



RESEARCH ARTICLE

Four decades of cultural evolution in House Finch songs

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ABSTRACT

Bird song is the primary animal model system for cultural evolution. Longitudinal studies of bird song across many generations can provide insights into patterns and mechanisms of change in socially transmitted traits. In this study, we conducted a comparative analysis of songs of the House Finch (*Haemorrhous mexicanus*) across an interval of 37 years (in 1975 and in 2012). Recordings from both years were collected in western Long Island, New York, which is thought to be the initial site of introduction of the House Finch around 1940 from the West Coast. Song types experienced a complete turnover during this period, although half of the syllable types were represented in both samples. Song length, frequency bandwidth and several other spectrographic features were the same in both years, and no structural features predicted recurrence of individual syllables. Consistent with the fact that our study population expanded substantially following a cultural founder effect, song and syllable sharing and similarity between individuals were lower in 2012 than in 1975, reflecting an increase in song diversity at the population level. However, in the more recent sample individual songs had fewer syllables, and were sung with less sequence stereotypy across renditions than in the earlier sample. Syllable prevalence in 2012 was associated both with complexity (as gauged by frequency excursion) and increased minimum frequency. Thus, over nearly 4 decades, Eastern House Finch songs remained structurally similar at the whole-song level, diversified between individuals, but became simpler and less consistent within an individual.

Keywords: bird song, *Carpodacus*, cultural evolution, FinchCatcher, *Haemorrhous*, House Finch, relaxed selection, syllable

Cuatro décadas de evolución cultural en los cantos de *Haemorrhous mexicanus*

RESUMEN

El canto de las aves es el principal sistema de modelo animal para la evolución cultural. Los estudios longitudinales del canto de las aves a través de varias generaciones pueden brindar información sobre los patrones y los mecanismos de cambio en rasgos transmitidos socialmente. En este estudio, realizamos un análisis comparativo de los cantos de *Haemorrhous mexicanus* a lo largo de un intervalo de 37 años (en 1975 y en 2012). Se usaron grabaciones de ambos años provenientes del oeste de Long Island, Nueva York, el cual se piensa que es el sitio inicial de introducción de *H. mexicanus* alrededor de 1940 desde la Costa Oeste. Los tipos de cantos experimentaron un recambio completo durante este período, aunque la mitad de los tipos de sílabas estuvieron representados en ambas muestras. La longitud, la frecuencia del ancho de banda y varias otras características espectrográficas del canto fueron las mismas en ambos años, y ninguna característica estructural predijo la recurrencia de las sílabas individuales. De modo consistente con el hecho de que nuestra población de estudio se expandió sustancialmente siguiendo un efecto fundador cultural, los cantos y las sílabas compartidas y la similitud entre individuos fueron más bajas en 2012 que en 1975, reflejando un aumento en la diversidad de cantos a nivel poblacional. Sin embargo, en la muestra más reciente, los cantos individuales tuvieron menos sílabas y éstas fueron cantadas con secuencias menos estereotipadas en las representaciones, que en la muestra más temprana. La prevalencia de sílabas en 2012 estuvo asociada tanto con la complejidad (según la frecuencia de la excursión) como con un aumento de la frecuencia mínima. Por ende, a lo largo de casi cuatro décadas, los cantos de los individuos de *Haemorrhous mexicanus* del este permanecieron estructuralmente similares a nivel de canto completo, se diversificaron entre individuos, pero se volvieron más simples y menos consistentes dentro de un mismo individuo.

Palabras clave: canto de las aves, *Carpodacus*, evolución cultural, FinchCatcher, *Haemorrhous*, selección relajada, sílaba

INTRODUCTION

Understanding the origins and maintenance of acoustic diversity is fundamentally important in the study of animal communication (Podos and Warren 2007, Campbell et al. 2010). In birds that learn their songs, acoustic variation is attributed mostly to events occurring during the process of vocal imitation. Recent studies on bird song focus on the lability of song structure through time (Janes and Ryker 2013, Williams et al. 2013, Janney et al. 2016, Leon et al. 2015). Temporal change in bird song structure between individuals is often considered to be analogous to genetic evolution (Munding 1982, Podos et al. 2004). Novel songs or song elements may result from immigration, learning “errors” or innovations, and more temporary improvisations; and these novel patterns of vocal structure can be transmitted by imitation to younger conspecifics. The accumulation of such changes through time in a population qualifies as cultural evolution (Janik and Slater 2000, Leadbeater and Chittka 2007, Rapaport and Brown 2008, Richerson and Boyd 2008). The forces that act upon bird song variation can essentially be viewed as the combined effects of drift and selection (Payne 1981, Baker and Cunningham 1985), including cultural drift (Lemon 1975), genetic drift (Podos et al. 2004), cultural selection (Slabbekoorn and Smith 2002) and natural selection (Nowicki et al. 1992), including sexual selection (Panhuis et al. 2001).

The few longitudinal studies of bird song have provided some of the most valuable insights into patterns of cultural evolution; in some cases such patterns have even indicated process (Payne 1996, Derryberry 2009, Byers et al. 2010, Williams et al. 2013). We contribute to this line of research with a comparative analysis of song in the House Finch (*Haemorrhous mexicanus*) between 1975 and 2012 on Long Island, New York. The House Finch is a non-territorial and socially monogamous passerine (Hill 1993b). It was introduced from its native range in western North America to Long Island, New York, in the early 1940s (Elliott and Arbib 1953), and has since become abundant in the East and expanded its range to the point of overlapping with the western population (National Audubon Society 2010). The male House Finch song is a long, rambling, hoarse warble composed of a series of short notes, or syllables (Thompson 1960, Munding 1975, Bitterbaum and Baptista 1979, Pytte 1997). Typically, the large syllable repertoire of an individual is divided into 2 or more song types, or themes, delivered with some stereotypy (Munding 1975, Pytte 1997, Tracy and Baker 1999). As House Finches are non-territorial, male song functions primarily in mate attraction and retention. Initial inquiries into whether song structure (e.g., complexity) is subject to sexual selection have yielded mixed results (Bitterbaum and Baptista 1979, Nolan and Hill 2004, Mennill et al. 2006); and species recognition might be a neglected function (Hill 2015).

Distinct song dialects with sharp boundaries were reported previously in Westchester County, New York (~25 km away from this study’s focal area) (Munding 1975). Within a given dialect area, the songs of the local population were stable over a short period of time (Munding 1975). However, this dialect variation might not be well maintained through time. For instance, the boundaries could erode as a result of the increased migratory activity and greater dispersal distance that have been observed in Eastern House Finches (Able and Belthoff 1998, Paradis et al. 1998), both of which factors would in turn complicate any female strategy of choosing local males based on their songs. Moreover, genetic studies (Wang et al. 2003) have shown that the Eastern population has neutralized the bottleneck effects of the founder event and recovered a high degree of genetic diversity. Data from the North American Breeding Bird Survey and Audubon’s Christmas Bird Count show that the House Finch population in New York grew substantially during the 1980s and early 1990s, but contracted nearly as drastically over the next 10 years (National Audubon Society 2010, Pardieck et al. 2016), owing to a conjunctivitis pandemic (Hawley et al. 2006). Any of these changes might have altered song patterns in the population, including possibly changing or disrupting the dialects that were present previously.

We explored the changes in House Finch song structure and sharing that have occurred across 4 decades during this expansion period following an introduction event. We predicted that song traditions and structure would not be preserved through time, but that contemporary songs would exhibit greater diversity in terms of song and syllable repertoires as the population size and therefore the variety of available acoustic information to a developing House Finch increased (Pytte 1997). The emergence of seasonal migratory activity and increase in dispersal distance also lead to this prediction. Since we divided songs into their component syllables for our analyses, we also investigated whether different levels of song organization (syllables vs. whole songs) exhibit heterogeneity in evolutionary rate or pattern (Catchpole and Slater 2008). Finally, in the light of past work on sexual selection in this species, we investigated whether a putative history of selection for longer or more complex songs has had a long-term effect on these parameters.

METHODS

Recording Equipment and Files

In 1975, P.C.M. used a Nagra III reel-to-reel tape recorder (9.5 cm s⁻¹) and Sennheiser 804 shotgun microphone to make field recordings. In 2013, the Cornell Laboratory of Ornithology’s Macaulay Library of Natural Sounds cleaned and repaired these tapes, and converted the entire audio

stream of the recordings into an uncompressed digital form (PCM 32-bit float, 96 kHz sample rate) using equipment that corrects for tape speed and other irregularities. We resampled these files to 16-bit before analysis. In 2012, F.C.G. made field recordings (PCM 16-bit, 44 kHz) with a Marantz PD661 solid state recorder and an ME66 Sennheiser shotgun microphone with K6 power supply.

Study Area

House Finches were recorded in western Long Island, New York, in 1975 (by P.C.M.) and in 2012 (by F.C.G.). The songs from 1975 were recorded in an area roughly 15 km (north to south) by 42 km (east to west): from Freeport (40.584°N, 73.560°W) in the south to Bay Shore (40.717°N, 73.243°W) in the north, and from Atlantic Beach West (40.588°N, 73.741°W) in the west to Bay Shore (40.717°N, 73.243°W)

in the east (Figure 1A). The songs from 2012 were recorded in an area roughly 34 km (north to south) by 40 km (east to west): from Long Beach in the south (40.589°N, 73.667°W) to Port Washington in the north (40.895°N, 73.635°W), and from Bay Ridge in the west (40.631°N, 74.036°W) to East Meadow in the east (40.729°N, 73.566°W). The overlap between these 2 study areas is ~10 km (north to south) by 15 km (east to west), as shown by the ellipse in Figure 1A. In both 1975 and 2012, the recordists (P.C.M. and F.C.G., respectively) attempted to record as many House Finches in western Long Island as possible. The distribution of House Finches was patchy in both years, and the locations where they were encountered were different, as represented in the geographic spread of our data. Specifically, the area from which recordings were collected was roughly twice as large for the 2012 sample as it was for the 1975

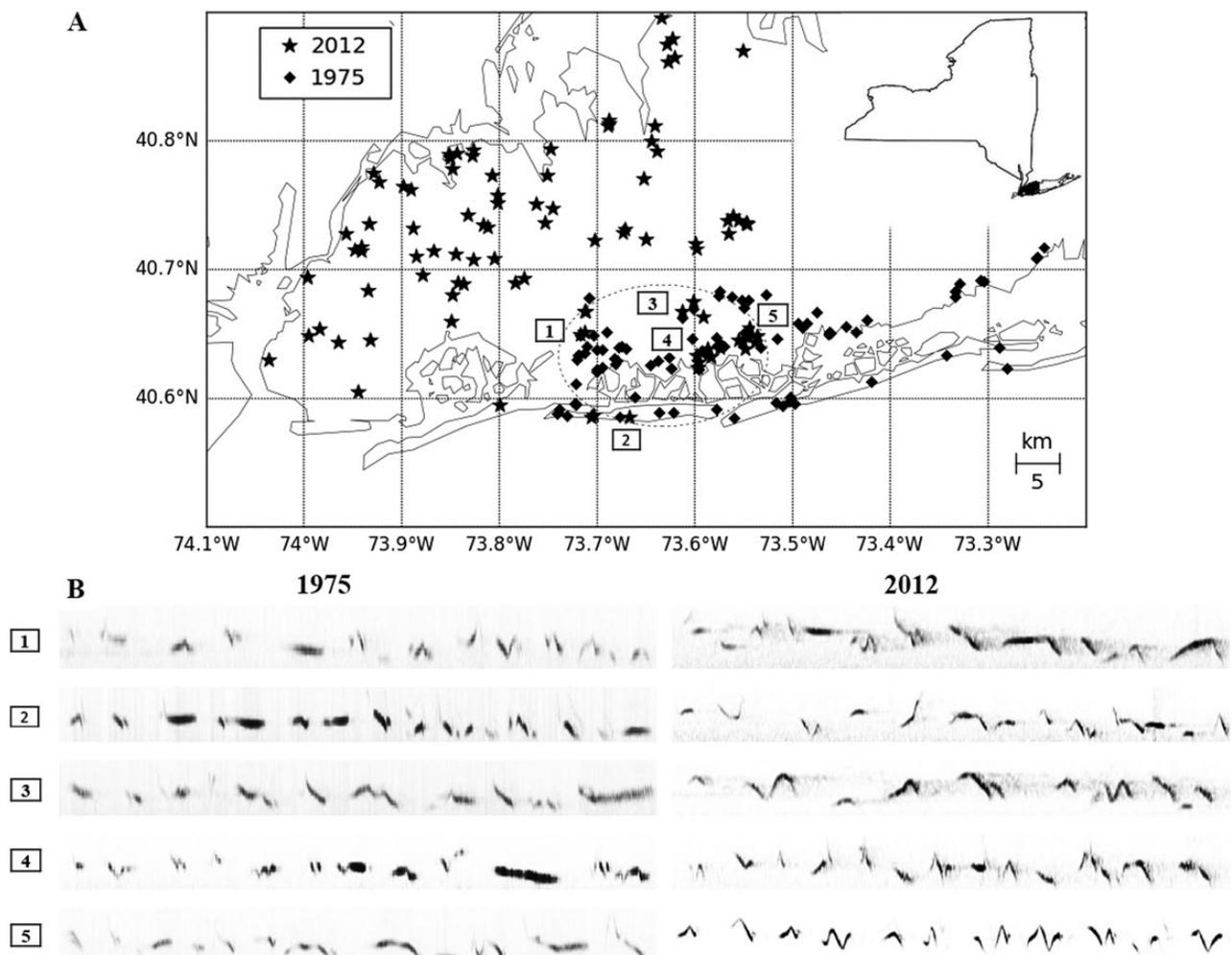


FIGURE 1. Study area and song examples. **(A)** House Finch recording locations, including 94 individuals (diamonds) from 1975, and 96 individuals (stars) from 2012, in western Long Island, New York. The samples overlap in the area designated by the ellipse. **(B)** Sample spectrograms of prominent song types of individuals in 5 locations where the song sample includes recordings from both years. (Locality: latitudes, longitudes): (1) Valley Stream: 40.678142°N, -73.708954°W; (2) Long Beach: 40.585620°N, -73.677043°W; (3) Freeport: 40.663354°N, -73.591043°W; (4) Baldwin: 40.633516°N, -73.598548°W; (5) Merrick: 40.644884°N, -73.552610°W.

sample. Such differences can confound an interpretation of differences between samples. However, we have evidence that no such confound occurred here: variation in songs and syllables was high even in a single geographical spot and across short distances (<10 km), but the variation does not significantly increase at larger distances within our sample (Ju 2015). Still, to test the effective equivalence of our samples another way, we reanalyzed a subsample of our data, restricting our comparison to individuals in each year that were recorded within 1 km of individuals recorded in the other year. The House Finch population in 1975 and 2012 was within the same order of magnitude in density before and after a spike in abundance. The 2012 population was 3 times the density of that of 1975 according to the North American Breeding Survey (Pardieck et al. 2016). The 2 populations were approximately the same density according to the Christmas Bird Count (National Audubon Society 2010).

Song Samples

The songs were recorded in the field during April–July in 1975 and in 2012. Individuals were recorded until they stopped singing or flew away. To reduce the chance of recording the same bird twice, we took several precautions, following Munding (1975). Each site was visited only once. Within a site, only one individual was recorded within a 160 m radius. We excluded recordings from the 1975 sample that contained multiple song bouts, in case they might have represented more than one individual.

Acoustic recordings of focal animals in natural or semi-natural environments are frequently accompanied by a variety of non-focal sounds (i.e. noise). This is of concern in our study because of the urban and suburban nature of our field site, and the possibility that noise has changed during the interim between our sample years. Masking that occurred in our sample owing to background noise should be considered as a detection issue, and recognition of signals depends substantially on the signal-to-noise ratio. In general, the level of noise is higher in our 2012 sample than it was in our 1975 sample (Figure 2). Thus, we examined the signal-to-noise ratio in the frequency bands (2,000–6,000 Hz) in which House Finch signals were detected (with FinchCatcher software, Ju 2016). The minimum ratio is 2 for almost all analyzed songs. Thus, masking by noise is unlikely to have confounded our analyses.

The objectives of this study were better served by collecting songs from a high number of individuals rather than requiring complete repertoires and thus decreasing the resolution of geographical coverage. Still, we wished to exclude individuals whose bouts were unlikely to represent a complete repertoire. To achieve this balance, we decided on a song sample threshold of 75%, such that we would analyze the recordings only of those birds from which we recorded enough songs to permit the retrieval of

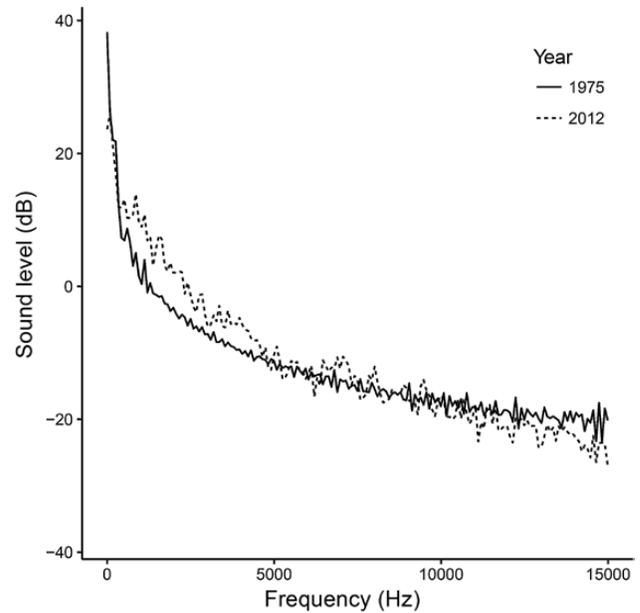


FIGURE 2. Background noise in song recordings from 1975 and 2012. Environmental noise spectra of sampling sites from the overlapping areas.

~75% or more of the full syllable repertoire. We generated this estimate for the population by plotting the cumulative number of syllable types detected in an individual's song bout against the n^{th} song sampled for this individual, for 10 representative individuals from the 2012 sample. We numbered birds in random order and calculated the cumulative proportion. This randomization procedure was iterated 10 times and we averaged the result for each bird. The 75% threshold was reached at 5 songs (Figure 3A), similar to birds sampled from 2 other Eastern populations: from Wisconsin in 1992 (Pytte 1997) and from Iowa in 2003 (Tracy et al. 2009). Because we only had recordings from 2 time points, our analyses of comparisons “between years” refer to comparisons of recordings from 1975 and from 2012, with no intervening data.

Identifying Song and Syllable Types

Syllable types. A syllable is defined here as a contiguous signal separated from others within a song by at least 20 ms (Munding 1975). We discovered through a pilot study that cataloguing House Finch syllable types (including between individuals, and without reference to sequence) is not amenable to an approach based on visual inspection of song spectrograms. Variation in syllable structure in the populations we examined appears to be either nearly continuous or represents enormous diversity, which would likely result in subjectivity in visual classification and low reproducibility among different investigators. We therefore based syllable classification on an automated similarity measurement procedure (FinchCatcher, Ju 2016) that

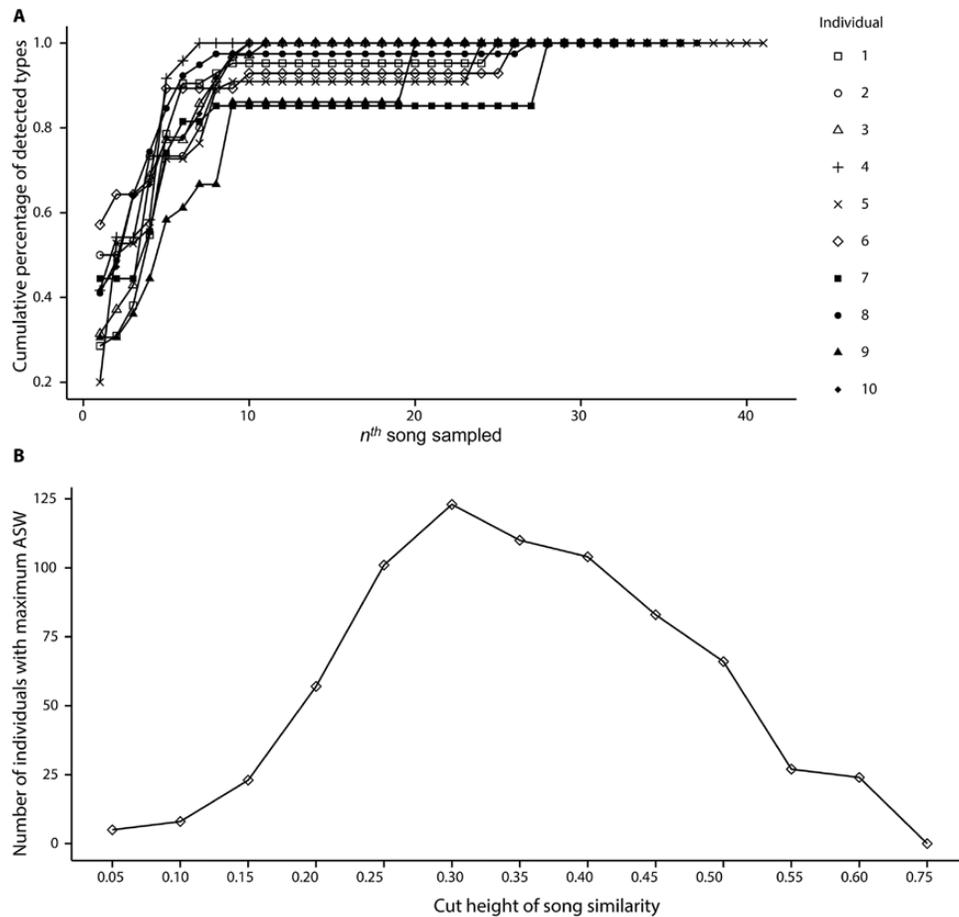


FIGURE 3. Criteria for selection of individuals and songs. **(A)** Cumulative percentage of syllable types detected by n^{th} song. The cumulative percentage of syllable types is plotted against the n^{th} song sampled for 10 different birds with large song samples. On average 76% (range: 61–90%) of an individual's syllable repertoire was captured in the first 5 songs. **(B)** Assessment of similarity criterion to define a song type. A line plot demonstrates how a given cut height applied to the dendrogram of all songs in each individual's repertoire influences the number of individuals that reach the maximum average silhouette width (ASW) score, a measure of effectiveness in separating songs into clusters. Maximum ASW indicates the best clustering quality and the optimal number of clusters. The peak for the combined dataset is at $x = 0.3$ and $y = 123$. Thus, by a similarity criterion of $1 - 0.3 = 0.7$, cluster analysis can optimally separate song types within the repertoires of the maximum number of individuals.

compares a number of shape-related acoustic features to generate overall similarity scores between syllables (Table 1; Ju and Lahti 2016), constructs a dendrogram by cluster analysis and classifies syllable types by “dynamic tree cut” (Langfelder et al. 2008). A typical or static tree cut would identify syllable types simply by drawing a line across the entire dendrogram, regardless of the density of the groupings or patterns of similarity across the tree. Dynamic tree cut, on the other hand, identifies syllable types in a bottom-up (tips to base) manner, in 2 stages. First, it respects the hierarchical structure of the dendrogram and detects groups of syllables with especially high similarity by applying a stringent threshold (within-type cutoff). Second, it assigns each of the remaining syllables to the nearest cluster (between-type cutoff) defined in the first stage, based on dissimilarity distance.

In this stage, the dendrogram hierarchy is ignored and only the dissimilarity information is used. Our syllables exhibited variation that was continuous or nearly so, and thus was not amenable to typical ways of determining the optimal number of clusters (Anderson 2008). Thus, we determined the optimal tree cut parameters by checking their performance on a subset of our data as follows. Using 30 manually identified syllable types, we estimated the distribution of within-type variance (i.e. the average of all pairwise dissimilarities between objects within a type) and between-type variance (i.e. the average of all pairwise dissimilarities between objects between the 2 nearest types in the dendrogram). We then determined the within-type threshold as the largest value for within-type variance that fell outside of the distribution of between-type variance, and the between-type threshold

TABLE 1. Measured features of House Finch syllable and song profiles.

Variables	Description
Average frequency (Hz) = AF	Mean frequency of a syllable/song
Start frequency (Hz) = SF	Frequency at the beginning of a syllable/song
End frequency (Hz) = EF	Frequency at the end of a syllable/song
Highest frequency (Hz) = HF	Maximum frequency of a syllable/song
Lowest frequency (Hz) = LF	Minimum frequency of a syllable/song
Bandwidth (Hz) = BW	Difference between maximum and minimum frequencies of a syllable/song
Frequency-time excursion length (cumulative Δ kHz per s) = FL	Arc length (on a per-time basis) of a syllable/song, treated as continuous by connecting amplitude peaks in the spectrogram, using line segments to create a polygonal path
Duration (s) = DU	Time duration of a syllable/song
Changes in concavity (per s) = CO	Number of changes (on a per-time basis) in the sign of the slope of frequency change throughout a syllable/song

as the value that optimized between the sensitivity and the specificity of classifying the 30 test syllable types in a Receiver Operating Characteristic (ROC) curve. The results of classification by dynamic tree cut were manually proofread. Those syllables whose recording quality was poor, or that were represented as lone representatives of their types in the classification, were excluded.

We combined all syllables from both datasets for classification. Such pooling enabled us to compare population-wide trends in syllable and song structure between 1975 and 2012. However, during such a temporal interval, or even within a geographical area during a single time period, phonologically similar syllables can arise independently. Such instances would represent homoplasy if incorporated into a phylogenetic tree. Thus, the syllable type dendrogram cannot be assumed to reflect the pattern of cultural evolutionary history. In this sense we are performing a phenetic analysis of syllable structure, and the cluster analysis must be interpreted only structurally and not historically. Classification by the automated similarity analysis in this study was highly concordant with analysis by a blind visual inspection of sound spectrograms (Ju 2015).

Song types. House Finch song types are generally distinctive (see below). Visual inspection has proved a successful way to yield reproducible song type classification among different observers (Munding 1982, Tracy and Baker 1999). Nevertheless, quantitative measurement of similarity between different song types would be impossible by this approach. To address this issue, we transformed each song into a string, each element of which indicates a distinct syllable type as defined by the syllable classification above. Then we calculated the edit (Levenshtein) distance (Ristad and Yianilos 1998) between each pair of song sequences, by which the minimum number of operations required to transform one string into the other was returned. Lastly, the similarity score of the pair of song sequences was estimated as follows:

$$S = \frac{1 - (E - D)}{L} \quad (1)$$

where E is the edit distance (the minimum number of operations required to transform one sequence into the other) between 2 sequences, D is the difference in lengths (numbers of syllable) between 2 songs, and L is the length of the shorter of the 2 songs in terms of the numbers of syllables. This equation adjusts similarity scores to account for difference in lengths of songs in comparison, to ensure that an incomplete song would not be misclassified as a different song type from the same song completed.

Traditionally, researchers have used a 75% similarity criterion to define distinct song types, whereby at least 75% of song elements must be shared and arranged in the same order between songs to be classified as the same song type (Munding 1982, Tracy and Baker 1999). While this threshold has proven useful to eliminate obvious misclassifications, it is inevitably somewhat arbitrary, and the resulting clusters might not reflect natural song type categories (Pytte 1997). To deal with this problem, we clustered song sequences within an individual's repertoire using a single-linkage hierarchical clustering algorithm (nearest neighbor clustering) and measured the Global Silhouette Index (Rousseeuw 1987) at different cut heights (0.05–0.75 at an interval of 0.05) to detect natural categories in the data. Average silhouette width (ASW) is a measure of how appropriately the data has been clustered. The higher the score of ASW, the better the separation among clusters. Therefore, the maximum ASW indicates the best clustering quality and the optimal number of clusters. A range of cut heights might result in the same best classification result (the highest averaged silhouette width) for an individual. For example, 2 different syllable types with between-type similarity scores <0.2 and with-type similarity scores >0.75 would be separated by any value of cut height from 0.2–0.75. For our data, the results of this analysis suggested that a cut height of 0.3 (corresponding to a similarity criterion of 0.7) is the optimally robust measure most likely to generate natural groups of songs (Figure 3B). Hence, we considered pairs of songs to be the same type if $S > 0.7$, where S is similarity in the equation above.

Syllable and Song Sequence Sharing

Song sequence sharing. We calculated the sequence similarity scores (S) of all pairwise song sequence comparisons between each pair of individuals. Since song sequence sharing is a rare occurrence at this spatial scale (see Results), we used the highest sequence similarity scores between individuals (i.e. the most similar of their song sequences) as the measure of song sequence similarity between individuals.

Syllable sharing. To determine the degree of syllable sharing among birds, we used Jaccard's similarity coefficient (S_j), a method commonly used to measure similarity for binary data (presence/absence) in acoustic analysis (Krebs 1989, Podos et al. 1992). S_j was calculated initially as follows:

$$S_j = \frac{a}{a + b + c} \quad (2)$$

where a is the number of shared syllables in both individual repertoires, b is the number of unique syllables in the first individual and c is the number of unique syllables in the second individual. The similarity score ranges from 0 (no sharing) to 1 (complete sharing). However, our data include unequal syllable repertoire sizes between individuals, and so the maximum possible S_j for the comparison would be necessarily <1 . To adjust for differences in repertoire size, we adjusted S_j as follows:

$$S_j(\text{adj}) = \frac{a}{a + b + c - d} \quad (3)$$

where d is the difference in detected repertoire size between individuals (Tracy and Baker 1999). We calculated $S_j(\text{adj})$ for each individual as the mean of comparisons with all other individuals ($n_{1975} = 4,371$; $n_{2012} = 4,560$ and $n_{1975 \text{ vs. } 2012} = 9,024$).

Differences between 1975 and 2012

Song sequence consistency. We consider song type sequence consistency (STSC) as the degree of stereotypy of a song type, i.e. the similarity among renditions of the same song type by the same individual. In order to evaluate the minimum number of renditions that would permit a precise assessment of consistency, we selected 20 song types that were represented by more than 15 renditions from a single bird, and randomly selected X songs from each type, where X ranged from 2 to 8. For each of these song types we calculated scores of STSC for each partial set of renditions (see the next paragraph for this scoring) and then compared the distribution of these scores with that of the scores based on the full set of renditions (>15) from these 20 song types using the Wilcoxon signed-rank test. This procedure was repeated 100 times for each X . The minimum required number of renditions was the smallest X at which the chance of yielding a significant difference between distributions of scores based

on subsampled and full sets of renditions is $<5\%$. This analysis showed that the distribution of scores for within-type consistency of simulated data at the sample size of 6 renditions has a probability of only 3% to be significantly different from that based on the full set of renditions (see Results; Figure 5E). Thus, we included only song types in this analysis for which we had at least 6 recordings by an individual bird.

We estimated STSC within individual birds following Anderson's test of multivariate dispersion (Anderson 2006). First, we performed a principal coordinates ordination (PCO) of the dissimilarity matrix ($1 - S$), where S is song sequence similarity (equation (1)) for all song sequences of a given song type within an individual. In this analysis, the score of STSC = $1 - D_i$, where D_i is the distance between each song and the spatial median of the respective song type (range: 0–1). More variable renditions of a given song type are represented as a larger distance to the spatial median in the first 2 components of the principal coordinates ordination of the dissimilarity matrix. We then averaged all scores within each individual to generate individual scores of STSC. We compared these scores between 1975 and 2012 samples using a t -test.

Song and syllable repertoire sizes. We measured the repertoire sizes of males, in terms of both song types and distinct syllable types; the latter measure has been considered an estimate of song complexity in House Finches (Mennill et al. 2006). However, if our recordings of individuals represented an incomplete sample of their repertoires, the sample size of songs recorded per individual could be positively associated with the number of song or syllable types. To test for this, we included sample size in our analysis. We tested for a difference in either song or syllable repertoires between the datasets by multiple linear regression (independent variables: year and sample size per individual; dependent variable: repertoire sizes of syllables or songs).

Acoustic features. We compared 9 vocal parameters at the song level between years (see Table 1). Two of these measures are new and potentially reflect phonological complexity: frequency-time excursion length (Ju 2015, Podos et al. 2016), and changes in concavity (Ju and Lahti 2016). Frequency-time excursion length of a tonal song is the total path length of the song through frequency-time space, including unvoiced durations over which the shortest path (Euclidean distance) is measured. Thus, if one were to trace an entire song spectrogram with a pencil, following the line of peak amplitude over time and moving across silent spaces using the shortest possible cuts, the frequency-time excursion would be the length of that trace. As for changes in concavity, if we treat a tonal song trace in a spectrogram as a function in frequency-time space, our value for changes in concavity is the number of times the slope of that function goes from positive to negative or vice versa (i.e. the number of critical points in the derivative of the trace). In other words, changes in concavity measure the number of times a song trace changes direction

(up vs. down) in frequency. These 2 measures are distinct; for instance, the same high frequency-time excursion length can be accomplished either by traversing a high frequency bandwidth with a few changes in concavity, or a low frequency bandwidth with many changes in concavity (high convolution). To avoid the bias introduced by the different sample size of songs recorded per individual, we averaged each of these measures for each individual prior to any test. We also studied the same 9 vocal parameters at the syllable level (Table 1). Specifically, we tested if any of them differed significantly between years or among 1975-specific, 2012-specific and recurring types. Multiple tests were corrected by the false discovery rate (FDR).

Syllable lexicon. We asked whether the presence of certain syllable types in both years was associated with their proportional representation among individuals (i.e. the proportion of individuals having the given type in their syllable repertoire) in each year. For this test we used logistic regression, where frequency of syllable appearance among individuals was regressed against the binary value of whether or not the syllables were present in both 1975 and 2012. We compared syllable types that were present in both years and those present only in one year using measurements of each of the 9 acoustic parameters listed in Table 1. We also examined whether any of these parameters were correlated with syllable representation (the proportion of individuals singing them) in each time period.

RESULTS

Our full analysis included 2,023 songs from 190 male House Finches: 1,042 songs from 94 individuals in 1975 (for a mean of 11.2 ± 5.1 songs per individual) and 981 songs from 96 individuals in 2012 (for a mean of 10.2 ± 4.5 songs per individual) (Figure 1). Song duration ranged from 1 to 5 s (2.33 ± 1.1) including inter-syllable intervals. Songs were comprised of 6–31 syllables (12.1 ± 3.8). Birds sang 1–7 different song types (3.1 ± 1.4). Song sequence variation within a type was common as previously noted (Bitterbaum and Baptista 1979, Munding 1975, Tracy and Baker 1999), and manifested as insertions, substitutions or deletions of 1–3 syllables, or as incomplete songs. Songs were parsed into 12,535 syllables from 1975 and 11,968 syllables from 2012, for a total of 24,503. Classification analysis of the pooled sample defined a total of 407 distinct syllable types, 29% ($n = 118$) of which were present in both 1975 and 2012.

Song Sequence Sharing Within and Between Years

According to the 70% similarity criterion (Figure 3B), individuals in our sample shared song types in 1975, although rarely, and shared no songs in 2012 or between years (Figure 4A). Out of 4,371 pair-wise comparisons between individuals in 1975, 132 pairs (3.0%) shared at least one song type, involving a total of 51 shared song types. Of

these pairs of individuals, 91% ($n = 120$) were <5 km apart. Sharing of the entire detected song repertoires was even rarer: only 2 pairs of individuals that sang more than one song type shared all of them with each other in 1975. No song type was present in both years, even between individuals recorded at the same locations (Figure 1). The degree of between-individual song similarity was lower in 2012 than in 1975 (Figure 4A; Table 3).

Syllable Sharing Within and Between Years

In total, 407 distinct syllable types were defined; 238 and 287 syllable types comprised the 1975 and 2012 lexicons, respectively. Among these, 118 syllable types were

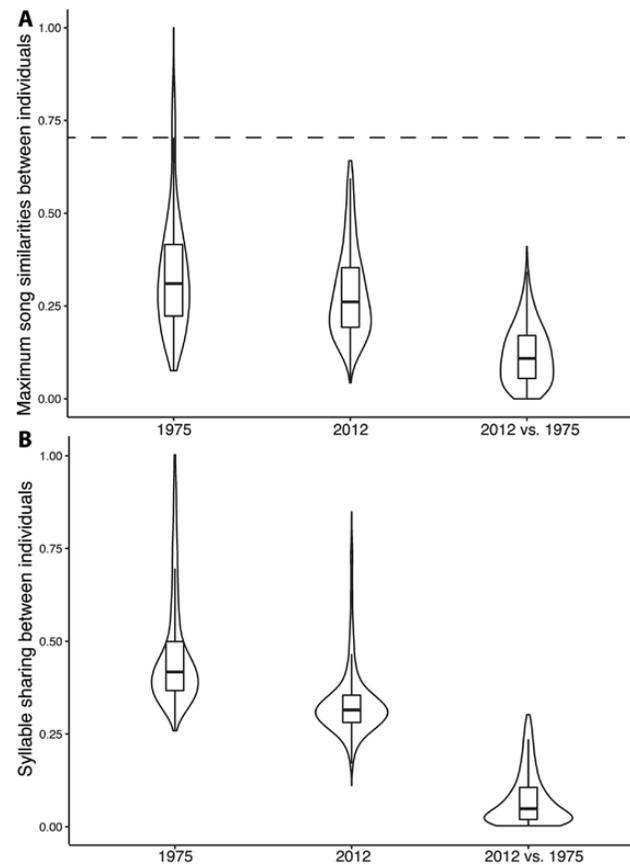


FIGURE 4. Song similarity and syllable sharing between individuals were lower in 2012 than in 1975. Violin plots showing distribution of maximum song similarity and syllable sharing between individuals within 1975 (number of comparisons = 4,371), within 2012 (number of comparisons = 4,560), and between 1975 and 2012 (number of comparisons = 9,024). The violin plot contains the same measures as a box plot, plus the probability density of the data at different values. (A) Maximum song similarity between individuals. Song sequence sharing ($S > 0.7$, indicated by the dashed line) is found between individuals in 1975, but not in 2012. No song types are shared between individuals from different years. (B) Syllable sharing (based on $S_j(adj)$) between individuals. Syllable sharing was lower in 2012 than in 1975.

present in both years (hereafter: recurring types). Sharing of syllables between individuals recorded in the same year, measured by Jaccard's similarity coefficient ($S_j(adj)$), was lower in 2012 than in 1975 (Figure 4B, Table 3). Not surprisingly, the degree of syllable sharing between years was even lower (Figure 4B), as less than half of the lexicon was shared between years.

Difference in Song Sequence Consistency

Song sequence consistency (STSC) between song renditions of the same type was lower in 2012 than in 1975 (Figure 5F, Table 3). This effect is illustrated by 2 song types collected in Freeport (40.663354°N, -73.591043°W) (Figure 5A-D). Our complete analysis included 51 individuals (58 song types) in 1975 and 42 individuals (45 song types) in 2012 that met our stringent criteria for sample selection (Figure 5E).

Difference in Song and Syllable Repertoire Sizes

The repertoire size of songs per individual did not differ between 1975 and 2012 after controlling for the number of songs recorded per individual (Figure 6A, Table 3). Despite the fact that the numbers of detected song types were highly variable for a given number of recorded songs per individual, the positive association between these 2 variables was significant, suggesting that the number of songs recorded for several individuals might be too small to have retrieved their full song type repertoires.

Syllable repertoire size per individual was significantly lower in 2012 than in 1975 after controlling for songs recorded per individual (Figure 6B, Table 3). The relationship

between sample size and the number of detected syllable types per individual was not significant, consistent with the analysis demonstrating that the first 5 songs could recover on average 75% of the detected syllable repertoire (see Methods and Figure 3A). We also excluded the possibility that the difference in syllable repertoire size might be a result of a difference in song length (1975: 12.0 ± 4.0 , $n = 94$; 2012: 12.2 ± 3.5 , $n = 96$; 2-sample t -test: $t_{186} = -0.96$, $P = 0.33$).

Difference in Acoustic Features

None of the 9 acoustic parameters measured differed significantly in means at the song or at the syllable level between 1975 and 2012 (Table 2). Mean minimum frequency was 158 kHz higher in 2012 than in 1975, but this difference was not significant after correcting for multiple comparisons.

Difference in Syllable Lexicon

Syllable types from 1975 which recurred in 2012 were present in more individuals' repertoires in 1975 than types found only in 1975 (Figure 7C, Table 3). Recurring syllable types also tended to be present in more individuals' repertoires in 2012 than syllables present only in 2012, but this trend was much weaker and did not reach significance (Figure 7A, Table 3). The proportion of individuals in each year that sang a given recurring syllable type was not correlated between years (linear regression: $F_{1,116} = 0.458$, $P = 0.49$) (Figure 7B); in other words, although syllable types which were more prevalent in 1975 were more likely to be present in 2012, they were not likely to be more prevalent than other syllable types in 2012.

TABLE 2. Population means of House Finch song and syllable parameters, and comparisons between 1975 and 2012.

Variables			Student's t -test			
	Mean in 1975	Mean in 2012	t	df	P (raw)	P (FDR)
Song						
AF (Hz)	3460.77	3498.11	-0.45	186.78	0.6558	0.6817
SF (Hz)	3539.87	3458.55	0.68	186.03	0.4962	0.6817
EF (Hz)	3231.58	3189.7	0.47	185.48	0.6412	0.6817
HF (Hz)	4083.61	4013.64	0.6	187.78	0.5515	0.6817
LF (Hz)	2859.15	3017.52	-1.95	172.12	0.0526	0.4734
BW (Hz)	1122.21	1172.75	-0.48	187.97	0.6326	0.6817
FL (Δ kHz per s)	21.66	23.3	-0.89	183.76	0.3761	0.6817
DU (s)	1.56	1.48	0.41	182.13	0.6817	0.6817
CO (per s)	18.16	20.22	-0.79	180.64	0.4281	0.6817
Syllable						
AF (Hz)	3471.13	3487.17	-0.29	465.17	0.7767	0.9079
SF (Hz)	3568.45	3595.50	-0.38	485.48	0.6996	0.9079
EF (Hz)	3318.36	3379.41	-0.91	488.96	0.3645	0.9079
HF (Hz)	3993.02	4025.43	-0.51	517.84	0.6070	0.9079
LF (Hz)	2689.66	2677.62	0.19	502.06	0.8487	0.9079
BW (Hz)	1085.03	1104.40	-0.31	505.62	0.7515	0.9079
FL (Δ kHz per s)	30.13	29.94	0.12	502.22	0.9079	0.9079
DU (s)	0.08	0.09	-1.01	476.03	0.3146	0.9079
CO (per s)	25.69	27.13	-0.54	517.61	0.5857	0.9079

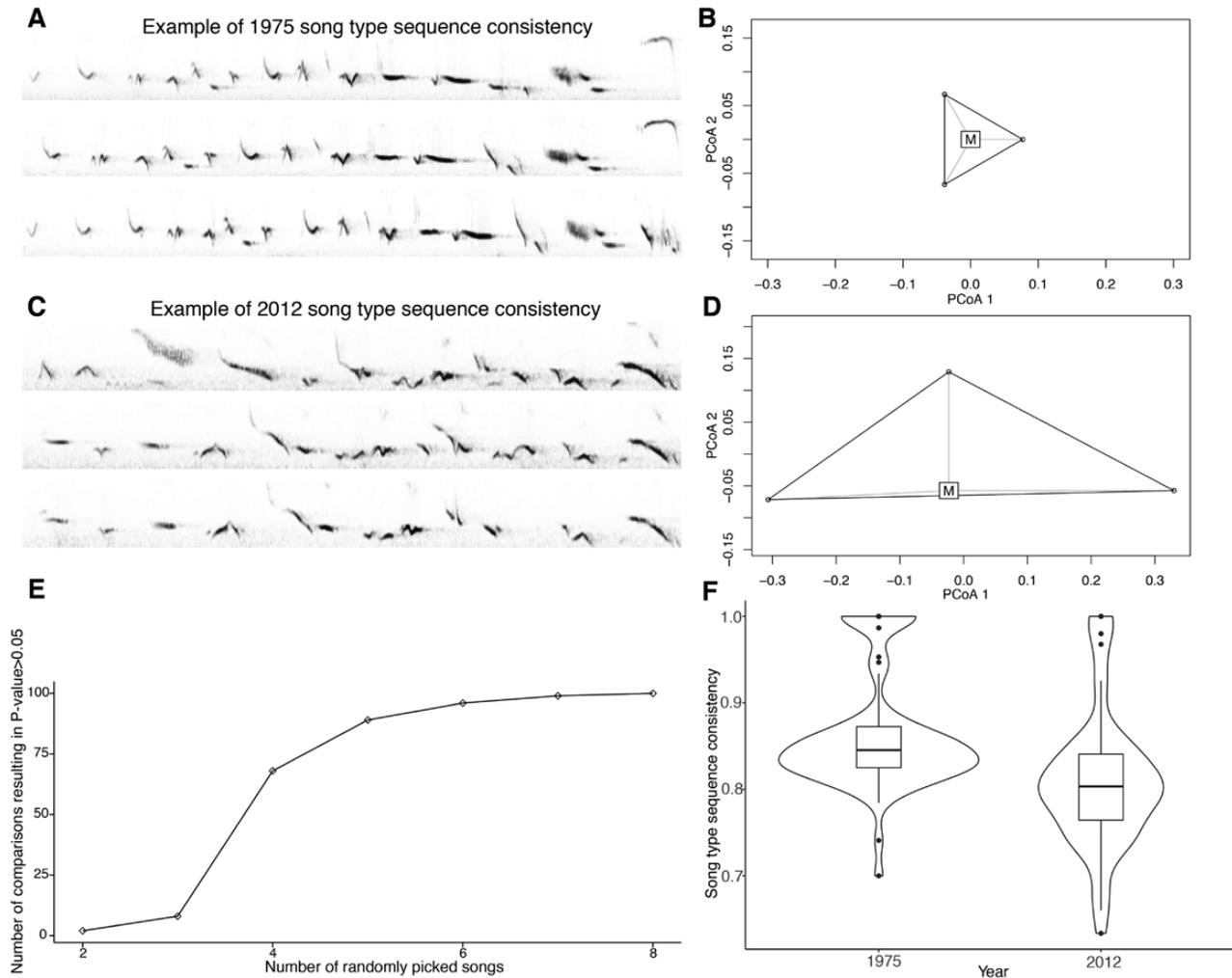


FIGURE 5. Song sequence consistency was lower in 2012 than in 1975. **(A, C)** Examples of 3 renditions of a single song type by a single individual in 1975 and 2012, respectively. **(B, D)** Illustration of the distance between each of these renditions and the spatial median (*M*) of the exemplary song types in **(A)** and **(C)** by Anderson's test of multivariate dispersion. **(E)** Validation of sample size for a test of song type consistency. This line plot shows the percent chance (*y*) of failing to obtain a significantly different distribution of scores for consistency (Wilcoxon signed-rank test: $P > 0.05$), based on *x* randomly picked songs as compared with our full sample by permutation (see Methods). When $x = 6$, $y = 97$, indicating only a 3% chance of obtaining a different distribution of consistency scores for the subsample relative to the complete sample; thus, we chose 6 songs as our minimum sample size of songs per individual. **(F)** Within-individual song sequence consistency. Violin plots show the distribution of distance to the spatial median (horizontal line) of the consistency with which individuals sang multiple renditions of the same song type, in 1975 and in 2012.

In 2012, the proportion of individuals with any given syllable in their repertoire was positively correlated with the lowest frequency of that syllable (Figure 8A, Table 3) and with its frequency excursion length (Figure 8B, Table 3). No such associations existed in 1975 (Figure 8C,D, Table 3). Neither of these 2 vocal parameters differed between recurring syllable types and year-specific types (2-sample *t*-tests, $FDR = \sim 0.70\text{--}0.99$) (Figure 8E,F).

Analyses of Song Samples in the Overlapping Regions Between Two Years

We subsampled our data, restricting our comparison to individuals in each year that were recorded within 1 km of

individuals recorded in the other year ($n_{1975} = 23$, $n_{2012} = 21$). The subsample contained 272 syllable types, with 101 and 111 exclusive to 1975 and 2012, respectively, and 60 shared between years. All results that were significant in the full comparative analysis were also significant in this restricted analysis, and means were also similar (Table 3).

DISCUSSION

Over the course of nearly 4 decades, the extent of sharing of songs and song elements, song and song element diversity, song lability, and song performance of House Finches

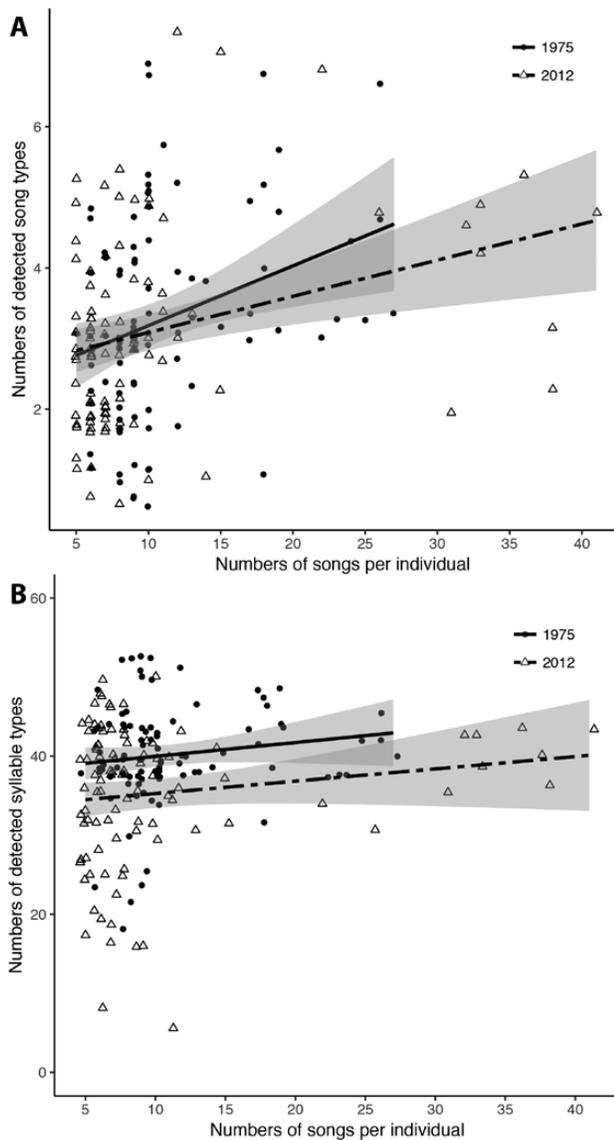


FIGURE 6. (A) Scatterplot showing song type repertoire size per individual in both study years, taking into account the number of songs recorded per individual. Data were jittered to unhide overlapping points. Linear regression lines are represented for 1975 and 2012 data, with the 95% confidence interval in gray. (B) Scatterplot showing the difference in syllable type repertoire size per individual between years, taking into account the number of songs recorded per individual. Data were jittered to unhide overlapping points. Linear regression lines are represented for 1975 and 2012 data, with the 95% confidence interval in gray.

on Long Island, New York, changed substantially. Song types present in the past were lost and replaced by others (Figure 4). Contemporary birds at the geographic scale we sampled do not share song types, whereas some of their ancestors did (Munding 1975, 1982). More generally, song similarity between individuals was lower in 2012 than in 1975, consistent with the greater observed song

diversity (Figure 6, Table 3). At the syllable level, half of the syllable types detected in 1975 recurred decades later in 2012, although any 2 similar acoustic structures across time could either be homologous or could have arisen independently. The syllables that recurred in 2012 were more prevalent in 1975, although they did not tend to maintain their prevalence (Figure 7). Syllable diversity was greater in the more recent sample, manifested as a larger lexicon size at the population level and as a lower degree of syllable type sharing among individuals. On the other hand, within an individual bird, a contemporary repertoire contains fewer syllable types and a tendency towards fewer song types than an ancestral repertoire (Figure 6, Table 3). Recent songs are also less consistent from rendition to rendition than they were earlier (Figure 5, Table 3). In terms of particular structural features of song, song length, frequency bandwidth and several other spectrographic features were similar in the 2 samples. No structural features predict recurrence of individual syllables, although in the contemporary population both the complexity metric of frequency excursion and an increase in minimum frequency were associated with syllable prevalence in individual repertoires (Figure 8, Table 3). Our 2 samples could represent either a temporal trend that would have been consistent in the intervening years or else 2 points in a fluctuating history of song structure in this population. In what follows we present some tentative interpretations that indicate some consistency between our results and expectations for a historical trend, based on what is already known about the Eastern House Finch population.

Increase in Song Diversity in a Growing Introduced Population

Given historical information about the founding and subsequent growth and spread of the Eastern House Finch population, our clearest prediction when comparing songs 3 decades vs. 7 decades from introduction was an increase in song diversity. This prediction also follows from the discovery of partial migratory behavior and longer-distance dispersal in this population, in contrast to the source population in the West (Able and Belthoff 1998). The 1975 songs in our study area were the product of roughly 3 decades of change since the colonization event on Long Island in the 1940s (Elliott and Arbib 1953). The few original founders were unlikely to have possessed all of the diversity represented in the 1975 recordings; the early song learning environment among the propagules and their immediate descendants was probably impoverished (Munding 1980, Pytte 1997). As the population grew and spread between the 1940s and 1970s (Munding and Hope 1982), locally distinctive dialects appear to have formed, perhaps around “founder nuclei”—early colonizers that themselves had different songs (Munding 1975). Throughout this

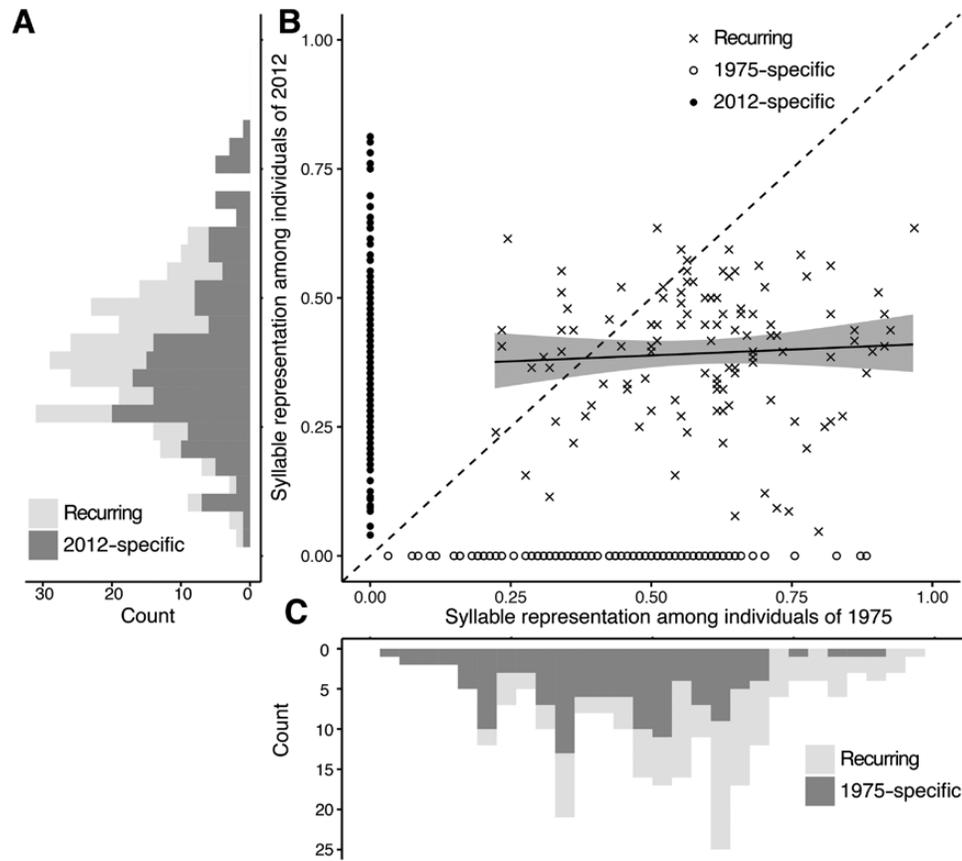


FIGURE 7. Recurring syllable types were the more prevalent ones in 1975. **(A)** Stacked histogram showing the distribution of the proportional representation of 287 syllable types among individuals in the 2012 sample, where “recurring” refers to types that are present in both years. **(B)** Scatterplot showing variation in proportional representation of syllable types (particularly recurring types) between years. A linear regression line is included for recurring types, with the 95% confidence interval in gray. The prevalence of recurring syllable types was not correlated between 1975 and 2012. **(C)** Stacked histogram showing the distribution of the proportional representation of 238 syllable types among individuals in the 1975 sample. Recurring syllable types were significantly more highly represented in repertoires in 1975 than 1975-specific syllable types.

period and afterwards, however, individual song distinctiveness would presumably have been increasing as well, through new or modified song elements accumulating as a result of departures from accurate imitation during song learning and production, as well as from recombination among parts of learned songs. The unit of song learning in House Finches appears to be below the whole-song level, such that an individual can assemble song parts gathered from various sources (Munding 1975, Bitterbaum and Baptista 1979, Tracy and Baker 1999). As the density of the introduced population increased, individuals would have had the opportunity to hear and choose among more songs and their constituent syllables during vocal development. This would have led to a higher diversity of song types, and lower sharing of whole song types between individuals, 2 of the most striking results in our study. Whereas 132 pairs of birds shared a total of 51 song types in 1975, no males in our sample shared song types in 2012 (or between years). Instances of song sharing have been observed between

New York House Finches <5 km apart in the 2010s (F. C. Geller personal observation), but no examples of this were present in the sample used in this analysis. Moreover, with more individuals learning syllables and modifying them, we would also predict an increase in total syllable types over time, which we likewise observed. Between 1975 and 2012, the number of syllable types in our samples rose from 238 to 287, despite 9.5% fewer syllables having been recorded in 2012. Even in the area of overlap between the 2 samples the number of syllable types was higher in 2012.

In short, our data in the light of past studies suggest 2 plausible engines for the increase in song diversity in Eastern House Finches over 4 decades, both of which are related to an increase in population density: (1) more individuals learning means more new variants in the population by copy error or innovation; and (2) more neighbors for any learner means a larger sample of components from which to construct songs. Another factor that would tend to intensify and spread this increase in diversity

TABLE 3. Significant differences between House Finch songs in 1975 and 2012 in western Long Island, including analysis of a subsample restricted to the geographical region of overlap. A test statistic of *t* indicates a 2-sample *t*-test, except in the cases of repertoire size where it indicates multiple linear regression; *z* indicates logistic regression, and *F* indicates linear regression. Values for *n* in the bottom 3 rows are the total number of syllable types in the dataset, which was significantly higher in 2012 than in 1975 (see text).

	Full sample			Subsample			P value
	1975 Mean ± SD (n)	2012 Mean ± SD (n)	Test statistics	1975 Mean ± SD (n)	2012 Mean ± SD (n)	Test statistics	
Song sequence sharing	0.34 ± 0.16 (4,371)	0.29 ± 0.12 (4,560)	<i>t</i> _{8,205} = 16.36	0.36 ± 0.22 (253)	0.25 ± 0.20 (210)	<i>t</i> _{4,45} = 4.71	< 0.001
Syllable sharing	0.46 ± 0.15 (4,371)	0.33 ± 0.09 (4,560)	<i>t</i> _{7,646} = 51.22	0.53 ± 0.23 (253)	0.40 ± 0.19 (210)	<i>t</i> _{4,60} = 6.19	< 0.001
Vocal consistency	0.86 ± 0.07 (51)	0.80 ± 0.08 (42)	<i>t</i> ₈₂ = 4.07	0.84 ± 0.05 (12)	0.78 ± 0.06 (8)	<i>t</i> ₁₄ = 2.33	0.036
Song repertoire size	3.2 ± 1.4 (94)	3.0 ± 1.3 (96)	<i>t</i> (year) ₂ = -0.64 <i>t</i> (sample size) ₁₈₇ = 4.26	3.4 ± 1.4 (23)	2.8 ± 1.3 (21)	<i>t</i> (year) ₂ = -1.41 <i>t</i> (sample size) ₄₁ = 3.15	<i>P</i> (year) = 0.17 <i>P</i> (sample size) = 0.003
Syllable repertoire size	40.2 ± 6.4 (94)	35.3 ± 9.0 (96)	<i>t</i> (year) ₂ = -4.17 <i>t</i> (sample size) ₁₈₇ = 1.97	42.3 ± 5.4 (23)	35.3 ± 8.2 (21)	<i>t</i> (year) ₂ = -3.48 <i>t</i> (sample size) ₄₁ = 1.20	<i>P</i> (year) < 0.001 <i>P</i> (sample size) = 0.24
Representation of recurring vs. non-recurring types	(238)	(287)	<i>z</i> (1975) = 5.94 <i>z</i> (2012) = 1.88	(161)	(171)	<i>z</i> (1975) = 4.38 <i>z</i> (2012) = 1.69	<i>P</i> (1975) < 0.001 <i>P</i> (2012) = 0.09
Representation correlated with lowest frequency	(238)	(287)	<i>F</i> (1975) _{1,236} = 0.033 <i>F</i> (2012) _{1,285} = 11.91	(161)	(171)	<i>F</i> (1975) _{1,159} = 1.05 <i>F</i> (2012) _{1,169} = 8.91	<i>P</i> (1975) = 0.31 <i>P</i> (2012) = 0.003
Representation correlated with frequency excursion	(238)	(287)	<i>F</i> (1975) _{1,236} = 0.53 <i>F</i> (2012) _{1,285} = 14.1	(161)	(171)	<i>F</i> (1975) _{1,159} = 0.1839 <i>F</i> (2012) _{1,169} = 8.103	<i>P</i> (1975) = 0.67 <i>P</i> (2012) = 0.005

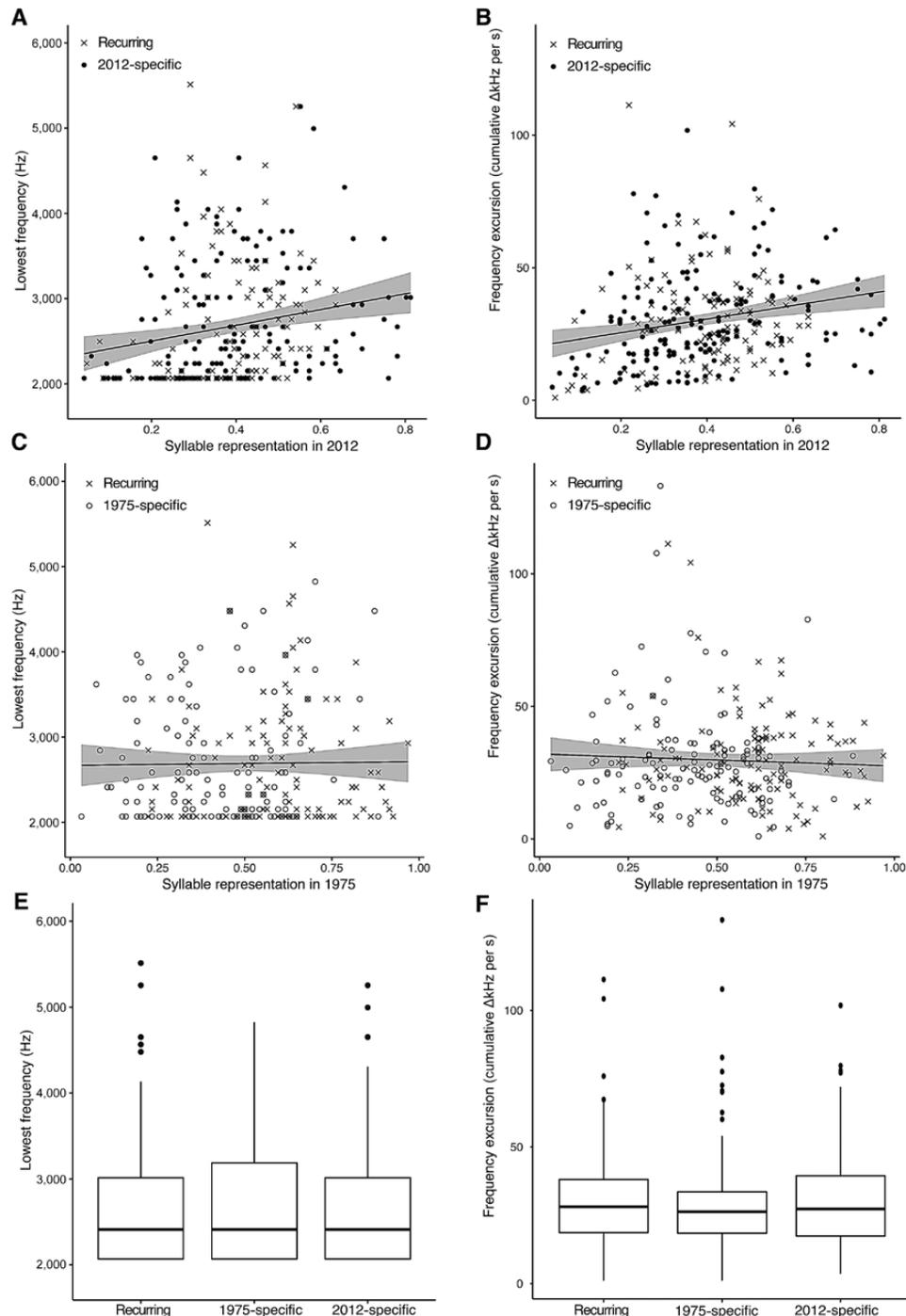


FIGURE 8. Two vocal parameters (lowest frequency and frequency excursion length) were positively correlated with syllable prevalence in 2012, but not in 1975. (**A, B, C, D**) Scatterplots showing the correlation between lowest frequency/frequency excursion of syllables and those syllables' proportional representation in repertoires in each year. Linear regression lines are represented, with the 95% confidence interval in gray. Both vocal parameters were significantly correlated with syllable prevalence in 2012 but not in 1975. (**E, F**) Boxplots showing no difference in either lowest frequency or frequency excursion among recurring, 1975-specific and 2012-specific syllable types.

is increased mixing of birds over a geographical area, whether by migration or dispersal. Munding (1975) inferred from banding studies that the Eastern House Finch population had become partially migratory, in

contrast to the sedentary habits of the ancestral Western population. This hypothesis was confirmed by Able and Belthoff (1998), who also found juvenile dispersal over longer distances in the East.

A Paradox: Changes in Song Diversity in the Population vs. the Individual

Although song diversity was higher at the population level in 2012 compared with 1975, the effect at the individual level was more complex. STSC or stereotypy in delivery was lower in the more recent sample, suggesting an increase in the looseness or plasticity of the individual vocal learning program (Figure 5). This would in turn increase the lability and thus eventually the diversity of song at the population level. However, the average number of syllable types per individual decreased, from 40.2 to 35.3, and our sample did capture entire individual syllable repertoires (Figure 6). Our test for a change in the number of song types, on the other hand, did not return a reliable result because our sample per individual was not extensive enough to ensure that we captured entire song repertoires. Still, the substantially lower number of syllable types per individual in 2012 than in 1975 contrasts sharply with the increase in syllable diversity at the population level. If our 2 samples indicate a historical trend, this paradoxical pair of results suggests 2 mechanisms operating in opposite directions—that despite the overall diversifying phenomena described above, individual songs are becoming simpler (with respect to syllable composition).

Mechanisms of Change at the Song Level

Oscine birdsong develops through an interplay of genetic inheritance, social learning and environmental influence (Marler and Munding 1971, Lahti et al. 2011, Munding and Lahti 2014). Change in song features between generations can be instigated by any combination of these features, including their interaction. Song genetically evolves insofar as a genetic change lies in the causal pathway of a change in song; song culturally evolves insofar as the change in song develops in the process of social acquisition; and a variety of other plastic changes can be caused by the non-social environment. This study cannot strictly distinguish among these mechanisms, although over the course of these 4 decades the scope for cultural evolution would be much greater than for genetic evolution (Cavalli-Sforza and Feldman 1981). Our results can also be tested against qualitative predictions from stochastic vs. selective mechanisms of song change.

As evolutionary theory predicts more generally, stochastic processes (e.g., drift and mutation) predict a frequency-dependent persistence of song elements through time, with a high turnover rate and no particular directionality to structural features in a large population (Lynch and Baker 1993, Byers et al. 2010). Our data meet this prediction in 4 main respects: (1) song types completely turned over between 1975 and 2012; (2) more prevalent syllable types in 1975 were more likely than rarer types to recur in 2012; (3) syllable recurrence did not strongly correlate with

prevalence in 2012 (NS trend), suggesting that the biased recurrence was mostly due to the higher earlier prevalence rather than something specifically advantageous about the syllables; and (4) none of the 9 measured vocal parameters correlated with syllable recurrence between years. These characteristics of song change are regularly observed in longitudinal studies of song, such as in the Indigo Bunting (*Passerina cyanea*, Payne 1996), the Chaffinch (*Fringilla coelebs*, Lynch and Baker 1993), the unaccented-ending songs of the Chestnut-sided Warbler (*Setophaga pensylvanica*, Byers et al. 2010), and the wild Canary (*Serinus canaria*, P. C. Munding personal observation).

As with any gene or trait, song features that are under positive selection are expected to maintain or increase their frequency in the population over time. In the House Finch, song length and complexity, at least in terms of syllable diversity, could be under sexual selection, although this is far from clear (Bitterbaum and Baptista 1979, Nolan and Hill 2004, Mennill et al. 2006). As stasis in song features could function in species recognition (Hill 2015), an increase in complexity or song length would be more suggestive of sexual selection in this case. Neither occurred: song length was the same in 1975 and in 2012 in terms of the numbers of syllables (mean = 12); and, as discussed above, song complexity in terms of individual syllable repertoire size actually decreased sharply (Figure 6, Table 3). None of the 9 measured song features were significantly different between 1975 and 2012 (Table 2). Minimum frequency increased by 158 Hz, but owing to the variance in this feature and considering multiple comparisons, it fell short of significance. Thus, predictions from selection are not met in terms of whole-song changes between years.

Mechanisms of Change at the Syllable Level

Since House Finch song learning appears to occur at a level below the whole song (Munding 1975, Bitterbaum and Baptista 1979, Tracy and Baker 1999), syllable structure and pattern might not change in lock-step with whole songs (Catchpole and Slater 2008). Testing syllables separately, none of the 9 acoustic features differed between 1975 and 2012 (Table 2), and no features are correlated either with syllable prevalence in 1975 or with recurrence between years (Figure 8). However, both frequency excursion and minimum frequency were significantly correlated with the prevalence of syllables among individuals in 2012 (Figure 8, Table 3). Although highly significant, these effects were not so strong as to influence whole-song or whole-repertoire trends within or between years. Frequency excursion is a measure of the acoustic complexity of a vocalization and indicates the agility of vocal tract modulation (Podos et al. 2016). If complexity is indeed under sexual selection, our results would suggest that females are scrutinizing syllables or phrases rather than whole songs, and their

choices have not been consistently enough applied over the decades to create population-level changes. This hypothesis that different syllable types might not be functionally equivalent, especially in the context of sexual selection, has been supported in the A-type “sexy syllables” of canaries (Vallet and Kreutzer 1995, Drăgănoiu et al. 2002), in contrast to a number of studies on other species that support the equivalent salience of syllable types (Slater et al. 1980, McGregor and Krebs 1982, Horn and Falls 1988, Payne et al. 1988, Catchpole and Rowell 1993, Lynch and Baker 1993).

The other acoustic change associated with syllable prevalence in 2012, an increase in minimum frequency, is commonly found in urban birds and is believed to function in avoiding the masking of song by the overwhelmingly low-frequency anthropogenic noise of the city (Slabbekoorn and Peet 2003). In House Finches particularly, Fernández-Juricic et al. (2005) and Bermúdez-Cuamatzin et al. (2009) both demonstrated a use of higher minimum pitch in noisy as opposed to quieter areas. Bermúdez-Cuamatzin et al. (2011) showed this to be a plastic adjustment rather than the genetic evolution of pitch. Our study shows that in the contemporary context the more common syllables tend also to have a higher minimum pitch. Several mechanisms are possible for this effect even if we assume a role for plasticity, such as differential hearing or learning of syllables in early development, preferential recruitment of high-minimum-frequency syllables when constructing songs, or on-the-spot adaptive frequency change in adults singing in the presence of noise.

Future Directions

Opportunities abound for further research and improvement of our understanding of this case study in the cultural evolution of bird song. So far we have not integrated a consideration of the effect of the mycoplasmal conjunctivitis outbreak that recently decimated the New York population (Hawley et al. 2006). In at least some respects this neglect is conservative. An increase in song diversity was evident despite this bottleneck; if the epidemic had not occurred, the increase in song diversity between 1975 and 2012 might have been even more marked. Our interpretation of the relationship between demographic factors and song change is also limited by the shortage of published research on this topic (Lomolino et al. 2015). Some studies have shown that song diversity is a potential estimator of population size (Laiolo et al. 2008, Sebastián-González and Hart 2017), but more directed studies would be needed to reveal how population dynamics influence song change at different levels, such as through innovation. Another limitation is that we have restricted ourselves to considering each population as a whole, and then comparing populations across time; but these same data should also be analyzed geographically, and any geographic patterns followed

across time. We will present those results elsewhere (see also Ju 2015). Finally, we have not considered an interaction between song and plumage color. The functional importance and tradeoffs involved in House Finch plumage color are well known (Hill 2002). Moreover, New York birds are far more colorful (redder) than birds in their ancestral population in California (Hill 1993a). A negative correlation between song complexity and elaboration of plumage has been reported in Cardueline Finches (Badyaev et al. 2002). Thus, a potentially fruitful avenue for future research on House Finches is the relationship between plumage and song over space and time.

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Ethics statement: No animals were handled or otherwise disturbed in the course of this study.

Author contributions: PCM collected the 1975 data. DCL conceived the study with help from all authors. FCG collected data. CJ manipulated the data, created and implemented software, performed analyses, and produced the results; this study was part of her doctoral dissertation research (CUNY Biology). CJ and DCL wrote the present manuscript. All authors contributed ideas.

LITERATURE CITED

- Able, K. P., and J. R. Belthoff (1998). Rapid evolution of migratory behaviour in the introduced House Finch of eastern North America. *Proceedings of The Royal Society of London. Series B: Biological Sciences* 265:2063–2071.
- Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253.
- Anderson D. R. (2008). *Model Based Inference in the Life Sciences: A Primer on Evidence*. Springer, New York, USA.
- Badyaev, A. V., G. E. Hill, and B. V. Weckworth (2002). Species divergence in sexually selected traits: Increase in song elaboration is related to decrease in plumage ornamentation in finches. *Evolution* 56:412–419.
- Baker, M. C., and M. A. Cunningham (1985). The biology of bird-song dialects. *Behavioral and Brain Sciences* 8:85–100.

- Bermúdez-Cuamatzin, E., A. A. Rioschelen, D. Gil, and C. M. Garcia (2009). Strategies of song adaptation to urban noise in the House Finch: Syllable pitch plasticity or differential syllable use? *Behaviour* 146:1269–1286.
- Bermúdez-Cuamatzin, E., A. A. Rioschelen, D. Gil, and C. M. Garcia (2011). Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters* 7:36–38.
- Bitterbaum, E., and L. F. Baptista (1979). Geographical variation in songs of California House Finches (*Carpodacus mexicanus*). *The Auk* 96:462–474.
- Byers, B. E., K. L. Belinsky, and R. A. Bentley (2010). Independent cultural evolution of two song traditions in the Chestnut-sided Warbler. *American Naturalist* 176:476–489.
- Campbell, P., B. Pasch, J. L. Pino, O. L. Crino, M. Phillips, and S. M. Phelps (2010). Geographic variation in the songs of neotropical singing mice: Testing the relative importance of drift and local adaptation. *Evolution* 64:1955–1972.
- Catchpole, C. K., and A. Rowell (1993). Song sharing and local dialects in a population of the European Wren Troglodytes. *Behaviour* 125:67–78.
- Catchpole, C. K., and P. Slater (2008). *Bird Song: Biological Themes and Variations*. Cambridge University Press, New York, USA.
- Cavalli-Sforza, L. L., and M. W. Feldman (1981). *Cultural Transmission and Evolution*. Princeton University Press, Princeton, New Jersey, USA.
- Derryberry, E. P. (2009). Ecology shapes birdsong evolution: Variation in morphology and habitat explains variation in White-crowned Sparrow song. *American Naturalist* 174:24–33.
- Drăgănoiu, T. I., L. Nagle, and M. Kreutzer (2002). Directional female preference for an exaggerated male trait in Canary (*Serinus canaria*) song. *Proceedings of The Royal Society B: Biological Sciences* 269:2525–2531.
- Elliott, J. J., and R. S. J. Arbib (1953). Origin and status of the House Finch in the eastern United States. *The Auk* 70:31–37.
- Fernández-Juricic, E., R. Poston, K. De Collibus, T. Morgan, B. Bastain, C. Martin, K. Jones, and R. Treminio (2005). Microhabitat selection and singing behavior patterns of male House Finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the Western US. *Urban Habitats* 3:49–69.
- Hawley, D. M., D. Hanley, A. A. Dhondt, and I. J. Lovette (2006). Molecular evidence for a founder effect in invasive House Finch (*Carpodacus mexicanus*) populations experiencing an emergent disease epidemic. *Molecular Ecology* 15:263–275.
- Hill, G. E. (1993a). Geographic variation in the carotenoid plumage pigmentation of male House Finches (*Carpodacus mexicanus*). *Biological Journal of The Linnean Society* 49:63–86.
- Hill, G. E. (1993b). Male mate choice and the evolution of female plumage coloration in the House Finch. *Evolution* 47:1515–1525.
- Hill, G. E. (2002). *A Red Bird in a Brown Bag: The Function and Evolution of Colorful Plumage in the House Finch*. Oxford University Press, Oxford and New York, UK, USA.
- Hill, G. E. (2015). Sexiness, individual condition, and species identity: The information signaled by ornaments and assessed by choosing females. *Evolutionary Biology* 42:251–259.
- Horn, A., and J. B. Falls (1988). Structure of Western Meadowlark (*Sturnella neglecta*) song repertoires. *Canadian Journal of Zoology* 66:284–288.
- Janes, S. W., and L. Ryker (2013). Rapid change in a type I song dialect of Hermit Warblers (*Setophaga occidentalis*). *The Auk* 130:30–35.
- Janik, V. M., and P. J. Slater (2000). The different roles of social learning in vocal communication. *Animal Behaviour* 60:1–11.
- Janney, E., H. Taylor, C. Scharff, D. Rothenberg, L. C. Parra, and O. Tchernichovski (2016). Temporal regularity increases with repertoire complexity in the Australian Pied Butcherbird's song. *Royal Society Open Science* 3:160357.
- Ju, C. (2015). *Cultural Evolution In Natural Populations: A Quantitative Bioacoustic Analysis*. Ph. D Thesis, City University of New York, New York, USA.
- Ju, C. (2016). FinchCatcher (version Beta 5). Queens College Department of Biology, New York, USA; <http://finchcatcher.net>.
- Ju, C., and D. C. Lahti (2016). *FinchCatcher Manual: Version Beta 5*. Queens College Department of Biology, New York, USA.
- Krebs, C. (1989). *Ecological Methodology*. Harper & Row, New York, USA.
- Lahti, D. C., D. L. Moseley, and J. Podos (2011). A tradeoff between performance and accuracy in bird song learning. *Ethology* 117:802–811.
- Laiolo, P., M. Vogeli, D. Serrano, and J. L. Tella (2008). Song diversity predicts the viability of fragmented bird populations. *PLoS One* 3:e1822.
- Langfelder, P., B. Zhang, and S. Horvath (2008). Defining clusters from a hierarchical cluster tree: The dynamic tree cut package for R. *Bioinformatics* 24:719–720.
- Leadbeater, E., and L. Chittka (2007). Social learning in insects— from miniature brains to consensus building. *Current Biology* 17:R703–R713.
- Lemon, R. E. (1975). How birds develop song dialects. *The Condor* 77:385–406.
- Leon, E., A. H. Beltzer, P. F. Olguin, C. F. Reales, G. Urich, V. Alessio, C. G. Cacciabue, and M. Quiroga (2015). Song structure of the Golden-billed Saltator (*Saltator aurantiirostris*) in the middle Parana river floodplain. *Bioacoustics* 24:145–152.
- Lomolino, M. V., B. C. Pijanowski, and A. Gasc (2015). The silence of biogeography. *Journal of Biogeography* 42:1187–1196.
- Lynch, A., and A. J. Baker (1993). A population memetics approach to cultural evolution in Chaffinch song: Meme diversity within populations. *American Naturalist* 141:597–620.
- Marler, P., and P. C. Munding (1971). *Vocal learning in birds*. In *The Ontogeny of Vertebrate Behavior* (H. Moltz, Editor). Academic Press, New York, USA, pp. 380–450.
- Mcgregor, P. K., and J. R. Krebs (1982). Song types in a population of Great Tits (*Parus Major*): Their distribution, abundance and acquisition by individuals. *Behaviour* 79:126–152.
- Mennill, D. J., A. V. Badyaev, L. M. Jonart, and G. E. Hill (2006). Male House Finches with elaborate songs have higher reproductive performance. *Ethology* 112:174–180.
- Munding, P. (1975). Song dialects and colonization in the House Finch, *Carpodacus mexicanus*, on the east coast. *The Condor* 77:407–422.
- Munding, P. (1982). Microgeographic and macrogeographic variation in the acquired vocalizations of birds. *Acoustic Communication in Birds* 2:147–208.

- Munding, P., and D. Lahti (2014). Quantitative integration of genetic factors in the learning and production of canary song. *Proceedings of The Royal Society B: Biological Sciences* 281:20132631.
- Munding, P. C. (1980). Animal cultures and a general theory of cultural evolution. *Ethology and Sociobiology* 1:183–223.
- Munding, P. C., and S. Hope (1982). Expansion of the winter range of the House Finch: 1947–79. *American Birds* 36:347–353.
- National Audubon Society (2010). The Christmas Bird Count Historical Results [Online]; <http://www.christmasbirdcount.org> (accessed 30 January 2018).
- Nolan, P. M., and G. E. Hill (2004). Female choice for song characteristics in the House Finch. *Animal Behaviour* 67:403–410.
- Nowicki, S., M. Westneat, and W. Hoese (1992). Birdsong: Motor function and the evolution of communication. *Seminars in Neuroscience* 4:385–390.
- Panhuis, T. M., R. Butlin, M. Zuk, and T. Tregenza (2001). Sexual selection and speciation. *Trends in Ecology & Evolution* 16:364–371.
- Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67:518–536.
- Pardieck, K. L., D. J. Ziolkowski Jr., M. Lutmerding, K. Campbell and M.-A. R. Hudson (2017). North American Breeding Bird Survey Dataset 1966 - 2016, version 2016.0. U.S. Geological Survey, Patuxent Wildlife Research Center; www.pwrc.usgs.gov/BBS/RawData/.
- Payne, R. B. (1981). Song learning and social interaction in Indigo Buntings. *Animal Behaviour* 29:688–697.
- Payne, R. B. (1996). Song traditions in Indigo Buntings: origin, improvisation, dispersal, and extinction in cultural evolution. In *Ecology and Evolution of Acoustic Communication in Birds* (D. E. Kroodsma and E. H. Miller, Editors). Cornell University Press, Ithaca, New York, USA, pp. 198–220.
- Payne, R. B., L. L. Payne, and S. Whitesell (1988). Interspecific learning and cultural transmission of song in House Finches. *The Wilson Bulletin* 100:667–670.
- Podos, J., S. K. Huber, and B. Taft (2004). Bird song: the interface of evolution and mechanism. *Annual Review of Ecology, Evolution, and Systematics* 35:55–87.
- Podos, J., D. L. Moseley, S. E. Goodwin, J. McClure, B. N. Taft, A. V. H. Strauss, C. Rega-Brodsky, and D. C. Lahti (2016). A fine-scale, broadly applicable index of vocal performance: Frequency excursion. *Animal Behaviour* 116:203–212.
- Podos, J., S. Peters, T. Rudnicki, P. Marler, and S. Nowicki (1992). The organization of song repertoires in Song Sparrows: Themes and variations. *Ethology* 90:89–106.
- Podos, J., and P. S. Warren (2007). The evolution of geographic variation in birdsong. *Advances in the Study of Behavior* 37:403–458.
- Pytte, C. L. (1997). Song organization of House Finches at the edge of an expanding range. *The Condor* 99:942–954.
- Rapaport, L. G., and G. R. Brown (2008). Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews* 17:189–201.
- Richerson, P. J., and R. Boyd (2008). *Not by Genes Alone: How Culture Transformed Human Evolution*. University of Chicago Press, Chicago, Illinois, USA.
- Ristad, E. S., and P. N. Yianilos (1998). Learning string-edit distance. *IEEE Transactions on Pattern Analysis and Machine Intelligence* 20:522–532.
- Rousseeuw, P. J. (1987). Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics* 20:53–65.
- Sebastián-González, E., and P. J. Hart (2017). Birdsong meme diversity in a habitat landscape depends on landscape and species characteristics. *Oikos* 126:1511–1521.
- Slabbekoorn, H., and M. Peet (2003). Ecology: Birds sing at a higher pitch in urban noise. *Nature* 424:267.
- Slabbekoorn, H., and T. B. Smith (2002). Habitat-dependent song divergence in the little greenbul: An analysis of environmental selection pressures on acoustic signals. *Evolution* 56:1849–1858.
- Slater, P. J. B., S. A. Ince, and P. W. Colgan (1980). Chaffinch song types: Their frequencies in the population and distribution between repertoires of different individuals. *Behaviour* 75:207–218.
- Thompson, W. L. (1960). Agonistic behavior in the House Finch. Part I: Annual cycle and display patterns. *The Condor* 62:245–271.
- Tracy, T. T., and M. C. Baker (1999). Geographic variation in syllables of House Finch songs. *The Auk* 116:666–676.
- Tracy, T. T., H. J. Zasadny, J. G. Erickson, and J. L. Siemers (2009). Syllable and song sharing in a recently established population of House Finches (*Carpodacus mexicanus*). *The Auk* 126:823–830.
- Vallet, E., and M. Kreutzer (1995). Female canaries are sexually responsive to special song phrases. *Animal Behaviour* 49:1603–1610.
- Wang, Z., A. J. Baker, G. E. Hill, and S. V. Edwards (2003). Reconciling actual and inferred population histories in the House Finch (*Carpodacus mexicanus*) by AFLP analysis. *Evolution* 57:2852–2864.
- Williams, H., I. I. Levin, D. R. Norris, A. E. Newman, and N. T. Wheelwright (2013). Three decades of cultural evolution in Savannah Sparrow songs. *Animal Behaviour* 85:213–223.