

Spatial Variation of House Finch (*Haemorhous mexicanus*) Song

Along the American Southwest Coast

By

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Abstract

The relatively young and burgeoning field of cultural evolution is interested in using non-human animal models to investigate the biological basis for cultural phenomena. Songbirds that learn to sing via social transmissions are particularly good organisms for exploring this topic, as song structure in these species has been found to vary over geographic distances and accumulate changes over time. These sorts of trait variation are considered hallmarks of cultural evolution. This study uses the syllables of house finch birdsong as cultural units and examines its geographic variation throughout the American southwest. Syllable sharing between house finches gradually decreases over a distance of 10 km. However, unlike previous studies, syllable sharing beyond 10 km conforms to a stochastic pattern. To explain these findings, the syllable saturation hypothesis is proposed, which suggests that there is a homoplasy of syllable types throughout the house finch vocal culture.

Introduction:

Cultural evolution is an interdisciplinary topic of increasing interest among evolutionary biologists (Mesoudi *et al.* 2006). Although definitions vary between disciplines, evolutionary biologists broadly characterize “cultural” to be the social transmission of behavioral traits and “cultural evolution” as the accumulation of changes and frequency of these traits in a population over time. This view makes cultural evolution analogous to Darwinian evolution, with variants capable of undergoing either selective or neutral processes (Grant & Grant, 1996; Baker & Cunningham, 1985; Boyd & Richerson, 1985; Payne, 1981; Cavalli-Sforza & Feldman, 1981). The present study uses birdsong as a model system for investigating cultural evolution. I employ a new quantitative method for analyzing the geographic variation of song among house finches (*Haemorhous mexicanus*) in the American southwest.

Birdsong is a well-established tool for studying the mechanisms of cultural evolution (Feher, 2008; Grant & Grant, 1996; Payne & Payne, 1993; Slater, 1986; Marler & Tamura, 1964). Many bird species learn their song via imitative processes, where individual birds attempt to mimic auditory stimuli after repeated exposure. Most species have genetically inherited traits that restrict their social learning of song to that of conspecifics by means of auditory or cognitive preferences expressed during early development (Nelson & Marler, 1993; Marler & Peters, 1987; Marler & Peters, 1977; Nottenbohm 1972). Among such birds, the vocal imitation process involves an activation and expression of neuromuscular motor patterns associated with singing that result in an overproduction of a wide variety of previously memorized sounds. These sounds then become subject to adjustments by a variety of social stimuli, causing selective attrition and reinforcement of song elements that gradually increases the resolution of the song, through a process referred to as action-based learning (Norby, 2007; Nelson, 2000; Nelson & Marler, 1994;

Marler & Nelson, 1993; Nelson, 1992; Marler, 1991). Error correction mechanisms complement this process in an attempt to maintain maximum song quality in adult birds (Sober & Brainard, 2009).

These mechanisms do not always result in a perfect replication of the model song, and many other factors can affect song plasticity (Payne, 1996). Gross deviations in song structure can occur in certain species when receiving inadequate exposure to suitable auditory models during specific developmental phases (Marler & Tamura, 1964; Payne 1981; Marler & Peters, 1988; Hughes, 2002). A variety of other types of changes can also occur at smaller scales, such as insertions and deletions of song elements. These alterations can be transmitted between imitating neighbors and accumulate within a population over time (Marler & Tamura, 1964; Thorpe 1956). This process constitutes cultural evolution; many variables have been found to influence its occurrence, such as access to nutritious food sources, exposure to environmental stressors, ecological variation, migration patterns, and geographic variation (MacDougall-Shackleton & Spencer, 2012; Derryberry, 2009; Nelson, 2001).

Cultural evolution, as with any other evolutionary phenomenon, can be studied allochronically and synchronically. The former method investigates changes along time within a cultural lineage; the latter fixes the study within a span of time and compares across lineages. These methods can be applied to studies of birdsong. As song changes over the generations in time, dispersal concurrently separates offspring from their parents in space. This creates a geographic spread of song differences that is amenable to a synchronic analysis. Using this approach, geographic variation becomes a suitable proxy for cultural evolutionary change.

Variation in song across geographic distance has been reported in many bird populations, especially in the song-learning oscine passerines. This can manifest as stochastic, clinal, or

dialectical patterns. The three types exist on a continuum, and the position of a song system on such a continuum can be affected by a variety of factors (Ju, 2015; Derryberry, 2011; Catchpole & Slater, 2008; Podos, 2007; Wright, Rodriguez, & Fleischer, 2005; Nelson & Soha, 2004; Lachlan & Feldman 2003; Warren & Nelson, 2002; Nelson, 2001; Cunningham, Baker, & Boardman, 1987; Mundinger, 1982). Stochastic variation is present when song variation is observed over an area but is not related to geographic distance between singing individuals. Examples of causal mechanisms for this phenomena include cultural and genetic drift. In cultural drift, variations emerge due to the rapid transmission of copying errors in divergent populations. In genetic drift, variations are expressed as random changes in anatomical, physiological, neural mechanisms underlying vocal ontogeny and production, or changes to the genetic loci underpinning these mechanisms (Grant and Grant, 1996; Payne, 1996; Lemon, 1975; Slabbekoorn & Smith, 2002; Podos & Norwicky, 2004b; Livingston *et al.*, 2000). Clinal variation is a gradual change in song across a geographic area. This pattern is expected based on the dispersal-related hypothesis presented above in cultural evolution, just as it is in genetic evolution (Rousset, 1997). Local stabilization of these patterns would be maintained by a preference for local songs (Slabbekoorn, 2004; Wiley & Richards, 1978; Butlin & Ritchie, 1994; Marler, 1957; Nowicki *et al.*, 2002). Dialects, at the opposite end of the continuum from stochastic variation, are typically characterized by sharp vocal boundaries and stepped variation, regionally distinct compared to other locales, and are a well-established vocal phenomenon (Podos & Warren, 2007; Leader, Wright, & Yom-Tov, 2000; Marler & Tamura, 1964; Mundinger, 1975). Despite these observations, the academic literature remains inconclusive as to the reason why dialects emerge in some species and not others, with the local adaptation hypothesis, social adaptation hypothesis, and epiphenomenon hypothesis all being offered as

potential explanations (Podos & Warren, 2007). No evidence exists of dialects among species that do not learn their songs via vocal imitation (Podos & Warren, 2007). In this study, I examine the pattern of geographic variation of birdsong among house finches in California.

The house finch is a small passerine bird native to the North American West that produces a long warbling song (Bitterbaum & Baptista, 1979; Pytte, 1997; Thompson, 1960). The basic element of a song is considered here a “syllable,” and is a continuous tonal trace or note. Several syllables are sung in succession, with .02-.20 sec silent intervals between them, constituting the song (Mundinger, 1975). An individual house finch is capable of producing song renditions that differ from one another slightly via insertion, deletion, or replacement of syllables; these are called variants. Groups of songs that are more distinct from one another, sharing only a minority of syllables, are considered separate song themes. An individual house finch possesses an average repertoire of two to seven song themes. Song themes can be shared between individuals as well. This study examines song structure at the syllable level in order to achieve a high resolution of structural (spectrographic) features.

House finches are present throughout the United States, although differences pertaining to the history of western and eastern populations make the species an interesting case study. Western house finches are native to the Southwest, having dispersed prehistorically from a Mexican origin to areas that now extend from California to parts of the Midwest. On the other hand, Eastern house finches were artificially introduced by humans. These birds were captured from their native sites by human traffickers for illegal pet trades during the 1940s, and were released into the wild by their owners during this time. There is some evidence that suggests as many as four separate founding events occurred in New York as a result (Mundinger, 1975; Elliott & Arbib, 1953). These birds spread from New York until they encompassed the entire

eastern half of the country, eventually coming into contact with western house finches in Oklahoma.

Studies on western and eastern house finches have revealed some differences in typical behavioral traits as well as birdsong structure. The older source population is non-migratory. The birds tend to possess greater syllable diversity, more song themes per locality, and more themes per individual (Tracy & Baker, 1999; Bitterbaum & Baptista, 1979). In contrast, the newer population is characterized as partially migratory, meaning that some individuals migrate and others do not. These house finches tend to have lower syllable diversity, fewer themes per locality, and fewer themes per individual than western birds (Ju, 2015; Tracy *et al.*, 2009; Munding 1975).

Although research on house finches residing in different states have revealed these characteristics to be consistent based on the population's place of origin, inquiries directed at exploring how their birdsong varies over geographic distance have produced divergent results. Munding (1975) reported the presence of distinct birdsong dialects among the New York house finches. This study prompted interest the birdsong community; Bitterbaum and Baptista (1979) followed up by exploring the same question in California birds. Their study revealed a gradual decline in syllable sharing over geographic distance. In 1997, a study was conducted on house finches residing in Wisconsin. These birds inhabited the leading edge of the eastern population at the time and no geographic variation was uncovered (Pytte, 1997). Tracy & Baker (1999) revealed a decline in sharing over distance among Colorado birds, considered to be a subset of the western population, in a pattern resembling Bitterbaum & Baptista (1979). Tracy *et al.* (2009) followed up with a comparative analysis using eastern-derived Iowa house finches and found no change in syllable sharing over distance. Since no investigation has revealed the

presence of dialects outside of Mundinger's (1975) study, Ju (2015) conducted another investigation of the New York population using new methods. Two studies were conducted, one on data from 2012 and another from 1975. Both revealed a decline of syllable sharing over distance, but to varying degrees. The results resembled neither Mundinger's dialects nor the stochastic variation in other eastern populations, but rather Bitterbaum & Baptista's (1979) and Tracy & Baker's (1999) findings in the West. A notable difference between Ju's (2015) study and others is that it demonstrated the continuum-like properties of geographic variation intermediate between dialects and clines.

Because the causes for these divergent results are still unclear, a more thorough investigation of the source population in the west could be helpful in providing additional clues, as would the use of methods that are comparable with studies in the east. My study utilizes the same quantitative methods on Californian birds as those used by Ju (2015) on New York birds. I use software that automatically identifies and extracts syllables from songs and measures several spectral features for each syllable. Comparisons among syllables in these features permits a cluster analysis and ultimately a syllable lexicon. I use this lexicon to compare the syllable repertoires of individual birds across geographic distances. Thus, this method circumvents potential problems that might have emerged in past studies due to multiple researchers conducting qualitative analyses of songs, analyses that might not yield comparable results. The goal of this study was to determine the nature of house finch song variation over space in California, in an effort to reconcile the history of conflicting reports on this species.

Methods:

Songs were recorded from wild house finches by a collaborator (Jacqueline Song) during April – May 2012. The sampling area consisted of 62 cities spanning nearly 700km northwest to southeast along the west coast of California. Birds were recorded only while the recorder maintained visual contact, and recording stopped when the bird stopped singing or flew away. To reduce the likelihood of recording the same bird twice, new birds were recorded at least 100 meters away from the previously recorded bird, and each city was visited by the recordists only once during the duration of the field study. Each song was manually parsed from the original recordings using Audacity® software, given unique labels, and saved as separate files in a database.

A total of 9434 songs from 855 unique birds, as well as their respective longitude/latitude coordinates, were recorded. Previous studies on house finches have established that most syllable types within a bird's song repertoire are present after recording the 15th song (Tracy & Baker, 1999; Tracy *et al.* 2009, Ju 2015). For this project, the sample was filtered using a higher song threshold of at least 20 songs; birds with fewer than 20 recorded songs were omitted, which resulted in 11 cities being excluded from the study. After filtering, 4443 songs from 130 birds in 51 cities remained and were used for the analysis (Fig. 1).

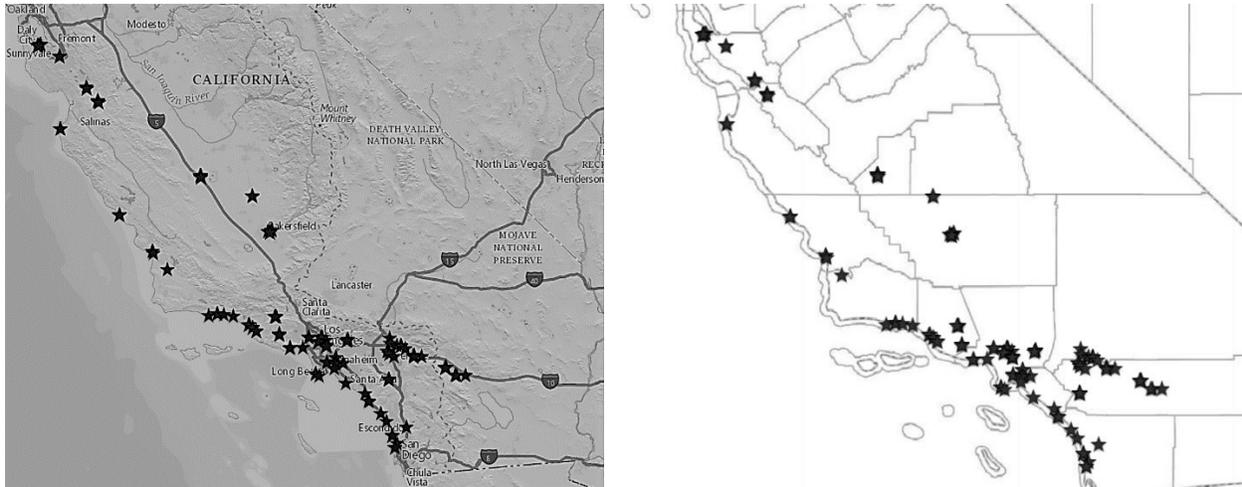


Figure 1: Sampling localities of 130 individuals in western California. Geographic terrain is represented (*left image*), as well as county borders (*right image*).

These songs were subsequently analyzed by a new quantitative analytical pipeline, FinchCatcher, created by a collaborator (Ju, 2015, 2016). FinchCatcher uses an algorithm that extracts signals from background noise and summarizes songs as a series of spectral shapes. The program is also optimized for field recordings of pure-tone bird signals with ambient noise and has been specialized specifically for analyzing house finch songs. Traditionally, signal extraction would be conducted by hand by the researcher, which would be physically laborious and prone to subjectivity between analysts. Software tools that have been designed to address this problem have typically been optimized for use under laboratory conditions, and often produce inconsistent or inaccurate results from field samples. FinchCatcher’s noise reduction and signal extraction features provide a powerful alternative method. After identifying syllables, I used FinchCatcher’s automated measurement procedure to analyze each syllable and characterize it in terms of 10 shape-related acoustic features. I then compared all ten variables across all individuals to generate overall similarity scores between syllables (Table 1). Statistical software R was then used to carry out all subsequent phases of the analysis (R Core Team, 2013).

Variables	Description
Average frequency (Hz)- AF	The average frequency of the entire song
Start frequency (Hz)-SF	The frequency at the beginning of the song
End frequency (Hz)-EF	The frequency at the end of the song
Bandwidth (Hz)-BW	The average difference between highest and lowest frequencies of each syllable in the song
Frequency-time excursion length- FL	Arc length of a song treated as continuous by connecting amplitude peaks in the spectrogram, using line segments to create a polygonal path
Duration (ms)-DU	Time duration of the song
Highest frequency (HZ)- HF	The average highest frequency of each syllable of the song
Lowest frequency (HZ) – LF	The average lowest frequency of each syllable of the song
Concavity-CO	The average number of changes in sign of slope of frequency changes per syllable throughout the song
Intersyllable-IS	The average duration of silence between consecutive syllables in the song

Table 1. Summary table of all 10 variables used by FinchCatcher to analyze syllables (Ju, 2016).

The results obtained from the FinchCatcher analysis was organized into an Unweighted Pair-Group Method using Arithmetic averages (UPGMA) dendrogram to determine degrees of relatedness between all syllables present in the population sample. The UPGMA dendrogram is a tree-like topological representation of data relationships, with groups of more closely related data points forming distinct clusters (Sneath & Sokal, 1973). It is created by using an unsupervised hierarchical clustering method over Euclidean distance and is a common tool used in ecology, bioinformatics, and phylogenetics (Legendre & Legendre, 1998). The data was centered and standardized using the scale() function to avoid over-representation of large values, in this case frequency-related variables, in the resulting cluster. With all 10 variables equally represented, a distance matrix was constructed from the standardized data using dist() and the UPGMA dendrogram was created from the distance matrix using an average linkage method in hclust(), an unsupervised hierarchical cluster analysis function. The average linkage method was selected

because of its increased accuracy for large sample sizes; it considers the distance between one cluster and another cluster to be equal to the average distance from any member of one cluster to any member of the other cluster (Legendre & Legendre, 1998).

A lexicon dictionary of syllables represented in the population sample was created from the dendrogram using dynamic tree cut. Unlike standard tree cuts, which separates clusters using a fixed height in ultrametric space relative to tree tips, a dynamic tree cut differentiates clusters based on height distance between nodes (Langfelder, Zhang, & Horvath, 2008). This method therefore uses dissimilarity information to create naturally occurring clusters relative to other clusters. Node clusters with a height less than the assigned value are reappointed to its higher-order cluster and all other extraneous outliers are labeled the same value for easy exclusion, effectively creating a complete lexicon of syllables. In this study, the *cutreeDynamic()* function in R was used to perform the dynamic tree cut. This function enables the user to select the parameters by which the dendrogram will be cut. The following parameters were used: *cutHeight* = 2; *minClusterSize* = 5; *minGap* = .5; and *maxCoreScatter* = 1. All values and variables were identical to those used by Ju (2015) with the exception of *cutHeight*, where the value was decreased from 3 to 2. The output for *cutreeDynamic()* results in each syllable being assigned a single numerical value, with members of the same cluster being represented by the same number.

Song repertoires for each bird were characterized using this lexicon dictionary. Then the Jaccard similarity coefficient (S_j), a measure commonly used for binary data in acoustic analysis (Krebs, 1989; Podos *et al.*, 1992), was used to compare degree of syllable sharing. S_j is calculated using this formula:

$$S_j = a / (a + b + c)$$

where a = the number of shared syllables in the lexicons of both localities, b = the number of unique syllable types in the first locality, c = the number of unique syllable types in the second locality. The similarity score ranges from 0 (not sharing at all) to 1 (perfect sharing). However, size of syllable lexicons are likely to be unequal between to be localities, making the maximum comparison value possible for S_j to be less than 1. Following Ju (2015), an adjustment was made to S_j to account for differences in size:

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

where d is the difference in detected lexicon size between localities. I calculated $S_j(\text{adj})$ for each individual compared with all other individuals.

To determine the relationship between syllable similarity and geographic distance, I graphed the relationship between $S_j(\text{adj})$ values against geographic distance. Two distance matrices were created: one for $S_j(\text{adj})$ values and another for geographic distance. Geographic distance was calculated by computing the distance on the surface of the earth between two points, representing the geographic coordinates of both syllables being compared, with each point consisting of longitude and latitude. The two matrices were then used to plot each pairwise comparison and correlation lines were produced.

Pearson's product-moment correlation and the Mantel test were used to reveal quantitative data trends. Pearson's correlation yields an output ranging from -1 (perfect negative correlation) to 1 (perfect positive correlation) with 0 representing no correlation. This method also produces a straight line when applied to scatterplot data and represents the underlying relationship between independent and dependent variables. Datapoints on the scatterplot, each one representing an individual observation, are assumed to be random deviations from this

underlying relationship. To avoid the possibility of ordering effects on the result, a Mantel test was also used. The Mantel test is a common test of statistical correlation between two matrices of equal rank and utilizes the Pearson product correlation coefficient across multiple data permutations (Legendre & Fortin, 1989).

Given the high density of data points and large distance included in this study, a correlation analysis alone may not adequately reveal the presence of local trends, so a nonparametric regression analysis using a locally weighted regression (loess) method was also conducted. The loess method is a multivariate smoothing procedure that is an extension of univariate locally weighted regression used to estimate a much wider class of regression surfaces (Cleveland & Devlin, 1986). Unlike Pearson’s method, which produces a line of best fit, this method uses a curve fitting procedure to represent the relationship between independent and dependent variables based on local density of datapoints. This method doesn’t return quantitative values, but can be useful in visually depicting data relationships at smaller scales more accurately than the aforementioned tools to supplement these findings.

Results:

This study included 130 birds representing 51 cities for analysis and analyzed a total of

TABLE 2: DESCRIPTIVE STATISTICS	
AVERAGE BIRDS/CITY	2.5
STANDARD DEVIATION OF BIRDS/CITY	1.5
AVERAGE SONGS/BIRD	34.2
STANDARD DEVIATION OF SONGS/BIRD	8.6
AVERAGE SONGS/CITY	87.1
STANDARD DEVIATION OF SONGS/CITY	55.7

4443 songs ($\bar{x} = 34.2, \sigma = 8.6$ per bird) (Table 2; Table 3). An average of 2.5 birds recorded at each city ($\sigma = 1.5$) were used for an average sample of 87.1 songs per city ($\sigma = 55.7$; see Fig. 2 for sample songs).

CITY	BIRDS	SONGS	AVERAGE SONGS/BIRD				
Azusa	4	151	38	Moreno Valley	1	43	43
Bakersfield	7	189	27	Newport Beach	1	46	46
Banning	1	36	36	Norwalk	2	65	33
Beaumont	3	102	34	Oceanside	2	78	39
Cambria	2	84	42	Oxnard	2	50	25
Cardiff, Encinitas	3	124	41	Pacific Palisades	1	21	21
Carmel-By- The-Sea	2	70	35	Palm Desert	2	70	35
Carpinteria	1	35	35	Palm Springs	4	103	26
Cerritos	2	82	41	Pismo Beach	2	58	29
Delano	2	86	43	Rancho Palos Verdes	2	89	45
Eagle Rock	1	39	39	Redlands	4	93	23
Escondido	1	39	39	Redwood City	7	194	28
Fillmore	4	160	40	Riverside	4	125	31
Fullerton	1	27	27	San Bernardino	2	46	23
Gilroy	3	80	27	San Clemente	2	48	24
Glendale	4	112	28	San Diego	3	67	22
Grover Beach	1	33	33	San Juan Capistrano	1	22	22
Hollister	4	155	39	San Pedro, Los Angeles	1	29	29
Hollywood	3	78	26	Santa Barbara	3	147	49
Indio	1	36	36	Santa Clara	2	54	27
Kettleman City	6	178	30	Santa Maria	1	26	26
Lake Elsinore	4	212	53	Thousand Oaks	3	161	54
Long Beach	3	139	46	Van Nuys, Los Angeles	2	65	33
Los Angeles	5	250	50	Ventura	4	106	27
Malibu	2	65	33	Yucaipa	1	43	43
Montecito	1	32	32				
				TOTAL:	51	130	4443

Table 3. Summary table of all cities sampled and the number of birds/songs representing each site.

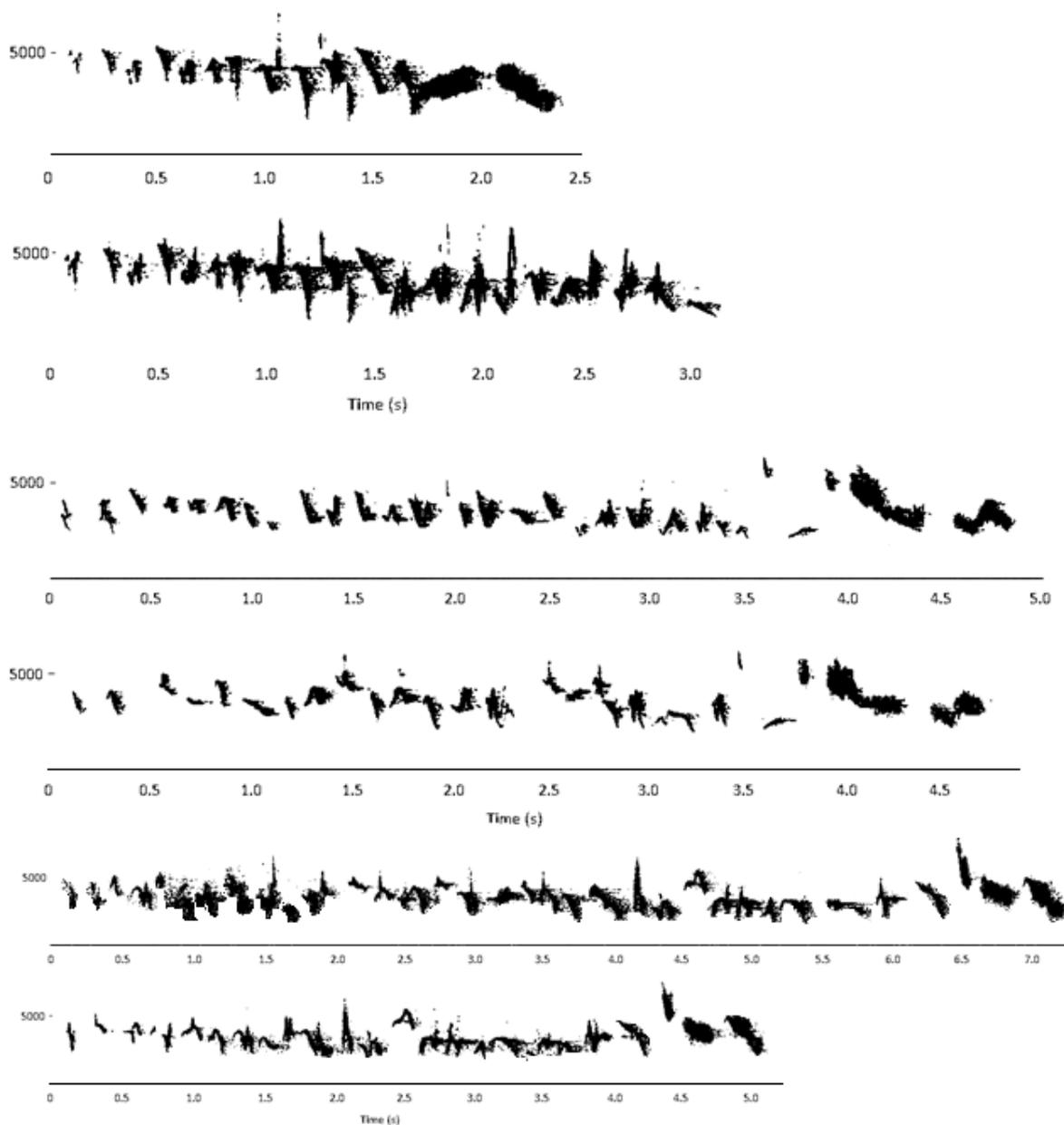


Figure 2: Song samples from three regions. San Diego, Carmel-By-The-Sea, and Santa Clara have been included for visual comparisons of typical songs that have been parsed from auditory files prior to syllable extraction. San Diego and Santa Clara are cities that are maximally distant from each other geographically in the sample at approximately 680km, whereas Carmel-By-The-Sea represents a site of intermediate distance between the other two locations.

FinchCatcher identified and extracted a total number of 74,068 syllables from the population sample. Cutting the tree with $cutHeight = 2$ revealed 495 unique syllable types. The tree cut also revealed that 2,286 syllables of the total 74,068 syllables were categorized as

outliers, accounting for 3% of the total data. These outliers were removed prior to the pairwise analysis.

The Jaccard similarity coefficient analysis resulted in a total of 8,385 comparisons and the geographic distance of the sample site ranged from 0 to 700km. $S_j(\text{adj})$ values spanned from 0.1 to 0.8 with an average value of .36. There was no correlation found between syllable sharing and geographic distance ($r = -0.027$, $t = -2.50$, $p = 0.01$, confidence level = .95). The trend line is flat, beginning at the average $S_j(\text{adj})$ value and continues straight through the dataset (Fig. 3). Datapoints throughout the scatterplot are equally spread out around the trend line, reflecting a homoscedastic pattern. These findings were confirmed by the Mantel test ($r = -0.06$, $p < 0.01$, number of permutations=999).

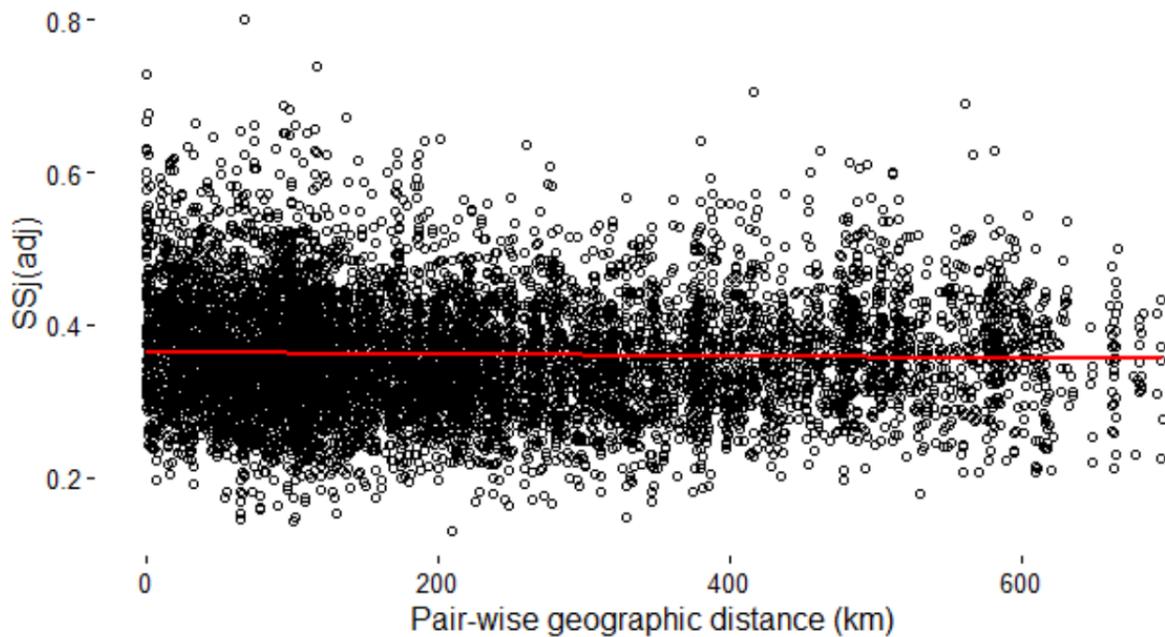


Figure 3: Comparison between syllable sharing (SSj(adj)) and geographic distance among California house finches using Pearson’s Correlation. Red line represents Pearson’s correlation coefficient $r = -0.03$, $t = -2.50$, $N = 8,385$, $p = 0.01$)

A partial analysis of this sample was conducted to increase the visual and quantitative resolution at shorter distances: 5km, 10km, 15km, 20km, and 50km. In a distance of up to 5km, the trend line begins above the $S_j(\text{adj})$ of .40 and maintains a statistically significant decrease over distance ($r = -0.42$, $t = -5.80$, $N = 160$, $p < .001$; $r^2 = .18$). The pattern is similar, but to a lesser extent, when analyzing distances up to 10km ($r = -0.19$, $t = -2.94$, $N = 242$, $p < 0.01$; $r^2 = .035$). These trends are not evident when analyzing up to longer distances. No decline in syllable sharing over distance is detectable through 15km ($r = -0.07$, $t = -1.20$, $N = 336$, $p = 0.23$) and 20km ($r = -0.05$, $t = -0.99$, $N = 465$, $p = 0.32$). At 50km, the obtained values resumes statistical significance, but there continues to be no change in the correlation pattern ($r = -0.09$, $t = -2.89$, $N = 1139$, $p < 0.01$). This resumption indicates that the results were not obtained by chance given the amount of data at 50km. Given this, it is also likely that the r values yielded at 15 and 20km are adequately representative samples of the overall population at those distances as well. The results of these partial results can be empirically summarized as: an observed relationship of decline over distance at 5km, which weakens over 10km, and has no relationship by 15km.

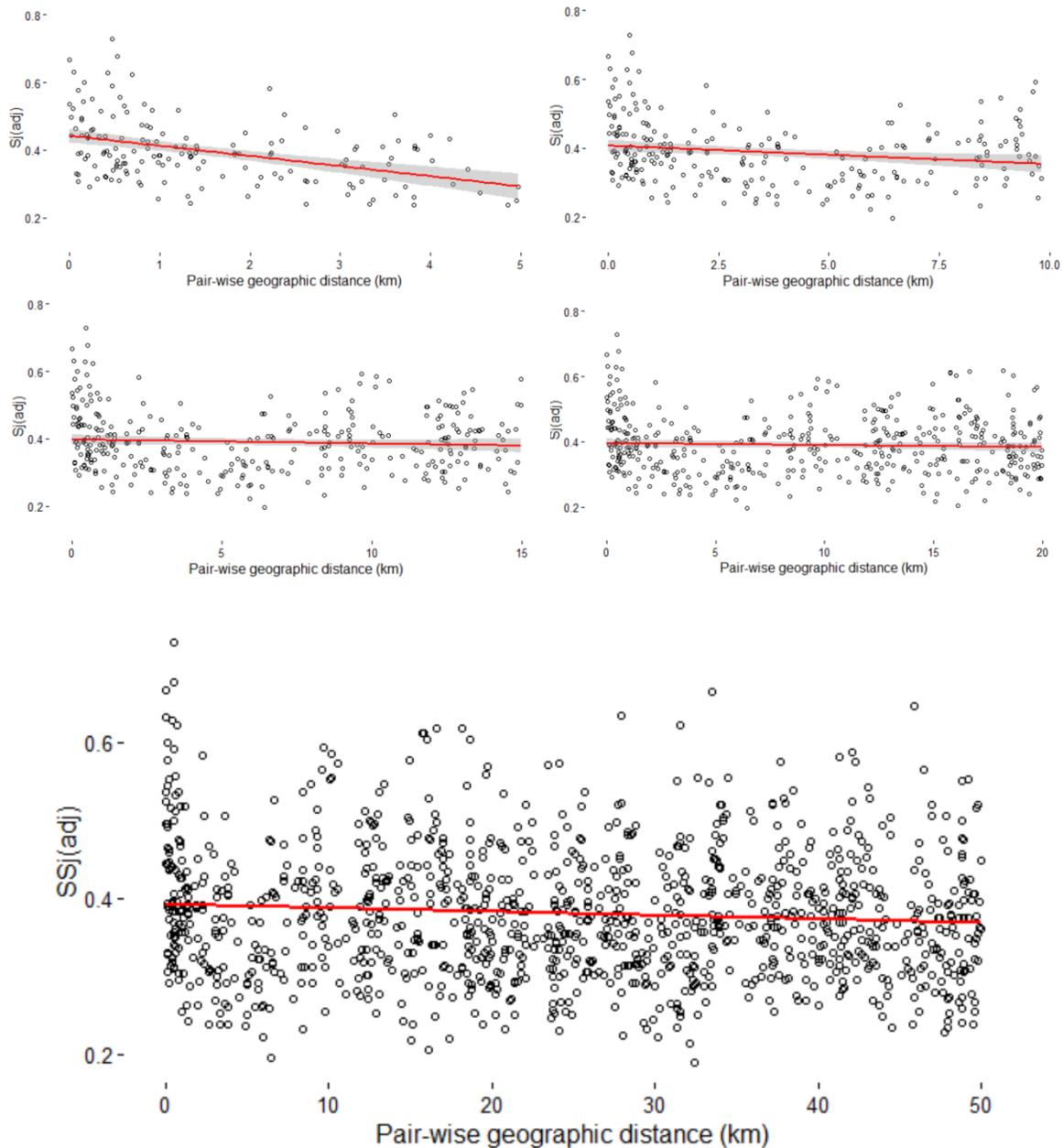


Figure 4: Scatterplots showing Pearson’s Correlation between $S_j(\text{adj})$ values for syllable sharing and geographic distance over shorter distances. A) 0-5km; B) 0-10km; C) 0-15km; D) 0-20km; E) 0-50km. The red line was plotted based on Pearson’s correlation coefficient.

When examining the data using a nonparametric analysis, the overall results obtained by the loess line are similar to those obtained via correlation methods. The loess line very gradually declines over increasing distance, but begins to increase at approximately 300km for up to 500km before leveling off (Fig. 5). The height of the loess line is consistently maintained

between $S_{j(\text{adj})}$ values of .4 and .3. The loess line, as a nonparametric analysis, does not produce quantitative results and assumes that the study sample is the population sample.

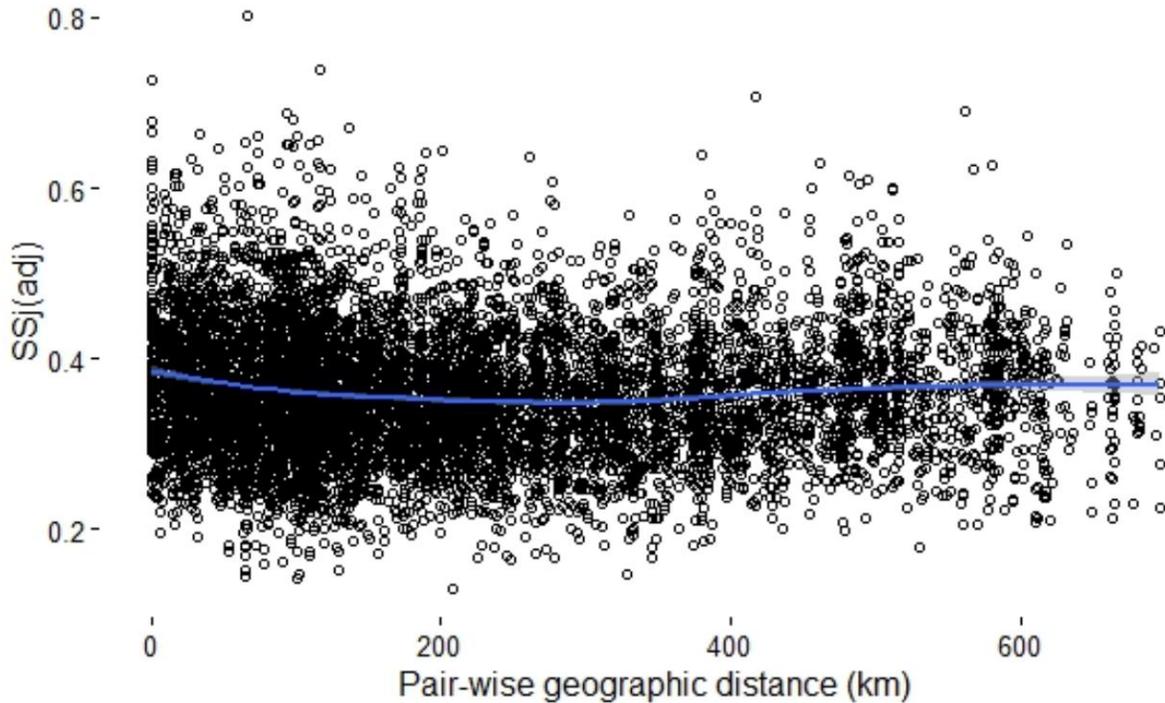


Figure 5: Nonparametric analysis showing degree of syllable sharing over geographic distance in western California. Blue line represents the loess line.

A partial analysis of the data was used to increase the visual resolution of the nonparametric analysis. At a distance of 5km, the loess line resembles a negative sigmoid curve, declining up to a distance of 1.5km and leveling off to a distance of 3km before continuing to decline. At 10km, the loess line assumes a parabolic form that begins and ends just above a $S_{j(\text{adj})}$ value of .40. At 15km and 20km, the graphs produced resemble the overall pattern present in Figure 5: the loess line gradually declines until a distance of 5km before beginning to increase up to a distance of 10km and subsequently levels off. The nonparametric model created at 50km resembles the linear model covering the same distance.

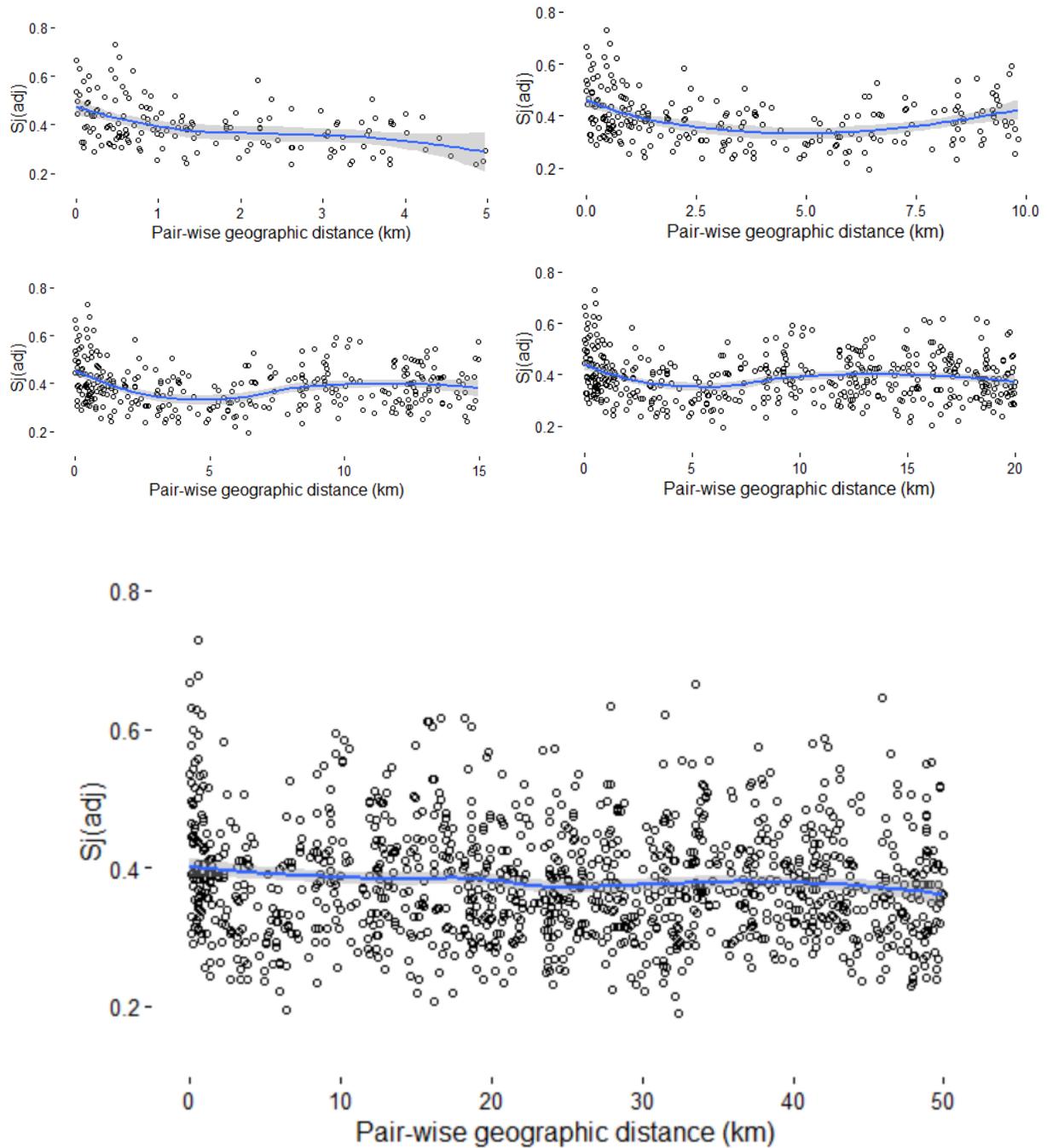


Figure 6: Scatterplots showing loess relationship between $S_j(\text{adj})$ values for syllable sharing and geographic distance over shorter distances. A) 0-5km; B) 0-10km; C) 0-15km; D) 0-20km; E) 0-50km. The blue line was plotted based on loess. Grey areas indicate the 95% confidence interval.

Discussion

The findings of this study indicate a largely stochastic pattern of geographic variation of house finch birdsong in the California population. These results were achieved by undergoing a series of three broad steps. First, song repertoires for each individual were characterized by using a population-wide lexicon to determine the total number of unique syllable types possessed by each bird. Each bird's songs were then compared to those of every other bird in the sample to determine the number of syllables shared, based on unique syllable types possessed by both individuals, and expressed in proportional terms as a single data point. Lastly, these proportions were compared to the geographic locations of the two birds at the moment of recording, represented in terms of longitude and latitude, by using linear and nonlinear regression methods. The analysis covered a distance spanning 700 kilometers. This analysis revealed no relationship between syllable sharing and the distance to which these birds have been separated throughout California. Additional analyses were then conducted on smaller scales as subsets of the original data to increase the resolution (decrease the geographical scale) of the test. This method revealed a negative correlation between syllable sharing and distance over 5 kilometers. The correlation dissipates over greater distances, becoming less marked at 10 km and disappearing at distances of 15 km and above.

Clinal variation at short distances suggest that house finch learning occurs within the context of locally limited model sources. In this regard, the present study is consistent with previous research results. Bitterbaum & Baptista (1979) demonstrated that syllable repertoires and songs between house finches gradually became less similar over increasing distances. Tracy & Baker's (1999) sample showed less syllable variation within sites than between distant sites. These observations are consistent with Mundinger's (1975) reports of song mimicry and syllable

learning among eastern juvenile males from nearby individuals. Quantitatively, this has been represented in the present study as a high proportion of syllable sharing between individuals at a single sampling site. A decline in this value up to 10km is likely due to a combination of action-based learned and selective attrition mechanisms (Marler, 1991; Nelson, 1992).

This pattern of decline of syllable similarity over distance is virtually extinguished when examining the data beyond 10 km. Given a gradual accumulation of copy errors, syllable sharing should decrease over distance until there is no syllable sharing. However, this is not the case in the current data. Apparently a largely random degree of syllable sharing occurs at every other distance beyond 10 km. Western house finches have been categorized as sedentary, so new syllables are probably not routinely penetrating both local and distant communities at equivalent levels throughout California because the population is in frequent flight. Instead, a lack of a relationship seems to suggest that there might be a second mechanism at work in the California population. This phenomenon would not cancel the effect of syllable decline over short distances, but would explain the observed stochasticity over longer distances. Stochasticity of geographic variation might indicate the presence of certain constraints being imposed on syllable genesis, transmission, and deterioration within a vocal culture of an otherwise sophisticated vocalizing species using complex birdsong.

The Syllable Saturation Hypothesis

I propose the “syllable saturation hypothesis” as an explanation for the observed stochasticity of syllable sharing in house finches. This hypothesis accepts the syllable to be a low-order song unit and the basic unit capable of cultural transmission in house finches as the underlying premise. Other studies have already suggested this could be the case in song learning (Mundinger, 1975; Lemon, 1975; Nelson, Marler, & Palleroni, 1995). There also appears to be

no interdependency between syllables immediately preceding and following individual syllable vocalizations, although limited levels of interdependency is possible and wouldn't necessarily affect the hypothesis if true (Ju, 2015). Evidence from other songbird species that lower-order units are more temporally stable these higher order units and could therefore be more promising research avenues to pursue for future studies (Ellers & Slabbekoorn, 2003; Nelson, Hallberg, & Soha, 2004). These observations qualify the syllable to be the most parsimonious unit available for study and it is partly for these reasons that I chose to exclusively examine syllable structure in this project.

The syllable saturation hypothesis assumes that all possible variations of a syllable that can possibly exist, considering the natural constraints of a syllable-producing birdsong species, does exist and results in repeated iterations of syllables. Therefore, when examining geographic variation of syllables, the phenomena would emerge as if birds separated by very large distances appear to be sharing their syllables to varying degrees. The term "saturation" refers to the maximum extent by which syllable structural variation can occupy physical space throughout a population at any given point in time. This hypothesis contains three broad components that would predict no geographic signal of variation over distance: 1) the two dimensional range of syllable variation is small; 2) variation of learning within an individual is large with no single syllable type conferring a selective advantage to the user over another; and 3) the species-specific learning mechanisms are both specialized for and restricted to conspecifics.

The two dimensions of syllable variation consist of syllable frequency and duration. These dimensions are constrained by two factors: anatomy and physiology of the user and response system of the receiver. It's already well known that the parameters of these variables are constrained by the physical apparatuses of vocalizing species as precursory conditions. In

songbirds, the shape of sound-producing organs, such as the syrinx and trachea, have large roles in determining auditory range (Podos, 1996). As a result, there are only a finite number of possible sounds any member of a songbird species can produce. This means that there are natural upper and lower physical boundaries limiting syllable structural genesis. Once a syllable has been produced and emitted into the environment, it serves as an auditory discriminative stimulus for conspecifics. Like any other discriminative stimulus, it is likely that the criterion defining a syllable and its constituent dimensions exist on a gradient scale, with the average grain being the most common natural phenomena (Honig & Urcuioli, 1981; Jenkins & Harrison, 1960; Guttman & Kalish, 1956). Exposure to imitable stimuli with a poor or above average grain would be automatically corrected by the receiver's response system and conform to the average (Ferster & Skinner, 1957; Skinner, 1953). Sober and Brainard (2009) has found that Bengalese finches adjust the fundamental frequency of their songs when their auditory feedback systems are disrupted, even throughout adulthood and post-crystallization. A smaller range of possible syllable variants due to these restrictions would increase the likelihood of finding repeat syllable types emerging between non-sharing members of the same species. Generalizability of stimulus properties would enable a songbird species to imitate the syllables of conspecifics and the cross-interactive effects of stimulus and response systems would prevent aberrant syllables from proliferating throughout the population while further restricting variation. Lee *et al.* (2009) demonstrated the ability of Zebra finches, Black-Capped Chickadees, and Mountain Chickadees to use frequency to generalize their species-specific auditory recognition abilities by using tones contiguous in frequency that were divided along 8 ranges, with each species varying their acquisition speed of frequency-range discrimination.

The constraints imposed upon on the syllable by these various mechanisms creates defined parameters of what can be summarized as “phonological space.” “Phonology” is a term borrowed from the linguistics field, as the study of sound patterns within languages, but its use it in a biological context is more general and refers only to the study of sound patterns (Yip, 2012). Phonological space can be imagined as a type of topological space (Schubert, 1968). With some of the important limitations of a syllable’s phonological space being identified, it’s clear that the syllable categorically cannot move beyond or exist outside this space in a given songbird species.

Perhaps house finch syllables, as they maneuver within the parameters of phonological space through minor innovation and imitation errors, eventually recolonize the same space occupied by syllables created by distant birds. If the house finch has a permissive learning mechanism that enables each individual to possess a high degree of variation in syllable production, and if the population size is large enough, this would eventually increase the probability of creating repeated iterations of syllables that eventually obliterates any geographic signal. Another way of imagining this phenomena is as a rampant homoplasy of syllable types, where analogous syllables exist in areas where there was no direct sharing between individuals. The massive amount of syllables in circulation completely saturates the available phonological space of this species and results in seemingly random duplications of syllable types by retarding the deterioration and extinction of syllables in the vocal culture. These random duplications become a statistical certainty given the right conditions, which could be determined mathematically.

There are two ways to interpret how a syllable can be categorized within phonological space: as a discrete variable or a continuous variable. If the syllable is a discrete variable, certain restrictive parameters would exist for each syllable type that would clearly classify syllables as

members of one type or another. This would make it more difficult for syllables to move within phonological space because the differences between two syllables, even if they are closely related structurally, would still be large enough to reduce the likelihood of a house finch from making innovation or copy errors during the imitative process. However, if the syllable is a continuous variable, then there would be no clear parameters that would clearly differentiate neighboring syllable types. This would increase the chance of individuals making extremely minor changes to the syllable as it's transmitted from one bird to the next. The syllable saturation hypothesis would predict that the syllable is a continuous variable functioning along a phonological continuum within the restrictive parameters set by anatomy, physiology, and learning response systems.

Experimental tests are needed to discover the extent to which certain constituent elements of this hypothesis are generalizable to house finches. However, there are some clues that this hypothesis may have some internal and external validity. The data here reveal a low number of unique syllable types found in the current study (495) relative to the high number of total syllables recorded (74,068), which suggest that the maximum number of syllable variants possible are already in circulation; a saturated phonological space. As was pointed out earlier, California house finches are unlikely to be in such frequent and distant flight that new syllable types are being regularly introduced to distant communities. One way to refute this claim would be to demonstrate that particular syllable types are unique to the geographic regions by which they were found. Interestingly, there appears to be evidence to the contrary. Tracy *et al.* (2009) has reported that some syllable types in Colorado were also found in Iowa, Wisconsin, New York, and California. The authors also stated that it is unlikely for the syllables to have infiltrated the other study sites, especially considering the population separation between eastern and

western birds. This seems to suggest that the syllable saturation hypothesis may have explanatory power that extends beyond the scope of the present study.

Past to Present: Research on Geographic Variation in House Finch Birdsng

The results of this study differ from previous research conducted on house finches. Bitterbaum & Baptista (1979) and Tracy & Baker (1999) found that western birds have syllable sharing within sites that declines over distance. Interestingly, with the exception of New York, the stochasticity present in this study bears greater resemblance to eastern populations (Pytte 1997; Tracy *et al.*, 2009). While Munding (1975) originally reported dialectical patterns in the New York population, Ju's (2015) study near this area revealed sharp declines in sharing over short distances that was followed by a leveling off over longer distances.

The exploration of birdsong produced by house finches and its relationship with geographic distance began with Munding (1975). Munding (1975) included 155 birds in the study and manually classified the song elements of each song by using a spectrographic analysis of audio recordings. A definition system was created to describe what a syllable, song element, silent period, and song length is and constitutes. This set a precedent for other researchers in this field to follow. The paper reported the presence of dialects in house finches sampled along 9 coastal sites of Long Island Sound. These sites spanned an area of 130 km and included Manhattan, Milford, and Poughkeepsie as the outermost sampling locales. Conclusions were derived from descriptions of local dialects in Chaffinches made by Poulsen (1951) and Marler (1952).

Bitterbaum & Baptista (1979) are the only researchers who have explored the question of geographic variation of house finch syllables in California prior to this study. The authors

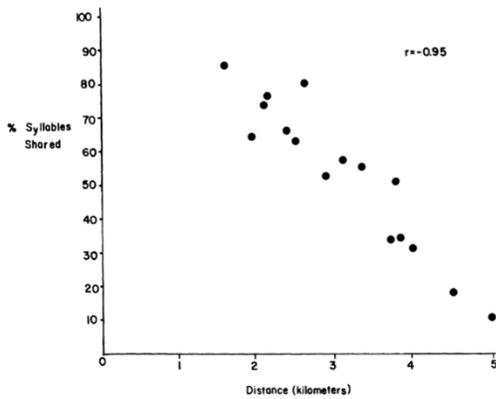


Figure 7. House finch Syllable sharing over geographic distance in California as presented by Bitterbaum & Baptista (1979)

included unbanded birds found in the wild, both male and female, and used testosterone injections to induce singing in females prior to song recordings. Using the criteria as defined by Mundinger (1975) to catalog syllables, 141 unique syllable types were found at Occidental College and this pool of syllables at distance 0 was used to model syllable sharing over a distance of 5 km. (Fig. 3). Bitterbaum and Baptista's

(1979) report infers that there were no unique syllable types found at other sites that weren't also present at distance 0. There were more unique syllable types found in this study than that found by Mundinger (1975), leading the authors to conclude that western house finches contain greater syllable diversity than those of eastern house finches. These finches also displayed more themes per individual ($\bar{x} = 4.01$) than those in the east ($\bar{x} = 2.23$). Variations in syllables and themes from individual to individual were explained as due to differences in individual learning.

Colorado house finches are also considered to be a part of the western house finch population and have had their geographic variation of song researched by Tracy & Baker (1999). Their study included 4,290 songs from both banded and unbanded males found at 21 sites in northern Colorado. A total of 23 birds were included in this study. 727 unique syllable types were cataloged, also using the same criteria created by Mundinger (1975). Tracy & Baker (1999) is the first study to use the adjusted Jaccard similarity coefficient ($Sj_{(adj)} = a/(a+b+c-d)$) to determine amount of syllable sharing between house finch songs over distance and compile a

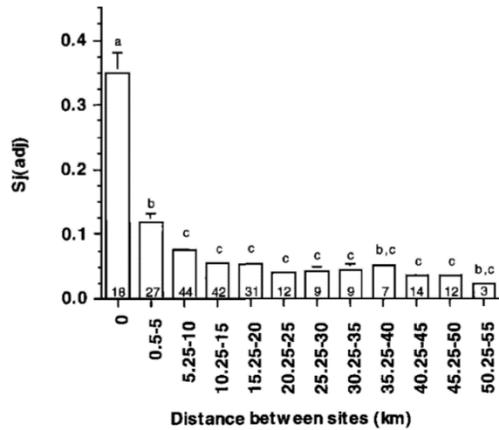


Figure 8: House finch syllable sharing over geographic distance in Colorado as presented by Tracy & Baker (1999). Results of test comparing means between sites grouped into 5-km distance intervals. Histogram bars with the same letters indicate groups that are not significantly different at ($\alpha = 0.05$ for experiment wise error rate (Tukey's W). Number of comparisons within distance intervals are indicated. Error bars were too small to represent.

syllable catalog. The authors used this approach to report average within-site sharing ($\bar{x} = 0.353$) as higher than between-site sharing ($\bar{x} = 0.272$).

Contrasted against Bitterbaum & Baptista's (1979) findings, Tracy & Baker (1999) reported that their birds did not share the majority of their syllable types with another bird and few syllable types were shared among all birds within a site. The study reveals a sharp decline in syllable sharing up to 5 km beyond distance 0 and levels off as the distance approaches 50 km.

Pytte (1997) recorded 274 songs from 20 individuals in five different geographic areas 15 - 90 km apart in southeastern Wisconsin. All birds

recorded were from unbanded males. Syllable sharing was determined using a chi-squared model, which Pytte (1997) reported did not decline over distance, unlike the findings of Bitterbaum & Baptista (1979). Exact figures for amount of syllable sharing between birds wasn't reported, nor was a graph produced to represent the relationship between sharing and distance. Individual birds produced an average of 11.4 ± 3.0 different syllables per song with 8 ± 7 unique syllable types per bird, but did not report the total number of unique syllable types found in the study. Pytte (1997) was the first study to conclude stochastic variation of house finch birdsong.

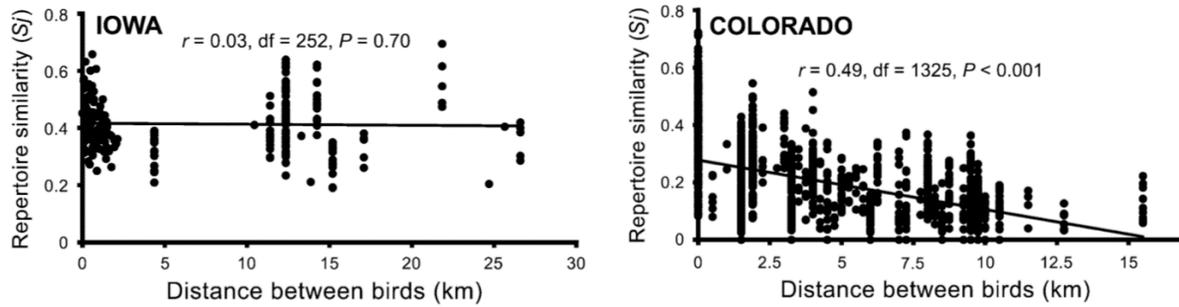


Figure 9: House finch syllable sharing over geographic distance in Iowa as presented by Tracy et al. (2009). The image on the left corresponds to the paper’s main study conducted at 6 towns in Iowa ($N = 23$ birds), while the image on the right is a reanalysis of Tracy & Baker (1999) using Jaccard’s similarity coefficient formula without the adjusted value ($N = 52$ birds).

Iowa house finches in Sioux County were examined by Tracy *et al.* (2009) at 6 towns ranging from 0 to 30 kilometers apart. 666 songs were recorded from 23 unbanded birds and the amount of syllable sharing was determined using Jaccard’s similarity coefficient ($S_j = a/(a+b+c)$). However, unlike the previous study done in Colorado, Tracy *et al.* (2009) opted out of using the adjusted Jaccard value they used in Tracy & Baker (1999). The reason they offered for this change in methodology is because they believed that their study had successfully detected almost all the syllables for most of the birds included and because unclassifiable syllable types were much less common in the present study (Tracy *et al.*, 2009). 132 unique syllable types were found in Sioux County and S_j scores ranged from 0.19 to 0.69 with no decline in syllable sharing over distance. The authors then reanalyzed the Tracy & Baker (1999) data, this time using 6 to 37 songs ($\bar{x} = 15.0 \pm 4.24$, median = 13) from 52 house finches, using the same methods as the present study. Even with this revised approach, Tracy *et al.* (2009) still found a decline in syllable sharing over distance among the Colorado birds (S_j values ranging from 0 to .54). While my methods are in disagreement with the revised approach that uses an adjusted versus unadjusted Jaccard correlation coefficient, it doesn’t appear that the unadjusted method has changed the overall trends found by Tracy & Baker (1999). Therefore, the Iowa analysis

would probably not reveal a different pattern if the adjusted S_j calculation were used. Tracy *et al.* (2009) hypothesized that the characteristics found in Iowa birds would be expected if the area had been colonized quickly by either a large number of birds from a single source population with extensive song sharing, or a small number of birds with a rapidly expanding population.

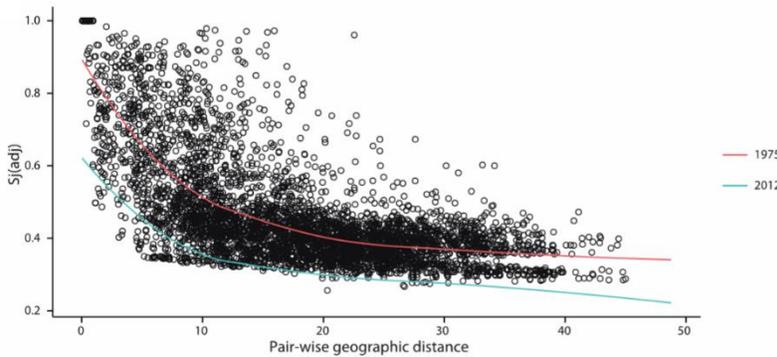


Figure 10: House finch syllable sharing over geographic distance in western Long Island as presented by Ju (2015). Samples were from 2012 ($N = 96$) and 1975 ($N = 94$)

Ju (2015) used 981 songs from 96 birds recorded in 2012 and 1042 songs from 94 birds recorded in 1975. Both datasets were collected in New York, but the sites sampled were different than those of Munding (1975). Data from

2012 spanned Queens, Brooklyn, and Nassau County, whereas the 1975 data sampled locales throughout western Long Island (Ju, 2015). This is the first study to use the automated similarity measurement procedure FinchCatcher to classify house finch syllables, yielding a total of 407 syllable types from a total of 11,968 from 2012 and 17,005 from 1975. 241 syllables were excluded from the study due to poor quality or classification as outliers. $S_{j(adj)}$ values in the 2012 dataset ranged from 0.1 to 0.85. The study sites spanned 50 kilometers. Both datasets for New York exhibited a sharp decline in syllable sharing up to 5 kilometers before the loess line levels off as it approaches 50 kilometers, resembling the results found by Tracy & Baker (1999) and Bitterbaum & Baptista (1975) (Fig. 10). Average $S_{j(adj)}$ values were higher in 1975 than in 2012. Ju (2015) reported that the results do not conform to purely a clinal pattern and instead represents an intermediary phase between clinal and dialectical variations. The multiple founder effect,

differential dispersal or migratory patterns, and developmental stress hypotheses were invoked as potential explanations to describe the results from the data obtained in 2012. A temporal study between the two datasets revealed a 20% increase in syllable types with a decrease in stochasticity from 1975 to 2012 (Ju, 2015). Demographic effects, migration patterns, developmental stress, and relaxed selection hypotheses were proposed to describe these changes over time. Although the 1975 data sampled Long Island, 40 kilometers away from Mundinger's (1975) study site, Ju's (2015) analysis suggests that the evidence of dialects in eastern house finches may not be as strong as previously thought.

California house finches in the present study exhibited some decline in syllable sharing at short distances, but not at larger distances ($S_{j(\text{adj})}$ ranging from .13 to .80; $\bar{x} = .36$). Compared to past studies, this study includes a larger sample of birds and songs spanning over a considerably greater geographic distance (Table 4).

Table 4: Summary of Past Findings

STUDY SITE/AUTHOR	POPULATION TYPE	TOTAL SONGS	SAMPLING DISTANCE	SYLLABLE CLASSIFICATION	ANALYTICAL METHODOLOGY	SYLLABLE TYPES	GEOGRAPHIC VARIATION
ROGINEK (2018)	Native	4443	700km	Automated	Jaccard Coefficient (adj)	495	Stochastic
TRACY & BAKER (1999)	Native	4290	50km	Manual	Jaccard Coefficient (adj)	727	Clinal
BITTERBAUM & BAPTISTA (1979)	Native	125	5km	Manual	Percent decline of syllables compared to Site 0	141	Clinal
JU (2015)	Introduced	2023	50km	Automated	Jaccard Coefficient (adj)	407	Hybrid Clinal
TRACY ET AL. (2009)	Introduced	666	30km	Manual	Jaccard Coefficient	132	Stochastic
PYTTE (1997)	Introduced	274	90km	Manual	Chi Squared	N/A	Stochastic
MUNDINGER (1975)	Introduced	N/A	130km	Manual	Manual Pattern Analysis	N/A	Dialectical

My methodological approach was mostly automated, as opposed to the studies prior to Ju (2015). This automation process frees the user from subjective interpretation in two major areas: syllable extraction and syllable classification. FinchCatcher can extract syllables from audio files containing background noise, but there were occasions where excessive interference required intervention to improve signal resolution. Errors in signal extraction would occur if the user failed to identify misalignments, using visual inspection, between the program's estimated extraction parameters and the actual syllable. The result would produce extracted syllables longer or shorter than the actual sample. However, these false syllables are more likely to have shapes that are radically different than the shapes of true syllables. Processing of extracted syllables via dynamic tree cut in R would subsequently label these false syllables as outliers, enabling easy identification and removal prior to Jaccard's comparison. Syllable classification is based on the manual input of several parameters, one of which included cutHeight. This parameter specifies the minimum distance between two nodes of a tree required to be classified as a separate syllable. Therefore, the higher the value assigned for cutHeight, the more syllables are grouped as the same type: fewer clusters and outliers are produced; a lower cutHeight value would result in fewer syllables being grouped together: more clusters and outliers are produced. Ju (2015) selected her cutHeight to be 3; whereas 2 was selected for the present study. Although it is possible that this may not have been the ideal choice, the alternatives do not seem to provide different results. Manipulations of this value would simply adjust the average $S_j(\text{adj})$ values of the data as well as start and end points for the trend line without having any effect on Pearson's correlation coefficient or shape of the loess line. Even when considering this possibility, the current cutHeight is likely to be at the correct value. A higher cutHeight would significantly reduce the number of syllable types, from 495 to only 140, which would suggest lower syllable

diversity exists in western populations than eastern populations and contradict past observations (Tracy & Baker, 1999; Tracy et al. 2009, Ju 2015).

The house finch populations in California, Iowa, and Wisconsin have common characteristics consistent with the hypothesis of saturation of phonological space. However, the previous California study, Colorado, and New York locales exhibit patterns that are not consistent with the syllable saturation hypothesis, suggesting the importance of other factors.

An Attempt to Synthesize Syllable Saturation within the Framework of Past Studies

The syllable saturation hypothesis does not contradict the previous findings and observations of a decline in syllable sharing over distance in some populations. Observations of juvenile house finches suggest that this species learn their song from neighboring conspecifics at a developmentally early age (Mundinger, 1975). Because of this, a decline of syllable sharing over distance is a reasonable expectation when: a) the geographic distance covered by a study is sufficiently small; b) the population density being sampled is low; c) a larger geographic distance is covered but the terrain contains natural barriers that obstruct auditory exposure to conspecifics, making syllable imitation challenging; or when d) birdsong is being subjected to relaxed selection. Interactions between these variables can further strengthen signals of declining syllable sharing over distance while weakening syllable saturation.

Bitterbaum and Baptista (1979) reported a substantial decline in syllable sharing over a distance of 5km ($r = .95$) in California. A partial analysis of my data up to 5km also demonstrates a decline in syllable sharing covering the same distance, but the correlation and proportion of variance accounted for is much lower ($r = -.42$). At 10km, the results continue to weaken substantially ($r = -.19$). This discrepancy can be explained via differences in research methods.

The authors of the former study chose to compare syllable pools obtained at each site to a single pool of syllables found at distance 0 that is said to contain all syllables represented throughout the study sample for a total of 16 comparisons. This method does not make comparisons between individual birds at each site and therefore doesn't address the extent of syllable sharing between birds within and between sites, an observation also pointed out by Tracy & Baker (1999). In contrast, each data point on Figure 4a represents a single bird-to-bird comparison and totals at 160 comparisons.

Colorado house finches may be inhabiting an acoustically impoverished environment. This could be caused by a lower density of birds occupying the same syllable community and further impaired by mountainous terrain. Although the Colorado population originated from California, differing altitudes and mountainous terrain might reduce song exposure and syllable acquisition from distant neighbors. Tracy & Baker (1999) found a sharp decline over short distances and a leveling off over further distances, and they also found a very high number of unique syllable types in Colorado (727) as compared to other studies. High numbers of syllable types relative to total number of syllables sampled could either indicate auditory isolation by distance or an incorrect classification of syllables due to human subjective processing. The former case would be due to fewer opportunities for individuals to be exposed to enough syllables to prevent the accumulation of copy errors affecting the phonological shape of each syllable. If the high number of syllable types are due to human classification differences, song processing through FinchCatcher would resolve these differences. The authors did seem to suspect that sample site altitude may have a role in affecting their results. Unlike other studies, Tracy & Baker (1999) reported study site altitudes, although they did not invoke an argument with these data.

The two datasets that Ju (2015) used were from two overlapping locales in western Long Island. A temporal analysis of the region seems to suggest that there is a decline in stochasticity over time. To explain this observation, Ju (2015) hypothesized that relaxed selection may be occurring among females for their preference in song in favor of plumage coloration. Past studies have pointed out that New York house finches are more colorful than western house finches and it has been thought that the reason for this may be because the founder birds were selected by merchants for their coloration before being sold as “Hollywood Finches” (Hill, 2002; Elliott & Arbib, 1953). A pilot study demonstrated some evidence for this: there was higher complexity and consistency of song found among western house finches versus their eastern counterparts (Ju, 2015). If relaxed selection on birdsong is occurring in this population, it could remove the regional effects of syllable saturation. Songs would shorten and be comprised of fewer syllables. Fewer syllables circulating throughout phonological space would enhance geographic signal by reducing the statistical chance of spontaneous emergence of duplicate syllables and increasing the signal strength of syllable sharing over shorter distances due to social learning.

Post-hoc Pilot Study: Spatial Analysis of house finch Syllables between New York and California

In the present study, syllable saturation was proposed as a hypothesis to explain stochasticity of sharing in a regional and continuous population. If syllable saturation is a species-wide phenomenon in house finches, then a spatial analysis of house finch syllables even between members of discontinuous populations, across vast distances, would continue to create the appearance of stochastic sharing.

To test this hypothesis, I conducted a post hoc pilot study using syllables from two disparate populations of house finches (New York and California). The discontinuity between

these populations increases the likelihood that house finch syllables are not culturally homologous between localities, either through common descent or by infiltration of syllables by bird movement. Thus, any incidence of syllable sharing between these areas is even more likely than among birds in California to be similar by analogy or convergence; and a lack of decline in sharing over such great distances would lend additional support to the syllable saturation hypothesis. By contrast, a lower level of sharing between these areas than among Californian birds would contradict the syllable saturation hypothesis.

Methods

A total of 20 birds and 200 songs were selected from New York and California recordings made in 2012. 10 birds were selected at random from each population, and 10 songs were used from each bird. This sampling strategy was designed to capture the greatest number of syllables in cultural circulation from the two populations with an economy of data.

The analysis used the same approach as the main study. All syllables from both populations were extracted from their songs using FinchCatcher. These syllables were pooled into a single dataset and was then subjected to a hierarchical cluster analysis using R. The syllable lexicon dictionary was created by separating nodes on the dendrogram using Dynamic Tree Cut. The following parameters were used: *cutHeight* = 2; *minClusterSize* = 5; *minGap* = .5; and *maxCoreScatter* = 1. Song repertoires for each bird was recreated using this lexicon dictionary and the adjusted Jaccard similarity coefficient ($S_j(\text{adj})$) was used to compare degree of syllable sharing. To determine the relationship between syllable similarity and geographic distance, I graphed the relationship between $S_j(\text{adj})$ values against geographic distance. Geographic distance was calculated by computing the distance on the surface of the earth between two points, representing the geographic coordinates of both syllables being compared,

with each point constituting of longitude and latitude. The two matrices were then used to plot each pairwise comparison and trend lines were produced. Pearson's product-moment correlation was used to reveal data trends.

Results

The Jaccard similarity coefficient analysis resulted in a total of 190 comparisons and the geographic distance of the sample site ranged from 0 to 6000km. $Sj_{(adj)}$ values spanned from 0.2 to 0.8 with an average value of .49. There was no correlation found between syllable sharing and geographic distance ($r = -0.14$, $t = -1.91$, $p = 0.05$, confidence level = .95; $r^2 = .02$). The trend line is flat, beginning near .5 on the y-axis and continues straight through the dataset (Fig. 10). Datapoints throughout the scatterplot are equally spread out around the trend line, reflecting a homoscedastic pattern.

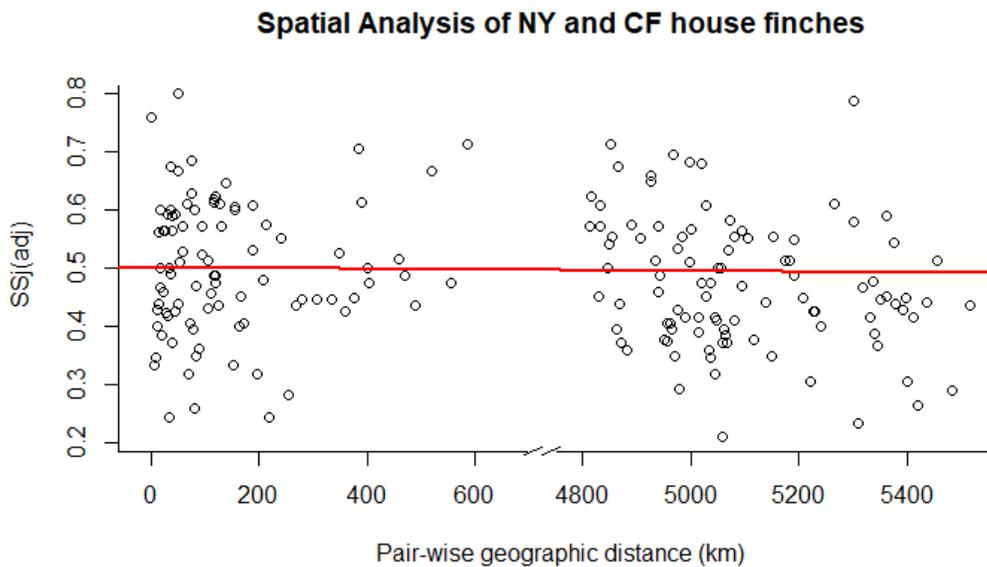


Figure 11: Spatial Analysis of NY and CF house finches. Syllable sharing ($SSj_{(adj)}$) and geographic distance compared within and between New York and California house finches. Red line represents Pearson's correlation coefficient $r = -0.14$, $t = -1.91$, $p = 0.05$

Discussion

The post hoc study of syllable sharing between New York and California house finches indicates a stochastic pattern of geographic variation of song across the continent ($r = -0.14$). Despite being separated by more than nearly 6000km, the analysis seems to suggest that a variable amount of syllable sharing is occurring between the two populations. This is difficult to believe. The eastern population was founded in the 1940s and has been separated from western house finches for approximately 70 years. A hypothesis positing that the syllables are somehow being shared between these two populations, when they have lived in isolation from one another for this long period of time, does not seem likely. Likewise, an assumption that the same syllables introduced to New York from California during founding could have persisted to the present also seems unlikely. Ju (2015) has demonstrated that diversity of syllable types have increased over time in New York from 1975 to 2012, while persistence of older syllables have decreased. There is no evidence to suggest that the opposite effect would have occurred prior to 1975. Increases in syllable diversity is more likely to also increase the likelihood of newly innovated syllables to be of the same form and type of other syllables from distant populations. Therefore, this post-hoc seems to support the idea that recolonizations of phonological space are occurring within the house finch cultural community throughout the United States.

Conclusion

Why is it that past researchers exploring house finch song have not explored a syllable saturation hypothesis? I suggest that the history of geographic variation in house finch song has undergone a series of historical accidents that directed the findings of future research, beginning with Mundinger's (1975) report of dialects in New York house finches. Being the first study of its kind, it inspired Bitterbaum & Baptista (1979) to investigate whether house finches in their

native population, California, exhibited dialect patterns as well. Small sample size, short distance covered, and their analytical method resulted in a continuous decline in syllable sharing over distance and established a behavioral contrast between east and western house finches. How syllable sharing changes over distance thus became the focus of subsequent studies. Pytte (1997) then conducted a study of Wisconsin house finches and reported no difference in syllable sharing over distance, refuting the founder effect hypothesis as a potential explanation for these observations. Tracy & Baker's (1999) Colorado study reported a decline in syllable sharing over distance. This study provided added support for Bitterbaum & Baptista's (1979) findings, as a pattern seems to be emerging that suggests a population-specific cultural attribute of declining syllable sharing over distance occurs in western house finches. Perhaps it was due to this agreement between these studies that Tracy & Baker's (1999) discussion focused on contrasting the differences between western and the dialectical eastern house finches, with Pytte's (1997) findings being largely overlooked. A follow-up study conducted in Iowa by Tracy *et al.* (2009) revealed no difference in syllable sharing over distance, but the findings were treated as a sort of anomaly by the authors. Results were only briefly compared to those found in Wisconsin by pointing out that Pytte's (1997) sample consisted of first and second generation immigrants. Tracy *et al.* (2009) argued that because the populations are too new, it is for this reason that dialects would not have yet emerged in Wisconsin and this may be also be the same reason why the Iowa sample yielded stochastic results as well. Finally, Ju's (2015) study found a clinal decrease in syllable sharing in New York in two different time periods. Explanations for this were then framed in terms of destruction of prior dialectical formations, but the research did not make an attempt to address the stochastic findings of Pytte (1997) and Tracy *et al.* (2009). Because these findings, from Munding (1975) to Ju (2015), have first revealed evidence of

dialects, then disproportionately uncovered greater evidence of clinal variation over stochastic variation, there was very little reason to seriously investigate the potential causes of stochasticity in house finches. The results of the current study forced a more rigorous examination of stochasticity's role in birdsong.

My study in California revealed a stochastic pattern of geographic variation of house finch syllables and I offered a new conceptual framework in an attempt to explain these findings. I proposed a new hypothesis called the syllable saturation hypothesis. Within its framework, I outlined the physical constraints affecting syllable genesis and transmission by defining the parameters restricting the phonological space of syllables and describing the continuum by which these syllables can change within this space. An attempt was made to synthesize the findings of past research in light of new evidence into this conceptual framework. Some predictions were made about the house finch that could explain why some previous research projects have revealed no geographic signal. Namely, given phonological constraints, house finches possess a combination of species-specific imitation and individual innovation leading to variation in syllable production. This would lead to a high probability of converging on syllable duplicates across distances where direct individual-to-individual sharing is highly unlikely. A post-hoc analysis was conducted and revealed supporting evidence for these ideas. Given these findings, stochasticity could be a more common condition of syllable geographic variation than initially thought. Future studies can examine differences of these patterns within the context of perturbations of this system.

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