Detecting cultural evolution in a songbird species using community-science data and computational modeling

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Abstract

Song in oscine birds is learned across generations, and aspects of the song-learning process parallel genetic transmission: variation can be introduced into both cultural and genetic traits via copy-error, and both types of traits are subject to drift and selective pressure. Similarly to allele frequencies in population genetics, observing frequencies of birdsong features can improve our understanding of cultural transmission and evolution. Uniquely, community-science databases of birdsong provide rich spatiotemporal data with untapped potential to evaluate cultural evolution in songbirds. Here we use both community-science and field-study recordings of chipping sparrows to examine trends across nearly seven decades of song. We find that some syllable types tend to persist in the population for much longer than others. Persistent songs tend to contain more syllables of shorter duration than songs which were observed across fewer years. To draw inferences about the effects of learning biases on chipping sparrow syllables, we construct a spatially explicit agent-based model of song learning. By comparing our empirical analysis to simulated song distributions using three different song-learning strategies—neutral transmission, conformity bias, and directional selection—we suggest that chipping sparrows are unlikely to select tutors neutrally or with a conformity bias and that they learn their songs with a remarkably low copy-error rate.

Keywords: birdsong, cultural evolution, learned behaviors, selective pressures, community science

Introduction

For oscine songbirds, song has many important functions, including territory defense, species identification, and mate attraction (Catchpole & Slater, 2003; Searcy & Andersson, 1986). In contrast to a closely related outgroup (suboscines), oscines must learn their songs, making the process of song learning critical to the reproductive success of individuals across this diverse clade (Kroodsma et al., 1982; Kroodsma & Miller, 1996; Mason et al., 2017; Thorpe, 1958). The evolutionary dynamics of learned song exhibit parallels to those of human cultural evolution, where long-lasting traditions can coexist (Aplin, 2016; Hoppitt & Laland, 2013; Kandler & Laland, 2009; Tomasello et al., 1993; Whiten, 2017). By studying song learning, we can better understand which aspects of human learning and cultural evolution are shared with other species and which properties are unique.

The transmission of information between individuals underpins both human and avian cultural evolution. Laboratory and field studies have shed light on how song is transmitted in avian populations. Some of these studies have measured the properties of cultural transmission: the similarity between learned song and tutor song, error rates in song matching, the invention of new songs, and the frequency of songs in a population, among other factors (Cardoso & Atwell, 2016; Marler & Peters, 1982; Marler & Tamura, 1962; Slater, 1986; Thorpe, 1958). Others have used field-site data to address questions of song change over time. For example, some studies have tracked cultural evolution using recordings taken in one population over multiple decades (Ju et al., 2019; Williams et al., 2013), and other studies have demonstrated that temporal changes in song are discerned by the current population by showing that birds react more strongly to modern recordings than to historical ones (Derryberry, 2007, 2011). Field-study recordings can ensure coverage of local song repertoires, facilitate direct observation of song tutors, and provide samples from the entire site's population. However, because of limits on the time period and geographic range they can cover, field studies cannot address certain questions about cultural evolution.

By tracking songs and reproductive success over time, as well as by determining which song features correspond to stronger responses in current populations, researchers have gained insight into the types of selective pressures that operate on song (Derryberry, 2007, 2011; Williams et al., 2013). In parallel, evolutionary biologists and population geneticists, without access to time-series data, have synthesized evolutionary models with evidence from existing

distributions of allele frequencies to understand whether regions of the genome have undergone selection (Bamshad & Wooding, 2003; Bustamante et al., 2001; Ford, 2002; Gutenkunst et al., 2009; Nielsen, 2005; Williamson et al., 2005). A genetic variant can become more frequent in a population because it is associated with a fitness advantage (selection) or due to random chance (genetic drift). A genetic region under selection will tend to have a different distribution of allele frequencies than those regions not under selection (Nielsen, 2005). Thus, one approach in population genetics is to simulate the evolution of a trait under different selection pressures and population histories. By comparing data from real populations to predictions from evolutionary models, researchers have identified which of these models best explains the data (Gutenkunst et al., 2009; Williamson et al., 2005). Some researchers apply this theoretical approach to the cultural evolution of song by examining the distribution of song within populations (Lynch & Baker, 1993, 1994) and by developing individual-based or agent-based simulations of song learning that are compared to field-site data (Crozier, 2010; Ellers & Slabbekoorn, 2003; Lachlan et al., 2018; Slater, 1986; Youngblood & Lahti, 2022). Such agent-based simulations have been used in conjunction with birdsong data to infer the learning strategies used by swamp sparrows and house finches (Lachlan et al., 2018; Youngblood & Lahti, 2022). With these comparisons of field recordings and results, researchers found evidence for different cultural transmission biases in different species: swamp sparrows showed evidence of conformity bias, a type of frequency bias in which common song variants are disproportionately preferred, whereas house finches showed evidence of content bias, in which certain song elements are preferentially learned regardless of their frequency in the population (Lachlan et al., 2018; Youngblood & Lahti, 2022).

Here, we present an extension to this approach by developing a model of cultural transmission of birdsong and comparing the results of this model to a large-scale song analysis of community-science recordings. We suggest that utilizing community-science data is a time- and cost-effective supplement to field studies in the study of birdsong evolution. Specifically, community-science data—which can cover a large geographic area over many years—can provide a unique insight into patterns of song transmission across large spans of time or space, particularly when these data are considered alongside evolutionary models. Researchers have analyzed community-science data to examine avian behaviors, whereas other studies have compared spatially explicit models to song recordings from the field to examine evolutionary hypotheses (Bolus, 2014; Dennhardt et al., 2015; Goodenough et al., 2017; Kaluthota et al.,

2016; Newson et al., 2016; Robinson et al., 2018; Silvertown et al., 2011). We synthesize these approaches by examining community-science data via models of song learning, providing insights into cultural evolutionary patterns.

As a focal species for this study, we chose the chipping sparrow, which has a simple repertoire of one repeated syllable. As a result, the full vocal repertoire of an adult bird can be captured by a single community-science recording. Since cultural transmission includes mechanisms of mutation, selection, and drift similar to those found in genetics, we employ techniques from population genetics—in particular, an adaptation of site frequency spectra (Bustamante et al., 2001; Nielsen, 2005)—to study song evolution. We identify unique syllable types that characterize the songs in a population, and use the occurrence and lifespans of these syllables to gain a deeper understanding of chipping sparrow learning. We compare the occurrence and longevity of songs to distributions produced by a computational model. This model simulates the transmission of syllables in a population under three types of learning—neutral evolution, conformity bias, and directional selection. We demonstrate how analysis of community-science data in association with a model can supplement field studies and extend the understanding of birdsong evolution.

Methods

Categorization of chipping sparrow syllables into types

In a previous study, we gathered and analyzed field-site and community-science recordings of chipping sparrows across the species' entire breeding range (**Fig. S1**), measuring numerous acoustic features of each song and classifying the syllables into distinct types and categories (Searfoss, Liu, et al., 2020; Searfoss, Pino, et al., 2020). A number of recorded songs in our previous analysis (Searfoss, Liu, et al., 2020) did not have a recording date listed; however, by revisiting the original field recording notes we were able to find the years for all recordings for our study presented here. We categorized songs as follows: all songs were viewed as spectrograms in Audacity on a fixed frequency- and time-scale (see **Appendix S1**). A single syllable was then selected as representative of a song, since chipping sparrow songs are fully characterized by repetition of a single syllable. We manually classified 820 syllables into 112 chipping sparrow syllable types based on the shape of the syllable (**Appendix S1**, similar to

methods of (Borror, 1959; Leitner & Catchpole, 2004; Liu, 2001; Vargas-Castro et al., 2012); for examples of spatial syllable distributions, see **Fig. S7**). We further grouped these syllable types into broader categories based on the syllable shape: up-down (up-slur followed by down-slur), down-up (down-slur followed by up-slur), sweep (single up-slur or down-slur), complex (more than two slurs), doubles (a slur with multiple frequencies), and buzz (syllable containing a noisy and/or high-entropy section, generally termed 'buzzy'). To ensure that we were correctly categorizing the repeated element, particularly in the case of up-down versus down-up syllables, we examined the beginning and end of the song to determine which part of the syllable came first.

In addition, we used the song-analysis software Chipper to extract eight song features from each recording: mean intersyllable silence duration, mean syllable duration, mean syllable frequency range, mean syllable minimum and maximum frequency, duration of song bout, mean syllable stereotypy, and total number of syllables. Chipper allows the user to visualize each song bout, and it predicts where syllable boundaries are located using fluctuations in the amplitude of the signal (Searfoss, Pino, et al., 2020). The user can change the signal-to-noise threshold, apply lowpass and highpass filters to exclude high-frequency and low-frequency noise, respectively, and manually correct these syllable boundaries if necessary. Then, Chipper analyzes the signal within each identified syllable and outputs a matrix of features for each song (see (Searfoss, Pino, et al., 2020) for more details on how each song feature is extracted from the spectrogram).

For the catalog numbers, database, recordist, URL, and license for the 820 song files, see **Supplementary Data Table 1**. For the metadata including recording latitudes and longitudes and the 8 song features (all log transformed except mean stereotypy of repeated syllables and the standard deviation of note frequency modulation), see **Supplementary Data Table 2**.

Calculating and analyzing the lifespan of chipping sparrow syllable types

The observed "lifespan" of a syllable type was defined as the period between the earliest and latest years in which a syllable type was recorded. To explore the properties of these lifespans, we plotted the distribution of syllable lifespans and the number of times in which these syllables were identified (**Fig. 2**). We proceeded to compare syllable features between songs that contained short-lived (lifespan=1 year) versus long-lived (lifespan≥50 years) syllable types. We performed Wilcoxon rank-sum tests on short- versus long-lived syllables for the eight song

features extracted from each recording. For stringency, we conducted a Bonferroni correction for multiple hypothesis testing by dividing the *P*-value threshold for significance (α=0.05) by the number of tests. Overall we performed one test on 8 song features, so the threshold for significance was lowered to $\alpha_{adjusted}=6.25\times10^{-3}$. In addition to our previously observed geographic patterns in chipping sparrow songs (Searfoss, Liu, et al., 2020), we also conducted Wilcoxon rank-sum tests to determine whether short- or long-lived syllables are more frequent on an east-west axis.

Model design

We developed an agent-based simulation to model song learning in the chipping sparrow population. The entirety of the model was implemented in Python 3.7 and uses the following primary packages: NumPy v1.16.3, Matplotlib v3.0.3, Pandas v0.24.2, and SciPy v1.2.1 (https://github.com/CreanzaLab/ChippingSparrowCulturalEvolutionModel). With this model, we simulate syllable transmission in a population under three learning regimes—neutral transmission, conformity bias, and directional selection. Under a neutral model of song learning, a juvenile randomly chooses a tutor's song to imitate; with conformity bias, a juvenile is disproportionately likely to choose a tutor with the most common song; and directional selection operates to favor certain song properties such as rate of syllable production or higher frequency bandwidth (Podos, 1997; Podos & Nowicki, 2004), such that juveniles are more likely to learn songs that exemplify better performance. Here, directional selection is somewhat analogous to the content bias observed in house finches (Youngblood & Lahti, 2022), since juveniles are choosing to learn a syllable based on its properties and not its frequency of occurrence; however, since chipping sparrows only learn one syllable, we track a continuous feature of a single syllable instead of the selection of certain syllables to compose a song.

A population of birds is initialized as a 500×500 matrix of syllable types. Each matrix location represented a single bird that sings a single syllable—represented by an integer initially assigned randomly from a discrete uniform distribution {1:500}. For the directional selection model, an additional matrix of identical size is used, containing rates of syllable production randomly sampled from a truncated normal distribution confined to the values observed in nature ($X \sim N(22.5, 25), 5<X<40$) (Searfoss, Liu, et al., 2020). In each timestep, roughly corresponding to a year, the following steps take place: a fraction of birds die, juvenile birds are tutored and fill

the empty territories, and a portion of the population disperses (**Fig. 1**). Note that there is a substantial burn-in period (discussed under 'Sampling the simulated bird population'), so initial distributions of syllables and song-rates have minimal impact on final, sampled values.

More specifically, first a fixed percentage of the birds are randomly selected for death. We set this mortality rate to 40% based on similar avian models (Lachlan et al., 2018; Slater, 1986). For every bird that is eliminated, a new juvenile bird replaces it; the new bird's repertoire is either a novel syllable in the case of copy error, or a syllable learned from one of its neighbors (birds present at the beginning of the timestep and adjacent to its hatching location in the two-dimensional matrix—up to eight birds). In order to maintain a spatial arrangement representative of natural territories, the matrix boundaries do not wrap, so birds at the edges of the matrix have fewer neighbors. Maintaining father-juvenile relationships was not necessary in our model, as oblique transmission of song, rather than vertical song transmission from parent to offspring, is predominant in chipping sparrows; juveniles after their first spring migration often change their song to match a neighbor, although the song does not change after the first year (Liu & Kroodsma, 2006; Liu & Nottebohm, 2007). Once all juveniles learn a syllable (see next sections for the three learning strategies), the new syllable types replace the matrix elements of the birds that died, representing juveniles moving into vacant territories. All territories vacated by birds that died are filled simultaneously, after tutor selection occurred for that time step. Since deaths in nature occur throughout the year and learning takes place over a short time, all birds present at the beginning of the timestep can influence the learning of juveniles during that timestep.

In addition, birds have an opportunity to disperse: some portion of birds (termed the 'dispersal fraction') is selected to move to a nearby location on the matrix. This promotes the mixing of regionally common syllable types with the larger population. Dispersal may sustain the local syllable diversity seen in chipping sparrow populations (Liu & Kroodsma, 2006). The addition of this dispersal step reflects what has been observed in the field: adults occasionally move to a new location, especially when they share a song with a neighbor (Liu & Kroodsma, 2006). We tested dispersal fractions between 0 and 0.5 in 0.1 increments, where 0.5 means that half of birds attempt to swap places with a bird that has not yet changed places, chosen randomly from a location within a set radius (up to 11 matrix units). These dispersal fractions and radius values were informed by field studies describing chipping sparrow territory size and dispersal patterns (Liu, 2004; Liu & Kroodsma, 2006; Swanson et al., 2004). For each set of parameters,

the simulation is run for 1000 timesteps, of which the final 68 are used for sampling (to compare with the 68 years of available community-science data) and the first 932 are a long burn-in period prior to sampling.

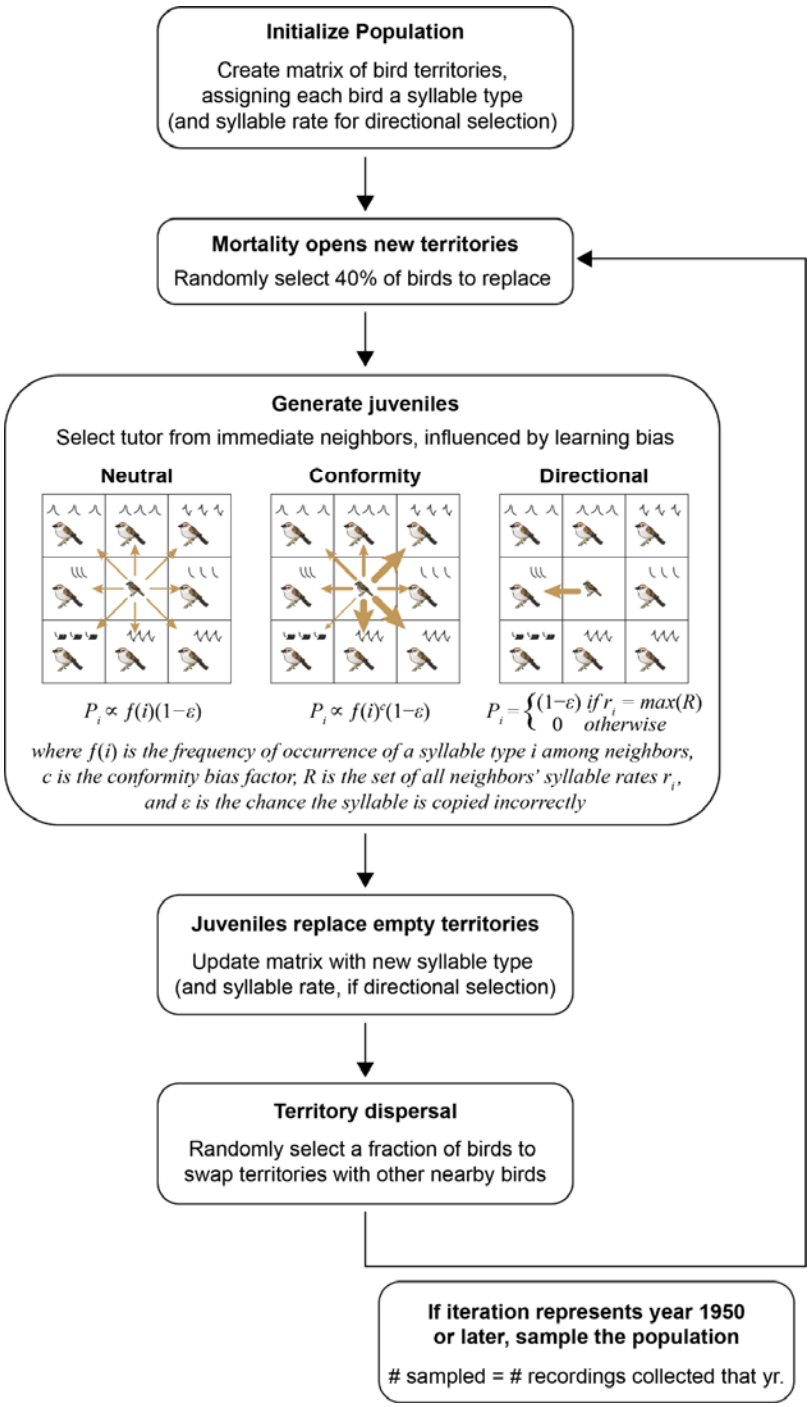

Figure 1. Model schematic with illustrated representation of learning biases. For neutral learning, the frequency of a syllable type among the juvenile's adjacent neighbors is proportional to the probability that it will be learned by the juvenile (equal weight for all neighbors; identical arrows). Conformity bias scales this probability by squaring the frequency of the syllable types' occurrence (more common syllables are preferred). In our implementation of directional bias, syllable rate is the song characteristic that is selected for (although this could easily represent any song feature): the neighbor with the highest syllable rate is chosen as the tutor. Both the syllable type (for all learning models) and syllable rate are learned with some probability of error; if the syllable type is incorrectly copied, a new syllable is invented.

Model implementation of neutral tutor selection

During each timestep, birds that die are replaced by a juvenile bird at each location. For neutral tutor selection, the syllable type learned by this juvenile is chosen at random from its eight immediate neighbors (or fewer, at edges and corners). To account for some likelihood of the new bird producing a novel syllable, we include a probability of error in learning. The probability of learning syllable type i in the case of neutral tutor selection can be represented as

$$P_i \propto f(i)(1-\varepsilon),$$

where $f(i)$ is the frequency of occurrence of a syllable type i among neighbors and ε is the chance the syllable is copied incorrectly. We varied this error rate parameter (ε) to explore the ranges of plausible error rates for each learning model (0.0001%, 0.001%, 0.01%, 0.1%, and 1.0%). Since only about 0.5% of observed songs were recorded only once (see **Fig. 2**), we did not test values of copy error higher than 1%.

Model implementation of conformity bias

Under conformity bias, juveniles preferentially learn more frequent songs. Each juvenile surveys the syllable types sung by his neighbors. The probability of learning syllable type i in the case of conformist tutor selection can be represented as

$$P_i \propto f(i)^c(1-\varepsilon)$$

where c is the conformity bias factor. In the simulations we report below, each syllable's frequency is squared (i.e. conformity factor c=2) and normalized to represent the likelihood of selecting each syllable, such that more common syllable types are learned more often than they appear among neighbors. We also tested a less severe conformity bias (conformity factor c=1.5) (see **Figs. S3-6**). The learning error and dispersal were examined identically those of the neutral tutor selection model.

Model implementation of directional tutor selection

For directional tutor selection, learning is based not on the frequencies of syllable types, but on a continuous variable representing the rate of syllable production. The probability of learning syllable type i under directional selection is given by

$$P_i \propto (1-\varepsilon) \text{ if } r_i = \max(R) \text{ and } P_i = 0 \text{ otherwise,}$$

where R is the set of all neighbors' syllable rates r_i. This process mimics a type of directional selection that has been proposed for chipping sparrows, in which the preferred song is most difficult to produce. This model could accommodate directional selection on any continuous song feature; as a case study, we use a simple metric—rate of syllable production, also called trill rate—as our putative feature that is under selection. This feature has been hypothesized to be relevant in chipping sparrows (Goodwin & Podos, 2014), but we note that our previous analysis showed a relatively wide distribution of trill rates in the chipping sparrow population over time, from ~5 to 40 syllables per second. In the model, the juvenile selects a tutor—the neighbor with the fastest syllable rate—and attempts to copy both the syllable type and the syllable rate of this tutor. The learning error for syllable type operates identically to the neutral and conformity models. With directional selection, there is also a learning error for syllable rate which is weighted such that it is more difficult to replicate or improve upon the tutor's performance than to perform worse than the tutor (as in (Henrich, 2004)). Thus, juveniles are most likely to sing at a slightly slower rate than the tutor, and the syllable rates are restricted to values observed in our chipping sparrow song database (between 1 and 40 syllables per second). Therefore, the learned song is sung at a rate similar to that of the tutor, and has either an identical or a novel syllable type. It is important to note that while we describe the song feature under selection as 'syllable rate', it can be interpreted that any continuously varying song feature is undergoing directional selection.

Sampling the simulated bird population

The method of data collection from the model population was chosen to replicate the sampling that occurred when songs were recorded by community-scientists. For each learning model, the simulated population is sampled such that the number of birds sampled per timestep is equal to the number of recordings we have from each year. Our recording data spans 68 years (1950–2017) with some years having no recordings; thus some number of birds (possibly 0) are selected at random from the model population for each of the last 68 of 1000 iterations of the model (here, the first 932 timesteps serve as a burn-in, which minimizes the effects of initialization for variables such as the number and distribution of syllables). For each bird sampled from the simulated population, the iteration from which it was collected and the syllable

type were documented. This was to ensure the lifespans and the counts of syllable types of this sampled model population could be calculated in the same manner as the recording data.

Quantitatively comparing model results to empirical data

For each simulation, we visualized and compared our results using the site-frequency spectrum technique from population genetics (Nielsen, 2005; Pepperell et al., 2013; Zhu & Bustamante, 2005) and created a "syllable frequency spectrum"—the frequency of birds that sing various syllable types in the sample—to compare our model results with empirical data. Additionally, we use a similar visualization to compare the frequencies of syllable-type lifetimes for each model across a range of learning error rates.

Specifically, we aimed to identify whether one or more tutor-selection models would be able to produce results similar to the empirical data, across both syllable frequency of occurrence and syllable lifetime distributions. These distributions have similarities to the empirical data: there are several frequent long-lasting syllables, many syllables observed very few times, and a small number of syllables with intermediate observed lifespans (**Fig. 2**). These intermediate-lifespan syllables were most difficult to replicate among these song-learning models in a way that could be detected by direct comparison of distributions, such as via two-sample Kolmogorov-Smirnov and *k*-sample Anderson-Darling tests; the sparsely populated intermediate values of syllable frequency and lifespan contained most of the relevant differences between models, whereas most mass used in comparisons of distributions lay at the extremes (**Figs. 2 & 6**). Instead of manually assigning categories of *short-longevity*, *intermediate-longevity*, etc., we placed the empirical data into bins using an algorithm; it assigned bin edges by minimizing the combined variance of bin count and bin width. First, we placed syllables that were recorded only once (for the syllable frequency spectrum) or only in a single year (for the distribution of syllable lifespans) into their own category, and all others were initially placed into six equally spaced bins. Then, the edges of these bins were progressively shifted 10^6 times (the edges were moved, and variances of the resulting bins' sizes and their number of data points were calculated). If the combined variance was lower, this became the new set of bins for the next permutation (see GitHub for details).

In this way, we used an algorithm to place the empirical chipping sparrow data into bins by syllable type using the optimally found edges, and the simulated samples were placed into the

same bins to compare their distributions with the empirical data. On the binned syllable-type and lifespan spectra, we conducted Fisher's exact tests between the empirical data (null hypothesis) and all simulated datasets to determine which combination of learning strategy, learning error, and dispersal fraction results in syllable-type and lifespan distributions that are concordant with the patterns found in the chipping sparrow population.

Results

Syllable types and cultural analysis

We categorized syllables from 820 recordings into 112 distinct syllable types (**Appendix S1**, also see previous analysis (Searfoss, Pino, et al., 2020)). We found that syllable types that continue to exist for much longer than the lifetime of a chipping sparrow (less than 9 years) are also those that are most commonly observed, whereas other syllables are transient, and are observed rarely (**Fig. 2**). In other words, we did not observe any syllables that were found in many recordings but existed for a short period of time. To identify differences between long- and short-lived syllables, we classify syllable types as short-lived (lifespan=1 year) or long-lived (lifespan≥50 years), and compare the features of these syllables (**Fig. 3**). We find that long-lived syllable types are significantly shorter in duration than short-lived syllables ($P<3.29\times10^{-3}$) (**Fig. 3A**, **Table 1**), and songs with a long-lived syllable type contain significantly more repetitions of that syllable per bout ($P<1.33\times10^{-3}$) (**Fig. 3B**). We also found that geographic differences did not explain the trends in longevity, since the longitude of recordings of different syllable types did not significantly differ between the two lifespan categories ($P=0.844$). Additionally, buzz syllables tend to be long-lived, whereas double or complex syllables tend to be short-lived, with up-down, down-up, and sweep syllables being prominent in both lifespan groups (**Fig. 3C**).

Table 1. Results of the Wilcoxon rank-sum tests between short- and long-lived syllable types.

Song Features	Short- vs Long-Lived *P*-value
Mean intersyllable silence duration	0.449
Mean syllable duration	**0.003**
Mean syllable frequency range	0.802
Mean syllable minimum frequency	0.476
Mean syllable maximum frequency	0.475
Duration of song bout	0.010
Mean stereotypy of repeated syllables	0.653
Total number of syllables	**0.001**

Bold indicates $P < 6.25 \times 10^{-3}$.

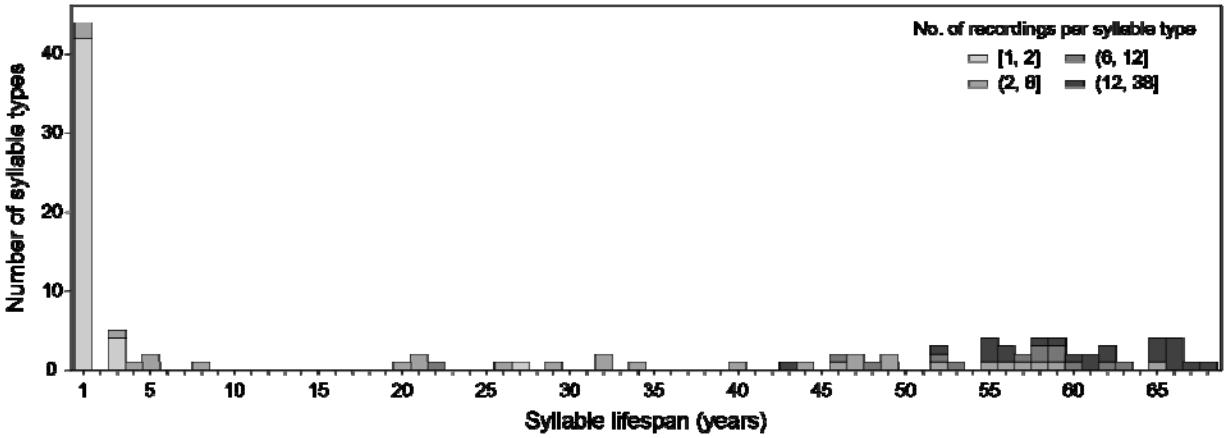

Figure 2. Distribution of chipping sparrow syllable type according to their lifespans. For our database of 820 recordings of 112 syllable types, we plot the number of syllable types versus syllable lifespan. Each syllable type is also shaded by the total number of recordings of that syllable type, illustrating that longer-lived syllable types are also more common, though less common long-lived syllables exist.

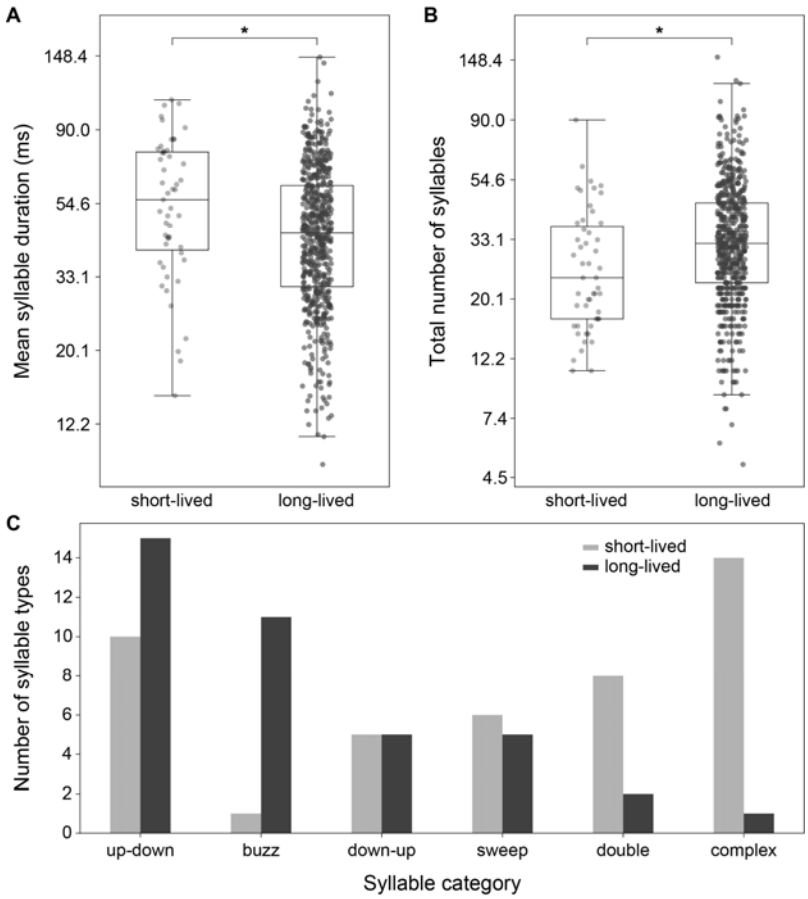

Figure 3. Syllable categories and song properties of short- and long-lived chipping sparrow syllable types. Songs with long-lived syllable types (>50-year lifespan) have (A) significantly shorter syllables (P=3.29×10^{-3}) and (B) significantly more syllables per song (P=1.33×10^{-3}) than songs with short-lived syllable types (1-year lifespan). Significant results are indicated (* denotes P<6.25×10^{-3} from Wilcoxon rank-sum tests). (C) The number of short- and long-lived syllable types in each syllable category.

Model results

Here, we ran several models of song transmission in order to test which model produces patterns most similar to empirical data. We conducted a parameter sweep, running the simulation for each of the three learning strategies with multiple error rates (or invention rates) spanning 0.001% to 1.0% and with territory dispersal fractions spanning 0 to 0.5 (i.e. 0 to 50% of individuals swap territories with a bird that has not already dispersed). We quantitatively determined which combinations of parameters (song-learning strategy, learning error rate, and dispersal fraction) produced results that did not deviate from the null hypothesis (empirical data). We provide the syllable type and syllable lifetime frequency spectra for the best-fit model for each learning type. We determined a 'best-fit' model by first ranking the P-values (from least to greatest) for both the analysis of syllable type frequencies and the analysis of syllable lifespans

and then combining the two ranks for each parameter set and choosing the one with the highest aggregate ranking, i.e. the largest sum of the two rankings (**Fig. 4 and 5**). (We note that the results of the Fisher's exact test indicate that the model results are potentially drawn from the same distribution as the real data when the null hypothesis is *not* rejected; when the *P*-value is not significant, the results of the model are statistically indistinguishable from the empirical data.) These best-fit model for each learning type was: neutral tutor selection with 0.001% learning error and 0.1 dispersal fraction (syllable frequency distribution $P=9.2\times10^{-17}$, lifespan frequency distribution $P=0.079$), conformity bias with 1.0% learning error and 0.2 dispersal fraction ($P=10^{-6}$ and $P=0.11$ respectively), and directional selection with 0.1% learning error and 0.5 dispersal fraction (statistically indistinguishable from the empirical data using both metrics; $P=0.36$ and $P=0.98$ respectively) (**Fig. 6,** see **Fig. S2** for corresponding binned spectra). See also **Figs. S3-6** for results of the reduced conformity bias ($c=1.5$); this model was not more effective at describing the observed data.

Only the directional selection model with learning error of 0.1% and 0.5 dispersal fraction simultaneously reproduced syllable counts and lifespans that could not be statically distinguished from those of the empirical data (Fisher's exact, $P=0.36$ and $P=0.98$, respectively) (**Fig. 4 and 5**). The simulation with directional selection of tutors appears to most closely match the frequency of syllable types found in our empirical data, with a distribution containing many singletons and a long, flat tail (**Fig. 6A**). While long-lived syllable types arise in all three song-learning models, directional selection has an enrichment for these syllable types compared to the neutral model, whereas conformity bias has an abundance of long-lived syllables and few syllables with intermediate lifespans; thus, directional selection's frequency spectrum of syllable-type lifespans best reflects what is observed in our community-science data sample (**Fig. 6B**).

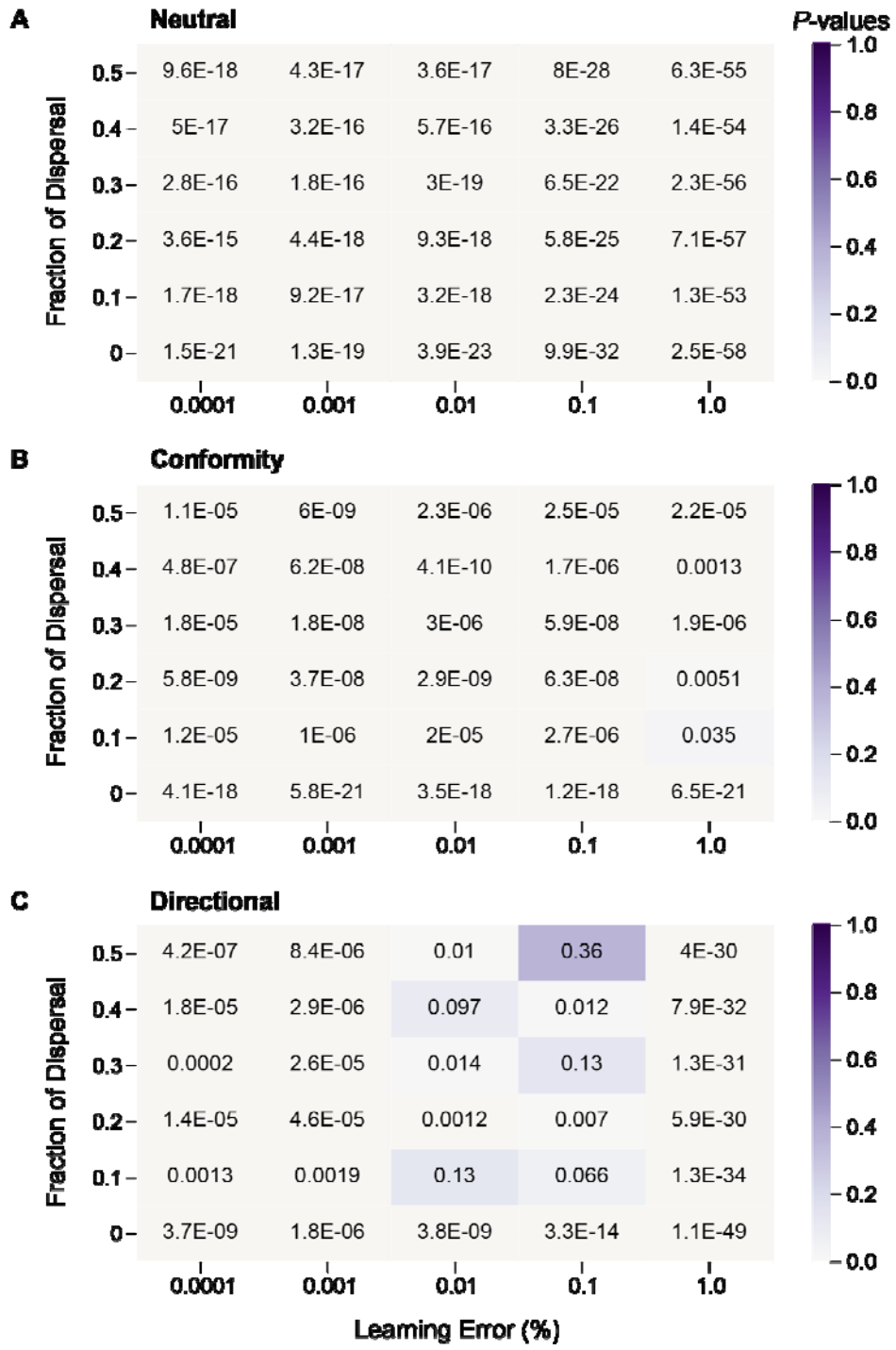

Figure 4. Statistical comparison of syllable frequency spectra between song-learning models and empirical data for simulations with a range of dispersal fractions and learning-error rates. *P*-values for Fisher's exact tests in which the null hypothesis is that the binned syllable frequency spectrum of empirical data and the simulated data are drawn from the same distribution. All simulations with (A) neutral learning or (B) conformity bias (c=2) were significantly different from the empirical data (P<0.05). Some, but not all, simulations with (C) directional selection were statistically indistinguishable from the empirical data (P>0.05).

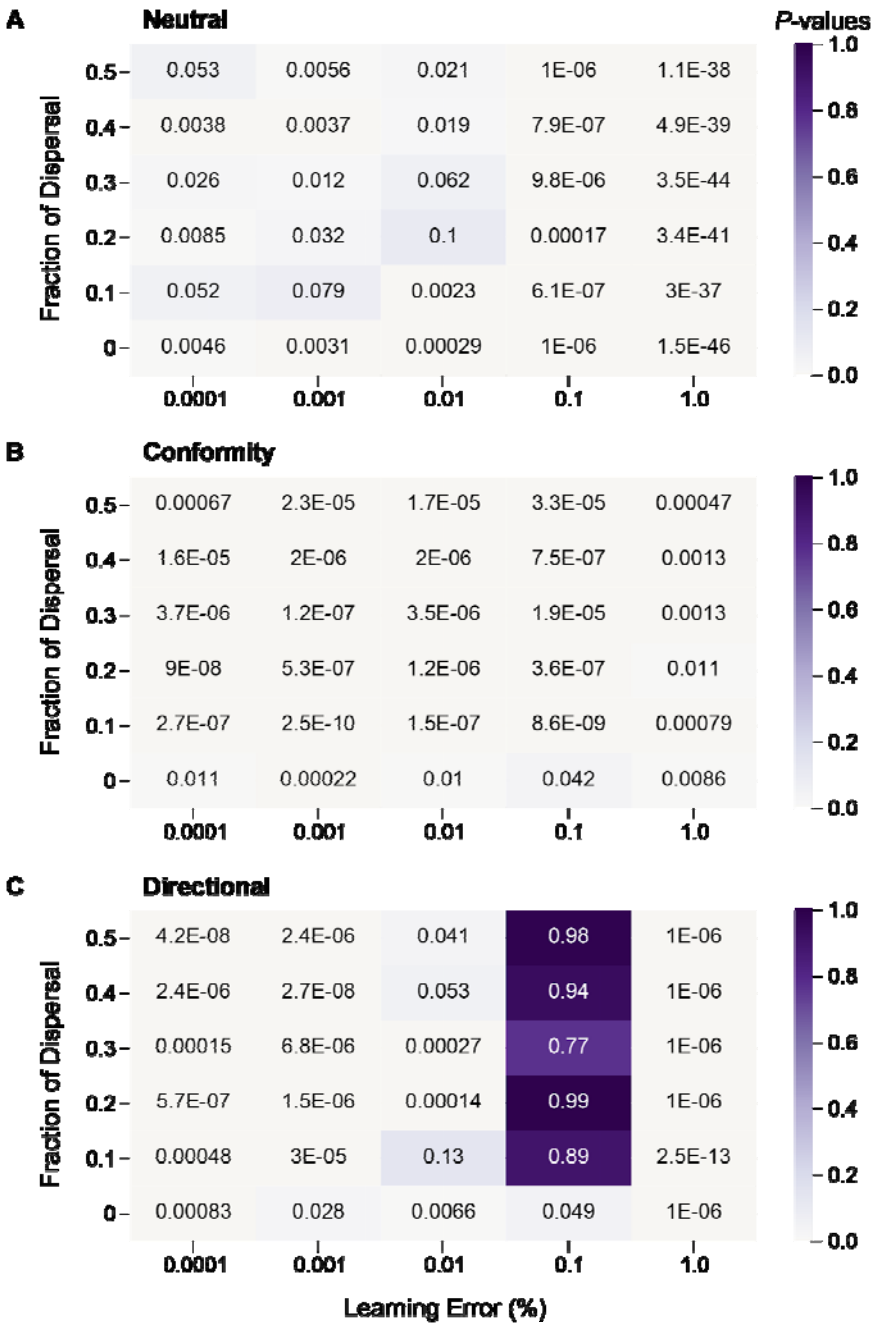

Figure 5. Statistical comparison of lifespan frequency spectra between song-learning models and empirical data for simulations with a range of dispersal fractions and learning-error rates. *P*-values for Fisher's exact tests in which the null hypothesis is that the binned lifespan frequency spectrum of empirical data and the simulated data are drawn from the same distribution. (A) Some simulations with neutral learning, territory dispersal, and low error in learning (≤0.01%) could not be distinguished from the empirical data ($P>0.05$). (B) All simulations with conformity bias differed significantly from the empirical data ($P<0.05$). (C) All simulations with directional learning and 0.1% learning error were indistinguishable from the empirical data except when no territory dispersal was allowed. Simulations with directional learning, 0.01% learning error, and either 0.4 or 0.1 dispersal fraction also emulated the empirical data.

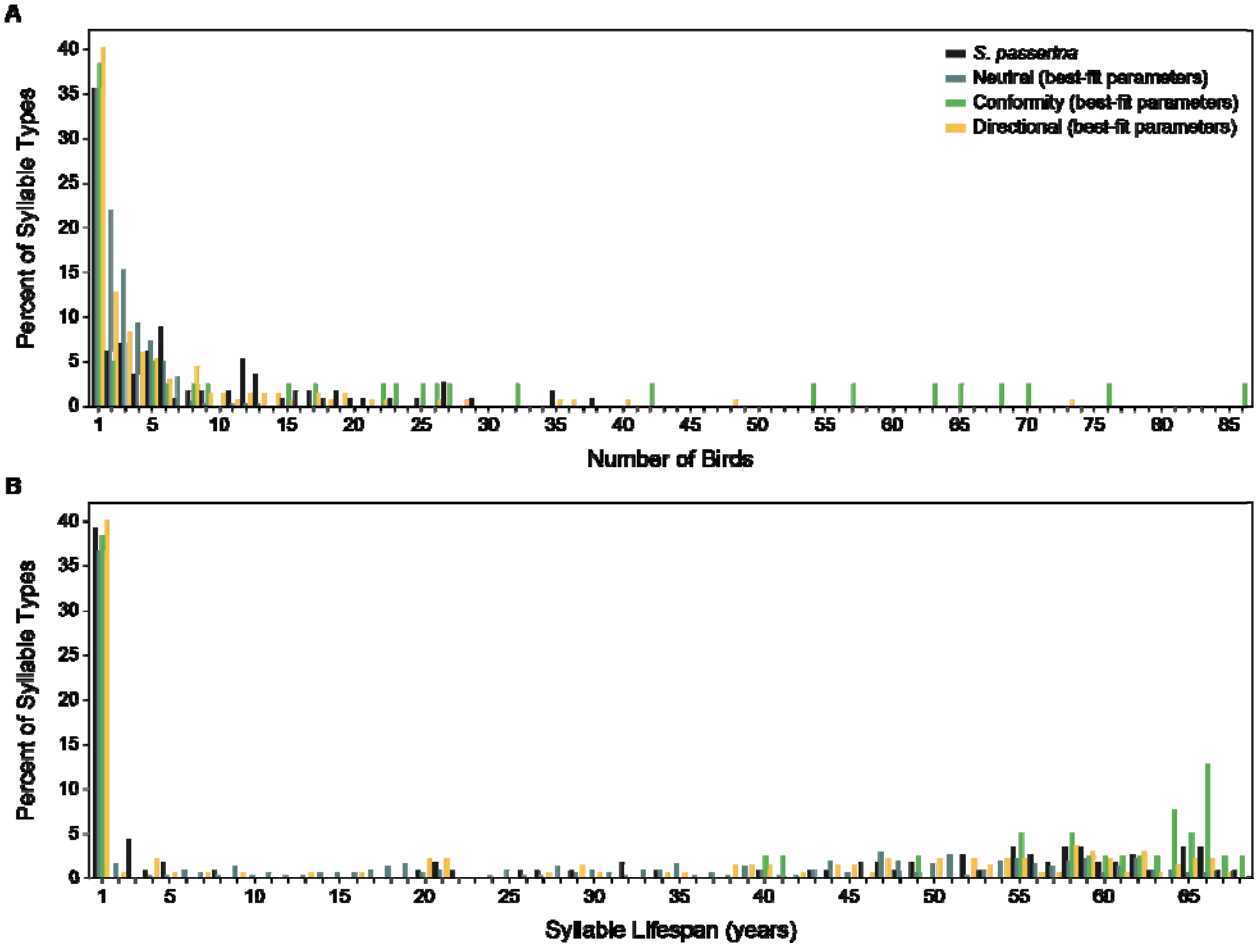

Figure 6. Comparison of syllable frequency spectra and syllable lifespan spectra between empirical data and samples from best-fit models. (A) The percent of syllable types versus the frequency at which the syllable types occur in the population (e.g. the number of birds sampled with that syllable type) for the best-fit models of each of the three song-learning strategies: (blue) neutral tutor selection with 0.001% learning error and 0.1 dispersal fraction, (green) conformity bias (c=2) with 1.0% learning error and 0.2 dispersal fraction, and (yellow) directional selection with 0.1% learning error and 0.5 dispersal fraction. In each panel, the histogram from community-science data is also provided (black). (B) The percent of syllable types versus the syllable lifespans (calculated as the last year − the first year in which the syllable type was sampled) for the best-fit models of each of the song learning strategies.

Discussion

Here, we perform an analysis of chipping sparrow song recordings across nearly seven decades to identify long-term patterns. We construct a spatially explicit model of cultural transmission of chipping sparrow songs with different types of learning bias—neutral evolution (unbiased transmission), directional selection (favoring a certain characteristic of song), and conformity bias (favoring locally common songs). By comparing our empirical and simulated results, we find that only a directional model of selection can replicate the patterns of both syllable frequency and longevity produced by chipping sparrow song learning. In addition, our computational analyses agree with evidence from field research in finding that chipping sparrows have high-fidelity song learning (predicted copy-error on the order of 0.1%) and likely disperse to new territories after initial learning. We extend the use of computational approaches to cultural evolution (Youngblood, 2019) with techniques from population genetics and rapidly growing community-science data (Searfoss, Liu, et al., 2020) to assess cultural change and stability in birdsong. Community-science recordings provide broad spatiotemporal coverage of a species' range, resulting in a dataset in which temporal changes can be identified across the entire population. By comparing these rich datasets with the predictions of cultural evolutionary models, we were able to evaluate the possible strategies underlying the social transmission of song.

Past studies have examined the diversity in syllables within the chipping sparrow population. For example, in the 1950s, Borror classified chipping sparrow syllables into categories and further subdivided the 58 recordings into 28 syllable types, demonstrating great song diversity and few observations of each syllable type (Borror, 1959). In a later analysis, the syllables of 157 chipping sparrows from the Eastern United States were analyzed and placed into around 30 distinct syllable types by eye (Liu, 2001). With 820 songs, we identified 112 syllable types (**Appendix S1**). While our larger community-scientist-informed sampling is far smaller than the current chipping sparrow population—which is on the scale of hundreds of millions—our analysis contains syllables that exist for decades and captures variation in birdsong that could not be identified via field studies of a species with such a large range. Similarly, we cannot exclude the convergence of chipping sparrow songs causing syllables to appear identical by chance rather than common descent—a sort of cultural homoplasy—and can only note the high fidelity of learning from tutors (Liu & Kroodsma, 2006) and non-random geographic syllable

distributions (**Fig. S7**), (Searfoss, Liu, et al., 2020). These data have allowed us to explore trends in chipping sparrow song over time that will inform future studies of their song and of cultural evolution. Our results demonstrate that the diversity of chipping sparrow syllable types was not fully sampled in previous studies, and it is likely that other syllable types will be discovered as contributing song recordings to community-science databases becomes more widespread.

With our analysis of chipping sparrow syllables, we found that many syllable types appear to be rare and short-lived, whereas others are quite common and can persist for decades (**Fig. 2**). Further, we found evidence that some broad characteristics were associated with longer syllable lifespans. Buzz syllables tended to be long-lived whereas complex syllables tended to be short-lived, and songs with long-lived syllable types had more repetitions of shorter syllables, which would be consistent with predictions that songs with faster syllable repetitions might be favored in birds (Byers et al., 2010). Notably, this pattern of shorter and faster syllables being long-lived is geographically distributed: the distribution of short- versus long-lived syllables was independent of longitude (Wilcoxon rank-sum test, p=0.992) despite songs from Western U.S./Canada having more, shorter syllables on average than songs from Eastern U.S./Canada (Searfoss, Liu, et al., 2020). These results raise an important question: are these syllables common and long-lived because of neutral transmission, culturally favorable properties (i.e. certain syllables are inherently salient or associated with successful birds), or conformity bias (i.e. common syllables are preferred when learning song)?

Selectively neutral processes of song learning, such as unbiased learning of a song with a relatively high rate of error, are predicted to result in a simple pattern of syllable prevalence: most sampled syllable types would be sung by only one bird, fewer syllables would be sung by two birds, even fewer by three birds, and so on, until only a small handful of syllables might be sung by many birds (Slater, 1986). Slater observed this distribution of syllables in chaffinches: in a population of 36 chaffinches, most songs were sung by only one bird, but one song was sung by 22 birds. Further, he modeled the song-learning process with a simulation in which newly settled birds learned a random nearby song with some error; this simulation demonstrated that a neutral learning process with a predictable rate of copy-error was sufficient to replicate the observed distribution of chaffinch syllables. A similar pattern is regularly observed in genetic data in a stable population in the absence of selection pressures: most genotypes are rare, and few genotypes predominate (Nielsen, 2005). Thus, for both genotypes and song types, one does

not need to invoke selection pressures to explain a pattern in which one or very few types are widespread but most are observed only once. In contrast, our results suggest that chipping sparrow song is not evolving neutrally: there are more frequently occurring syllables than would be expected from a neutral model of song evolution (**Fig. 6A**). Our results suggest that the evolutionary pressures on syllable types in chipping sparrows are not neutral, and that certain properties of a song could be favored by chipping sparrows.

Our 70-year sampling timespan gave us the opportunity to analyze the observed longevity of chipping sparrow syllable types alongside their frequency of occurrence. We find that most rare syllables are also short-lived and most common syllables exist for decades (**Fig. 2**). While this distribution of syllable lifespans can be replicated by both neutral learning and directional selection, (**Fig. 6B**), only directional selection simultaneously produces similar rates of syllable occurrence (**Fig. 6A**). Together, the syllable frequency and lifespan spectra appear to indicate a non-conformist transmission bias in chipping sparrows. Lachlan *et al.* demonstrated a model of conformity bias in swamp sparrows that leads to a qualitatively similar lifespan distribution as ours, in which certain syllables tend to be longer-lived, even predicting that these syllables are maintained for upwards of 500 years (Lachlan et al., 2018). In contrast, we do not find strong support for conformity-biased song learning in chipping sparrows. Instead, our model of non-neutral song learning strategies—directional selection and conformity bias—support directional selection as the most likely source of the observed patterns in lifespan and occurrence of chipping sparrow syllables (**Fig. 4 and 5**). Our results can be compared to those in house finches, which demonstrated content bias—certain syllables were more likely to be learned because of their acoustic features, not because of their frequency of occurrence in the population (Youngblood & Lahti, 2022). In chipping sparrows, since only one syllable is learned per bird, we track potential selection on the acoustic features themselves to test whether directional selection favoring the learning of faster songs or more extreme values of a syllable feature can explain the observed syllable distributions in the empirical song data.

While our best-fit model of directional selection (positive directional selection on song rate, with a learning error of 0.1% and a dispersal fraction of 0.5) reproduced frequency spectra of syllable-types and syllable lifespans representative of our empirical data, this model does not accurately describe all features of chipping sparrow song. The range of song rates (~36.5–40 syllables per second) observed in the entire simulated population (before sampling) is much higher and

narrower than that observed in the chipping sparrow population (~5–38 syllables per second) (Searfoss, Liu, et al., 2020). This supports our intuition that syllable rate is not under directional selection on its own, since we previously observed a wide range of syllable rates in chipping sparrow songs that persisted over many years in nature (Searfoss, Liu, et al., 2020). This divergence between our model and community-science data suggests that more complex evolutionary pressures or cultural transmission biases might be at play, such as performance tradeoffs or differing selection pressures for tutor selection compared to mate choice, which could be integrated into the model for future research. One such explanation is a hypothesized performance tradeoff in chipping sparrow song between frequency bandwidth and the rate of syllable delivery (Podos, 1996, 1997); due to physiological constraints, a high-performance song might have a large frequency bandwidth but slower syllable rate or a faster syllable rate but reduced frequency bandwidth. In this case, directional selection is likely occurring on multiple axes and operating on both traits at once. If there is a tradeoff between two song parameters under selection, we would not expect to see tight distributions of a single syllable parameter (syllable rate or frequency modulation) as there will be a boundary along which the properties are balanced. Furthermore, although long-lived syllables had significantly shorter durations overall, we find a wide distribution of mean syllable durations, implying that both long and short syllables can persist over time.

While only models of directional selection resemble the lifespan and occurrence patterns from our empirical data, it is difficult to determine whether a certain song feature is being favored by directional selection without corresponding field experiments. We framed directional tutor selection in our model such that a parameter was the determining factor for the learned syllable type. As a result, our simulations only suggest that a song characteristic could be under directional selection, not that syllable rate in particular is under selection. To test which song features might be favored in learning and tutor selection, we propose playback experiments to determine whether there is a difference in juveniles' responses to recordings of different song rates, frequency bandwidths, and syllable complexities as well as to historical versus current song recordings (as in (Derryberry, 2007)). These results could then be compared to females' responses to determine whether tutor selection and mate choice are favoring similar song characteristics. Ideally, this would be carried out at multiple locations across the chipping sparrow's range, given the geographical patterns observed earlier. We aim to extend this model

to incorporate content bias more broadly, allowing selection on the syllables themselves rather than aspects of syllable production such as syllable rate, as this may better align with empirical data in which buzz syllable types are long-lived. To execute this extension to the model, it would be necessary to create a measure of syllable quality to drive tutor choice.

The question of whether directional selection plays a strong role in chipping sparrow song evolution has been a topic of debate in the literature (Akçay & Beecher, 2015; Goodwin & Podos, 2014, 2015; Kroodsma, 2017). In chipping sparrows, syllable rate in particular has been shown to correlate with displays of territory defense: "birds responded more vigorously when simulated intruders sang the more difficult to produce, faster songs, and also when there was a stronger disparity between intruder trill rates and their own" (Goodwin & Podos, 2014). Some evidence suggests that chipping sparrows are subject to a performance constraint, specifically one in which there is a tradeoff between large sweeps in frequency (Hz) and high rate of syllable delivery (Goodwin & Podos, 2014; Podos, 1997). It is proposed that physiological constraints contribute to this balance in song performance (Podos, 1996, 1997). Further studies have suggested that this performance tradeoff between frequency bandwidth and syllable rate could be meaningful: under the stress of competing with the noise of an urban environment, chipping sparrows under-performed, singing "twice as far below the trade-off frontier" than those in less-noisy environments (Davidson et al., 2017). Kroodsma presents a contrary view based on results from field studies that demonstrate juvenile chipping sparrows imitate their neighbors with great success, and suggests that physiological constraints do not inhibit juveniles from performing fast songs (Kroodsma, 2017). Instead, he suggests that their performance is determined by that of their neighbor. Our analysis could potentially reconcile the performance-driven and neighbor-dependent hypotheses. Our results suggest that chipping sparrows might *select* which of their neighbors will be a tutor based on some aspect of their song performance: certain tutors may be preferred for reasons other than the how frequently the song is heard in the local population. The distributions of syllable types and syllable lifespans produced by the model with directional selection are more similar to those of the chipping sparrow population than the neutral process of random song matching. In nature, juvenile chipping sparrows sing several neighbors' songs before selecting a final song, which suggests that a selective process is taking place (Liu & Nottebohm, 2007). This selective process, along with juveniles' modification of their song during the plastic phase of song learning, have been proposed to play a part in determining their

final song (Podos, 2017). The extent to which these potential selective processes affect song learning is controversial, suggesting that the combination of song data with learning simulations could shed light on the evolutionary dynamics of vocal learning.

We demonstrate that coupling an agent-based model with analyses of community-science data is a tool to better understand the evolution of behavior in a songbird. By developing a model of cultural transmission of song and comparing patterns produced by three learning strategies to those found in our empirical data, we demonstrate that the observed frequencies and lifespans of chipping sparrow syllable types show evidence of transmission bias. In particular, our results are indicative of a song-learning strategy in which tutor selection is under directional pressure in the chipping sparrow population, with juveniles preferentially selecting tutors with certain song features, and in which copy-errors or invention rates are quite low, on the order of 0.1%. While our simulation does not specify which syllable or song features are specifically under selection, we find that neutral song-learning processes and conformity-biased learning, both of which have been observed in other species, cannot explain the distribution of songs observed in chipping sparrows (Lachlan et al., 2018; Slater, 1986). Despite their deceptively simple song, our computational analyses suggest that chipping sparrows appear to be exhibiting learning biases and complex cultural transmission patterns, warranting further investigation in the field.

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Author Contributions:
N.C. and A.M.S conceived and designed the project with input from Y.P. Y.P and A.M.S. coded the model and conducted all analyses with assistance from N.C. Y.P. and A.M.S and N.C. wrote the manuscript.

Competing Interest Statement:
The authors declare no competing interests.

Data and materials availability:

All code is available at https://github.com/CreanzaLab/ChippingSparrowCulturalEvolutionModel. For the catalog numbers, database, recordist, URL, and license for the 820 song files, see **Supplementary Data Table 1**. For the metadata including recording latitudes and longitudes and the 8 song features (all log transformed except mean stereotypy of repeated syllables and the standard deviation of note frequency modulation), see **Supplementary Data Table 2**.

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