the minimum syllable duration and the minimum inter-syllable silence duration. When satisfied with the segmentation, the user submits the parameters. For this study, the following four features for each song were calculated using the onsets and offsets of each syllable: song duration, total number of syllables in the song, mean syllable duration, and mean inter-syllable silence duration. The distribution of the data was not normal for any of these song features; therefore, the data were log-transformed and analyzed with non-parametric statistics.

Classifying song as before-sunrise, morning, or afternoon

We categorized our songs by time of day based on the definitions used in Liu 2004 (Liu, 2004) and Liu and Kroodsma 2007 (Liu & Kroodsma, 2007): the dawn chorus was defined as “the period of continuous singing that occurs 30-60 min before sunrise.” Then, the end of the dawn chorus was defined as the time when a paired male stopped singing or when an unpaired male “stopped singing from the ground and flew to a tree where they resumed singing.” The day song was defined as “an unpaired male’s singing after sunrise.” Daytime recordings were collected between 6 and 9 a.m. (Liu, 2004) or after the dawn chorus until as late as 11 a.m. (Liu & Kroodsma, 2007) depending on the study. As we did not have behavioral data (location of the singing bird or mating status) for recordings from citizen-science databases, we relied solely on the time of the recording and associated metadata to categorize the songs similarly into “before-sunrise” (classified as recordings made from midnight to sunrise), “morning” (from sunrise to noon), and “afternoon” (from noon to midnight). The earliest recording in our database was

04:06, and the latest recording was 20:30. Therefore, our before-sunrise category corresponds to the definition of dawn song from fieldwork and our morning category primarily corresponds to the day song.

The time of sunrise was calculated for each recording based on the date, latitude, and longitude of the recording using Python functions from the Observation Planning package (astroplan) (Morris et al., 2018) and The Astropy Project (Robitaille et al., 2013; The Astropy Collaboration et al., 2018). This categorization scheme assumes that the time of recording annotated by the recordist is the actual time the bird sang, which might not be the case if the recordist rounded to the nearest hour or only documented the beginning or ending time of an outing.

Verifying Xeno-canto MP3 recordings do not impact measurements

All Xeno-canto recordings were downloaded as MP3's. Thus, to test whether the compressed format had a systematic effect on our measurements (see, e.g., (Araya-Salas et al., 2017)), we compare the song features collected from Xeno-canto to those from Macaulay Library within each time-of-day category. We performed Wilcoxon rank-sum tests to determine whether song duration, total number of syllables, mean syllable duration, and mean inter-syllable silence duration differed between Xeno-canto and Macaulay Library recordings. After Bonferroni correction for 3 Wilcoxon rank-sum tests (for each time-of-day category) on each of 4 song features, $\alpha_{\text{adjusted}}=4.17\times10^{-3}$.

Analysis of daily patterns in chipping sparrow songs

Here, we test whether the results from previous fieldwork on individual chipping sparrows (n=15) (Liu, 2001; Liu & Kroodsma, 2007) are broadly consistent across the species range: the duration of chipping sparrows' dawn songs are shorter than their day songs. We performed Wilcoxon rank-sum tests for song duration between pairs of time-of-day categories (before-sunrise vs. morning, before-sunrise vs. afternoon, and morning vs. afternoon). We used a Bonferroni correction for testing multiple hypotheses, which lowered the threshold for significance to $\alpha_{\text{adjusted}}=0.0167$ (3 Wilcoxon rank-sum tests). We also tested for differences in variance of song duration between pairs of time-of-day categories using the Brown-Forsythe test for equality of variance in non-normal distributions and used the same Bonferroni correction (α_{adjusted}=0.0167).

Next, to determine which song feature is responsible for the increase in song length after sunrise, we compared the total number of syllables per song, mean syllable duration, and mean inter-syllable silence duration using Wilcoxon-rank sum tests between pairs of time-of-day categories. Once again, we used a Bonferroni correction for testing multiple hypotheses, (α_{adjusted}=0.0167, 3 Wilcoxon rank-sum tests on each song feature). We also tested for differences in variance for these three song features between pairs of time-of-day categories using the Brown-Forsythe test for equality of variance in non-normal distributions and used the same Bonferroni correction (α_{adjusted}=0.0167).

To estimate the amount of individual variability in chipping sparrow song, we examined multiple songs for a subset of chipping sparrow recordings. For five of the longest recordings from each time-of-day category, we parsed all recorded songs (excluding those that were interrupted by other birds), resulting in data from 15 birds with 5 to 46 songs each. We measured song duration and number of syllables using the same methods as above.

All statistical tests were conducted using the Python Statistical functions package SciPy.stats (v1.0.0) (Jones et al., 2001): scipy.stats.ranksums for Wilcoxon rank-sum tests and scipy.stats.levene(center=‘median’) for Brown-Forsythe tests.

To account for differences in the timing of breeding, we tested whether month and latitude contributed to the differences in song between before-sunrise and morning by testing a Generalized Linear Mixed Model (GLMM) using the R package MCMCglmm (Hadfield, 2010). We assigned as fixed effects the month of recordings, the latitude at which the recordings were collected, the interaction between these two variables, and the classification into either before-sunrise or morning, with no random effects. Default priors were used, and the model was run for 100,000 iterations.

RESULTS

For the recordings from citizen-science databases with date and time annotations, we used the latitude, longitude, and date to estimate the time of sunrise. We determined that 57 of these recordings were captured before sunrise (including the dawn chorus), 224 in the morning (after sunrise but before noon), and 38 after noon. We found no systematic differences in song features (song duration, total number of syllables, mean syllable duration, and mean inter-syllable silence duration) between recordings from Xeno-canto (downloaded as MP3 files) and Macaulay Library (downloaded as WAV files) within each time-of-day category ($p>0.227$ for all comparisons).

We compared song duration between these three time-of-day categories and found that song durations were significantly shorter before sunrise than either in the morning (Wilcoxon $p=0.0078$) or in the afternoon ($p=0.0013$). There was no significant difference between morning and afternoon ($p=0.0211$) (**Fig. 3.2A, Table 3.1**). Additionally, the variance of the song duration was significantly greater before sunrise than during the morning (Brown-Forsythe $p=4.77\times10^{-6}$) (**Table 3.2**).

We found that the total number of syllables per song was significantly different between the before-sunrise and morning periods (Wilcoxon $p=0.0026$) and the before-sunrise and afternoon periods ($p=5.95\times10^{-4}$). There were no significant differences in the mean syllable duration and mean inter-syllable silence duration between time-of-day categories (**Fig. 3.3, Table 3.1**). There was no significant difference in variance between the time-of-day categories for mean syllable duration, mean inter-syllable silence duration, or total number of syllables (**Table 3.2**).

Examining individual birds, we found the within-bird variability in song duration and number of syllables was much smaller than the total variability between birds (**Fig. 3.4**).

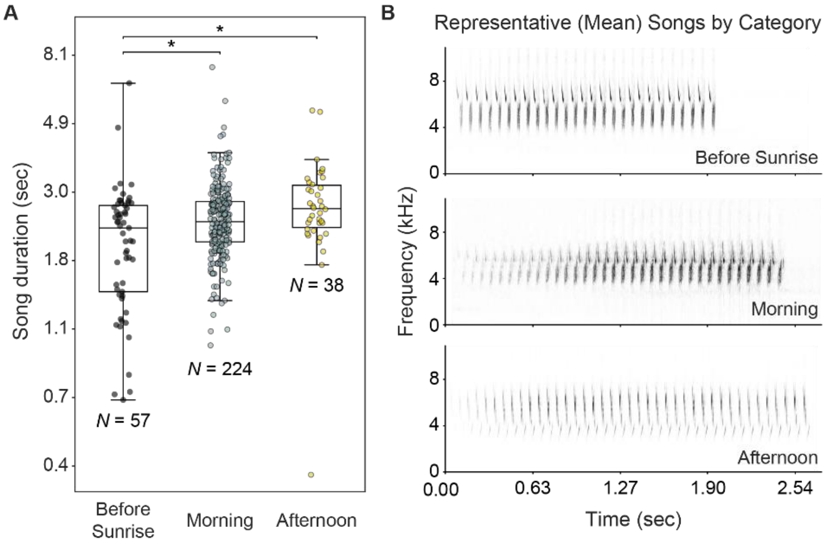

Figure 3.2 Chipping sparrow songs are shorter in length before sunrise than after sunrise. (A) The song duration was significantly shorter before sunrise than after sunrise (morning or afternoon). Box plots show the median, upper and lower quartiles, whiskers (25% quartile − 1.5×IQR, 75% quartile + 1.5×IQR), and all data points including outliers. The *y*-axis is on a log scale. Significant results are indicated between populations (* denotes $p<0.0078$ for Wilcoxon rank-sum test). (B) Spectrograms from each time-of-day category (before-sunrise, morning, and afternoon) of the song that is closest to the category's mean of two song features—song duration and total number of syllables. Before-sunrise recording: ML176261 contributed by Geoffrey A. Keller. Morning recording: ML73829 contributed by Wil Hershberger. Afternoon recording: ML15435 contributed by Robert C. Stein.

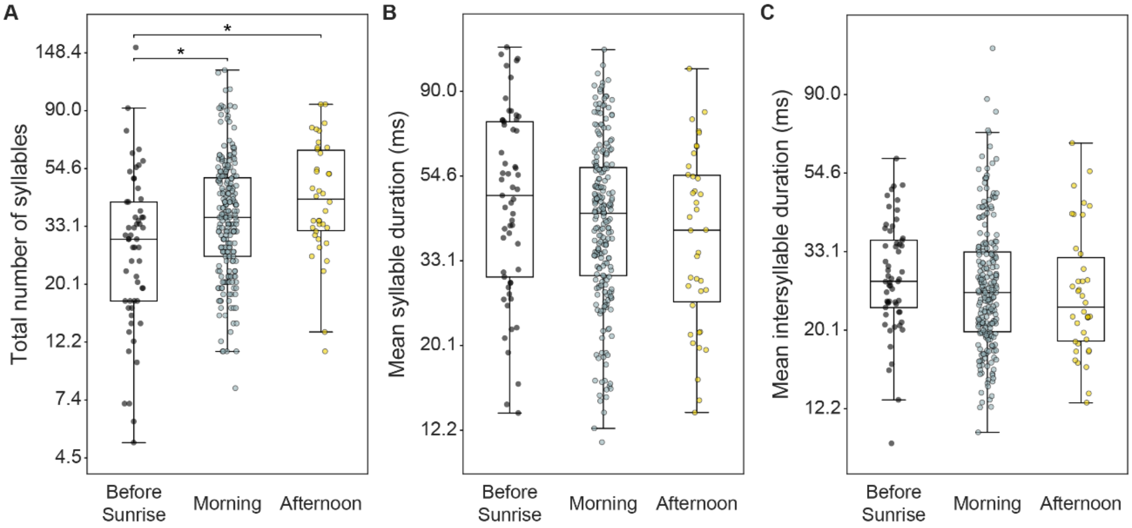

Figure 3.3 The total number of syllables accounts for the difference in song duration. (A) Songs recorded before sunrise had significantly fewer syllables than songs in the morning or in the afternoon. Significant results are indicated between populations (* denotes $p<0.0026$ for Wilcoxon rank-sum test). Neither (B) the mean syllable duration nor (C) the mean inter-syllable silence duration was significantly different before sunrise versus after sunrise (both morning and afternoon), and therefore, do not account for the difference in song duration. The *y*-axes are on a log scale.

Table 3.1 Comparing medians between times of day song distributions. Medians of the distributions of song features and Wilcoxon rank-sum test results between songs recorded either before sunrise, in the morning, or in the afternoon

Song feature	Medians			*p*-values		
	Before Sunrise	Morning	Afternoon	Before Sunrise vs. Morning	Before Sunrise vs. Afternoon	Morning vs. Afternoon
Song duration (s)	2.25	2.35	2.59	**0.0078**	**0.0013**	0.0211
Mean syllable duration (ms)	47.95	43.17	39.07	0.1186	0.0527	0.3002
Mean inter-syllable silence duration (ms)	26.95	25.10	22.86	0.0791	0.0706	0.4946
Total number of syllables	29	35	41	**0.0026**	**0.0006**	0.0522

Bold indicates $p<0.0167$.

Table 3.2 Comparing variances between times of day song distributions. Variances of the distributions of song features and Brown-Forsythe test results for equality of variance between songs recorded either before sunrise, in the morning, or in the afternoon

Song feature	Variances			*p*-values		
	Before Sunrise	Morning	Afternoon	Before Sunrise vs. Morning	Before Sunrise vs. Afternoon	Morning vs. Afternoon
Song duration (s)	0.2106	0.0741	0.1570	**4.77E-06**	0.0715	0.4722
Mean syllable duration (ms)	0.2976	0.2262	0.2638	0.1090	0.8841	0.2262
Mean inter-syllable silence duration (ms)	0.1216	0.1643	0.1575	0.2541	0.3874	0.9889
Total number of syllables	0.4488	0.2542	0.2368	0.0193	0.1256	0.8862

Bold indicates $p<0.0167$. Variance calculations were performed on log-transformed data, so the values are in $\ln(\text{units})^2$.

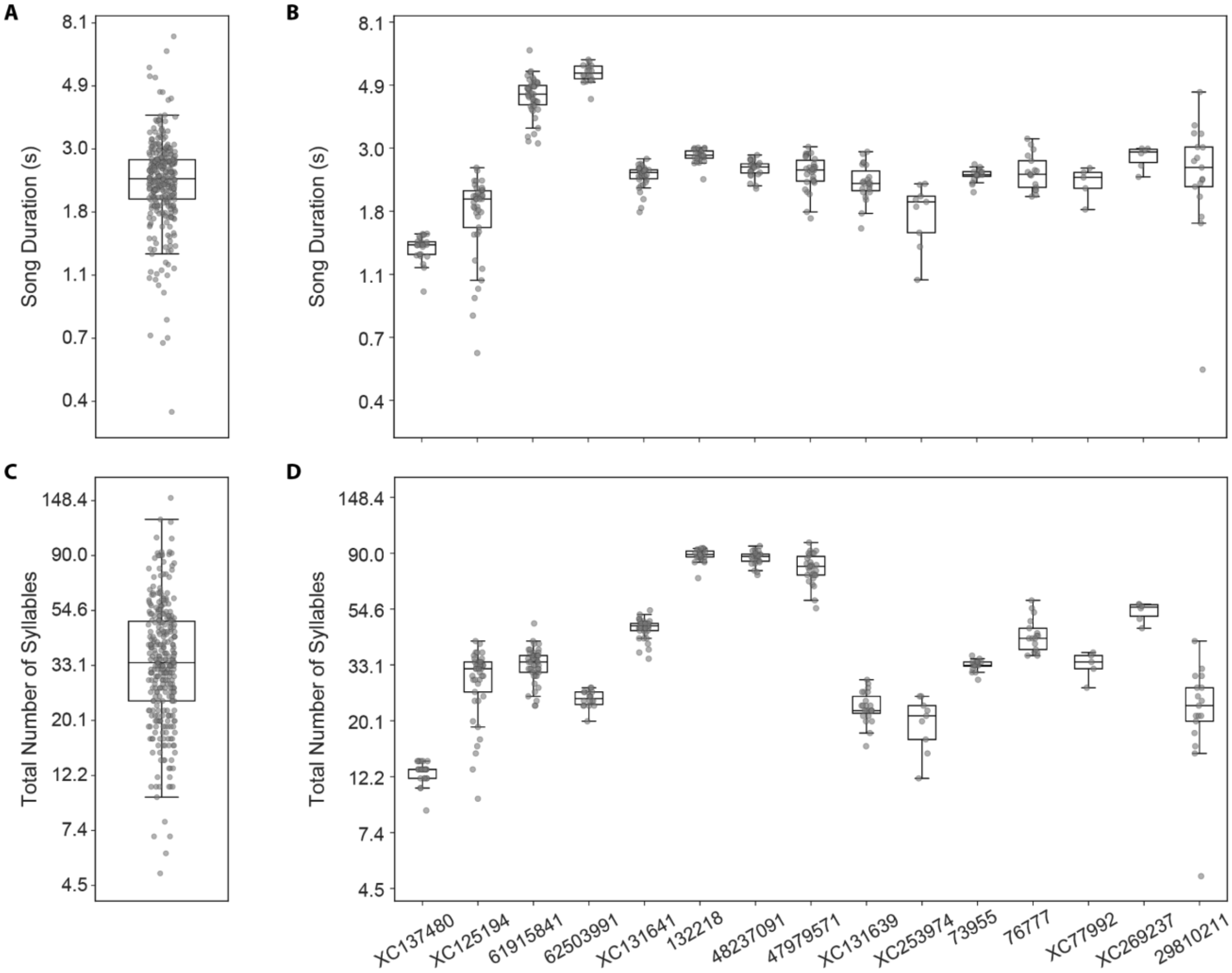

Figure 3.4 Variation among songs produced by an individual chipping sparrow compared to the variation among the population. We took 5 of the longest recordings from each time-of-day category and parsed all songs in a recording. This resulted in 15 total birds (catalog numbers listed) with 5 to 46 songs each for which we measured song duration and total number of syllables. Boxplots are provided for each bird (B and D) alongside boxplots of our 319 individual measurements (A and C).

Additionally, as the diel patterns in chipping sparrow song are associated with social behaviors of territory defense and mate attraction (Liu, 2004), we used GLMM to examine whether the differences in song duration and total number of syllables were due to variables associated with breeding season—the time of collection (month) or location (latitude). As the breeding season is affected by arrival time after migration and food availability, the breeding state of a recorded bird could be dependent on both month and latitude; thus, we were also interested in the interaction between these two variables. The GLMM analysis reaffirmed our results that the time of day (before-sunrise or morning) is significantly linked to the duration of the song (*pMCMC*=0.0002) due to the difference in the total number of syllables in the song (*pMCMC*=0.0004) (**Table 3.3**). GLMM also confirmed that variables closely associated with time of breeding—the month of the recording, the latitude, and the interaction of the two—do not have a significant effect on the song duration or total number of syllables.

Table 3.3 Results for the GLMM analysis.

Song Feature	Group	Post Mean	l-95% CI	u-95% CI	pMCMC
Duration of song bout	(Intercept)	6.9339	5.8652	8.0474	**0.0001**
	Latitude	0.0191	-0.0090	0.0470	0.1829
	RecordingMonth	0.0959	-0.1067	0.2974	0.3565
	Before Sunrise/Morning	-0.2126	-0.3054	-0.1195	**0.0002**
	Latitude:RecordingMonth	-0.0021	-0.0071	0.0031	0.4359
Mean syllable duration	(Intercept)	3.0803	1.4364	4.8487	**0.0001**
	Latitude	0.0183	-0.0252	0.0621	0.4110
	RecordingMonth	0.2118	-0.1098	0.5208	0.1910
	Before Sunrise/Morning	0.1208	-0.0263	0.2632	0.1060
	Latitude:RecordingMonth	-0.0057	-0.0136	0.0023	0.1640
Mean inter-syllable silence duration	(Intercept)	2.6800	1.3260	3.9980	**0.0001**
	Latitude	0.0147	-0.0221	0.0465	0.4006
	RecordingMonth	0.2471	-0.0003	0.4967	0.0493
	Before Sunrise/Morning	0.0597	-0.0558	0.1729	0.2994
	Latitude:RecordingMonth	-0.0061	-0.0127	0.0000	0.0575
Total number of syllables	(Intercept)	3.3846	1.6452	5.2461	**0.0004**
	Latitude	0.0003	-0.0475	0.0449	0.9934
	RecordingMonth	-0.1395	-0.4914	0.1802	0.4212
	Before Sunrise/Morning	-0.3006	-0.4551	-0.1454	**0.0004**
	Latitude:RecordingMonth	0.0041	-0.0041	0.0129	0.3437

DISCUSSION

A recent review of the opportunities and challenges in applying citizen-science data to avian studies notes that "big data have been used to study and model bird diversity and distributions across space and time, explore the patterns and determinants of broad-scale migration strategies, and examine the dynamics and mechanisms associated with geographic and phenological responses to global change" (La Sorte et al., 2018). However, such data have generally not been used to extend the findings of behavioral field observations (Frigerio et al., 2018; Hecht & Cooper, 2014), such as diel patterns in birdsong, to a continental scale. As a proof-of-principle, we demonstrate that large citizen-science datasets can be used to reveal facets of birdsong that previously would have required extensive fieldwork to uncover. Specifically, we test the predictions of local scale observations of diel patterns in birdsong on a continental scale: chipping sparrows noticeably reduce the duration of their songs before sunrise (**Fig. 3.2B**). By comparing our results to a previous site-specific field study (Liu, 2001; Liu & Kroodsma, 2007), we suggest that this change in song duration is not a local phenomenon but occurs throughout the chipping sparrow's geographic range (**Fig. 3.5**). Furthermore, we confirm that the significant reduction in song duration before sunrise is attributable to the total number of syllables per song, as there was no significant difference in either mean syllable duration or mean inter-syllable silence duration between songs sung before and after sunrise (**Fig. 3.3, Table 3.1**). In other words, chipping sparrows reduce the duration of their dawn songs by singing fewer syllables, not by shortening their syllables or the silences between them. In addition, we found that chipping sparrow song duration has greater variance before sunrise than during the morning. Overall, the proof-of-concept study presented here serves to demonstrate that the vast number of citizen-science recordings can be used both to detect significant diel patterns across a species' entire geographic range, which could motivate researchers to choose a certain species for complementary fieldwork studies, and to examine whether field results obtained at a local level apply across an entire species.

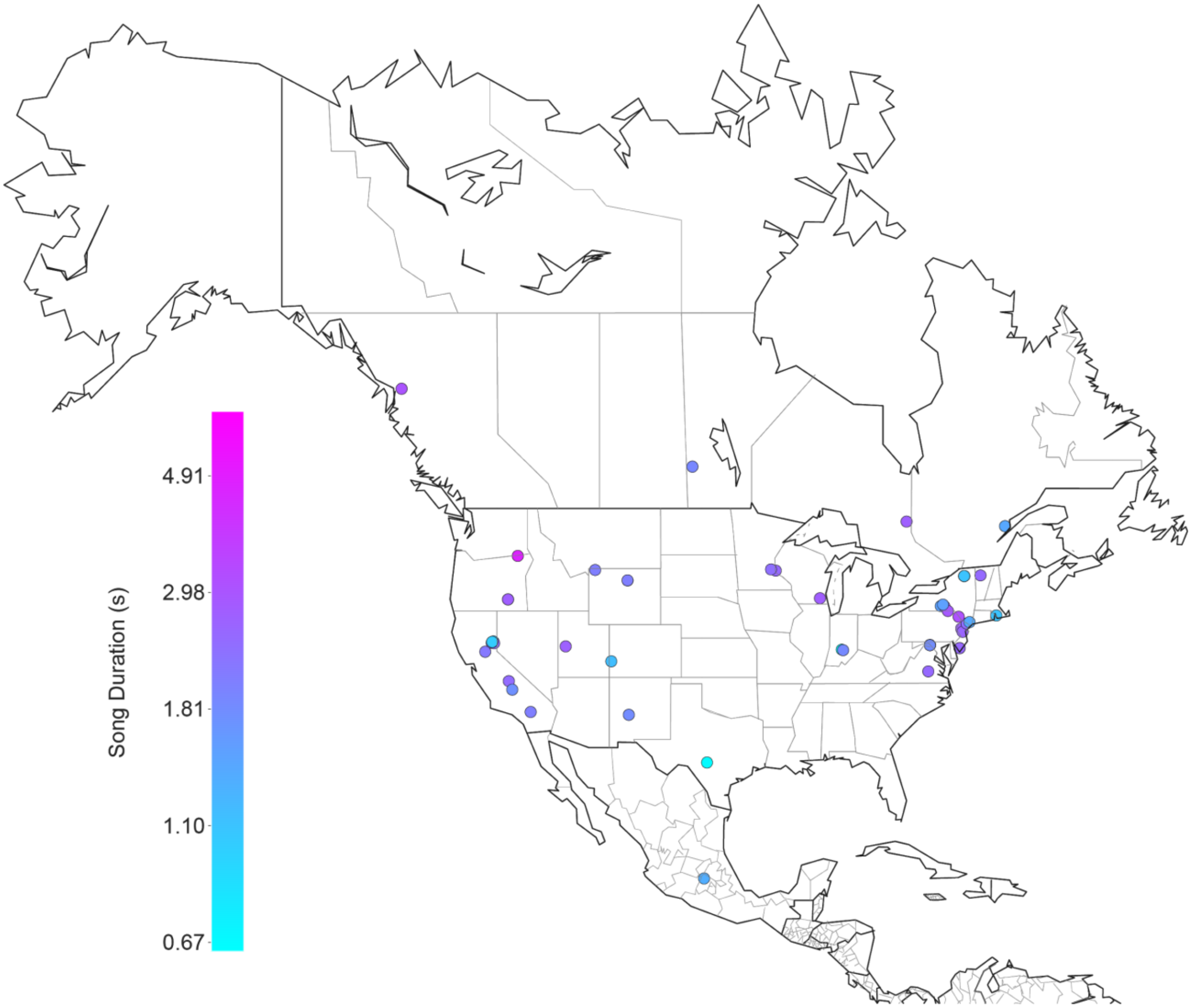

Figure 3.5 Geographic distribution of the recordings taken before sunrise and associated durations. The locations (latitudes and longitudes) of the 57 citizen-science recordings acquired before sunrise. The color corresponds to the song duration. The duration of dawn songs seems to be geographically well-distributed; there is no particular subset of the region that has systematically shorter songs causing the trend.

When using citizen-science data, it is important to note possible caveats; here we examine the limitations of our data and the resulting impact on our findings. In the case of our study, the timestamp of the recording could be the actual time the bird sang or it could mark the beginning or end of a birdwatcher's outing. In addition, the position from which the bird sang (e.g. on top of a tree or on the ground) is rarely included, but this behavior has been historically used to distinguish between dawn and day song (Liu, 2004; Liu & Kroodsma, 2007). Both of these limitations of citizen-science data could have resulted in our misclassification of a song into time-of-day categories, potentially diminishing our ability to detect real differences in song features. Similarly, pooling citizen-science recordings by time of day, without behavioral observations or within-individual song comparisons at different timepoints, could make it difficult to find more nuanced differences in song that are related to an interaction between diel patterns and other factors such as social contexts. For instance, males could sing territorial song primarily at dawn but also at any time another male arrived on its territory, in which case we would be less likely to see a difference in dawn and day songs. In addition, a chipping sparrow might shorten its dawn song primarily at specific points in its breeding cycle, such as before it formed a pair bond or while it was establishing a territory, diminishing our power to detect the diel pattern. Furthermore, meaningful but region-specific diel patterns would be more likely to be overlooked when using citizen-science data pooled across large spatial scales than when conducting fieldwork. Pooled data could also mask effects that might readily be distinguishable by comparing songs within individuals. For instance, the fieldwork on chipping sparrows included recordings collected over ~5 years of banded birds, allowing for direct comparisons between dawn and day song within individuals. If there are different but overlapping distributions of song durations before versus after sunrise, a larger sample size than available might be necessary to detect the difference using citizen-science data. In spite of these limitations of citizen-science data, we identified significant differences in chipping sparrow song duration due to an increased number of syllables after sunrise, suggesting that this trend could be even stronger than we are able to detect.

While citizen-science data have proven to be a powerful research tool independent of fieldwork, we see the potential in using it in all stages of the research process. Here, we propose how large-scale data-driven analyses could inform different types of focal field studies and, in turn, how field studies could address the shortcomings of citizen-science data. First, our analysis pipeline for citizen-science recordings could be used to analyze songs across numerous taxa to assess candidate species for intensive fieldwork. For instance, analysis of citizen-science data could be used to examine whether species in any songbird clade of interest change their song between the dawn and day. Rather than conducting fieldwork on multiple species at different locations, which could take many years, an initial analysis could be conducted using the citizen-science recordings. For example, we could test our findings in chipping sparrows across New World Sparrow species more broadly, and the results could then motivate targeted field studies of specific sparrow species to validate the song differences within individuals. More importantly, these field studies could shed light on whether similar song functions observed in chipping sparrows (primarily territory defense at dawn and mate attraction during the day) are also associated with predictable song differences for all sparrow species that exhibit similar diel patterns in song. On the other hand, if previous research on a species has revealed diel patterns in behavior, such as singing from different locations within their territory at different times of day, citizen-science data could be useful to explore whether there are parallel diel differences in song structure.

Citizen-science data not only can be used to confirm and extend the results of focal field studies, but is also an increasingly valuable resource in ornithology and other fields (Bonney et al., 2009; Bonter, 2017; Bonter & Cooper, 2012; Dickinson et al., 2010; Lang et al., 2019; La Sorte et al., 2013; Newson et al., 2017; La Sorte et al., 2018; Suzuki-Ohno et al., 2017). This is especially true with rapid phenological shifts due to climate change and the ecological impact of human behavior on species diversity and numbers (Callaghan et al., 2017; Danielsen et al., 2011; Hames et al., 2002; Horton et al., 2019; Mayor et al., 2017). Our results add to the literature highlighting the capacity of such resources (Dickinson et al., 2010; Hochachka et al., 2012; La Sorte et al., 2018) and the importance of thoughtfully designing data collection methods (Azzurro et al., 2013; Boakes et al., 2010; Bonter & Cooper, 2012; Frigerio et al., 2018; Hecht & Cooper, 2014; La et al., 2016; Sauer et al., 1994; Shirk et al., 2012; Tulloch et al., 2013; Williams et al., 2012), in order to maximize the scientific value of citizen-science data beyond biodiversity and migration studies. Our analysis brought to the forefront limitations in data acquisition that could be addressed relatively easily with modifications to the recording submission process. Foremost, very little behavioral data are obtained (e.g. verbal or written comments) in parallel with recordings. Our case study on chipping sparrows shows that such behavioral notes would be useful when combined with recording metadata. Such data facilitate testing additional hypotheses hinging on behavioral context, such as the functional relevance of observed diel song differences. Moreover, behavioral data—such as whether the bird is singing from the ground, a tree, or other perch, as well as the estimated height of perch—are not difficult to document; such annotations could be encouraged by integrating them into the reporting mechanism on citizen-science smartphone apps. Studies such as (Benedetti et al., 2018; Bonter & Cooper, 2012; Celebrate Urban Birds, 2016, FeederWatch, n.d.; Leighton et al., 2018) show the power of citizen scientists collecting even simple behavioral observations to test long-standing hypotheses. Another drawback of citizen-science recordings is that many are short clips only including one or few songs. This makes it difficult to calculate average song properties for each bird, measure inter-song interval, recognize song patterns within longer bouts, or determine repertoire size. For example, between dawn and day, chipping sparrows recorded in the field changed not only the duration of their individual songs but also the rate of song delivery (Liu & Kroodsma, 2007). Similarly, black-capped chickadees produce more frequent and larger frequency shifts in their dawn song (Horn et al., 1992); however, neither of these diel patterns would be easily discovered using existing, publicly available data since most recordings are too short. Perhaps online databases could encourage recordists to avoid splitting their recordings into multiple submissions and to record individual birds for longer, for example by tracking the user's average recording length or number of songs per recording.

In conclusion, we believe there is untapped potential for citizen-science databases of birdsong to complement and inform field research. Toward this end, we use publicly available recordings to detect diel patterns in the chipping sparrow song, extending the results of a focal field study of chipping sparrow behavior. We find that, across their geographic range, chipping sparrows on average sing shorter and more variable songs with fewer syllables before sunrise, illustrating that this phenomenon is not confined to the region and time period of the field study. By extension, we predict that behavioral differences found in field studies might also apply across the species range: singing before sunrise is used in territorial defense whereas morning singing serves the purpose of mate attraction. The methods used in this paper can serve as a template for future studies, to uncover diel song patterns in other species. Overall, we demonstrate the ability of citizen-science data to detect diel patterns in birdsong, providing motivation for using citizen-science data in tandem with fieldwork to extend behavioral studies across geographies and species.

MANUSCRIPT DATA AVAILABILITY AND ACKNOWLEDGMENTS

All data and associated code for statistical anlayses are available at https://github.com/CreanzaLab/chipping_sparrows_time_of_day. Documentation and code for Chipper can be found at http://github.com/CreanzaLab/chipper.

We would like to thank Matt Young for assistance accessing song files from Macaulay Library, Brett M. Morris for Python code using astroplan to calculate time of sunrise based on temporal and geographic information for time of day analyses, and members of the Creanza lab for helpful discussions.

CHAPTER 4

GEOGRAPHICALLY WELL-DISTRIBUTED CITIZEN SCIENCE DATA REVEALS RANGE-WIDE VARIATION IN THE CHIPPING SPARROW'S SIMPLE SONG

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A modified version was previously published as:
Searfoss, A. M., Liu, W.-c., Creanza, N. (2020) Geographically well-distributed citizen science data reveals range-wide variation in the chipping sparrow's simple song. *Animal Behaviour*, 161, 63–76. https://doi.org/10.1016/j.anbehav.2019.12.01

INTRODUCTION

In the extensive body of literature on avian vocalizations, geographic variation has been a specific focus of many studies. The formation and accumulation of geographic variation in song is related to factors of song learning, such as locally transmitted copy errors or selective attrition, as well as to the dispersal patterns of birds at different life stages. (Aplin, 2019; Marler & Tamura, 1964; Nelson, 2000; Slabbekoorn & Smith, 2002; Slater, 1989, 1986). Furthermore, since song often serves the purpose of species identification and mate attraction (Catchpole & Slater, 2008), geographic variation in learned song can potentially play a role in biological evolution: if females preferentially select males with local songs, then the local song could eventually act as a cultural barrier to gene flow (Baker & Mewaldt, 1978; Edwards et al., 2005; Irwin, Irwin, & Price, 2001; MacDougall-Shackleton & MacDougall-Shackleton, 2001; Marler & Tamura, 1962; Nottebohm, 1969; Patten, Rotenberry, & Zuk, 2004; Stewart & MacDougall-Shackleton, 2008). Overall, variation in song can potentially be linked to reproductive isolation and speciation events either directly, by reinforcing population divergence (Irwin, Thimgan, & Irwin, 2008; Lipshutz, Overcast, Hickerson, Brumfield, & Derryberry, 2017; Martens, 1996), or indirectly, as a by-product of other environmental selection pressures that result in acoustic or morphological adaptations (Bertelli & Tubaro, 2002; Cutler, 1970; Nottebohm, 1985; Ryan & Brenowitz, 1985;

Schluter, 2000; Slabbekoorn, 2004; Wiley & Richards, 1978).

Geographic variation in song has been described by three primary patterns: random, in which song characteristics have no correlation with geographic location; clinal, in which song varies gradually yet predictably with geographic distance; and distinct dialects, in which songs differ between geographically defined regions (Podos & Warren, 2007). Distinct dialects have been the most commonly studied, since the sharp differences between dialects seemed likely to provide insights into evolutionary processes (Podos & Warren, 2007). Previous research posits that song dialects could have evolved through multiple mechanisms, including through adaptation to the local environment, as a response to social factors such as female preferences, or simply by neutral cultural drift, in which song is locally learned and copy errors accumulate regionally (Andrew, 1962; Marler & Tamura, 1962; Nottebohm, 1969; Podos & Warren, 2007; Rothstein & Fleischer, 1987). Most tests of these hypotheses have relied upon fieldwork, as it is well suited to capture the variability between populations with distinct song differences and to characterize the sharp transitions between dialects (Baker, 1975; Borror & William, 1965; Chilton, Wiebe, & Handford, 2002; MacDougall-Shackleton & MacDougall-Shackleton, 2001; Marler & Tamura, 1964; McGregor, 1980; Nicholls, Austin, Moritz, & Goldizen, 2006; Nottebohm, 1969; Shizuka, Ross Lein, & Chilton, 2016; Wilkins et al., 2018). However, discrete local dialects are relatively rare in songbird species (Slater, 1989, 1986). In fewer studies, fieldwork has detected clinal patterns, with more continuous shifts in song properties across geographic regions, generally across a range of 10 to several hundred kilometers (Cicero & Benowitz-Fredericks, 2000; Dalisio, Jensen, & Parker, 2015; Falls, Krebs, & McGregor, 1982; Janes, Ryker, & Ryan, 2017; Lee, Podos, & Sung, 2019; Mcgregor & Krebs, 1982; Schook et al., 2008; Sung & Handford, 2006). Together, this leaves song variation understudied in the numerous species that lack these short-range geographic song patterns. We propose that for the remaining populations, in which songs have random variation at a local scale, there could be long-range geographic patterns that would not be immediately apparent, even when comparing multiple focal studies (**Fig. 4.1A**). More broadly, site-specific field studies are not ideally suited to finding long-range geographic patterns in songs, and a more continuous geographical sampling of songs across the species range could reveal such patterns (**Fig. 4.1B**).

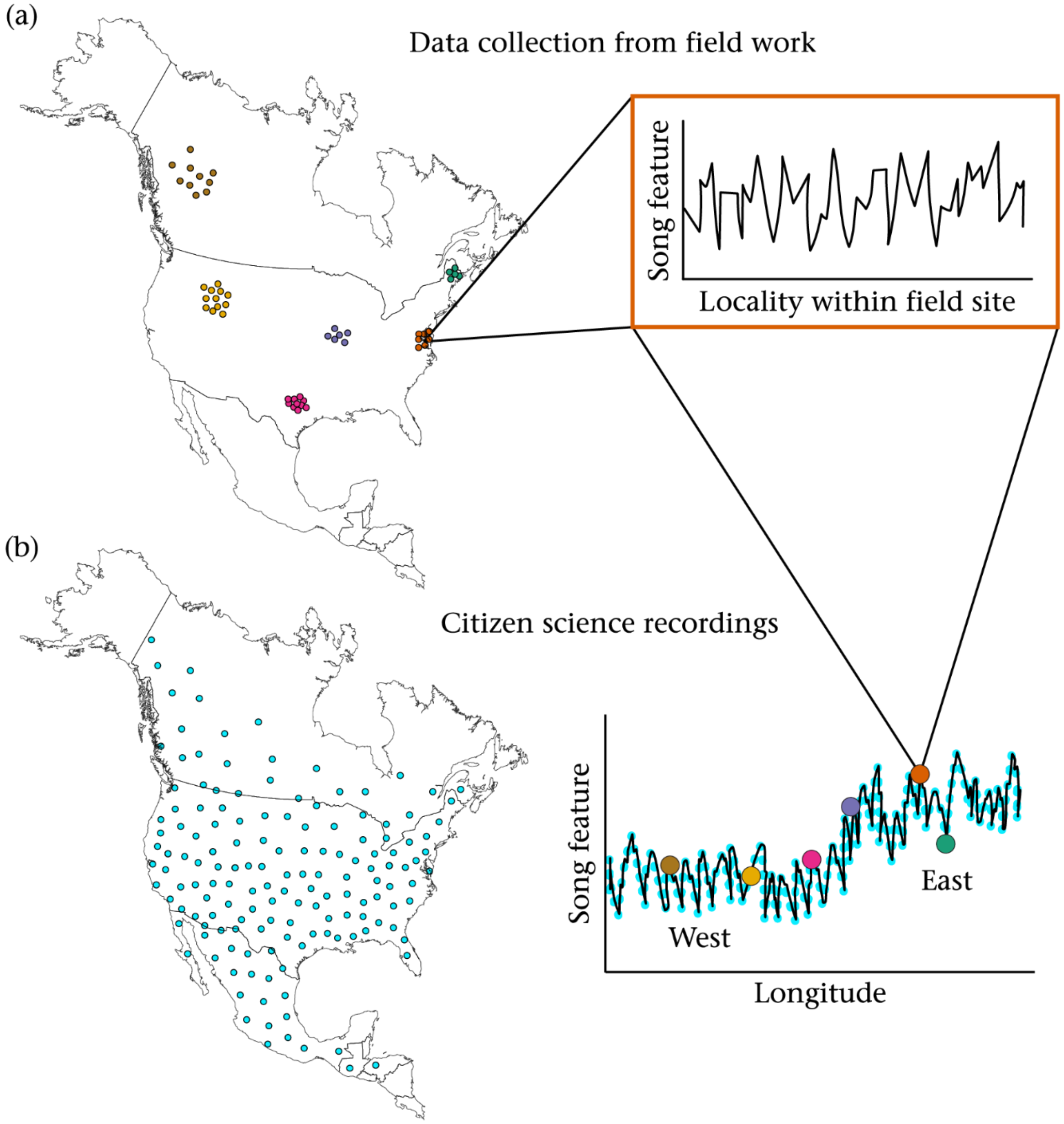

Figure 4.1 Schematic illustrating how citizen-science data could reveal geographic patterns when song variation appears random at the local scale of field studies. Field studies have proven useful in characterizing many types of geographic variation in song including random, clinal, and dialect patterns (Podos & Warren, 2007); however, these site-specific studies are less well suited for finding large-scale structure across a continent. Citizen-science data, which provides recordings collected more continuously across a species' range, is better suited to finding long-range patterns in song for species that seem to have short-range random variation. (A) As an example, we show a map of North America, which encompasses the entire chipping sparrow range (Fig. 4.2), with points indicating theoretical field sites, within which songs have no geographic structure. (B) Citizen-science recording locations that are often well distributed across a species' entire range could better detect large-scale geographic trends in song, such as higher values in the East than in the West, than the punctate measurements from fieldwork. Geographic maps in Figures 4.1–4.3 were made using ArcMap v.10.7; country outlines are from Esri, DeLorme Publishing Company, Inc. (map projection, North_America_Lambert_Conformal_Conic, WKID: 102009 Authority: Esri.

Recently, some groups have begun taking advantage of well-distributed data sets accumulated by citizen scientists and have found spatial variation in song across large geographic ranges (Bolus, 2014; Kaluthota, Brinkman, dos Santos, & Rendall, 2016; Roach & Phillmore, 2017; Weir, Wheatcroft, & Price, 2012). We take a similar approach to ask whether range-wide trends in song can be uncovered for species with high degrees of local song variation. Here, we synthesize and leverage recordings from previous field studies (Liu, 2004; Liu & Kroodsma, 2006, 2007; Liu & Nottebohm, 2007) and public repositories of birdsong (Cornell Lab of Ornithology, 2009; Nelson & Gaunt, 1997; Planqué & Vellinga, 2005) to facilitate a large-scale examination of geographic song variation across North and Central America in the chipping sparrow. The chipping sparrow is well suited to this type of study, as there is local variation of syllable types within the population, but each individual sings one, relatively simple song type, composed of a single syllable repeated at a relatively constant rate (Borror, 1959; Marler & Isaac, 1960) (see Results, **Fig. 4.8M**). The chipping sparrow has been recorded extensively, with database entries covering the chipping sparrow's entire range in Canada, the United States, Mexico, and parts of Central America. Past site-specific studies have been conducted on the chipping sparrow to investigate both song development and performance (Goodwin & Podos, 2014; Liu, 2004; Liu & Kroodsma, 2006, 2007) as well as to compare songs across multiple states (Borror, 1959); however, no vocalization study has explored geographic variation across the entire chipping sparrow range.

While chipping sparrows have very simple songs, they exhibit two layers of complexity that make them particularly interesting to study in the context of geographic variation: they have seasonal migration in a subset of their geographic range (**Fig. 4.2**), and they can briefly modify their songs after they establish a territory. During their hatch year, chipping sparrows can learn song from conspecific tutors as juveniles, and then, immediately after their first spring migration, they have the potential to show learning plasticity (Liu & Kroodsma, 1999; Liu & Nottebohm, 2007). Studies of chipping sparrows show that first-year males often produce a song with syllables that closely match the song of a bird on a neighboring territory, even if that song type differs from those of the yearling's father and other males near his natal territory (Liu & Kroodsma, 2006). After this first breeding season, the chipping sparrow's song crystallizes, and each male sings one song for the rest of his life (Liu & Kroodsma, 2006).

Since a male chipping sparrow's song can be influenced by his neighbors after his first migration, the syllable types of successful birds, such as those with large or long-held territories, could gain prominence in one region. Over time, this pattern of song learning could lead to regional differences in chipping sparrow syllable types that would be analogous to the local dialect structure observed in other sparrow species (Baptista, 1977; Baptista & King, 1980; DeWolfe, Kaska, & Peyton, 1974; Marler & Tamura, 1962; Shizuka et al., 2016; Tubaro, Segura, & Handford, 1993). However, chipping sparrows show a more complex geographic distribution of songs, with many syllable types coexisting in the same region (Borror, 1959; Liu & Kroodsma, 2006). This local variation is thought to be attributed in part to copy errors but even more so to low territory site-fidelity; males will often abandon their territory after an unsuccessful breeding season, resulting in short-range dispersal (Liu & Kroodsma, 2006). Studying chipping sparrows on a large spatial scale could reveal interesting regional patterns of conformity in certain song features (e.g. syllable durations and frequency) despite varied syllable types on a local scale.

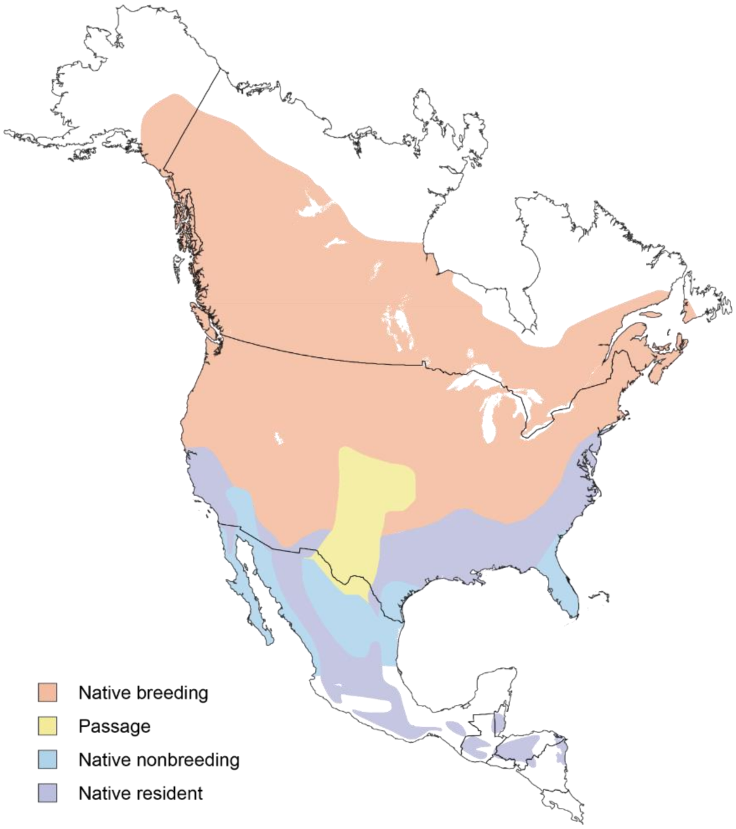

Figure 4.2 Chipping sparrow range map. Range map was adapted from BirdLife International and Handbook of the Birds of the World (2018) Bird species distribution maps of the world (version 2018.1). Available at http://datazone.birdlife.org/species/requestdis.

With corresponding genetic information, one could examine the role of song variation in biological evolution. However, chipping sparrow genetic variation remains understudied and somewhat unresolved. For example, an early study of chipping sparrow genetic variation used restriction fragment analysis of mitochondrial DNA (mtDNA) and found no geographic variation across the United States and Canada (Zink & Dittmann, 1993). A more recent study analyzed mitochondrial control region (mtDNA CR) sequences from across both North and Central America to examine the ancestry of the migratory chipping sparrow population, finding evidence that the migratory population descended from the sedentary population that resides in Mexico, not Guatemala (Milá, Smith, & Wayne, 2006). Their results suggest that the expansion of chipping sparrows from Mexico into the United States and Canada occurred in the 18,000 years since the last glacial maximum. Some studies of invasive species indicate that signatures of geographic population structure can arise on much shorter timescales (i.e. the few hundred years since the invasion event) (Rollins, Woolnough, Wilton, Sinclair, & Sherwin, 2009; Van Leeuwen et al., 2012), indicating that it could be possible to detect genetic differentiation in chipping sparrows since the last glacial maximum. Lastly, chipping sparrow cytochrome oxidase I (COI) sequences have been gathered, primarily for phylogenetic studies aimed at determining taxonomic relationships, divergence times, and selection pressures (Kerr, 2011; Kerr et al., 2007; Tavares & Baker, 2008), but these sequences have not been used to study chipping sparrow genetic variation.

We hypothesize that both song and genetic variation should have a geographic signature in the cross-continental chipping sparrow population. In particular, we predict that birds that are further apart geographically should show greater genetic distance as well as greater song divergence. However, the combination of first-year song plasticity, seasonal long-distance migration, and short-range dispersal in chipping sparrows could disrupt the relationship between geography, genes, and song. For example, the population could be genetically well-mixed due to nonphilopatric migration while still maintaining song structure due to the postmigration song plasticity. Even with low site-fidelity, song types could vary locally while general song characteristics (e.g. duration and frequency measures) could be spread and maintained across long ranges. Thus, we aim to use quantitative song analysis of citizen-science recordings to assess large-scale geographic signatures of chipping sparrow songs and evaluate these patterns in the context of their genetic structure.

METHODS

Gathering chipping sparrow song data

To determine whether there are patterns in song variation across the chipping sparrow's entire geographic range, we leveraged the data collected by citizen scientists across the United States, Canada, and Central America. Specifically, we assembled chipping sparrow recordings from an intensive field study conducted between 1997 and 2008 (Liu, 2004; Liu & Kroodsma, 2006, 2007; Liu & Nottebohm, 2007) as well as from available databases: the Macaulay Library at the Cornell Lab of Ornithology (Cornell Lab of Ornithology, 2009), Borror Laboratory of Bioacoustics (Nelson & Gaunt, 1997), and Xeno-canto (Planqué & Vellinga, 2005). For each of the songs used in this analysis, we compiled the year of the recording and the latitude and longitude of the recording location (**Fig. 4.3A**). All songs had a provided latitude and longitude or a stated location for which we could estimate a latitude and longitude. If songs did not have the necessary metadata available for a particular test, they were not included in the corresponding analyses.

The recordings and their metadata were manually examined for evidence that multiple recordings were of the same individual bird. In the absence of observable syllable differences to discriminate between individuals or field notes dictating that two individuals were recorded, seemingly identical song samples recorded in a single location (matching latitude and longitude coordinates) within one calendar year were considered duplicate recordings of one bird. Similarly, all files with matching location but without a date were considered to be recorded in the same year as each other. Then for all duplicates, either the least noisy bout was kept, or if there was no clear difference, one bout was randomly selected, eliminating all others. We implemented this conservative method to reduce the chance that our analysis would be biased by multiple recordings of one individual, with some risk that we eliminated neighboring pairs of individuals in which one bird had accurately imitated another.

In total, we gathered 1078 recordings of chipping sparrows; we excluded 132 song files due to repeated recording of the same bird and 126 recordings due to noise levels, leaving 820 song files (see **Appendix B** for references), each a representative song of an individual chipping sparrow, for analysis.

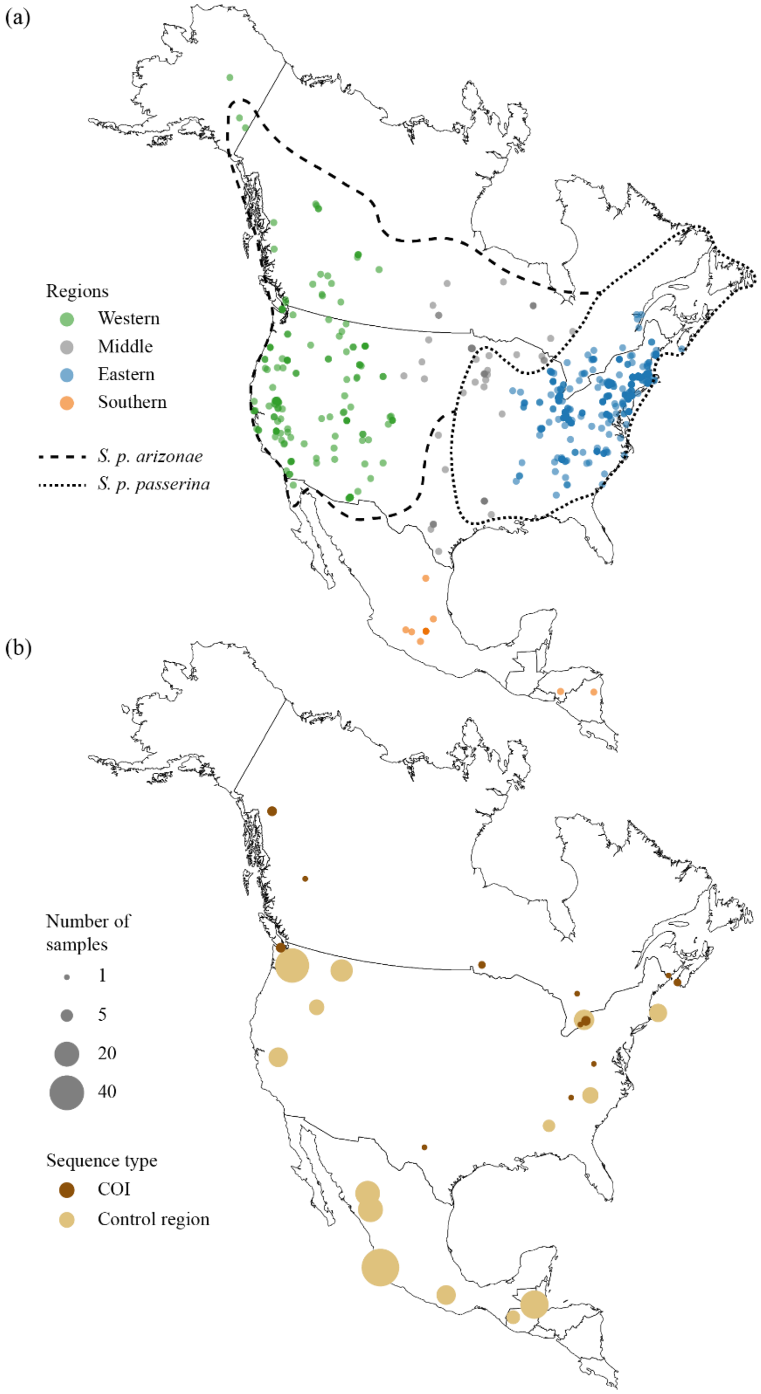

Figure 4.3 Geographic location of song recordings and mitochondrial genetic data. (A) The geographic distribution of song recordings is shown. For most geographic analyses, we used latitude and longitude, but for discrete geographic comparisons of song, we analyzed recordings between regions defined based on putative subspecies' ranges (see Methods): Southern (orange), Western (green), Eastern (blue), and Middle (gray). The ranges for the subspecies north of Mexico are adapted from Zink and Dittmann (1993). (B) The sampling location of each previously published mtDNA control region sequence (tan) (Milá et al., 2006) and cytochrome oxidase I (COI) sequence (brown) is indicated on the map (see Methods for GenBank accession numbers). The size of each circle indicates the number of sequences sampled at that location.

Bout selection and analysis

To analyze chipping sparrow song features, we imported the recordings into Audacity (www.audacityteam.org) and chose the song bout of best quality from each, which was ideally free of interfering birdsong, human voices, or excessive noise, since any competing signals complicate syllable segmentation and comparison. When multiple acceptable bouts were present in a recording, we selected one bout of typical length to include in the analysis. We exported the selected bout in WAV format sampled at 44,100 Hz. We conducted signal processing, noise reduction (high-pass filter and signal reduction), and segmentation of bouts into syllables in Chipper (**Chapter 1, Appendix A**), software we developed for this purpose in Python. In brief, this software computes a Gaussian-windowed spectrogram (based on code from Gardner & Magnasco, 2006) and binarizes this spectrogram such that the top 3% of signal is retained for assessing syllable boundaries. Syllable beginnings (onsets) and endings (offsets) are then automatically detected by summing the columns of the spectrogram (resulting in a vector of total signal intensity over time) and then finding the element positions (or time points) at which there is a change from no signal to signal or vice versa. A syllable is removed if it is shorter than 6.3 ms, and two syllables are merged if the silence between them is shorter than 3.2 ms. Next, we could adjust this automatic segmentation, if necessary, in several ways: by normalizing the signal amplitude, by using a high-pass filter to remove low-frequency noise, by changing the amount of signal retained in the binary matrix, and by adjusting the minimum syllable duration and the minimum intersyllable silence duration within Chipper. Once the semi-automated segmentation is complete, intersyllable comparison is calculated by using a constrained sliding window algorithm to find the maximum overlap between two binary syllables. Syllables are considered the same if the overlap is greater than a user-defined threshold. Chipper further divides syllables into notes defined as any four-connected signal in the binary matrix with a number of pixels greater than a user-specified threshold. For our analysis of chipping sparrow songs, we used a low intersyllable maximum overlap threshold of 40%, as we knew the characteristic song only contains one syllable type. We set the threshold for note size to 120 pixels. Ultimately, Chipper calculated 16 song features for each recording, defined below. Each feature was log-transformed if the distribution of data was not normal; the only syllable features that did not need to be log-transformed were mean stereotypy of repeated syllables and the standard deviation of note frequency range.

We calculated 16 song features in the following manner: (1) mean note duration, calculated as mean(time of note ending − time of note beginning); (2) mean note frequency range, calculated as mean(note maximum frequency − note minimum frequency); (3) mean note minimum frequency, calculated as mean(minimum frequency of each note); (4) mean note maximum frequency, calculated as mean(maximum frequency of each note); (5) mean intersyllable silence duration, calculated as mean(time of syllable onset − time of previous syllable offset); (6) mean syllable duration, calculated as mean(time of syllable offset − time of syllable onset); (7) mean syllable frequency range, calculated as mean(syllable maximum frequency − syllable minimum frequency); (8) mean syllable minimum frequency, calculated as mean(minimum frequency of each syllable); (9) mean syllable maximum frequency, calculated as mean(maximum frequency of each syllable); (10) duration of song bout, calculated as (time of last syllable offset − time of first syllable onset); (11) mean stereotypy of repeated syllables, calculated as the mean percent similarity for sets of syllables that were deemed repetitions of the same syllable; (12) number of notes per syllable, calculated as (total number of notes)/(total number of syllables); (13) syllable rate, calculated as (number of syllables)/(bout duration); (14) total number of syllables, calculated as the number of syllable onsets in a bout; (15) standard deviation (SD) of note duration, calculated as SD(time of note ending − time of note beginning); (16) standard deviation of note frequency range, calculated as SD(note maximum frequency − note minimum frequency). Each of these features was calculated for the 820 songs.

Comparing Xeno-canto song properties to other databases

To determine whether the compressed format (MP3) of recordings downloaded from Xeno-canto affects the song features measured (see, e.g. Araya-Salas, Smith-Vidaurre, & Webster, 2017), we compared the song features of recordings collected from Xeno-canto to those from Macaulay Library, Borror Lab of Bioacoustics, and Dr. Wan-chun Liu. We restricted this analysis to the eastern U.S./Canada to avoid confounding geographical patterns with recording quality differences. We performed a Wilcoxon rank-sum test (function ‘ranksums’, SciPy module from Python; Jones, Oliphant, & Peterson, 2001) to determine whether each of the song features differed between Xeno-canto recordings and the recordings from other databases. For stringency, we conducted a Bonferroni correction for multiple hypothesis testing by dividing the P value threshold for significance (α=0.05) by the number of tests. Overall, we performed three Wilcoxon rank-sum tests on each of 16 song features; the threshold for significance was lowered to $\alpha_{\text{adjusted}}=1.0\times10^{-3}$.

Analysis of geographic structure in song, note, and syllable properties

In visualizing the geographic spread of the pooled recordings, we found a few over-represented locations in our data set, especially in the eastern United States (**Fig. 4.4A**). The locations (rounding latitude and longitude to two decimals) with 25 or more recordings were as follows: central Columbus, Ohio, U.S.A. (39.96N, 83.00W, 42 samples); northern Columbus, Ohio, U.S.A. (40.08N, 82.92W, 47 samples); Ashley, Ohio, U.S.A. (40.42N, 82.91W, 25 samples); Amherst, Massachusetts, U.S.A. (42.37N, 72.52W, 51 samples); and Ware, Massachusetts, U.S.A. (42.28N, 72.31W, 26 samples). Over-representation was generally due to a field study of chipping sparrows conducted in that location. Thus, we conducted both Wilcoxon rank-sum tests and Brown–Forsythe tests for equality of variance in non-normal distributions (function 'levene(center='median')', SciPy module from Python; Jones et al., 2001) between each of these five sites and the other eastern U.S./Canada recordings. After Bonferroni correction for five tests on each of the 16 song features, $\alpha_{\text{adjusted}}=6.25\times10^{-4}$.

To avoid pseudoreplication in our subsequent song analyses, we conducted statistical tests before and after downsampling the song data by location. To perform this downsampling, we rounded the latitudes and longitudes to two decimal places (~1 km) and then randomly selected one song from each rounded latitude/longitude pair; this resulted in a downsampled data set of 335 songs (**Fig. 4.4B**). We repeated this sampling procedure 1000 times, performing the statistical test on each subset of songs and recording the maximum and minimum values for each test conducted.

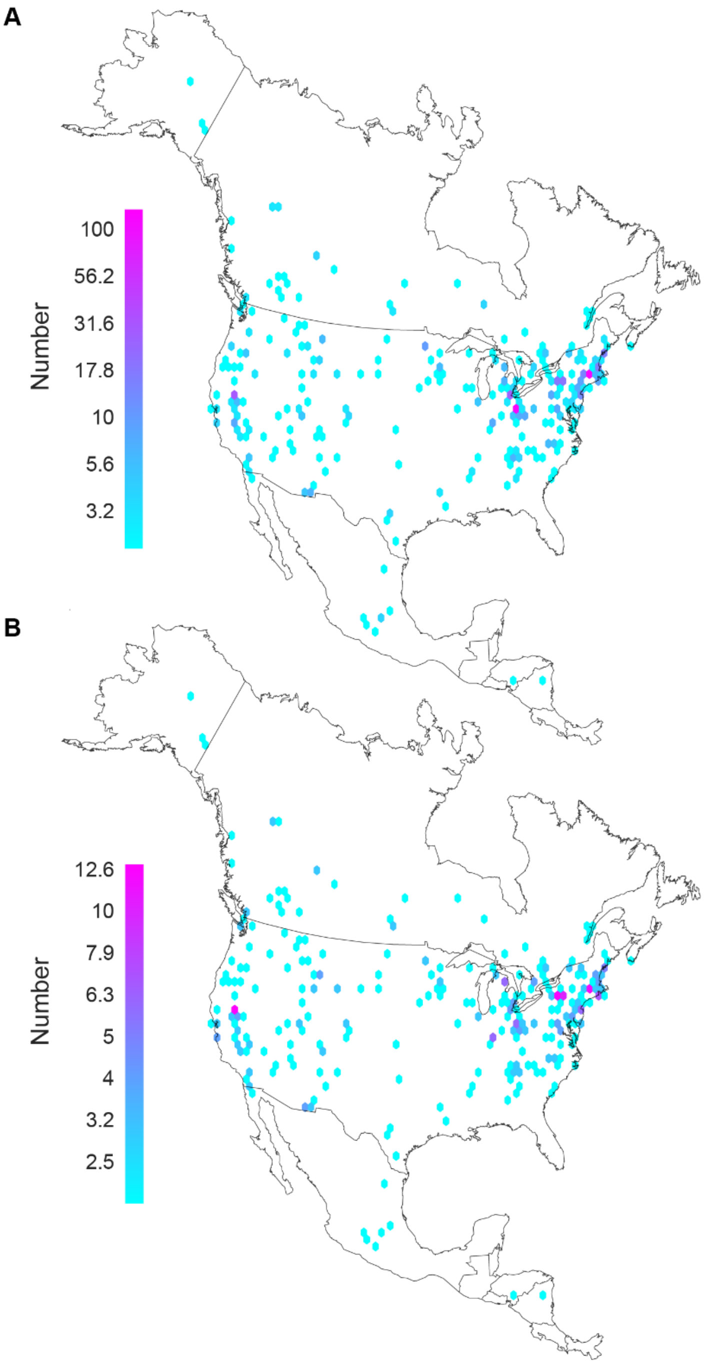

Figure 4.4 Geographic distribution of song recordings before and after downsampling. (A) Heat map of the geographical distribution of the 820 song recordings, with the color of the hexagon bins indicating the number of song recordings in a local area. (B) Distribution of geographical locations of song recordings after downsampling; note that the color scale differs from that in (A). Downsampling was conducted by randomly selecting a song from each location (geographical coordinates rounded to two decimal places). This sampling process was conducted 1000 times; this figure represents one of these random samplings. Although there were a large number of recordings near Ithaca, New York, U.S.A., they were ~1 km away from each other and thus were not downsampled. We suspect that the large number of song recordings in this area were due to the large number of recordists near the Cornell Lab of Ornithology.

To determine whether songs vary across their geographic range, we calculated Spearman rank correlations between the 16 song features and the latitude and longitude of the recordings. We conducted a Bonferroni correction for multiple hypothesis testing: two tests on 16 song features, $\alpha_{\text{adjusted}}=1.56\times10^{-3}$. For continuous analyses, all 820 song recordings were used.

To further examine the relationship between location and song variation, we calculated a pairwise geographic distance matrix between latitudes and longitudes of collection sites for all song recordings using the great-circle distance (the shortest distance between two points on a sphere). For each song feature, a song distance matrix was calculated using Euclidean distance (function ‘dist’, R package ‘stats’; R Core Team, 2019), resulting in 16 song feature distance matrices that each corresponded to the geographic distance matrix. We then tested whether the song distance between chipping sparrows for each of the 16 song features was significantly correlated with the geographic distance between their sampling locations using Mantel tests (Mantel, 1967) (function ‘mantel’, R package ‘vegan’; Dixon, 2003) with 100,000 permutations. When performed on the 1000 downsampled data sets, each Mantel test was run with 10,000 permutations. After Bonferroni correction for16 Mantel tests on the song data, the threshold for significance was lowered to $\alpha_{\text{adjusted}}=3.13\times10^{-3}$.

Since we observed clustering in song features across longitudes that potentially corresponded to subspecies boundaries, we also conducted discrete analyses. To inform our categorization of recordings into discrete geographic regions, we examined subspecies classifications of chipping sparrows. There have been several subspecies classifications proposed for chipping sparrows in the United States and Canada, but there is no clear consensus. Currently, the Clements Checklist lists two weakly demarcated subspecies in this region (Clements et al., 2019), but the American Ornithologists’ Union checklist has not listed any chipping sparrow subspecies since 1983 (Chesser et al., 2019). Furthermore, a mitochondrial study found no genetic differentiation within the United States and Canada (Zink & Dittmann, 1993). The study also provides the only subspecies map available for chipping sparrows; thus, we used this map to identify potential boundaries for the two putative subspecies (*S. p. passerina* and *S. p. arizonae*). It should be noted that their map divides the western United States into *S. p. arizonae* and *S. p. boreophila*, but these subspecies have since been combined into *S. p. arizonae* (Clements et al., 2019). Additionally, since their map boundaries were hand-drawn, we leave some recordings near the boundaries unclassified to be conservative. The adjusted boundaries to include this conservative categorization roughly align with the following: Eastern (latitude > 25°, longitude > −90°), Western (latitude > 25°, longitude < −105°), and Southern (latitude < 25°, all longitudes) (**Fig. 4.3A**). To avoid ambiguity, the Middle region was excluded from any discrete geographic analysis. For each pair of regional categories, we performed a Wilcoxon rank-sum test to determine whether each of the song features differed between regions. After Bonferroni correction for three Wilcoxon rank-sum tests for location on each of 16 song features, $\alpha_{\text{adjusted}}=1.0\times10^{-3}$.

We performed a Wilcoxon rank-sum test to compare the years of recordings between the Eastern and Western regions both before and after downsampling by location.

Song features as geographic classifiers

To evaluate how well the song features serve as predictors for classifying song recordings into their respective regions (Eastern or Western U.S./Canada) that correspond to putative subspecies ranges, we created a Gaussian Naive Bayes classifier (function 'GaussianNB', Scikit-learn module in Python; Pedregosa et al., 2011). To train the classifier, we fit the Gaussian Naive Bayes model to 67% of our song data, leaving 33% of the data for testing. Only songs classified as from Eastern or Western U.S./Canada were used in the training and test sets as the Middle U.S./Canada had no ground truth for being considered Eastern or Western and there were too few Southern songs to split into a training and test set. We trained our model four different ways: (1) with all 16 song features, (2) with each of the song features independently, (3) with all pairs of song features, and (4) with all combinations of three song features. Using each trained model, we predicted the region for each song in our test set, and reported the accuracy of the classifier.

Principal component and Procrustes analyses

Since some song features were correlated with one another, we reduced the dimensionality of the song data by performing a principal component analysis (function 'PCA', Scikit-learn module in Python; Pedregosa et al., 2011) on the matrix of 16 song features calculated for each of the 820 songs. To quantify the relationship between these principal components and geography, we performed a Procrustes analysis (function 'procrustes', SciPy module in Python; Jones et al., 2001) of the song feature PCs versus the geographic coordinates of the recording sites. This analysis compares the two-dimensional locations of each song in principal component space (PC1 versus PC2) to their corresponding geographic sampling locations, rotating and rescaling the PC plot to find the best overlap by minimizing the sum of squared errors (Wang et al., 2010); we calculated a dissimilarity statistic *D*, the minimized sum of squares of the pointwise differences between the PCs and geographic distances. We calculated empirical *P* values by running 10^5 permutations of geographic locations and assessing the number of randomized locations that provided a better fit to the data than the actual sampling locations. When performed on the 1000 downsampled data sets, each Procrustes analysis was run with 10,000 permutations. We also calculated the Pearson correlation coefficients between the first two principal components and the latitudes and longitudes of the recordings.

Syllable types

To detect spatial dynamics in chipping sparrow syllable types, we first determined which birds were singing the same syllables. By comparing one representative syllable from each chipping sparrow song in Audacity, we classified the 820 songs into 112 chipping sparrow syllable types by hand. These 112 types were further grouped into similar categories based on the shape of the syllable: up-down (up-slur followed by down-slur), down-up (down-slur followed by up-slur), sweep (single up-slur or down-slur), complex (more than two slurs), doubles (a slur with multiple frequencies), and buzz (syllable containing some buzzy phrase). To show the relative number of recordings of each syllable type and also the number of syllable types in each syllable category, we plotted a stacked histogram of the number of recordings of a syllable type colored by the region. The syllable types are organized by category; these categories are ordered from the one with the most to least number of recordings. Within each category, the syllable types are also ordered from highest to lowest frequency. To determine the most common syllable categories in each region, we controlled for number of recordings from each region and plotted the percentage of syllable types from that region that were in each category.

Collection and sequence alignment of publicly available chipping sparrow genetic data

We obtained all publicly available chipping sparrow sequences from GenBank and recorded the corresponding sampling location of each based on information provided in the genetic databases and accompanying publications. This included one set of 247 mtDNA control region sequences (328 base pairs, accession numbers AY862812-AY862852; Milá et al., 2006) and 21 cytochrome oxidase subunit I sequences (610-831 base pairs; accession numbers AY666225, AY666348, DQ433193, DQ434762-DQ434766, EU525508-EU525509, HM033820-HM033829, JN850724). JN850724 did not have detailed location information, only country and state; thus, we were not able to include it in analyses that required geographic distance. For each set of sequences, we performed multiple sequence alignments with MAFFT (Katoh & Toh, 2008) using G-INS-i, a method optimized for sequences that can be fully aligned.

Correlations between genetic and geographic distance

We calculated a pairwise geographic distance matrix between latitudes and longitudes of collection sites for the mtDNA CR sequences using the great-circle distance (the shortest distance between two points on a sphere), and we repeated this procedure for the sampling locations of the COI sequences. A corresponding genetic distance matrix was calculated for each (function ‘dist.dna’, R package ‘ape’; Paradis, Claude, & Strimmer, 2004) with Kimura’s two-parameter distance (Kimura, 1980).

We then tested whether the genetic distance between chipping sparrows was significantly correlated with the geographic distance between their sampling locations using a Mantel test (Mantel, 1967) with 1,000,000 permutations for both data sets. We performed Mantel tests for mtDNA CR and COI sequences separately, using only sequences from the United States and Canada.

The Mantel test results provide a continuous measure of correlation between geographic and genetic distance. To better understand the genetic variation in the chipping sparrow between regions, we performed an analysis of molecular variance (AMOVA) and calculated F_{ST} for the grouping into Eastern and Western regions (Excoffier & Lischer, 2010; Excoffier, Smouse, & Quattro, 1992). These are commonly used statistics in population genetics that enable researchers to quantify and compare the genetic variation within versus between groups to assess whether two populations are genetically differentiated. We used Arlequin v.3.5.2.2 (Excoffier & Lischer, 2010) to conduct the AMOVA (Excoffier et al., 1992) and calculated the fixation index, F_{ST} (Weir, 1996;

Weir & Cockerham, 1984) for both mtDNA CR sequences and COI sequences. For both the mtDNA CR sequences and the COI sequences, we used the same division of samples into Eastern and Western regions of the U.S./Canada as was conducted for songs: the Eastern region corresponded to the *S. p. passerina* range and the Western region corresponded to the *S. p. arizonae* range. Two COI sampling locations fell outside of these defined regions, so they were not included in the AMOVA. For all tests, Kimura's two-parameter distance was calculated with pairwise deletion of gaps and missing data, and 10,100 permutations were run to calculate an empirical *P* value. We set the parameter for 'allowed missing level per site' to 0.5 such that no sites were eliminated due to missing data. Sequence transversion, transitions, and deletions were all given the same weight of 1.

We created minimum spanning networks (epsilon=0) (Bandelt, Forster, & Rohl, 1999) with Population Analysis with Reticulate Trees (PopART) (Leigh & Bryant, 2015) to visualize haplotype maps for both mtDNA CR and COI sequences.

RESULTS

Comparing Xeno-canto song properties to other databases

When testing whether the MP3 file format of Xeno-canto recordings led to systematic song feature differences, we found that only the mean stereotypy of repeated syllables was significantly different between Eastern songs collected from Xeno-canto versus Macaulay Library, Borror Laboratory of Bioacoustics, or Dr. Wan-chun Liu (Wilcoxon rank-sum test: $P<10^{-3}$; **Table 4.1**). Thus, significant differences in mean stereotypy in subsequent results should be interpreted with caution. Similarly, from parsing these recordings in Chipper, we noticed that, for chipping sparrows, corresponding syllable and note measurements (e.g. syllable maximum frequency and note maximum frequency) showed similar patterns, but note measurements from low-quality recordings were less reliable than corresponding syllable measurements.

Table 4.1 Comparing Recordings from Xeno-canto to Other Databases

Results of the Wilcoxon rank-sum tests between Eastern recordings collected from Xeno-canto versus Eastern recordings collected from Macaulay Library (including eBird), from Borror Laboratory of Bioacoustics or from Dr Wan-chun Liu

Song features	Xeno-canto vs		
	Macaulay Library *P* value	Borror Lab *P* value	Wan-chun Liu *P* value
Mean note duration	0.127	0.148	0.712
Mean note frequency range	0.012	0.139	0.001
Mean note minimum frequency	0.087	0.088	0.031
Mean note maximum frequency	0.208	0.415	0.510
Mean intersyllable silence duration	0.683	0.704	0.743
Mean syllable duration	0.348	0.146	0.525
Mean syllable frequency range	0.010	0.630	0.208
Mean syllable minimum frequency	0.028	0.020	0.089
Mean syllable maximum frequency	0.322	0.194	0.839
Duration of song bout	0.563	0.941	0.014
Mean stereotypy of repeated syllables	**$<10^{-3}$**	**$<10^{-3}$**	**$<10^{-3}$**
Number of notes per syllable	0.293	0.356	0.154
Syllable rate	0.677	0.294	0.447
Total number of syllables	0.526	0.371	0.142
Standard deviation of note duration	0.221	0.121	0.073
Standard deviation of note frequency range	0.995	0.074	0.474

Bold indicates $P < 1.0 \times 10^{-3}$.

Analysis of geographic structure in song, note, and syllable properties

There was no significant difference in the variance (Brown–Forsythe test) of any song feature between the Eastern U.S./Canada recordings and those from the five over-represented sites (central and north Columbus, OH; Ashley, OH; Amherst, MA; and Ware, MA). The mean stereotypy of repeated syllables was greater in northern Columbus, Ohio than in the rest of the Eastern U.S./Canada (Wilcoxon rank-sum test: $P=4.17\times10^{-4}$; **Fig. 4.5**).

Geographic variation in song features was evident across the range of the chipping sparrow: many song features correlated with longitude, whereas no song features correlated with latitude (**Figs. 4.6–4.8, Tables 4.2, 4.3**). Specifically, mean intersyllable silence duration, mean syllable duration, mean syllable frequency range, mean syllable maximum frequency, mean note minimum frequency, number of notes per syllable, and standard deviation of note duration all had a significant positive correlation with longitude (Spearman rank correlation: $r_S\geq0.139$, $P<10^{-3}$) whereas syllable rate and total number of syllables had a significant negative correlation with longitude ($r_S\leq-0.359$, $P<10^{-25}$), even after downsampling by location (**Table 4.4**).

There was a statistically significant correlation between geographic distance and distances of mean intersyllable silence duration, mean syllable duration, mean syllable maximum frequency, syllable rate, total number of syllables, and mean note minimum frequency (Mantel test: $P<10^{-5}$, indicating that no permutation was better associated with geography than the real data) (**Tables 4.2, 4.3**). These song features remained significant after downsampling (**Table 4.5**).

After applying a Bonferroni correction ($\alpha_{\text{adjusted}}=1.0\times10^{-3}$), most song features differed significantly between longitudinal categories (Eastern versus Western), with mean intersyllable silence duration, mean syllable duration, mean syllable frequency range, mean syllable maximum frequency, syllable rate, total number of syllables, mean note duration, mean note minimum frequency, and mean note maximum frequency showing strong significance (Wilcoxon rank-sum test: $P<10^{-10}$; all remained significant after downsampling by location; **Figs. 4.8, 4.9, Tables 4.2, 4.3**, results for downsampled data set in **Table 4.6**). Number of notes per syllable and standard deviation of note duration between Eastern and Western U.S./Canada were also significantly different ($10^{-10}<P<10^{-3}$), even after downsampling by location. For comparisons between Western and Southern songs, only mean intersyllable silence duration, syllable rate and total number of syllables were significantly different ($10^{-10}<P<10^{-3}$) (**Figs. 4.8, 4.9, Table 4.2**), even after downsampling by location (**Table 4.6**). No significant differences were found between the Eastern and Southern categories (**Tables 4.2, 4.3**).

A Wilcoxon rank-sum test indicated that the distributions of recording years were statistically different ($P<10^{-7}$); certain years were more represented in the Eastern versus Western regions. We hypothesized that this difference was due to the over-representation of field studies conducted at specific time points in specific locations. After downsampling by location, there was no significant difference in the year of recordings between Eastern and Western regions ($P_{\text{min}}=0.535$, $P_{\text{max}}=0.925$).

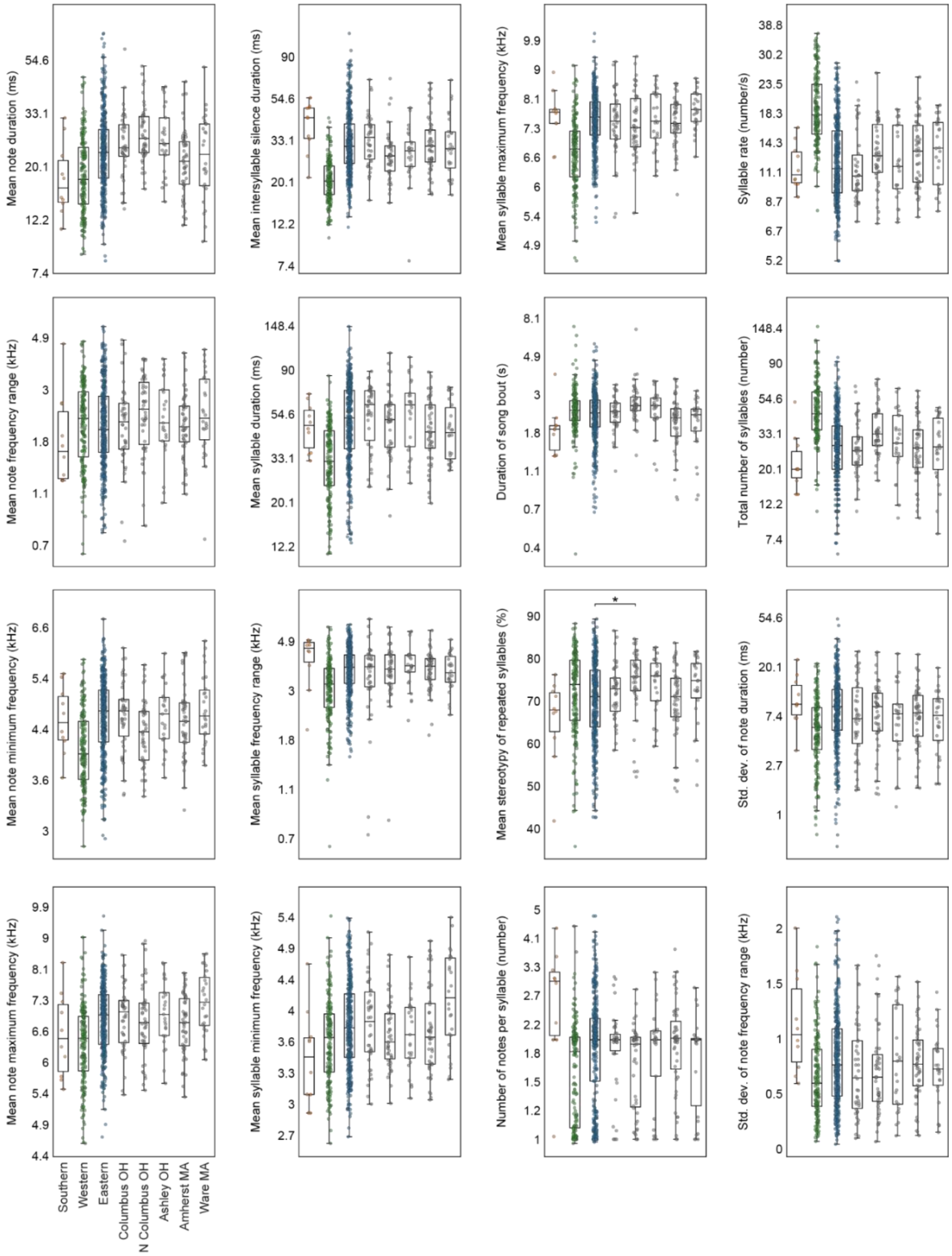

Figure 4.5 Box plots demonstrating variation in chipping sparrow song structure and frequency between five over-represented recording locations and the defined regions of interest. The five over-represented sites included central Columbus, OH, U.S.A. (39.96N, 83.00W, 42 samples), northern Columbus, OH, U.S.A. (40.08N, 82.92W, 47 samples), Ashley, OH, U.S.A. (40.42N, 82.91W, 25 samples), Amherst, MA, U.S.A. (42.37N, 72.52W, 51 samples) and Ware, MA, U.S.A. (42.28N, 72.31W, 26 samples). Overall, these sites were not systematically different from the Eastern recordings as a whole. Significant results are indicated between populations (*$P < 6.25 \times 10^{-4}$ for Wilcoxon rank-sum tests; there were no significant results for the Brown–Forsythe test). Color indicates region of the recording data: Southern (orange); Western (green); Eastern (blue); each of the five over-represented sites (grey).

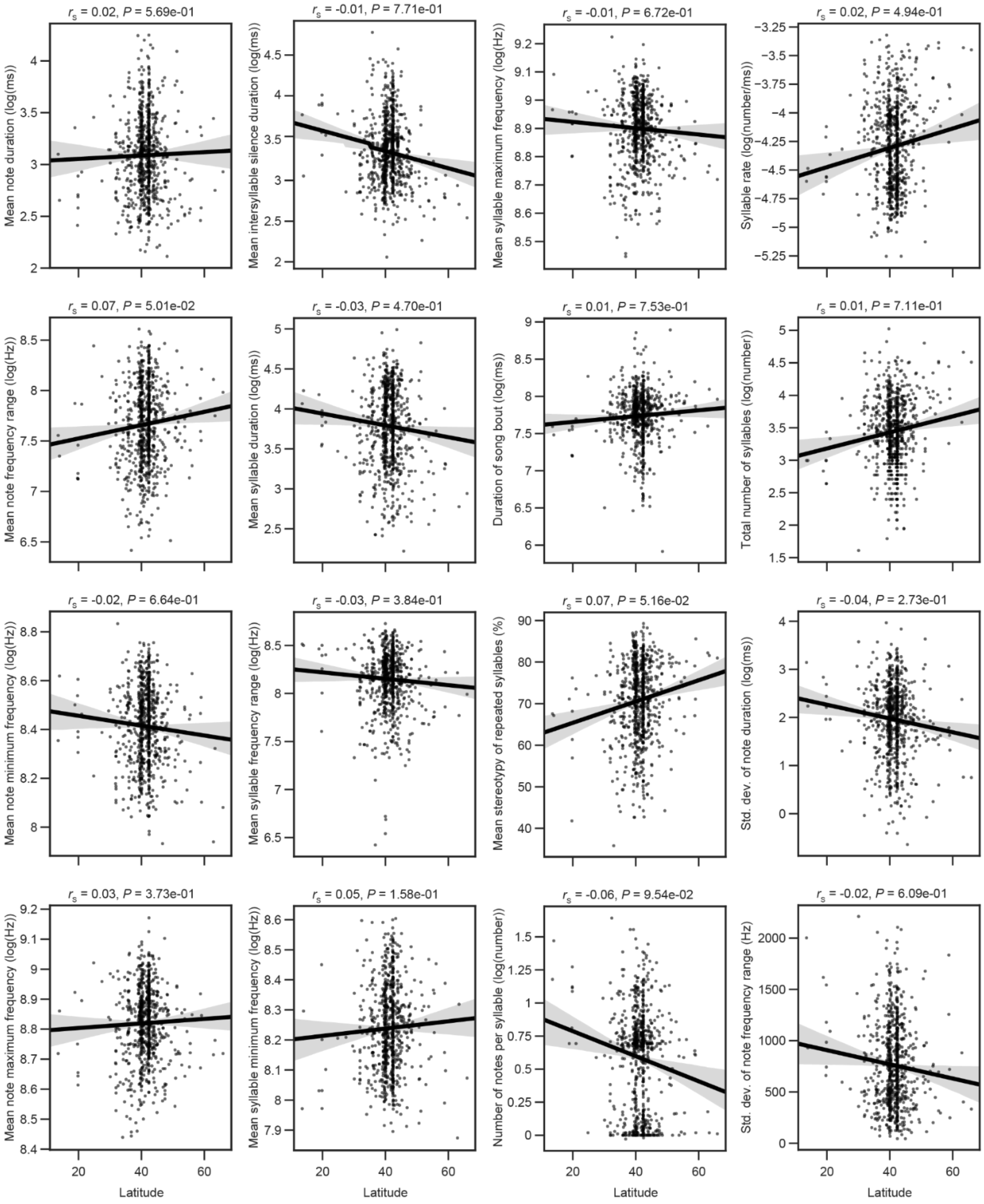

Figure 4.6 Scatter plots of the 16 song features versus latitude. A linear regression model fit and 95% CI are plotted. Spearman's rank correlation coefficients are listed above each plot along with the *P* value. There were no significant correlations.

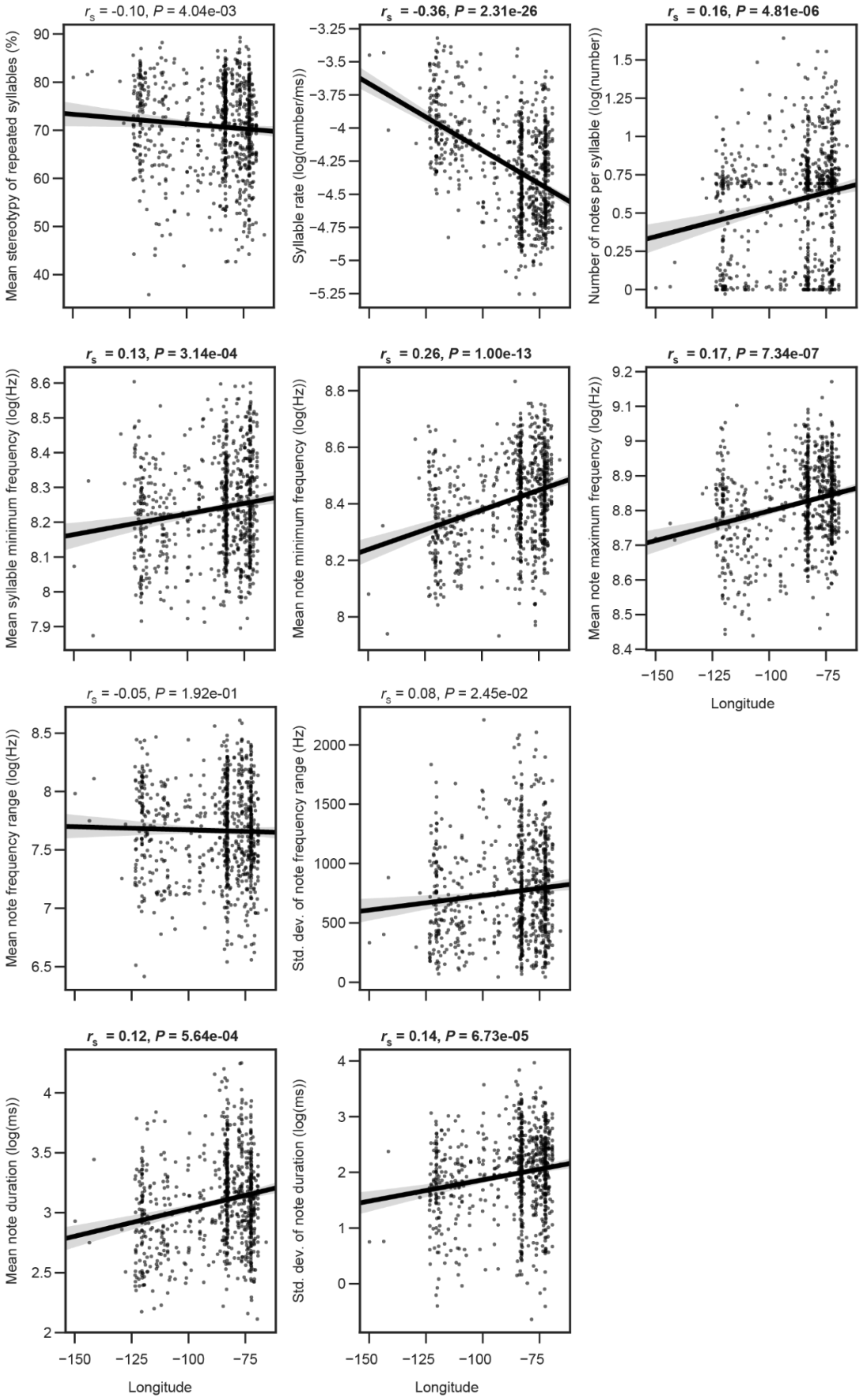

Figure 4.7 Scatter plots of 10 song features versus longitude. See Fig. 4.8 for the other six song features versus longitude. A linear regression model fit and 95% CI are plotted. Spearman's rank correlation coefficients are listed above each plot along with the *P* value. Significant results ($P < 1.56 \times 10^{-3}$) are shown in bold.

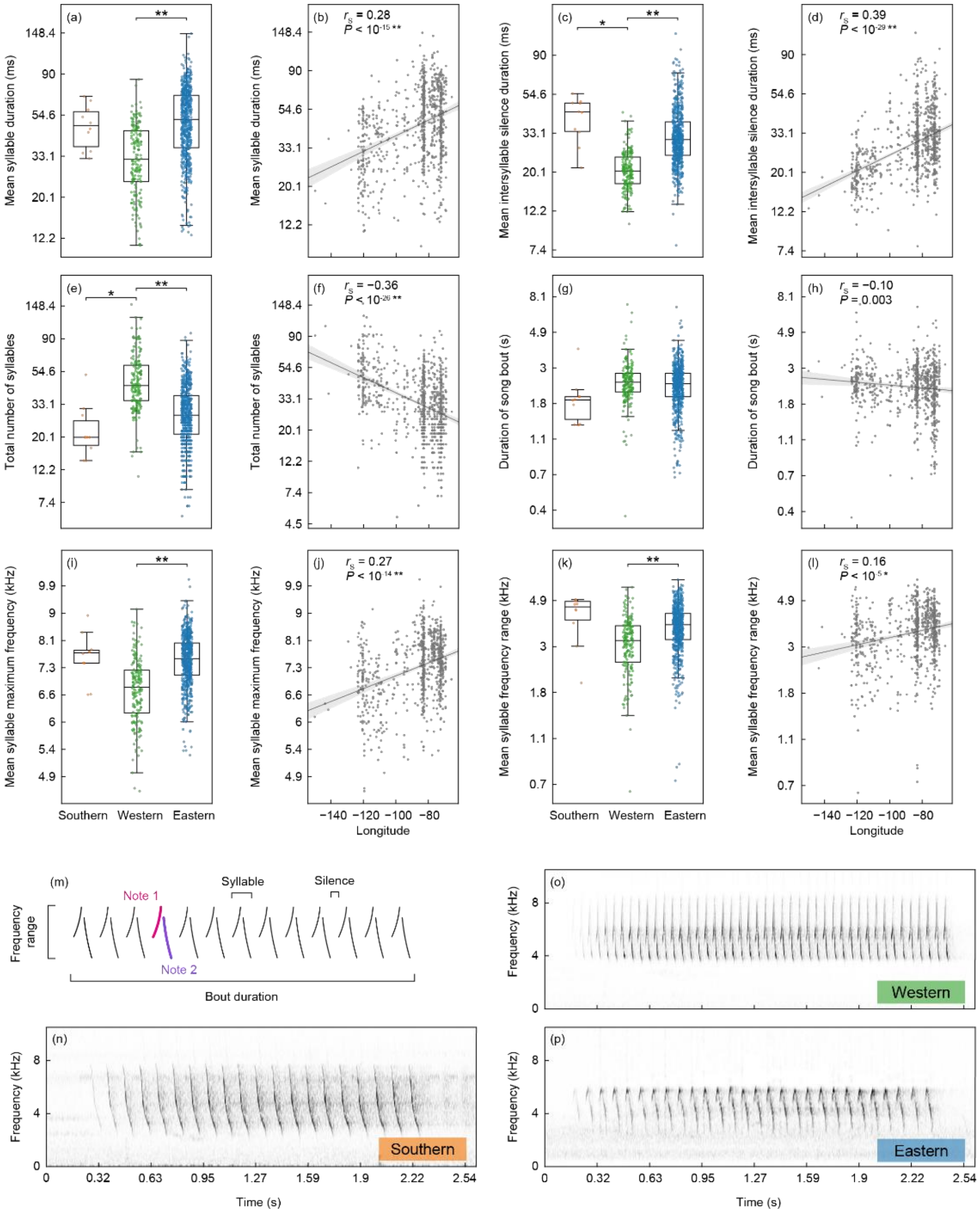

Figure 4.8 Chipping sparrow song structure and regional differences. (A–L) Regional differences in chipping sparrow song structure and frequency. Southern region (Mexico and Guatemala): orange dots; Western U.S./Canada: green dots; Eastern U.S./Canada: blue dots. Box plots show the median, upper and lower quartiles, whiskers (25% quartile − 1.5×IQR, 75% quartile + 1.5×IQR), and all data points including outliers. Significant results are indicated between populations (Wilcoxon rank-sum tests: $*P<10^{-3}$; $**P<10^{-10}$). Scatter plots show all 820 data points, a linear regression model fit, and 95% CI. Spearman's rank correlation coefficients (r_S) are listed above each plot along with the P value ($*P<10^{-3}$; $**P<10^{-10}$). (M) Schematic of a chipping sparrow song. Syllables are the repeated element in the song, and they are composed of notes, units of connected signal (for more examples of syllable types see Fig. 4.11). (N–P) The song of each region (Southern, Western, Eastern, respectively) that was closest to the region's mean for four song features—total number of syllables, mean syllable duration, mean intersyllable silence duration, and duration of song bout. Southern recording: ML527118 contributed to Macaulay Library by Mark Robbins. Western recording: ML72202241 contributed to Macaulay Library by Gregory Budney. Eastern recording: XC313467 contributed to Xeno-canto by Matt Wistrand.

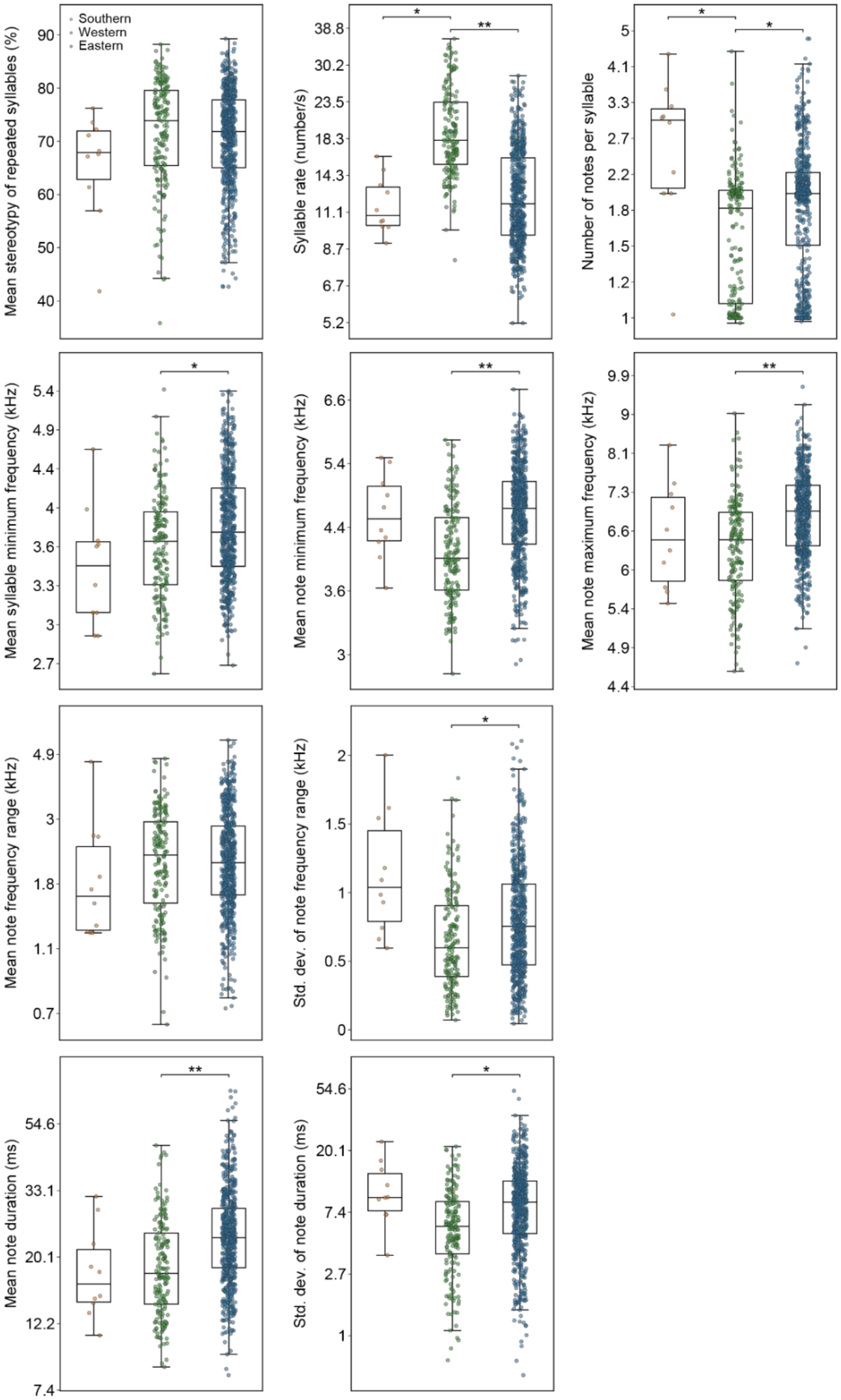

Figure 4.9 Box plots demonstrating regional differences in chipping sparrow song structure and frequency. (Complements Fig. 4.8.) Significant results are indicated between populations (Wilcoxon rank-sum tests: $*P < 1.0 \times 10^{-3}$; $**P < 1.0 \times 10^{-10}$). Color indicates region of the recording data: Southern (orange); Western (green); Eastern (blue). The results for syllable rate support our results (see main text) indicating that birds in the Eastern U.S./Canada sing fewer syllables than birds in the Western U.S./Canada, but they maintain a similar song bout duration.

Table 4.2 Geographic analyses of syllable and song features

Results of Spearman’s rank correlations between song features and latitude and longitude of recordings, Mantel tests quantifying the correlation between song feature distances and geographic distances, and Wilcoxon rank-sum tests between regions for the nine song features that relate to syllables or the entire song.

Song feature	Correlation with latitude (Spearman)		Correlation with longitude (Spearman)		Correlation with geographic distance (Mantel)		Differences between regions (Wilcoxon rank-sum test)		
	r_S	*P* value	r_S	*P* value	*r*	*P* value	E vs W *P* value	E vs S *P* value	W vs S *P* value
Mean intersyllable silence duration	-0.010	0.771	0.387	**$<10^{-29}$**	0.155	**$<10^{-5}$**	**$<10^{-43}$**	0.027	**$<10^{-5}$**
Mean syllable duration	-0.025	0.470	0.279	**$<10^{-15}$**	0.132	**$<10^{-5}$**	**$<10^{-26}$**	0.514	0.003
Mean syllable frequency range	-0.030	0.384	0.161	**$<10^{-5}$**	0.096	**$<10^{-4}$ †**	**$<10^{-13}$**	0.040	0.002
Mean syllable minimum frequency	0.049	0.158	0.126	**$<10^{-3}$ †**	0.025	0.056	**$<10^{-3}$ †**	0.028	0.171
Mean syllable maximum frequency	-0.015	0.672	0.267	**$<10^{-14}$**	0.166	**$<10^{-5}$**	**$<10^{-26}$**	0.747	0.002
Duration of song bout	0.011	0.753	-0.102	0.003	0.003	0.418	0.152	0.011	0.002
Mean stereotypy of repeated syllables	0.068	0.052 †	-0.100	0.004 †	0.023	0.086	0.080	0.103	0.056
Syllable rate	0.024	0.494	-0.359	**$<10^{-25}$**	0.205	**$<10^{-5}$**	**$<10^{-40}$**	0.737	**$<10^{-5}$**
Total number of syllables	0.013	0.711 †	-0.363	**$<10^{-26}$**	0.155	**$<10^{-5}$**	**$<10^{-30}$**	0.047	**$<10^{-4}$**

E: Eastern; W: Western; S: Southern. For all *P* values, bold indicates those less than the corresponding α_{adjusted} *P* value after Bonferroni correction (see Methods). (For song features related to notes, see Table 4.3.)

† Indicates *P* values that changed in significance with downsampling by location (see Tables 4.4–4.6 for minimum and maximum *P* values).

Table 4.3 Geographic analyses of note features

Results of Spearman's rank correlations between song features and latitude and longitude of recordings, Mantel tests quantifying the correlation between song feature distances and geographical distances and Wilcoxon rank-sum tests between regions for the seven song features that relate to notes

Song feature	Correlation with latitude (Spearman)		Correlation with longitude (Spearman)		Correlation with geographic distance (Mantel)		Differences between regions (Wilcoxon rank-sum test)		
	r_S	*P* value	r_S	*P* value	r	*P* value	E vs W *P* value	E vs S *P* value	W vs S *P* value
Mean note duration	0.020	0.569	0.120	**$<10^{-3}$**†	0.053	**0.001**†	**$<10^{-12}$**	0.018	0.743
Mean note frequency range	0.068	0.050	-0.046	0.192†	0.006	0.343	0.738	0.134	0.148
Mean note minimum frequency	-0.015	0.664	0.256	**$<10^{-12}$**	0.100	**$<10^{-5}$**	**$<10^{-18}$**	0.801	0.017
Mean note maximum frequency	0.031	0.373	0.172	**$<10^{-6}$**†	0.090	**$<10^{-5}$**†	**$<10^{-13}$**	0.185	0.546
Number of notes per syllable	-0.058	0.095	0.159	**$<10^{-5}$**	0.048	**0.001**†	**$<10^{-6}$**	0.006	**$<10^{-3}$**†
Standard deviation of note duration	-0.038	0.273†	0.139	**$<10^{-4}$**	0.028	0.057†	**$<10^{-8}$**	0.265	0.005
Standard deviation of note frequency range	-0.018	0.609	0.079	0.025†	0.002	0.436	**$<10^{-4}$**†	0.020	0.001

E: Eastern; W: Western; S: Southern. For all *P* values, bold indicates those less than the corresponding α-adjusted values after Bonferroni correction (see Methods).

†Indicates *P* values that changed in significance with downsampling by location (see Tables 4.4–4.6 for minimum and maximum *P* values).

Table 4.4 Results of Spearman's rank correlations with downsampling

The maximum and minimum *P* values of the Spearman's rank correlations between 16 song features and latitude and longitude of recordings for 1000 iterations of random sampling of recordings

Song features	Latitude		Longitude	
	Max. *P* value	Min. *P* value	Max. *P* value	Min. *P* value
Mean note duration	0.999	0.383	0.021†	**<10^{-6}**
Mean note frequency range	0.286	0.019	0.214	**<10^{-3}†**
Mean note minimum frequency	0.718	0.070	**<10^{-6}**	**<10^{-11}**
Mean note maximum frequency	1.000	0.334	0.048†	**<10^{-4}**
Mean intersyllable silence duration	0.064	0.004	**<10^{-18}**	**<10^{-28}**
Mean syllable duration	0.672	0.111	**<10^{-11}**	**<10^{-20}**
Mean syllable frequency range	0.271	0.034	**<10-3**	**<10^{-6}**
Mean syllable minimum frequency	0.595	0.115	0.472†	0.006†
Mean syllable maximum frequency	0.243	0.029	**<10^{-6}**	**<10^{-10}**
Duration of song bout	0.159	0.006	0.998	0.103
Mean stereotypy of repeated syllables	**<10^{-3}†**	**<10^{-5}†**	0.047	**<10^{-3}†**
Number of notes per syllable	0.258	0.023	**<10^{-3}**	**<10^{-9}**
Syllable rate	0.176	0.012	**<10^{-17}**	**<10^{-27}**
Total number of syllables	0.096	**1.53×10^{-3}†**	**<10^{-12}**	**<10^{-20}**
Standard deviation of note duration	0.225	**<10^{-3}†**	**<10^{-3}**	**<10^{-7}**
Standard deviation of note frequency range	0.449	0.009	0.173	**<10^{-3}†**

Bold indicates $P < 1.56 \times 10^{-3}$.

†Indicates song variables that had significant *P* values before but not after downsampling or vice versa (see Tables 4.2 and 4.3).

Table 4.5 Results of Mantel tests with downsampling

The maximum and minimum *P* values of the Mantel tests quantifying the correlation between song feature distances and geographical distances for 1000 iterations of random sampling of recordings

Song features	Max. *P* value	Min. *P* value
Mean note duration	0.369†	**0.002**
Mean note frequency range	0.789	0.108
Mean note minimum frequency	**0.002**	**$<10^{-4}$**
Mean note maximum frequency	0.275†	**0.002**
Mean intersyllable silence duration	**$<10^{-4}$**	**$<10^{-4}$**
Mean syllable duration	**$<10^{-4}$**	**$<10^{-4}$**
Mean syllable frequency range	0.134†	**$<10^{-4}$**
Mean syllable minimum frequency	0.462	0.011
Mean syllable maximum frequency	**$<10^{-3}$**	**$<10^{-4}$**
Duration of song bout	0.572	0.109
Mean stereotypy of repeated syllables	0.494	0.042
Number of notes per syllable	0.220†	**$<10^{-3}$**
Syllable rate	**$<10^{-4}$**	**$<10^{-4}$**
Total number of syllables	**$<10^{-4}$**	**$<10^{-4}$**
Standard deviation of note duration	0.362	**$<10^{-3}$†**
Standard deviation of note frequency range	0.814	0.060

Bold indicates $P < 3.13 \times 10^{-3}$.

†Indicates song variables that had significant *P* values before but not after downsampling or vice versa (see Tables 4.2 and 4.3).

Table 4.6 Results of Wilcoxon rank-sum tests with downsampling

The maximum and minimum *P* values of the Wilcoxon rank-sum tests between regions for 1000 iterations of random sampling of recordings

Song features	Eastern vs Western		Eastern vs Southern		Western vs	
	Max. *P* value	Min. *P* value	Max. *P* value	Min. *P* value	Max. *P* value	Min. *P* value
Mean note duration	**$<10^{-4}$**	**$<10^{-9}$**	0.192	0.062	1.000	0.705
Mean note frequency range	0.721	0.045	0.943	0.469	0.643	0.316
Mean note minimum frequency	**$<10^{-8}$**	**$<10^{-13}$**	1.000	0.272	0.135	0.019
Mean note maximum frequency	**$<10^{-4}$**	**$<10^{-8}$**	0.785	0.355	0.514	0.170
Mean intersyllable silence duration	**$<10^{-20}$**	**$<10^{-29}$**	0.171	0.062	**$<10^{-4}$**	**$<10^{-4}$**
Mean syllable duration	**$<10^{-13}$**	**$<10^{-18}$**	0.762	0.370	0.015	0.006
Mean syllable frequency range	**$<10^{-5}$**	**$<10^{-10}$**	0.283	0.061	0.021	0.009
Mean syllable minimum frequency	0.125†	**$<10^{-3}$**	0.200	0.042	0.557	0.170
Mean syllable maximum frequency	**$<10^{-11}$**	**$<10^{-16}$**	1.000	0.674	0.015	0.009
Duration of song bout	1.000	0.172	0.078	0.014	0.029	0.010
Mean stereotypy of repeated syllables	0.162	0.004	0.704	0.146	0.260	0.038
Number of notes per syllable	**$<10^{-3}$**	**$<10^{-7}$**	0.154	0.072	0.011†	0.004†
Syllable rate	**$<10^{-20}$**	**$<10^{-24}$**	1.000	0.726	**$<10^{-3}$**	**$<10^{-4}$**
Total number of syllables	**$<10^{-13}$**	**$<10^{-17}$**	0.284	0.076	**$<10^{-3}$**	**$<10^{-3}$**
Standard deviation of note duration	**$<10^{-5}$**	**$<10^{-9}$**	0.986	0.430	0.030	0.011
Standard deviation of note frequency range	0.002†	**$<10^{-5}$**	0.255	0.031	0.011	0.002

Bold indicates $P < 1.0 \times 10^{-3}$.

†Indicates song variables that had significant *P* values before but not after downsampling (see Tables 4.2 and 4.3).

Song features as geographic classifiers

Our Gaussian I Bayes classifier was 82.5% accurate (72.2–83.3% accurate after downsampling) at predicting the region of the recorded song when all 16 song features were used to train the model (**Table 4.7**). Certain features were more accurate predictors than others; when mean intersyllable silence duration, syllable rate, and total number of syllables were used individually to train the model, the classifier was at least 78% accurate (80.5%, 79.7%, and 78.5%, respectively; 75.0–88.0%, 74.1–83.3%, and 69.4–79.6% accurate after downsampling). For all other individual features, classification was greater than 73% accurate (**Table 4.7**). When two features were used in combination to train the model, some pairs were more accurate than any individual feature, whereas other pairs were less accurate. All classifiers trained on a pair of song features were more than 70% accurate, with the most accurate being 84.9% accurate (79.6–88.9% accurate after downsampling) when mean intersyllable silence duration and mean note minimum frequency were paired. When three features were used in combination to train the model, all classifiers were again more than 70% accurate; the most accurate combination was mean intersyllable silence duration, mean note minimum frequency, and mean note duration, with 87.6% accuracy (82.4–92.6% accuracy after downsampling).

Table 4.7 Song features as geographic classifiers

Percentage accuracy of the Gaussian Naive Bayes classifier trained with all 16 song features together or with an individual song feature

Song feature	All data	Downsampled data	
	% Accuracy	Max. % Accuracy	Min. % Accuracy
All 16 song features together	82.47	83.33	72.22
Mean intersyllable silence duration	80.48	87.96	75.00
Syllable rate	79.68	83.33	74.07
Total number of syllables	78.49	79.63	69.44
Mean syllable maximum frequency	76.49	75.00	65.74
Mean note minimum frequency	76.49	77.78	65.74
Mean syllable duration	76.49	75.93	67.59
Mean syllable minimum frequency	74.50	67.59	56.48
Mean note duration	74.50	77.78	62.04
Standard deviation of note frequency range	74.50	66.67	50.00
Number of notes per syllable	74.50	69.44	54.63
Mean note frequency range	74.50	65.74	64.81
Duration of song bout	74.50	67.59	60.19
Mean stereotypy of repeated syllables	74.50	66.67	61.11
Mean syllable frequency range	74.10	73.15	65.74
Mean note maximum frequency	73.71	71.30	64.81
Standard deviation of note duration	73.31	70.37	61.11

The maximum and minimum percentage accuracy for the same song features from 1000 iterations of random sampling of recordings are also provided.

Principal component and Procrustes analyses

Conducting a principal component analysis (PCA) of 16 song features for all 820 songs, we found the first two principal components explained 32.1% (31.2–34.4% after downsampling) and 20.3% (21.2–22.8% after downsampling) of the variance, respectively. When we examined the PC loadings, the song features that were correlated with longitude (**Tables 4.2, 4.3**) were also most heavily weighted in the first principal component even after downsampling by location (**Table 4.8**). When we plotted these first two PCs, we found some regional structure, but the samples from different regions did not form fully separate clusters (**Fig. 4.10**). Using Procrustes analysis, we found a significant association (D=0.883, $P<10^{-5}$) between the first two principal components and the geographic locations of recording sites. With downsampling, there was still a significant association (D_{min}=0.837, D_{max}=0.883, $P<10^{-4}$). By far, the strongest geographic association was between the first principal component and longitude (Pearson correlation: r_{818}=0.42, $P<10^{-35}$; downsampled: $P_{\mathrm{min}}<10^{-25}$, $P_{\mathrm{max}}<10^{-16}$). The first principal component was weakly correlated with latitude (r_{818}=−0.10, P=0.003; downsampled: $P_{\mathrm{min}}<10^{-4}$, P_{max}=0.004). The second principal component was weakly correlated with both longitude (r_{818}=−0.13, $P<10^{-3}$; downsampled: $P_{\mathrm{min}}<10^{-4}$, P_{max}=0.037) and latitude (r_{818}=0.13, $P<10^{-3}$; downsampled: $P_{\mathrm{min}}<10^{-3}$, P_{max}=0.029).

Table 4.8 Results from Principal Component Analysis

The loadings for the first and second principal components when conducing the PCA on all 820 recordings

Song features	All data		Downsampled data			
	PC1	PC2	PC1 Max.	PC1 Min.	PC2 Max.	PC2 Min.
Mean note duration	-0.243	0.281	0.271	-0.268	0.295	-0.268
Mean note frequency range	-0.119	0.511	0.121	-0.113	0.515	-0.507
Mean note minimum frequency	-0.074	-0.295	0.120	-0.103	0.279	-0.311
Mean note maximum frequency	-0.199	0.306	0.185	-0.182	0.370	-0.337
Mean intersyllable silence duration	-0.228	-0.093	0.277	-0.272	0.135	-0.139
Mean syllable duration	-0.383	-0.144	0.399	-0.395	0.167	-0.167
Mean syllable frequency range	-0.346	0.180	0.341	-0.338	0.265	-0.204
Mean syllable minimum frequency	0.170	-0.101	0.195	-0.195	0.104	-0.155
Mean syllable maximum frequency	-0.284	0.147	0.273	-0.267	0.231	-0.191
Duration of song bout	0.040	0.068	0.068	-0.073	0.071	-0.056
Mean stereotypy of repeated syllables	-0.007	0.408	0.038	-0.045	0.420	-0.413
Number of notes per syllable	-0.210	-0.389	0.235	-0.225	0.400	-0.401
Syllable rate	0.384	0.147	0.398	-0.402	0.176	-0.182
Total number of syllables	0.310	0.154	0.337	-0.340	0.176	-0.173
Standard deviation of note duration	-0.307	-0.125	0.341	-0.340	0.129	-0.164
Standard deviation of note frequency range	-0.265	0.042	0.299	-0.297	0.121	-0.083

The maximum and minimum loadings for the first and second principal components from 1000 iterations of random sampling of recordings. Song features that were correlated with longitude (see Tables 4.2 and 4.3) were also most heavily weighted in the first principal component.

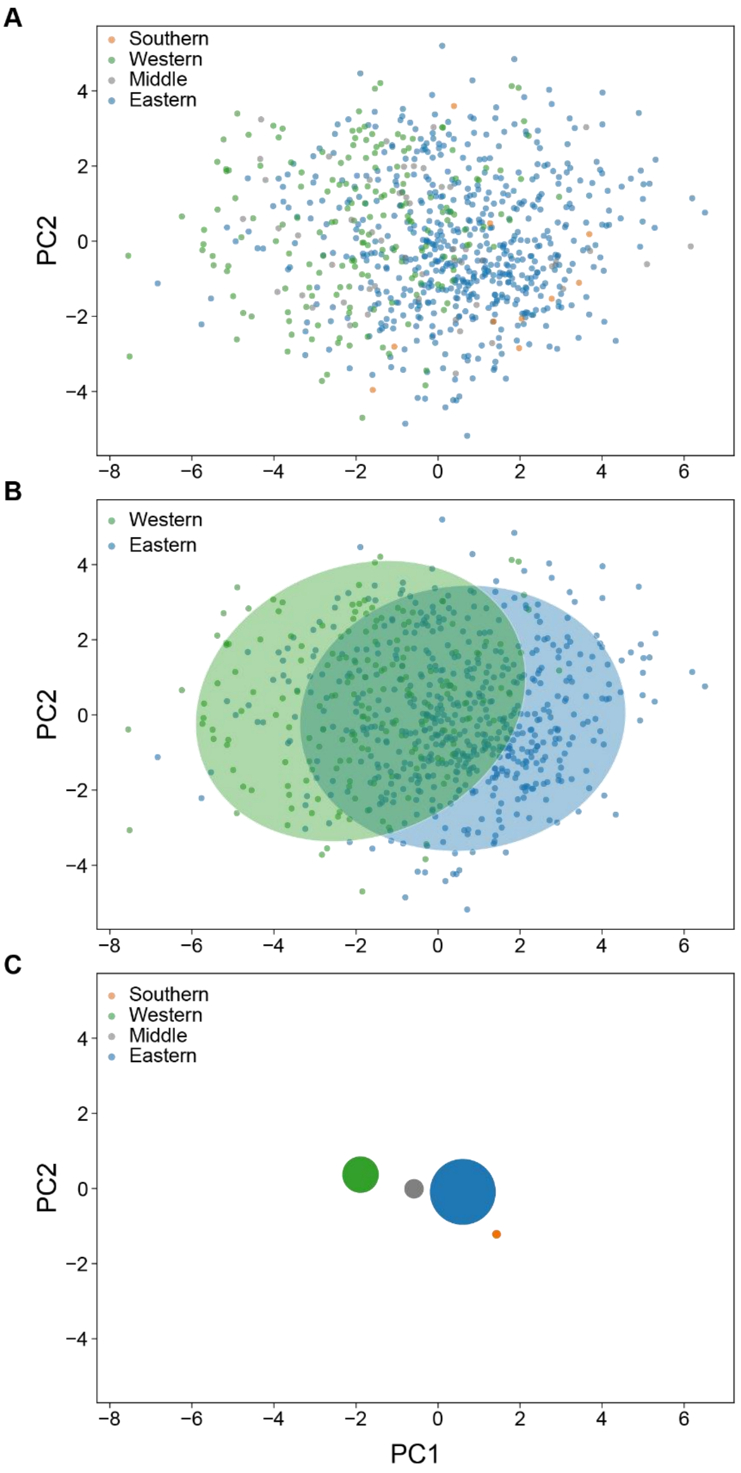

Figure 4.10 Geographical structure in the first and second principal components of the 16 song features. (A) The first and second principal components are plotted against each other for all 820 recordings from all regions. (B) Only data from the Eastern and Western U.S./Canada are plotted. The shaded regions are 2σ covariance ellipses centered at the mean of each region. The dimensions of the ellipses are scaled by the eigenvalues of the covariance matrix with the semi-major axis along the largest eigenvector. (C) A point is centered at the mean of each region with area scaled by the number of recordings.

Syllable types

We categorized syllables from 820 recordings into 112 distinct syllable types (**Fig. 4.11A, Appendix C**). The syllable categories ranked by overall commonality were up-down, buzz, down-up, sweep, double, and complex (**Fig. 4.11**). We found the most common syllable categories in the Eastern U.S./Canada to be up-downs, those in Western U.S./Canada to be buzz, and those in the Southern region to be both up-downs and sweeps (**Fig. 4.11B**).

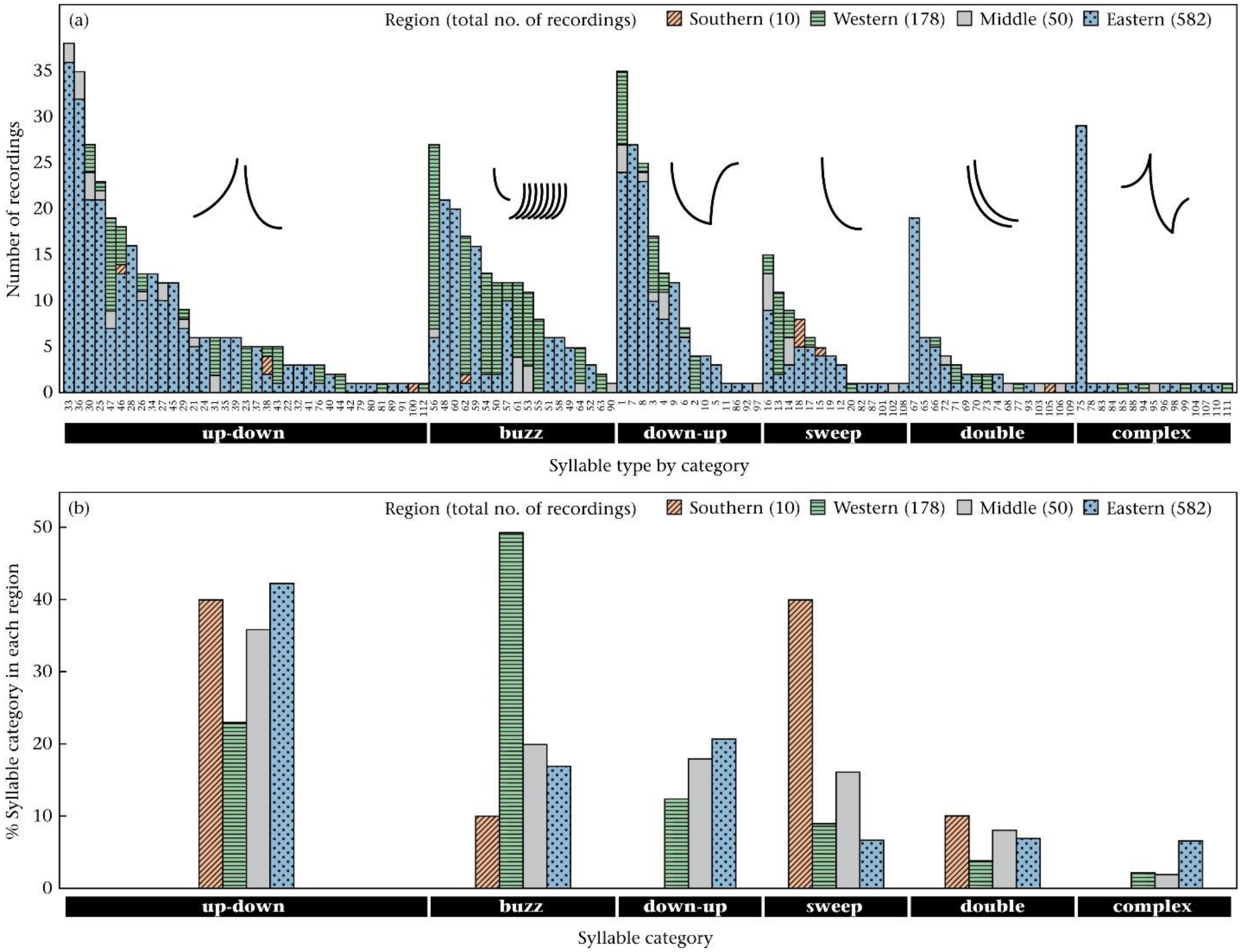

Figure 4.11 The regional distribution of chipping sparrow syllable types. (A) The number of recordings of each of the 112 syllable types (see Appendix C) colored by the region of the recordings. The syllable types are first ordered from most common to least common syllable category (up-down, buzz, down-up, sweep, double, complex) and then ordered within category by the syllable type with the most recordings. An example syllable shape is shown for each syllable category. (B) The percentage of a syllable category in each region, rescaled such that the percentages for each region sum to 100. (Syllable types are not shown.)

Correlations between genetic and geographic distance

We reanalyzed the publicly available sequence data over the same region in which we found song differences (**Fig. 4.3B**)—the United States and Canada. The geographic locations of the COI data, with samples from only Canada and the United States, did not correlate with genetic distances (Mantel test: $r=-0.095$, $P=0.838$; **Table 4.9**). We also tested the U.S./Canada subset of the control region sequences and found no significant relationship between genetic and geographic distance ($r=-0.077$, $P=0.963$).

When the United States and Canadian populations were divided into Eastern and Western regions, there was no significant population genetic structure ($P=0.121$) in the mtDNA CR, with 99.11% of variance from within populations; thus, we cannot reject the null hypothesis that the United States and Canada represent a single interbreeding population of chipping sparrows. This was also true for the COI sequences when divided into Eastern and Western groups ($P=0.983$); in these sequences, there was more variation within Eastern and Western groups than between them (**Table 4.9**).

The haplotype maps support the AMOVA and F_{ST} results, showing that many of the COI and CR samples from the Eastern and Western United States and Canada had identical genetic sequences (**Fig. 4.12**).

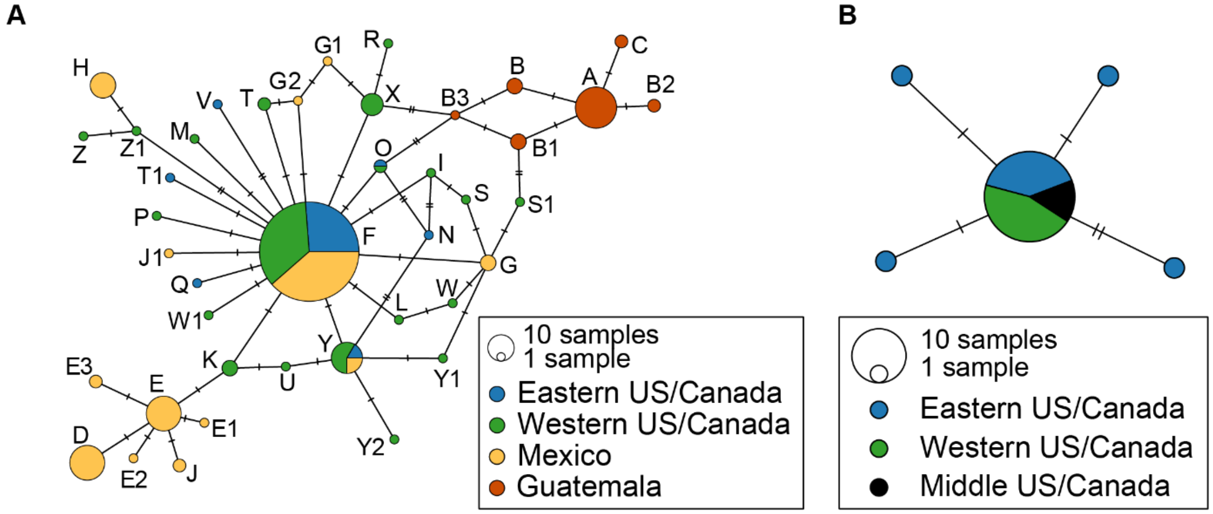

Figure 4.12 Haplotype maps of chipping sparrow genetic sequences. (A) Minimum-spanning haplotype network of chipping sparrow control region sequences. Letters indicate haplotype assignments from Milá et al. (2006). (B) Minimum-spanning haplotype network of chipping sparrow cytochrome oxidase I sequences. (A–B) Each tick mark on the vertices represents one base pair difference between the two connected sequences. Circle size indicates the number of samples with each identical sequence.

Table 4.9 Geographic analyses of genetic data

Results of Mantel test comparing geographic and genetic distance, and results of AMOVA for geographic groupings into Eastern and Western United States/Canada

	Mantel (continuous U.S./Canada)		AMOVA (Eastern vs Western U.S./Canada)				
	r	*P* value	Source of variation	*df*	% Variation	F_{ST}	*P* value
Mitochondrial control region sequences							
	−0.077	0.963	Among populations	1	0.89	0.01	0.121
			Within populations	113	99.11		
Cytochrome oxidase I sequences							
	−0.095	0.838	Among populations	1	−8.83	−0.088	0.983
			Within populations	16	108.83		

DISCUSSION

Oscine songbirds are an ideal model system to test the broad hypothesis that population structure can extend to cultural traits: some species learn song from their fathers and nearby neighbors and then disperse short distances to establish a new territory, which could lead to both short-range and long-range patterns of geographic variation (Baker & Mewaldt, 1978; Lipshutz et al., 2017; MacDougall-Shackleton & MacDougall-Shackleton, 2001; Marler & Tamura, 1964; Nottebohm, 1969; Podos & Warren, 2007). While much research has been conducted on geographic variation in avian vocalizations, most studies use fieldwork that is limited in geographic coverage compared to a species' entire range. Even when multiple field sites are surveyed across a species' range, the sampling between locations is often discontinuous (Chilton et al., 2002; Irwin, 2000; Nicholls et al., 2006; Shizuka et al., 2016; Sosa-López, Mennill, & Navarro-Sigüenza, 2013; Wilkins et al., 2018). This method of data collection has proven useful for establishing and comparing short-range patterns in which the geographic variation has clear boundaries between populations, ultimately favoring the study of dialects. We believe the abundance of well-distributed citizen-science contributions to libraries of natural sounds provides a unique opportunity to study long-range geographic variation, particularly in populations that appear to have no clear differences within and between discrete sites (**Fig. 4.1**).

Here, we present the largest analysis of chipping sparrow song recordings to date. We leverage large, publicly available data sets of natural sounds along with recordings from past field studies (820 recordings in total) to examine song variation across the full range of the chipping sparrow (**Fig. 4.2, Fig. 4.3A**), a songbird that appears to have random song variation at a local scale (Liu & Kroodsma, 2006).

By quantifying and analyzing song features across a relatively even geographical distribution of recordings, we observed a broad pattern of geographic song differentiation across the species' range previously unnoticed by more localized studies (Borror, 1959). We found strong differences in song across longitudes in the U.S./Canada but minimal differences across latitudes (**Figs. 4.6–4.9, Tables 4.2, 4.3**). We note that the chipping sparrow is sedentary in the southernmost subset of its range (Middleton, 1998; Milá et al., 2006); since we had few song recordings from Mexico and Guatemala, we focused our analysis on the United States and Canada, where the chipping sparrow is seasonally migratory (**Fig. 4.2, Fig. 4.3A**). Across our sample in the U.S. and Canada, Western birds produced bouts of similar length to Eastern birds (**Fig. 4.8G–**

H). However, on average, the songs of the Western birds contained more syllables (**Fig. 4.8E–F**) that were shorter (**Fig. 4.8A–B**) and sung at a faster pace (**Fig. 4.8C–D**); these differences are visually apparent between average songs from these regions (**Fig. 4.8O–P**). The pitch of chipping sparrow songs also correlated with longitude, with most frequency measures being higher in the Eastern recordings (**Fig. 4.8I–L**). It is not surprising that our findings differ from those of Borror's (1959) study, which only included geographic comparisons between songs of similar pattern, reducing the sample to eight songs from Maine and Ohio, both classified as Eastern in our analysis. Furthermore, we classified the set of chipping sparrow songs into unique syllable types and examined the prevalence of different syllable types over the species' geographic range. We found that the syllable types could be grouped into six syllable categories, all of which were represented in both Eastern and Western U.S./Canada; however, certain syllable categories were more common in different regions (**Fig. 4.11**). For example, the most common syllable category in the Eastern U.S./Canada was up-down and the most common syllable category in the Western U.S./Canada was buzz.

Our song results are consistent with two possible scenarios: either (1) the song characteristics of the two putative chipping sparrow subspecies are distinct, with *S. p. arizonae* performing syllables at a faster pace and lower frequency and *S. p. passerina* performing syllables at a slower pace and higher frequency, or (2) there is a clinal gradient in several song features, with gradual song changes from east to west (**Fig. 4.8**). These two possibilities would be distinguishable with more recordings from the middle of the United States and Canada, and we encourage citizen scientists in those areas to contribute song recordings to public databases. Nevertheless, we can reject the null hypothesis that chipping sparrow songs are not differentiated across their migratory range.

Our finding that chipping sparrow songs are differentiated by both syllable rate and mean frequency range follows the predictions of the song-performance literature: physiological constraints suggest a trade-off between repetition rate and frequency bandwidth across numerous species (Ballentine, 2004; Podos, 1996, 1997), such that it is possible for a syllable to sweep a larger frequency space if the syllable is repeated more slowly. This performance trade-off has even been shown to occur in chipping sparrows (Goodwin & Podos, 2014). Thus, our results hint that Eastern and Western chipping sparrows are occupying different portions of the species' song-performance space: Eastern chipping sparrows navigate the song-performance trade-off by generally having a slower syllable rate (fewer, longer syllables) and a larger frequency range, whereas Western chipping sparrows distinguish themselves with a faster syllable rate but a smaller frequency range.

Furthermore, there are differences in song that have been associated with differences in morphology—birds with larger beaks tend to have decreased trill speeds and smaller frequency ranges (Huber & Podos, 2006; Podos, 1997, 2001). We note that the two weakly demarcated subspecies of chipping sparrows in the United States and Canada are genetically indistinguishable with available data (Clements et al., 2019; Middleton, 1998; Zink & Dittmann, 1993). The subspecies *S. p. arizonae* (which roughly corresponds to our Western recording category) are said to be larger than *S. p. passerina* (which roughly corresponds to our Eastern recording category) (Floyd, 2008). If we were to assume Western chipping sparrows also have larger beaks, we would expect to see a decrease in their frequency range and trill speeds compared to Eastern chipping sparrows; however, the Western population has decreased frequency range and increased trill speeds (shorter syllables and shorter intersyllable silences). This raises the interesting possibility that Western chipping sparrows may have larger bodies but similarly sized (or smaller) beaks than Eastern chipping sparrows, warranting additional investigation. Alternatively, Eastern chipping sparrows could be singing slower than the limits of their performance capabilities.

Overall, our results suggest that longitude is a salient factor when studying the cultural changes in chipping sparrow songs. We note, however, that this analysis does not have the resolution to test which factors may have driven these changes, such as whether these song differences can be attributed to stochastic cultural drift, whether habitat and body size factors differ systematically between these two populations, or whether sexual selection pressures differ, favoring fast-paced and lower-frequency songs in the west and slower, higher-frequency songs in the east. A first step to determining which factors lead to song divergence would be to test chipping sparrow responses to playbacks with characteristics of both Eastern and Western songs. For example, if individuals respond more strongly to their own regional song (or songs that have been modified to have regional song characteristics, such as syllable rate or frequency) than to songs of another region, it would suggest that individuals can discriminate between songs based on these regionally varying properties, and that behavioral differences may play an active role in maintaining spatial patterns (Derryberry, 2011; Martens, 1996; Searcy, Nowicki, & Hughes, 1997). This would also aid in determining whether there are discrete boundaries in song preference between the putative subspecies or whether there is a gradient in song preference across the country.

We attempt to contextualize our results by evaluating population-level song structure alongside genetic variation to best address evolutionary patterns in chipping sparrows. If cultural variation is acting as a reproductive isolation mechanism, then genetic differentiation should increase as cultural differentiation increases (Creanza et al., 2015). To test whether our Eastern versus Western patterns in song correspond to similar patterns of genetic variation, we reanalyzed the publicly available genetic data sets, which included mtDNA CR and COI sequences, across longitudes in the United States and Canada. Our results indicate that there is no significant correlation between genetic and geographic distance for samples from the United States and Canada (**Table 4.9**, Mantel test). Conducting an AMOVA further determined that there was no genetic population structure between the Eastern and Western U.S./Canada (**Table 4.9**). Although we observe significant song divergence across the geographic range of the migratory population of chipping sparrows, we do not see corresponding genetic differentiation.

It is important to note that, while mitochondrial DNA has proven useful in many phylogeographic studies (Alvarez, Salter, McCormack, & Milá, 2016; Barreira, Lijtmaer, & Tubaro, 2016; Campagna et al., 2010; Hung, Drovetski, & Zink, 2016; Lait & Hebert, 2018; Licona-Vera & Ornelas, 2017; Lijtmaer, Kerr, Barreira, Hebert, & Tubaro, 2011; Stoeckle & Kerr, 2012; Valentini, Pompanon, & Taberlet, 2009; Williford, Deyoung, Honeycutt, Brennan, & Hernández, 2016), mtDNA is not perfectly suited to evaluating geographic structure in recently isolated or partially connected populations, such as in intraspecies studies (Balloux & Lugon-Moulin, 2002; Hung et al., 2016). Thus, since the chipping sparrow population continuously spans North and Central America, it would be best to use genome sequences to provide greater resolution. However, since there are only two nuclear DNA sequences (GenBank accession FJ376498 and KJ910331) and one sequenced genome (Zhang et al., 2015) in the public repositories for chipping sparrows, we used the numerous previously collected mtDNA CR and COI sequences to contextualize our results with a call for future studies to collect and analyze nuclear DNA. Therefore, the genetic context in which we try to evaluate the cultural evolution of chipping sparrow song is not conclusive but does suggest that either the population diverged too recently to detect genetic change, or it is a panmictic population. Another possible caveat of using mitochondrial versus nuclear DNA is that it is maternally inherited, whereas song is passed along through the paternal line in chipping sparrows. Thus, if one sex is more philopatric than the other, this could cause differences in the population structure seen in genes versus song. Along with nuclear DNA collection, we suggest that studies of migratory patterns would help to clarify the lack of genetic variation in the migratory population.

If our result, that there is little mitochondrial genetic differentiation across migratory chipping sparrows, is supported by genome-scale data, it raises the question of what process is taking place to maintain a genetically well-mixed population with cultural population structure. Several patterns of seasonal migration and site fidelity could lead to our observed results. For example, if individuals settled far from their previous territory with each seasonal migration event, and could not alter their song, this would lead to both a genetically and culturally well-mixed population. However, from previous studies of chipping sparrow song development, we know that it is possible for chipping sparrows to change their song during their first breeding season but not during subsequent breeding seasons (Liu & Kroodsma, 1999; Liu & Nottebohm, 2007). This song modification after the first migration enables an individual male to adjust his song to be similar to the song of nearby conspecifics (Liu & Kroodsma, 2006), culturally matching his local area even if his genetic relatives are far away. Thus, if a chipping sparrow male migrates to a completely new location in his first spring, modifies his song, and then returns to that general area in subsequent seasonal migrations, it would still be possible for cultural variation to become structured across large geographic scales while the genetic population becomes well mixed. We found the migratory population of chipping sparrows in U.S./Canada to be culturally structured but genetically well mixed in mitochondrial variation, which is consistent with a pattern in which long-distance seasonal migration is less faithful to natal location in the first migration than it is to a subsequent migration location once the bird has established an adult territory. We note, though, that we found very little mitochondrial genetic variation in chipping sparrows in the U.S./Canada, with numerous samples across this range having an identical haplotype. These low levels of genetic variation are consistent with a very recent divergence of Eastern and Western populations, since cultural differences can accumulate more quickly than genetic differentiation. Furthermore, since there are minimal studies on chipping sparrow migration and dispersal (Liu & Kroodsma, 2006), additional studies using Argos satellite tracking or geolocators (e.g. in other sparrows; Cormier, Humple, Gardali, & Seavy, 2016; Fraser et al., 2018; Ross, Bridge, Rozmarynowycz, & Bingman, 2014; Seavy, Humple, Cormier, & Gardali, 2012) could determine the likelihood that chipping sparrows migrate to entirely new locations and whether the probability of these events differs with the age of the bird.

Even though chipping sparrows have been observed to match a neighbor’s syllable type after their first migration (Liu & Kroodsma, 2006), we found extensive local syllable-type diversity in both Eastern and Western regions. If territorial adult males fail to successfully breed on a certain territory, they are likely to abandon that territory and disperse a few miles or more to resettle in a new territory (Liu & Kroodsma, 2006), potentially playing an important role in supporting local song diversity. Because their song will not change after the first breeding season, these males, after abandoning their previous territory and settling a new territory, will be less likely to share a syllable type with their new neighbors. However, this dispersal event is likely to occur within a few miles, whereas the potential change in territory location during the first seasonal migration could be much greater; therefore, small changes in territory location would increase local diversity of syllable types but would not disrupt the regional similarity in song features such as syllable durations and frequencies.

Overall, we demonstrate that long-range geographic patterns can be uncovered using analyses of spatially well-distributed citizen-science recordings, even in species with high levels of short-range song variability and no discernible genetic differentiation. Furthermore, our results suggest a complex landscape of cultural variation in chipping sparrows: local syllable diversity and long-range cultural differentiation with no accompanying mitochondrial genetic population structure. Taken together, our work motivates the need for more complete genetic studies of chipping sparrows to determine whether the Eastern and Western populations, which exhibit song differences, are also showing early stages of genetic divergence. This would provide support for the subspecies classifications. Additionally, our results suggest that the chipping sparrow is an ideal species for tracking migratory behavior and studying the role of dispersal in shaping geographic patterns of song. Lastly, we encourage the use of citizen-science data to assess song variation, particularly in species that have been the subject of multiple field studies, to extend and situate the results within the species’ larger geographic range.

MANUSCRIPT DATA AVAILABILITY AND ACKNOWLEDGMENTS

The accession numbers for genetic sequences used are as follows: AY862812-AY862852, AY666225, AY666348, DQ433193, DQ434762-DQ434766, EU525508-EU525509, HM033820-HM033829, and JN850724. All scripts and input files, including the metadata with recording latitudes and longitudes and the 16 song features (all log-transformed except mean stereotypy of repeated syllables and the standard deviation of note frequency range), for statistical analyses can be found at http://github.com/CreanzaLab/ChippingSparrows. Documentation and code for Chipper can be found at http://github.com/CreanzaLab/chipper. For the catalog numbers, databases, recordists, URLs, and licenses for the 820 song files, see **Appendix B**.

We are grateful to Jill Soha for assistance with Borror Laboratory files, Desmond Fugar for initial testing of the song data, and Fernando Nottebohm for advice on the preliminary analysis.

CHAPTER 5

DETECTING CULTURAL EVOLUTION IN A SONGBIRD SPECIES USING CITIZEN-SCIENCE DATA AND COMPUTATIONAL MODELING

INTRODUCTION

Song plays many important roles in avian biology—territory defense, species identification, and mate attraction (Catchpole & Slater, 2003). Thus, the signals produced by an individual bird are critical to its survival and success; moreover, the way in which these signals are transmitted and maintained is vital to the entire species. Indeed, a subset of passerines, the oscines, transmit their species-specific signal by a process of song learning. Researchers have been interested in understanding the social learning of song as it parallels human cultural transmission, in which long-lasting traditions arise yet variation is maintained (Aplin, 2016; Hoppitt & Laland, 2013; Kandler & Laland, 2009; Tomasello et al., 1993; Whiten, 2017). By studying song learning, we can begin to understand which aspects of human learning and cultural evolution are shared with other animals and which properties are unique.

Many studies have been conducted in the laboratory and in the field to better understand the social learning taking place in avian populations: researchers examine the frequency of songs in a population, the similarity between learned song and tutor song, error rate in song matching, invention of new song, among other factors (Cardoso & Atwell, 2016; Marler & Peters, 1982; Marler & Tamura, 1962; Slater, 1986; Thorpe, 1958). Others have taken creative approaches to expand the use of field-site data to ask evolutionary questions. For example, some studies have studied cultural evolution over time using recordings taken over multiple decades (Ju et al., 2019; Williams et al., 2013), even confirming that temporal changes in song are salient to the current population by playing historical recordings to modern birds (Derryberry, 2007). Other researchers are taking a more theoretical approach to the cultural evolution of song by developing individual-based or agent-based simulations to compare to empirical data (Crozier, 2010; Lachlan et al., 2018). There are many benefits of using field study recordings, including the ability to collect enough songs to ensure coverage of song repertoire, observation of song tutors, and sampling the entire local site population. However, field studies generally remain limited in both the time period and the geographic range they cover.

We propose the utilization of citizen-science data as a time- and cost-effective supplement to field studies to study change in species' song over time. Specifically, we hypothesize that citizen-science data with a wider spatiotemporal coverage can be advantageous in gaining an understanding of the process in which song is being learned within a species. As song learning allows for mutation through copy errors similar to genetic mutation, we employ methods of genetic evolution, examining the frequency of unique songs (or syllables) as well as the lifetimes of such syllable types in the chipping sparrow population. We then compare our empirical results to those of a computational model that we developed to mimic the spread of syllables in a population under three types of learning or tutor selection—neutral, conformity, and directional.

METHODS

Categorization of chipping sparrow syllables into types

For this analysis, we used the same citizen-science recordings gathered in Chapter 4 as well as the syllable types and categories we found for those songs. Here we describe the method of categorization in brief: All songs were viewed in Audacity on the same frequency and time scale. A single syllable was then taken to represent an individual chipping sparrow song. Using the 820 syllables, we manually classified the 820 songs into 112 chipping sparrow syllable types. We further grouped these syllable types into similar categories based on the syllable shape: up-down (up-slur followed by down-slur), down-up (down-slur followed by up-slur), sweep (single up-slur or down-slur), complex (more than two slurs), doubles (a slur with multiple frequencies), and buzz (syllable containing some buzzy phrase).

Calculating lifespan of chipping sparrow syllable types

The lifespan of a syllable type was calculated using the earliest and latest year of the recordings that contained the syllable type. There were four recordings and thus four syllable types that did not have a corresponding year; these were excluded from this analysis. Using the lifespan, we then divided the syllables to compare features between songs that contained short-lived (lifespan=1 year) versus long-lived (lifespan≥50 years) syllable types. We performed Wilcoxon rank-sum tests on short- versus long-lived syllables for the 16 song features. For stringency, we conducted a Bonferroni correction for multiple hypothesis testing by dividing the P value threshold for significance (α=0.05) by the number of tests. Overall we performed one test on 16 song features, so the threshold for significance was lowered to $\alpha_{\mathrm{adjusted}}=3.13\times10^{-3}$. We did not control for region in the lifespan analysis.

Model design

The entirety of the model was implemented in Python 3.7 and uses the following primary packages: NumPy v1.16.3, Matplotlib v3.0.3, Pandas v0.24.2, and SciPy v1.2.1. For details, please refer to https://github.com/CreanzaLab/chippies_cultural_transmission_model. A population of birds is initialized as a 500x500 matrix of syllable types. The syllable types are represented as integers and are randomly assigned from a discrete uniform distribution (function ‘random.randint’, NumPy module). A second matrix of the same size is initialized with syllable rates randomly sampled from a truncated normal distribution (function ‘stats.truncnorm.rvs’, SciPy module). This second matrix only informs learning in the model with directional selection. Each timestep, a fixed percentage of the birds are selected for death. We set this mortality rate to 40% based on similar avian models (Lachlan et al., 2018; Slater, 1986). For every dead bird, a new bird replaces it with a new syllable learned from the neighbors present at the beginning of the timestep (at a distance of 1 in the two-dimensional matrix—up to eight birds—by default). For dead birds at the edge of the matrix, the number of neighbors is fewer as the matrix does not wrap in order to maintain a spatial arrangement representative of natural territories. All dead birds are replaced at the same time; thus, birds that die in the current timestep could still influence learning. This is to represent the possibility that if nearby birds die, they would most likely not have died simultaneously in nature. Once all learned syllables are determined (see next sections for the three learning models), the new syllable types replace the matrix elements of the dead birds.

Model implementation of neutral tutor selection

During each timestep, the birds that died must be replaced by a juvenile bird at each location, which is represented in the model by assigning a new syllable type to the now open position in the matrix. For neutral tutor selection, the syllable type that is learned by this juvenile is randomly chosen (function ‘random.choice’, NumPy module) from the eight neighbors (or fewer for edge cases). However, we include error in learning, representing the likelihood of the new bird producing a completely novel syllable. This was implemented by choosing a random float in the half open interval [0.0, 1.0) (function ‘random.random’, NumPy module); if the float was less than the decimal error rate, the syllable was not correctly learned resulting in the invention of a new syllable type.

Model implementation of conformity

Conformity is implemented in the learning step of the model. Our implementation mimics conformity biased cultural transmission in which the probability of choosing to copy a common cultural phenotype exceeds the probability of choosing that phenotype in a frequency-dependent manner: First, the syllable types of the neighbors and the counts of all unique syllable types are determined. Second, the probability of randomly selecting a syllable type is then weighted by the square of their frequency of occurrence. The power used to scale the probabilities—in this case 2—can be adjusted in the model. The error rate for learning is applied in the same manner as in the neutral tutor selection model.

Model implementation of directional tutor selection

For directional tutor selection, a continuous variable representing the rate of syllable production, rather than the syllable type, became the basis of learning. This mimics a type of directional selection hypothesized to occur in chipping sparrows, in which the preferred song is the most difficult one to produce. The learning bird selects a tutor—the neighbor with the fastest syllable rate—from whom to copy; the learning bird attempts to copy both the syllable type and the syllable rate of this tutor. The learning error for syllable type functions identically to the neutral and conformity models. The learning error for syllable rate was weighted such that it was easier to perform worse rather than better than the tutor; specifically, a random number was chosen from a uniform distribution over the half-open interval [-2, 0.25) which was then added to the tutor’s syllable rate. The syllable rate was limited to the interval between one to 40 syllables per second, as these are the naturally occurring rates of syllable production (**Chapter 4**). Therefore, the learned song is sung at a rate similar to that of the tutor, and either has the same, or a new, syllable type.

Sampling the model bird population

The method of data collection from the model population was chosen to replicate the sampling that occurs when songs are recorded by citizen-scientists. Thus the model was built such that the sampling frequency of birds, or number of birds randomly sampled from the population, is set by the user. More specifically, in this chapter, we have sampled the population such that the number of birds sampled per timestep are equal to the number of real recordings we have from each year. Our data spans 1950-2017 with some years having no recordings; thus some number of birds (possibly 0) were randomly selected from the population for the last 68 iterations of the model.

RESULTS

Syllable types and cultural analysis

We categorized syllables from 820 recordings into 112 distinct syllable types (**Appendix C**). Examining the lifespans of the syllable types and the number of recordings of that syllable type (**Fig. 5.1**) demonstrates that syllable types that continue to exist for much longer than the lifetime of a chipping sparrow are those that are most commonly observed, whereas the syllables that exist briefly are also rare. In other words, we did not observe any syllables that were very common but existed for a short period of time. When we classify syllable types as short-lived (lifespan=1 year) or long-lived (lifespan≥50 years), we find songs with a long-lived syllable type have significantly more syllables per bout ($P<6.98\times10^{-4}$) (**Fig. 5.2B**). It seems these long-lived syllable types also tend to be shorter, although this finding was not significant after Bonferroni correction (**Fig. 5.2A**, **Table 5.1**). Additionally, buzz syllables tend to be long-lived, whereas double or complex syllables tend to be short-lived, with up-down, down-up, and sweep syllables being prominent in both lifespan groups (**Fig. 5.2C)**.

Table 5.1 Results of the Wilcoxon rank-sum tests between short- and long-lived syllable types.

Song Features	Short- vs Long-Lived *P*-value
Mean note duration	0.568
Mean note frequency range	0.056
Mean note minimum frequency	0.166
Mean note maximum frequency	0.059
Mean intersyllable silence duration	0.707
Mean syllable duration	0.004
Mean syllable frequency range	0.516
Mean syllable minimum frequency	0.878
Mean syllable maximum frequency	0.332
Duration of song bout	0.003
Mean stereotypy of repeated syllables	0.453
Number of notes per syllable	0.010
Syllable rate	0.008
Total number of syllables	**0.001**
Standard deviation of note duration	0.698
Standard deviation of note frequency range	0.158

Bold indicates $P < 3.13 \times 10^{-3}$.

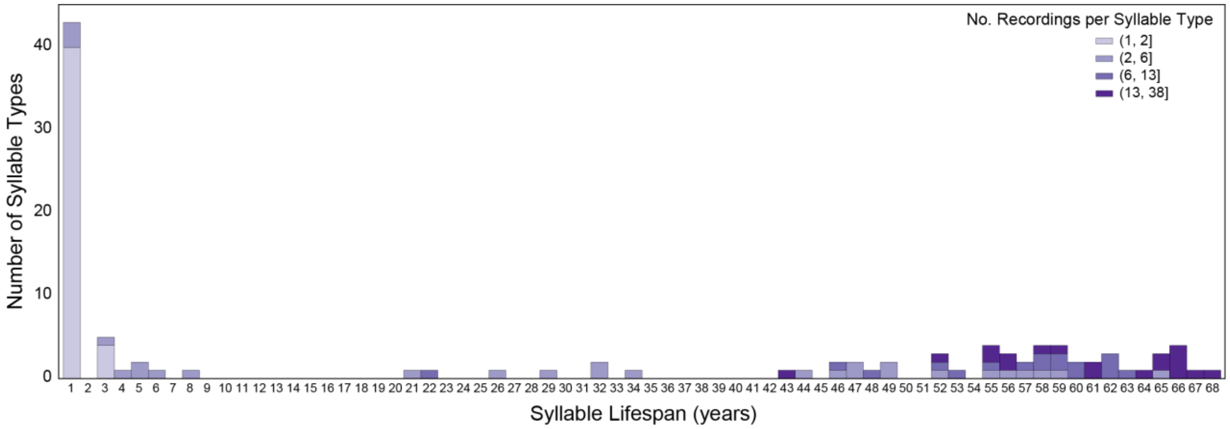

Figure 5.1 Temporal distribution of chipping sparrow syllable types. The number of syllable types versus syllable lifespan. Each syllable type is also shaded by the total number of recordings of that syllable type.

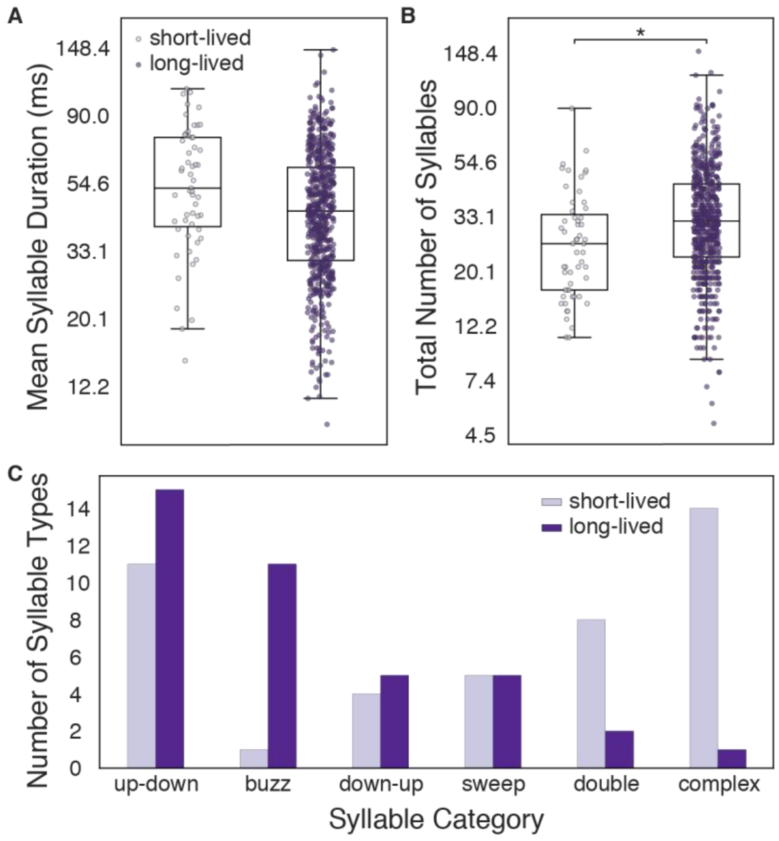

Figure 5.2 Syllable categories and properties of short- and long-lived chipping sparrow syllable types. Songs with long-lived (dark-purple) syllable types have significantly shorter syllables (A) and more syllables per bout (B) than those with short-lived syllable types (light purple). Significant results are indicated between populations (* denotes $p<3.13\times10^{-3}$ from Wilcoxon rank-sum tests). (C) The number of short- or long-lived syllable types in each syllable category.

Model results

We ran the preliminary model for each of the three learning systems with multiple error rates (or invention rates) spanning 0.001% to 1.0%. We then borrowed techniques from population genetics (particularly the site frequency spectrum) (Nielsen, 2005; Pepperell et al., 2013; Zhu & Bustamante, 2005) and created "syllable frequency spectra"—the frequency of songs of various syllable types in the sample—to compare our model results and empirical data (**Fig. 5.3**). Qualitatively, none of the learning schemes appear to perfectly replicate our results from citizen-science data. However, the model with directional selection of tutors appears to most closely match our empirical data, with a large number of singletons and a long-tailed distribution.

Additionally, we compare the frequency of lifetimes of various syllable types in the sample for each model and learning error rate (**Fig. 5.4**). While long-lived syllable types arise in all three song-learning models, only directional selection has an enrichment for these syllable types reflecting what is observed in our citizen-science data sample (**Fig. 5.4**; yellow and purple respectively).

To better estimate the learning error rate, we ran additional simulations with more error rates. Qualitatively, we found the copy error rate of 0.05% seems to most resemble the chipping sparrow population (**Fig. 5.5**). To quantify which learning schema at this learning error rate best fits our empirical data, we calculated the percent overlap of each histogram with the histogram of the citizen-science data (**Table 5.2**).

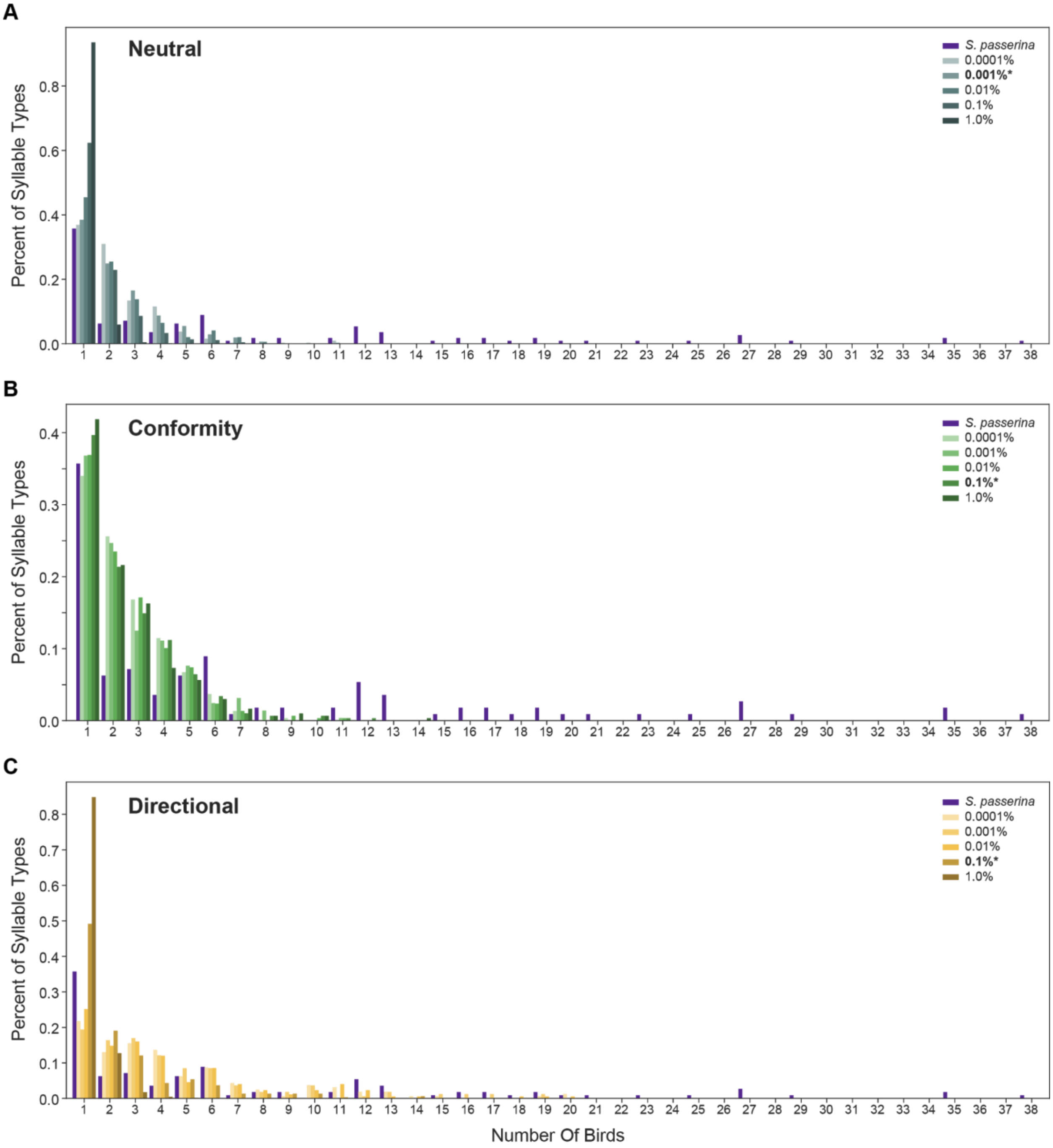

Figure 5.3 Comparison of model and empirical syllable frequency spectra. The percent of syllable types versus the frequency at which the syllable types are sung in the population (e.g. the number of birds sampled with the syllable type) for the three models of song learning: (A) neutral tutor selection, (B) conformity bias, and (C) directional selection. In each panel, the histogram from citizen-science data is also provided (purple). (An asterisk * indicates, for each model type, the simulation with the learning error rate that most resembling the empirical data based on percent overlap between the histograms.) Note, the *y*-axes differ between panels.

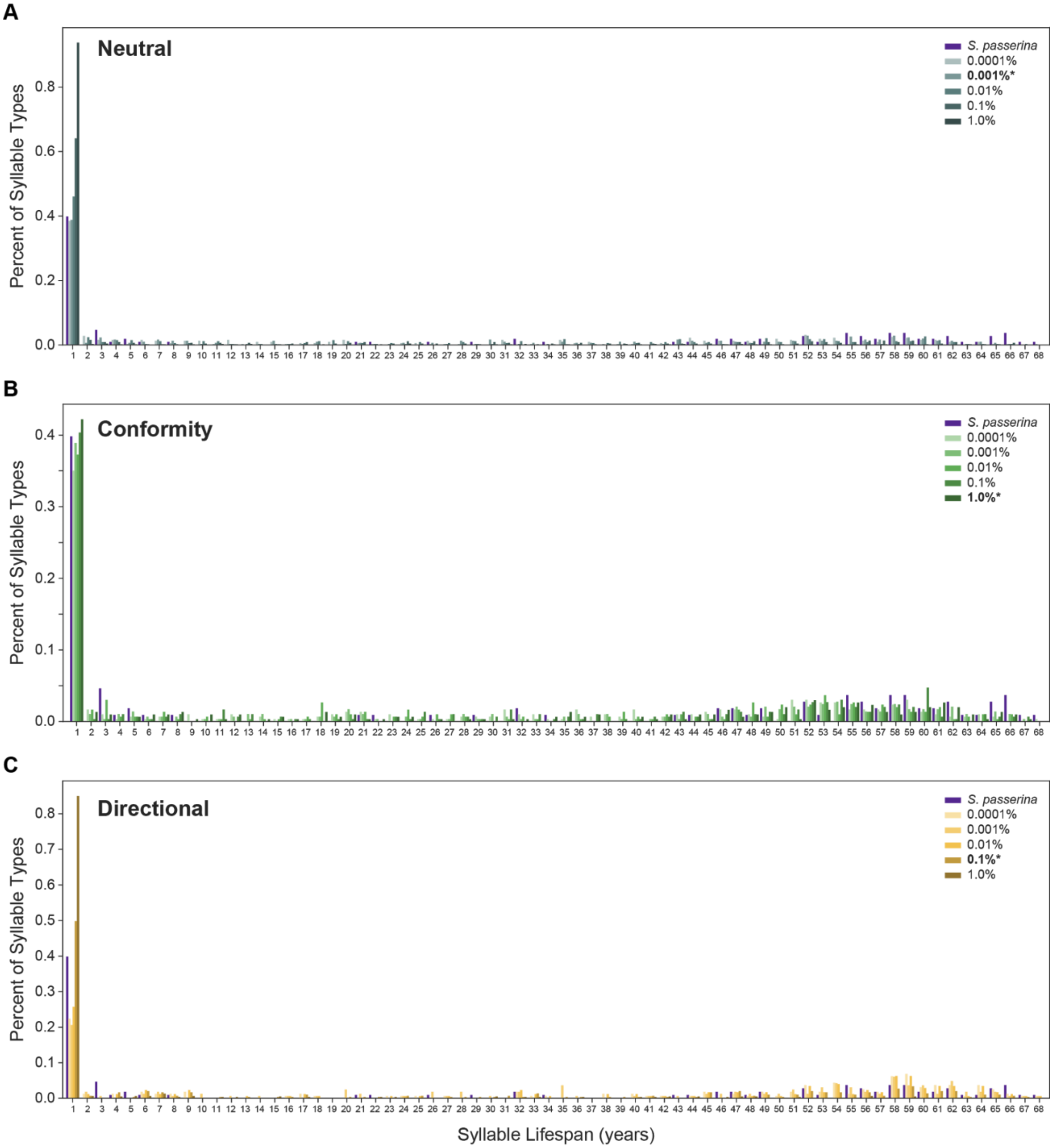

Figure 5.4 Comparison of model and empirical syllable lifespans. The percent of syllable types versus the syllable lifespans (e.g. the last year − first year in which the syllable type was sampled) for the three models of song learning: (A) neutral tutor selection, (B) conformity bias, and (C) directional selection. In each panel, the histogram from citizen-science data is also provided (purple). (An asterisk * indicates, for each model type, the simulation with the learning error rate that most resembling the empirical data based on percent overlap between the histograms.) Note, the *y*-axes differ between panels.

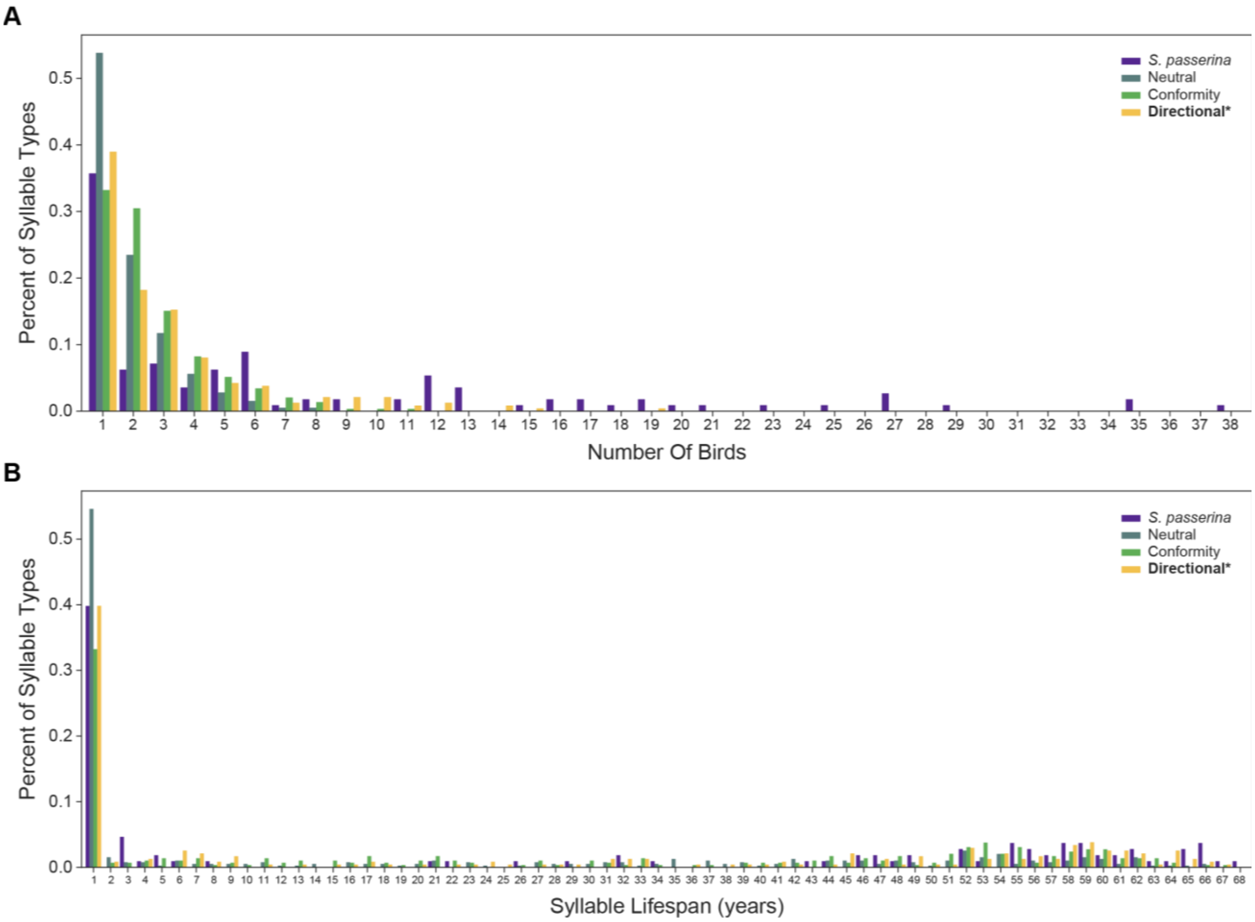

Fig. 5.5 Comparison of model types with 0.05% learning error to empirical data. (A) The percent of syllable types versus the frequency at which the syllable types are sung in the population for the empirical data (purple) and three models of song learning: neutral tutor selection (blue), conformity bias (green), and directional selection (yellow). (B) The percent of syllable types versus the syllable lifespans for the three models of song learning. (* indicates, for each model type, the simulation with the learning schema that most resembling the empirical data based on percent overlap between the histograms.)

Table 5.2 Similarity between chipping sparrow syllable frequency spectra and model results. For the three models of song learning run with a 0.05% learning error, the percent of overlap in syllable frequency spectrum (Fig. 5.5A) and histograms of syllable lifespan (Fig. 5.5B).

Learning Scheme	Percent Overlap	
	Number of Birds	Syllable Lifespan
Neutral	58.0%	63.1%
Conformity	61.7%	67.1%
Directional	68.2%	73.2%

DISCUSSION

Our study shows the utility of citizen science data for measuring cultural change and stability in birdsong. Particularly, citizen-science recordings provide large spatiotemporal coverage of a species' range, providing a data set in which temporal changes can be identified across the entire population. By comparing these rich datasets with cultural evolution models, we can make and evaluate insights into the strategies underlying the social transmission of song

Past studies have examined the diversity in syllables within the chipping sparrow population. For example, Borror classified chipping sparrow syllables into categories and further subdivided the 58 recordings into 28 syllable types, demonstrating great song diversity and few observations of each syllable type (Borror, 1959). In a later analysis, the syllables of 157 chipping sparrows from the Eastern United States were analyzed and placed into around 30 distinct syllable types by eye (Liu, 2001). With 820 songs, we identified 112 syllable types (**Appendix C**). Our results demonstrate that the diversity of chipping sparrow syllable types was not fully sampled in previous studies, and it is likely that other syllable types will be discovered as contributing song recordings to citizen-science databases becomes more widespread, particularly since many syllable types appear to be rare and short-lived.

We found evidence that some broad characteristics were associated with longer syllable lifespans. For example, buzz syllables tended to be long-lived whereas complex syllables tended to be short-lived, and songs with long-lived syllable types had more, shorter syllables. Interestingly, many of these characteristics of long-lived syllables also tend to be characteristic of Western U.S./Canada songs (**Chapter 4**), but when tested, the distributions of longitude coordinates for short- versus long-lived syllables did not differ (Wilcoxon rank-sum test, p=0.992), indicating that syllable types are not longer-lived in the Western U.S./Canada. Together, our results raise an important question for future field and computational studies: can we disentangle whether common, long-lived syllables in a region are well adapted to the local environment (e.g. the syllable is an easier signal to transmit given the foliage density), culturally favored (e.g. the syllable is easier to learn or is often sung by successful males and thus frequently imitated), or under conformity bias (e.g. common syllables are matched more often than expected by random chance when learning song)?

To determine whether the frequency of chipping sparrow syllable types is indicative of neutral evolution or selection, we first compared our results to those of predictions of previously studied neutral processes (genes and chaffinch song). Selectively neutral processes of song learning, such as unbiased learning of a song with some error rate, would predict a relatively simple pattern of syllable prevalence: most syllable types would be sung by only one bird, fewer syllables would be sung by two birds, even fewer by three birds, and so on, until only a small handful of syllables might be sung by many birds (Slater, 1986). Slater observed this distribution of syllables in chaffinches: in a population of 36 chaffinches, most songs were sung by only one bird, but one song was sung by 22 birds. Further, he modeled the song-learning process with a simulation in which newly settled birds learned a random nearby song with some error; this simulation demonstrated that a neutral learning process with a predictable rate of copy-error was sufficient to replicate the observed distribution of chaffinch syllables. A similar pattern is regularly observed in genetic data in the absence of selection pressures: rare genotypes are observed very frequently, and very few genotypes are common (Nielsen, 2005). Thus, for both genotypes and song types, one does not need to invoke selection pressures to explain a pattern in which one or very few types are widespread but most are observed only once. However, we observed a slightly different pattern in chipping sparrow syllables, finding that the distribution of syllable type frequencies has a long tail with numerous common chipping sparrow syllable types (**Fig. 5.5A, purple**). Thus, qualitatively, our results might suggest that the evolutionary pressures on syllable types in chipping sparrows might not be selectively neutral, and certain syllable types or song characteristics may be under positive selection. We note, though, that the frequency distribution predicted to be characteristic of neutral evolution generally includes samples from a single time point, whereas our data is a compilation of many sampling locations over ~70 years. Therefore, we also analyzed chipping sparrow syllable types over time, finding that most rare syllables are short-lived and common syllables are persistent, existing for decades. This distribution of syllable lifespans (**Fig. 5.2C)** also appears contrary to what is expected from the perspective of neutral evolution, in which all syllables have an equal chance of being passed to the next generation. Instead, this appears indicative that a transmission bias could be present in chipping sparrows; Lachlan *et. al.* demonstrates a model of conformity bias in swamp sparrows that leads to a similar distribution as ours in which certain syllables tend to be longer-lived, even predicting that these syllables are maintained for upwards of 500 years (Lachlan et al., 2018).

To determine whether chipping sparrow syllables show evidence of transmission bias—either a directional learning bias or a conformity bias—we developed an agent-based model of cultural transmission of song and compared the results of three different learning strategy to the patterns found in our empirical data. Often, models have been constructed to represent a small local community of birds and is then compared to data from a local fieldsite (Robinson & Creanza, 2020). To compare the wide-ranging spatiotemporal dataset collected by citizen scientists, we developed a larger, spatially explicit model of song evolution, and compared our empirical data to simulated samples from this model. Here we present our preliminary results from single runs of each model type at various learning error rates; note, our next steps include running each of these a number of times to create consensus distributions. However, we can still conclude from our preliminary results that chipping sparrows are most likely learning song with a directional bias in tutor choice and a low copy-error rate (or invention rate) of 0.05%.

Here we discuss the most conspicuous qualitative differences between our empirical data and our best fit model (positive directional selection on song rate, with a 0.05% learning error). First, the range of song rates (~36.5–40 syllables per second) observed in the model population is much lower than that of the natural chipping sparrow population (~5–38 syllables per second). This brings into question whether syllable rate is indeed under selection for song learning. (See below for further discussion on this difference.) Second, the number of unique syllable types (236) in the sample population from the model is close to double the number found in our citizen-science data (112). This could be a result of the number of syllables with which we initialized the model or our definition of copy-rate error as a representation of invention and not a probability of learning a slightly less favorable syllable type. Both of these should be explored further with additional parameter testing. Lastly, we note that in our chipping sparrow data there is a steep dropoff between the fraction of syllable types that are sung by just one bird and the fraction of syllable types that are sung by two or three birds; this pattern was not captured by any of the simulations. Together, these diverging qualities between our model findings and citizen-science data suggests the need for additional model refinement, but even more so, a consideration of other factors at play or missing from the model structure.

While it appears directional selection most closely replicates the pattern in our empirical data for both the frequency and the lifetimes of syllable types, evidence for selection towards high syllable rate is not well supported. From previous analyses of song recordings (**Chapter 4**), we find a large variability in song rate. In addition, when examining long-lived syllables, we observe a wide distribution of mean syllable durations, implying both long and short syllables can persist over time. To confirm that song rate is not favored in learning and thus has not been driven to change significantly over recent years, we propose playback experiments to determine whether there is a difference in individuals' responses to recordings of different song rates and to historical versus current song recordings (Derryberry, 2007). While we present the model as specifically selecting for syllable rate, our implementation could be generalized to any song feature. Because we do not hypothesize other song features as candidates for such selection pressure from previous results (**Chapter 4**), we propose a change to how directional tutor selection is executed. Instead of constructing independent syllable type and song-feature vectors in which only the song-feature is under pressure, syllable types themselves could be under selection. To execute this in the model, it would be necessary to create a measure of syllable quality; this syllable quality would then drive tutor choice.

Lastly, one current and significant deficiency of our preliminary model presented here is the lack of a mechanism for maintaining local diversity, which has been observed in nature (Liu & Kroodsma, 2006). For example, the results of the conformity simulations show rapid evolution of patchiness in the matrices, similar to a pattern of regional dialects in which nearby birds all sing the same song, whereas chipping sparrows in nature do not show this pattern. To address this model inaccuracy, we first propose two small improvements that are already easily attainable in the current model structure: (1) increasing the number of neighbors from which the new bird chooses a tutor and (2) splitting the learning error into two parts such that there is still a chance for a novel syllable, but now also the possibility of not choosing the most desirable tutor according to the model criteria (conformity or highest syllable rate). We note that increasing the neighborhood from which a tutor is chosen should increase diversity under neutral selection; however, this may have the opposite effect under directional and conformity bias. While either of these adjustments would most likely improve the model's local diversity, we believe it will still be instructive to add an additional step to the model—an opportunity for individual dispersal. For instance, in each timestep, some small fraction of birds could move to a new location some distance from its original territory. This would promote the mixing of regionally prominent syllable types throughout the larger population, and disrupt the formation of dominant dialects in any region. The addition of this step would directly reflect what has been observed in local chipping sparrow populations: nestlings disperse from a few meters up to two kilometers from natal nesting site to establish their own breeding area, and adults, more often than not (e.g. 23 of 38 banded birds) have been observed to disperse ~1.5km to establish a new breeding area in subsequent years (Liu & Kroodsma, 2006). To match these dispersal patterns and the matching of songs from neighbors at juveniles' first breeding site, the implementation of a dispersal step in the model could occur before or after learning or at both instances; all combinations should be tested and compared to the empirical data. Thus, implementing dispersal is ecologically justifiable, and may allow the model to more closely mirror local and global patterns.

Overall, we demonstrate that coupling an agent-based model with citizen-science data can be advantageous for better understanding the evolution of behavior in a songbird. In particular, our preliminary results are indicative of a song-learning scheme in which tutor selection is under directional pressure in the chipping sparrow population. In order to gain further insights, the model can accommodate extensions and additional parameter testing. The two most significant and most likely necessary changes to better represent the chipping sparrow population would be altering the way in which directional tutor selection is implemented such that the syllable type itself is under selection and also the introduction of dispersal both before and after song learning. Together, these two features could improve the model fit to our empirical data set of citizen-science recordings of chipping sparrows.

DATA AVAILABILITY AND ACKNOWLEDGMENTS

All scripts for this work can be found at https://github.com/CreanzaLab/chippies_cultural_transmission_model.

We are grateful to Yakov Pichkar for his assistance in refactoring the model to improve efficiency as well as discussions during development of the model.

CHAPTER 6

CONCLUDING REMARKS

As technology advances, research is driven forward. In ornithology, and more specifically the study of birdsong, these advances have manifested over the decades in the development and improvement of recording and playback devices as well as song visualization methods. Most recently, the reduction in size of recording devices, the integration of audio and GPS technology into the smartphone, and the popularization of birding databases have worked together to drive the accumulation of citizen-science data. While the resultant citizen-science repositories have provided a valuable resource for avian research (Callaghan & Gawlik, 2015; Gasc et al., 2013; Kelling et al., 2012; Lagoze, 2014; Sullivan et al., 2017; Velásquez-Tibatá et al., 2012), databases of birdsong recordings remain underutilized in large-scale analyses (Benedetti et al., 2018; Mason et al., 2014; Tobias et al., 2014; Weir & Wheatcroft, 2011). Thus, the aim of this thesis was to improve the workflow of using citizen-science recordings for quantitative birdsong research and to demonstrate the power of citizen-science data as a resource for behavioral analyses at scale. I directly accomplished this goal by developing the open-source software Chipper (**Chapter 2**). Chipper has streamlined the analysis of birdsongs collected on devices of varying quality and made spatiotemporal analyses across a species' entire geographic range more feasible. Employing Chipper, I demonstrated that citizen-science recordings could be used to detect diel patterns in song that were previously discovered by intensive field work (**Chapter 3**). Importantly, my work demonstrated that such patterns could be uncovered using single recordings of individual birds across the entire species' range rather than by numerous recordings of the same bird within one fieldsite. After validating the approach, I then extended the study of chipping sparrow songs using citizen-science data to determine whether there were song differences among the species' vast North American range (**Chapter 4**). I successfully determined that the song rate and frequency varied with longitude, but not latitude. Finally, I developed a model of chipping sparrow song evolution and compared the results of this model to the distribution of unique syllables across citizen-science recordings in order to shed light on song-learning strategies and accuracy in the chipping sparrow population (**Chapter 5**).

Ideally, with citizen-science data being much easier to analyze, Chipper will change how researchers approach questions. Specifically, we hope that the use of citizen-science recordings to test hypotheses does not only begin to answer questions more quickly and cost-effectively but also generates new questions that then must be tested in the field. Thus, we propose that assessing citizen-science data should be seen as a first avenue in developing a research question, ideally occurring before fieldwork and informing long-term experiments. For instance, the work presented in Chapter 3 suggests the Eastern and Western chipping sparrows are a genetically well-mixed but culturally varied population, with Eastern chipping sparrows singing fewer, longer syllables. In order to determine whether these differences in song are meaningful to the species, playback studies should be conducted. For example, recordings from across the distribution of Eastern and Western songs could be played to the same and opposite population of chipping sparrows and the response measured. If the differences in syllable length and numbers of syllables are salient to the birds, one would predict a difference in behavioral response to playbacks, with birds approaching the speaker more closely or singing in response to certain songs. This would allow us to directly address the question: do birds respond most strongly to playbacks from their own region, or are the faster Western songs universally more appealing?

The results of Chapter 3 also suggest the importance of migration studies. Additional studies of chipping sparrow migration patterns and fidelity could bring to light the factors at play in maintaining a genetically well-mixed population. The interplay between migration patterns and song-learning window are not often explored. For instance, species with faithful migration patterns and short song-learning windows may produce the most significantly distinct dialects; whereas species with unfaithful migration patterns and long song-learning windows would most likely lead to lack of song structure across the range. It is still not well understood how migration and song learning interact to form (or prevent the formation of) a dialect. With the use of Chipper to quickly analyze songs of multiple species, candidate species could be easily chosen for further migration studies to explore this interaction.

Beyond the work presented here, Chipper and citizen-science data have jointly opened additional areas of study in the Creanza lab. By combining eBird data on both bird sightings and birdsongs, others in the lab are now able to investigate whether the amount of overlap in geographic range correlates with song differences as the need for conspecific identification becomes more imperative with increased habitat sharing. Similarly, another student is examining the interplay between differentiated song and plumage in Junco subspecies. As Chipper is applicable to many species and increases the speed at which hundreds of songs can be analyzed, phylogenetically controlled studies of song characteristics are even more of an immediate interest to the lab. One such project underway is the study of how urbanization is affecting birdsong similarly across the avian phylogeny with specific interest in whether song learning is necessary for adaptation on short time scales. Across these research questions, Chipper has been applied to many species' songs, covering approximately 17 different families.

Furthermore, with a user-friendly interface, Chipper has been a valuable tool in the classroom. It has allowed for the development of a seminar course (BSCI3965) in which the entire research process can be easily achieved by the students over the course of a semester. Students first learn about birdsong, both its functions and many forms and begin to establish a research question of interest. Second, students are able to take part in data collection just like other citizen scientists, by recording songs on campus with handheld recorders or their phones. By combining their recordings with those from citizen-science databases, they easily have enough data to analyze. Chipper allows them to quickly extract syllable and song measurements. This leaves time for students to learn the basics of coding and statistical analysis to test their hypothesis and to practice data-visualization skills.

Similarly, Chipper could provide a means for crowdsourcing data analysis of birdsongs. Other areas of science have already taken this approach: the Milky Way Project and Galaxy Zoo asks the public to score and classify astrophysical phenomena in satellite images (Beaumont et al., 2014; Robles et al., 2019; Walmsley et al., 2020), and FoldIt has created a video game to harness human problem-solving for the computationally limited problem of protein folding (Cooper et al., 2010). NASA GLOBE Cloud Protocol has even integrated data collection into the classroom by having students observe and report cloud coverage (Robles et al., 2019). The partnership of Chipper with citizen-science databases such as Macaulay Library or Xeno-canto could mean the gamification of song parsing. While the birding community continues to increase in computer-savvy members, more and more birders are already using online tools that sync with these databases, such as eBird. Either migrating Chipper over to a web-based application or creating a site for easy download of recordings and upload of Chipper outputs could allow the community to contribute beyond data collection.

With heavy use in the Creanza lab, we have recognized areas in which Chipper could be improved to extend its applicability. For instance, one of the most imperative improvements would be to make Chipper compatible with longer song bouts. This would allow the user to study birds that sing continuously for long periods of time such as the European starling or the Northern mockingbird. Suggestions on how to implement this improvement are as follows: (1) change the windows being used to display the spectrograms to Kivy ScrollView widgets such that a horizontal scroll bar can be used to view the entire song and all segmentations, or (2) automatically break the provided recording into smaller audio clips before rendering and calculating the segmentation; then after segmentation of each clip, automatically stitch the segmentations back together resulting in one set of measurements for the entire recording.

Another way to improve Chipper's user experience would be to encompass more of the song analysis workflow in the single application. Specifically, the inclusion and automation of bout selection before segmentation would reduce the need to use another program such as Audacity and would further streamline analysis, reducing the number of times the user has to open or manipulate a single recording. Additionally, the current method used in Chipper for determining syntax includes the relatively costly computation of cross-correlation of syllable spectrograms. However, research in bout selection and syllable categorization is ongoing and often requires large amounts of data to inform the automated selections and classifications (Adavanne et al., 2017; Daou et al., 2012; Mackevicius et al., 2019; Nicholson, 2016; Pearre et al., 2017; Sainburg et al., 2019; Wu et al., 2008). Since our current syllable classification in Chipper is restricted to one-dimensional alignment (in time), a simple improvement could be the inclusion of methods borrowed from image registration (Brown, 1992; Zitová & Flusser, 2003) such that the user has the option to allow displacement in time and/or frequency as well as geometric transformations (*e.g.* scaling) such that syllable shape becomes the primary classifier. For studies in which there is a vast number of songs of the same species, machine learning could even be considered and implemented to improve syllable classification. Thus, while I see these as possible improvements for Chipper, I also recognize that the robust automation of species identification, bout selection, and syllable classification are currently some of the greatest challenges in song analysis. Chipper was developed using open-source software to facilitate addressing these existing hurdles and unforeseen new challenges, and we hope users will contribute by integrating their own analysis methods and improving it for the community as a whole.

While we conducted a test of accuracy, repeatability, and reproducibility of Chipper, I believe additional analyses could be done to compare Chipper to other methods that use the waveform rather than the spectrogram for extracting quantitative measurements. Previous work has demonstrated that these two fundamentally different methods of feature extraction can lead to varied measurements (Zollinger et al., 2012). However, such work has primarily been carried out with field recordings with professional equipment or recordings from well-controlled sound chambers. Thus, there is a need for further studies to better understand whether different measurement methods affect larger studies that use non-ideal recordings (such as smartphone recordings) from citizen scientists (Araya-Salas et al., 2019). Are such recordings already of poor enough quality that the difference in measurement from using a waveform versus spectrogram is not significant? If there is a difference in measurement, is the impact on the result negligible as long as there are considerable amounts of data that are analyzed in the same manner? I find this area of investigation particularly interesting with respect to using citizen-science data to study the impact of urbanization on birdsong, an area in which frequency and amplitude are thought to be important factors, since these song features are the same ones that are the most susceptible to errors introduced by low-quality recordings and high background noise (Brumm et al., 2017; Zollinger et al., 2012).

Using Chipper and citizen-science data could greatly expand the research efforts on assessing the impact of urbanization on cultural evoltuion. While evolution often evokes the initial thought of long temporal scales, it has been shown to be dynamically occurring over shorter timescales as well (Blount et al., 2008; Ford & Ford, 1930; P. R. Grant & Grant, 2006; P. R. Grant & Rosemary Grant, 2002). Moreover, intense environmental pressure often drives swift evolutionary change (Creed, 1975; R. B. Grant & Grant, 1993; Kettlewell, 1973). Recently, scientists have been interested in how our impact as humans is driving evolution (Diamond, 1986; Rabin & Greene, 2002; Swaddle et al., 2015). Human impact has often led to habitat loss and consequently displacement of species (Dixo et al., 2009; Fahrig, 2003; Marzluff, 2001; Stone, 2000). However, many avian species seem to be adapting to changes in their environment that accompany urban development such as the disruption of light patterns, food sources, and nesting habitats (Arroyo-Solís et al., 2013; Lancaster & Rees, 1979; Nordt & Klenke, 2013; Wang et al., 2008); often this adaptation involves changing their song due to the necessity to be heard over anthropogenic noise (Nemeth & Brumm, 2009; Patricelli & Blickley, 2006; Roca et al., 2016;

Slabbekoorn & Peet, 2003). Assessing the impact of urbanization on wildlife is a fundamentally important problem in biology, as humans continue to alter and fragment animal habitats. Since songs provide birds with a means to identify conspecifics, defend territories, and attract mates, studying changes in birdsong will elucidate the pressures facing birds to reproduce and persist in urban environments.

The study of the impact of urbanization on song is one area of birdsong research that could benefit greatly from the use of Chipper and citizen-science data. The large amounts of citizen-science birdsong data collected over large spatial and temporal scales is an ideal resource for studying fast-changing qualities in birdsong across many species. Pairing this valuable dataset with others related to urbanization—maps of human population, roads, building footprints, and land use—could further studies of how we are impacting birds and specifically their song. Furthermore, the level of resolution possible may even provide insights into whether efforts to maintain city greenspaces is worthwhile or whether there are qualities such as size, type of landscape, etc. that are predictors for maintaining a sufficient environment without pressures for species to change their singing behavior.

A growing body of literature has started to uncover changes in birdsong pitch and amplitude in response to urbanization, particularly anthropogenic noise (Francis et al., 2011; Nemeth & Brumm, 2009; Roca et al., 2016; Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006). However, most of these studies have focused on individual species, were conducted using only one or two field sites, and often included the use of artificial noise. With birdsongs being recorded across the globe and archived in public repositories, a large-scale study spanning multiple species, years, and locations is now feasible. Thus, we can now conduct studies of the same species across different levels of urbanization instead of relying on birds' responses to increased artificial noise, and we can then compare adaptations across the phylogeny, for instance between oscines (vocal-learning songbirds) and suboscines (a closely related clade of non-learners).

While the vast amount of data allows for a number of interesting scientific questions, the impact should reach beyond the academy: data-driven conservation efforts should be an integral part of the discussion around urban planning and public involvement. Additionally, as we have limited ability to stop cities from growing into surrounding habitats, I propose taking an unconventional approach: look beyond the urban-versus-rural dichotomy and ask whether city greenspaces provide sufficient habitat to dampen the impact of urbanization on local birds and their behavior, in the hope of influencing urban planning policies (Blair & Launer, 1997; Fernández-Juricic et al., 2005). Therefore, we present our aim to address this topic at two fundamentally different spatial scales: a large-scale study of urban and rural populations across North America and a local field study in Nashville.

More specifically, preliminary work has been conducted using both citizen science data from public repositories and local data collection to pilot a multispecies study examining birdsong across rural and urban locations. We have downloaded songs of both oscines and suboscines across nearly 20 families from Macaulay Library, eBird, and Xeno-canto and measured song features using Chipper. We are working with Vanderbilt's Spatial Analysis Research Laboratory to use geographical information system maps to categorize the location each bird inhabited. Specifically, we are using a combined measure of distance from population centers, distance to roads, surrounding building footprint, and land use to determine the level of urbanization. Once this is complete, we can use phylogenetic comparative analyses to determine whether similar changes are occurring across closely related species and whether these changes can be predicted by evolutionary relationships (e.g. between oscines and suboscines (Ríos-Chelén et al., 2012)).

Simultaneously, we have been collecting our own recordings of birdsong in Nashville as another approach to determining whether there is a level of urban greenspace (size, level of noise, other human footprint markers) that mitigates changes in birdsong. We procured a research agreement with Metro Parks and a number of surrounding State Parks to conduct fieldwork on public lands. Using a light-pollution map (www.lightpollutionmap.info) as a proxy for level of urbanization, we identified multiple locations covering the rural to urban spectrum (Bortle class 4-9). Throughout the summer of 2018 (March–August), Wildlife Acoustics SM4 recorders were set to passively record birds at a different park each week. In order to analyze such a large dataset, we have used Wildlife Acoustics' Kaleidoscope Pro Analysis Software, to run precursory clustering and classification of hours of recordings. To do this, we have relied on our own knowledge to identify the resultant clusters as specific species' songs. It would be best to consult local birders with far greater experience in the future. After further rounds of classification, the resulting song clips can be used to evaluate species diversity at each location. Then using Chipper to analyze the identified clips, more quantitative analyses on song and syllable durations and frequencies can be used to compare between levels of urbanization. This project represents a major future direction in the long-term goal of merging citizen-science data with Chipper analyses to address large-scale questions in the evolution of behavior.

In sum, I have developed Chipper, a much-needed tool in the field of song analysis, to semi-automate syllable parsing and feature measurements with particular attention to applicability to a variety of species and recording qualities. I demonstrated Chipper's utility on a large-scale citizen-science data set: recorded songs of the chipping sparrow across North and Central America. I tested Chipper's validity by detecting diel patterns in chipping sparrow song using citizen-science data; moreover, I illustrated that such patterns could be identified in a population without multiple recordings of the same individual but rather with single recordings representing a sample of the population. By combining Chipper and citizen-science data, I also presented a new biological discovery that was not previously feasible: I found that chipping sparrow song differs across North America, with individuals in the Eastern United States/Canada tending to sing songs with fewer, longer syllables than in the Western U.S./Canada but with the same overall song duration. We then contextualized these results by re-examining the genetic differentiation across the chipping sparrows's range. Our results suggest that there are two culturally distinct sub-populations of migratory chipping sparrows that are genetically indistinguishable using mitochondrial DNA, motivating future studies on migration patterns and additional sequencing of nuclear DNA. Overall, the population-level song structure seems to support the weakly demarcated and debated subspecies classifications, while the lack of genetic population structure does not. Thus, future field studies of song performance and song playbacks could elucidate whether there are morphological differences between the two populations and whether song is or could be acting as a reproductive barrier. Lastly, I have demonstrated that citizen-science data in conjunction with agent-based models can be used to examine the cultural evolution of avian vocalizations. From preliminary results, it appears chipping sparrows learn song with very low error rate but with some directional selection of tutors for song learning. Taken together, the analysis techniques provided by Chipper and the continued dedication to improving the use of citizen-science recordings promise to shed new light on the evolution of learned behaviors and drive large spatiotemporal and multi-species studies in unforeseen domains.

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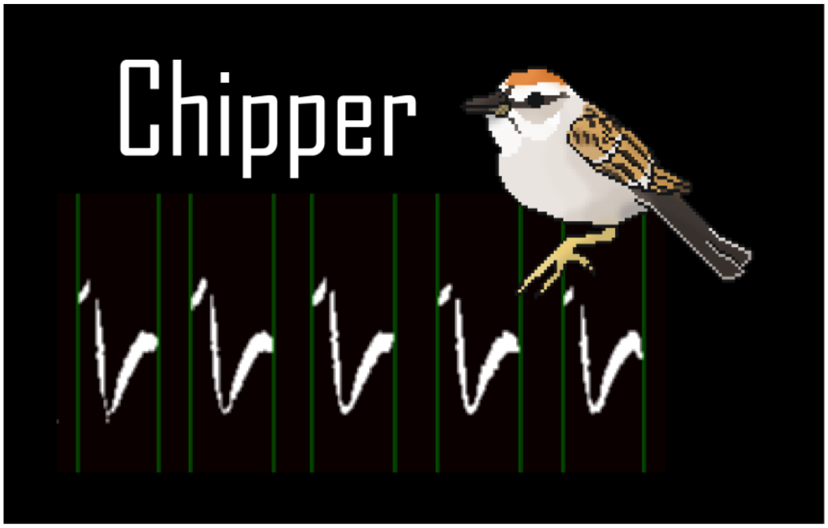
APPENDIX A

CHIPPER MANUAL

Chipper v1.0 Manual



Updated: January 2020

Table of Contents

How to Install

Option 1: Download Chipper

1. Download the version of Chipper for your operating system (found at https://github.com/CreanzaLab/chipper/releases).

2. Unzip the folder, extracting all files.

3. Run the application file.

   Windows
   - Navigate into the start_chipper folder and double click the Application file (.exe) named start_chipper, which may have a bird as an icon.
   - The first time you try to open the file, you may receive the message "Windows Defender SmartScreen prevented an unrecognized app from starting. Running this app might put your PC at risk." Click "More info" and then select "Run anyway".
   - You will now see a terminal window open.

   Mac
   - Navigate into the start_chipper folder and double click the Unix executable file named start_chipper.
   - The first time you try to open the file, you may receive the message "start_chipper can't be opened because it is from an unidentified developer". If so, right click on the file and select "Open". Click "Open" again on the popup to confirm.
   - You will now see a terminal window open.
   - If you continue to receive pop-ups indicating the developer cannot be identified or verified, you will need to update which apps you allow. (Common for macOS Catalina.)
     - Open System Preferences > Security & Privacy > General. Under “Allow apps downloaded from:” select “Anywhere”. If this is not an option, continue to the next step.
     - Open Terminal and enter the following:

       ```
       $ sudo spctl --master-disable
       ```
     - Reopen System Preferences. The third option "Anywhere" should now be available. Click the lock, type your password, and select this option.
     - Try again to click and run the executable file named start_chipper.
     - Once you successfully run Chipper, you can change the “Allow apps downloaded from” setting back to the default to restore security.

Linux:

- Open the terminal and type "/path/to/start_chipper/start_chipper" without the quotes and replacing "/path/to" with the full file location.
- Hit enter.

4. The Chipper landing page will soon open. Note, this can take some time to load the first time. If it does not open, close the terminal and try opening the start_chipper file again. For best performance, we recommend using Chipper in full-screen mode, especially if you are working on a low resolution display. You are ready to go!

Option 2: Install from source (primarily for developers)

1. Install Anaconda
   Our recommended approach is to use Anaconda, which is a distribution of Python containing most of the numeric and scientific software needed to get started. If you are a Mac or Linux user, have used Python before and are comfortable using pip to install software, you may want to skip this step and use your existing Python installation.

2. Next, download our code, including the requirements.txt file. From within a terminal or command prompt window, create a conda environment.

   ```
   $ conda create -n chipper_env python=3.7
   ```

   For Mac and Linux, install packages with conda:

   ```
   $ conda install -r requirements.txt
   $ conda install  pypiwin32 kivy.deps.sdl2 kivy.deps.glew
   kivy.deps.gstreamer kivy.deps.glew_dev kivy.deps.sdl2_dev
   kivy.deps.gstreamer_dev
   ```

   For Windows users, you may need to use pip to install: requirement

   ```
   $ pip install -r requirements.txt
   $ pip install  pypiwin32 kivy.deps.sdl2 kivy.deps.glew kivy.deps.gstreamer
   kivy.deps.glew_dev kivy.deps.sdl2_dev kivy.deps.gstreamer_dev
   ```

3. Install kivy packages:

   ```
   $ garden install --kivy graph
   $ garden install --kivy filebrowser
   $ garden install --kivy matplotlib
   $ garden install --kivy progressspinner
   ```

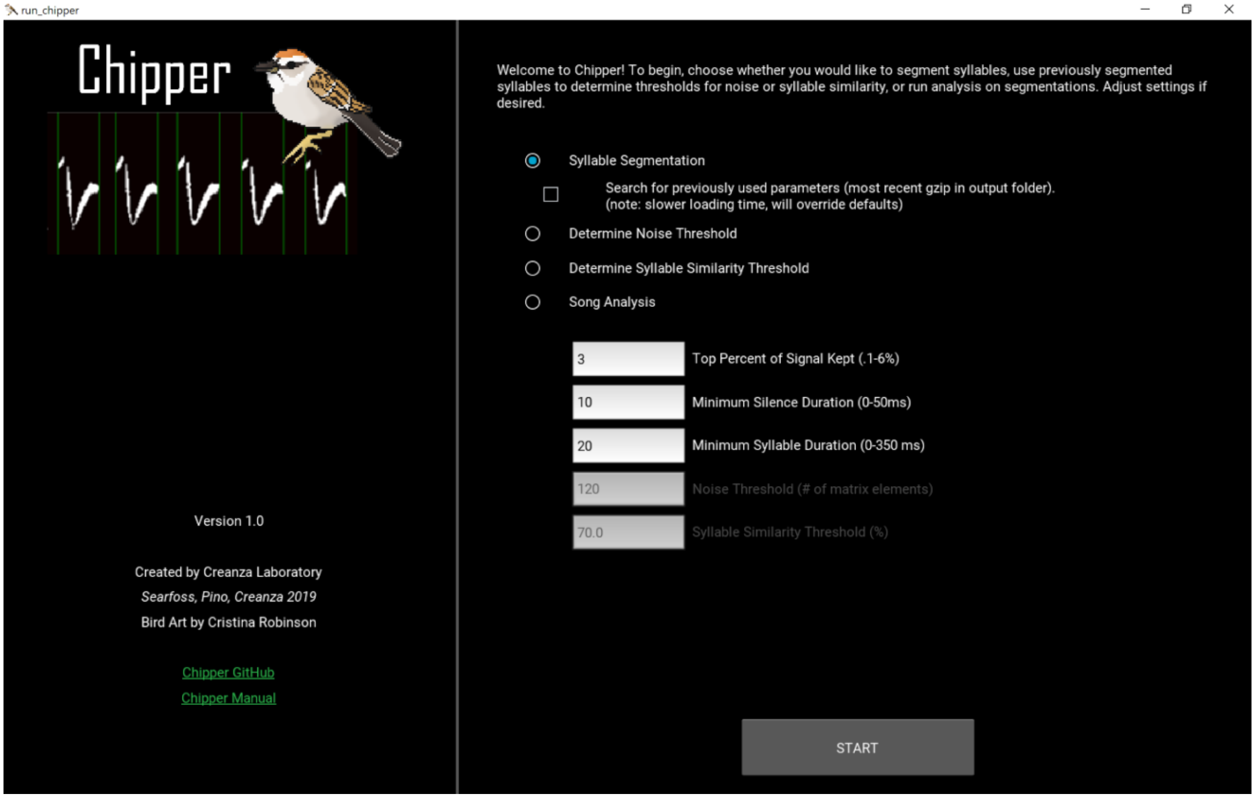
For full code visit https://github.com/CreanzaLab/chipper.

Overview

The Chipper landing page allows you to choose whether you want to

1) segment songs (or other acoustic signals)
2) determine the threshold for noise
3) determine the threshold for syllable similarity, or
4) complete analysis of already segmented files.

These steps should generally be conducted in the order listed. Steps 2 and 3 can be skipped if you have already determined appropriate thresholds for your study.



Welcome to Chipper! To begin, choose whether you would like to segment syllables, use previously segmented syllables to determine thresholds for noise or syllable similarity, or run analysis on segmentations. Adjust settings if desired.

● Syllable Segmentation
  ☐ Search for previously used parameters (most recent gzip in output folder). (note: slower loading time, will override defaults)
○ Determine Noise Threshold
○ Determine Syllable Similarity Threshold
○ Song Analysis

3 Top Percent of Signal Kept (.1-6%)
10 Minimum Silence Duration (0-50ms)
20 Minimum Syllable Duration (0-350 ms)
120 Noise Threshold (# of matrix elements)
70.0 Syllable Similarity Threshold (%)

Version 1.0

Created by Creanza Laboratory
Searfoss, Pino, Creanza 2019
Bird Art by Cristina Robinson

For **Syllable Segmentation**, the user can choose parameter defaults for top percent of signal kept, minimum silence duration, and minimum syllable duration; these defaults will start the parsing of every song. You can also select “Search for previously used parameters” which will look for gzips in any *SegSyllsOuput_YYYYMMDD_THHMMSS* folders in the selected folder for segmentation. If any gzips are found, the most recent one will be used to load the previous settings and segmentation conducted for the song.

For **Song Analysis**, the user can choose parameters for noise threshold (to distinguish between signal and noise) and percent syllable similarity (to determine syntax). We suggest first using the noise and syllable similarity threshold widgets for best results; after finishing each widget, the new parameter for analysis will be populated.

Syllable Segmentation

Starting Syllable Segmentation will first take you to a file explorer to choose either a single WAV file or folder of WAV files. The length of the songs and the size of the files Chipper can handle depends greatly on your computing resources and screen size. We recommend songs between ~0.5s and 10s long or files no larger than 3MB. Depending on the computing resources, you may experience lag with files between 2-3MB. Thus, we recommend selecting bouts of song to segment using another program such as Audacity (www.audacityteam.org) or monitoR (https://CRAN.R-project.org/package=monitoR). Similarly, if a bout is very short, it may appear stretched; you can always reduce this effect when selecting a bout in Audacity by not cutting the bout too close or by adding time to the beginning or end of the bout.

Note: We have set a warning message for files over 3MB in which the user can select to either toss or process the file; this is a safety to ensure the user knows they may experience a lag or even crash Chipper if the file is much larger than recommended and has not been previously parsed. If you are consistently parsing files larger than this with no issue and want to change this threshold, see line 338 of control_panel.py (and line 275 in run_chipper.kv for popup message).

Each file will load using the default parameters from the landing page to automatically parse the song. Next adjust the sliders to finalize your segmentation. For detailed calculations involving the parameters underlying these sliders and how they are applied to the spectrogram code at https://github.com/CreanzaLab/chipper.

Here is a suggested order in which to adjust the sliders (for a detailed example with screenshots, see next section):

1. Adjust the high-pass and low-pass filter slider (left of top spectrogram).

2. If there are some portions of the song that seem very low in amplitude, try normalizing the signal.

3. Adjust the signal threshold to reduce noise.

   Tip: You can use the crop sliders (under the bottom spectrogram) to remove the onsets/offsets temporarily to see if you like what the signal threshold is giving you without having the lines crowd your view. Be sure to put these sliders back after you are done, as the onsets and offsets must be in place to submit a segmentation.

4. Adjust minimum silence duration to the ***minimum value*** that segments the way you think is correct. Using the smallest value that gives you good parsing will help if you have spots of noise right on the edge of a syllable; it will cut the speck of noise out of the actual syllable. On the other hand, if you are trying to get two parts of a syllable that are far apart from one another to parse together, try increasing the minimum silence duration quite a bit.

5. You may need to iterate between steps #3 and #4.

6. Adjust the minimum syllable duration if you are still not satisfied with the parsing. Usually you will not have to adjust this parameter much or at all. (However, this will depend on the song type you are parsing.) It is often useful in getting rid of little bits of noise that are parsing as syllables (by increasing the minimum syllable duration) or to include small syllables that are not parsing (by decreasing the minimum syllable duration).

7. Use the crop sliders (under the bottom spectrogram) to remove onsets and offsets capturing any signal before or after the song.

8. Add/Delete any onsets/offsets that are missing or extraneous. Try to add as few manual onsets/offsets as possible. It is better to have too many and have to remove.

   Tip: Use the left and right arrow keys to move between the selected onset/offset and the others. Use "Enter" to accept addition or deletion of onsets/offsets. Use "x" to cancel addition or deletion of onsets/offsets.

9. Submit your parsed song, or toss if you think it is too noisy and you are not getting good data!

   *Careful not to hit submit or toss twice in a row. If you think the button did not work, it might just be loading the next file. The **buttons should turn blue if they have been selected** and will be gray again when the new image is loaded. However, if you do accidentally skip or toss a song, you can use the "Back" button to return to the previous song.*

Once you have parsed all the files in a folder, there will be a new folder within that directory called *SegSyllsOutput_YYYYMMDD_THHMMSS*, where *YYYYMMDD* is replaced with the current date and *HHMMSS* is replaced by the current time. For every WAV file that was successfully segmented, there will be an associated gzip which will be used in the next steps in Chipper. Specifically, each gzip is written after the user hits "Submit". These gzips are used to review the segmentation again using Syllable Segmentation or to determine Thresholds and run Analysis in the next steps.

In addition, four human-readable text files are output once the last file is either submitted or tossed.

1. *segmentedSyllables_parameters_all* includes a list of all the Chipper parameters used to reach the submitted segmentation.

FileName	name of WAV file
FrequencyFilter	[high-pass, low-pass] in number of matrix elements from the bottom of the spectrogram
BoutRange	[left crop, right crop] in number of matrix elements from the left of the spectrogram
PercentSignalKept	top percent of signal kept
MinSilenceDuration	number of spectrogram matrix elements
MinSyllableDuration	number of spectrogram matrix elements
Normalized	‘yes’ or ‘no’ indicating whether the song was normalized or not

2. *segmentedSyllables_syllables_all* with a list of onsets and a list of offsets in number of matrix elements from the left of the spectrogram.

3. *segmentedSyllables_conversions_all* includes the conversions necessary to change the parameters from spectrogram matrix elements into milliseconds or Hz for each WAV file processed.

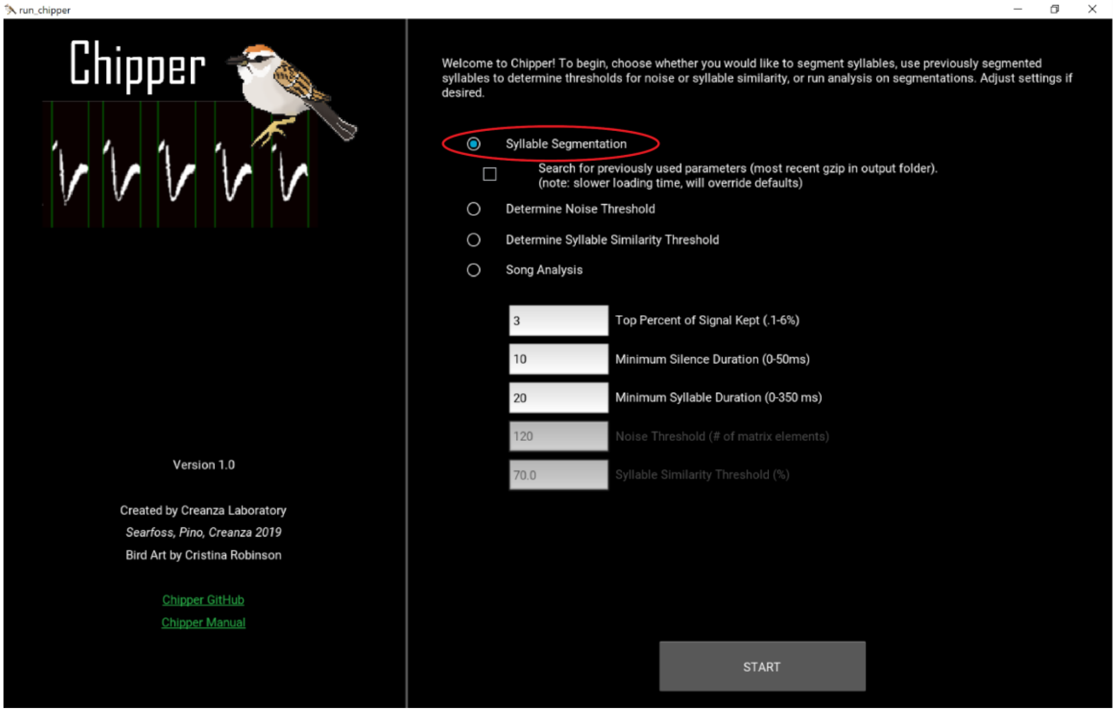
FileName	name of WAV file
timeAxisConversion	number of milliseconds per matrix element
freqAxisConversion	number of Hz per matrix element

4. *segmentedSyllables_tossed* with a list of the files that were tossed. There should be no gzips provided for the files in this list.

Note: If Chipper crashes during segmentation (or the user exits Chipper), the text files will not be output; however, gzips for any segmentations that were submitted will be present in the output folder. To run the next steps, only gzips are needed. The text outputs are solely for the user’s information.

Example of Syllable Segmentation

1. Select “Syllable Segmentation”.



Welcome to Chipper! To begin, choose whether you would like to segment syllables, use previously segmented syllables to determine thresholds for noise or syllable similarity, or run analysis on segmentations. Adjust settings if desired.

● Syllable Segmentation

☐ Search for previously used parameters (most recent gzip in output folder).
(note: slower loading time, will override defaults)

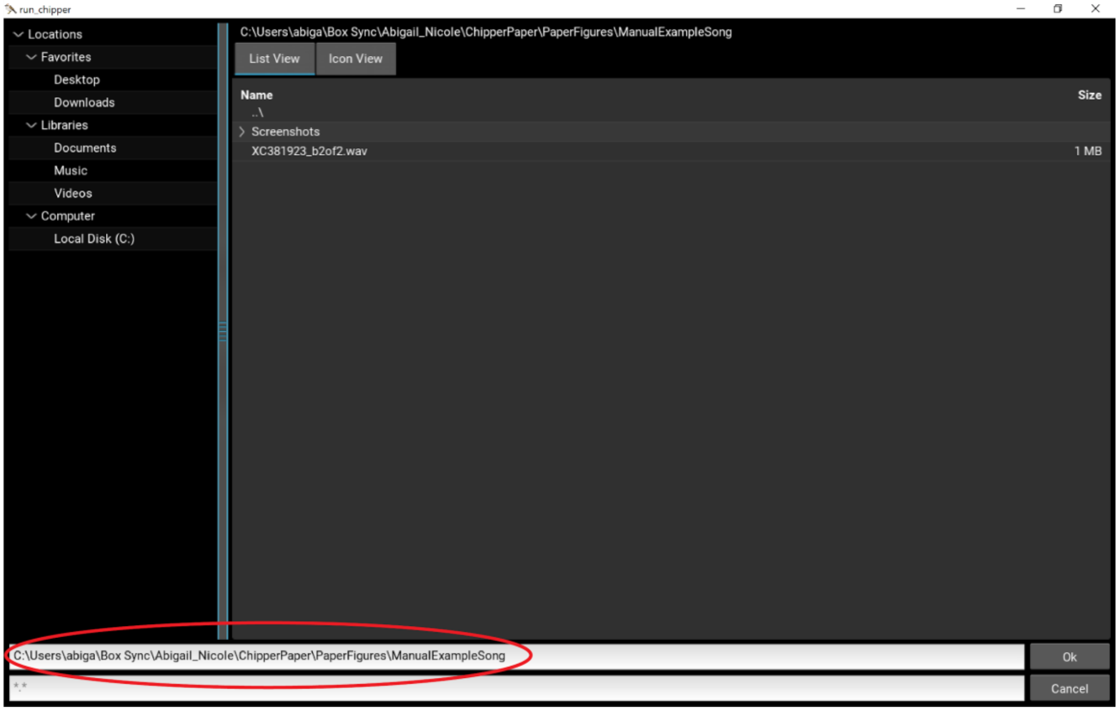
○ Determine Noise Threshold

○ Determine Syllable Similarity Threshold

○ Song Analysis

3	Top Percent of Signal Kept (.1-6%)
10	Minimum Silence Duration (0-50ms)
20	Minimum Syllable Duration (0-350 ms)
120	Noise Threshold (# of matrix elements)
70.0	Syllable Similarity Threshold (%)

2. Navigate to and select a WAV file or folder of WAV files to parse. Double click ..\ (for PC) or ../ (for Mac or Linux) to move back up a folder. Here we use the second bout from the Xeno Canto recording 381923. (XC381923 contributed by Lucas, Creative Commons Attribution-NonCommercial-ShareAlike 4.0, https://www.xeno-canto.org/381923).



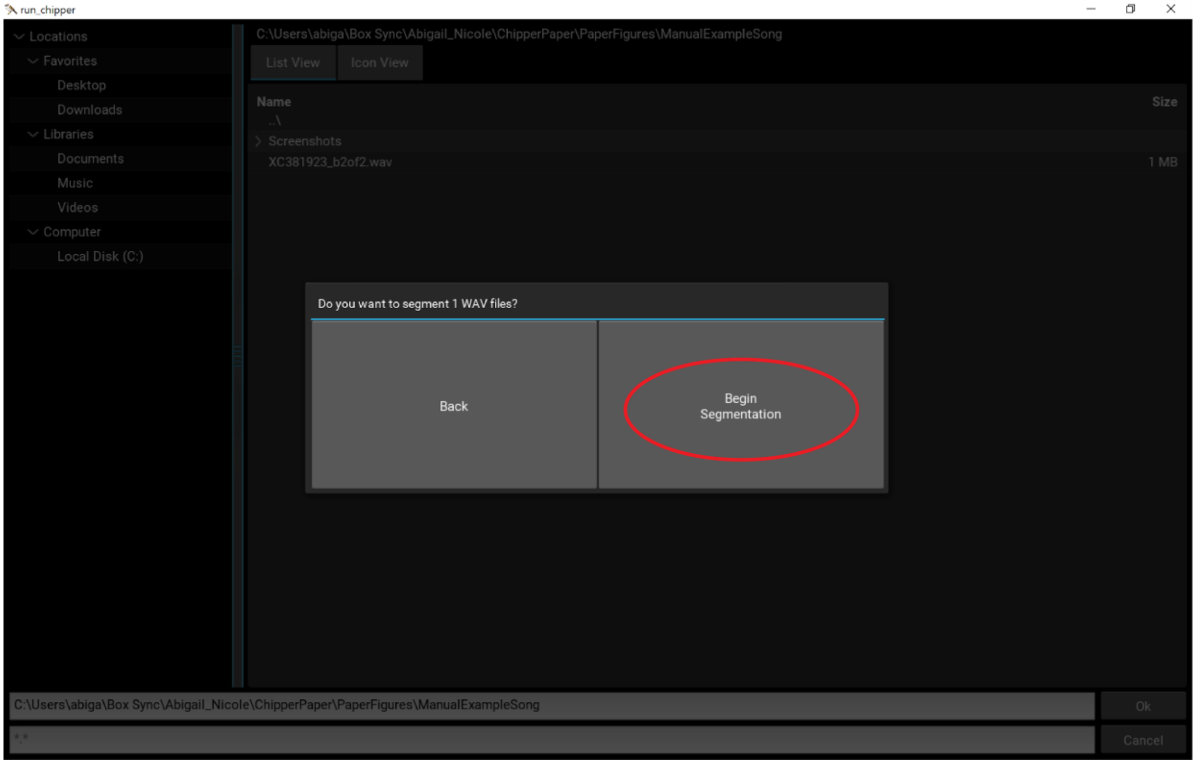
C:\Users\abiga\Box Sync\Abigail_Nicole\ChipperPaper\PaperFigures\ManualExampleSong

Name	Size
..\	
Screenshots	
XC381923_b2of2.wav	1 MB

C:\Users\abiga\Box Sync\Abigail_Nicole\ChipperPaper\PaperFigures\ManualExampleSong

.

3. Click “Begin Segmentation”.



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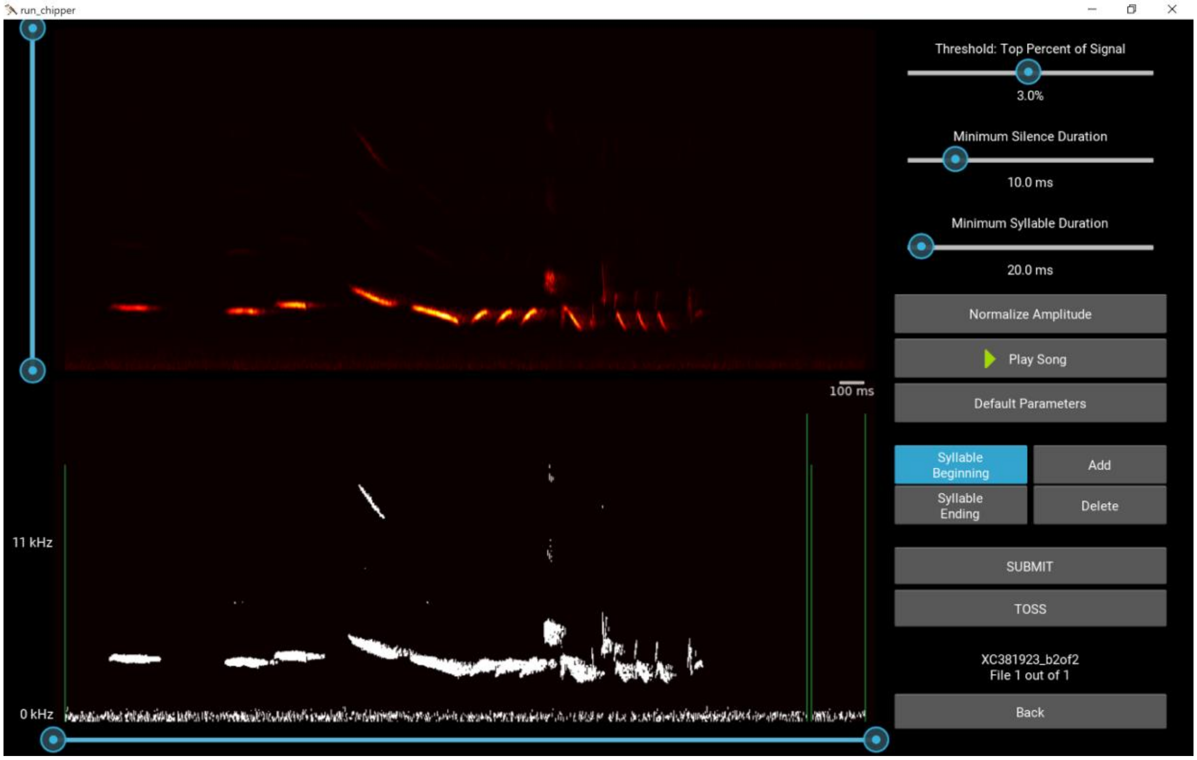
Do you want to segment 1 WAV files?

C:\Users\abiga\Box Sync\Abigail_Nicole\ChipperPaper\PaperFigures\ManualExampleSong

4. The file is loaded with segmentation using the default parameters. In this case, we did not change the defaults on the landing page.



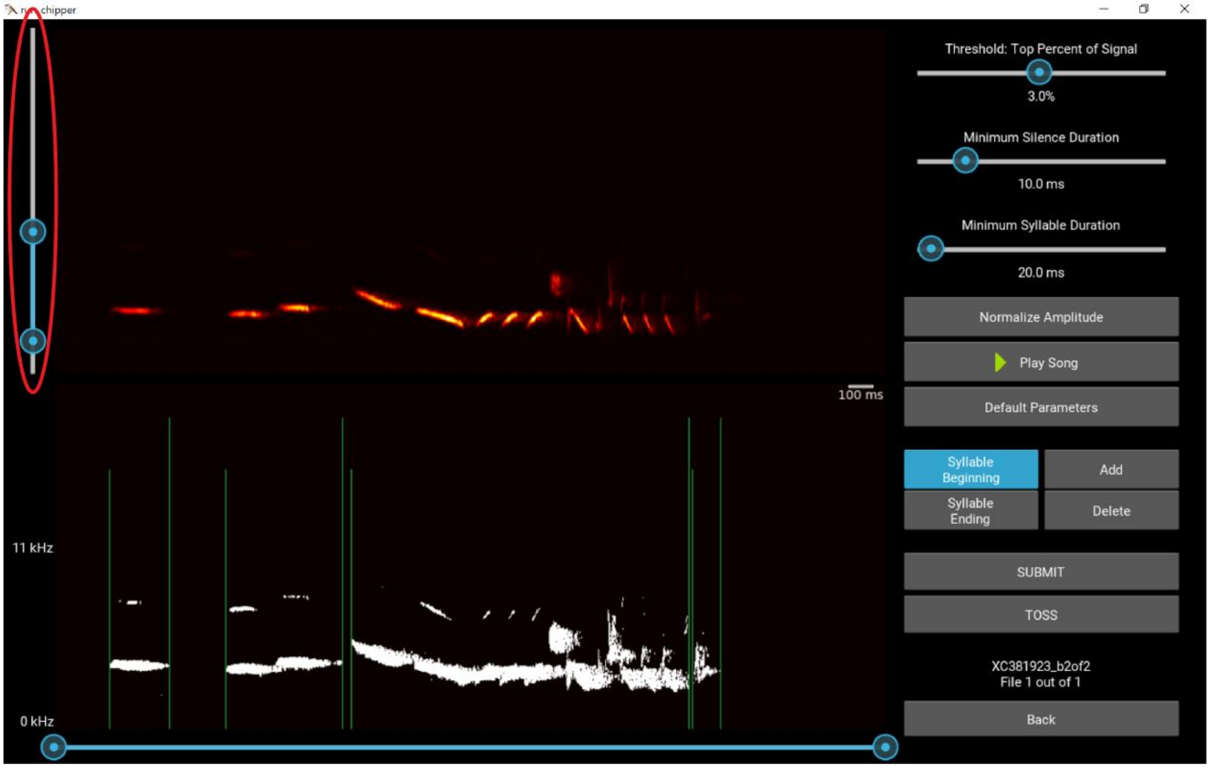
Threshold: Top Percent of Signal 3.0%

Minimum Silence Duration 10.0 ms

Minimum Syllable Duration 20.0 ms

XC381923_b2of2
File 1 out of 1

5. Adjust the low-pass and high-pass filters.



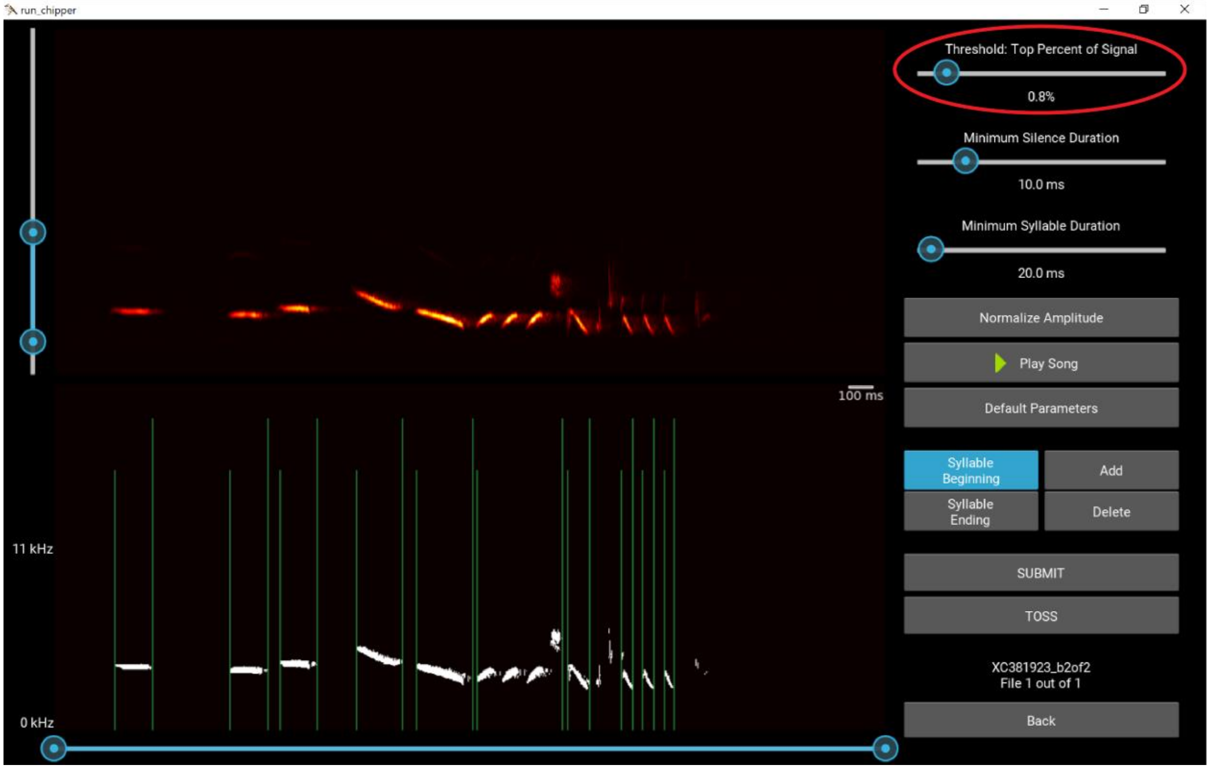
Threshold: Top Percent of Signal 3.0%

Minimum Silence Duration 10.0 ms

Minimum Syllable Duration 20.0 ms

XC381923_b2of2
File 1 out of 1

6. Adjust the signal threshold to reduce noise. (You may come back and tweak this again.)



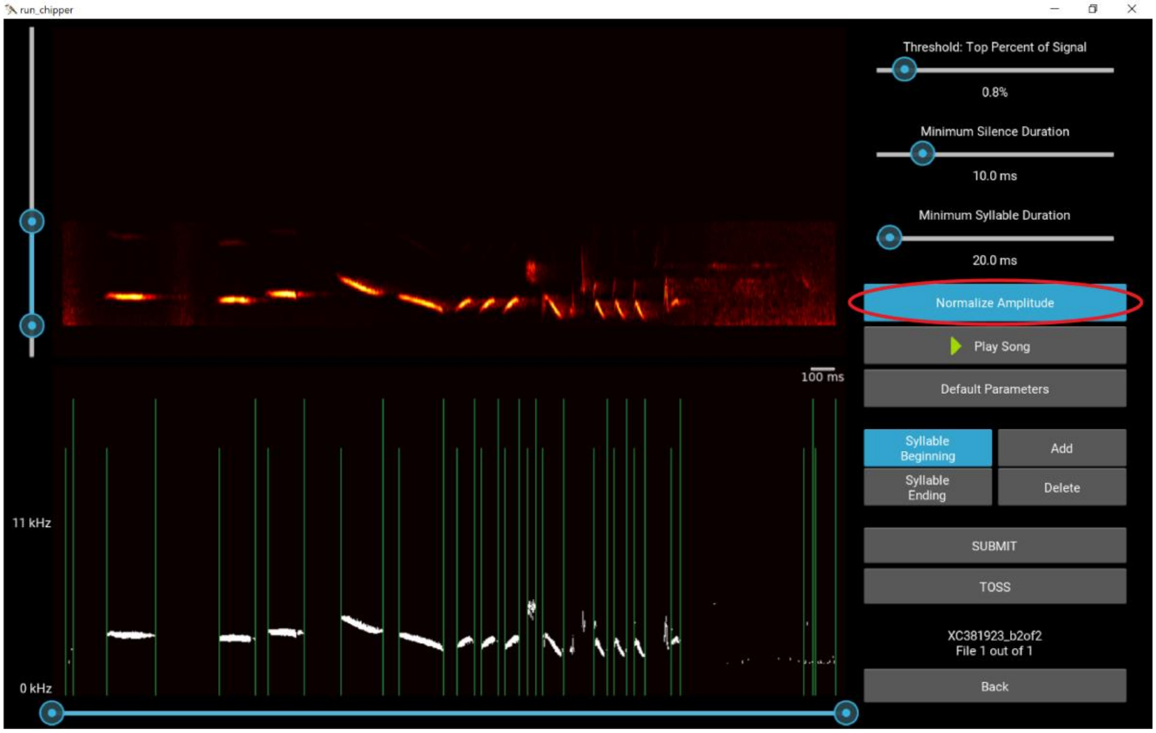
Threshold: Top Percent of Signal 0.8%

Minimum Silence Duration 10.0 ms

Minimum Syllable Duration 20.0 ms

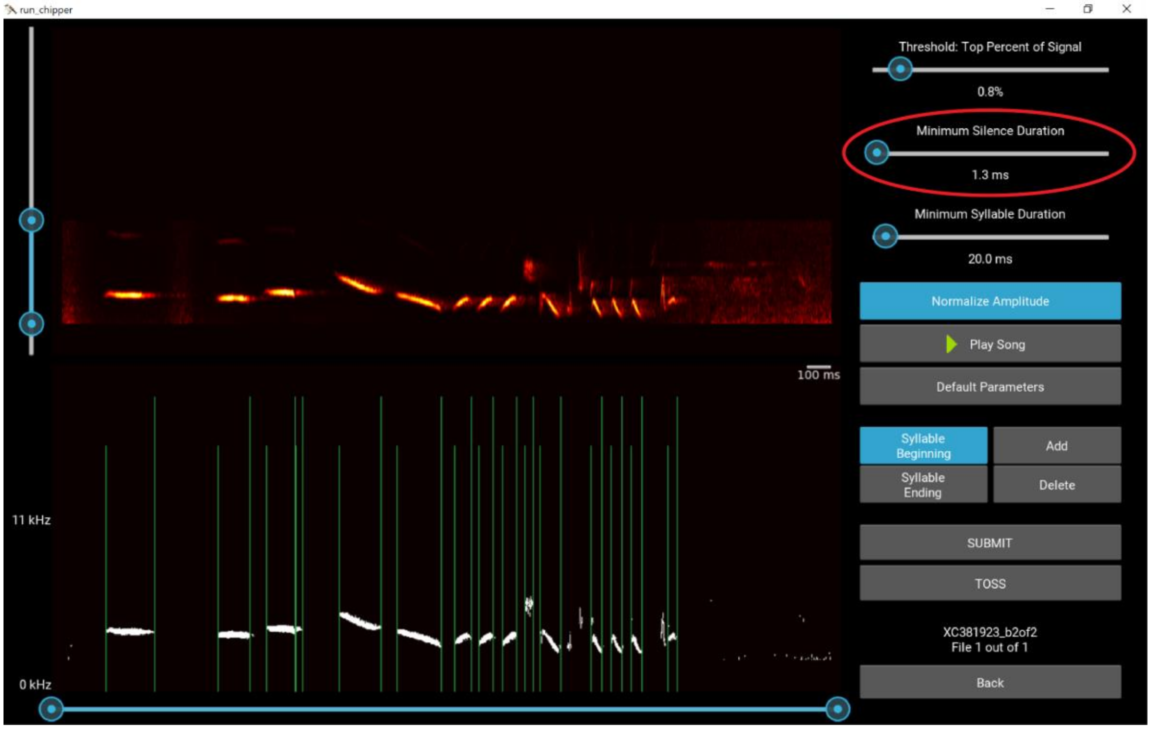
XC381923_b2of2
File 1 out of 1

7. Select Normalize Amplitude as some of the small syllables (especially the one on the right end) are fading away with the reduction in signal threshold.



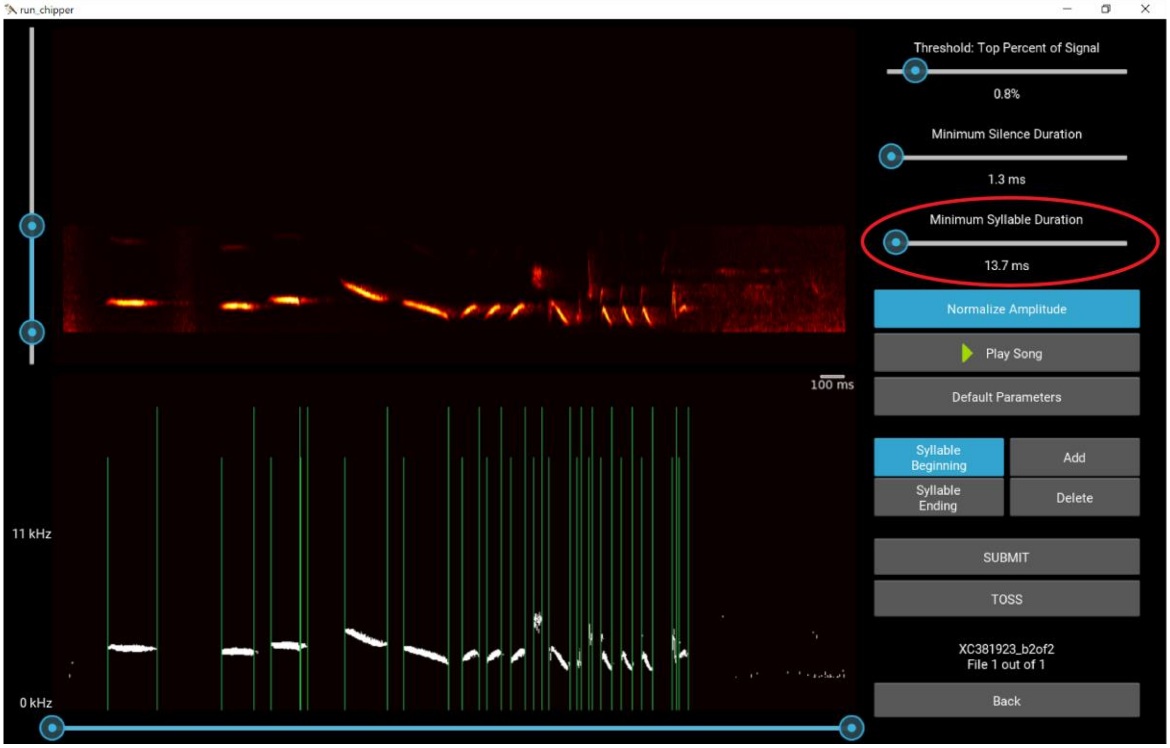
Threshold: Top Percent of Signal
0.8%
Minimum Silence Duration
10.0 ms
Minimum Syllable Duration
20.0 ms
XC381923_b2of2
File 1 out of 1

8. Adjust minimum silence duration. This both got rid of some of the onsets and offsets around noise on the ends of the song as well as some of the noise at the end of syllables that appears to be an echo.



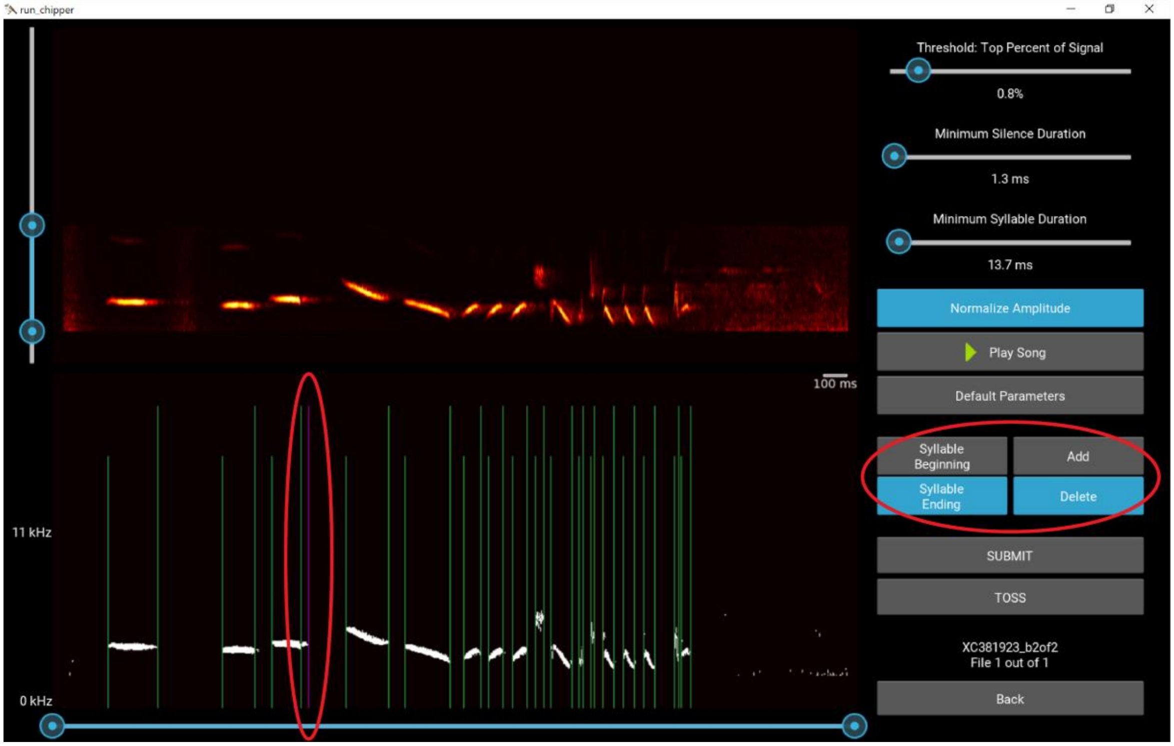
Threshold: Top Percent of Signal
0.8%
Minimum Silence Duration
1.3 ms
Minimum Syllable Duration
20.0 ms
XC381923_b2of2
File 1 out of 1

9. Use minimum syllable duration to correctly parse the beginning of the last syllable and the two small syllables in the middle of the song that have no onsets or offsets.

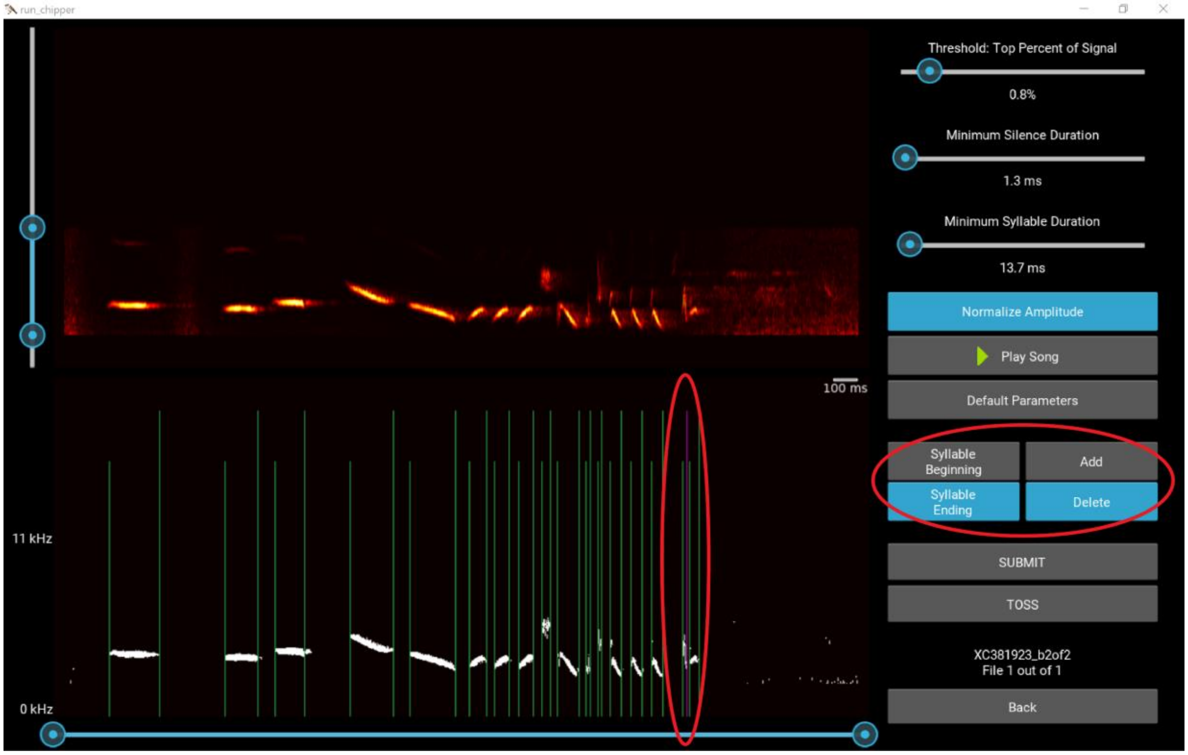


Threshold: Top Percent of Signal
0.8%
Minimum Silence Duration
1.3 ms
Minimum Syllable Duration
13.7 ms
XC381923_b2of2
File 1 out of 1

10. Add/Delete any onsets/offsets that are missing or extraneous. Here we delete two syllable beginnings and two syllable endings.



Threshold: Top Percent of Signal
0.8%
Minimum Silence Duration
1.3 ms
Minimum Syllable Duration
13.7 ms
XC381923_b2of2
File 1 out of 1

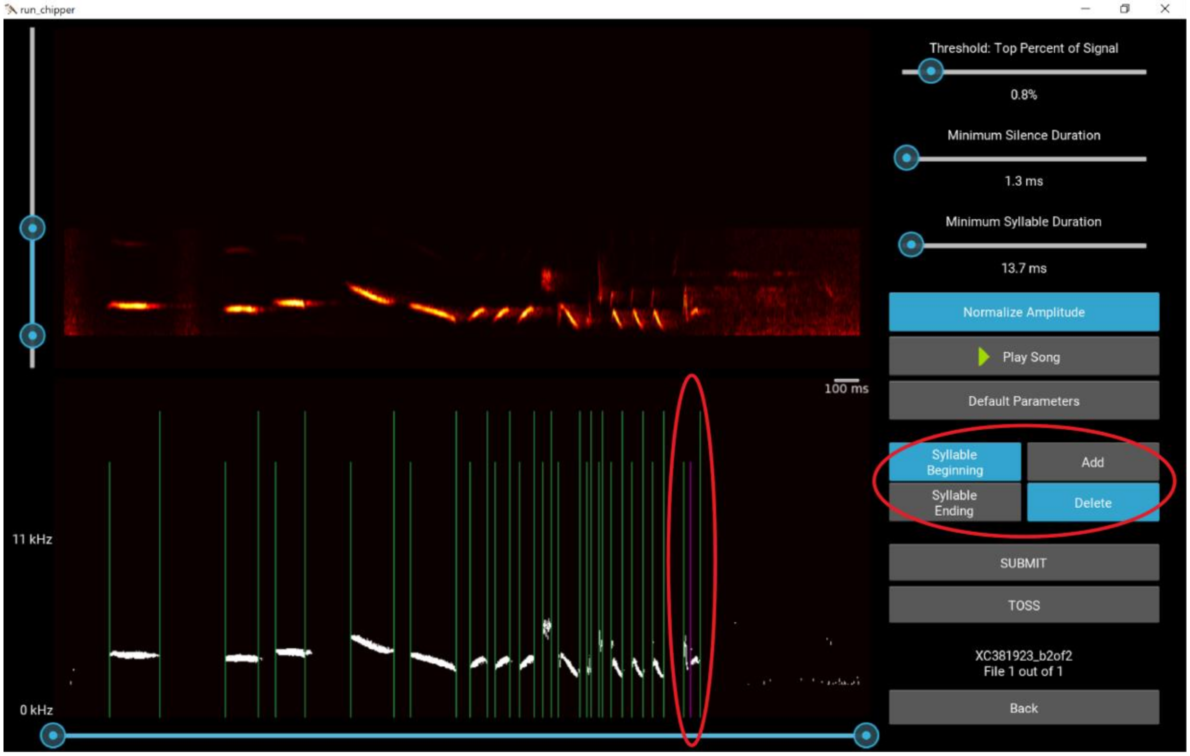


Threshold: Top Percent of Signal
0.8%

Minimum Silence Duration
1.3 ms

Minimum Syllable Duration
13.7 ms

XC381923_b2of2
File 1 out of 1



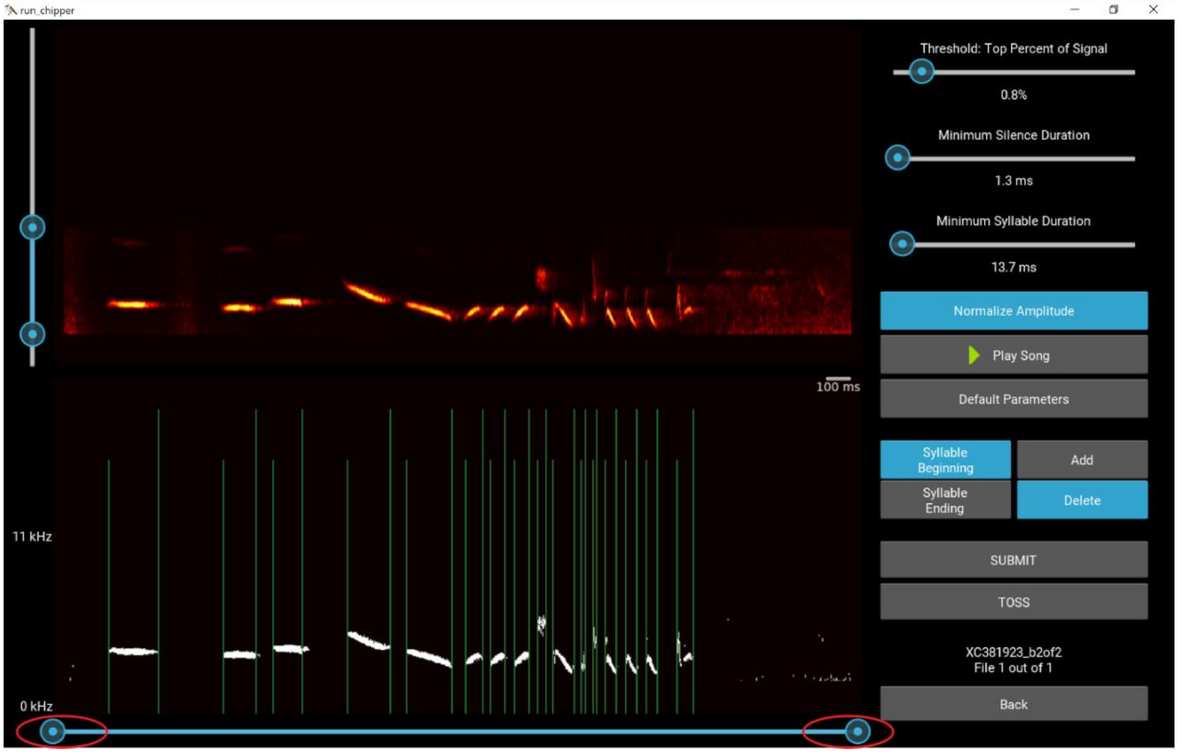
Threshold: Top Percent of Signal
0.8%

Minimum Silence Duration
1.3 ms

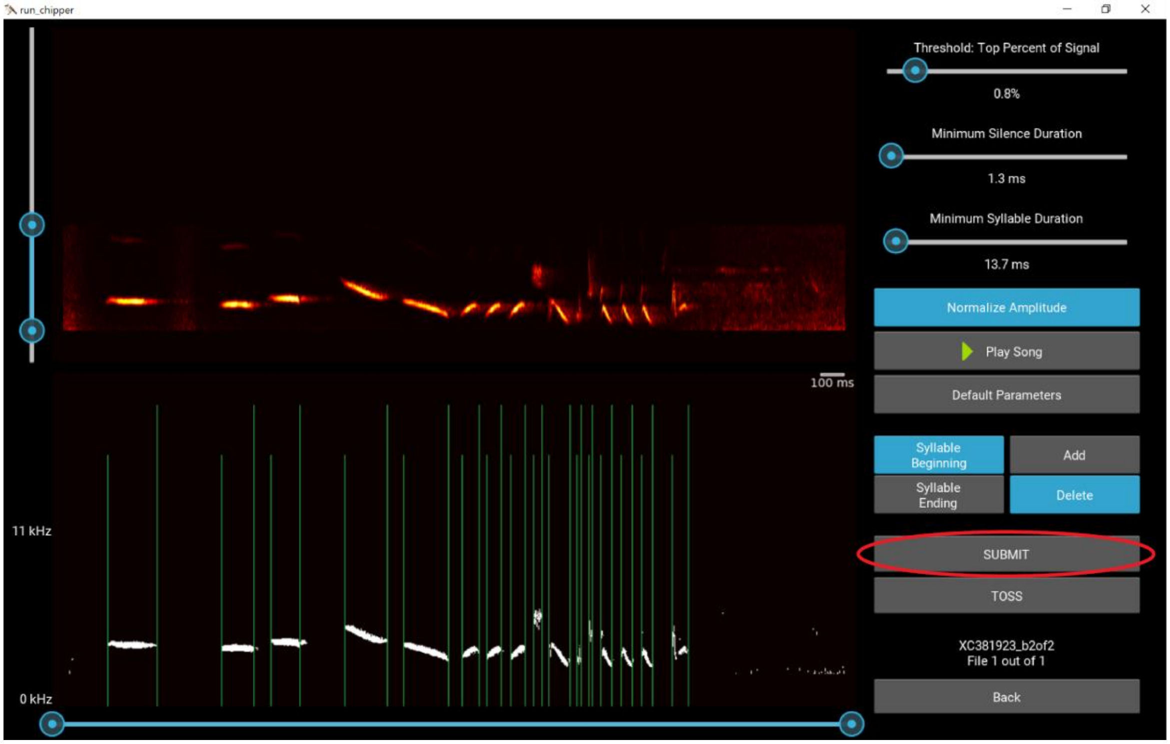
Minimum Syllable Duration
13.7 ms

XC381923_b2of2
File 1 out of 1

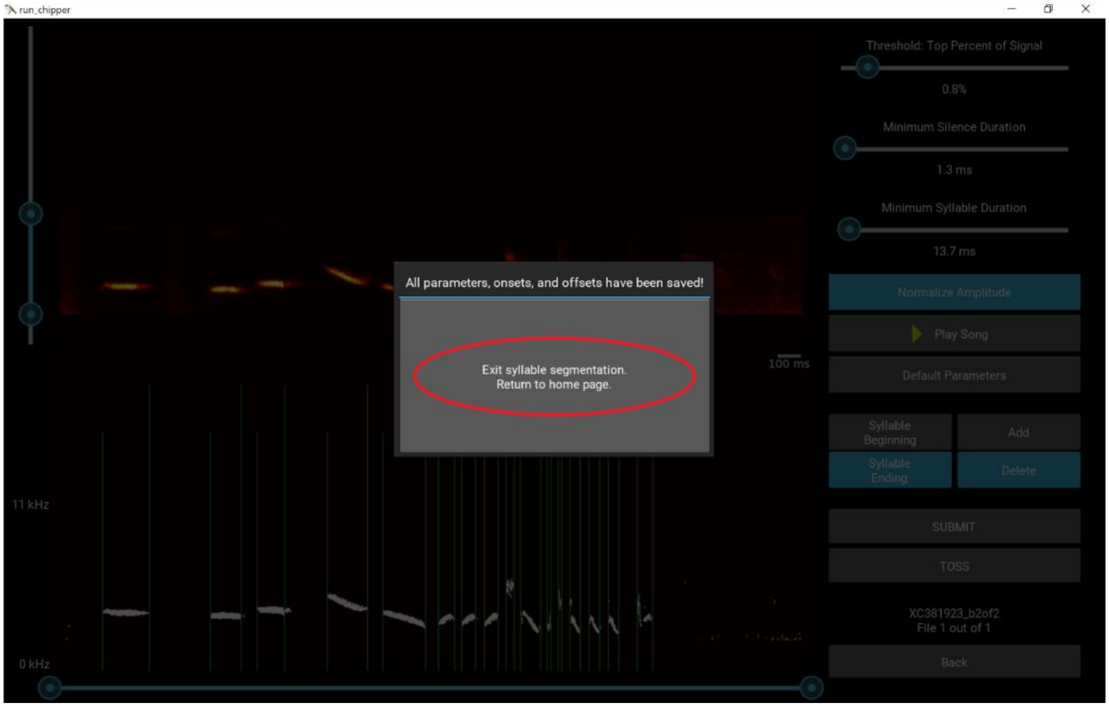
11. If the noise at the beginning and end of the song were still being parsed as syllables (which is not the case here), you could adjust the bottom slider to crop from the left and right.



12. Segmentation looks good, select Submit!



13. Exit Syllable Segmentation and return to the landing page where you can continue to parse another folder of WAV files or can continue with this set in the threshold widgets and analysis.



Threshold: Top Percent of Signal 0.8%

Minimum Silence Duration 1.3 ms

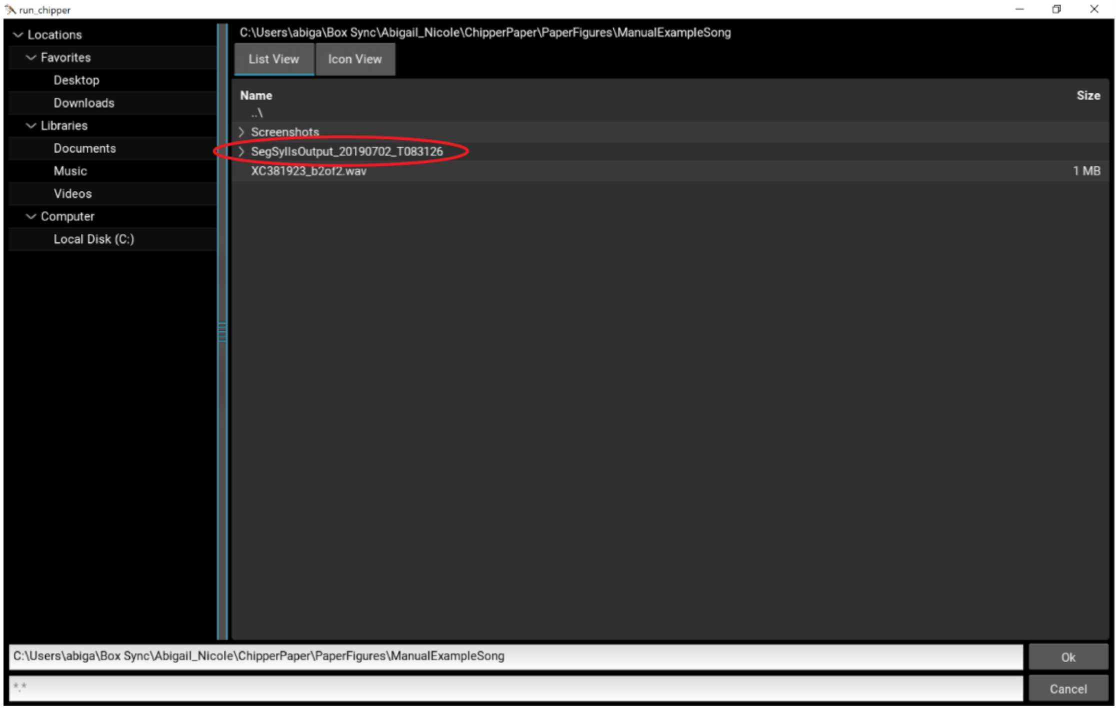
Minimum Syllable Duration 13.7 ms

XC381923_b2of2
File 1 out of 1

All parameters, onsets, and offsets have been saved!

Exit syllable segmentation.
Return to home page.

14. The output folder, *SegSyllsOutput_YYYYMMDD_THHMMSS* can now be found in the same folder as the WAV files you ran. This folder contains the four human-readable text file outputs as well as the gzips for each submitted WAV file.



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Name	Size
..\	
Screenshots	
SegSyllsOutput_20190702_T083126	
XC381923_b2of2.wav	1 MB

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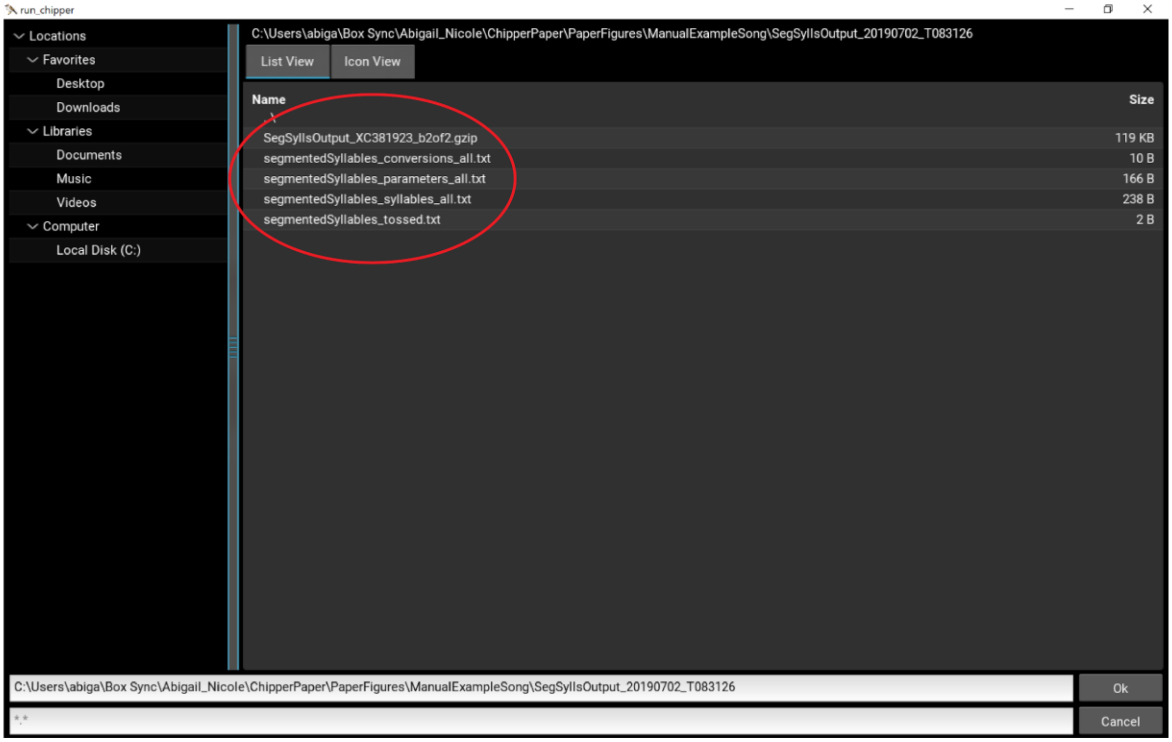

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Name	Size
SegSyllsOutput_XC381923_b2of2.gzip	119 KB
segmentedSyllables_conversions_all.txt	10 B
segmentedSyllables_parameters_all.txt	166 B
segmentedSyllables_syllables_all.txt	238 B
segmentedSyllables_tossed.txt	2 B

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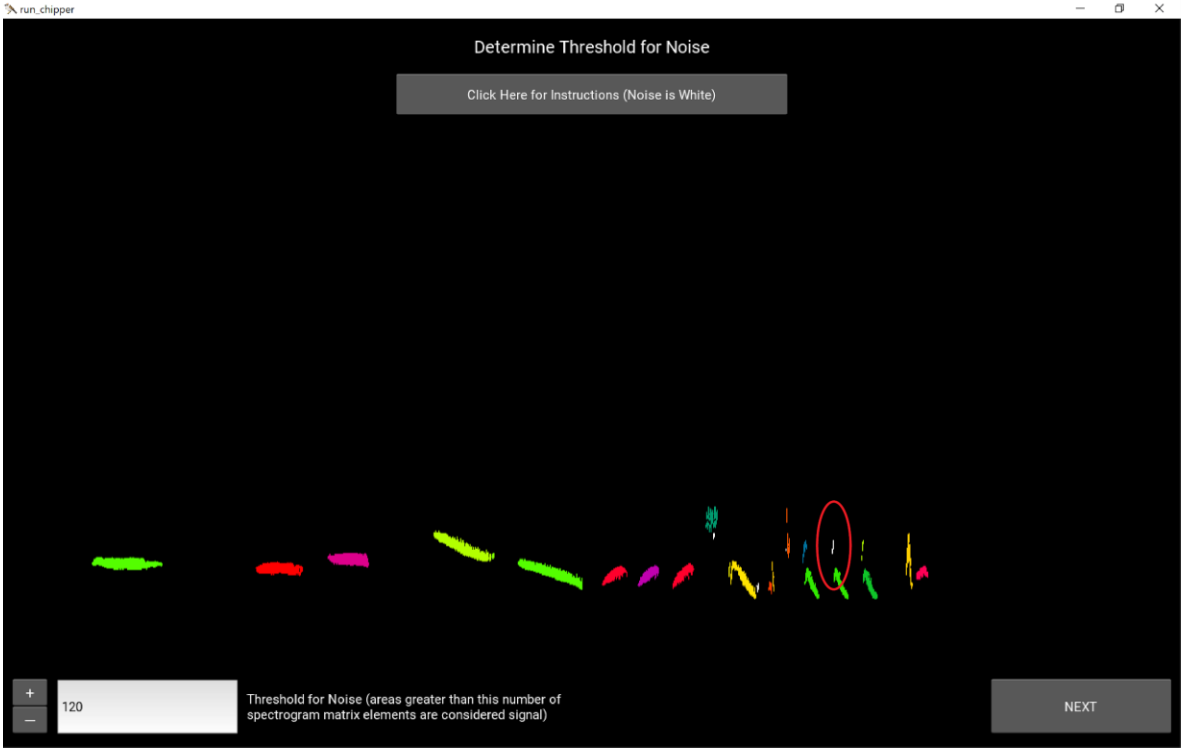
Noise Threshold Widget

The purpose of the widget is to help you determine a common size threshold for noise for all of your data. Since audio noise often appears on a spectrogram as small pieces of signal, we enable the user to set a size threshold such that sets of connected signal below (or equal to) a certain size are considered noise and not meaningful signal in your recording. Ideally, you have been able to remove all or most noise in the Syllable Segmentation process, such that this widget is primarily functioning to determine separate notes. However, removing small pieces of noise can also be accomplished by setting this threshold.

We recommend you perform this step for a set of songs from the same species. Specifically, you can use a subset of your data (~20 songs) to determine the threshold. You will adjust the threshold for each song until satisfied with the results. A summary of the thresholds used for the sample songs will be given at the end. Then, you will be given the chance to adjust the final threshold to be used in song analysis. You can return to this widget as many times as you wish to visualize the chosen threshold for any songs of interest.

The colors are to help you distinguish separate notes. A note is considered to be a set of connected elements (by edges not corners, e.g. 4-connected) in the binary spectrogram having an area greater than the noise threshold. So, if two notes very close to one another appear separate and are the same color, they are most likely one note. This may be due to the limits of screen resolution. If the area of a note is less than or equal to the noise threshold, it will be considered noise, appearing white in the spectrogram. Noise will not be considered in the analysis calculations.

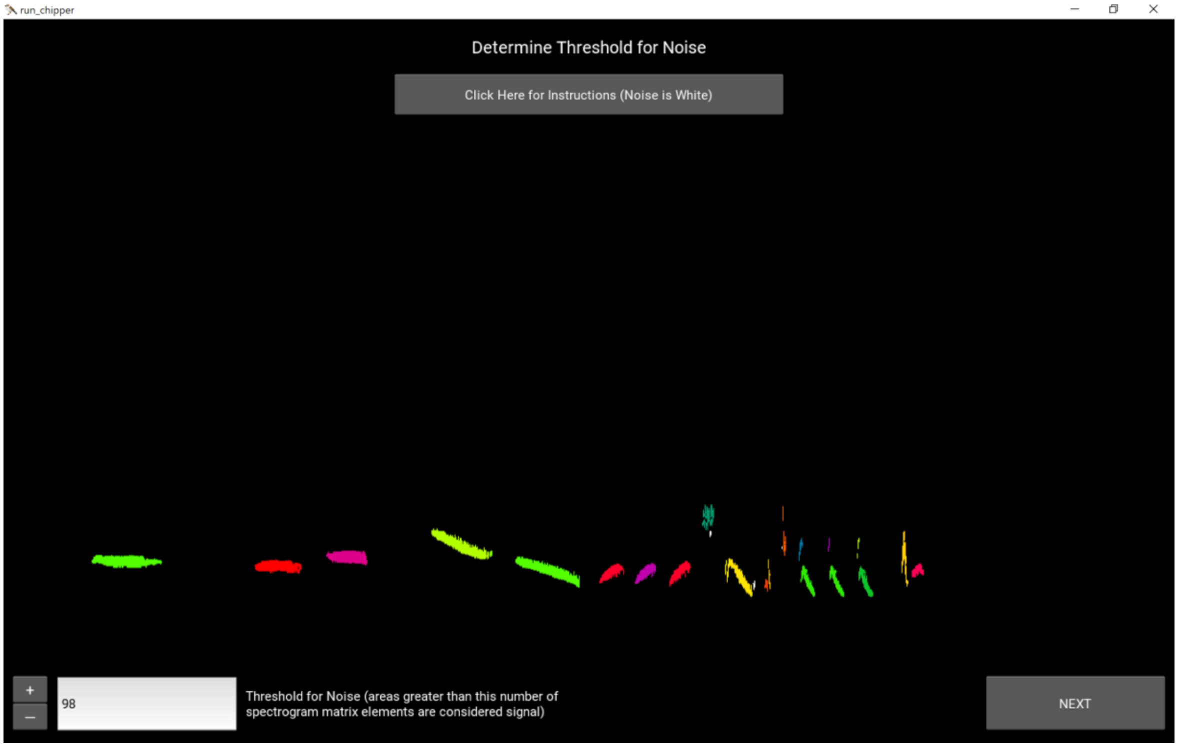
Below is the example song with the *default* noise threshold. In this case, there only looks to be one syllable with signal that is incorrectly labeled as noise. This signal (circled below) is shown in white, indicating it has few enough spectrogram matrix elements to be considered noise. If we reduce the threshold, smaller notes will be considered signal instead of noise.



120

Threshold for Noise (areas greater than this number of spectrogram matrix elements are considered signal)

Reducing the noise threshold, the second note of the syllable is now correctly labeled. Here is the example song with the *adjusted* noise threshold.



98

Threshold for Noise (areas greater than this number of spectrogram matrix elements are considered signal)

Syllable Similarity Threshold Widget

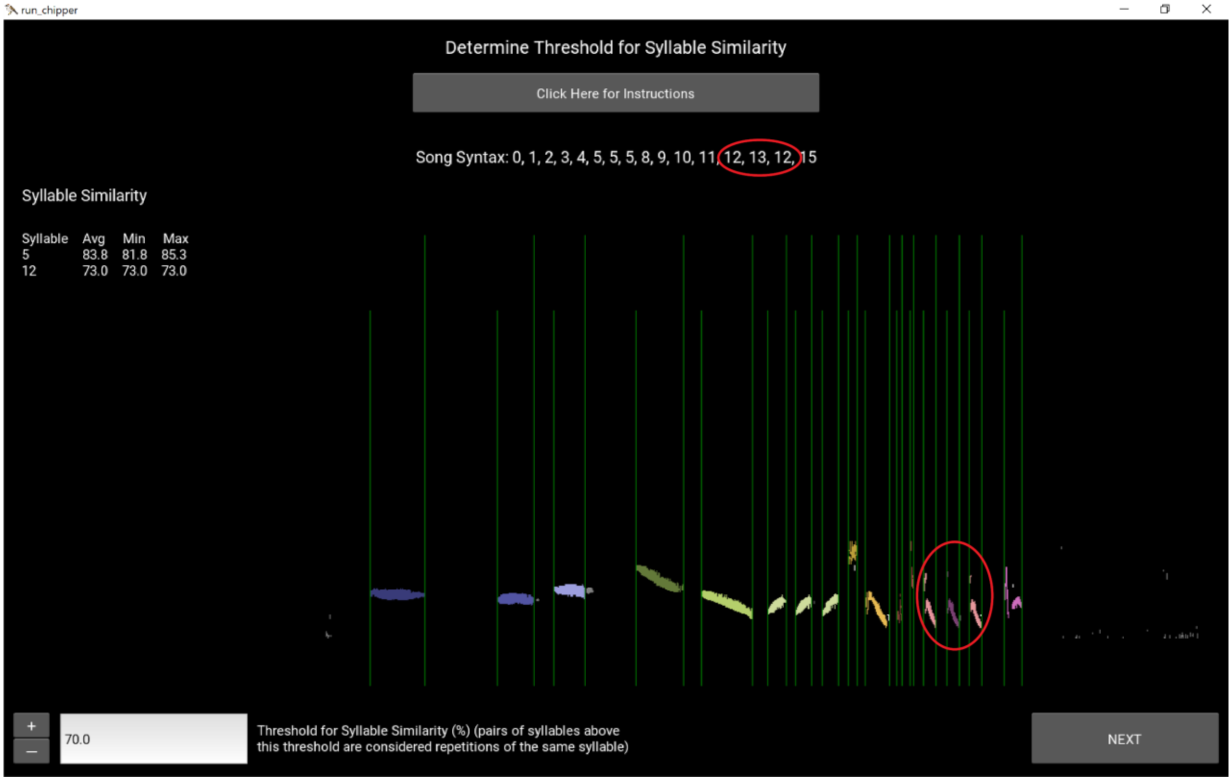
The purpose of the widget is to help you determine a common threshold for syllable similarity for all of your data. When syllables are compared with one another in Chipper, syllables that are more similar to each other than this threshold value (or equal to) will be considered repetitions of the same syllable.

We recommend you perform this step for a set of songs from the same species. Specifically, you can use a subset of your data (~20 songs) to determine the threshold. You will adjust the threshold for each song until satisfied with the results. A summary of the thresholds used for the sample songs will be given at the end. Then, you will be given the chance to adjust the final threshold to be used in song analysis. You can return to this widget as many times as you wish to visualize the segmentation and chosen threshold for any songs of interest.

The colors are to help you distinguish the syntax of the song, which is also written numerically above the spectrogram. Two syllables are considered to be identical if they overlap with an accuracy greater than or equal to the syllable similarity threshold. The syntax is found sequentially, meaning if the second syllable is found to be the same as the first, and the third syllable is found to be the same as the second but not the first, the third will still be the same as both the first and second syllables. To help, the average, minimum, and maximum percent similarity between like syllables is also provided. Note: the minimum can potentially be less than the threshold because syntax is found sequentially.

In the spectrograms shown in this widget, any signal between syllables will be grey and will not be considered in the analysis. Similarly, any noise (determined using the Noise Threshold from the previous step) will be white and will not be considered in the analysis.

Below is the example song with the *default* syllable similarity threshold. In this case, the syntax is close to what we would consider correct for this bird; however, there are a set of three similar syllables at the end that are labeled “12, 13, 12”.



Determine Threshold for Syllable Similarity

Song Syntax: 0, 1, 2, 3, 4, 5, 5, 5, 8, 9, 10, 11, 12, 13, 12, 15

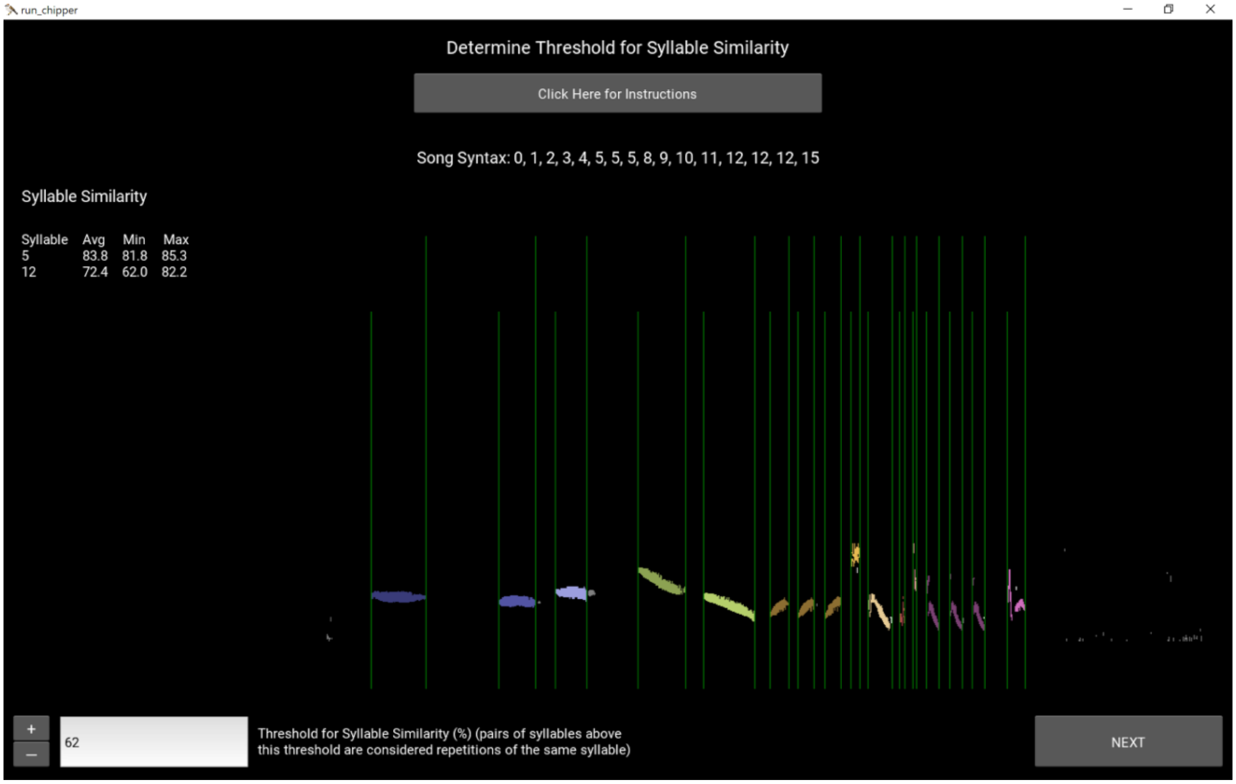
Syllable Similarity

Syllable	Avg	Min	Max
5	83.8	81.8	85.3
12	73.0	73.0	73.0

70.0

Threshold for Syllable Similarity (%) (pairs of syllables above this threshold are considered repetitions of the same syllable)

Adjusting the syllable similarity threshold allows us to reach the correct syntax. Here is the example song with the *adjusted* syllable similarity threshold.



Determine Threshold for Syllable Similarity

Song Syntax: 0, 1, 2, 3, 4, 5, 5, 5, 8, 9, 10, 11, 12, 12, 12, 15

Syllable Similarity

Syllable	Avg	Min	Max
5	83.8	81.8	85.3
12	72.4	62.0	82.2

62

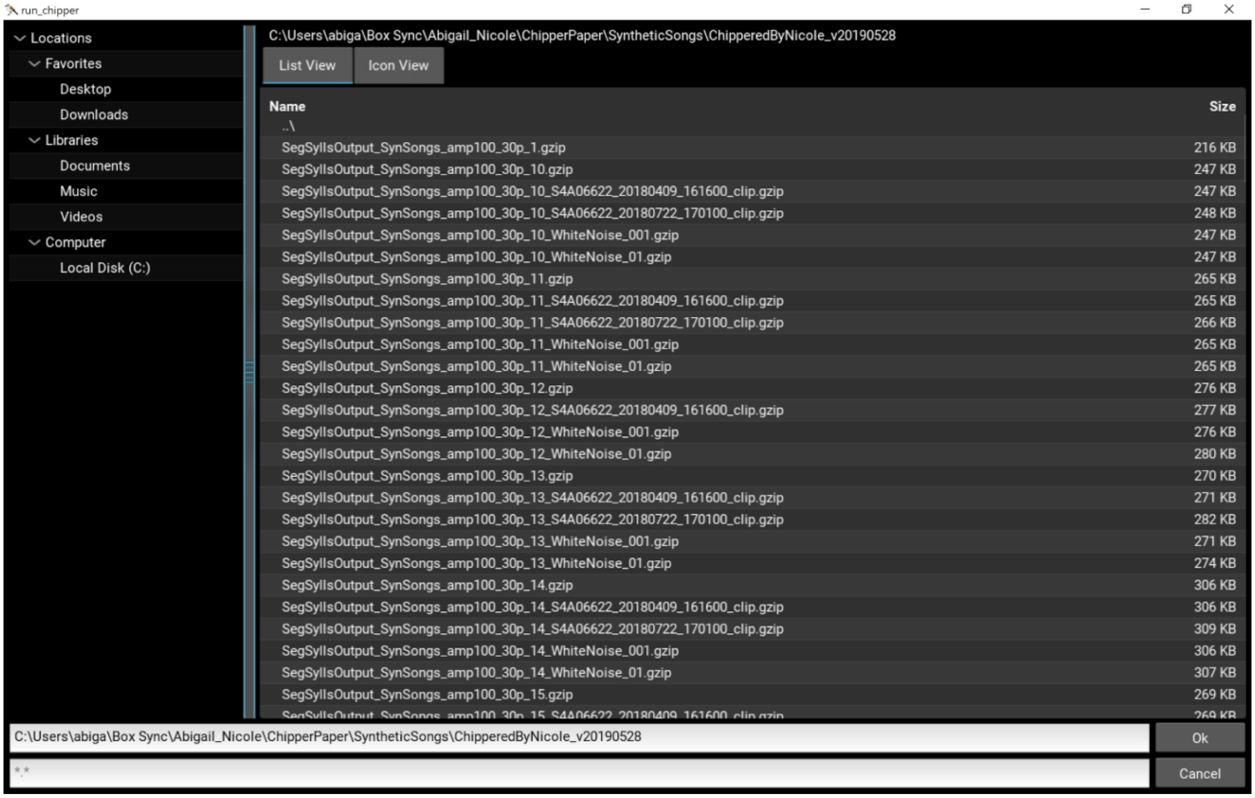
Threshold for Syllable Similarity (%) (pairs of syllables above this threshold are considered repetitions of the same syllable)

Running Analysis

The Noise Threshold and Syllable Similarity Threshold specified on the landing page will be used in Song Analysis. If you have not used the two widgets to determine appropriate thresholds, we recommend doing so before running Song Analysis. Users should be cautious of any note and syntax measurements made in analysis without first finding appropriate thresholds for their data. Similarly, if the user is not concerned with note and syntax information and they are confident they have removed all noise that would artificially raise or lower the frequency measurements, these thresholds can be lowered for analysis.

Starting Song Analysis will first take you to a file explorer to choose a folder of gzip outputs from Syllable Segmentation.

Note: The gzips do not have to be in their original output folder; the user could have moved them to a new location. If other file types are in the same folder, they will be ignored.



C:\Users\abiga\Box Sync\Abigail_Nicole\ChipperPaper\SyntheticSongs\ChipperedByNicole_v20190528

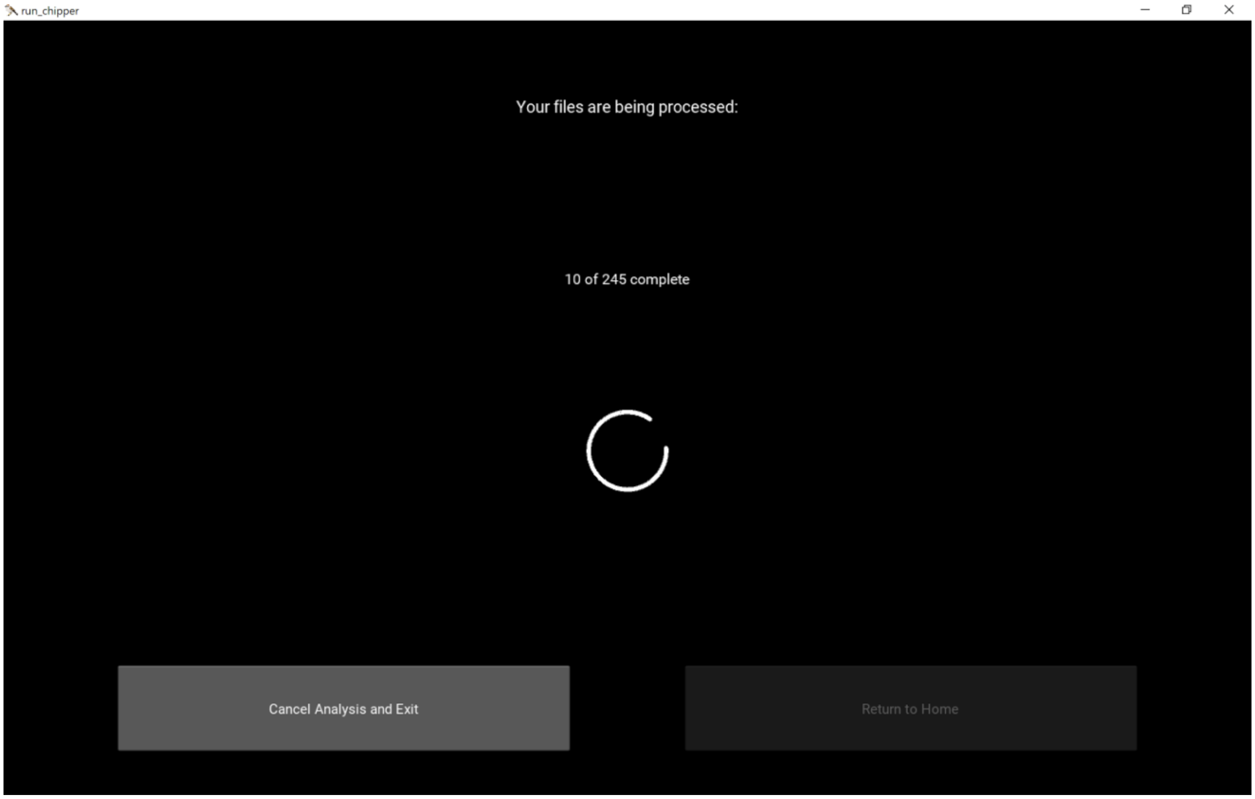
Name	Size
..\	
SegSyllsOutput_SynSongs_amp100_30p_1.gzip	216 KB
SegSyllsOutput_SynSongs_amp100_30p_10.gzip	247 KB
SegSyllsOutput_SynSongs_amp100_30p_10_S4A06622_20180409_161600_clip.gzip	247 KB
SegSyllsOutput_SynSongs_amp100_30p_10_S4A06622_20180722_170100_clip.gzip	248 KB
SegSyllsOutput_SynSongs_amp100_30p_10_WhiteNoise_001.gzip	247 KB
SegSyllsOutput_SynSongs_amp100_30p_10_WhiteNoise_01.gzip	247 KB
SegSyllsOutput_SynSongs_amp100_30p_11.gzip	265 KB
SegSyllsOutput_SynSongs_amp100_30p_11_S4A06622_20180409_161600_clip.gzip	265 KB
SegSyllsOutput_SynSongs_amp100_30p_11_S4A06622_20180722_170100_clip.gzip	266 KB
SegSyllsOutput_SynSongs_amp100_30p_11_WhiteNoise_001.gzip	265 KB
SegSyllsOutput_SynSongs_amp100_30p_11_WhiteNoise_01.gzip	265 KB
SegSyllsOutput_SynSongs_amp100_30p_12.gzip	276 KB
SegSyllsOutput_SynSongs_amp100_30p_12_S4A06622_20180409_161600_clip.gzip	277 KB
SegSyllsOutput_SynSongs_amp100_30p_12_WhiteNoise_001.gzip	276 KB
SegSyllsOutput_SynSongs_amp100_30p_12_WhiteNoise_01.gzip	280 KB
SegSyllsOutput_SynSongs_amp100_30p_13.gzip	270 KB
SegSyllsOutput_SynSongs_amp100_30p_13_S4A06622_20180409_161600_clip.gzip	271 KB
SegSyllsOutput_SynSongs_amp100_30p_13_S4A06622_20180722_170100_clip.gzip	282 KB
SegSyllsOutput_SynSongs_amp100_30p_13_WhiteNoise_001.gzip	271 KB
SegSyllsOutput_SynSongs_amp100_30p_13_WhiteNoise_01.gzip	274 KB
SegSyllsOutput_SynSongs_amp100_30p_14.gzip	306 KB
SegSyllsOutput_SynSongs_amp100_30p_14_S4A06622_20180409_161600_clip.gzip	306 KB
SegSyllsOutput_SynSongs_amp100_30p_14_S4A06622_20180722_170100_clip.gzip	309 KB
SegSyllsOutput_SynSongs_amp100_30p_14_WhiteNoise_001.gzip	306 KB
SegSyllsOutput_SynSongs_amp100_30p_14_WhiteNoise_01.gzip	307 KB
SegSyllsOutput_SynSongs_amp100_30p_15.gzip	269 KB
SegSyllsOutput_SynSongs_amp100_30p_15_S4A06622_20180409_161600_clip.gzip	269 KB

C:\Users\abiga\Box Sync\Abigail_Nicole\ChipperPaper\SyntheticSongs\ChipperedByNicole_v20190528

.

A popup will appear with the number of gzips that will be processed. You can either select "Back" or "Run". When "Run" is selected, a new progress page will appear (see below). The number of files will be incremented as the analysis is completed. Any errors in analysis should throw an exception, printing the error to the analysis page and skipping the current gzip; the error messages will also be logged in a text file named

AnalysisOutput_YYYYMMDD_THHMMSS_error_log. While Song Analysis is running, if needed, use the active button to “Cancel Analysis and Exit” Chipper.



When all gzips are completed, the spinning wheel will no longer be present, and the button “Return to Home” will become active. Two Song Analysis output files can now be found in the folder you analyzed:

1. *AnalysisOutput_YYYYMMDD_THHMMSS_songsylls* with measurements pertaining to the song and syllables.
2. *AnalysisOutput_YYYYMMDD_THHMMSS_notes* with measurements pertaining to the notes. The user should be careful using these measurements, as noisy song files will not have accurate note information due to disconnected signal. In other words, when a syllable is segmented from a noisy file, the signal is likely to be broken up into pieces that are not actually separate notes sung by the bird. Thus, note measurements should be used with caution from field recordings unless the user is confident that syllables are parsed correctly into notes. The user can always visualize the notes using the Noise Threshold widget.

Analysis Output

Together the *AnalysisOutput_YYYYMMDD_THHMMSS_songsylls* and *AnalysisOutput_YYYYMMDD_THHMMSS_notes* files include 42 measurements for all gzips run through Song Analysis and the two thresholds submitted by the user for the calculations.

Noise Threshold is used to remove any connected signal with an area less than or equal to the submitted parameter. This is done first, such that all note-related and frequency-related calculations will be affected by this last bit of “cleaning”. Any calculations that exclusively use the onsets and offsets (e.g. syllable duration, silence duration) will not be affected.

Syllable Similarity Threshold is used to determine if two syllables are considered to be repetitions of the same syllable. This affects syllable pattern (syntax) and any measures associated with it—syllable pattern, sequential repetition, syllable stereotypy, and mean and standard deviation of syllable stereotypy.

All Syllable calculations are conducted on the signal between onsets and offsets (i.e. signal that occurs between syllables is not analyzed).

For definitions of each of the measurements see the table below; for more detailed information see https://github.com/CreanzaLab/chipper/blob/master/chipper/analysis.py.

Term	Calculation
avg_note_duration(ms)	mean(time of note ending − time of beginning)
avg_notes_freq_range(Hz)	mean(maximum frequency − minimum frequency for each note)
avg_notes_lower_freq(Hz)	mean(minimum frequency of each note)
avg_notes_upper_freq(Hz)	mean(maximum frequency of each note)
avg_silence_duration(ms)	mean(time of syllable onset − time of previous syllable offset)
avg_syllable_duration(ms)	mean(time of syllable offset − time of syllable onset)
avg_sylls_freq_range(Hz)	mean(maximum frequency − minimum frequency for each syllable)
avg_sylls_lower_freq(Hz)	mean(minimum frequency of each syllable)
avg_sylls_upper_freq(Hz)	mean(maximum frequency of each syllable)
bout_duration(ms)	(time of last syllable offset − time of first syllable onset)
largest_note_duration(ms)	max(time of note ending − time of note beginning)
largest_notes_freq_range(Hz)	max(maximum frequency − minimum frequency for each note)
largest_silence_duration(ms)	max(time of syllable onset − time of previous syllable offset)
largest_syllable_duration(ms)	max(time of syllable offset − time of syllable onset)

largest_sylls_freq_range(Hz)	max(maximum frequency − minimum frequency for each syllable)
max_notes_freq(Hz)	max(maximum frequency of each note)
max_sylls_freq(Hz)	max(maximum frequency of each syllable)
mean_syllable_stereotypy	mean(stereotypy values for each repeated syllable) [see syllable_stereotypy definition below]
min_notes_freq(Hz)	min(minimum frequency of each note)
min_sylls_freq(Hz)	min(minimum frequency of each syllable)
noise_threshold	provided by user (Noise Threshold) [see Noise Threshold Widget] Note: Clusters of signal (4-connected elements of the spectrogram) that have an area larger than this threshold are considered notes, and those less than or equal to this threshold are considered noise and removed from analysis.
num_notes	number of 4-connected elements of the spectrogram with an area greater than the noise threshold
num_notes_per_syll	(total number of notes)/(total number of syllables)
num_syllable_per_bout_duration(1/ms)	(number of syllables)/(song duration)
num_syllables	number of syllable onsets in a song
num_syllables_per_num_unique	(number of syllable onsets in a song)/(number of unique values in syllable pattern)
num_unique_syllables	number of unique values in syllable pattern
overall_notes_freq_range(Hz)	max(maximum frequency of each note) − min(minimum frequency of each note)
overall_sylls_freq_range(Hz)	max(maximum frequency of each syllable) − min(minimum frequency of each syllable)
sequential_repetition	(number of syllables that are followed by the same syllable)/(number of syllables - 1)
smallest_note_duration(ms)	min(time of note ending − time of note beginning)
smallest_notes_freq_range(Hz)	min(maximum frequency − minimum frequency for each note)
smallest_silence_duration(ms)	min(time of syllable onset − time of previous syllable offset)
smallest_syllable_duration(ms)	min(time of syllable offset − time of syllable onset)
smallest_sylls_freq_range(Hz)	min(maximum frequency − minimum frequency for each syllable)
stdev_note_duration(ms)	standard deviation(time of note ending − time of note beginning)
stdev_notes_freq_range(Hz)	standard deviation(maximum frequency − minimum frequency for each note)
stdev_silence_duration(ms)	standard deviation(time of syllable onset − time of previous syllable offset)
stdev_syllable_duration(ms)	standard deviation(time of syllable offset − time of syllable onset)

stdev_syllable_stereotypy	standard deviation(stereotypy values for each repeated syllable) [see syllable_stereotypy definition below]
stdev_sylls_freq_range(Hz)	standard deviation(maximum frequency − minimum frequency for each syllable)
syll_correlation_threshold	provided by user (Syllable Similarity Threshold) [see Syllable Similarity widget] Note: The percent similarity between any pair of syllables is defined as maximum(cross-correlation between each pair of syllables)/maximum(autocorrelation of each of the compared syllables) × 100. If this percent similarity is greater than or equal to the syll_correlation_threshold, the two syllables are considered the same.
syllable_pattern	list of the syllables in the order that they are sung, where each unique syllable (found sequentially) is assigned a number (i.e. the song syntax) [see *Syllable Similarity* widget]
syllable_stereotypy	list of the mean(pairwise percent similarities) for each repeated syllable, where percent similarity is the maximum(cross-correlation between each pair of syllables)/maximum(autocorrelation of each of the compared syllables) × 100

Contributing or Customizing Chipper

We created Chipper using open-source software so that the community can contribute to improving and adding new functionality to Chipper.

An easy place to start would be to adjust or add measurements output from Chipper's analysis. You can do this by editing the analysis.py script (https://github.com/CreanzaLab/chipper/blob/master/chipper/analysis.py). All information from segmentation and threshold determination have been added as attributes of the Song class and can be used for additional calculations.

If you would like to contribute your changes to Chipper so others can also benefit, please submit a pull request to https://github.com/CreanzaLab/chipper.

If you find any bugs or would like to suggest changes or improvements to Chipper, please create a new issue at https://github.com/CreanzaLab/chipper/issues.

APPENDIX B

CHIPPING SPARROW METADATA

We have included all metadata for the chipping sparrow songs used in Chapters 3–5. We list the Catalog numbers for every recording, the database from which the recording was acquired, the recordist, the URL where the raw song file can be found, the license type, and whether the recording was used in Chapter 3 for analysis of diel patterns.

Table B.1 Metadata for chipping sparrow songs used in all analyses.
eBird: eBird; ML: Macaulay Library; W-c.L.: Wan-chun Liu; BLB: Borror Laboratory of Bioacoustics; XC: Xeno-canto

CatalogNo	From	Recordist	URL	License Type	Diel
75281061	eBird	Alice Andrade	https://macaulaylibrary.org/asset/75281061	Student/Researcher	Yes
75263881	eBird	Alice Andrade	https://macaulaylibrary.org/asset/75263881	Student/Researcher	Yes
75257731	eBird	Alice Andrade	https://macaulaylibrary.org/asset/75257731	Student/Researcher	Yes
72202241	eBird	Gregory Budney	https://macaulaylibrary.org/asset/72202241	Student/Researcher	Yes
70160751	eBird	Katie Henderson	https://macaulaylibrary.org/asset/70160751	Student/Researcher	Yes
67470971	eBird	Nick Roth	https://macaulaylibrary.org/asset/67470971	Student/Researcher	Yes
67370131	eBird	Nick Roth	https://macaulaylibrary.org/asset/67370131	Student/Researcher	Yes
65614601	eBird	Adam Richardson	https://macaulaylibrary.org/asset/65614601	Student/Researcher	Yes
65614601	eBird	Adam Richardson	https://macaulaylibrary.org/asset/65614601	Student/Researcher	Yes
65256221	eBird	Pamela Ford	https://macaulaylibrary.org/asset/65256221	Student/Researcher	
64713371	eBird	Justin Watts	https://macaulaylibrary.org/asset/64713371	Student/Researcher	Yes
64640681	eBird	LynnErla Beegle	https://macaulaylibrary.org/asset/64640681	Student/Researcher	Yes
64129161	eBird	Kaylin Ingalls	https://macaulaylibrary.org/asset/64129161	Student/Researcher	Yes
64041271	eBird	Hal Mitchell	https://macaulaylibrary.org/asset/64041271	Student/Researcher	Yes
63757551	eBird	Christine Stoughton Root	https://macaulaylibrary.org/asset/63757551	Student/Researcher	Yes
63496741	eBird	Brad Walker	https://macaulaylibrary.org/asset/63496741	Student/Researcher	Yes
63391781	eBird	Jim Tietz	https://macaulaylibrary.org/asset/63391781	Student/Researcher	Yes

62976331	eBird	Brad Walker	https://macaulaylibrary.org/asset/62976331	Student/Researcher	Yes
30946051	eBird	Jay McGowan	https://macaulaylibrary.org/asset/30946051	Student/Researcher	Yes
51073421	eBird	Michael Morris	https://macaulaylibrary.org/asset/51073421	Student/Researcher	Yes
56336181	eBird	Brad Walker	https://macaulaylibrary.org/asset/56336181	Student/Researcher	Yes
62880971	eBird	Damon Haan	https://macaulaylibrary.org/asset/62880971	Student/Researcher	Yes
62788091	eBird	Linda Ireland	https://macaulaylibrary.org/asset/62788091	Student/Researcher	Yes
62595431	eBird	Kenny Frisch	https://macaulaylibrary.org/asset/62595431	Student/Researcher	Yes
62534811	eBird	Steven Biggers	https://macaulaylibrary.org/asset/62534811	Student/Researcher	Yes
62507851	eBird	Mhairi McFarlane	https://macaulaylibrary.org/asset/62507851	Student/Researcher	Yes
62503991	eBird	Wil Hershberger	https://macaulaylibrary.org/asset/62503991	Student/Researcher	Yes
62047421	eBird	Cory "Chia" Chiappone	https://macaulaylibrary.org/asset/62047421	Student/Researcher	Yes
61916011	eBird	Jay McGowan	https://macaulaylibrary.org/asset/61916011	Student/Researcher	Yes
61752381	eBird	manuel grosselet	https://macaulaylibrary.org/asset/61752381	Student/Researcher	Yes
61683011	eBird	Sarah Taylor	https://macaulaylibrary.org/asset/61683011	Student/Researcher	Yes
61229511	eBird	Guillermo Funes	https://macaulaylibrary.org/asset/61229511	Student/Researcher	Yes
61110051	eBird	Dave Slager	https://macaulaylibrary.org/asset/61110051	Student/Researcher	Yes
61069461	eBird	David McQuade	https://macaulaylibrary.org/asset/61069461	Student/Researcher	Yes
60991241	eBird	Glen Chapman	https://macaulaylibrary.org/asset/60991241	Student/Researcher	Yes
60937361	eBird	Bill Tollefson	https://macaulaylibrary.org/asset/60937361	Student/Researcher	Yes
60835531	eBird	Jeff Ellerbusch	https://macaulaylibrary.org/asset/60835531	Student/Researcher	Yes
60825391	eBird	Alex Merritt	https://macaulaylibrary.org/asset/60825391	Student/Researcher	Yes
59630451	eBird	Dennis Leonard	https://macaulaylibrary.org/asset/59630451	Student/Researcher	Yes
59229281	eBird	Neill Vanhinsberg	https://macaulaylibrary.org/asset/59229281	Student/Researcher	Yes
59170581	eBird	Ryan Andrews	https://macaulaylibrary.org/asset/59170581	Student/Researcher	Yes
59078691	eBird	Shane Sater	https://macaulaylibrary.org/asset/59078691	Student/Researcher	Yes
58447071	eBird	Alix d'Entremont	https://macaulaylibrary.org/asset/58447071	Student/Researcher	Yes
58183101	eBird	Mike Schanbacher	https://macaulaylibrary.org/asset/58183101	Student/Researcher	Yes
57546521	eBird	Shane Sater	https://macaulaylibrary.org/asset/57546521	Student/Researcher	Yes
57546081	eBird	Shane Sater	https://macaulaylibrary.org/asset/57546081	Student/Researcher	Yes
57536381	eBird	Andrew Dreelin	https://macaulaylibrary.org/asset/57536381	Student/Researcher	Yes
57327041	eBird	Mike Hearell	https://macaulaylibrary.org/asset/57327041	Student/Researcher	Yes

57170271	eBird	Jay McGowan	https://macaulaylibrary.org/asset/57170271	Student/Researcher	Yes
57116861	eBird	Nick Kachala	https://macaulaylibrary.org/asset/57116861	Student/Researcher	Yes
57105731	eBird	David Eberly	https://macaulaylibrary.org/asset/57105731	Student/Researcher	Yes
56760661	eBird	David McCartt	https://macaulaylibrary.org/asset/56760661	Student/Researcher	Yes
56682831	eBird	Mark Greene	https://macaulaylibrary.org/asset/56682831	Student/Researcher	Yes
56466101	eBird	Luis Mendes	https://macaulaylibrary.org/asset/56466101	Student/Researcher	Yes
56335081	eBird	Andrew Aldrich	https://macaulaylibrary.org/asset/56335081	Student/Researcher	Yes
56023061	eBird	David McCartt	https://macaulaylibrary.org/asset/56023061	Student/Researcher	Yes
55941541	eBird	Fyn Kynd	https://macaulaylibrary.org/asset/55941541	Student/Researcher	Yes
55891391	eBird	Neill Vanhinsberg	https://macaulaylibrary.org/asset/55891391	Student/Researcher	Yes
55863891	eBird	Michael Rieser	https://macaulaylibrary.org/asset/55863891	Student/Researcher	Yes
55584461	eBird	Krzysztof Bystrowski	https://macaulaylibrary.org/asset/55584461	Student/Researcher	Yes
55554691	eBird	John P Richardson	https://macaulaylibrary.org/asset/55554691	Student/Researcher	Yes
55470981	eBird	Ethan M	https://macaulaylibrary.org/asset/55470981	Student/Researcher	Yes
55344231	eBird	Luis Mendes	https://macaulaylibrary.org/asset/55344231	Student/Researcher	Yes
55340881	eBird	Luis Mendes	https://macaulaylibrary.org/asset/55340881	Student/Researcher	Yes
55265651	eBird	Ed Pandolfino	https://macaulaylibrary.org/asset/55265651	Student/Researcher	Yes
55176911	eBird	Nick Varvel	https://macaulaylibrary.org/asset/55176911	Student/Researcher	Yes
55143861	eBird	Darrell Peterson	https://macaulaylibrary.org/asset/55143861	Student/Researcher	Yes
54947101	eBird	Laura Gooch	https://macaulaylibrary.org/asset/54947101	Student/Researcher	Yes
54868471	eBird	Luis Mendes	https://macaulaylibrary.org/asset/54868471	Student/Researcher	Yes
54719121	eBird	Mike McDowell	https://macaulaylibrary.org/asset/54719121	Student/Researcher	Yes
54636381	eBird	Krzysztof Bystrowski	https://macaulaylibrary.org/asset/54636381	Student/Researcher	Yes
54632481	eBird	Richard Ackley	https://macaulaylibrary.org/asset/54632481	Student/Researcher	Yes
54615501	eBird	Glen Chapman	https://macaulaylibrary.org/asset/54615501	Student/Researcher	Yes
54367981	eBird	Jeffrey Roth	https://macaulaylibrary.org/asset/54367981	Student/Researcher	Yes
54245591	eBird	Eliza Fraser	https://macaulaylibrary.org/asset/54245591	Student/Researcher	Yes
53817481	eBird	Colin Sumrall	https://macaulaylibrary.org/asset/53817481	Student/Researcher	Yes
53817461	eBird	Colin Sumrall	https://macaulaylibrary.org/asset/53817461	Student/Researcher	Yes
53487311	eBird	Matthew Schenck	https://macaulaylibrary.org/asset/53487311	Student/Researcher	Yes
53420611	eBird	Guy McGrane	https://macaulaylibrary.org/asset/53420611	Student/Researcher	Yes

53366871	eBird	Ted Nichols II	https://macaulaylibrary.org/asset/53366871	Student/Researcher	Yes
53021931	eBird	Tabitha Olsen	https://macaulaylibrary.org/asset/53021931	Student/Researcher	Yes
52971811	eBird	Paul Sellin	https://macaulaylibrary.org/asset/52971811	Student/Researcher	Yes
52867771	eBird	Hal Mitchell	https://macaulaylibrary.org/asset/52867771	Student/Researcher	Yes
52595781	eBird	Kelly Krechmer	https://macaulaylibrary.org/asset/52595781	Student/Researcher	Yes
48237091	eBird	Laura Gooch	https://macaulaylibrary.org/asset/48237091	Student/Researcher	Yes
47744191	eBird	Laura Gooch	https://macaulaylibrary.org/asset/47744191	Student/Researcher	Yes
36028431	eBird	Dominic Garcia-Hall	https://macaulaylibrary.org/asset/36028431	Student/Researcher	Yes
31668351	eBird	Andrew Aldrich	https://macaulaylibrary.org/asset/31668351	Student/Researcher	Yes
30045451	eBird	Kyle Lima	https://macaulaylibrary.org/asset/30045451	Student/Researcher	Yes
29912751	eBird	Luis Mendes	https://macaulaylibrary.org/asset/29912751	Student/Researcher	Yes
29891771	eBird	Clifford Hirst	https://macaulaylibrary.org/asset/29891771	Student/Researcher	Yes
29855421	eBird	Glen Chapman	https://macaulaylibrary.org/asset/29855421	Student/Researcher	Yes
29810211	eBird	Jay McGowan	https://macaulaylibrary.org/asset/29810211	Student/Researcher	Yes
29804411	eBird	Paul Marvin	https://macaulaylibrary.org/asset/29804411	Student/Researcher	Yes
29405651	eBird	Carl Hughes	https://macaulaylibrary.org/asset/29405651	Student/Researcher	Yes
28478521	eBird	Colin Sumrall	https://macaulaylibrary.org/asset/28478521	Student/Researcher	Yes
27647091	eBird	Evan Lipton	https://macaulaylibrary.org/asset/27647091	Student/Researcher	Yes
27646801	eBird	Evan Lipton	https://macaulaylibrary.org/asset/27646801	Student/Researcher	Yes
27575581	eBird	David Eberly	https://macaulaylibrary.org/asset/27575581	Student/Researcher	Yes
27447641	eBird	Jay McGowan	https://macaulaylibrary.org/asset/27447641	Student/Researcher	Yes
27191601	eBird	Colin Sumrall	https://macaulaylibrary.org/asset/27191601	Student/Researcher	Yes
26292371	eBird	Martin Wall	https://macaulaylibrary.org/asset/26292371	Student/Researcher	Yes
25574571	eBird	Colin Sumrall	https://macaulaylibrary.org/asset/25574571	Student/Researcher	Yes
61915841	eBird	Jay McGowan	https://macaulaylibrary.org/asset/61915841	Student/Researcher	Yes
61136181	eBird	Glen Chapman	https://macaulaylibrary.org/asset/61136181	Student/Researcher	Yes
61082981	eBird	Eric Michael	https://macaulaylibrary.org/asset/61082981	Student/Researcher	Yes
59701521	eBird	Jon G.	https://macaulaylibrary.org/asset/59701521	Student/Researcher	Yes
58237601	eBird	David Brown	https://macaulaylibrary.org/asset/58237601	Student/Researcher	Yes
56464981	eBird	Luis Mendes	https://macaulaylibrary.org/asset/56464981	Student/Researcher	Yes
47979571	eBird	Laura Gooch	https://macaulaylibrary.org/asset/47979571	Student/Researcher	Yes

31356151	eBird	Matthew Hunter	https://macaulaylibrary.org/asset/31356151	Student/Researcher	Yes
28295391	eBird	David Lugo	https://macaulaylibrary.org/asset/28295391	Student/Researcher	Yes
27432141	eBird	Colin Sumrall	https://macaulaylibrary.org/asset/27432141	Student/Researcher	Yes
527118	ML	Mark Robbins	https://macaulaylibrary.org/asset/527118	Student/Researcher	Yes
15421	ML	Arthur A. Allen	https://macaulaylibrary.org/asset/15421	Student/Researcher	Yes
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44360	ML	Bill Roe	https://macaulaylibrary.org/asset/44360	Student/Researcher	Yes
38511	ML	Lewis Kibler	https://macaulaylibrary.org/asset/38511	Student/Researcher	Yes
87491	ML	Matthew D. Medler	https://macaulaylibrary.org/asset/87491	Student/Researcher	Yes
64237	ML	William W. H. Gunn	https://macaulaylibrary.org/asset/64237	Student/Researcher	Yes
167877	ML	Alec Wyatt	https://macaulaylibrary.org/asset/167877	Student/Researcher	Yes
213694	ML	Bob McGuire	https://macaulaylibrary.org/asset/213694	Student/Researcher	Yes
141608	ML	Jeremy Minns	https://macaulaylibrary.org/asset/141608	Student/Researcher	Yes
141599	ML	Jeremy Minns	https://macaulaylibrary.org/asset/141599	Student/Researcher	Yes
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177868	ML	Ingrid Holzmann	https://macaulaylibrary.org/asset/177868	Student/Researcher	Yes
179993	ML	Brad Walker	https://macaulaylibrary.org/asset/179993	Student/Researcher	Yes
179374	ML	logan kahle	https://macaulaylibrary.org/asset/179374	Student/Researcher	Yes
179382	ML	logan kahle	https://macaulaylibrary.org/asset/179382	Student/Researcher	Yes
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31	ML	William V. Ward	https://macaulaylibrary.org/asset/31	Student/Researcher
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44647	ML	Ernest Franzgrote	https://macaulaylibrary.org/asset/44647	Student/Researcher
63030	ML	Dave Herr	https://macaulaylibrary.org/asset/63030	Student/Researcher
80351	ML	Randolph Little	https://macaulaylibrary.org/asset/80351	Student/Researcher
107969	ML	Steven R. Pantle	https://macaulaylibrary.org/asset/107969	Student/Researcher
105316	ML	Geoffrey A. Keller	https://macaulaylibrary.org/asset/105316	Student/Researcher
106527	ML	Randolph Little	https://macaulaylibrary.org/asset/106527	Student/Researcher
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76556	ML	Curtis Marantz	https://macaulaylibrary.org/asset/76556	Student/Researcher
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106878	ML	Randolph Little	https://macaulaylibrary.org/asset/106878	Student/Researcher
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94460	ML	Wil Hershberger	https://macaulaylibrary.org/asset/94460	Student/Researcher
106965	ML	Randolph Little	https://macaulaylibrary.org/asset/106965	Student/Researcher
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118862	ML	Geoffrey A. Keller	https://macaulaylibrary.org/asset/118862	Student/Researcher
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129063	ML	Michael Andersen	https://macaulaylibrary.org/asset/129063	Student/Researcher
129066	ML	Michael Andersen	https://macaulaylibrary.org/asset/129066	Student/Researcher
49496	ML	Curtis Marantz	https://macaulaylibrary.org/asset/49496	Student/Researcher
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9708bMorril1	W-c.L.	Wan-chun Liu	Wan-chun Liu
9708bPO	W-c.L.	Wan-chun Liu	Wan-chun Liu
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9709bPufftonLI	W-c.L.	Wan-chun Liu	Wan-chun Liu
9709bPufftonPG	W-c.L.	Wan-chun Liu	Wan-chun Liu
9709bPufftonnewLI	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713aRiver1	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713aRiver2	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713bMontague1	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713bMontague2	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713bMontague3	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713bMontague4	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713bQuabbinYYweird	W-c.L.	Wan-chun Liu	Wan-chun Liu

bird4b	W-c.L.	Wan-chun Liu		Wan-chun Liu
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1_395655680_4_27_13_37_56	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655690_4_27_13_39_26	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655699_4_27_13_40_46	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655723_4_27_13_44_12	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655744_4_27_13_47_10	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655750_4_27_13_48_2	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655759_4_27_13_49_26	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655776_4_27_13_51_48	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655956_4_27_14_17_40	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395655967_4_27_14_19_22	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395656010_4_27_14_25_34	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395656029_4_27_14_28_16	W-c.L.	Wan-chun Liu		Wan-chun Liu
thayer1	W-c.L.	Wan-chun Liu		Wan-chun Liu
10a	W-c.L.	Wan-chun Liu		Wan-chun Liu
11b	W-c.L.	Wan-chun Liu		Wan-chun Liu

12a	W-c.L.	Wan-chun Liu		Wan-chun Liu
13a	W-c.L.	Wan-chun Liu		Wan-chun Liu
18a	W-c.L.	Wan-chun Liu		Wan-chun Liu
19a	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395656282_4_27_15_4_40	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395656465_4_27_15_31_4	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395656487_4_27_15_34_16	W-c.L.	Wan-chun Liu		Wan-chun Liu
20a	W-c.L.	Wan-chun Liu		Wan-chun Liu
5b	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston14a	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston16	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston18	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston2	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston20a	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston21acton	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston26	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston4	W-c.L.	Wan-chun Liu		Wan-chun Liu
fourth male	W-c.L.	Wan-chun Liu		Wan-chun Liu
third male	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395664089_4_28_9_48_56	W-c.L.	Wan-chun Liu		Wan-chun Liu
IESgh1b	W-c.L.	Wan-chun Liu		Wan-chun Liu
IESgh4	W-c.L.	Wan-chun Liu		Wan-chun Liu
IESgh6	W-c.L.	Wan-chun Liu		Wan-chun Liu
IESgh7	W-c.L.	Wan-chun Liu		Wan-chun Liu
IESgh8	W-c.L.	Wan-chun Liu		Wan-chun Liu
IESpsb1	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395636144_4_25_14_44_48	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395656234_4_27_14_57_44	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395664618_4_28_11_5_8	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395667426_4_28_17_49_26	W-c.L.	Wan-chun Liu		Wan-chun Liu
9705aQuabbin9	W-c.L.	Wan-chun Liu		Wan-chun Liu

9705awildwood1	W-c.L.	Wan-chun Liu	Wan-chun Liu
Boston1	W-c.L.	Wan-chun Liu	Wan-chun Liu
Boston12	W-c.L.	Wan-chun Liu	Wan-chun Liu
Boston13b	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395645285_4_26_12_41_8	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395664295_4_28_10_18_34	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395664306_4_28_10_20_8	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395664407_4_28_10_34_40	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395664471_4_28_10_43_52	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395664990_4_28_11_58_34	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395667362_4_28_17_40_10	W-c.L.	Wan-chun Liu	Wan-chun Liu
9705aQuabbin6	W-c.L.	Wan-chun Liu	Wan-chun Liu
9705aQuabbindrive1	W-c.L.	Wan-chun Liu	Wan-chun Liu
9708bQuabbinRR	W-c.L.	Wan-chun Liu	Wan-chun Liu
9709bQuabbinSBnotsure	W-c.L.	Wan-chun Liu	Wan-chun Liu
9709bQuabbinSkew	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713awildwoodYS	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713bMontague5	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713bQuabbinCorner nei	W-c.L.	Wan-chun Liu	Wan-chun Liu
9713bwildwoodGY	W-c.L.	Wan-chun Liu	Wan-chun Liu
WR1	W-c.L.	Wan-chun Liu	Wan-chun Liu
bird3a	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395645193_4_26_12_27_52	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395645261_4_26_12_37_40	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395645406_4_26_12_58_36	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395645491_4_26_13_10_50	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395645540_4_26_13_17_48	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395645565_4_26_13_21_28	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395655528_4_27_13_16_6	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395655532_4_27_13_16_38	W-c.L.	Wan-chun Liu	Wan-chun Liu
1_395655609_4_27_13_27_48	W-c.L.	Wan-chun Liu	Wan-chun Liu

1_395656002_4_27_14_24_22	W-c.L.	Wan-chun Liu		Wan-chun Liu
16a	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395656197_4_27_14_52_26	W-c.L.	Wan-chun Liu		Wan-chun Liu
8a	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston22	W-c.L.	Wan-chun Liu		Wan-chun Liu
Boston6	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395636185_4_25_14_50_40	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395645368_4_26_12_53_4	W-c.L.	Wan-chun Liu		Wan-chun Liu
1_395645457_4_26_13_5_54	W-c.L.	Wan-chun Liu		Wan-chun Liu
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17096	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB17096.mp3	CC BY-NC-SA 3.0
17448	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB17448.mp3	CC BY-NC-SA 3.0
17449	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB17449.mp3	CC BY-NC-SA 3.0
18666	BLB	McCallum, D. A. (D. Archibald)	http://osuc.osu.edu/blbmp3s/BLB18666.mp3	CC BY-NC-SA 3.0
18728	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB18728.mp3	CC BY-NC-SA 3.0
18736	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB18736.mp3	CC BY-NC-SA 3.0
18819	BLB	Baptista, L. F. (Luis F.)	http://osuc.osu.edu/blbmp3s/BLB18819.mp3	CC BY-NC-SA 3.0
28741	BLB	Colver, K. (Kevin)	http://osuc.osu.edu/blbmp3s/BLB28741.mp3	CC BY-NC-SA 3.0
29060	BLB	Colver, K. (Kevin)	http://osuc.osu.edu/blbmp3s/BLB29060.mp3	CC BY-NC-SA 3.0
24426	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB24426.mp3	CC BY-NC-SA 3.0
33842	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB33842.mp3	CC BY-NC-SA 3.0
34083	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34083.mp3	CC BY-NC-SA 3.0
34085	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34085.mp3	CC BY-NC-SA 3.0
34087	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34087.mp3	CC BY-NC-SA 3.0
34088	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34088.mp3	CC BY-NC-SA 3.0
34089	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34089.mp3	CC BY-NC-SA 3.0
34090	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34090.mp3	CC BY-NC-SA 3.0
34091	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34091.mp3	CC BY-NC-SA 3.0

34092	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34092.mp3	CC BY-NC-SA 3.0
34913	BLB	Baptista, L. F. (Luis F.)	http://osuc.osu.edu/blbmp3s/BLB34913.mp3	CC BY-NC-SA 3.0
31210	BLB	Colver, K. (Kevin)	http://osuc.osu.edu/blbmp3s/BLB31210.mp3	CC BY-NC-SA 3.0
34094	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34094.mp3	CC BY-NC-SA 3.0
34096	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34096.mp3	CC BY-NC-SA 3.0
34098	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34098.mp3	CC BY-NC-SA 3.0
34100	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34100.mp3	CC BY-NC-SA 3.0
34147	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34147.mp3	CC BY-NC-SA 3.0
34150	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34150.mp3	CC BY-NC-SA 3.0
34154	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34154.mp3	CC BY-NC-SA 3.0
34156	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34156.mp3	CC BY-NC-SA 3.0
25456	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB25456.mp3	CC BY-NC-SA 3.0
26911	BLB	Colver, K. (Kevin)	http://osuc.osu.edu/blbmp3s/BLB26911.mp3	CC BY-NC-SA 3.0
27948	BLB	Colver, K. (Kevin)	http://osuc.osu.edu/blbmp3s/BLB27948.mp3	CC BY-NC-SA 3.0
29562	BLB	Colver, K. (Kevin)	http://osuc.osu.edu/blbmp3s/BLB29562.mp3	CC BY-NC-SA 3.0
3279	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB03279.mp3	CC BY-NC-SA 3.0
4703	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB04703.mp3	CC BY-NC-SA 3.0
17475	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB17475.mp3	CC BY-NC-SA 3.0
30356	BLB	Nelson, D. A. (Douglas A.)	http://osuc.osu.edu/blbmp3s/BLB30356.mp3	CC BY-NC-SA 3.0
34576	BLB	Baptista, L. F. (Luis F.)	http://osuc.osu.edu/blbmp3s/BLB34576.mp3	CC BY-NC-SA 3.0
34988	BLB	Baptista, L. F. (Luis F.)	http://osuc.osu.edu/blbmp3s/BLB34988.mp3	CC BY-NC-SA 3.0
608	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB00608.mp3	CC BY-NC-SA 3.0
16865	BLB	Gaunt, S. L. L. (Sandra L. L.)	http://osuc.osu.edu/blbmp3s/BLB16865.mp3	CC BY-NC-SA 3.0
1703	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB01703.mp3	CC BY-NC-SA 3.0
2045	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB02045.mp3	CC BY-NC-SA 3.0
7086	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB07086.mp3	CC BY-NC-SA 3.0
7135	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB07135.mp3	CC BY-NC-SA 3.0
8147	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB08147.mp3	CC BY-NC-SA 3.0
8148	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB08148.mp3	CC BY-NC-SA 3.0
8161	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB08161.mp3	CC BY-NC-SA 3.0
22191	BLB	McLean, E. B. (E. Bruce)	http://osuc.osu.edu/blbmp3s/BLB22191.mp3	CC BY-NC-SA 3.0

33766	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB33766.mp3	CC BY-NC-SA 3.0	
33843	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB33843.mp3	CC BY-NC-SA 3.0	
33844	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB33844.mp3	CC BY-NC-SA 3.0	
34149	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34149.mp3	CC BY-NC-SA 3.0	
34153	BLB	Liu, W. (Wan-chun)	http://osuc.osu.edu/blbmp3s/BLB34153.mp3	CC BY-NC-SA 3.0	
1974	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB01974.mp3	CC BY-NC-SA 3.0	
2477	BLB	Borror, D. J. (Donald J.)	http://osuc.osu.edu/blbmp3s/BLB02477.mp3	CC BY-NC-SA 3.0	
363865	XC	Brian Murphy	https://www.xeno-canto.org/363865	CC BY-NC-SA 4.0	Yes
378424	XC	Jeremy Minns	https://www.xeno-canto.org/378424	CC BY-NC-SA 4.0	Yes
376219	XC	William Whitehead	https://www.xeno-canto.org/376219	CC BY-NC-SA 4.0	Yes
327741	XC	Antonio Xeira	https://www.xeno-canto.org/327741	CC BY-NC-SA 4.0	Yes
325097	XC	Antonio Xeira	https://www.xeno-canto.org/325097	CC BY-NC-SA 4.0	Yes
322659	XC	Richard E. Webster	https://www.xeno-canto.org/322659	CC BY-NC-SA 4.0	Yes
320440	XC	Jonathon Jongsma	https://www.xeno-canto.org/320440	CC BY-SA 4.0	Yes
315096	XC	J.R. Rigby	https://www.xeno-canto.org/315096	CC BY-NC-SA 4.0	Yes
313309	XC	Antonio Xeira	https://www.xeno-canto.org/313309	CC BY-NC-SA 4.0	Yes
308852	XC	Jerald R	https://www.xeno-canto.org/308852	CC BY-NC-SA 4.0	Yes
294364	XC	Paul Marvin	https://www.xeno-canto.org/294364	CC BY-NC-SA 4.0	Yes
293008	XC	Martin St-Michel	https://www.xeno-canto.org/293008	CC BY-NC-SA 4.0	Yes
269238	XC	Frank Lambert	https://www.xeno-canto.org/269238	CC BY-NC-ND 4.0	Yes
269237	XC	Frank Lambert	https://www.xeno-canto.org/269237	CC BY-NC-ND 4.0	Yes
246585	XC	Nikhil Jain	https://www.xeno-canto.org/246585	CC BY-NC-ND 4.0	Yes
195560	XC	Richard E. Webster	https://www.xeno-canto.org/195560	CC BY-NC-SA 4.0	Yes
189596	XC	Richard E. Webster	https://www.xeno-canto.org/189596	CC BY-NC-SA 4.0	Yes
189062	XC	Richard E. Webster	https://www.xeno-canto.org/189062	CC BY-NC-SA 4.0	Yes
188824	XC	Richard E. Webster	https://www.xeno-canto.org/188824	CC BY-NC-SA 4.0	Yes
188159	XC	Richard E. Webster	https://www.xeno-canto.org/188159	CC BY-NC-SA 4.0	Yes
188094	XC	Richard E. Webster	https://www.xeno-canto.org/188094	CC BY-NC-SA 4.0	Yes
179122	XC	John van Dort	https://www.xeno-canto.org/179122	CC BY-NC-SA 4.0	Yes
170986	XC	Elvis Herrera Rodríguez	https://www.xeno-canto.org/170986	CC BY-NC-SA 3.0	Yes
163938	XC	Jerome Fischer	https://www.xeno-canto.org/163938	CC BY-NC-SA 3.0	Yes

142341	XC	Amy Davis	https://www.xeno-canto.org/142341	CC BY-NC-SA 3.0	Yes
141461	XC	Mike Nelson	https://www.xeno-canto.org/141461	CC BY-NC-SA 3.0	Yes
139882	XC	Gabriel Leite	https://www.xeno-canto.org/139882	CC BY-NC-SA 3.0	Yes
138781	XC	Ryan P. O'Donnell	https://www.xeno-canto.org/138781	CC BY-NC-ND 3.0	Yes
131641	XC	Jonathon Jongsma	https://www.xeno-canto.org/131641	CC BY-SA 3.0	Yes
131573	XC	Eric DeFonso	https://www.xeno-canto.org/131573	CC BY-NC-SA 3.0	Yes
125194	XC	Richard E. Webster	https://www.xeno-canto.org/125194	CC BY-NC-SA 3.0	Yes
125192	XC	Richard E. Webster	https://www.xeno-canto.org/125192	CC BY-NC-SA 3.0	Yes
125190	XC	Richard E. Webster	https://www.xeno-canto.org/125190	CC BY-NC-SA 3.0	Yes
125188	XC	Richard E. Webster	https://www.xeno-canto.org/125188	CC BY-NC-SA 3.0	Yes
104951	XC	Eric DeFonso	https://www.xeno-canto.org/104951	CC BY-NC-ND 2.5	Yes
83519	XC	Jelmer Poelstra	https://www.xeno-canto.org/83519	CC BY-NC-ND 2.5	Yes
77992	XC	Ryan P. O'Donnell	https://www.xeno-canto.org/77992	CC BY-NC-ND 2.5	Yes
61635	XC	Luke Owens	https://www.xeno-canto.org/61635	CC BY-NC-ND 2.5	Yes
56891	XC	Ian Davies	https://www.xeno-canto.org/56891	CC BY-NC-ND 2.5	Yes
47096	XC	Todd Wilson	https://www.xeno-canto.org/47096	CC BY-NC-ND 2.5	Yes
16985	XC	Allen T. Chartier	https://www.xeno-canto.org/16985	CC BY-NC-SA 3.0	Yes
14415	XC	Chris Parrish	https://www.xeno-canto.org/14415	CC BY-NC-ND 2.5	Yes
13646	XC	Chris Parrish	https://www.xeno-canto.org/13646	CC BY-NC-ND 2.5	Yes
12579	XC	Andrew Spencer	https://www.xeno-canto.org/12579	CC BY-NC-ND 2.5	Yes
373249	XC	Bobby Wilcox	https://www.xeno-canto.org/373249	CC BY-NC-SA 4.0	Yes
364591	XC	Brian Murphy	https://www.xeno-canto.org/364591	CC BY-NC-SA 4.0	Yes
359412	XC	Linda Stehlik	https://www.xeno-canto.org/359412	CC BY-NC-SA 4.0	Yes
326708	XC	Martin St-Michel	https://www.xeno-canto.org/326708	CC BY-NC-SA 4.0	Yes
325938	XC	James Bradley	https://www.xeno-canto.org/325938	CC BY-NC-SA 4.0	Yes
325446	XC	Daniel Parker	https://www.xeno-canto.org/325446	CC BY-NC-SA 4.0	Yes
324926	XC	Bernard Bousquet	https://www.xeno-canto.org/324926	CC BY-NC-SA 4.0	Yes
321209	XC	Joshua Jaeger	https://www.xeno-canto.org/321209	CC BY-NC-SA 4.0	Yes
320337	XC	Antonio Xeira	https://www.xeno-canto.org/320337	CC BY-NC-SA 4.0	Yes
315158	XC	Antonio Xeira	https://www.xeno-canto.org/315158	CC BY-NC-SA 4.0	Yes
314922	XC	Bobby Wilcox	https://www.xeno-canto.org/314922	CC BY-NC-SA 4.0	Yes

313880	XC	Jarrod Swackhamer	https://www.xeno-canto.org/313880	CC BY-NC-SA 4.0	Yes
313469	XC	Matt Wistrand	https://www.xeno-canto.org/313469	CC BY-NC-SA 4.0	Yes
313468	XC	Matt Wistrand	https://www.xeno-canto.org/313468	CC BY-NC-SA 4.0	Yes
312321	XC	John Hogan	https://www.xeno-canto.org/312321	CC BY-NC-SA 4.0	Yes
309778	XC	Jerald R	https://www.xeno-canto.org/309778	CC BY-NC-SA 4.0	Yes
294302	XC	Paul Marvin	https://www.xeno-canto.org/294302	CC BY-NC-SA 4.0	Yes
206093	XC	Eric DeFonso	https://www.xeno-canto.org/206093	CC BY-NC-SA 4.0	Yes
195836	XC	Richard E. Webster	https://www.xeno-canto.org/195836	CC BY-NC-SA 4.0	Yes
189595	XC	Richard E. Webster	https://www.xeno-canto.org/189595	CC BY-NC-SA 4.0	Yes
184387	XC	Manuel Grosselet	https://www.xeno-canto.org/184387	CC BY-NC-SA 4.0	Yes
182933	XC	Lauren Harter	https://www.xeno-canto.org/182933	CC BY-NC-SA 4.0	Yes
177381	XC	Jorge de Leon Cardozo	https://www.xeno-canto.org/177381	CC BY-NC-SA 4.0	Yes
176359	XC	Jorge de Leon Cardozo	https://www.xeno-canto.org/176359	CC BY-NC-SA 4.0	Yes
137480	XC	Martin St-Michel	https://www.xeno-canto.org/137480	CC BY-NC-SA 3.0	Yes
133534	XC	Dan Lane	https://www.xeno-canto.org/133534	CC BY-NC-SA 3.0	Yes
131640	XC	Jonathon Jongsma	https://www.xeno-canto.org/131640	CC BY-SA 3.0	Yes
131639	XC	Jonathon Jongsma	https://www.xeno-canto.org/131639	CC BY-SA 3.0	Yes
131638	XC	Jonathon Jongsma	https://www.xeno-canto.org/131638	CC BY-SA 3.0	Yes
125186	XC	Richard E. Webster	https://www.xeno-canto.org/125186	CC BY-NC-SA 3.0	Yes
125185	XC	Richard E. Webster	https://www.xeno-canto.org/125185	CC BY-NC-SA 3.0	Yes
125183	XC	Richard E. Webster	https://www.xeno-canto.org/125183	CC BY-NC-SA 3.0	Yes
125180	XC	Richard E. Webster	https://www.xeno-canto.org/125180	CC BY-NC-SA 3.0	Yes
107570	XC	Mike Nelson	https://www.xeno-canto.org/107570	CC BY-NC-ND 2.5	Yes
104707	XC	Paul van Els	https://www.xeno-canto.org/104707	CC BY-NC-ND 2.5	Yes
102952	XC	Eric DeFonso	https://www.xeno-canto.org/102952	CC BY-NC-ND 2.5	Yes
100725	XC	Daniel Lane	https://www.xeno-canto.org/100725	CC BY-NC-ND 2.5	Yes
83733	XC	David Geale	https://www.xeno-canto.org/83733	CC BY-NC-ND 2.5	Yes
81357	XC	Mike Nelson	https://www.xeno-canto.org/81357	CC BY-NC-ND 2.5	Yes
79970	XC	Jonathon Jongsma	https://www.xeno-canto.org/79970	CC BY-SA 3.0	Yes
76506	XC	Jonathon Jongsma	https://www.xeno-canto.org/76506	CC BY-SA 3.0	Yes
72165	XC	Richard E Webster	https://www.xeno-canto.org/72165	CC BY-NC-ND 2.5	Yes

70985	XC	Mary Beth Stowe	https://www.xeno-canto.org/70985	CC BY-NC-ND 2.5	Yes
52371	XC	Mike Nelson	https://www.xeno-canto.org/52371	CC BY-NC-SA 3.0	Yes
31306	XC	Allen T. Chartier	https://www.xeno-canto.org/31306	CC BY-NC-SA 3.0	Yes
31305	XC	Allen T. Chartier	https://www.xeno-canto.org/31305	CC BY-NC-SA 3.0	Yes
1256	XC	Don Jones	https://www.xeno-canto.org/1256	CC BY-NC-ND 2.5	Yes
326776	XC	Daniel Parker	https://www.xeno-canto.org/326776	CC BY-NC-SA 4.0	Yes
302537	XC	Lauren Harter	https://www.xeno-canto.org/302537	CC BY-NC-SA 4.0	Yes
289051	XC	Lauren Harter	https://www.xeno-canto.org/289051	CC BY-NC-SA 4.0	Yes
253975	XC	Terry Davis	https://www.xeno-canto.org/253975	CC BY-NC-SA 4.0	Yes
236651	XC	Maxime Aubert	https://www.xeno-canto.org/236651	CC BY-NC-SA 4.0	Yes
210094	XC	Juan Carlos Pérez M.	https://www.xeno-canto.org/210094	CC BY-NC-SA 4.0	Yes
138703	XC	Garrett MacDonald	https://www.xeno-canto.org/138703	CC BY-NC-SA 3.0	Yes
111473	XC	Richard E Webster	https://www.xeno-canto.org/111473	CC BY-NC-ND 2.5	Yes
82109	XC	Mike Nelson	https://www.xeno-canto.org/82109	CC BY-NC-ND 2.5	Yes
52370	XC	Mike Nelson	https://www.xeno-canto.org/52370	CC BY-NC-SA 3.0	Yes
16984	XC	Allen T. Chartier	https://www.xeno-canto.org/16984	CC BY-NC-SA 3.0	Yes
16983	XC	Allen T. Chartier	https://www.xeno-canto.org/16983	CC BY-NC-SA 3.0	Yes
308415	XC	Jim Holmes	https://www.xeno-canto.org/308415	CC BY-NC-SA 4.0	Yes
253942	XC	Bobby Wilcox	https://www.xeno-canto.org/253942	CC BY-NC-SA 4.0	Yes
6244	XC	Manuel Grosselet	https://www.xeno-canto.org/6244	CC BY-NC-ND 2.5	Yes
17172	XC	Allen T. Chartier	https://www.xeno-canto.org/17172	CC BY-NC-SA 3.0	Yes
376768	XC	Manuel Grosselet	https://www.xeno-canto.org/376768	CC BY-NC-SA 4.0	Yes
313467	XC	Matt Wistrand	https://www.xeno-canto.org/313467	CC BY-NC-SA 4.0	Yes
376766	XC	Manuel Grosselet	https://www.xeno-canto.org/376766	CC BY-NC-SA 4.0	Yes
322656	XC	Richard E. Webster	https://www.xeno-canto.org/322656	CC BY-NC-SA 4.0	Yes
205466	XC	Eric DeFonso	https://www.xeno-canto.org/205466	CC BY-NC-SA 4.0	Yes
133489	XC	Dan Lane	https://www.xeno-canto.org/133489	CC BY-NC-SA 3.0	Yes
253974	XC	Terry Davis	https://www.xeno-canto.org/253974	CC BY-NC-SA 4.0	Yes
177136	XC	Daniel Parker	https://www.xeno-canto.org/177136	CC BY-NC-SA 4.0	Yes

APPENDIX C

CHIPPING SPARROW SYLLABLE TYPES METADATA AND IMAGES

We provide information on each of the 112 syllable types. For each type, we report the following: syllable category, number of recordings of that type, the years of the earliest and latest recordings of songs with that type, and the number of recordings from the Eastern, Western, Southern, and Middle regions with that type (**Table C.1**). We also include screenshots of each syllable type from recordings visualized in Audacity, all at with the same time and frequency scale (**Fig. C.1**).

Table C.1 Summary of the syllable types providing associated information on category, counts, time period and geographical range

Syllable type	Syllable category	Number of recordings	Year of earliest recording	Year of latest recording	Number of Eastern recordings	Number of Western recordings	Number of Southern recordings	Number of Middle recordings
1	Downup	35	1952	2017	24	8	0	3
2	Downup	4	1972	2017	0	4	0	0
3	Downup	17	1957	2017	10	6	0	1
4	Downup	13	1954	2015	8	2	0	3
5	Downup	3	1971	2017	3	0	0	0
6	Downup	7	1958	2016	6	1	0	0
7	Downup	27	1954	2009	27	0	0	0
8	Downup	25	1956	1998	23	1	0	1
9	Downup	12	1954	1975	12	0	0	0
10	Downup	4	1998	1998	4	0	0	0
11	Downup	1	1956	1956	1	0	0	0
12	Sweep	3	1965	1969	3	0	0	0
13	Sweep	11	1965	2017	2	9	0	0
14	Sweep	9	1958	2015	3	3	0	3
15	Sweep	5	1958	2013	4	0	1	0
16	Sweep	15	1954	2017	9	2	0	4
17	Sweep	6	1959	1990	5	1	0	0
18	Sweep	8	1961	2017	5	0	3	0
19	Sweep	4	1964	2010	4	0	0	0
20	Sweep	1	2016	2016	0	1	0	0
21	Updown	6	1997	2017	5	0	0	1
22	Updown	3	2017	2017	3	0	0	0
23	Updown	5	1967	2015	0	5	0	0

24	Updown	6	1958	2016	6	0	0	0
25	Updown	23	1953	2017	21	1	0	1
26	Updown	13	1956	2017	10	2	0	1
27	Updown	12	1956	2017	10	0	0	2
28	Updown	16	1959	2017	16	0	0	0
29	Updown	9	1958	2017	7	1	0	1
30	Updown	27	1953	2017	21	3	0	3
31	Updown	6	1986	2017	0	4	0	2
32	Updown	3	Not provided	Not provided	3	0	0	0
33	Updown	38	1952	2017	36	0	0	2
34	Updown	13	1956	2010	13	0	0	0
35	Updown	6	1957	1990	6	0	0	0
36	Updown	35	1950	2017	32	0	0	3
37	Updown	5	2017	2017	5	0	0	0
38	Updown	5	1951	2015	2	1	2	0
39	Updown	6	1974	2017	6	0	0	0
40	Updown	2	1973	1973	2	0	0	0
41	Updown	3	1989	2017	3	0	0	0
42	Updown	1	1964	1964	1	0	0	0
43	Updown	5	1960	2017	1	4	0	0
44	Updown	2	2017	2017	0	2	0	0
45	Updown	12	1966	2017	12	0	0	0
46	Updown	18	1963	2017	13	4	1	0
47	Updown	19	1956	2016	7	10	0	2
48	Buzz	21	1954	2009	21	0	0	0
49	Buzz	5	1957	2011	5	0	0	0
50	Buzz	12	1959	2017	2	10	0	0
51	Buzz	6	1960	1965	6	0	0	0
52	Buzz	3	1964	1971	3	0	0	0
53	Buzz	11	1960	2017	0	8	0	3
54	Buzz	13	1958	2017	2	11	0	0
55	Buzz	8	1970	2015	0	8	0	0
56	Buzz	27	1952	2017	6	20	0	1
57	Buzz	12	1955	2017	10	2	0	0
58	Buzz	6	1968	2016	6	0	0	0
59	Buzz	16	1952	2009	16	0	0	0
60	Buzz	20	1952	2017	20	0	0	0
61	Buzz	12	1970	2017	0	8	0	4
62	Buzz	17	1964	2015	1	15	1	0
63	Buzz	2	1965	1967	0	2	0	0
64	Buzz	5	1958	2014	0	4	0	1
65	Double	6	1963	1967	6	0	0	0
66	Double	6	2014	2016	5	1	0	0

67	Double	19	1963	2017	19	0	0	0
68	Double	1	2015	2015	0	0	0	1
69	Double	2	2015	2017	2	0	0	0
70	Double	2	2015	2017	1	1	0	0
71	Double	3	2014	2017	1	2	0	0
72	Double	4	1966	2017	3	0	0	1
73	Double	2	2014	2016	0	2	0	0
74	Double	2	2016	2016	2	0	0	0
75	Complex	29	1951	2017	29	0	0	0
76	Updown	3	1963	1988	1	2	0	0
77	Double	1	2017	2017	0	1	0	0
78	Complex	1	1987	1987	1	0	0	0
79	Updown	1	1956	1956	1	0	0	0
80	Updown	1	Not provided	Not provided	1	0	0	0
81	Updown	1	2001	2001	0	1	0	0
82	Sweep	1	1958	1958	1	0	0	0
83	Complex	1	1987	1987	1	0	0	0
84	Complex	1	1963	1963	1	0	0	0
85	Complex	1	1971	1971	0	1	0	0
86	Downup	1	Not provided	Not provided	1	0	0	0
87	Sweep	1	Not provided	Not provided	1	0	0	0
88	Complex	1	2016	2016	1	0	0	0
89	Updown	1	2017	2017	1	0	0	0
90	Buzz	1	2017	2017	0	0	0	1
91	Updown	1	2017	2017	1	0	0	0
92	Downup	1	2017	2017	1	0	0	0
93	Double	1	2017	2017	1	0	0	0
94	Complex	1	2017	2017	0	1	0	0
95	Complex	1	1956	1956	0	0	0	1
96	Complex	1	1998	1998	1	0	0	0
97	Downup	1	2005	2005	0	0	0	1
98	Complex	1	2009	2009	1	0	0	0
99	Complex	1	2007	2007	0	1	0	0
100	Updown	1	2006	2006	0	0	1	0
101	Sweep	1	2011	2011	1	0	0	0
102	Sweep	1	2013	2013	0	0	0	1
103	Double	1	2013	2013	0	0	0	1
104	Complex	1	2013	2013	1	0	0	0
105	Double	1	2014	2014	0	0	1	0
106	Double	1	2015	2015	0	0	0	1
107	Complex	1	2016	2016	1	0	0	0
108	Sweep	1	2016	2016	1	0	0	0
109	Double	1	2017	2017	1	0	0	0

110	Complex	1	2017	2017	1	0	0	0
111	Complex	1	2017	2017	0	1	0	0
112	Updown	1	1994	1994	0	1	0	0

Figure C.1 Examples of the 112 syllable types. Clips of the recordings were taken in Audacity, and all are shown on the same frequency (*y*-axis) and timescale (*x*-axis).

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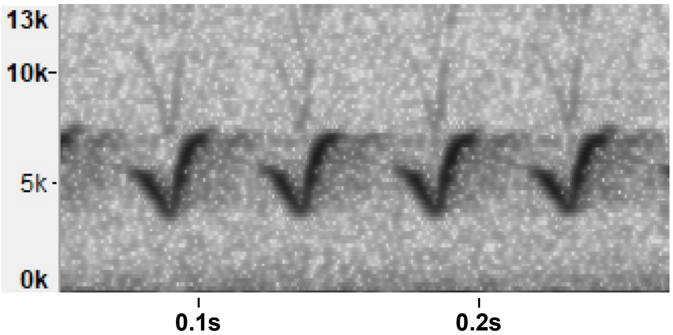

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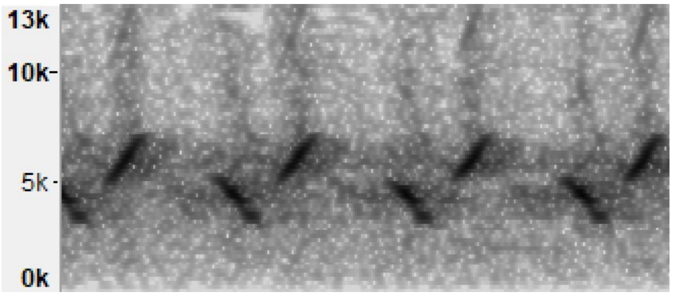

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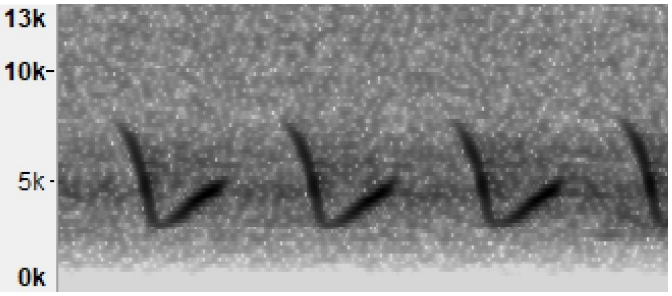

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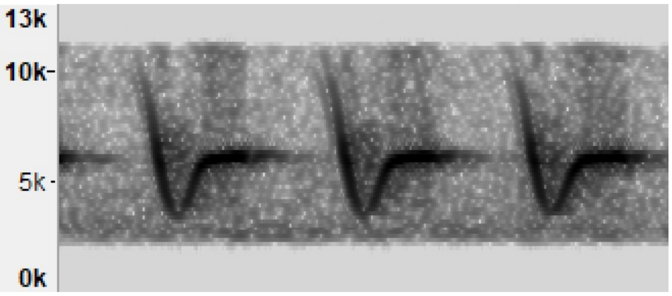

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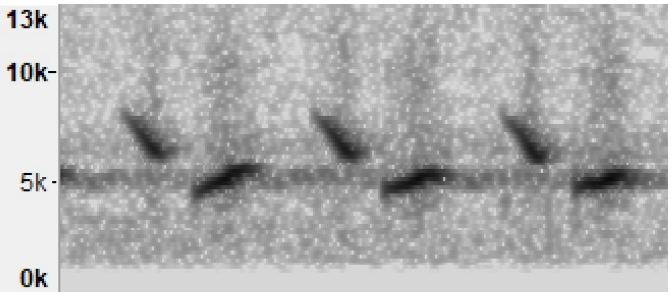

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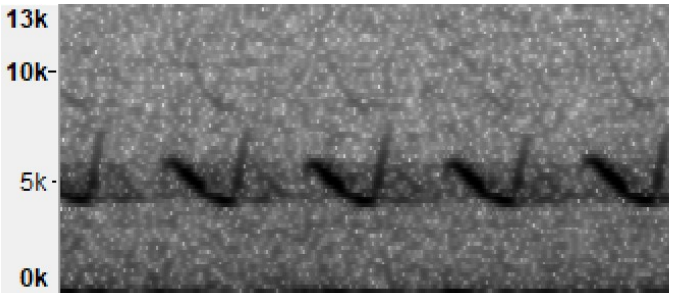

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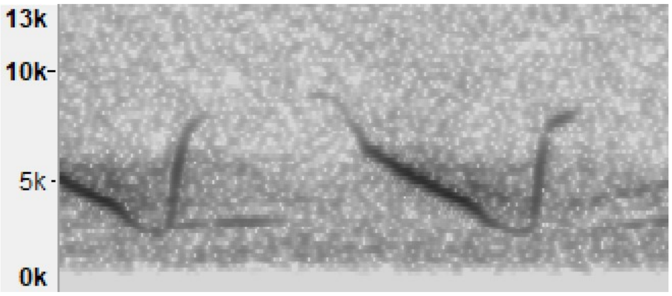

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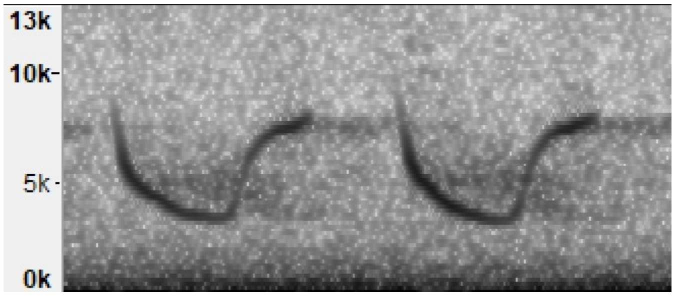

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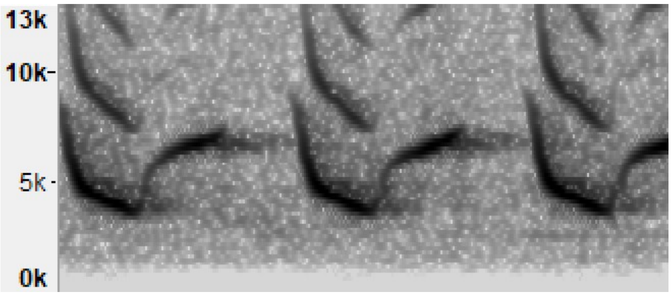

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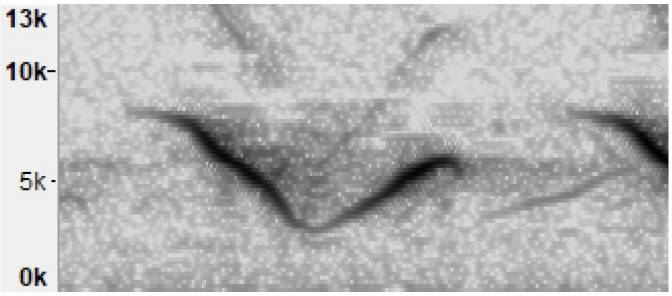

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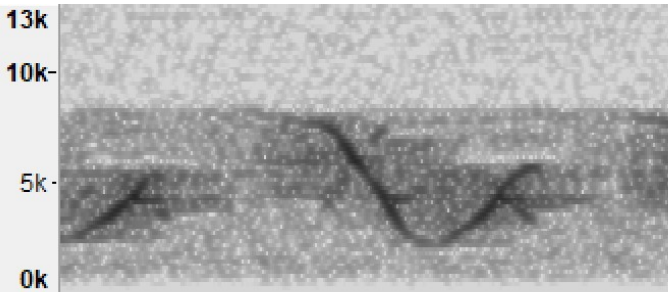

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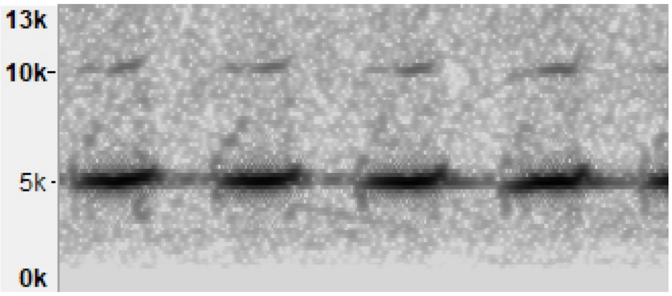

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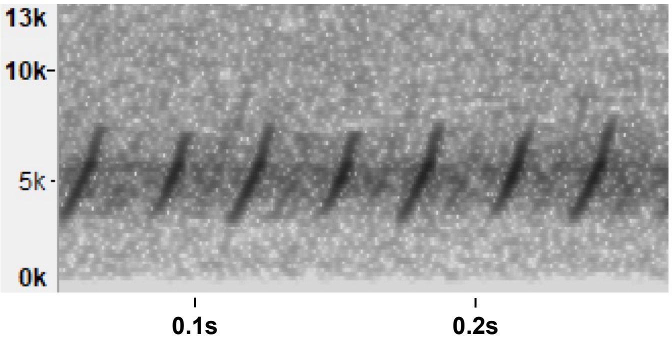

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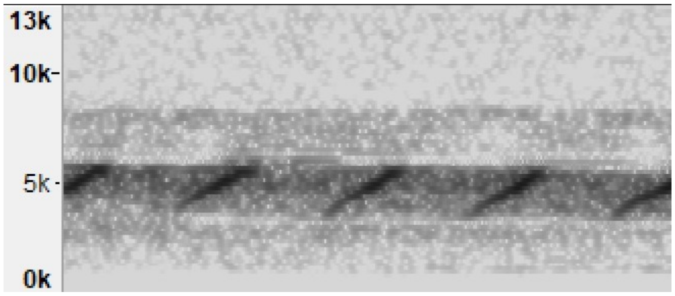

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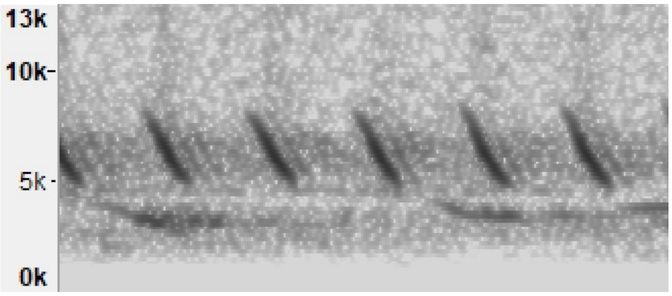

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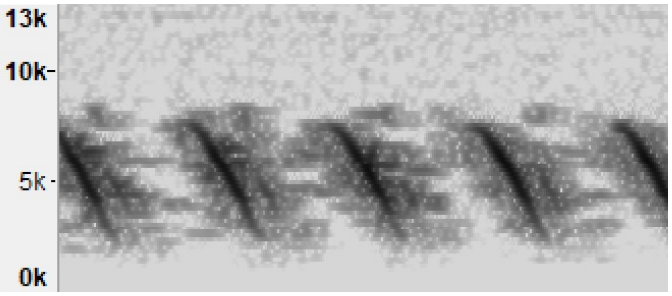

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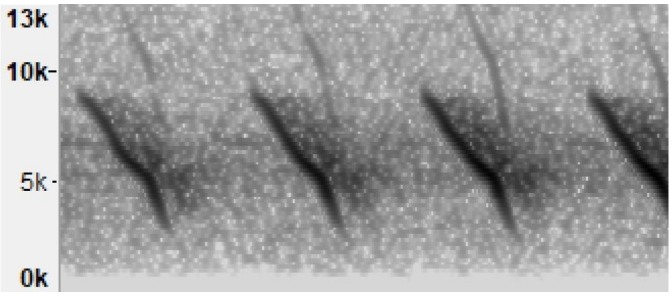

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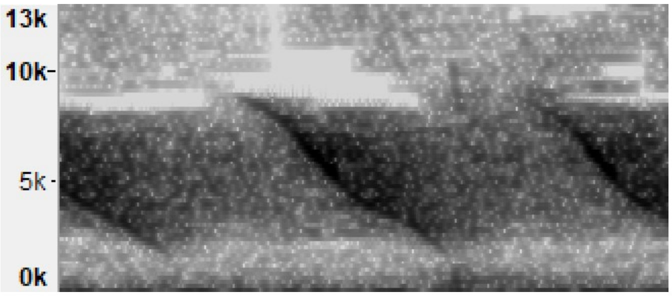

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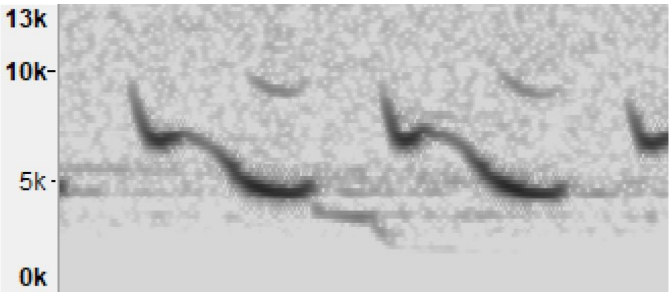

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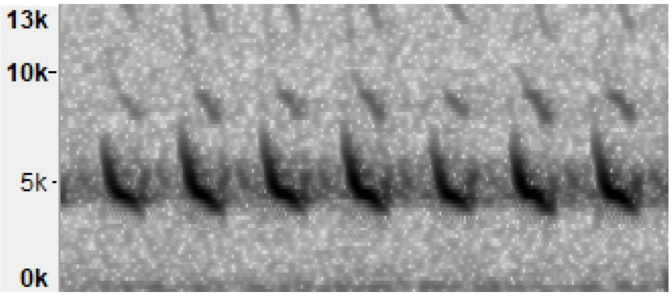

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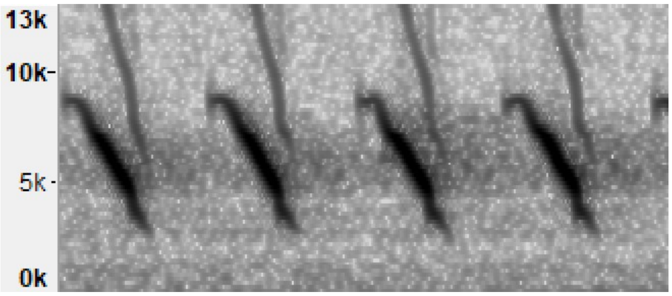

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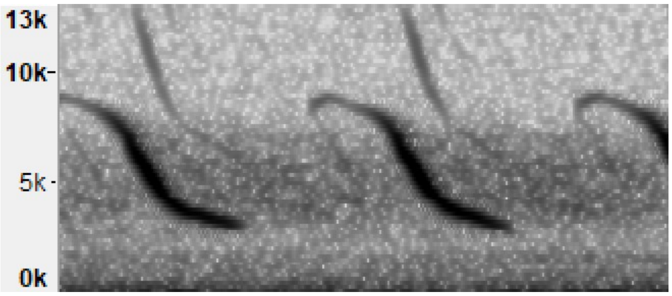

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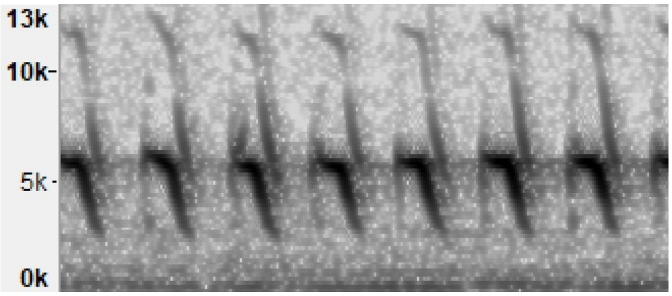

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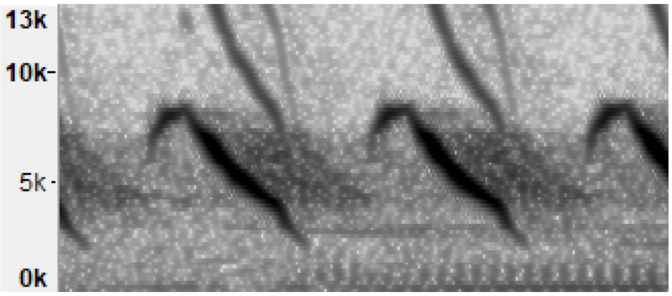

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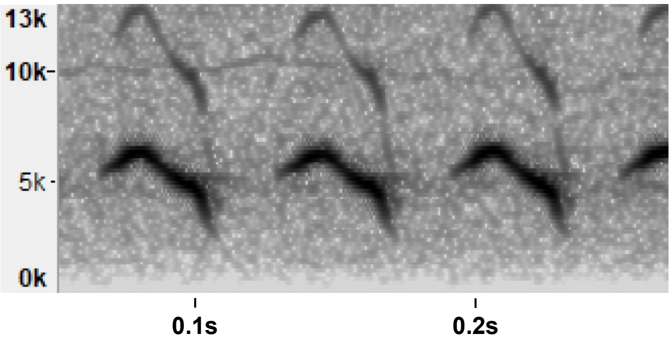

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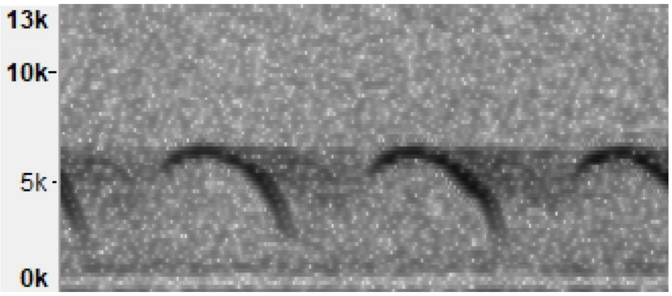

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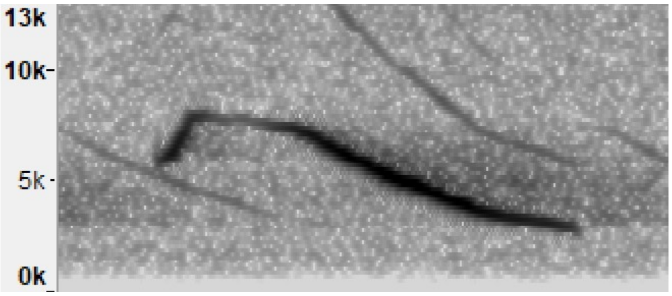

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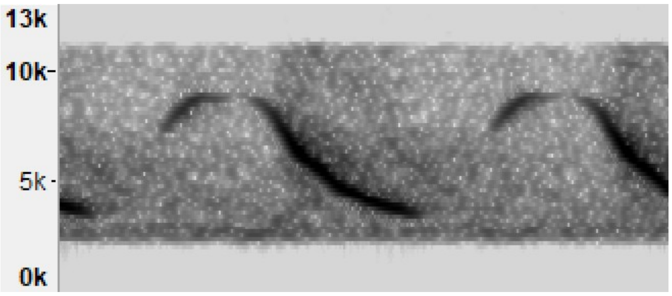

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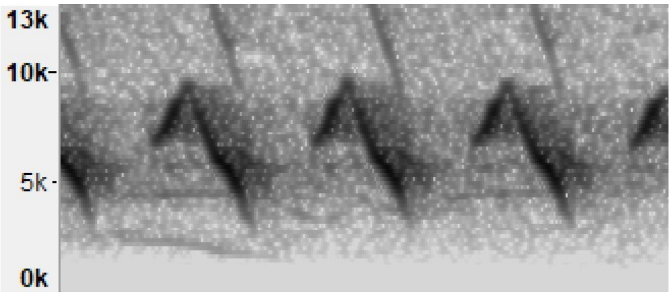

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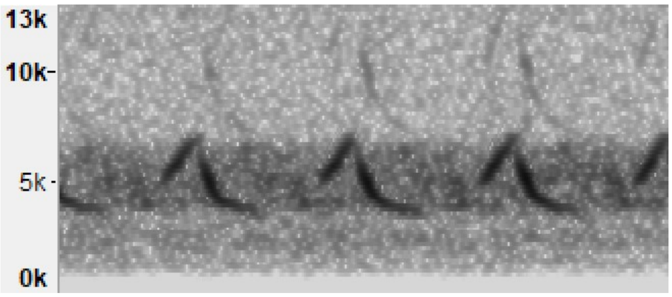

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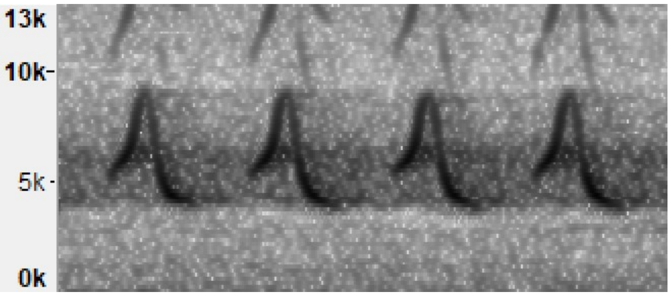

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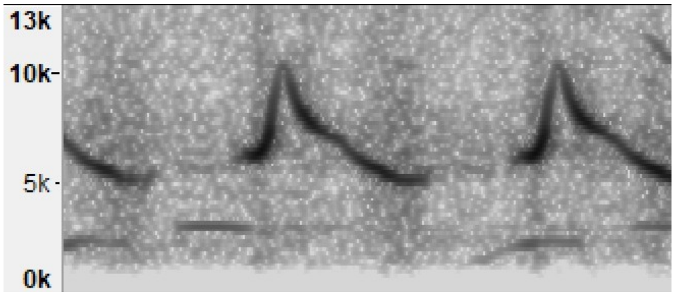

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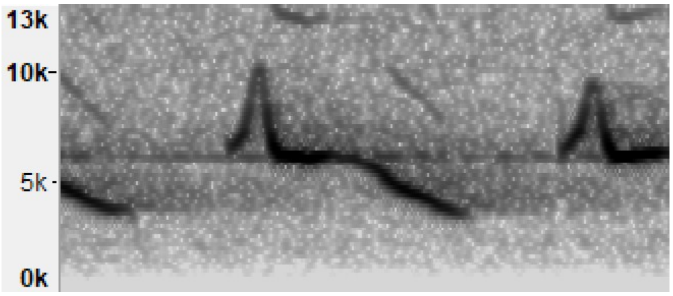

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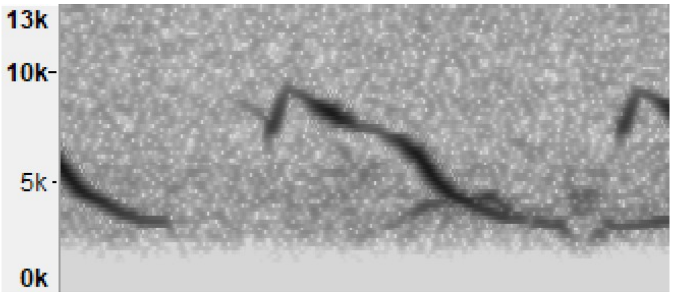

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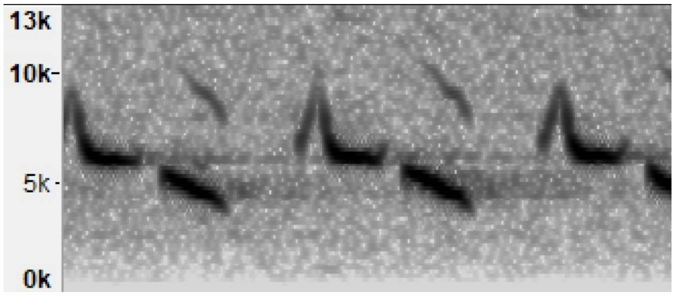

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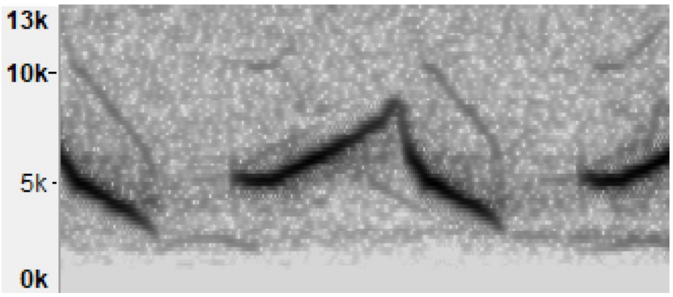

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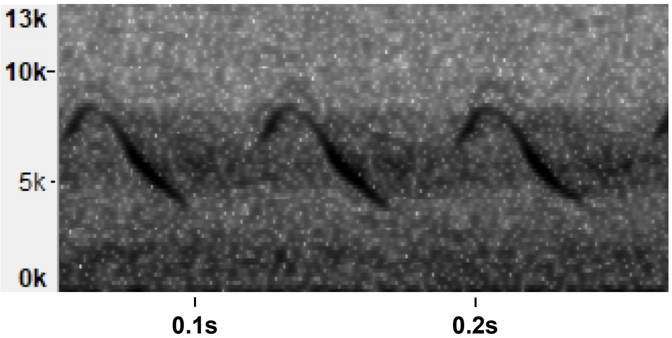

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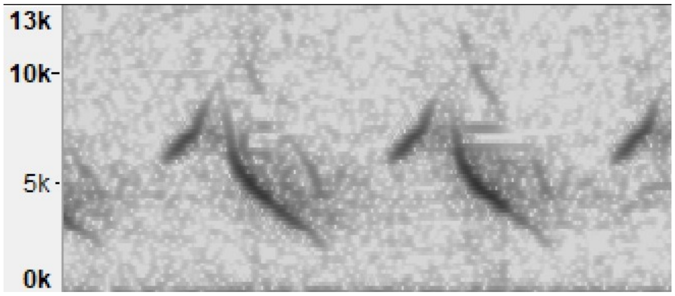

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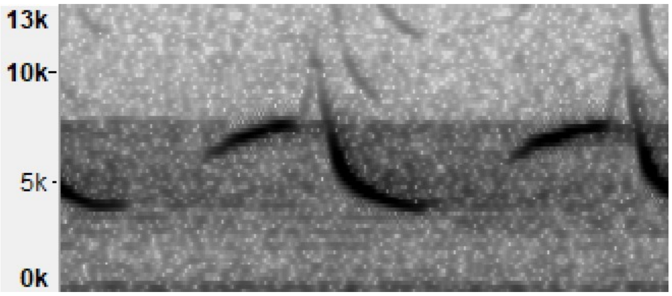

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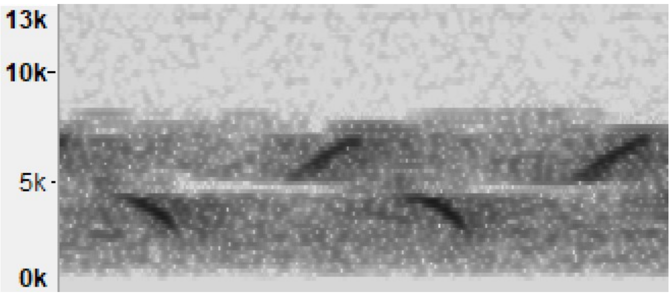

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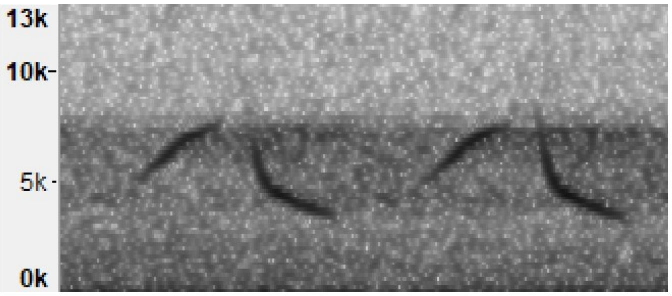

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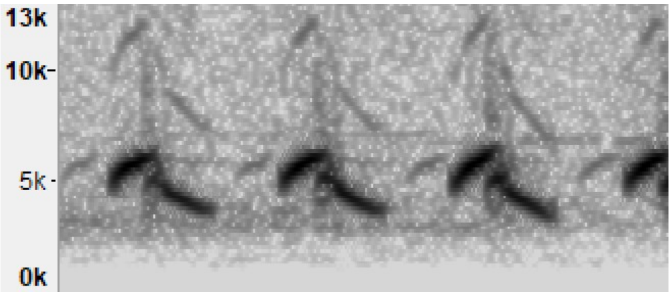

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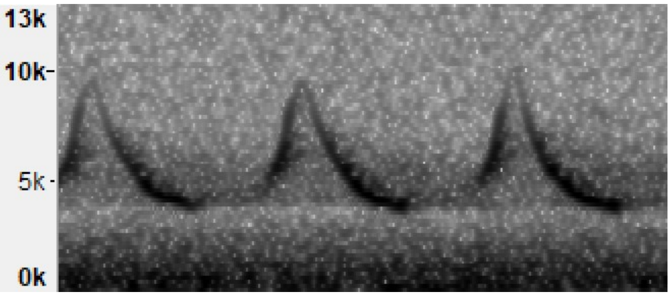

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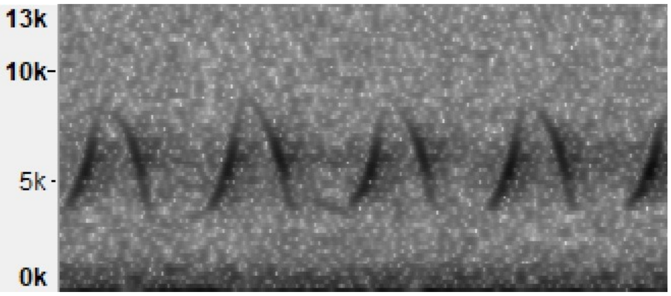

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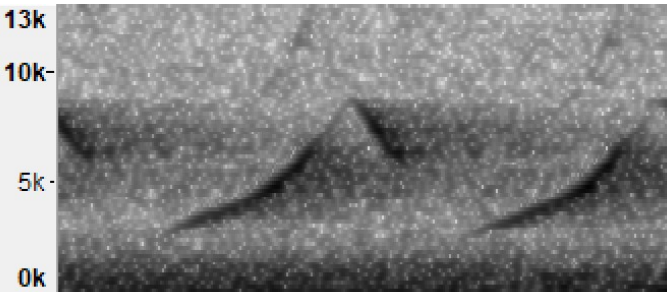

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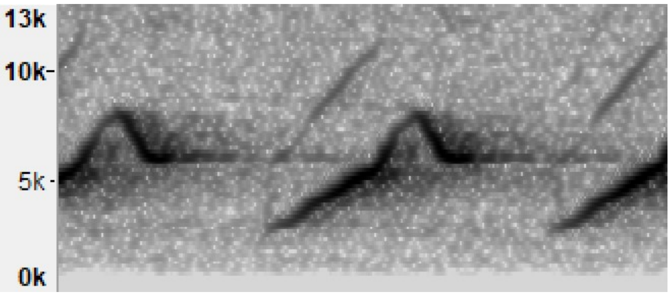

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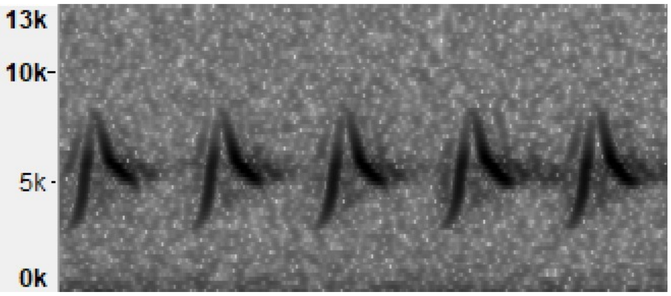

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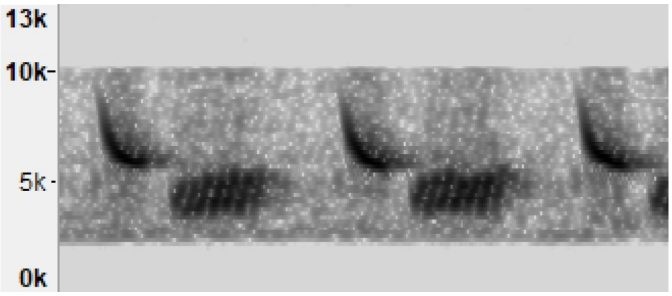

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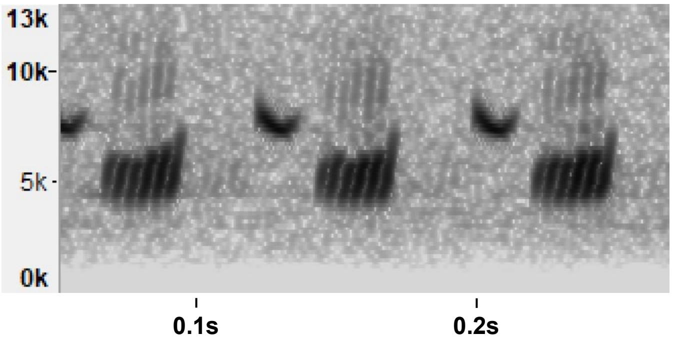

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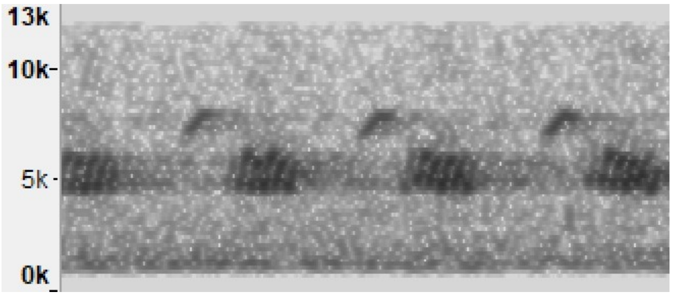

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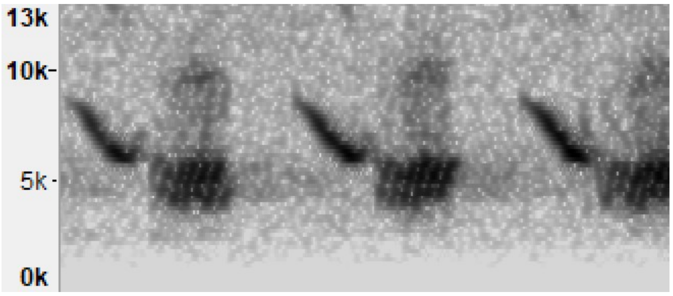

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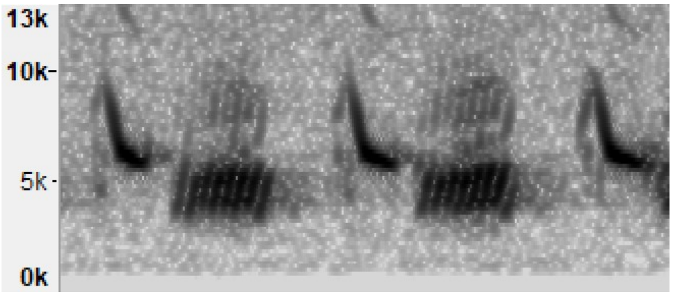

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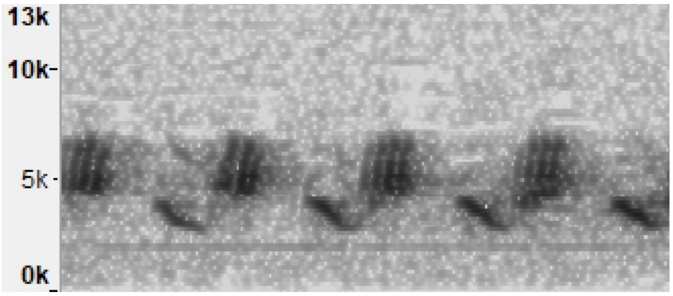

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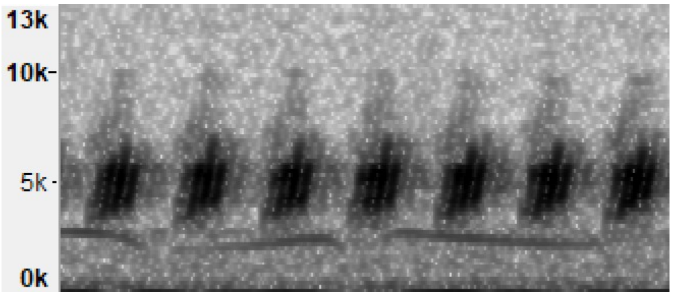

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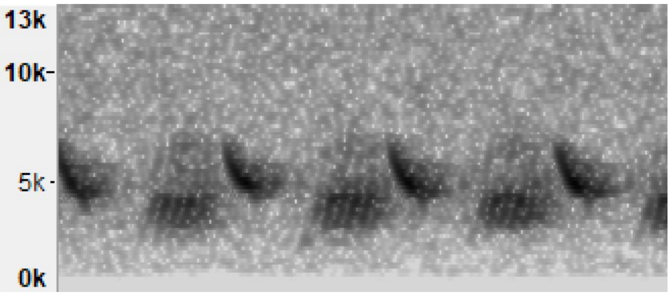

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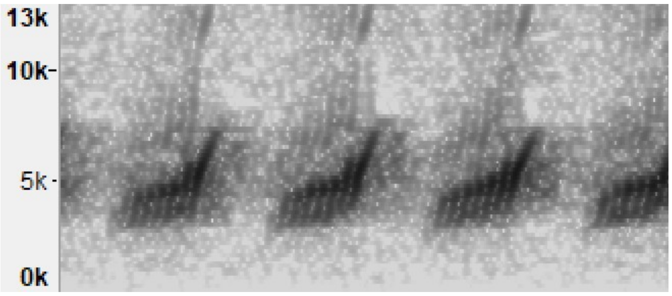

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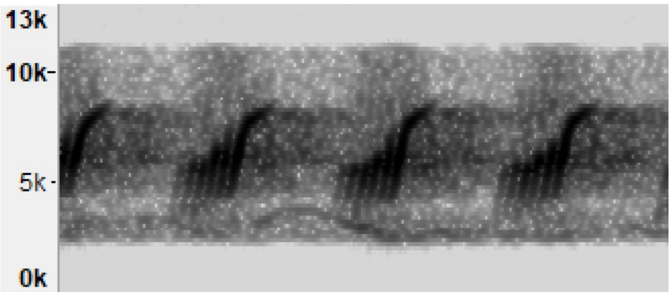

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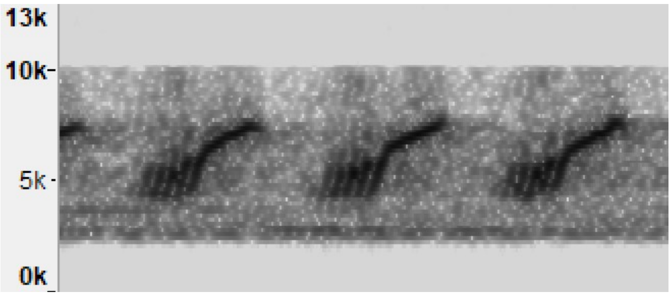

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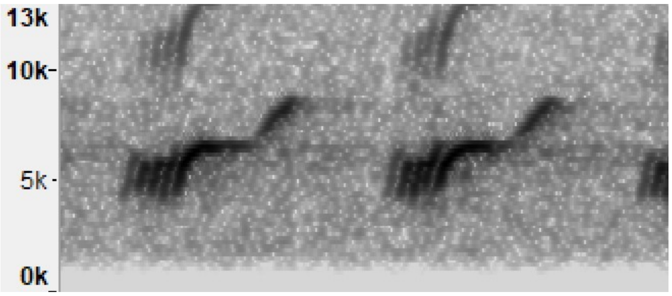

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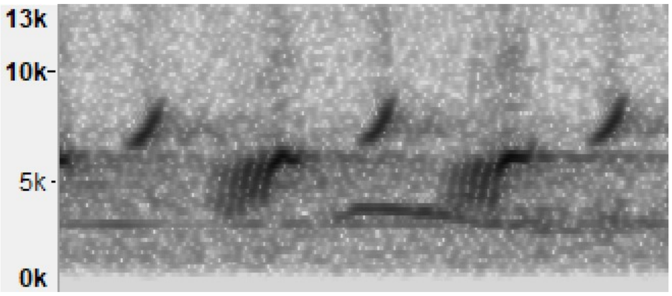

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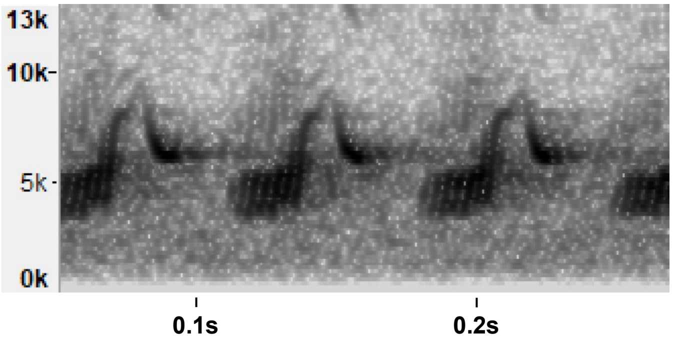

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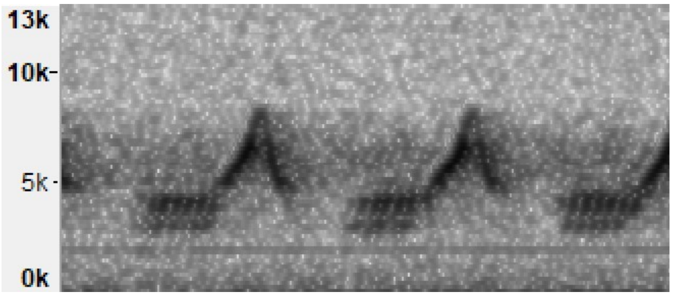

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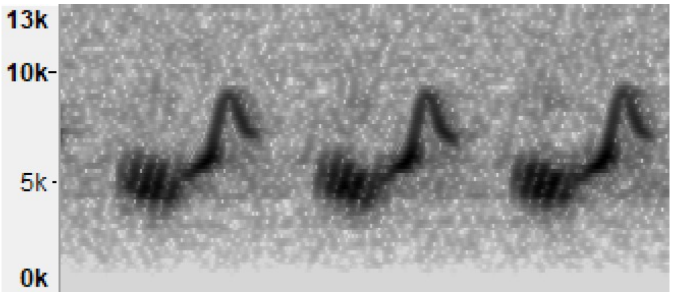

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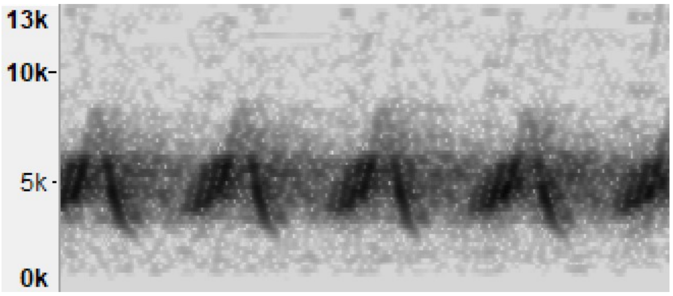

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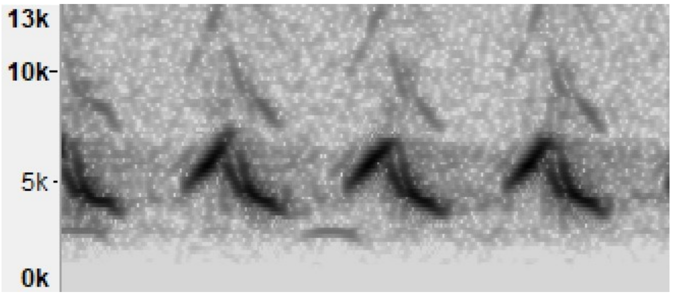

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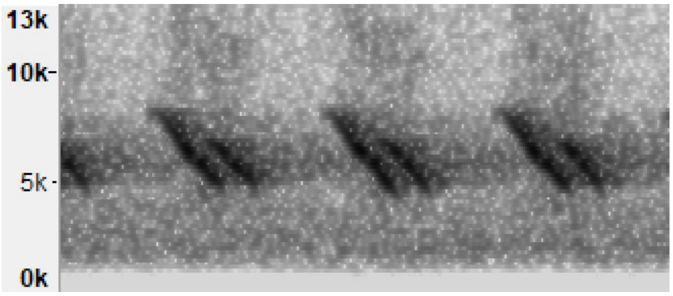

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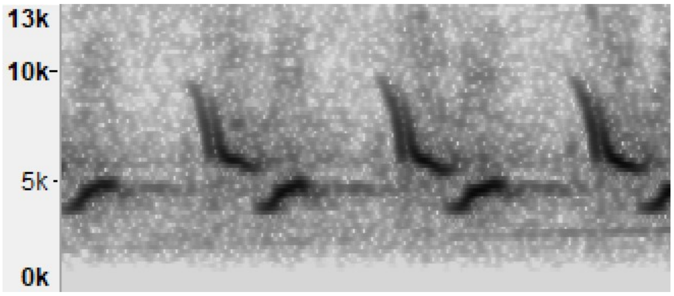

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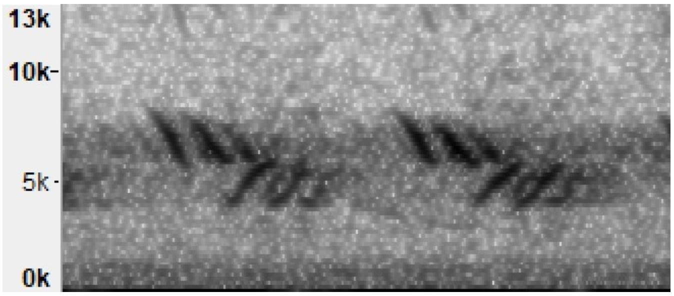

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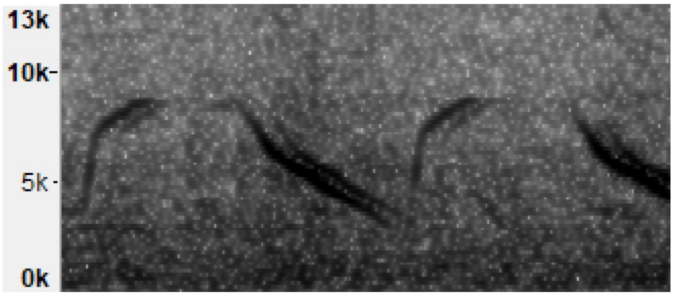

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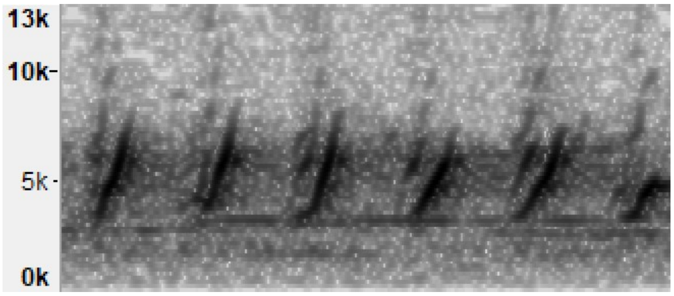

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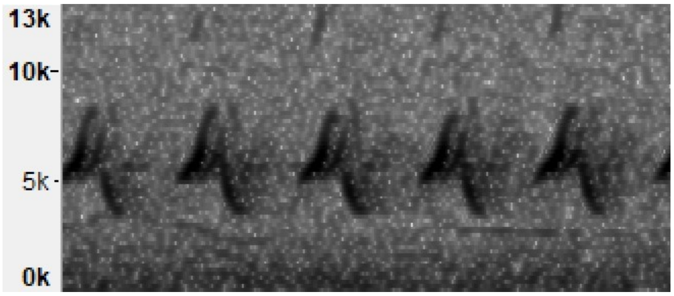

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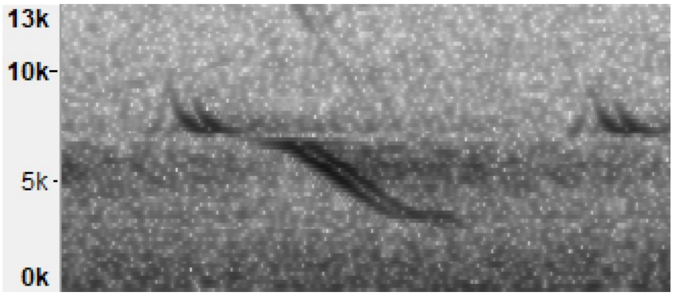

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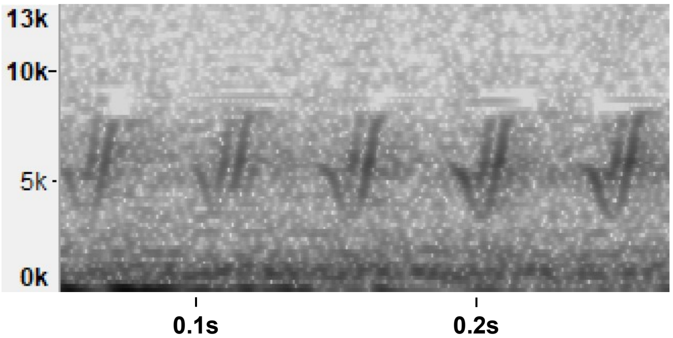

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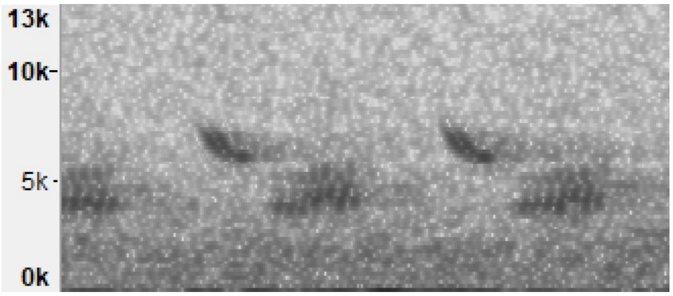

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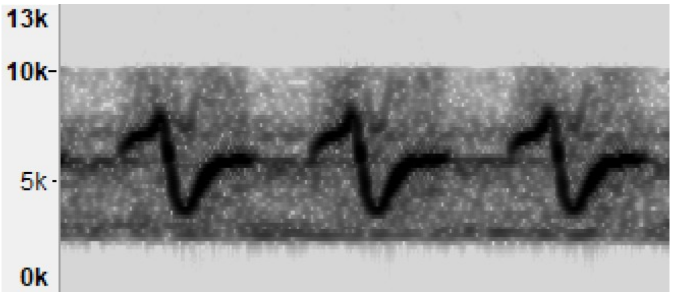

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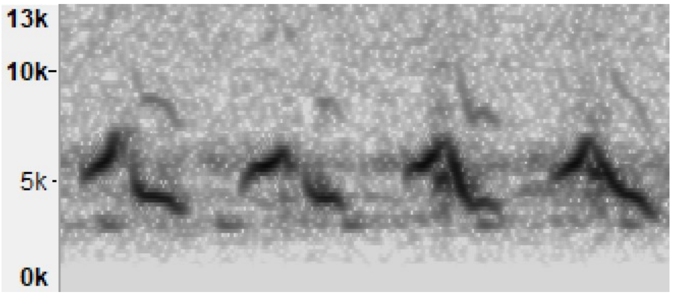

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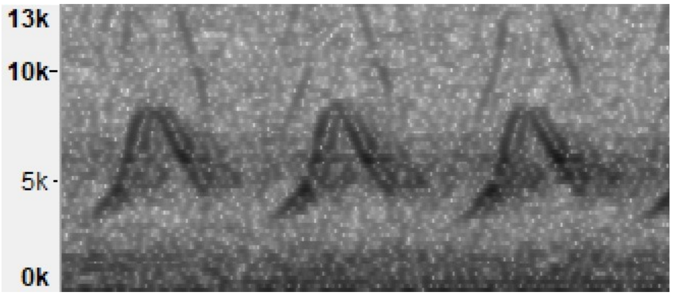

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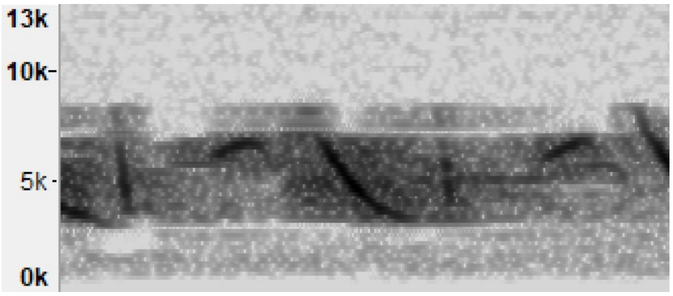

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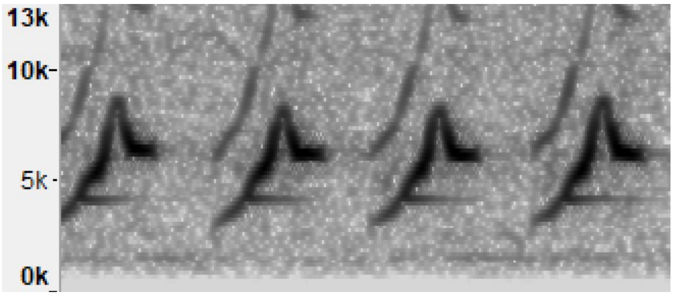

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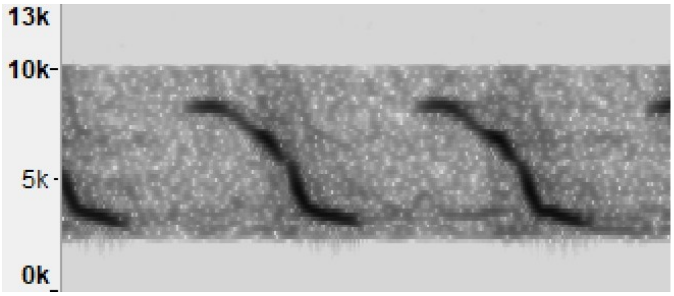

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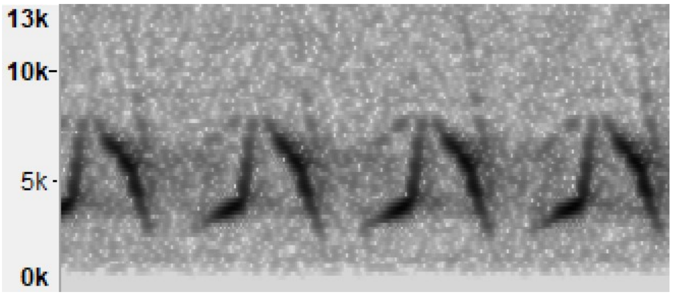

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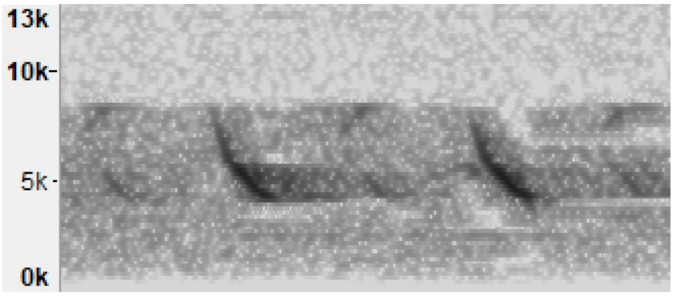

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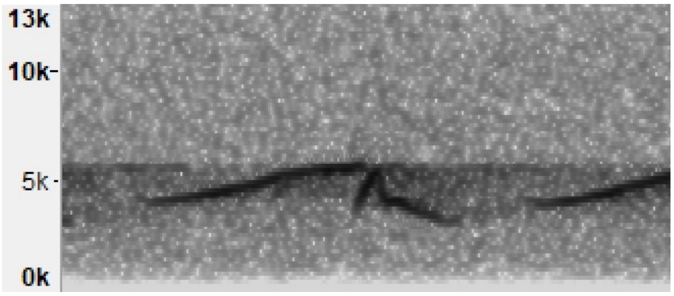

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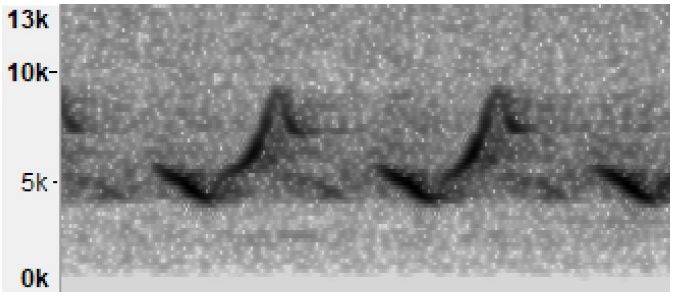

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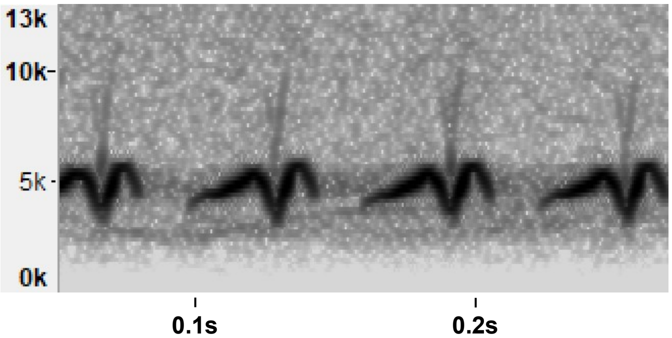

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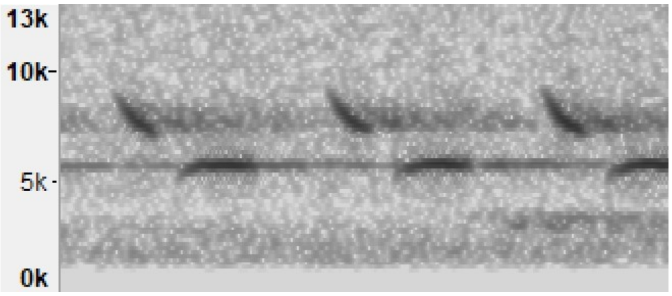

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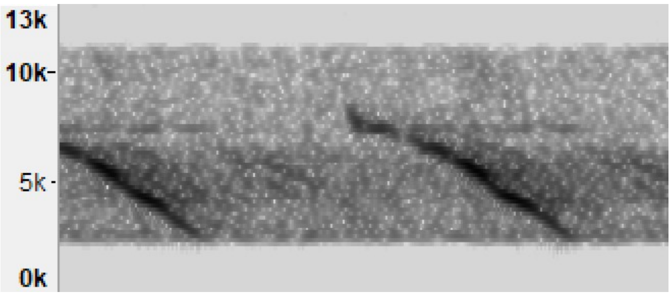

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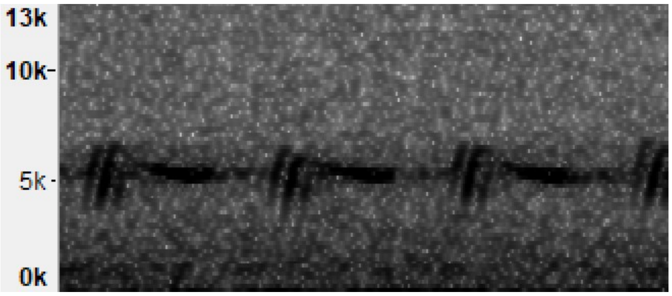

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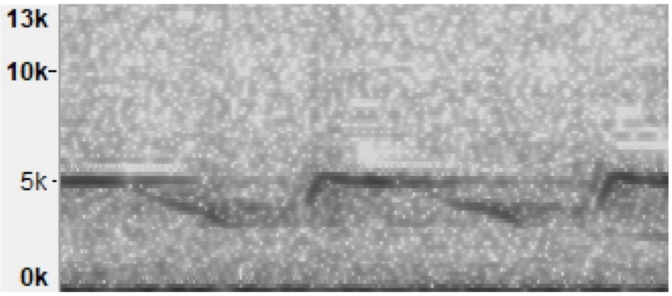

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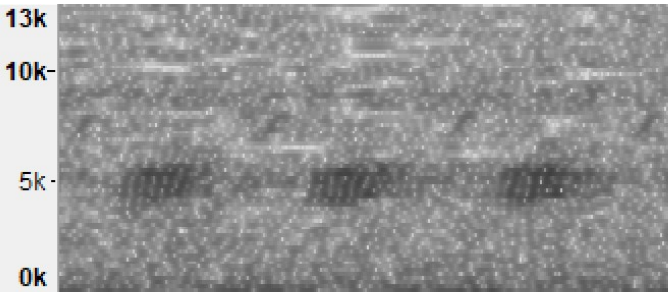

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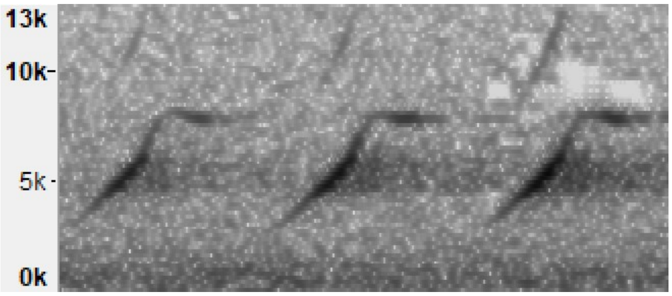

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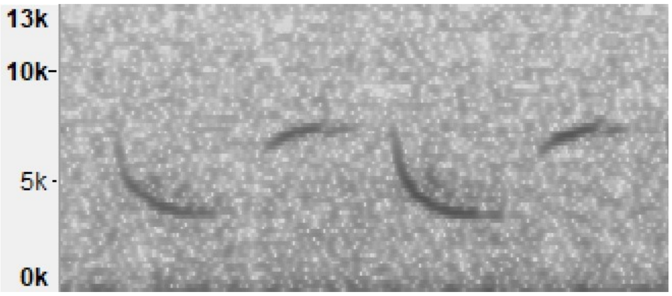

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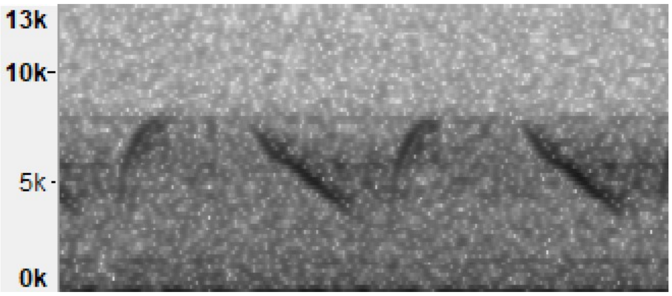

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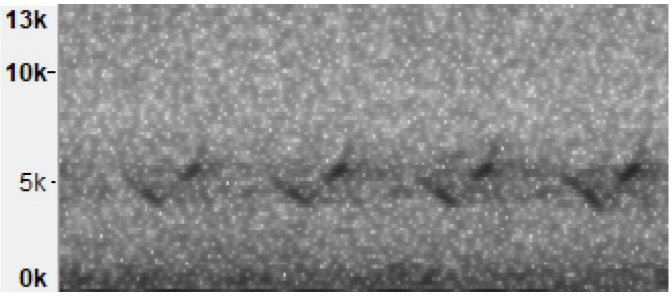

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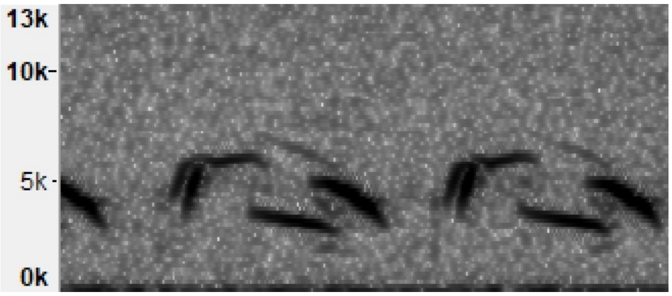

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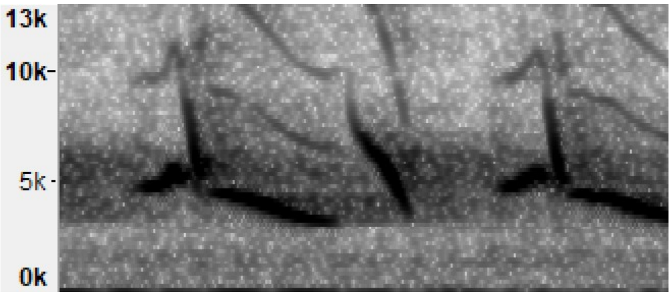

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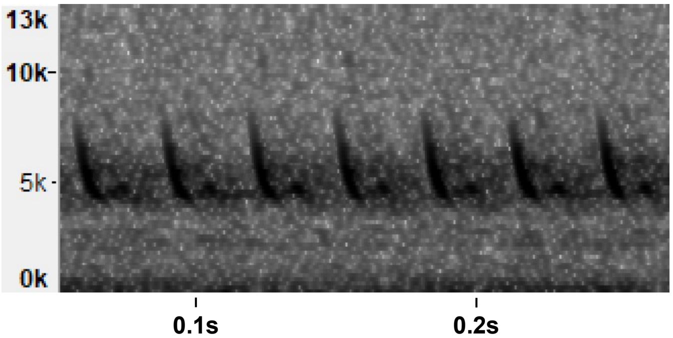

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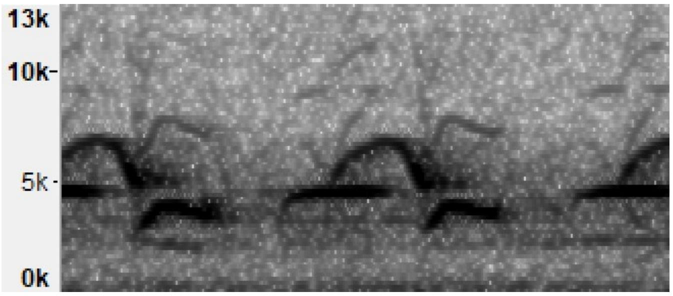

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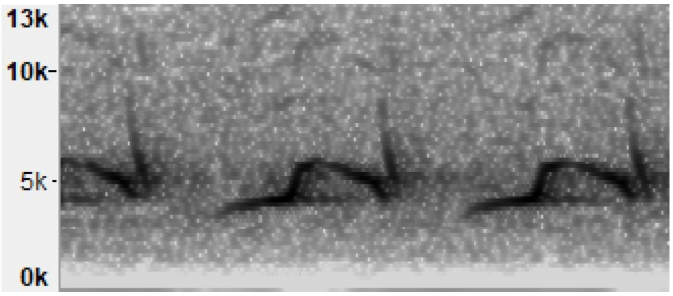

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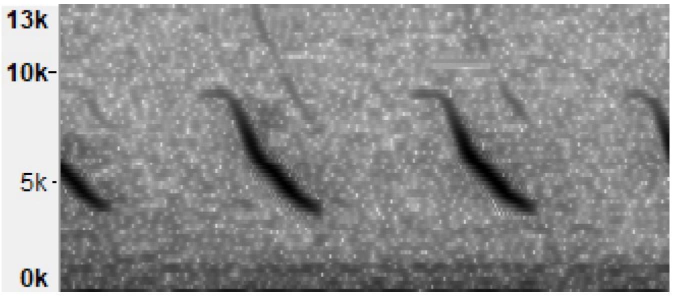

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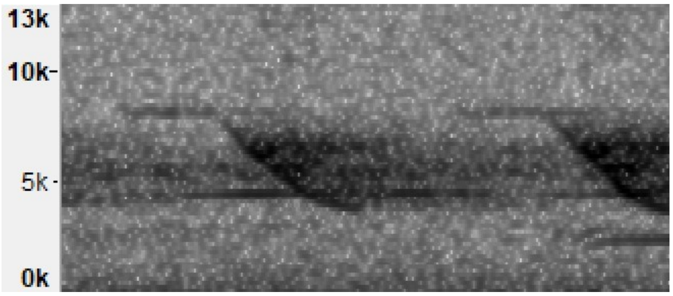

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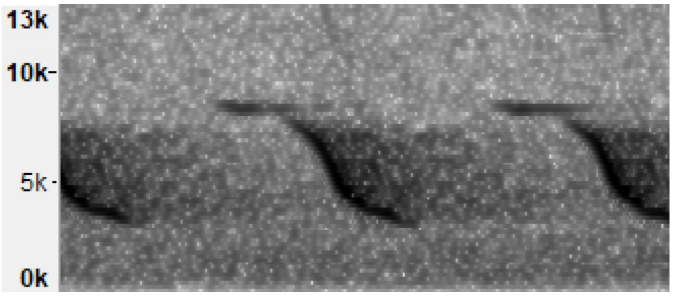

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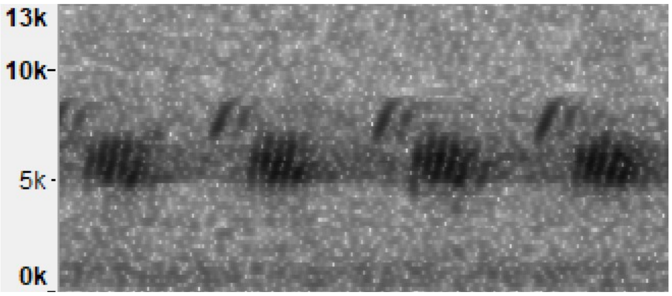

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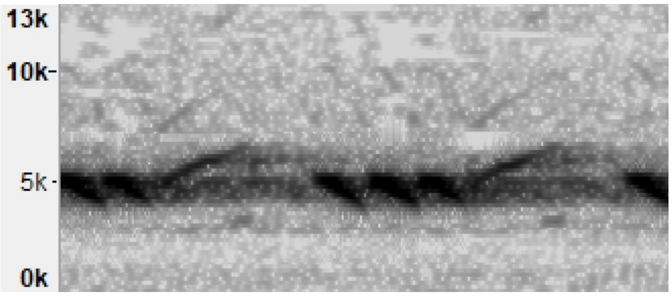

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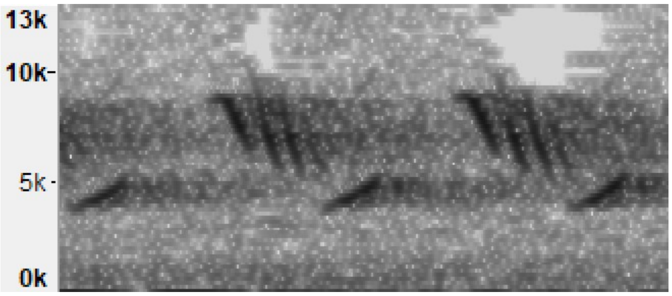

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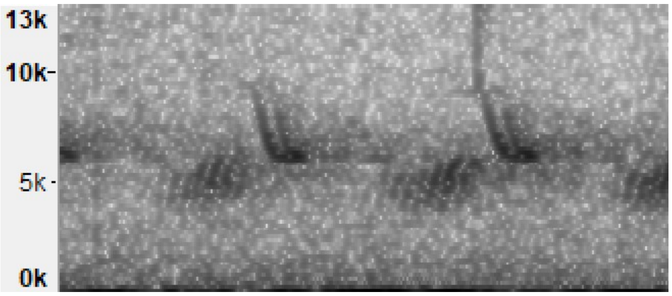

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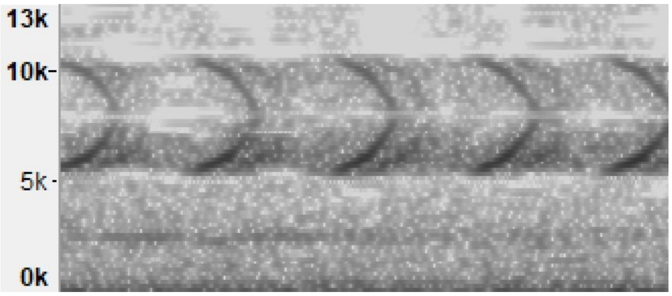

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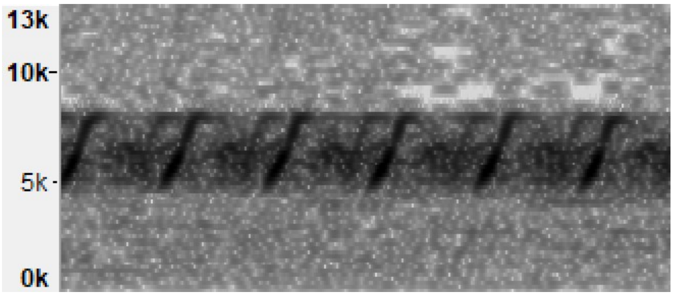

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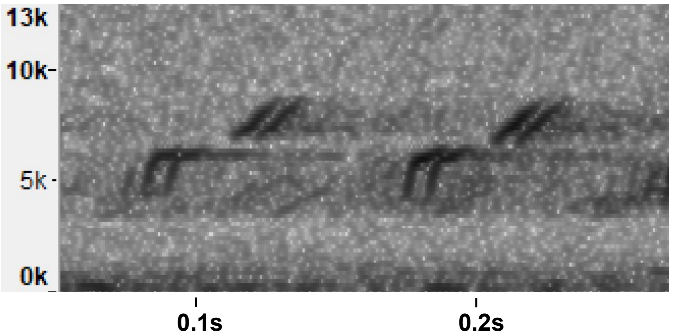

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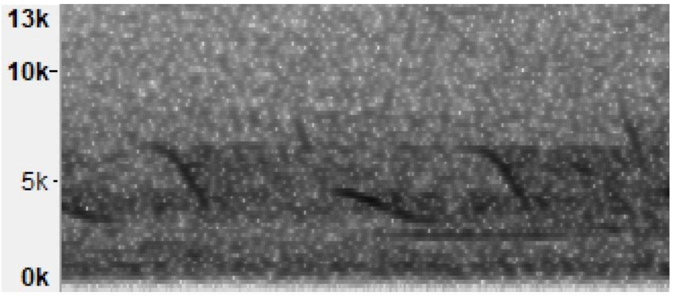

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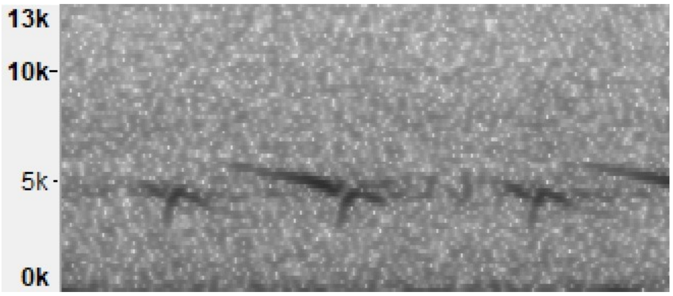

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