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Avian Behavior, Ecology, and Evolution

Cultural shifts after punctuated environmental stress: a study of song distributions in Dark-eyed Junco and Song Sparrow populations

Cambios culturales tras estrés ambiental puntuado: un estudio de las distribuciones del canto en poblaciones de Junco Ojioscuro y Gorrión Cantor

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ABSTRACT. Environmental stress, especially during development, can cause important phenotypic changes in individuals. In songbirds, these stress-induced changes have been shown to include impaired learning of song and reduced song complexity in several species. Typically, developmental stress has been studied in terms of individual variation within a population; however, birdsong, a culturally transmitted trait, may undergo relatively rapid changes if widespread learning impairment results from population-level environmental stress, and these changes could potentially be amplified if affected individuals become the song tutors for future generations. We thus hypothesize that ecosystem-wide stressors may cause population-level changes to birdsong. Here, we use publicly available birdsong recordings to determine whether song differences were evident after an abnormal and severe 2016 drought in western New York State. We analyzed birdsong recordings of two species, the Dark-eyed Junco (*Junco hyemalis*) and the Song Sparrow (*Melospiza melodia*), recorded between 2006–2020 in the drought-affected region and, for comparison, in two nearby regions less affected by the drought. The population-level song features of the species with more complex songs (Song Sparrow) changed in the drought area after 2016, but not in the control area. In the species with a more simple song (Dark-eyed Junco), we detected song changes in both regions, suggesting that the drought did not have an outsized effect on song in this species. These findings support a more nuanced hypothesis that stress-induced deficits may disproportionately affect species with songs that are more difficult to learn. These conclusions are tempered by the relatively sparse recording availability from years prior to 2016, but we predict that future longitudinal studies of song evolution in natural populations will be more tractable given the nearly exponential increase in the number of song recordings deposited in public repositories in recent years, making this experimental design a useful framework for future studies.

RESUMEN. El estrés ambiental, especialmente durante el desarrollo, puede provocar importantes cambios fenotípicos en los individuos. En las aves cantoras, estos cambios inducidos por el estrés han demostrado incluir el aprendizaje deficiente del canto y la reducción de la complejidad del canto en varias especies. Típicamente, el estrés del desarrollo ha sido estudiado en términos de variación individual dentro de una población; sin embargo, el canto de los pájaros, un rasgo transmitido culturalmente, puede sufrir cambios relativamente rápidos si se produce un deterioro generalizado del aprendizaje como resultado del estrés ambiental a nivel de población, y estos cambios potencialmente se podrían amplificar si los individuos afectados se convierten en los tutores del canto de las generaciones futuras. Así, hipotetizamos que los factores de estrés que afectan a todo el ecosistema pueden provocar cambios en el canto de las aves a nivel poblacional. Aquí, utilizamos grabaciones disponibles públicamente del canto de aves para determinar si las diferencias en el canto eran evidentes después de una sequía anormal y severa en 2016 en el oeste del estado de Nueva York. Analizamos los cantos de dos especies, el Junco Ojioscuro (*Junco hyemalis*) y el Gorrión Cantor (*Melospiza melodia*), grabados entre 2006 y 2020 en la región afectada por la sequía y, para comparar, en dos regiones cercanas menos afectadas por la sequía. Las características del canto a nivel poblacional de la especie con cantos más complejos (Gorrión Cantor) cambiaron en la zona de sequía después de 2016, pero no en el área control. En la especie con un canto más simple (Junco Ojioscuro), detectamos cambios en el canto en ambas regiones, sugiriendo que la sequía no tuvo un efecto desproporcionado en el canto de esta especie. Estos resultados apoyan una hipótesis más matizada según la cual los déficits inducidos por el estrés pueden afectar desproporcionadamente a especies con cantos que son más difíciles de aprender. Estas conclusiones se ven atenuadas por la disponibilidad relativamente escasa de grabaciones de años anteriores a 2016, pero predecimos que los futuros estudios longitudinales de la evolución del canto en poblaciones naturales serán más tratables dado el aumento casi exponencial en el número de grabaciones de canto depositadas en repositorios públicos en los últimos años, haciendo de este diseño experimental un marco útil para futuros estudios.

Key Words: *birdsong, community science, environmental change, evolution*

INTRODUCTION

In the context of global climate change, numerous studies have identified effects of environmental change on important avian behaviors such as the timing of migration and breeding (Carey 2009, Tuomainen and Candolin 2011, Knudsen et al. 2011); however, how these environmental changes affect learned behaviors, such as the songs of the Oscine songbirds (Order: Passeriformes), remains understudied (Møller 2010, Snell-Rood 2012). Learned behaviors can evolve in similar patterns to genetically heritable traits; for example, culturally transmitted traits that confer a selective advantage are likely to become more common, and bottleneck events can reduce the "pool" of

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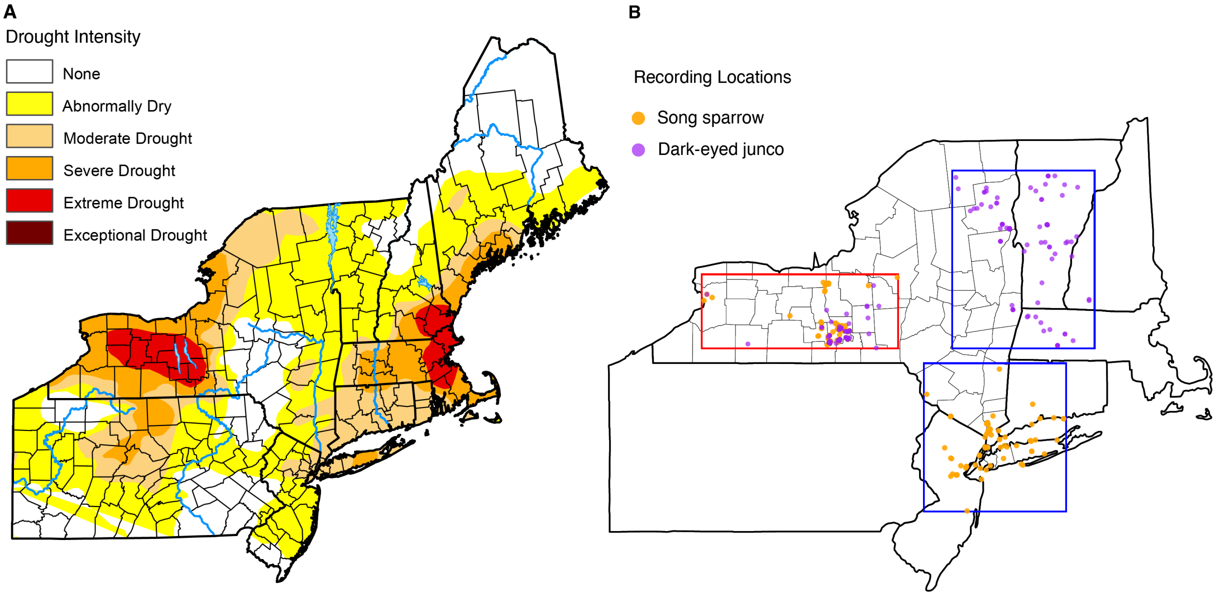
phenotypes in a population (Feldman and Cavalli-Sforza 1976, Creanza and Feldman 2014, Hudson and Creanza 2022). In contrast to genetic traits, cultural traits have the potential to undergo changes more rapidly through cultural evolutionary mechanisms such as low-fidelity copying or transmission within a generation (Tomasello 1999, Perreault 2012). Birdsong is a species-specific vocalization that generally functions in mate attraction, species recognition, and territory defense (Catchpole and Slater 2003), and the characteristics of these songs are extremely diverse across the >4500 species of songbirds (Marler and Slabbekoorn 2004). Learning duration varies between species, with some species learning only in the first year of life, after which they do not modify their songs (termed "closed-ended learners"), and others learning for several years or throughout their lifetimes ("open-ended learners") (Nottebohm 1981, Robinson et al. 2019, Rundstrom and Creanza 2021). Since birdsong can play an important role in mate choice (Kroodsma and Byers 1991; Catchpole and Slater 2003, Collins 2004), its species-level features are hypothesized to change in response to sexual pressures (Catchpole 1987, Ten Cate 2004, Price 2015, Robinson and Creanza 2019, Robinson et al. 2019). Songs are composed of syllables, defined as periods of continuous sound that are separated from one another by a short period of silence (Franz and Goller 2002, Searfoss et al. 2020). The diversity of song is typically characterized using a set of metrics that include measurements of pitch, frequency modulation, duration, spectral entropy, and syllable diversity (Read and Weary 1992, Tchernichovski et al. 2001, Weir and Wheatcroft 2011, Snyder and Creanza 2019). One widely used metric is "syllable repertoire," or the total number of unique syllables an individual produces, which is considered a metric of song complexity and learning capacity (Soma and Garamszegi 2011, Moore et al. 2011, Schmidt et al. 2013, Creanza et al. 2016, Robinson et al. 2019).

Birdsong is an energetically costly behavior, requiring significant investment in specialized neural development and time dedicated toward practicing song (Nowicki and Searcy 2004). Stress induced by nutritional deficit, ectoparasite infection, thermal extremes, or exposure to elevated corticosterone during development has been shown to impair learning ability in several species, using song learning accuracy or song complexity as metrics (Nowicki et al. 1998, Buchanan et al. 2003, Spencer et al. 2003, Holveck et al. 2008, Boogert et al. 2008, 2018, Brumm et al. 2009, MacDougall-Shackleton and Spencer 2012, Lachlan and Nowicki 2012). The conditions causing stress, such as food availability and parasite load, are usually assumed to vary across a population, such that some birds experience little stress during development and can subsequently learn higher-quality songs than birds who experienced higher levels of developmental stress. However, certain extreme environmental events might effectively apply stress to an entire population simultaneously, which could result in an entire cohort of birds exhibiting impaired song learning. If this occurred, would there be a detectable perturbation in population song in the next breeding season? If these perturbed songs became the models for future generations, could such a punctuated stressor ultimately induce lasting changes in the populations' songs? We hypothesize that ecosystem-wide stressors could cause population-level changes to bird song as an entire cohort experiences developmental stress, and, further, that these altered songs could potentially spread and persist in the population, providing a possible driver of accelerated birdsong divergence. This systems-level hypothesis is inherently complex and dependent upon the species-specific physiological and behavioral impacts of different ecological stressors. We thus also hypothesize that species might have different levels of sensitivity to these population-wide environmental disturbances and thus song changes might be observed in only a subset of species. Directly linking population-level song changes concurrent with an environmental event to stress and impaired learning, as opposed to alternative explanations such as biased mortality or dispersal away from affected regions, would likely require intensive, long-term field studies. However, we propose that community-science song-recording data could be used to identify species that exhibit population-level song changes before and after a large-scale stressor and enable field biologists to choose target species that would be well suited to studying the mechanisms underlying these changes.

We identified an ecological opportunity through which to test our hypothesis that song in a population may change after a widespread environmental stressor, and that these changes may be detectable using community-science birdsong recordings. From June through November 2016, New York State, which occupies a humid continental climate region (Kottek et al. 2006), experienced a severe drought that was very abnormal for the region (Fig. 1). The most severely affected region—central-western New York State—spent over two months under the classification of "Extreme Drought" (Appendix 1: Fig. S1). Air temperatures in 2016 in this region were also higher than normal, around the 90th percentile relative to the previous 60 years (Sweet et al. 2017), although not an outlier relative to other years between 2010 and 2021 (Appendix 1: Fig. S2). These combined factors had significant effects on vegetation: in the most heavily impacted region, New York Drought Region VII, which encompasses Tompkins, Cayuga, Onondaga, Schuyler, Seneca, Yates, Ontario, Livingston, and Wyoming counties, farms reported average non-irrigated crop losses ranging from 45% loss of field crops to 69% loss of fruit crops (Sweet et al. 2017). Incidentally, this area is also a hotspot for songbird recordings: the area surrounding Ithaca, New York—which is home to Cornell University, the Cornell Lab of Ornithology, and the Macaulay Library of Natural Sounds—has an uncommonly high spatial density of publicly available bird song recordings obtained by both academics and community bird enthusiasts over the past few decades, with a sharp increase in submitted recordings over the past five years.

While there does not seem to have been a robust analysis or systematic documentation of effects on passerines during this drought, research on passerine species from other drought events can provide some predictions as to the potential effects. In many species, including Song Sparrows, reproduction and reproductive physiology is negatively affected by the absence of water (Wingfield et al. 2012, Prior et al. 2013, Kozlovsky et al. 2018). Dry conditions can also lead to decreased and/or delayed nesting behavior and egg-laying, and factors such as lack of food availability during drought can increase nest failure (George et al. 1992, Christman 2002, Bolger et al. 2005, Winter et al. 2005, Langin et al. 2009, McCreedy and van Riper 2014, Colón et al. 2017). A study of drought-related effects on juvenile birds observed lower nestling body condition, smaller brood size, and delayed post-fledging dispersal from natal territories during the

Fig. 1. Maps of drought severity and recording locations. (A) Map from U.S. Drought Monitor (Svoboda et al. 2002) from September 2016 showing the severity and geographic extent of the drought in western New York. (B) Map of songs for Song Sparrows (*Melospiza melodia*) and Dark-eyed Juncos (*Junco hyemalis*) in our analyses. The red box encompasses the recordings of both Song Sparrows (orange) and Dark-eyed Juncos (purple) in the Drought region. For a similarly sized control region that did not experience a drought, we found the densest sampling of Song Sparrow recordings in northern New Jersey and southern New York and Connecticut and of Dark-eyed Junco recordings in eastern New York, Vermont, New Hampshire, and western Massachusetts.



drought year, suggesting that the drought had a negative effect on surviving nestlings in addition to reducing the likelihood of nestling survival (Vernasco et al. 2017). Drought leads to physiological stress and mortality in individuals through dehydration and by reducing the availability of plant and arthropod biomass that serve as food sources for many bird species (Boag and Grant 1984, Langin et al. 2009). These effects may be most pronounced in specialist species, but generalists are also affected negatively by lack of water availability and tree and plant mortality (Roberts et al. 2019).

In this study, we present analyses of the songs of two focal species, the Dark-eyed Junco (*Junco hyemalis hyemalis*) and the Song Sparrow (*Melospiza melodia*), recorded in central-western New York State between 2006 and 2019, as well as in one less-affected "control" region for each species. Our goals are twofold: first, we aim to demonstrate the use of community-generated birdsong recordings to detect changes in song in spatially constrained longitudinal studies, and second, we aim to provide a roadmap toward directly testing our broader hypotheses of how environmental events might affect cultural transmission of birdsong. When an extreme environmental event occurs, biologists often do not have behavioral or other phenotypic data from before the event unless it occurs by chance at an established field site (e.g., Price et al. 1984, Grant and Grant 1989, 1993, Donihue et al. 2018). We thus propose community-science recordings as a potential source of data for longitudinal studies, which would enable researchers to begin a study of a focal region once an environmental event had already occurred. Studies of past events, such as our focal drought, are hindered by the relatively small numbers of recordings available prior to the past several years; however, we anticipate that the continuing upward trend in contributions to community-science repositories of natural sounds will facilitate longitudinal studies of bird songs going forward.

Here, we analyze song recordings obtained from publicly accessible repositories with a specific prediction that the population distributions of certain song features will shift from before the 2016 drought to after the drought. As song complexity has previously been shown to negatively correlate with metrics of stress in Song Sparrows and to decrease in birds that had been subjected to a stress treatment (Schmidt et al. 2012, 2013), we predict that metrics of song complexity in the target species would shift toward simpler song following the drought. We might also expect a larger variance in these feature distributions after the drought, since recordings after 2016 might represent a mix of individuals that learned their songs prior to 2016, individuals that learned their songs during the drought period, and individuals that may have learned their songs from the drought-year birds. In contrast, we expect that songs in the control regions would not be significantly different before versus after 2016.

METHODS

Site Selection

In the summer of 2016, a large area of New York State experienced a drought that was unprecedented in recorded history for the region. This provided a unique opportunity for a natural experiment to study the effects of environmental stress on birdsong on a population-wide scale. Tompkins County, home to the Cornell Lab of Ornithology, was classified as being under drought conditions from late June until well into November of that year, with over two months spent under the classification of "Extreme Drought." Using the ample community-science birdsong recording data available in this area, collected before, during, and after the drought, we quantified features of the songs of individual species to assess whether the drought had a detectable effect on songs in the affected populations. We compared the songs from the drought area with songs in a control region of approximately similar land area. The control regions were selected by finding the area with the next highest density of recordings after western New York from the pool of available recordings on Macaulay Library and Xeno-canto (The Cornell Lab of Ornithology n.d., Vellinga and Planqué n.d.). We assessed the density of recordings for each target species and both time periods, 2006-June 2016 (before drought) and 2017-2019 (after drought) and selected the regions that were not impacted or were less severely impacted by the 2016 drought and that had the greatest number of available recordings before and after the drought period. For both species, we only considered regions in the eastern half of the continental U.S. since there are well-documented differences in song dialects and singing behavior between east and west coast populations of Song Sparrows (Hughes et al. 1998), and different Dark-eyed Junco subspecies are present in the West (Ferree 2013). Since no regions outside of western New York had at least 20 recordings for Dark-eyed Juncos from 2006-2016, we chose the Dark-eyed Junco control region based on the abundance of recordings from 2017-2019, and, of those options, chose the region that did not also experience severe drought during 2016 (Appendix 1: Figs. S3A-B). For Song Sparrows, only one potential control area had relatively dense recording availability both before and after 2016, and it had experienced moderate drought during 2016 (Appendix 1: Figs. S3C-D). For subsequent analyses, we defined the Drought region for both species as 42.2°N-43.2°N and 74.45°W-78.9°W. To compare the Drought region with an area that did not experience extreme drought in the studied timeframe, we defined the Control region for Dark-eyed Juncos to be 42.0°N-44.6°N and 72.0° W-74.5°W and the Control region for Song Sparrows to be 40.0° N-42.0°N and 72.5°W-75.0°W.

Species selection

We selected Song Sparrows and Dark-eyed Juncos as target species based on several factors related to 1) feasibility of a community-science-based study of song, 2) likelihood of drought impact on individuals, and 3) likelihood that any drought-associated impact of song could be detected in years following the drought. Regarding the feasibility of study, we considered the number of song recordings available and song structure. In early 2017, we retrieved metadata for all audio recordings from Tompkins County, New York which were tagged as containing "song" in the Macaulay Library online repository. We excluded any species with less than 100 recordings. We also eliminated any species that sing continuously or that do not have a clear separation between song bouts (e.g., Red-eyed Vireo) to facilitate consistent song analysis using our acoustic analysis program, Chipper (Searfoss et al. 2020). Drought-associated impacts on song within a population would be diluted by high rates of immigration or emigration, so we sought species that were year-round residents of the drought region and/or for which there existed some evidence of annual philopatry (eliminating e.g., Chestnut-sided Warbler, Common Yellowthroat, Ovenbird, Indigo Bunting, Black-throated Blue Warbler, Blue-headed Vireo, Blackburnian Warbler, Blue-winged Warbler, Ruby-crowned Kinglet, Purple Finch), so that adult birds recorded in a location are likely to have hatched near that location. We also focused on species that do not modify their song repertoires after their first breeding season (i.e., "closed-ended" learners), since we hypothesized that effects of the drought on song learning could be less pronounced in "open-ended" learners, who can continue to modify their song in subsequent breeding seasons (e.g., Gray Catbird, Red-winged Blackbird, Chestnut-sided Warbler; Brenowitz and Beecher 2005, Robinson et al. 2019). The Dark-eyed Junco and the Song Sparrow, both in the family Passerellidae and the two songbird species with the most recordings in the drought area that were not eliminated for any of the reasons outlined above, are both closed-ended learners and show evidence of philopatry (Weatherhead and Forbes 1994, Liebgold et al. 2013). Song Sparrows tend to learn songs and syllable types from several neighboring adults, such that elements or entire songs are learned with relatively high fidelity (Beecher et al. 1994, Beecher 2008). Dark-eyed Juncos learn songs faithfully but also appear to improvise some songs, which are thought to be of higher performance difficulty than shared songs (Cardoso and Atwell 2016).

Environmental limitations to food sources may have been a major contributor to developmental stress during the drought (White 1984, Huberty and Denno 2004). The 2016 drought has been shown to have had a large detrimental effect on agricultural vegetation and wild vegetation alike (Sweet et al. 2017). The Dark-eyed Junco diet is composed primarily of plant matter, which comprises 76% of their diet, 62% of which is seeds, and they have been known to supplement their diet with insects on occasion (Del Hoyo et al. 1992). Although the Song Sparrow diet is also primarily composed of plant matter for most of the year, during the breeding season their diets rely more heavily on animal food sources, such as beetles, butterflies, and small gastropods (Del Hoyo et al. 1992). The generalist diets of both species could have provided a buffer against substantially increased mortality as a result of the drought, increasing the likelihood that members of the cohorts experiencing the drought during development would have survived the drought.

Dark-eyed Junco and Song Sparrow populations may be expected to include many of the same individuals from year to year. Some subspecies of the Dark-eyed Junco, as well as many Western populations of Song Sparrows, are either short-distance altitudinal migrants or are sedentary. While the drought and control regions used in this study lie fully within the ranges in which each species is present year-round, breeding populations in these areas likely do migrate in a "leap-frog" pattern, with the northernmost breeding populations moving to the year-round presence area during the winter while the breeding populations in the year-round presence area migrate to the southern U.S. (Yunick 1988, Arcese et al. 2020, Nolan et al. 2020). Therefore, it becomes important to consider rates of philopatry in these species and populations. Several types of evidence—capture-recapture, experimental displacement, and population genomic methods—have indicated that Dark-eyed Junco populations in the Eastern

Table 1. Summary of recordings of Dark-eyed Juncos (*Junco hyemalis*) and Song Sparrows (*Melospiza melodia*) in the drought and control regions. ML = Macaulay Library, XC = Xeno-canto.

Species	Number of unique recordings	Drought region	Control region
Dark-eyed Junco	2006-June 2016 (pre-drought)	131 bouts from 46 recordings (45 ML, 1 XC)	11 bouts from 8 recordings (8 ML)
Dark-eyed Junco	2017-2019 (post-drought)	199 bouts from 73 recordings (64 ML, 1 XC, 8 this study)	62 bouts from 48 recordings (47 ML, 1 XC)
Song Sparrow	2006-June 2016 (pre-drought)	409 bouts from 37 recordings (34 ML, 3 XC)	72 bouts from 16 recordings (1 ML, 15 XC)
Song Sparrow	2017-2019 (post-drought)	740 bouts from 158 recordings (148 ML, 4 XC, 6 this study)	330 bouts from 83 recordings (74 ML, 9 XC)

U.S. likely have moderately high rates of philopatry (Ketterson and Nolan 1992, Keiser et al. 2005, Liebgold et al. 2013, 2019). Song Sparrow populations in Eastern North America have also been found to exhibit high rates of philopatry and site fidelity using capture-recapture data, stable isotope analysis, and song-sharing analysis (Beecher et al. 1994, Potvin et al. 2015, Sarquis-Adamson and MacDougall-Shackleton 2016, Kelly et al. 2019, Weatherhead and Boak 1986). Both of our target species engage in similar singing behavior in which males advertise location and territory by producing high-amplitude songs for extended periods of time. However, the two focal species for our study have notable variation in song complexity. The Dark-eyed Junco has a relatively simple song, typically consisting of one repeated syllable, whereas Song Sparrow songs are composed of multiple syllables. Dark-eyed Juncos have small repertoires of around 4 songs per individual, and have been observed to sing the same song up to 120 times in a row before switching to a new song (Williams and MacRoberts 1977, Newman et al. 2008, Cardoso et al. 2009). Song Sparrows, on the other hand, typically cycle between 5-13 different song types, often singing several renditions of one type before switching to the next (Wood and Yezerinac 2006). Dark-eyed Juncos have two types of songs, short-range and long-range, with the short-range songs being much softer and often more complex than the long-range songs (Cardoso et al. 2009). Short-range songs, likely due to their quiet and subtle nature, are rarely found in community science recording repositories; thus, in this study, we only consider long-range songs in Dark-eyed Juncos. Dark-eyed Junco females sing only short-range song, so are not included in our dataset (Nolan et al. 2020). Song Sparrow females have been observed to sing, though infrequently and generally before breeding begins (Arcese et al. 1988, 2020). None of the Song Sparrow recordings we used were labeled as being of a female by the recordist, but we cannot rule out the possibility that some female songs were included, since the lack of sexual dichromatism in this species can make visual sexing difficult.

Obtaining recordings

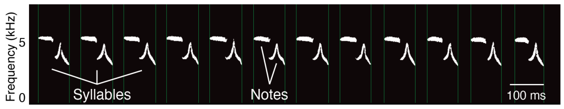
Two community-science recording libraries, Macaulay Library and Xeno-canto, provided most of the recordings for this study. We used the search engines of these digital databases with the search terms "*Junco hyemalis*" and "*Melospiza melodia*" with the filters "Location = United States" and "Sounds/Type = Song." From these digital databases, we were able to obtain a total of 203 recordings for Dark-eyed Juncos, and 564 recordings for Song Sparrows from within the two analysis regions from 2006-2019. All of the Dark-eyed Junco recordings we include were identified by the recordists as being of the slate-colored subspecies, *Junco hyemalis hyemalis*. After visually examining each recording, we discarded any that misidentified the species, only contained calls, were noted in the recording metadata to contain juvenile or plastic song, or had excessive background noise. In cases where multiple recordings existed from the same recordist on the same date and at the same time or location, we used only one recording in order to avoid double-counting individual birds who may have been recorded more than once, unless it was clearly noted in the remarks that the recordings were of different individuals.

We supplemented these recordings with ones recorded in the field by one author (KTS) in July 2017. During this trip, the author visited several publicly accessible locations in Tompkins County within the region that had experienced the heaviest drought during 2016. This added usable recordings from an additional 8 Dark-eyed Juncos and 6 Song Sparrows. Recordings from January 2006 through June 2016 were categorized as before the drought. Those recorded from July 2016 through December 2016 were considered to have occurred during the drought and removed from analysis. Any recordings from 2017 or later were defined as after the drought. Due to the sparseness of recordings in public repositories from earlier years, we did not include any recordings prior to 2006 (Table 1). Lists of the recordings used for each species are available in a data repository (https://doi.org/10.6084/m9.figshare.22151684).

Processing song recordings

Many of the recordings collected contained multiple song bouts from the same bird. For the purposes of this study, we define a bout as a continuous period of syllable production that is temporally separate from other periods of song. Within these bouts, syllables are separated from one another by silence, and discrete pulses of signal that are not separated by silence are termed notes (Fig. 2).

Fig. 2. Example spectrogram of a single bout of Dark-eyed Junco (*Junco hyemalis*) song with parts of the song highlighted. Syllables are periods of signal separated by silences. Within each of the syllables shown, there are two notes, i.e., discrete pulses of signal that are not separated from one another by silences.



Individual bouts were extracted from recordings using Audacity version 2.4.2 and exported as separate WAV files with sampling rate set to 44100 Hz. Due to inherent differences between species song, different bout-selection protocols were implemented for juncos and Song Sparrows. Since Dark-eyed Juncos repeat the same song type many times in a row, most of the recordings in community-science databases are of a single song type (Williams and MacRoberts 1977, Cardoso et al. 2009). If there were multiple distinct song types in a single recording, we collected at least one bout of each type, but otherwise, we collected up to three bouts per recording, preferentially choosing ones that were least affected by background noise. Song Sparrows, in contrast, cycle between song types more frequently (Wood and Yezerinac 2006). In order to obtain the greatest possible variation in songs, we extracted every available bout from Song Sparrow recordings. Spectrograms of extracted bouts are available in a data repository (https://doi.org/10.6084/m9.figshare.22151684).

Syllable segmentation in Chipper

Bouts were segmented into discrete syllables by a researcher blind to the region and year of each recording using the open source software Chipper (Searfoss et al. 2020). Chipper uses a Fast Fourier Transform to generate a spectrogram from the WAV file of each song bout and then predicts syllable boundaries using fluctuations in the signal amplitude. The user can first implement high-pass and low-pass filters to reduce low-frequency and high-frequency background noise, respectively, and then modify the predicted syllable boundaries by adjusting parameters such as the signal-to-noise threshold, the minimum silence duration required to distinguish between syllables, and the minimum duration of syllables. Song bouts were discarded if they had a signal-to-noise ratio that made it difficult to reliably detect syllable boundaries. In addition, any files that had birds singing in the background that interfered with the song of the bird of interest in the recording were removed. Since Dark-eyed Juncos generally sing a single repeated syllable, we could extract syllable properties even when only a subset of the song bout was usable, which was the case for 5 files; for these files, we manually counted the number of syllables and number of unique syllables and excluded them from analyses of two other song features, number of notes and bout duration.

The resulting spectrogram of each song is stored as a matrix in which (at a sampling rate of 44100 Hz) every row represents ~43 Hz and every column represents 0.317 milliseconds (Searfoss et al. 2020). The value in each element of this matrix represents the signal intensity at that frequency and time; each element in the matrix becomes a pixel in the spectrogram image (Fig. 2). After the user adjusts the signal-to-noise threshold, signal intensities above this value are retained in a binary spectrogram where ‘1’ or ‘0’ indicates that signal is present or absent at that frequency and time.

Chipper also executes an additional stage of noise reduction by measuring each note, defined as an area of continuous sound across the time and frequency axes, and discarding any that have an area in pixels less than a user-specified noise threshold. Chipper allows the user to empirically determine this average noise threshold (the minimum area in pixels that a note must be in order to not be discarded as noise) as well as an average syllable similarity threshold (the percent overlap that determines whether two syllables are considered the same or different). To assess these thresholds, we selected ~80-100 single-bout files for each species and manually set the noise threshold and syllable similarity threshold for each file. Across these test files, the average noise threshold for Song Sparrows was 59.1 pixels, and the average similarity threshold was 47.3% syllable overlap. The average noise threshold for Dark-eyed Juncos was 142 pixels, and the average similarity threshold was 29% syllable overlap. We used these average values as the thresholds in subsequent analyses. Occasionally, a syllable would only contain notes with areas below the noise threshold; we manually checked these recordings to decide whether the songs should be reanalyzed with different parameters or discarded.

Song analysis

For those recordings that contained more than one bout, we averaged the song feature values from each bout and used these values in all subsequent analyses. After syllable segmentation, we used Chipper to measure a slightly different set of song features for Dark-eyed Juncos and Song Sparrows, choosing metrics that were more likely to be meaningful based on the structure and features of each species’ song. For both species, we measured bout duration, total number of syllables, number of unique syllables, total number of notes, number of notes per syllable, mean syllable duration, standard deviation of syllable duration, rate of syllable production (calculated as the number of syllables divided by the duration of the song bout), degree of syllable repetition (calculated as the number of syllables divided by the number of unique syllables), overall frequency range, average maximum frequency of syllables, and average minimum frequency of syllables. For Dark-eyed Juncos, which generally sing multiple repetitions of the same syllable, we also measured the mean syllable stereotypy, defined as the mean syllable overlap value for syllables that were deemed to be repetitions of the same syllable. For Song Sparrows, which generally sing both short and long syllables, we also measured the duration of the shortest syllable and the duration of the longest syllable. Features that describe duration are measured in milliseconds, and features that describe frequency are measured in Hertz.

Since song is an inherently multidimensional trait, we performed principal components analyses for several purposes. First, we performed PCAs on the full datasets of song features and performed subsequent analyses on all PCs with eigenvalues >1.5, which included PCs 1-3 for both species, alongside individual analyses of each song feature. We also performed a multivariate test to assess the homogeneity of song variances before versus after the drought using vegan::betadisper() on the PCoA-transformed song feature data (log-transformed when applicable). For each focal species and song feature, we used a set of Shapiro-Wilk tests to assess the distribution of our song-feature data before and after the drought in both the drought region and the control region. When at least one group in each comparison was not normally distributed, we log-transformed the song-feature data by taking the natural log of the feature values. We used nlme::gls() to test whether there were significant differences in any features between the four groups made by intersecting “Region” (Drought or Control) and “Era” (Before 2016 or After 2016): Drought-Before, Drought-After, Control-Before, and Control-After. We first performed this generalized least squares (GLS) regression as both a simple model, with each group assumed to have equal weight, and a complex model, with weights set individually for each group by varIdent(form = ~1 | Era*Region) to account for heterogeneous variances of the different groups. For each song feature, we performed an ANOVA to test whether the complex model was a better fit to the data than the simple model, and we used the complex model only if it was a significantly better fit. We performed an ANOVA on the appropriate GLS model to test whether any of the groupings (by Era, Region, or their interaction) significantly differed in that song feature, and we used a Holm-Bonferroni correction to account for multiple hypothesis testing on the 13 (Dark-eyed Juncos) or 14 (Song Sparrows) song features. We then performed pairwise post-hoc tests using estimated marginal means (R package 'emmeans') on those features that were significant in order to compare Drought-Before to Drought-After and Control-Before to Control-After, adjusting the p-value outputs using the 'mvt' (multivariate *t* distribution) method.

Finally, to visualize the song differences from before and after the drought, we performed a principal components analysis on the full set of song recordings for each species but included only the features that exhibited significant or trending-significant differences in either region from before to after 2016 based on the results from the GLS model. We transformed these feature values for each analyzed bout based on the loadings from the PCA, scaled the PCA dimensions based on their contributions to the observed variance, and identified the bout with the smallest Euclidean distance to the medians of the PC dimensions in each group in order to identify a representative song bout from each group.

All statistical analyses were implemented in R, with code available on GitHub (https://github.com/CreanzaLab/Birdsong_DroughtStress).

Population trends

Intense droughts can cause high mortality and reduce breeding behaviors in some passerine species (Boag and Grant 1981). We used two sources of population sampling data to assess whether there were any notable deviations from typical species abundance and breeding trends in our regions of interest during 2016. First, we obtained banding data for all species from the United States Geological Society (USGS) from 2010-2020. We assessed species abundance using the USGS banding data by counting the total number of captures of each species in a region per year. We controlled for effort by dividing by the total number of Location-Days for that region and time period, defined as the total number of unique banding location-dates in which at least one passerine individual was documented. We assessed the approximate rate of recruitment of young birds into the breeding population for each yearly cohort by summing the numbers of individuals classified as "Hatch Year" or "Local" (defined as "A nestling or young bird incapable of sustained flight") within each region.

We also obtained observation data in the form of community-scientist-submitted species checklists from 2006-2022 from eBird. From these, we considered only data from "completed" checklists, i.e., for which the observer attested that all species encountered during that sampling event were recorded in the checklist. Approximately 80% of the checklists from each of our regions are noted as complete (Control [Dark-eyed Junco]: 79.6%, Control [Song Sparrow]: 81.2%, Drought [both]: 78.7%). We measured the abundance of each species by summing the number of individuals of each species encountered across all complete checklists for each month of each year. We controlled for effort by dividing this number by the total number of complete checklists over the same region and time period. We assessed breeding behavior trends for each species by counting the number of encounters that were labeled with a "Confirmed" or "Confirmed/Probable" breeding behavior, which includes: Nest with Young, Nest with Eggs, Carrying Fecal Sac, Feeding Young, Carrying Food, Recently Fledged Young, Occupied Nest, Used Nest, Distraction Display, Nest Building, and Carrying Nesting Material (Wood et al. 2011, eBird Help Center 2021).

RESULTS

Recordings obtained

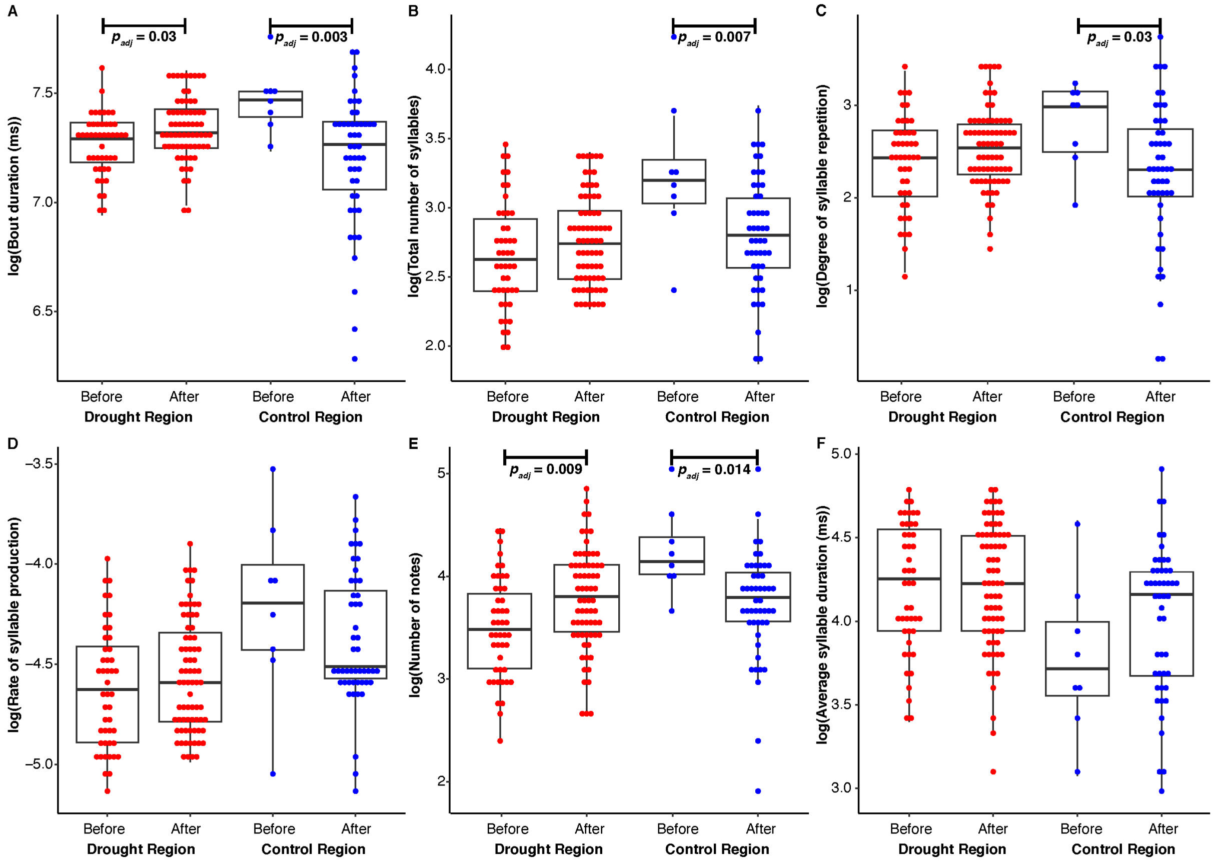
We initially collected 203 recordings of Dark-eyed Juncos and 564 recordings of Song Sparrows from the target areas. We discarded a subset of these recordings for several reasons. Occasionally recordings were submitted by the same recordist (or a group of recordists in the same location) on the same day, and we eliminated all but one from our sample unless we could confirm that the recordings were different birds based on the information provided by the recordists. In addition, we eliminated songs that were either recorded during the drought (5 junco recordings, 7 Song Sparrow recordings), recorded slightly outside the drought region, or had no analyzable song due to excessive background noise or poor signal-to-noise ratio. In all, we omitted 28 Dark-eyed Junco recordings and 270 Song Sparrow recordings.

The Dark-eyed Junco's long-range song is relatively simple, with each song bout characterized by a single syllable repeated multiple times. We analyzed 403 Dark-eyed Junco bouts from 175 unique recordings in total (Table 1). Song Sparrows sing a relatively complex song, particularly for closed-ended learners (Marler and Peters 1987). Many of their syllables are composed of multiple notes, and they cycle through their syllable repertoire of approximately 35-38 syllables by singing different song types containing overlapping subsets of their syllable repertoire. To capture this variation, we analyzed as many bouts as possible from each individual recording. We analyzed Song Sparrow songs from 294 unique recordings in total (Table 1).

Dark-eyed Junco song analysis

The principal components analysis produced three components with eigenvalues > 1.5, which together explained 67.9% of variance (Appendix 1: Table S1A). There was a significant difference in the first and third principal components of Dark-eyed Junco song between the four groups (GLS interaction term (Era*Region) PC1 $p = 0.0059$, PC2 $p = 0.72$, PC3 $p = 0.0013$), and our post-hoc test showed that both PC1 and PC3 differed significantly from before to after 2016 in the Control region, but not the Drought region (estimated marginal means adjusted *p*-values: PC1 - Drought region $p = 0.50$, Control region $p = 0.021$; PC3 - Drought region $p = 0.056$, Control region $p = 0.015$) (Appendix 1: Fig. S4). The most influential features in PC1 were number of syllables, average syllable duration, rate of syllable production, and degree of syllable repetition. The most influential features in PC3 were bout duration, average maximum syllable frequency, frequency range, and number of notes (Appendix 1: Table S1). When testing individual features, we found that Dark-eyed Junco songs appeared to change over time in both regions in several of the same features: in the drought region, Dark-eyed

Fig. 3. Song feature distributions within Dark-eyed Junco populations before and after the 2016 drought. Each boxplot shows Dark-eyed Junco (*Junco hyemalis*) mean song-feature values per recording: (A) bout duration, (B) number of syllables, (C) degree of repetition (number of syllables divided by the number of unique syllables), (D) rate of syllable production (number of syllables divided by the bout duration in ms), (E) total number of notes per bout, and (F) mean syllable duration. Song features were log-transformed by taking the natural log of the feature values when they were not normally distributed (all panels). The midline of each boxplot represents the median, with the boxes representing the interquartile range (IQR). Labeled p-values are calculated with the emmeans package and are significant when adjusted for multiple comparisons. The whiskers are 1.5 * IQR. These specifications also apply to the box plots in Figure 5.



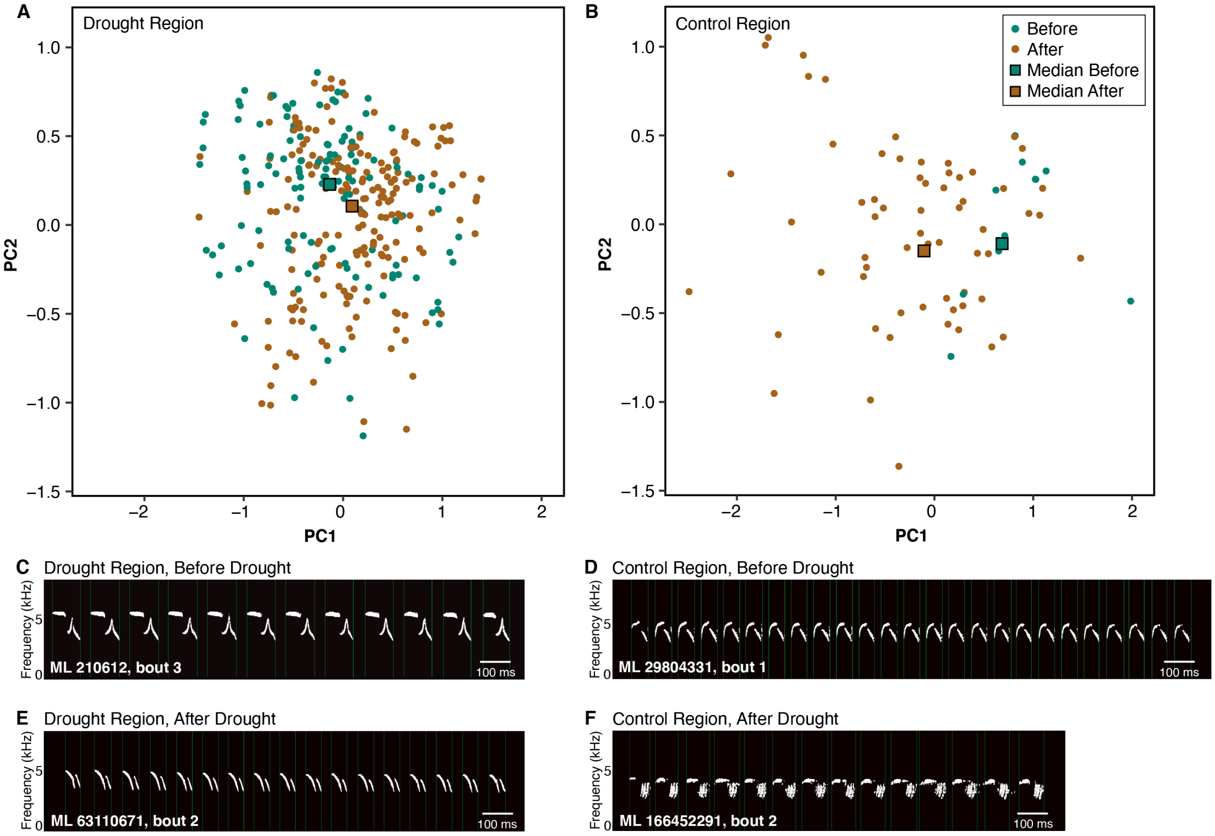
Junco songs exhibited increases in the number of notes per bout and bout duration after 2016 relative to before 2016, and in the control region, Dark-eyed Junco songs exhibited decreases in bout duration, the total number of syllables, degree of syllable repetition, and the total number of notes per bout after 2016 relative to before (Fig. 3, Appendix 1: Table S2). There were no differences in song feature variances before vs after 2016 in either region (ANOVA, vegan::betadisper() test $p > 0.05$, Appendix 1: Fig. S5).

We identified representative bouts to provide examples of the song differences between each region and era combination (Fig. 4). These song spectrograms effectively show the decrease in bout duration, number of syllables, and number of notes in the Control region, as the before-2016 representative bout is visibly longer than the others (Fig. 4D, F). The differences between the two time periods in the Drought region appear more subtle (Fig. 3A, E), and indeed, the bouts have very similar numbers of notes and bout durations. The qualitative differences in syllable structure demonstrate how songs with quantitatively similar song features may still look and sound very different (Fig. 4C, E).

Song Sparrow song analysis

The principal components analysis produced three components with eigenvalues > 1.5, which together explained 64.8% of variance (Appendix 1: Table S1B). The GLS model revealed a significant interaction between the region and time period for the first and third principal components of Song Sparrow song (GLS interaction term (Era*Region) PC1 $p = 0.0013$, PC2 $p = 0.56$, PC3 $p = 0.028$). The subsequent pairwise post-hoc test showed that both PC1 and PC3 differed significantly from before to after 2016 in the drought region but not the control region (estimated marginal means adjusted p-values: PC1 - Drought region $p = 0.0049$, Control region $p = 0.12$; PC3 - Drought region $p = 0.00063$, Control region $p = 0.75$) (Appendix 1: Fig. S4). The most influential features in PC1 were average syllable duration, rate of

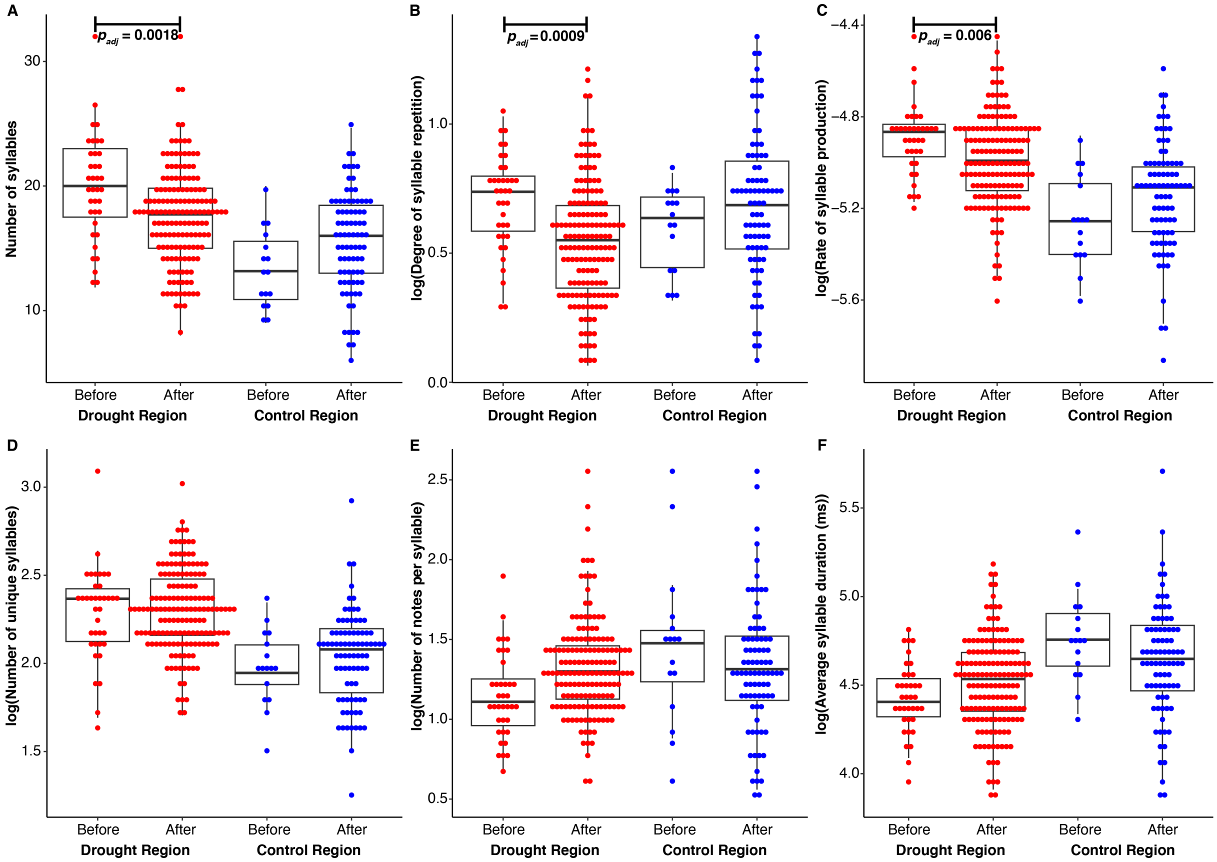
Fig. 4. Visualizing Dark-eyed Junco (*Junco hyemalis*) song features. To visualize typical songs from each region, we performed a principal components analysis on the full set of song recordings but including only the features that exhibited significant or trending-significant differences in the Drought or Control regions from before to after the drought (number of notes per bout, bout duration, degree of syllable repetition, number of syllables, mean syllable stereotypy) (Appendix 1: Table S2). We transformed these feature values for each analyzed bout based on the loadings from the PCA, then plotted PC1 and PC2 of each individual bout in the (A) drought and (B) control regions. The squares indicate the median values of both principal components for the before- and after-drought periods within each region. The songs that were closest to the median values of the five PCs in each region and time period are shown for each region (C-F). The spectrograms from the control region show the most apparent and significant differences, with the (D) pre-2016 median bout having a duration of 1805ms, 53 notes, and 25 syllables, and (F) the post-2016 median bout with a duration of 1345ms, 33 total notes, and 14 syllables.



syllable production, number of notes per syllable, standard deviation of syllable duration, number of syllables, and largest syllable duration. The most influential features in PC3 were degree of syllable repetition, average minimum syllable frequency, and largest syllable duration (Appendix 1: Table S1B). When testing individual features, three of these song features were significantly different in the drought region: after the drought, we observed a decrease in the number of syllables, the rate of syllable production, and the degree of repetition (Fig. 5, Appendix 1: Table S3). In the drought region, the reduction in the degree of syllable repetition after the drought (Fig. 5B), when taken in concert with the trends toward longer average syllable durations and a lower rate of syllable production (Fig. 5C, F), may indicate that the shift occurs most prominently in the trill section that exists in most Song Sparrow songs. In trills, a single syllable is rapidly repeated on average 7-9 times (Borror 1965), so a smaller number of syllable repetitions in the trill would decrease the overall degree of repetition and, if the trill was approximately the same duration, the rate of syllable production in the trill. We performed a follow-up analysis to check whether this interpretation is borne out in the data by obtaining for each bout the number of times the most-repeated syllable type was produced in that bout. We averaged these values across all bouts within each recording to obtain, for each recording, the "mean number of repetitions of the most-repeated syllable type per bout" and found that this was significantly lower after the drought in the drought region only (Appendix 1: Fig. S6).

PC-transformed bout-level data and representative Song Sparrow bouts from each region and time period are shown in Figure 6. The representative bouts from the drought region effectively show the decrease in the number of syllables and related metrics from before to after the drought (Fig. 6C, E). The representative bouts in the control region show how songs can be qualitatively different

Fig. 5. Song feature distributions within Song Sparrow (*Melospiza melodia*) populations before and after the 2016 drought. Each boxplot shows Song Sparrow mean song-feature values per recording: (A) number of syllables, (B) degree of repetition (number of syllables divided by the number of unique syllables), (C) rate of syllable production, (D) number of unique syllables, (E) number of notes per syllable, and (F) mean syllable duration. The number of syllables, degree of repetition, and rate of syllable production (A-C) were significantly different from before to after the drought in the drought region only, with Bonferroni-Holm correction for multiple hypothesis testing. In the drought region, the differences in average syllable duration and the number of notes per syllable from before to after the drought were trending towards significance, but were not significant after Bonferroni-Holm correction for multiple hypothesis testing. The number of unique syllables was normally distributed (Shapiro-Wilk test p > 0.05) in both time periods and this feature was thus not log-transformed (Appendix 1: Table S3).

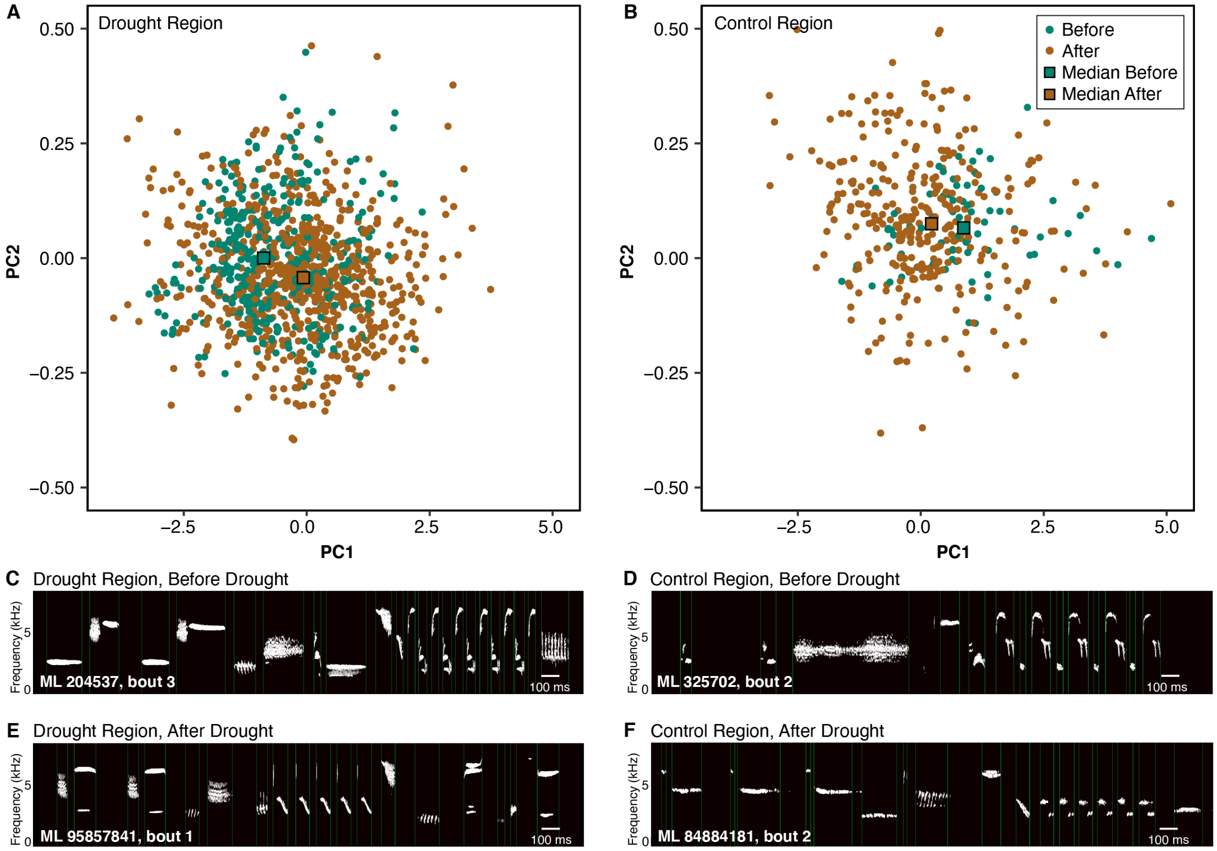


without those differences meaningfully changing the measured song features (Fig. 6D, F). Finally, we used a multivariate test to assess the homogeneity of song variances before versus after 2016 using vegan::betadisper() on the log-scaled and PCoA-transformed feature data and found that the variances of the pre-2016 and post-2016 data were significantly different in the drought region ($p = 0.0423$), but not the control region ($p = 0.5173$) (Appendix 1: Fig. S5).

Population trends

We attempted to assess whether deviations from typical population or breeding dynamics occurred during the 2016 drought by analyzing both USGS banding data and eBird observation data. We found that, overall, the amount of "effort" in banding is declining (fewer unique Location-Days per year) across all three of our studied regions, but there were fewer banding Location-Days in 2016 than would have been expected based on the overall trend (Appendix 1: Fig. S7). This could have been caused by either a higher rate of failed banding sessions, in which no passerines were captured, or by banding sessions being performed less frequently that year. In contrast, "effort" in documenting bird observations with eBird is increasing (more complete checklists per year across all regions; Appendix 1: Fig. S8). Species abundance trends in these data are somewhat noisy, but neither Song Sparrows nor Dark-eyed Juncos were encountered at a notably reduced rate during 2016 in the drought region when controlling for effort (Appendix 1: Fig. S9). There was no reduction in captures of juvenile birds in the drought region in 2016, but there were slightly fewer juvenile Song Sparrows and Dark-eyed Juncos captured in 2017 in the drought region than in 2016 or 2018; however, these values are within the typical year-to-year variation in the data (Appendix 1: Fig. S10). Similar trends are present in the eBird observation data; there are no noteworthy fluctuations in sighting frequency and breeding behaviors during and after 2016 (Appendix 1: Figs. S11-S12).

Fig. 6. Visualizing Song Sparrow (*Melospiza melodia*) song features. To visualize typical songs from each region, we performed a principal components analysis on the full set of song recordings but included only the features that exhibited significant or trending-significant differences in the Drought region from before to after the drought (total number of syllables, rate of syllable production, degree of syllable repetition, average syllable duration, average number of notes per syllable) (Appendix 1: Table S3). We transformed these feature values for each analyzed bout based on the loadings from the PCA, then plotted PC1 and PC2 of each individual bout in the (A) drought and (B) control region. In the drought region, Song Sparrow songs on average had significantly less syllable repetition, fewer syllables, and a lower number of syllables per bout duration after the drought, which is potentially due to changes in the trill section of the song (Appendix 1: Figure S6). There were no significant differences in the control region. The songs displayed in panels C-F were closest by Euclidean distance to the median value of the 5 PCs, scaled by the contribution of each PC dimension. In the drought region, the 'median' song from before the drought (C) has 22 syllables, a degree of syllable repetition of 2.0, a rate of syllable production of 7.5 syllables/sec, an average syllable duration of 99.8 ms, and 2.5 notes per syllable; the 'median' song after the drought (E) has 18 syllables, a degree of syllable repetition of 1.6, a rate of syllable production of 6.5 syllables/sec, an average syllable duration of 84.5 ms, and 3.9 notes per syllable. The observed reduction in the number of syllables in the trill section is shown here, with the trill in the song from before the drought containing 6 repeated syllables and the trill in the song from after the drought containing 5 repeated syllables.



DISCUSSION

Here, we propose a method for testing the hypothesis that environmental stress may affect the cultural transmission of birdsong in natural populations through stress-induced learning impairment. Because physiologically stressful conditions during development can disrupt song learning on an individual level, we hypothesized that a population-wide stressor could have measurable effects on the distribution of song features in a population. Studying a learned behavior, such as song, in the context of population-wide environmental pressures is particularly interesting since the resulting cultural evolutionary dynamics could be significantly more rapid than genetic evolution (Perreault 2012). Even without selection for a novel song type, the combination of drift and oblique transmission—from an adult to an unrelated juvenile—could lead to the spread of novel song variants more quickly than possible with a genetic mutation (Cavalli-Sforza and Feldman 1981). Since large-scale stressors may not occur in a location that is being actively monitored and recorded by field biologists, comparative studies of before vs. after a localized environmental stressor may be most possible by using community-science data. We analyzed community-science birdsong recordings from two common species of songbird, the

Dark-eyed Junco and the Song Sparrow, recorded before and after a severe and abnormal drought that affected western New York in 2016, and assess whether we find evidence for temporal differences in song features in the drought-affected region and, for comparison, from lesser-affected regions. We demonstrate that shifts in population song may be detectable using aggregated community-science birdsong recordings. While we cannot conclude that these shifts are due to environmental stress-induced impaired learning given the scope of these data, these results provide intriguing hints that environmental events may affect the songs present in a region.

Interpretation of results by species

For Dark-eyed Juncos, a species that generally sings a simple song of one repeated syllable, we observed several song-feature changes in both the drought region and the control region, suggesting that the drought did not have an outsized effect on the songs of this species compared to typical changes over time. In contrast, in the Song Sparrow, a species that has a relatively large syllable repertoire and produces complex multi-note syllables, we observed significant differences in some song features related to song complexity (number of syllables, degree of syllable repetition) in the drought region, but not the control region. Specifically, Song Sparrows in the drought region after 2016 sang songs with less syllable repetition, a lower rate of syllable production, and fewer syllables per bout overall. In addition, in the drought region but not the control region, we observed higher variance in song features after the drought. Since we hypothesized that species with complex songs would be more sensitive to the potential stress-associated learning disruption, these differences are notable. However, other song features that are related to song complexity, such as the number of unique syllables per song or the total number of notes, did not change after drought as we had predicted. Thus, the changes we observed suggest that Song Sparrow songs did not become universally simpler after the drought. We hypothesized that changes in the Song Sparrow's "trill" section (made up of numerous repetitions of the same syllable) could explain these observed patterns, and we found that the mean number of repetitions in the trill was significantly lower after the drought in the drought region only. This suggests that trills may have meaningfully changed due to the drought, becoming either shorter in duration or slower in the rate of syllable production. Though the relevance of trill rate hasn't been studied specifically in Song Sparrows, trills that cover large frequency ranges are considered to be physically difficult to perform across species, and thus a higher rate of trill production is hypothesized to be sexually selected because it is indicative of higher male quality, greater skill, or superior developmental history (Podos 1997, Ballentine et al. 2004, Caro et al. 2010, Searcy et al. 2010, Cramer 2012).

Alternative explanations for song feature shifts after drought

Song in a population could shift significantly after an environmental stressor for reasons other than impaired learning. First, if there was heightened mortality in the population, songs could undergo a bottleneck effect akin to the stochastic loss of genetic diversity after extreme population reduction. In such a case, we might expect to see a narrower distribution of one or more of the song features after the reduction in population diversity that occurs during this type of bottleneck event. Alternatively, if song features were correlated with another trait that was under selection pressure during drought conditions, such as body size, there could be indirect effects on song independent of learning ability. Second, a drought could induce individuals to emigrate from the region in pursuit of more hospitable conditions, or to not return to it after migration. If these individuals did not return in the following year once drought conditions had abated, others may disperse into and opportunistically colonize those territories, changing the region's song distribution by changing the residents of the region. Third, adult songs, despite being crystallized and thus not expected to radically change, could theoretically be different during drought conditions, for example if the ambient temperature and humidity altered airflow through the syrinx or sound transmission through the air (Pandit et al. 2022). In this case, juveniles perceiving those song differences could hypothetically learn the song as perceived in the context of drought conditions and propagate any differences to future pupils.

Caveats and limitations

The high baseline level of complexity of Song Sparrow songs may prevent us from accurately assessing changes in song using only mean song feature values across recordings, since, for example, meaningful changes in syntax or syllable composition could occur but not be reflected in the average values we analyzed. However, the observed shifts in certain features may hint at more nuanced changes happening in song or syllable structure. Future analysis of individual song elements, such as buzzes and trills (Burt et al. 2002), could probe these facets in greater depth. This could also be true for the Dark-eyed Juncos, since the individual syllables in the median bouts were qualitatively very different (Figs 4C-F). Additional song features such as entropy and frequency modulation may provide insights into trends related to syllable composition, though these may be somewhat difficult to reliably quantify in noisy recordings.

When performing community-science-based analyses, we often lack metadata that would be useful in interpreting the song data, such as the age or identity of the bird in the recording. One potential challenge of studying severe environmental stress is that members of a population might conserve resources by reducing their reproductive output, for example by abandoning nest-building activities or failing to provision chicks (Ouyang et al. 2012, Angelier et al. 2016). In the context of this study, this would mean that there would be fewer juveniles developing during the height of the drought, and thus less of an effect on the represented songs in the following years. However, the timing of the drought in New York might have mitigated this challenge; since the drought did not reach its highest level of severity until mid-summer, many species would likely have already bred and raised chicks to at least fledgling age, increasing the likelihood that enough juveniles were exposed to drought stress to significantly affect population song. Our analysis of the USGS banding and eBird data suggests that any fluctuations in species abundance or breeding behaviors were within the range of typical annual variation.

To detect shifts in song that could potentially be linked to impaired learning due to the drought, as opposed to occurring due to normal stochasticity in population song, we compared the drought region to a control region for each species; however, the best-sampled control regions we could find still had much smaller numbers of recordings than the drought region, reducing our power to detect any potential shifts in the songs in these control regions. Further, the only reasonably well-sampled potential control regions also experienced abnormally dry and moderate drought conditions, respectively, during 2016, since this drought was a regional phenomenon that affected much of the northeast United States. Additionally, while the control regions are in fairly similar climates to the drought region, potential differences between the regions (in elevation, urbanization, land use, and other ecological, geological, and meteorological factors) make it so these are not perfectly matched "controls." Still, in principle, they may be useful for testing whether or how much song in a region varies under typical environmental conditions, or how spatial variation in sampling can affect the results.

This raises another limitation of using community science data: since songs are known to have regional differences, variation in the spatial distribution of recordings could create the appearance of a shift in song features, when in actuality the observed changes could be a result of inconsistent sampling of subpopulations and their local dialects. Indeed, in both Dark-eyed Junco and Song Sparrow songs, the first three principal component dimensions were mostly significantly different between the regions, irrespective of time period. This suggests that there may be differences in songs between the regions that may make them less informative to directly compare (Appendix 1: Fig. S4). Further, in order to maximize sample size in the more sparse Control regions, we chose to expand these sampling regions to include recordings from a larger area than in the Drought region, which could have contributed to variation seen in the Control regions (Appendix 1: Table S4).

Tips for future investigators

We have several specific recommendations for future research that might aim to detect changes in song over time and/or to test the specific hypothesis that environmental stress could lead to impaired transmission of song. First, the massive increase in community-contributed recordings in the last 3-5 years is promising and may pave the way for more robust studies of this nature. These studies would ideally track fluctuations in songs by year to reveal trends on a finer temporal scale. Ideally there would be such ample recordings available in a small enough region that local dialects would not impact results, or that recordings could be downsampled to ensure that subpopulations are equally represented across years. More likely would be that a study using community-science data could help inform decisions on target species and locations for a more robust field study, which may be necessary in order to disentangle the possible mechanisms underlying any observed changes in song after a climatic event.

To test the impaired-learning hypothesis in either a community-science or a targeted field study, an ideal focal location would likely be the site of a long-term field study on an isolated or island population where effects of immigration and emigration from the region would be negligible. Historical environmental data including water availability, temperature, and, if available, surveys on vegetation and arthropod abundance, would help establish how anomalous any particular climatic event was and the type of stress that individuals might have experienced during it. There would ideally exist historical data on rates of mortality, nest failure, and recruitment per year, especially during years when a stressful environmental event occurred, in order to verify that breeding, nesting, and fledging of juveniles were not completely impaired by the climatic event. There would also ideally be ample historical recordings of songs from years prior to the environmental stressor and concerted recording effort after. While comparisons to control populations or regions could be informative, especially if multiple control populations are used, differences in regional dialects and environmental features may reduce their applicability. Potentially more informative would be to extend the study period and compare year-to-year trends within a region in the context of periods of environmental stress or abundance.

The differences between species songs and life histories may substantially affect the expected effects of any given population-wide stressor. As described in the methods, we considered factors including diet, philopatry, breeding time, song complexity, song structure, and learning window duration, but there are some other factors that might allow for analyses that could more specifically test the impaired-learning hypothesis. If a species predominantly exhibits high-fidelity vertical learning, or learning from parent to offspring with little improvisation on the part of the pupil, having field data on parentage and identity-linked song recordings would allow for comparisons between songs of the tutor and pupil directly. By measuring the similarity between these songs, it would be possible to more directly attribute any changes in song to mistakes in learning and track the frequency of mistakes over stressful and non-stressful years. Species with predominantly vertical learning may, however, be less likely to have perturbed songs spread rapidly in a population relative to species with ample oblique learning. Future studies might also benefit from incorporating more information-dense song measurements, such as tracking the presence and evolution of individual syllable or song types. If dispersal to or from the population is possible, this could help determine whether the recordings from each time period belong to the same broader regional dialect or whether it's more likely that new individuals colonized the area. Alternatively, it could allow for analysis of individual syllable transmission; some species tend to synthesize songs from syllables learned from multiple sources, so impaired learning might be detected at the syllable level, as opposed to song averages.

CONCLUSIONS

Here, we present a study of the songs of two well-recorded species in a region that experienced a severe drought compared to regions that did not. After the drought, we observe a suite of song changes in the drought region but not the control region in the species with the more complex song, the Song Sparrow. In contrast, in the species with simpler songs, the Dark-eyed Junco, we observed song changes in both regions, suggesting that the drought did not alter the song of this species in a way that could be differentiated from typical shifts in song features over time.

If the trends we observed in Song Sparrows in the three years since the drought were to persist and a population's song underwent lasting changes, there could be meaningful implications for conservation, particularly in the face of climate change, which is likely to make severe weather events more common. If these changes were particularly salient in a given species' song—for example, if the song changed in features that are important for mate choice—a population's song could theoretically become unattractive to a sister population that maintained the typical ancestral song. This would suggest a potential side effect of anthropogenic climate change that has not been well studied: that the sublethal experiences of individuals could impact the development of behaviors that are culturally transmitted to future generations, leading to an increase in reproductive isolation by sexual selection of this trait that is both plastic and sensitive to hostile conditions (Mendelson and Safran 2021). This study provides a first step toward testing these hypotheses, and we aim for our initial findings to prompt further investigation in other species and systems, particularly in datasets in which individuals are identified and hatch-year conditions are known. We propose that song data from prior long-term population studies could be reanalyzed in light of historical environmental factors to further investigate this phenomenon of accelerated song divergence and clarify the interaction between song complexity and stress-induced changes to song across species. Alternatively, as depositions of song recordings by community-scientists become increasingly common, using public repositories may become more tractable and informative by allowing for increased sample sizes and associated analysis of temporal dynamics in population songs on a finer scale.

Author Contributions:

N.C. and K.T.S. conceived and designed the project. M.L.S. processed song data. K.T.S. and M.L.S. conducted all analyses with assistance from N.C.; K.T.S. and N.C. made figures and wrote the manuscript with input from M.L.S.

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Data Availability:

All statistical analyses were implemented in R, with code available at https://github.com/CreanzaLab/Birdsong_DroughtStress. Data, including the catalog numbers, database, recordist, URL, and license for the analyzed song files, are available at https://doi.org/10.6084/m9.figshare.22151684

LITERATURE CITED

Angelier, F., J. C. Wingfield, S. Tartu, and O. Chastel. 2016. Does prolactin mediate parental and life-history decisions in response to environmental conditions in birds? A review. Hormones and Behavior 77:18-29. https://doi.org/10.1016/j.yhbeh.2015.07.014

Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten. 2020. Song Sparrow (Melospiza melodia). Birds of the world. Cornell Laboratory of Ornithology. https://doi.org/10.2173/bow.sonspa.01

Arcese, P., P. K. Stoddard, and S. M. Hiebert. 1988. The form and function of song in female song sparrows. Condor 90(1):44-50. https://doi.org/10.2307/1368431

Ballentine, B., J. Hyman, and S. Nowicki. 2004. Vocal performance influences female response to male bird song: an experimental test. Behavioral Ecology 15(1):163-168. https://doi.org/10.1093/beheco/arg090

Beecher, M. D. 2008. Function and mechanisms of song learning in Song Sparrows. Advances in the Study of Behavior 38:167-225. https://doi.org/10.1016/S0065-3454(08)00004-1

Beecher, M. D., S. E. Campbell, and P. K. Stoddard. 1994. Correlation of song learning and territory establishment strategies in the Song Sparrow. Proceedings of the National Academy of Sciences of the United States of America 91:1450-1454. https://doi.org/10.1073/pnas.91.4.1450

Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's Finches (Geospizinae) in the Galapagos. Science 214:82-85. https://doi.org/10.1126/science.214.4516.82

Boag, P. T., and P. R. Grant. 1984. The classical case of character release: Darwin's finches (Geospiza) on Isla Daphne Major, Galápagos. Biological Journal of the Linnean Society. Linnean Society of London 22(3):243-287.

Bolger, D. T., M. A. Patten, and D. C. Bostock. 2005. Avian reproductive failure in response to an extreme climatic event. Oecologia 142:398-406. https://doi.org/10.1007/s00442-004-1734-9

Boogert, N. J., L.-A. Giraldeau, and L. Lefebvre. 2008. Song complexity correlates with learning ability in zebra finch males. Animal Behaviour 76:1735-1741. https://doi.org/10.1016/j.anbehav.2008.08.009

Boogert, N. J., R. F. Lachlan, K. A. Spencer, C. N. Templeton, and D. R. Farine. 2018. Stress hormones, social associations and song learning in zebra finches. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 373:20170290. https://doi.org/10.1098/rstb.2017.0290

Borror, D. J. 1965. Song variation in Maine Song Sparrows. Wilson Bulletin 77:5-37.

Brenowitz, E. A., and M. D. Beecher. 2005. Song learning in birds: diversity and plasticity, opportunities and challenges. Trends in Neurosciences 28:127-132. https://doi.org/10.1016/j.tins.2005.01.004

Brumm, H., S. A. Zollinger, and P. J. B. Slater. 2009. Developmental stress affects song learning but not song complexity and vocal amplitude in zebra finches. Behavioral Ecology and Sociobiology 63:1387-1395. https://doi.org/10.1007/s00265-009-0749-y

Buchanan, K. L., K. A. Spencer, A. R. Goldsmith, and C. K. Catchpole. 2003. Song as an honest signal of past developmental stress in the European Starling (Sturnus vulgaris). Proceedings of the Royal Society of London. Series B: Biological Sciences 270:1149-1156. https://doi.org/10.1098/rspb.2003.2330

Burt, J. M., S. C. Bard, S. E. Campbell, and M. D. Beecher. 2002. Alternative forms of song matching in Song Sparrows. Animal Behaviour 63:1143-1151. https://doi.org/10.1006/anbe.2002.3011

Cardoso, G. C., and J. W. Atwell. 2016. Shared songs are of lower performance in the Dark-eyed Junco. Royal Society Open Science 3(7):160341. https://doi.org/10.1098/rsos.160341

Cardoso, G. C., J. W. Atwell, E. D. Ketterson, and T. D. Price. 2009. Song types, song performance, and the use of repertoires in Dark-eyed Juncos (Junco hyemalis). Behavioral Ecology 20 (4):901-907. https://doi.org/10.1093/beheco/arp079

Carey, C. 2009. The impacts of climate change on the annual cycles of birds. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 364:3321-3330. https://doi.org/10.1098/rstb.2009.0182

Caro, S. P., K. B. Sewall, K. G. Salvante, and K. W. Sockman. 2010. Female Lincoln's sparrows modulate their behavior in response to variation in male song quality. Behavioral Ecology 21 (3):562-569. https://doi.org/10.1093/beheco/arq022

Catchpole, C. K. 1987. Bird song, sexual selection and female choice. Trends in Ecology & Evolution 2:94-97. https://doi.org/10.1016/0169-5347(87)90165-0

Catchpole, C. K., and P. J. B. Slater. 2003. Bird song: biological themes and variations. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/CBO9780511754791

Cavalli-Sforza, L. L., and M. W. Feldman. 1981. Cultural transmission and evolution: a quantitative approach. Monographs in Population Biology 16:1-388. https://doi.org/10.1515/9780691209357

Christman, B. J. 2002. Extreme between-year variation in productivity of a Bridled Titmouse (Baeolophus wollweberi) population. Auk 119(4):1149-1154.

Collins, S. 2004. Vocal fighting and flirting: the functions of birdsong. Pages 39-79 in Nature's music: the science of birdsong. Elsevier, New York, New York, USA. https://doi.org/10.1016/B978-012473070-0/50005-0

Colón, M. R., A. M. Long, and M. L. Morrison. 2017. Responses of an endangered songbird to an extreme drought event. Southeastern Naturalist 16(2):195-214. https://doi.org/10.1656/058.016.0207

Cramer, E. R. A. 2012. Vocal deviation and trill consistency do not affect male response to playback in house wrens. Behavioral Ecology 24(2):412-420. https://doi.org/10.1093/beheco/ars178

Creanza, N., and M. W. Feldman. 2014. Complexity in models of cultural niche construction with selection and homophily. Proceedings of the National Academy of Sciences of the United States of America 111(3):10830-10837. https://doi.org/10.1073/pnas.1400824111

Creanza, N., L. Fogarty, and M. W. Feldman. 2016. Cultural niche construction of repertoire size and learning strategies in songbirds. Evolutionary Ecology 30:285-305. https://doi.org/10.1007/s10682-015-9796-1

Del Hoyo, J., A. Elliott, and J. Sargatal. 1992. Handbook of the birds of the world. Lynx Edicions, Barcelona, Spain.

Donihue, C. M., A. Herrel, A.-C. Fabre, A. Kamath, A. J. Geneva, T. W. Schoener, et al. 2018. Hurricane-induced selection on the morphology of an island lizard. Nature 560:88-91. https://doi.org/10.1038/s41586-018-0352-3

eBird Help Center. 2021. eBird breeding and behavior codes. https://support.ebird.org/en/support/solutions/articles/48000837520-ebird-breeding-and-behavior-codes

Feldman, M. W., and L. L. Cavalli-Sforza. 1976. Cultural and biological evolutionary processes, selection for a trait under complex transmission. Theoretical Population Biology 9:238-259. https://doi.org/10.1016/0040-5809(76)90047-2

Ferree, E. D. 2013. Geographic variation in morphology of Dark-eyed Juncos and implications for population divergence. Wilson Journal of Ornithology 125(3):454-470. https://doi.org/10.1676/12-179.1

Franz, M., and F. Goller. 2002. Respiratory units of motor production and song imitation in the zebra finch. Journal of Neurobiology 51:129-141. https://doi.org/10.1002/neu.10043

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275-284. https://doi.org/10.2307/1941861

Grant, B. R., and P. R. Grant. 1989. Natural selection in a population of Darwin's Finches. American Naturalist 133 (3):377-393. https://doi.org/10.1086/284924

Grant, B. R., and P. R. Grant. 1993. Evolution of Darwin's finches caused by a rare climatic event. Proceedings of the Royal Society of London. Series B: Biological Sciences 251:111-117. https://doi.org/10.1098/rspb.1993.0016

Holveck, M.-J., A. C. Vieira de Castro, R. F. Lachlan, C. ten Cate, and K. Riebel. 2008. Accuracy of song syntax learning and singing consistency signal early condition in zebra finches. Behavioral Ecology 19(6):1267-1281. https://doi.org/10.1093/beheco/arn078

Huberty, A. F., and R. F. Denno. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85:1383-1398. https://doi.org/10.1890/03-0352

Hudson, E. J., and N. Creanza. 2022. Modeling how population size drives the evolution of birdsong, a functional cultural trait. Evolution 76:1139-1152. https://doi.org/10.1111/evo.14489

Hughes, M., S. Nowicki, W. A. Searcy, and S. Peters. 1998. Song-type sharing in song sparrows: implications for repertoire function and song learning. Behavioral Ecology and Sociobiology 42:437-446. https://doi.org/10.1007/s002650050458

Keiser, J. T., C. W. S. Ziegenfus, and D. A. Cristol. 2005. Homing success of migrant versus nonmigrant Dark-eyed Juncos (Junco Hyemalis). Auk 122(2):608-617.

Kelly, T. R., K. A. Hobson, G. W. Casbourn, E. A. MacDougall-Shackleton, and S. A. MacDougall-Shackleton. 2019. Long-term winter-site fidelity in Song Sparrows (Melospiza melodia). Auk 136(2):ukz010. https://doi.org/10.1093/auk/ukz010

Ketterson, E. D., and V. Nolan. 1992. Hormones and life histories: an integrative approach. American Naturalist 140(1):S33-62. https://doi.org/10.1086/285396

Knudsen, E., A. Lindén, C. Both, N. Jonzén, F. Pulido, N. Saino, et al. 2011. Challenging claims in the study of migratory birds and climate change. Biological Reviews of the Cambridge Philosophical Society 86:928-946. https://doi.org/10.1111/j.1469-185X.2011.00179.x

Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15(3):259-263. https://doi.org/10.1127/0941-2948/2006/0130

Kozlovsky, D. Y., C. L. Branch, A. M. Pitera, and V. V. Pravosudov. 2018. Fluctuations in annual climatic extremes are associated with reproductive variation in resident mountain chickadees. Royal Society Open Science 5(5):171604. https://doi.org/10.1098/rsos.171604

Kroodsma, D. E., and B. E. Byers. 1991. The function(s) of bird song. American Zoologist 31(2):318-328. https://doi.org/10.1093/icb/31.2.318

Lachlan, R. F., and S. Nowicki. 2012. How reliable is song learning accuracy as a signal of male early condition? American naturalist 180:751-761. https://doi.org/10.1086/668010

Langin, K. M., T. S. Sillett, J. Yoon, H. R. Sofaer, S. A. Morrison, and C. K. Ghalambor. 2009. Reproductive consequences of an extreme drought for orange-crowned warblers on Santa Catalina and Santa Cruz islands. Pages 293-300 in C. C. Damiani and D. K. Garcelon, editors. Proceedings of the Seventh California Islands Symposium. Institute for Wildlife Studies, Arcata, California, USA.

Liebgold, E. B., N. M. Gerlach, and E. D. Ketterson. 2013. Similarity in temporal variation in sex-biased dispersal over short and long distances in the Dark-eyed Junco, Junco hyemalis. Molecular Ecology 22(22):5548-5560. https://doi.org/10.1111/mec.12508

Liebgold, E. B., N. M. Gerlach, and E. D. Ketterson. 2019. Density-dependent fitness, not dispersal movements, drives temporal variation in spatial genetic structure in Dark-eyed Juncos (Junco hyemalis). Molecular Ecology 28(5):968-979. https://doi.org/10.1111/mec.15040

MacDougall-Shackleton, S. A., and K. A. Spencer. 2012. Developmental stress and birdsong: current evidence and future directions. Journal of Ornithology 153(1):105-117. https://doi.org/10.1007/s10336-011-0807-x

Marler, P., and S. Peters. 1987. A sensitive period for song acquisition in the song sparrow, Melospiza melodia: a case of age-limited learning. Ethology 76(2):89-100. https://doi.org/10.1111/j.1439-0310.1987.tb00675.x

Marler, P. R., and H. Slabbekoorn. 2004. Nature's music: the science of birdsong. Elsevier, Cambridge, Massachusetts, USA.

McCreedy, C., and C. van Riper. 2014. Drought-caused delay in nesting of Sonoran Desert birds and its facilitation of parasite- and predator-mediated variation in reproductive success. Auk 132 (1):235-247. https://doi.org/10.1642/AUK-13-253.1

Mendelson, T. C., and R. J. Safran. 2021. Speciation by sexual selection: 20 years of progress. Trends in Ecology & Evolution 36:1153-1163. https://doi.org/10.1016/j.tree.2021.09.004

Møller, A. P. 2010. When climate change affects where birds sing. Behavioral Ecology 22(1):212-217. https://doi.org/10.1093/beheco/arq200

Moore, J. M., T. Székely, J. Büki, and T. J. Devoogd. 2011. Motor pathway convergence predicts syllable repertoire size in oscine birds. Proceedings of the National Academy of Sciences of the United States of America 108:16440-16445. https://doi.org/10.1073/pnas.1102077108

Newman, M. M., P. J. Yeh, and T. D. Price. 2008. Song variation in a recently founded population of the Dark-eyed Junco (Junco hyemalis). Ethology 114(2):164-173. https://doi.org/10.1111/j.1439-0310.2007.01457.x

Nolan, V., Jr, E. D. Ketterson, D. A. Cristol, C. M. Rogers, E. D. Clotfelter, R. C. Titus, et al. 2020. Dark-eyed Junco (Junco hyemalis) in A. F. Poole and F. B. Gill, editors. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://birdsoftheworld.org/bow/species/daejun/1.0/introduction

Nottebohm, F. 1981. A brain for all seasons: cyclical anatomical changes in song control nuclei of the canary brain. Science 214:1368-1370. https://doi.org/10.1126/science.7313697

Nowicki, S., S. Peters, and J. Podos. 1998. Song learning, early nutrition and sexual selection in songbirds. American Zoologist 38 (1):179-190. https://doi.org/10.1093/icb/38.1.179

Nowicki, S., and W. A. Searcy. 2004. Song function and the evolution of female preferences: why birds sing, why brains matter. Annals of the New York Academy of Sciences 1016:704-723. https://doi.org/10.1196/annals.1298.012

Ouyang, J. Q., M. Quetting, and M. Hau. 2012. Corticosterone and brood abandonment in a passerine bird. Animal Behaviour 84:261-268. https://doi.org/10.1016/j.anbehav.2012.05.006

Pandit, M. M., E. S. Bridge, and J. D. Ross. 2022. Environmental conditions lead to shifts in individual communication, which can cause cascading effects on soundscape composition. Ecology and Evolution 12:e9359. https://doi.org/10.1002/ece3.9359

Perreault, C. 2012. The pace of cultural evolution. PLoS ONE 7: e45150. https://doi.org/10.1371/journal.pone.0045150

Podos, J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). Evolution 51(2):537-551. https://doi.org/10.2307/2411126

Potvin, D. A., P. W. Crawford, S. A. MacDougall-Shackleton, and E. A. MacDougall-Shackleton. 2015. Song repertoire size, not territory location, predicts reproductive success and territory tenure in a migratory songbird. Canadian Journal of Zoology 93 (8):627-633. https://doi.org/10.1139/cjz-2015-0039

Price, J. J. 2015. Rethinking our assumptions about the evolution of bird song and other sexually dimorphic signals. Frontiers in Ecology and Evolution 3:40. https://doi.org/10.3389/fevo.2015.00040

Price, T. D., P. R. Grant, H. L. Gibbs, and P. T. Boag. 1984. Recurrent patterns of natural selection in a population of Darwin's finches. Nature 309:787-789. https://doi.org/10.1038/309787a0

Prior, N. H., S. A. Heimovics, and K. K. Soma. 2013. Effects of water restriction on reproductive physiology and affiliative behavior in an opportunistically-breeding and monogamous songbird, the zebra finch. Hormones and Behavior 63:462-474. https://doi.org/10.1016/j.yhbeh.2012.12.010

Read, A. F., and D. M. Weary. 1992. The evolution of bird song: comparative analyses. Philosophical Transactions of the Royal Society B 338:165-187. https://doi.org/10.1098/rstb.1992.0137

Roberts, L. J., R. Burnett, J. Tietz, and S. Veloz. 2019. Recent drought and tree mortality effects on the avian community in southern Sierra Nevada: a glimpse of the future? Ecological Applications 29:e01848. https://doi.org/10.1002/eap.1848

Robinson, C. M., and N. Creanza. 2019. Species-level repertoire size predicts a correlation between individual song elaboration and reproductive success. Ecology and Evolution 9:8362-8377. https://doi.org/10.1002/ece3.5418

Robinson, C. M., K. T. Snyder, and N. Creanza. 2019. Correlated evolution between repertoire size and song plasticity predicts that sexual selection on song promotes open-ended learning. eLife 8: e44454. https://doi.org/10.7554/eLife.44454

Rundstrom, P., and N. Creanza. 2021. Song learning and plasticity in songbirds. Current Opinion in Neurobiology 67:228-239. https://doi.org/10.1016/j.conb.2021.02.003

Sarquis-Adamson, Y., and E. A. MacDougall-Shackleton. 2016. Song Sparrows Melospiza melodia have a home-field advantage in defending against sympatric malarial parasites. Royal Society Open Science 3:160216. https://doi.org/10.1098/rsos.160216

Schmidt, K. L., A. A. Furlonger, J. M. Lapierre, E. A. MacDougall-Shackleton, and S. A. MacDougall-Shackleton. 2012. Regulation of the HPA axis is related to song complexity and measures of phenotypic quality in song sparrows. Hormones and Behavior 61:652-659. https://doi.org/10.1016/j.yhbeh.2012.02.027

Schmidt, K. L., S. D. Moore, E. A. MacDougall-Shackleton, and S. A. MacDougall-Shackleton. 2013. Early-life stress affects song complexity, song learning and volume of the brain nucleus RA in adult male song sparrows. Animal Behaviour 86:25-35. https://doi.org/10.1016/j.anbehav.2013.03.036

Searcy, W. A., S. Peters, S. Kipper, and S. Nowicki. 2010. Female response to song reflects male developmental history in swamp sparrows. Behavioral Ecology and Sociobiology 64:1343-1349. https://doi.org/10.1007/s00265-010-0949-5

Searfoss, A. M., J. C. Pino, and N. Creanza. 2020. Chipper: open-source software for semi-automated segmentation and analysis of birdsong and other natural sounds. Methods in Ecology and Evolution 11(4):524-531. https://doi.org/10.1111/2041-210X.13368

Snell-Rood, E. C. 2012. The effect of climate on acoustic signals: does atmospheric sound absorption matter for bird song and bat echolocation? Journal of the Acoustical Society of America 131:1650-1658. https://doi.org/10.1121/1.3672695

Snyder, K. T., and N. Creanza. 2019. Polygyny is linked to accelerated birdsong evolution but not to larger song repertoires. Nature Communications 10:884. https://doi.org/10.1038/s41467-019-08621-3

Soma, M., and L. Z. Garamszegi. 2011. Rethinking birdsong evolution: meta-analysis of the relationship between song complexity and reproductive success. Behavioral Ecology 22 (2):363-371. https://doi.org/10.1093/beheco/arq219

Spencer, K. A., K. L. Buchanan, A. R. Goldsmith, and C. K. Catchpole. 2003. Song as an honest signal of developmental stress in the zebra finch (Taeniopygia guttata). Hormones and Behavior 44:132-139. https://doi.org/10.1016/S0018-506X(03)00124-7

Svoboda, M., D. LeComte, M. Hayes, R. Heim, K. Gleason, J. Angel, B. Rippey, R. Tinker, M. Palecki, D. Stooksbury et al. 2002. The drought monitor. Bulletin of the American Meteorological Society 83(8):1181-1190. https://doi.org/10.1175/1520-0477-83.8.1181

Sweet, S. K., D. W. Wolfe, A. DeGaetano, and R. Benner. 2017. Anatomy of the 2016 drought in the northeastern United States: implications for agriculture and water resources in humid climates. Agricultural and Forest Meteorology 247:571-581. https://doi.org/10.1016/j.agrformet.2017.08.024

Tchernichovski, O., P. P. Mitra, T. Lints, and F. Nottebohm. 2001. Dynamics of the vocal imitation process: how a zebra finch learns its song. Science 291:2564-2569. https://doi.org/10.1126/science.1058522

Ten Cate, C. 2004. Birdsong and evolution. Pages 296-317 in P. Marler and H. Slabbekoorn, editors. Nature's music: the science of birdsong. Elsevier Academic Press, Cambridge, Massachusetts, USA. https://doi.org/10.1016/B978-012473070-0/50013-X

The Cornell Lab of Ornithology. Macaulay Library: a scientific archive for research, education, and conservation, powered by you. https://www.macaulaylibrary.org/

Tomasello, M. 1999. The cultural origins of human cognition. Harvard University Press, London, England. https://doi.org/10.4159/9780674044371

Tuomainen, U., and U. Candolin. 2011. Behavioural responses to human-induced environmental change. Biological Reviews 86 (3):640-657. https://doi.org/10.1111/j.1469-185X.2010.00164.x

Vellinga, W. P., and R. Planqué. Xeno-canto: sharing wildlife sounds from around the world. https://xeno-canto.org/

Vernasco, B. J., T. S. Sillett, P. P. Marra, and T. B. Ryder. 2017. Environmental predictors of nestling condition, postfledging movement, and postfledging survival in a migratory songbird, the Wood Thrush (Hylocichla mustelina). Auk 135(1):15-24.

Weatherhead, P. J., and K. A. Boak. 1986. Site infidelity in Song Sparrows. Animal Behaviour 34:1299-1310. https://doi.org/10.1016/S0003-3472(86)80201-9

Weatherhead, P. J., and M. R. L. Forbes. 1994. Natal philopatry in passerine birds: genetic or ecological influences? Behavioral Ecology 5(4):426-433. https://doi.org/10.1093/beheco/5.4.426

Weir, J. T., and D. Wheatcroft. 2011. A latitudinal gradient in rates of evolution of avian syllable diversity and song length. Proceedings of the Royal Society B: Biological Sciences 278:1713-1720. https://doi.org/10.1098/rspb.2010.2037

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90-105. https://doi.org/10.1007/BF00379790

Williams, L., and M. H. MacRoberts. 1977. Individual variation in songs of Dark-eyed Juncos. Condor 79:106-112. https://doi.org/10.2307/1367537

Wingfield, J. C., K. Sullivan, J. Jaxion-Harm, and S. L. Meddle. 2012. The presence of water influences reproductive function in the Song Sparrow (Melospiza melodia morphna). General and Comparative Endocrinology 178:485-493. https://doi.org/10.1016/j.ygcen.2012.07.007

Winter, M., D. H. Johnson, and J. A. Shaffer. 2005. Variability in vegetation effects on density and nesting success of grassland birds. Wildlife Management 69:185-197.

Wood, C., B. Sullivan, M. Iliff, D. Fink and S. Kelling. 2011. eBird: engaging birders in science and conservation. PLoS Biology 9: e1001220. https://doi.org/10.1371/journal.pbio.1001220

Wood, W. E., and S. M. Yezerinac. 2006. Song Sparrow (Melospiza Melodia) song varies with urban noise. Auk 123 (3):650-659. https://doi.org/10.1093/auk/123.3.650

Yunick, R. P. 1988. Differential spring migration of Dark-eyed Juncos. Journal of Field Ornithology 59:314-320.

Appendix: Supplemental Figures and Tables

Cultural shifts after punctuated environmental stress: a study of song distributions in Dark-eyed Junco and Song Sparrow populations

Supplemental Tables

	PC1	PC2	PC3
Bout duration (ms)	-0.1665459	-0.0036175	**-0.527575**
Rate of syllable production (Number of syllables divided by bout duration)	**-0.4292783**	0.15686655	0.08475945
Average syllable duration (ms)	**0.43914745**	-0.1548555	-0.1179026
Standard deviation of syllable duration (ms)	0.21535134	0.28518245	-0.0033744
Average syllable upper frequency (Hz)	0.1801962	-0.0907469	**-0.5171299**
Average syllable lower frequency (Hz)	-0.1943956	0.21603638	-0.0846287
Overall syllable frequency range (Hz)	0.26030926	-0.0903027	**-0.3856307**
Number of notes	-0.1073708	**0.4212219**	**-0.3498447**
Number of notes per syllable	0.24612039	**0.3398911**	-0.2007135
Number of syllables	**-0.4480448**	0.12904599	-0.207895
Number of unique syllables	0.06202007	**0.43995637**	0.10039593
Degree of repetition (Number of syllables divided by number unique)	**-0.3512576**	-0.2797122	-0.2353986
Mean syllable stereotypy	-0.1032396	**-0.4749758**	-0.0766961
Proportion of Variance	0.3065	0.2408	0.1317
Eigenvalues	3.984	3.130	1.713

Table S1A: Dark-eyed Junco principal component loadings by song feature. PC1 and PC3 were significantly different in the control region from before to after 2016, while none were significant in the drought region. The proportion of variance explained by each principal component is given in the last row. All loadings that have an absolute value greater than 0.30 are indicated in bold font. See **Figure S4**.

	PC1	PC2	PC3
Bout duration (ms)	0.00532734	**-0.4228521**	0.16240812
Number of syllables	**-0.3458911**	**-0.3243144**	0.20378128
Rate of syllable production (Number of syllables divided by bout duration)	**-0.4226098**	-0.0564736	0.11013442
Average syllable duration (ms)	**0.42324314**	-0.0529731	-0.0739714
Standard deviation of syllable duration (ms)	**0.36019293**	-0.1267016	0.24656715
Number of unique syllables	-0.18839	**-0.4027593**	-0.3541724
Degree of repetition (Number of syllables divided by number unique)	-0.1685814	0.11461891	**0.61940589**
Average syllable upper frequency (Hz)	0.11807169	-0.2409636	0.29407423
Average syllable lower frequency (Hz)	0.04844985	0.15346658	**0.37252899**
Overall syllable frequency range (Hz)	-0.0826014	**-0.3750778**	-0.0079921
Number of notes	0.09335848	**-0.4648783**	0.00834772
Number of notes per syllable	**0.36555865**	-0.1786854	-0.1467235
Largest syllable duration (ms)	**0.33641169**	-0.1659606	**0.31019402**
Smallest syllable duration (ms)	0.22430933	0.14398953	-0.0381991
Proportion of Variance	0.3275	0.2108	0.1097
Eigenvalues	4.585	2.951	1.535

Table S1B: Song Sparrow principal component loadings by song feature. PC1 and PC3 were significantly different in the Drought region from before to after 2016, while none were significant in the control region. The proportion of variance explained by each principal component is given in the last row. All loadings that have an absolute value greater than 0.30 are indicated in bold font. See **Figure S4**.

Feature	log Transformed	GLS Model ANOVA p-value	ANOVA EraRegion_Pval	Holm-Bonferroni p-value threshold for ANOVA	ANOVA significant after Holm-Bonferroni	Before vs. After Drought adjusted p-value	Before vs. After Control adjusted p-value
Bout duration (ms)	TRUE	0.00000	**0.00002**	0.00385	**TRUE**	**0.02972**	**0.00250**
Rate of syllable production (Number of syllables divided by bout duration)	TRUE	0.21972	0.08965	0.00625	FALSE	0.49660	0.30911
Average syllable duration (ms)	TRUE	0.55248	0.17608	0.00714	FALSE	0.98802	0.21707
Standard deviation of syllable duration (ms)	TRUE	0.38112	0.22953	0.00833	FALSE	0.85697	0.21497
Average syllable upper frequency (Hz)	TRUE	0.28981	0.83666	0.05000	FALSE	0.98253	0.93992
Average syllable lower frequency (Hz)	FALSE	0.48985	0.80492	0.02500	FALSE	0.95494	0.98707
Overall syllable frequency range (Hz)	FALSE	0.20999	0.23523	0.01000	FALSE	0.82179	0.50029
Number of notes	TRUE	0.93393	**0.00026**	0.00417	**TRUE**	**0.00903**	**0.01367**
Number of notes per syllable	TRUE	0.02066	0.38254	0.01250	FALSE	0.07828	0.93970
Number of syllables	TRUE	0.13100	**0.00074**	0.00455	**TRUE**	0.15941	**0.00671**
Number of unique syllables	TRUE	0.00007	0.59496	0.01667	FALSE	0.99997	0.81726
Degree of repetition (Number of syllables divided by number unique)	TRUE	0.00006	**0.00169**	0.00500	**TRUE**	0.18574	**0.03243**
Mean syllable stereotypy	TRUE	0.35367	0.08171	0.00556	FALSE	0.62669	*0.03667*

Table S2. Statistical analysis of Dark-eyed Junco songs. We performed Shapiro-Wilk tests on the subset of data in the control region and the subset of data in the drought region. When either of these were significant, indicating non-normality, we log-transformed the feature values (‘TRUE’ in column ‘log transformed’). We used nlme::gls() to test whether there were significant differences in any features between the four groups. We first performed this gls() as a simple model with no weights and as a complex model, with weights set by varIdent(form = ~1 | Era*Region). We performed an ANOVA to test whether the complex model was a significantly better fit than the simple model and used the simple model if this was not significant, and the complex model if it was (p-values in column “GLS model ANOVA p-value”). We performed an ANOVA on the selected model for each song feature and corrected for multiple hypothesis testing with a Holm-Bonferroni correction. Four song features varied significantly between groups, bout duration, the total number of syllables, degree of syllable repetition, and the total number of notes per bout. (bolded) One other feature, syllable stereotypy, trended towards significance (italics). For the four song features with significant ANOVA results, we performed a post-hoc test to test whether they were significantly different before vs. after the drought in the drought and control regions using emmeans::emmeans(), adjusting p-values using emmeans::test() p-adjustment method “mvt”. All four song features differed in the control region, and bout duration and total number of notes also differed in the drought region. Syllable stereotypy approached significance in the control region only.

Feature	log Transformed	GLS Model ANOVA p-value	ANOVA EraRegion_Pval	Holm-Bonferroni p-value threshold for ANOVA	ANOVA significant after Holm-Bonferroni	Before vs. After Drought adjusted p-value	Before vs. After Control adjusted p-value
Bout duration (ms)	TRUE	0.29550	0.17625	0.00833	FALSE	0.38504	0.66716
Number of syllables	FALSE	0.65918	**0.00035**	0.00385	**TRUE**	**0.00181**	0.06993
Rate of syllable production (Number of syllables divided by bout duration)	TRUE	0.03806	**0.00160**	0.00417	**TRUE**	**0.00605**	0.11626
Average syllable duration (ms)	TRUE	0.00579	*0.00773*	0.00455	FALSE	*0.03925*	0.16804
Standard deviation of syllable duration (ms)	TRUE	0.00010	0.11816	0.00556	FALSE	0.30681	0.46208
Number of unique syllables	TRUE	0.35866	0.66125	0.01250	FALSE	0.89607	0.66437
Degree of repetition (Number of syllables per number unique)	TRUE	0.00582	**0.00006**	0.00357	**TRUE**	**0.00009**	0.11308
Average syllable upper frequency (Hz)	TRUE	0.00135	0.70977	0.01667	FALSE	0.96779	0.94271
Average syllable lower frequency (Hz)	TRUE	0.05068	0.79582	0.02500	FALSE	0.40549	0.45888
Overall syllable frequency range (Hz)	TRUE	0.00011	0.35661	0.01000	FALSE	0.48824	0.87767
Number of notes	TRUE	0.13728	0.87595	0.05000	FALSE	0.70086	0.93917
Number of notes per syllable	TRUE	0.00032	*0.02713*	0.00500	FALSE	*0.00151*	0.53597
Largest syllable duration (ms)	TRUE	0.00145	0.14997	0.00714	FALSE	0.25391	0.59648
Smallest syllable duration (ms)	TRUE	0.44932	0.12925	0.00625	FALSE	0.81418	0.05474

Table S3. Statistical analysis of Song Sparrow songs. Methods are the same as in **Table S2**. Three song features varied significantly between groups, number of syllables, rate of syllable production (number of syllables divided by bout duration), and degree of syllable repetition (number of syllables divided by number of unique syllables) (bolded), and two others (average syllable duration and mean number of notes per syllable) showed trends towards significance (italics). For the three song features with significant ANOVA results, we performed a post-hoc test to test whether they were significantly different before vs. after the drought in the drought and control regions using emmeans::emmeans(), adjusting p-values using emmeans::test() p-adjustment method “mvt”. All three song features differed in the drought region but not in the control region.

	Dark-eyed Junco - Drought	Dark-eyed Junco - Control	Song Sparrow - Drought	Song Sparrow - Control
Mean distance between all points (km)	24.47	103.6	39.90	63.51
Max distance between any points (km)	257.3	296.2	278.9	218.0
Mean distance to nearest neighbor (km)	3.024	4.660	1.144	5.063
Area of convex hull polygon (sq km)	18360	31320	14920	24920

Table S4: Spatial metrics of each region. Latitude and longitude of each recording transformed using UTM zone 18 projection and sp:spTransform(). Convex hull polygon calculated using rgeos:gConvexHull() and rgeos:gArea().

Supplemental Figures

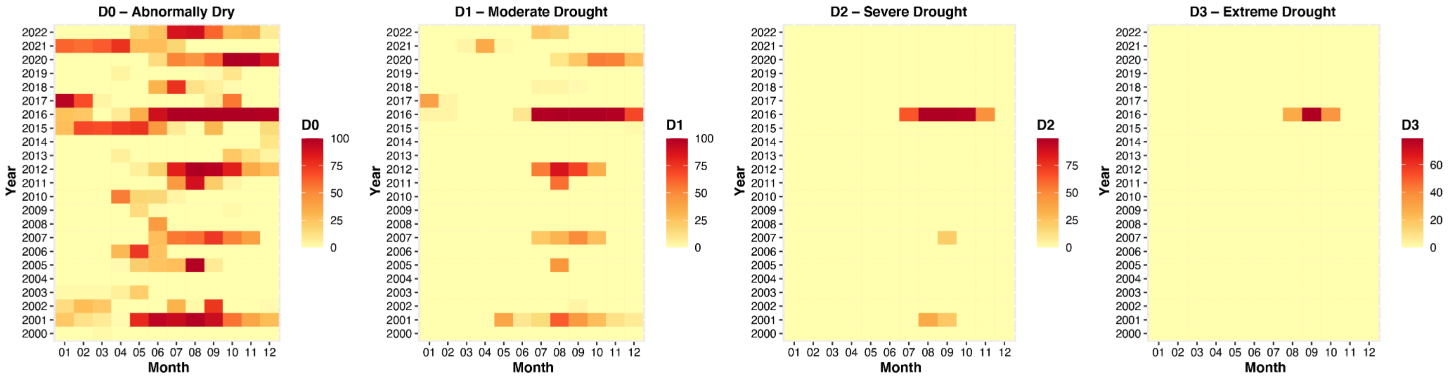

Figure S1: Mean percent of land area in New York counties in the drought region classified as drought level D0-D3 or higher by month and year from 2000-2022. Counties included are Cayuga, Erie, Genesee, Livingston, Ontario, Schuyler, Seneca, Tompkins, Wyoming, and Yates. The year 2016 was a clear outlier in drought severity and area, as it was the only year that most of the land area across these counties was in drought level D2 ("severe") and the only year that any of the listed counties had land classified as drought level D3 ("extreme") or higher. The drought levels referenced here are assigned by National Oceanic and Atmospheric Administration's National Integrated Drought Information System (NIDIS) program and take into account variables including temperature, precipitation, soil moisture, water levels in streams and lakes, and others, with drought level D3 indicating extreme drought, corresponding to major crop and pasture losses and widespread water shortages or restrictions. Data obtained from the Drought Monitor (Svoboda et al. 2002), accessed via https://droughtmonitor.unl.edu/NADM/Home.aspx. The colorbar indicates the average percentage of each county that met or exceeded the indicated level of drought.

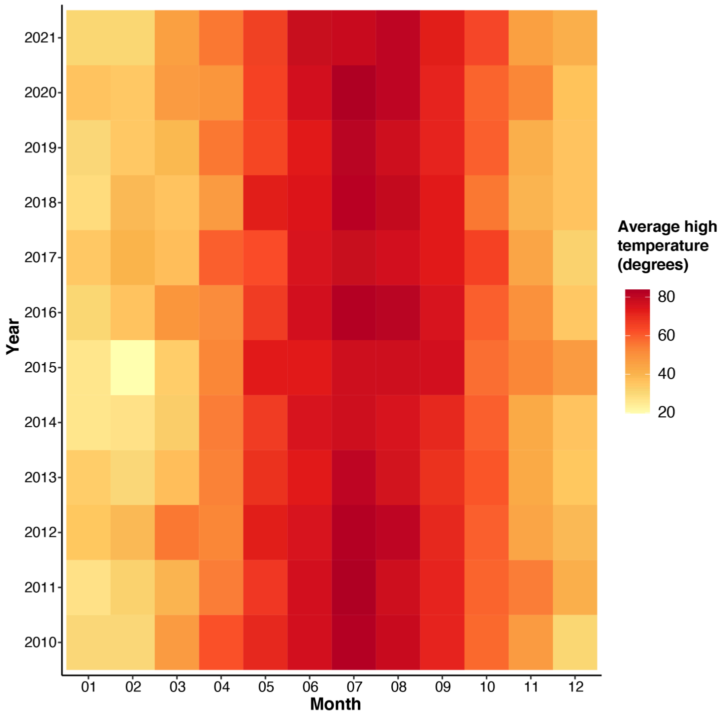

Figure S2: Mean of mean maximum daily recorded temperature per month across stations with complete records in Tompkins County, New York. There is no year that is a clear outlier in the period between 2010 and 2021. Data from the National Oceanic and Atmospheric Administration's National Centers for Environmental Information, accessed via https://www.ncei.noaa.gov/cdo-web/datatools.

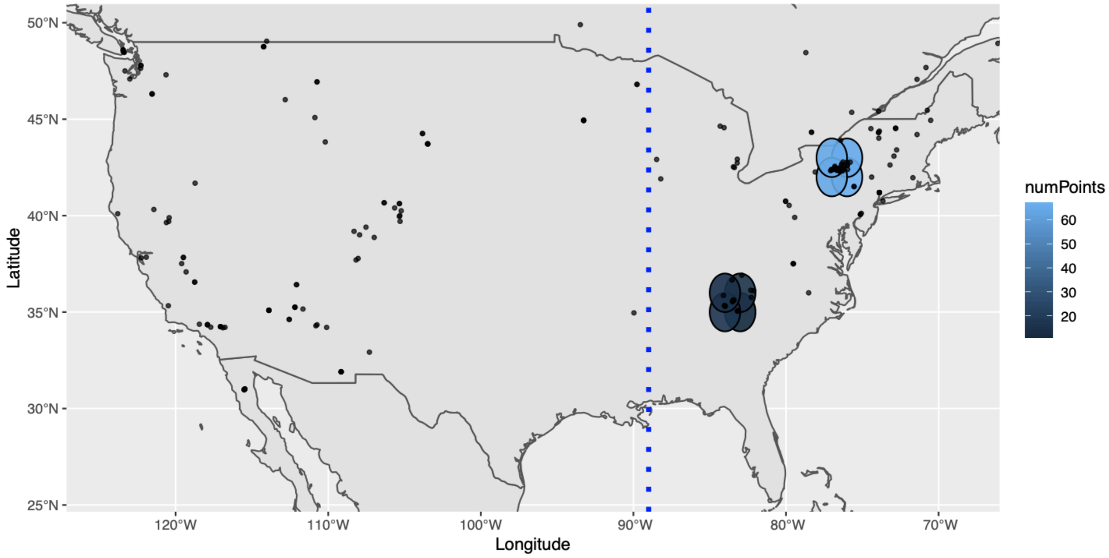

Figure S3A: Dark-eyed Junco recordings publicly available on Macaulay Library or Xeno-canto recorded between 2006 and 2016. Of all regions centered on each integer value of (Longitude, Latitude) ranging from 70°W through 89°W (the westernmost longitude we considered in deciding target regions, denoted by the dotted blue line) and 30°N through 47°N, the plotted, filled oval regions (area with a radius of 1°) are the only regions that contain at least 10 recordings between 2006 and 2016 (pre-Drought). The fill color is scaled to the number of recordings available within that area.

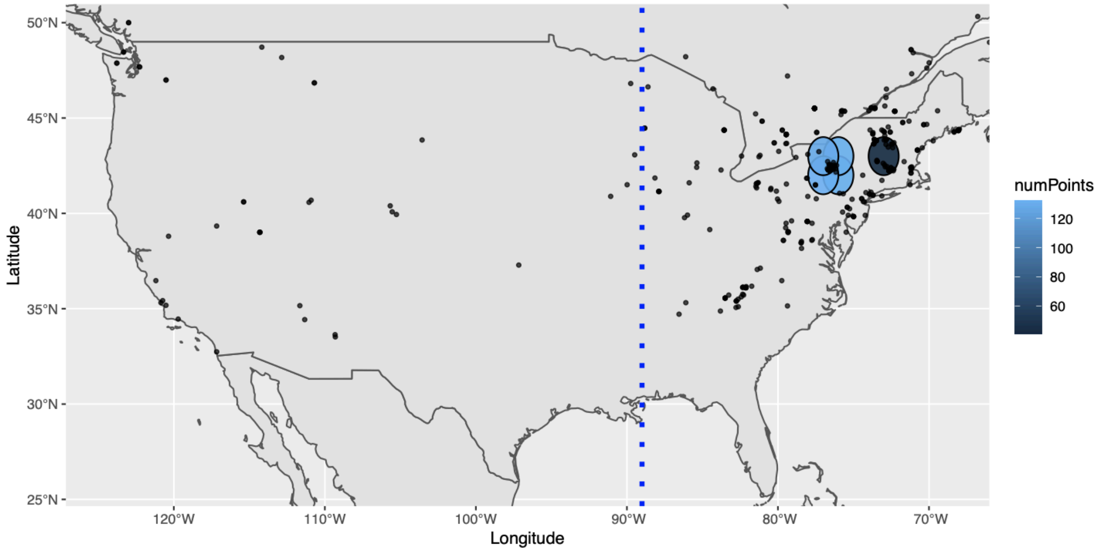

Figure S3B: Dark-eyed Junco recordings publicly available on Macaulay Library or Xeno-canto recorded between 2017 and 2019. Of all regions centered on each integer value of (Longitude, Latitude) ranging from 70°W through 89°W (the westernmost longitude we considered in deciding target regions, denoted by the dotted blue line) and 30°N through 47°N, the plotted, filled oval regions (area with a radius of 1°) are the only regions that contain at least 40 recordings between 2017 and 2019 (post-Drought).

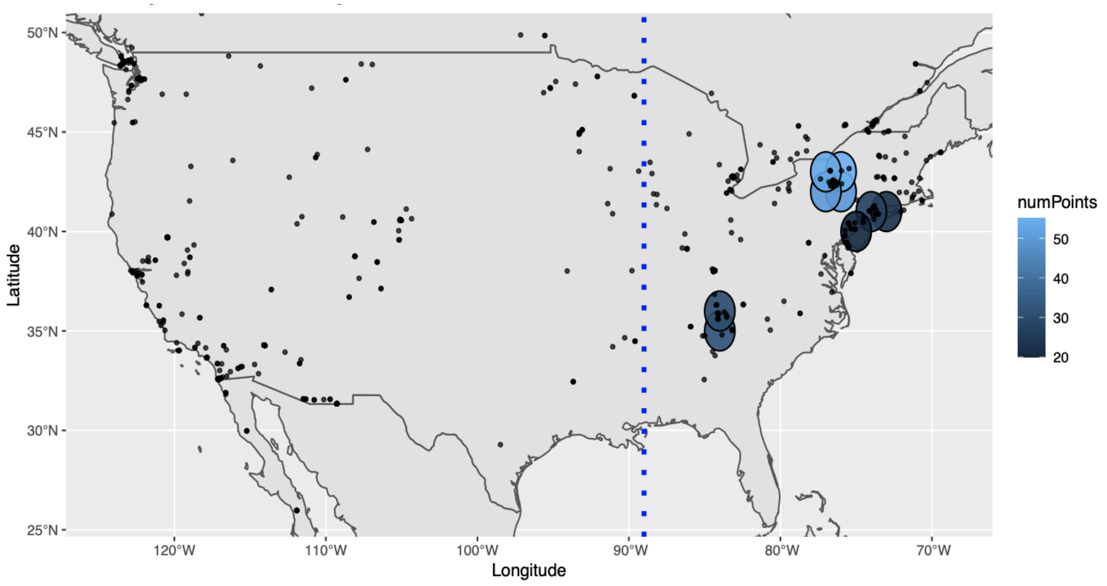

Figure S3C: Song Sparrow recordings publicly available on Macaulay Library or Xeno-canto recorded between 2006 and 2016. Of all regions centered on each integer value of (Longitude, Latitude) ranging from 70°W through 89°W (the westernmost longitude we considered in deciding target regions, denoted by the dotted blue line) and 30°N through 47°N, the plotted, filled oval regions (area with a radius of 1°) are the only regions that contain at least 20 recordings between 2006 and 2016 (pre-Drought).

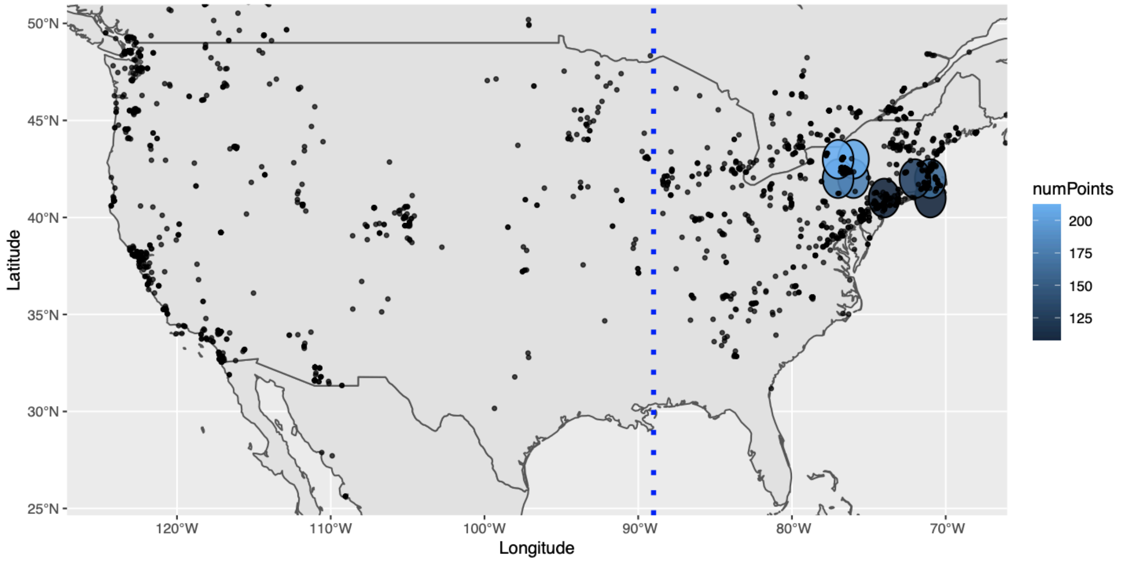

Figure S3D: Song Sparrow recordings publicly available on Macaulay Library or Xeno-canto recorded between 2017 and 2019. Of all regions centered on each integer value of (Longitude, Latitude) ranging from 70°W through 89°W (the westernmost longitude we considered in deciding target regions, denoted by the dotted blue line) and 30°N through 47°N, the plotted, filled oval regions (area with a radius of 1°) are the regions that contain at least 100 recordings between 2017 and 2019 post-Drought).

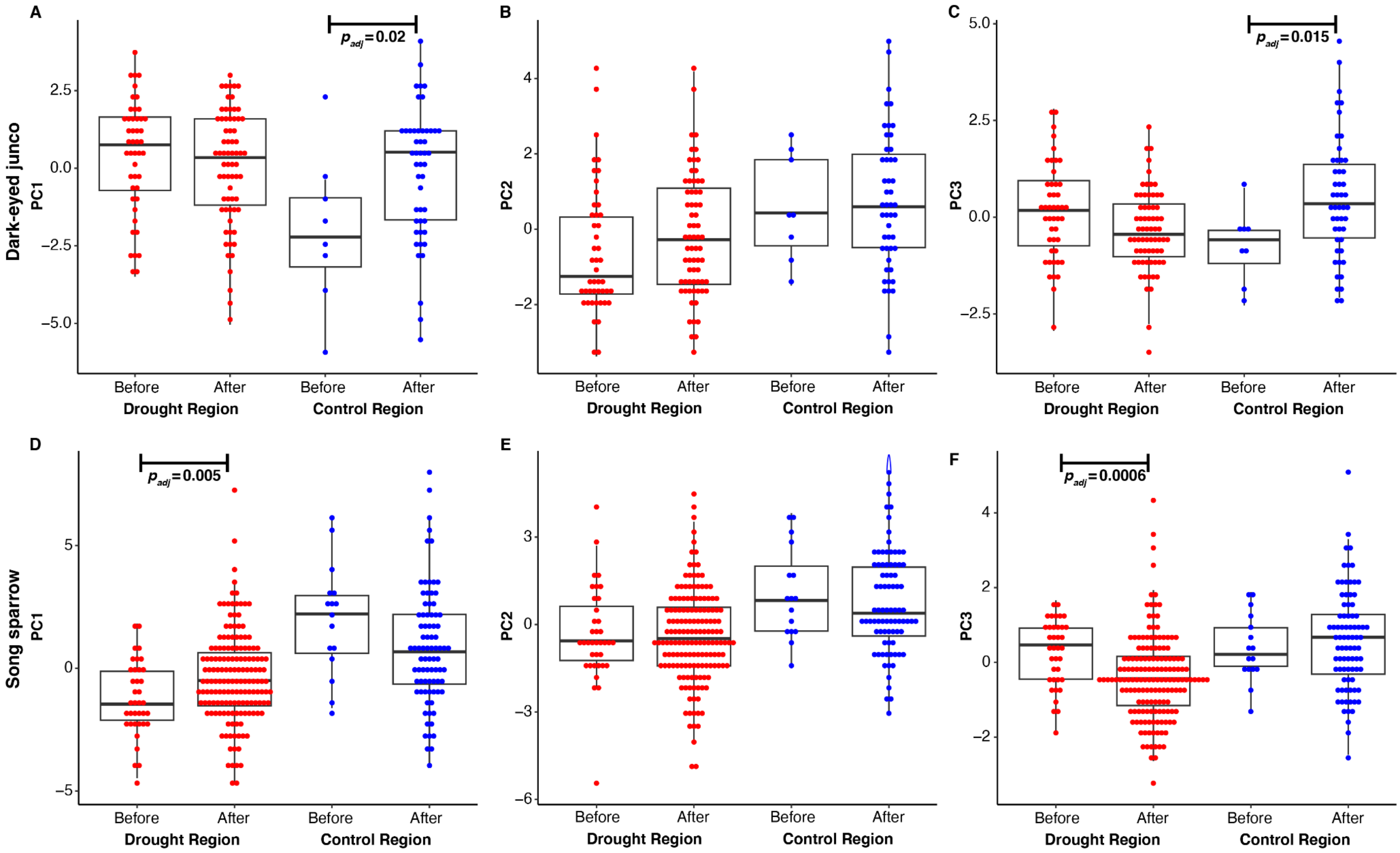

Figure S4: Distributions of the first three principal components of the song feature data for Song Sparrows and Dark-eyed Juncos. Statistical analyses performed as in the individual song features. For each set of Principal Component scores, we assessed whether there were differences between groups using a GLS model and post-hoc tests, as in **Figures 3** and **5** in the main text. We used the simple GLS model, which assumed equal weights for each group) unless an ANOVA indicated that the variable-weight model was a significantly better fit (variable-weights model used in panels C, D, F). Weights of song features in each dimension are provided in **Table S1**. Overall, there were significant regional differences in song features, with two of the three dimensions differing significantly between regions in Dark-eyed Juncos (ANOVA by Region: PC1 $p = 0.068$, PC2 $p = 0.0011$, PC3 $p = 0.020$), and three of the three dimensions differing by region in Song Sparrows (ANOVA by Region: PC1, PC2, PC3 $p < 1 \times 10^{-7}$).

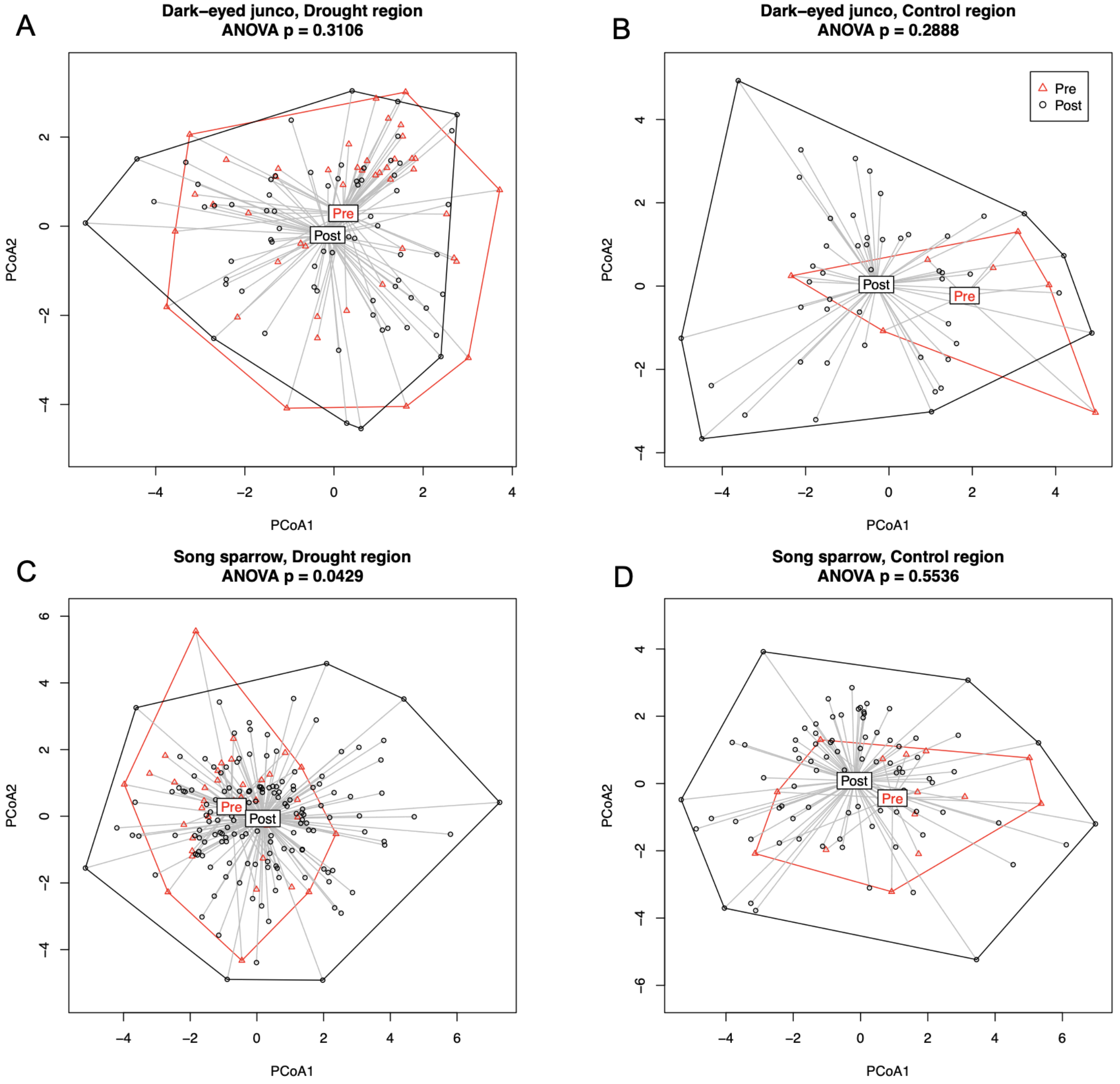

Figure S5: Multivariate test of homogeneity of song feature variances by Region and Era. This analysis was conducted with the function betadisper (R package "vegan") on the PCoA-transformed song-feature data. The ANOVA of this output tests for differences in the distances from members of each group to its group's centroid. Only the variances in Song Sparrow songs in the drought region were significantly different before versus after 2016 (Panel C).

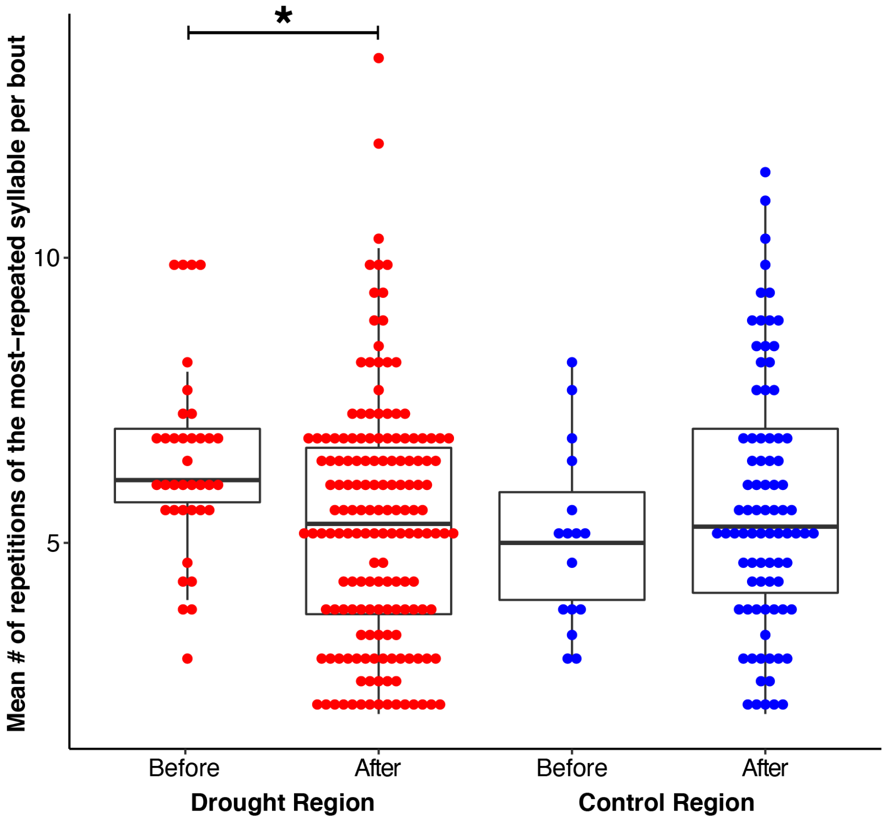

Figure S6: Distributions of average counts of the most-repeated syllable per bout per recording within Song Sparrow populations before and after the 2016 drought. For each bout, we found the most repeated syllable type based on the syllable type assignment from the Chipper analysis, counted the number of times the most repeated syllable was produced, and averaged those counts across all bouts sampled from a given recording. Overall, in recordings after the drought, the most-repeated syllable type per bout was repeated fewer times on average (GLS ANOVA: $p = 0.016$; nlme::gls with no weights: Drought region pre vs post $p = 0.009$, Control region pre vs post $p = 0.542$) .

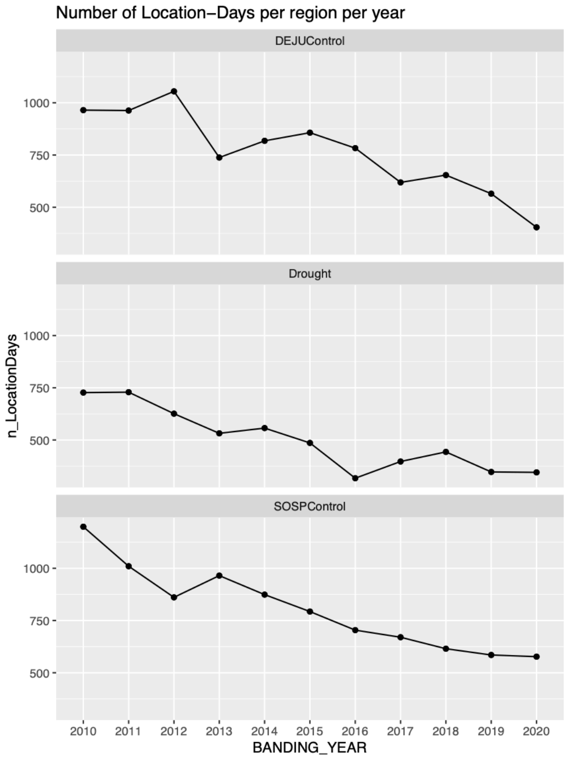

Figure S7: The number of unique banding location-days in the USGS database per year per region, used as a proxy for effort.

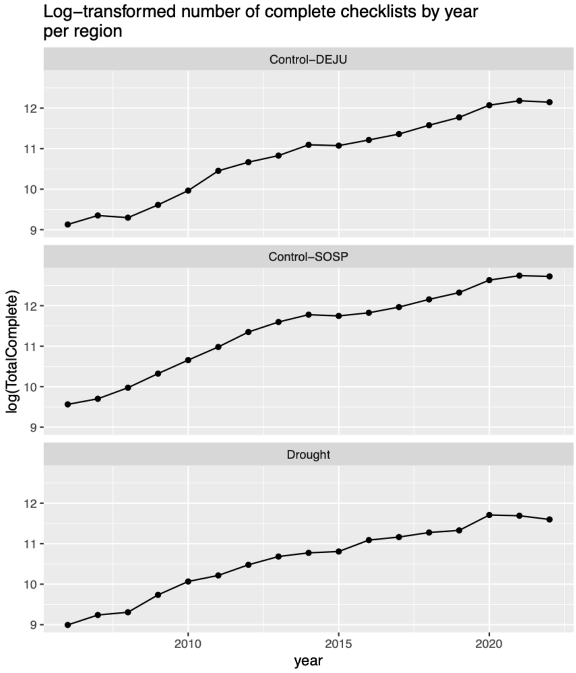

Figure S8: The number of complete checklists in the eBird database per year per region, used as a proxy for effort. Numbers were log-transformed (natural log) for ease of visualization.

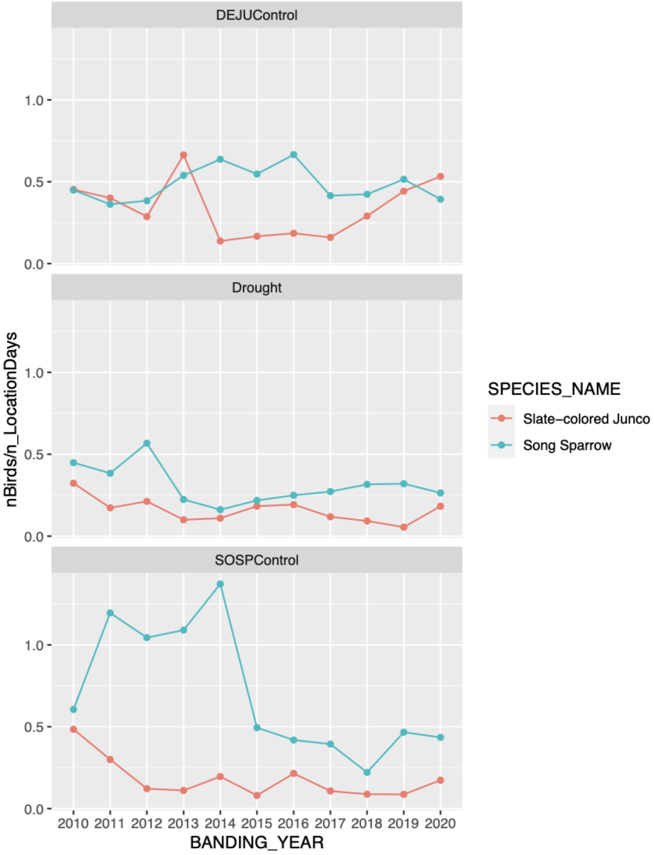

Figure S9: Relative species abundances in each of our three regions as reported by United States Geological Society (USGS) bird banding data. For each year between 2010 and 2020, we divided the number of Dark-eyed Juncos (*Junco hyemalis hyemalis*, Slate-colored Junco subspecies, shown in red) and Song Sparrows (shown in teal) of any age class banded in a region by the total number of days at each unique banding site that banding was conducted in that region. For example, a value greater than one indicates that, on average, more than one bird of that species was banded each time a banding effort was conducted in the region.

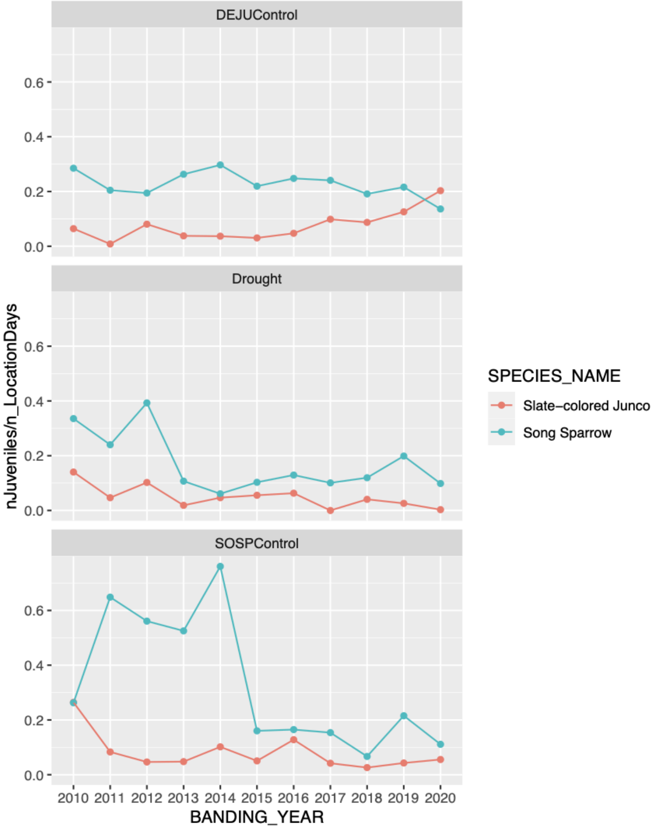

Figure S10: Juvenile bird abundances in each of our three regions as reported by United States Geological Society (USGS) bird banding data. For each year between 2010 and 2020, we divided the number of juvenile Slate-colored Juncos and Song Sparrows observed in a region by the total number of days at each unique banding site that banding was conducted in that region. Observations labeled “Hatch year” or “Local” (defined as “A nestling or young bird incapable of sustained flight”) were counted as juvenile observations.

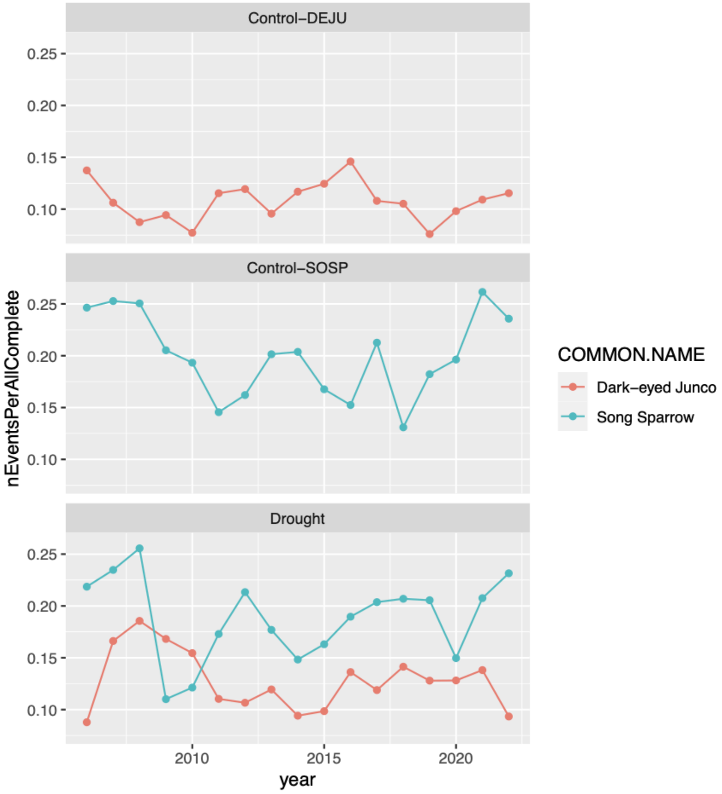

Figure S11: Relative species abundances in each of our three regions as reported by eBird user observation data. For each year between 2006 and 2022, we divided the number of completed eBird checklists that included Dark-eyed Juncos (red) and Song Sparrows (teal) by the total number of checklists that were completed in that region.

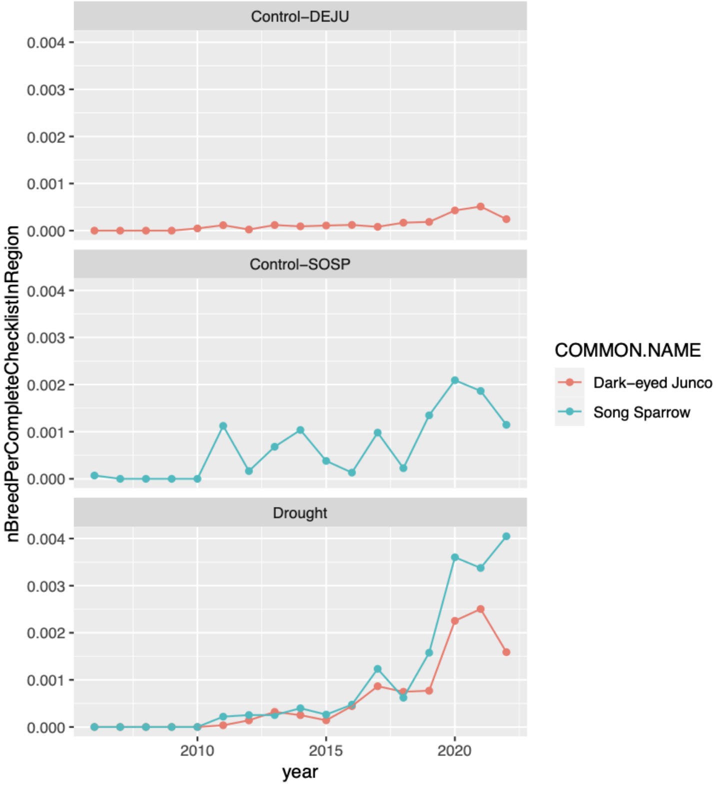

Figure S12: Breeding behavior observations in each of our three regions as reported by eBird user observation data. For each year between 2006 and 2022, we divided the number of completed eBird checklists that mentioned breeding behaviors in Dark-eyed Juncos (red) and Song Sparrows (teal) by the total number of checklists that were completed in that region.