

SONG ORGANIZATION OF HOUSE FINCHES AT THE EDGE OF AN EXPANDING RANGE¹

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Abstract. Colonization patterns of House Finches (*Carpodacus mexicanus*) provide a rare opportunity to study regional differences in songs associated with differences in colonization histories. House Finches have undergone two different types of colonization events in the mainland United States which have given rise to differences in singing among three regions. In this study, I describe songs of House Finches that have recently colonized southeastern Wisconsin at the western edge of their expanding eastern range. Song stereotypy, repertoire size, and song sharing patterns in Wisconsin differ from those of eastern and western House Finches. An earlier House Finch colonization of the East Coast, by the parental West Coast stock, resulted in an increased rigidity of song syntax, decreased repertoire size, and increased song sharing. Colonization of Wisconsin by East Coast stock, however, has led to a decreased rigidity of syntax, increased repertoire size and decreased song sharing. The two colonization events differ markedly in the numbers of founders and the size of the area from which potential colonizers may have originated. Differences in singing between these two areas may have been influenced by the amount of heterogeneity of song types present during the early stages of colony establishment.

Key words: colonization, song, dialect, syntax, House Finch.

INTRODUCTION

Many songbird species have song dialects, or regional differences in songs. Whereas comparisons among dialects provide information about intraspecific variability, such accounts usually are unable to offer insight into the historical context in which changes in song structure have occurred. Colonization of new areas by songbirds is thought to be one process through which regional differences in songs may arise (Thielcke 1969, Baker and Cunningham 1985). Most evidence for dialect formation due to colonization lies in differences in songs between mainland and insular populations where species introductions have occurred (Baptista and Johnson 1982, Jenkins and Baker 1984, Baker and Jenkins 1987). Studies of songs during the colonization process are particularly informative in that they present an opportunity to associate changes in social and ecological variables with changes in songs and may provide a time frame in which song changes take place (Mundinger 1975). This paper documents differences in song stereotypy, repertoire size and song sharing patterns between House Finches (*Carpodacus mexicanus*) that have recently colonized southeastern Wisconsin, and House Finches on the East and West

Coasts of the United States described by Mundinger (1975) and Bitterbaum and Baptista (1979), respectively.

House Finches are native to the western United States, southern Canada, and Mexico. East Coast House Finches are descendants of a small number of California House Finches released from pet shops on Long Island, New York in 1941 (Elliot and Arbib 1953). The East Coast introduction resulted in a dramatic change in song organization of eastern House Finches from that of the parental California House Finches (Mundinger 1975, Bitterbaum and Baptista 1979). Eastern songs are more stereotyped and less syntactically variable than California House Finch songs. In addition, eastern repertoire sizes are smaller and song sharing patterns more discrete than in California.

The eastern population increased rapidly and expanded north and south along the East Coast and westward throughout the Midwestern states. Recordings of House Finches in Wisconsin show differences in song variability, individual repertoire sizes, and song sharing patterns from these characteristics recorded 19 years earlier in East Coast House Finches (Mundinger 1975). Whereas much research documents regional differences in the structure of song elements or in the presence or absence of song elements (review in Thielcke 1969, Mundinger 1982), this paper

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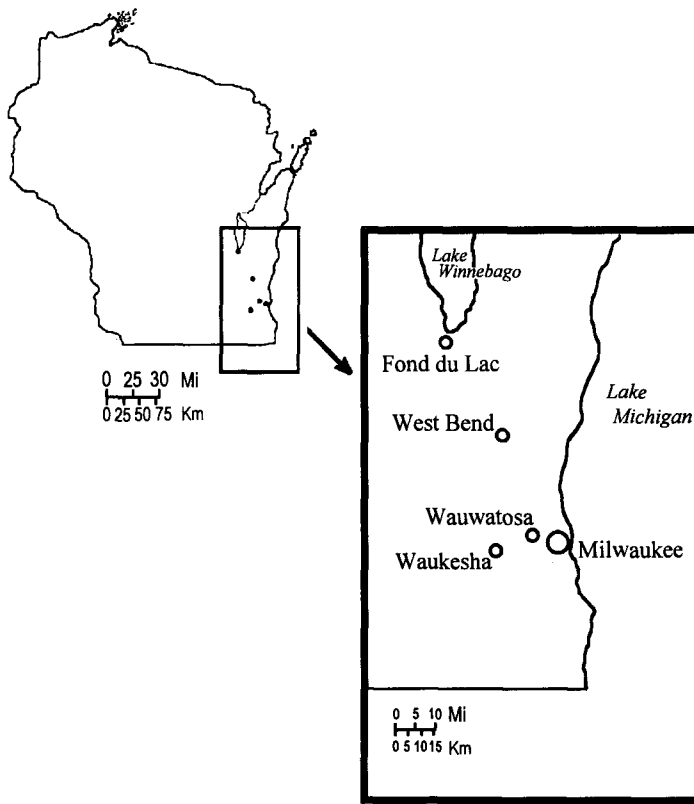


FIGURE 1. Map of House Finch study sites in Wisconsin.

adds to the small number of studies reporting intraspecific variation in the strictness or leniency of syntax rules (Bitterbaum and Baptista 1979, Kroodsma 1980, Baptista and Johnson 1982, Jenkins and Baker 1984, Lynch and Baker 1993).

Differences between Wisconsin and the East Coast colonization patterns, including availability of song model tutors and heterogeneity of colonizing flocks, are discussed as potential influences on song learning. The results of this study underscore the importance of examining social and behavioral factors in considering the extent of a species' plasticity in acquiring the organizing principles of song production.

METHODS

Recordings were made between 06:00 and 15:00 from March through July, 1992. Adult male House Finches were recorded using an Audiotecnica line cardioid microphone (AT385) and a Nakamichi cardioid microphone (CM 100)

with a Sony Professional Walkman cassette tape recorder. Songs were analyzed with a Kay Elemetrics Sona-Graph 7800 using a 300 Hz bandwidth filter.

All birds recorded were unbanded. To avoid recording the same individual twice, each bird was recorded only while it was within view and recordings were made in each area only once. Adult males were identified by plumage and behavior. Sample sizes and distances among recording sites were chosen to be similar to those of Mundinger (1975) and Bitterbaum and Baptista (1979) so that the three studies can be compared. I analyzed 274 songs from 20 individuals recorded in five different geographic areas, 15–90 km apart, throughout southeastern Wisconsin (Fig. 1). These 20 individuals were selected from a total of 42 birds recorded based on the criteria that I was able to record five or more songs from each (mean \pm SD = 13.7 ± 9.4 songs/bird, $n = 20$). Songs from 22 birds which sang fewer than five songs were not included in

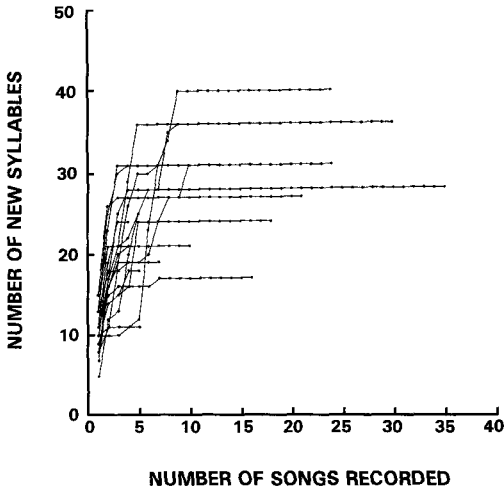


FIGURE 2. The number of new syllables produced with each successive song. A line represents an individual's increase in syllable repertoire per additional song produced. Dots along lines represent each song.

this study; however, inspection of their songs indicated that song organization was similar to that of the other birds. The 5-song criteria was chosen because this number satisfactorily represented a bird's syllable repertoire. A mean of 90.2% of the total number of syllables recorded from each individual were sung within the first five successive songs (Fig. 2). The number of new syllables produced is highly correlated with the number of songs produced when all songs are analyzed (least squares linear regression: $r^2 = 0.42$, $P = 0.002$). When songs produced after the first five are analyzed, there is no correlation between the number of new syllables and the total number of songs recorded (least squares linear regression: $r^2 = 0.027$, $P > 0.05$). This indicates that the number of new syllables increases with the first five songs recorded, then decreases. Munding (1975) recorded songs from 3–5 males from each of nine sites 10–20 km apart, and 112 males from an area 12.2×12.2 km surrounding one of the recording sites. Recordings ranged from 1–195 songs per bird. Bitterbaum and Baptista (1979) recorded 746 songs from 73 birds across four recording sites within a 5 km transect, 69 songs from 5 males from a site outside the transect, and 42 songs from 14 males on an island 28 km from the California coast.

The definitions of syllable and song type follow Munding (1975) and Bitterbaum and Bap-

tista (1979). A syllable is either a single trace on a sonagraph or multiple traces that are separated temporally by less than 0.02 sec and always appear together (Munding 1975). Syllables were assigned a letter or number allowing songs to be translated into representative sequences. Because the classification of syllables affects the degree of song variation found within an individual, among individuals, and among recording sites, the range of variation within syllable types produced by each individual was determined by visual inspection of sonagraphs before comparisons were made among individuals. The amount of variation permissible within a syllable category depended upon whether variation was graded or discrete. Similar syllables which were produced with graded variability were scored as the same syllable (e.g., Fig. 3A and 3C, syllable 1). On the other hand, similar syllables were judged to be distinct if even small differences between them were consistent (e.g., Fig. 3A, syllables 4 and 5). Syllables were catalogued in an individual "dictionary," and syllable repertoires were counted.

Syllable dictionaries were compared among individuals in each recording area to determine shared and unique syllables, providing a measure of intrasite variability. Individual dictionaries then were pooled from birds within a recording site, and each combined dictionary was compared across sites to reveal intersite differences in the occurrence of each syllable. In a small number of cases (3.0%, $n = 66$ syllables shared across sites), syllable order was considered in determining whether similar syllables from different sites were categorized as variants of the same syllable, or as different syllables (Fig. 4).

Songs were considered to be the same song type if they shared more than 75% of their constituent syllables (after Munding 1975, Bitterbaum and Baptista 1979). Syllable sharing was determined by comparing two songs at a time. The total number of different syllables in the two songs was counted, i.e., repeated syllables were counted only once. The number of different syllables common to both songs was then counted, and a percentage of the total combined number of syllables was calculated. This was repeated for every song pair within the set of 274 songs. The total number of pairs in 274 songs is

the sum of $1 + 2 + 3 + 4 \dots 273$ $\sum_{i=1}^{273} i$ pairwise

combinations). All song types were assigned a letter and shared songs were identified among individuals within and across recording sites. Birds which sang more than 20 songs (21–35 songs, $n = 5$ birds) did not sing more song types than birds which sang 5–20 songs ($n = 15$; $t_{18} = 0.26$, $P > 0.05$). All results are presented as means (\pm SD) unless noted otherwise.

RESULTS

SONG ORGANIZATION

House Finch song is described by Hill (1993) as a hoarse warble that shifts rapidly between high and low frequency syllables ending in a syllable with a downward frequency sweep. A downward frequency syllable ends about 80% of the 274 songs analyzed (e.g., syllables u, v, or w in Fig. 5). Songs produced by Wisconsin House Finches typically last about 2–3 sec and range in frequency from approximately 1.4 to 8.2 kHz. Songs are composed of 11.4 ± 3.0 ($n = 274$) different syllable types and 14.0 ± 3.9 ($n = 274$) total syllables.

Songs may be roughly divided into three sections, each containing characteristic syllables specific to that section. The beginning section generally contains 2–8 syllables taken from a larger pool of syllables found almost exclusively in introductory positions. Introductory syllables are not produced in a stereotyped order and segregate independently across songs (Fig. 3, Table 1). Many syllables in the beginning section are unique to individuals and are not associated with particular song types.

The middle section is characterized by strictly ordered sequences of either 2, 3, 4, or 5 syllables (e.g., Fig. 4, Table 1). All sequences are mutually exclusive, i.e., no syllable is found in more than one sequence. A total of 12 two-syllable sequences, 5 three-syllable sequences, 5 four-syllable sequences, and 1 five-syllable sequence were identified. Any syllable from a sequence of four or five is sometimes omitted without altering the order of the remaining syllables. The middle section of a song is usually comprised of a combination of 1–4 syllable sequences. A syllable may be repeated at the beginning or end of a sequence. In addition, a single syllable, or a two-syllable sequence is often repeated in a series.

The end section consists of seven syllables which constitute a single stereotyped sequence

(Fig. 5). Any number of syllables from this terminal sequence may be omitted and the remaining syllables maintain their order. Whereas the middle section of songs are composed of varying combinations of different sequences, the end portion is highly stereotyped within and among song types. Eighty-one percent of all songs recorded end with syllables from this sequence ($n = 222$ songs of 274). All individuals produce the first six of these syllables whereas the seventh is rare. In 2 of 274 songs (< 1%), part of the end sequence is repeated.

REPERTOIRE SIZE AND SONG STEREOTYPY

The mean number of syllables in an individual repertoire is $25.2 (\pm 7.2)$ and the mean individual song repertoire is $3.0 (\pm 1.4)$ song types. The amount of variability within one song type produced by any individual is very high. Rarely is the same song repeated exactly (3% of 274 songs). Songs that are classified as the same type vary on a continuum from 75% to 100% shared syllables. Songs that are different types may share as many as 74% of their constituent syllables. Therefore, song type categories do not represent clusters of songs which are more similar within a category than between categories. Instead, song types grade into one another. Although song types reported in this study appear to be largely an artificial construct, the 75% shared syllable criteria was upheld in order to allow comparisons with eastern and western House Finches.

SYLLABLE AND SONG SHARING

The mean number of syllables unique to an individual is $8 (\pm 7.0)$, which is nearly 32% of the mean number of syllables in a repertoire. Whereas approximately two thirds of an individual's syllable repertoire is shared with at least one other bird in the same recording area, different combinations of syllables are shared with different neighbors. Thus, the percentage of overlap in syllable repertoires decreases rapidly when more than two birds are compared (Table 2).

Different song types also are shared among neighboring birds. Song types are often determined by the middle section syllables because introductory syllables vary within song types and end syllables are stereotyped across song types. Therefore, birds sharing middle-section syllable types generally share the same song

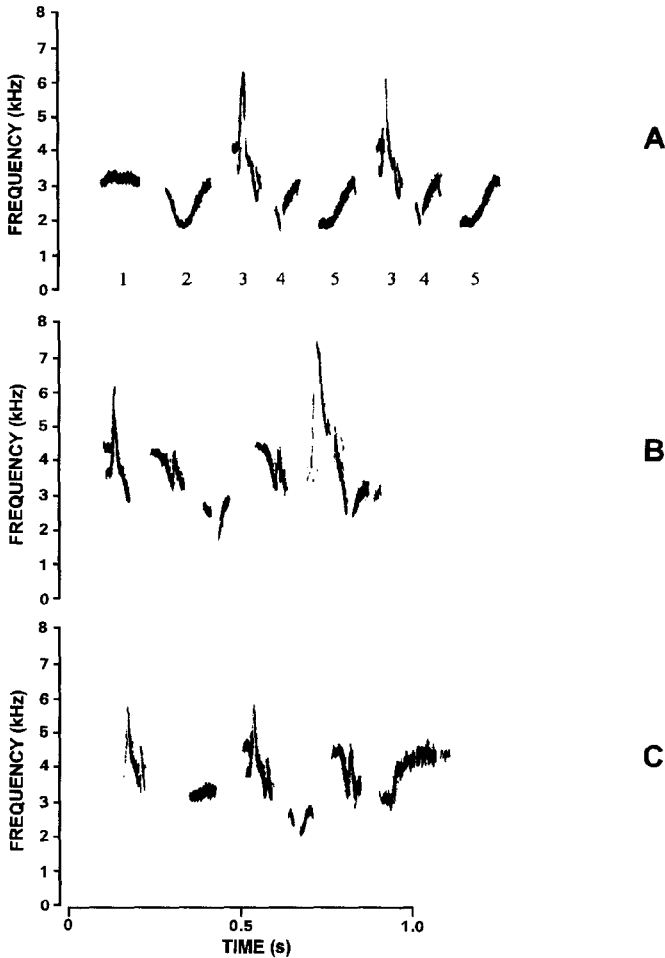


FIGURE 3. Sequences A, B, and C are introductory syllables from the same song type produced by a single male recorded in Milwaukee, Wisconsin. The introductory portions of songs typically vary in syllable type and syllable order within song types produced by an individual.

types. However, no identical songs are shared. Instead, shared song types vary in syllable number, syllable order, and syllable type.

REGIONAL SYLLABLE CHARACTERISTICS

Syllables are no more likely to be shared with immediate neighbors within a recording site than with House Finches at other recording sites ($\chi^2_1 = 0.01, P > 0.05$). Of the syllables present in only a single recording area, few are shared among birds recorded at that site. The majority of syllables unique to each area also is unique to individual birds (Table 3). No syllables specific to a recording site were shared by all birds within that site. Therefore, dialects could not be detected as regionally distinct syllables or songs.

However, the acoustic structure of seven syllables seen in all five recording sites did reveal regional variations shared by birds in each area and not found in other areas. Two of these syllables (g and h) are shown in Figures 6 and 7. The other five syllables are similar to g and h in the degree of intra- and inter-regional variation. In three recording sites, identical syllable variants were sung by all individuals within that area ($n = 6, 3, 2$). Within each of two areas, West Bend and Fond du Lac, two groups of males shared a different set of syllable variants (Figs. 6 and 7). Within West Bend, two birds sang one variant, and three birds sang another variant. Within Fond du Lac, three males sang a variant and one male sang another. Therefore, syllable

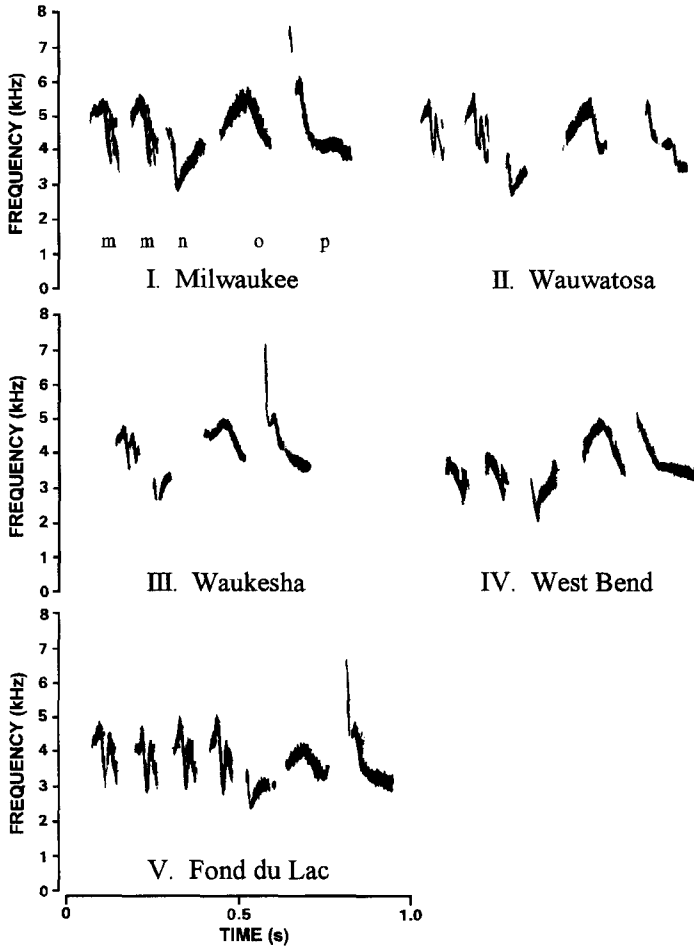


FIGURE 4. Syllable order was considered in categorizing these syllables as regional variants of the same syllable types, m, n, o, and p.

TABLE 1. Examples of song variation within song types. Each number or lower case letter represents a syllable. Each sequence is a different song and is displayed with beginning, middle, and end sections separated by commas. Song types are identified as capital letter A, B, or C. These songs were sung by a single male during one song bout, not in this order.

Song type	Song sequences		
	Beginning	Middle	End
A	4 8 7 1 2 5,	g h m n o p 45 46,	st u v w
A	8 3 5 2 7 1,	m m n o p g h 45 46,	st u
A	1 5 8 2 7,	m m m n o p g h 21 22 45 46,	st u v
A	7 1 7 2 8,	g h m m n o p 45 46,	st u v
B	10 2 8 7 8,	b c d g h f i f i f,	st u v w x
B	1 2 1 7 8,	b c d g h f i f,	st u v w x
B	7 2 8,	b c g h f i f i f i f i f,	st u v w x
B	2 8 7,	g h f i f i f i f i f,	st u v w x
C	1 10 1 2 7,	r r r r j k f i f,	st u v w x
C	7 1 10 2,	r r 17 18 17 19 j k f i f,	st u v w
C	2 1 10 1,	r r j k j k 17 18 17 19 f i f,	st u v w x
C	10 1 2,	17 18 17 19 r r r r j k f i f i f,	st u v w x

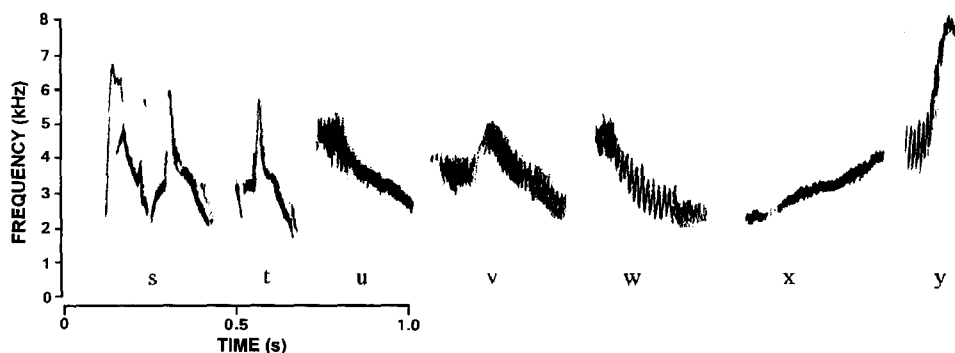


FIGURE 5. Stereotyped terminal sequence. Any syllable in the sequence may be omitted and the order of the remaining syllables remains unchanged.

variants may be shared on a small scale between neighboring birds.

DISCUSSION

COMPARISON OF RESULTS IN DIFFERENT REGIONS

Song characteristics reported by Mundinger (1975), Bitterbaum and Baptista (1979), and this study are summarized in Table 4. The mean number of syllables per individual was calculated for the East Coast population based on reported song sequences of nine banded males from which Mundinger (1975) recorded 711 songs over two years. There is no significant difference in the syllable repertoire sizes between eastern and Wisconsin House Finches ($t_{27} = 0.60$, $P > 0.05$).

Statistical analyses cannot be conducted to determine whether the differences in song repertoire size between eastern and western House Finches are significant because variances were not given by Mundinger (1975) or Bitterbaum and Baptista (1979). Nevertheless, the trend is interesting. California House Finches appear to

have nearly double the song repertoire of eastern House Finches, while Wisconsin House Finches are intermediate.

Mundinger (1975) describes eastern House Finch songs as highly stereotyped. This is strikingly different from the songs produced in Wisconsin and California. In the East Coast populations, stereotypy occurred on several levels. The same syllable type was repeated nearly exactly by the same individual and by individuals within a population. In addition, each song type was repeated nearly exactly by all individuals that included the song in their repertoire. Therefore, song types consisted of a single song with very few variations. Occasionally 1, 2, or 3 introductory notes were repeated in the beginning of a song, or 1, 2, or 3 syllables were omitted throughout the song (Mundinger 1975). Mundinger also reports occasional variations in syllable order in the introduction. In general, however, the high degree of stereotypy is emphasized in his description.

In contrast, Wisconsin House Finches rarely sing the same song twice. Variations occur in the

TABLE 2. Mean number of syllables shared between two individuals in a population and number of syllables shared among all individuals within each population.

Population	Between pairs			Within population			
	Mean no. (\pm SD) shared syllables	Mean combined syllable repertoire	Percent of repertoire shared	No. of syllables shared	Combined syllable repertoire	Percent of repertoire shared	No. of birds recorded
Milwaukee	15.9 \pm 6.4	50.0	31.8%	6	77	7.8%	6
Wauwatosa	11.3 \pm 4.4	42.0	26.9%	8	42	19.0%	3
Waukesha	17.0 \pm 0.0	50.0	34.0%	17	50	34.0%	2
West Bend	16.3 \pm 2.8	34.2	47.7%	8	44	18.2%	5
Fond du Lac	13.0 \pm 5.2	36.5	35.6%	8	55	14.5%	4

TABLE 3. Syllables unique to populations and also shared within populations.

Populations	Number of syllables unique to the population	Number of syllables unique to the population and also shared by two or more birds within the population
Milwaukee	14	4
Wauwatosa	3	0
Waukesha	15	0
West Bend	14	5
Fond du Lac	16	2

types of syllables comprising the song, the order of syllables, and the repetition of syllables. Variations in constituent syllables are found primarily in introductory syllables as well as in the combinations of syllable sequences present in the middle portion of the song.

As in Wisconsin House Finches, California House Finch songs also are highly variable. A single bird seldom repeats himself precisely when singing successive renditions of a particular song type (Bitterbaum and Baptista 1979).

There are two notable differences in the types of variation existing between California and Wisconsin House Finches. Bitterbaum and Baptista (1979) reported that variations in songs of the same type are due to the omission or addition of syllables in the introductory and end portions of the song. Wisconsin birds, however, have highly stereotyped end portions and a high degree of variability in the introduction and middle portions. In addition, syllables in California House Finch songs segregate independently, whereas in Wisconsin, syllables segregate in groups of ordered syllable combinations as well as independently.

Song sharing patterns, like song stereotypy, also are very different between the eastern and Wisconsin populations. Munding (1975) stated that in eastern House Finches, identical songs may be sung by a large number of males (estimated to be approximately several hundred) within the same geographical region. The entire repertoire of song types (2–6) of any individual is shared among many, or all, other members of the region. No song types unique to an individ-

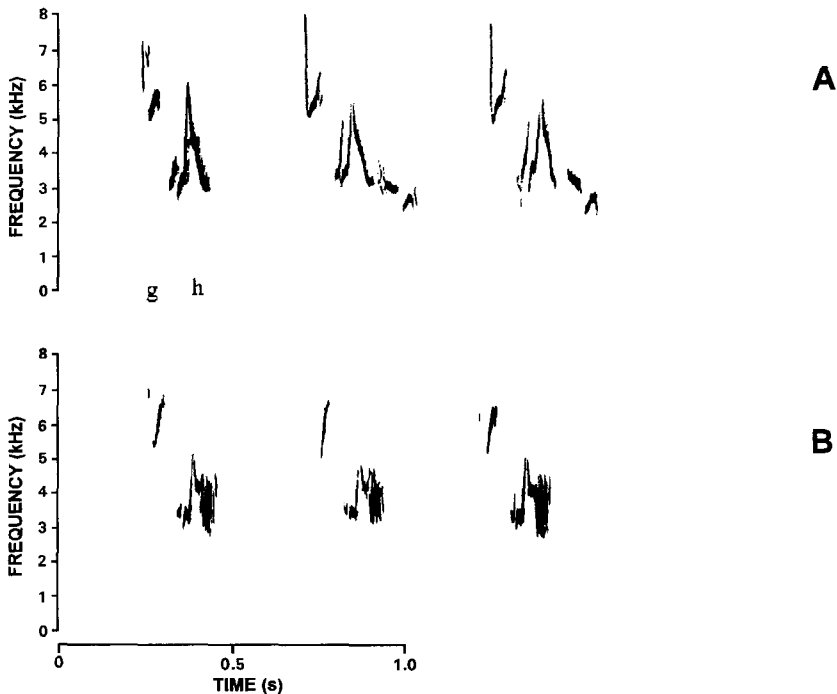


FIGURE 6. Intrasite stereotypy of regional syllable variants. Row A shows syllables g and h produced by three males in the West Bend recording site. Row B shows variants of the same syllable types, g and h, produced by three males in the Fond du Lac population.

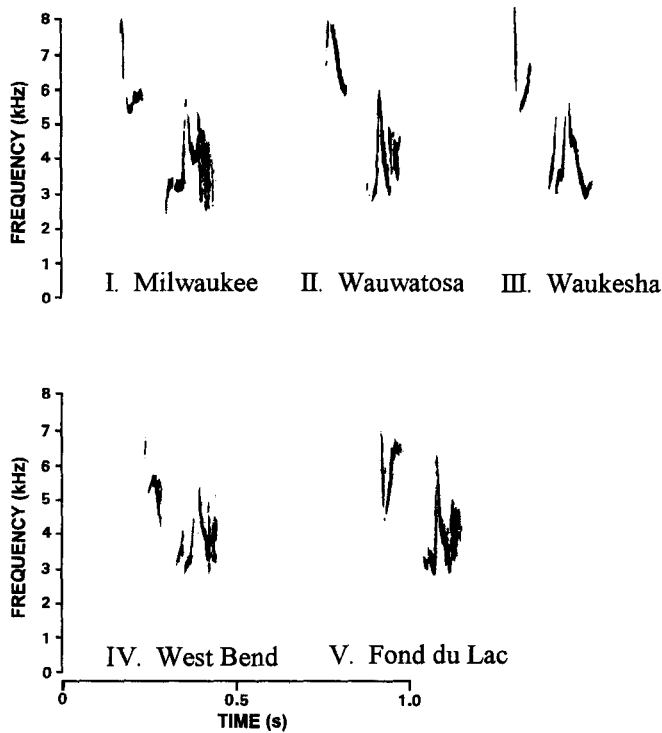


FIGURE 7. Regional variants of syllables g and h. The syllables shown here recorded in the West Bend and Fond du Lac sites were recorded from a different male than the variants from these sites shown in Figure 6.

ual were reported (Mundinger 1975). The high degree of song sharing results in dialects comprised of a few shared song types (4–7) separated by distinct boundaries where dialect areas adjoin.

Wisconsin House Finches do not have discrete

dialect boundaries. Clusters of syllables, not entire songs, are shared among groups of birds. Furthermore, frequencies of shared syllables in Wisconsin do not follow an apparent clinal distribution as syllables are no more likely to be shared with immediate neighbors than with

TABLE 4. Song characteristics of House Finches in three geographic regions. Numbers given for West Coast and East Coast populations were determined from data provided in Bitterbaum and Baptista (1979) and Mundinger (1975), respectively.

	West Coast mean (\pm SD) ^a	East Coast mean (\pm SD)	Wisconsin mean (\pm SD)
Individual song repertoire	4.0	2.2	3.0 (\pm 1.4)
Individual syllable repertoire	—	26.7 (\pm 2.8)	25.2 (\pm 7.2)
Song length: total syllable number	13.0	—	14.0 (\pm 3.9)
Variability in different song sections:			
beginning	Variable	Variable	Variable
middle	Stereotyped	Stereotyped	Variable
end	Variable	Stereotyped	Stereotyped
Portion of song that is shared	Middle	Entire song	End
Amount of individual variation within a song type	High	Low	High
No. of birds recorded	92	9	20
No. of songs recorded	857	711	274

^a Standard deviations for mean song repertoire and syllable number combined across sample sites were not provided by Bitterbaum and Baptista (1979), and standard deviation for mean song repertoire was not provided by Mundinger (1975).

House Finches at other recording sites. Whereas regional differences are not found in syllable use, site-specific syllable variants may be distinguished by the acoustic structure of a small number of syllables.

California House Finch populations are similar to those in Wisconsin in that there are no dialect boundaries identifying areas of song sharing. However, unlike in Wisconsin, the degree of syllable sharing among individuals decreases with distance from any starting sample point. The differences in syllable frequencies lie on a gradient or cline, with no strict delineations among syllable pools. Dialects may be identified as clusters of relatively higher use of particular syllables. No area-specific syllable variants were reported (Bitterbaum and Baptista 1979).

In sum, song stereotypy, repertoire size, and song sharing patterns of Wisconsin House Finches differ from those of both East Coast and California House Finches. Although I have isolated these features, they are likely not independent. A decrease in song stereotypy may result in larger individual repertoires (Kroodsma 1982) and a loss of discrete dialects (Krebs and Kroodsma 1980, Williams and Slater 1990). This relationship between stereotypy, repertoire size, and song sharing is consistent with the differences between singing characteristics of East Coast, Wisconsin, and California House Finches. The highly variable syntax in Wisconsin populations compared with that of East Coast populations may result in the classification of more song types from similarly sized syllable repertoires. The increased song variability in Wisconsin also may account for the lack of shared songs among neighboring birds because even birds that share a song type sing different renditions of the song.

HYPOTHESES OF VARIATION IN SONG CHARACTERISTICS

Bitterbaum and Baptista (1979) invoked the founder effect hypothesis to explain the difference between eastern and western song characteristics. According to this hypothesis, the founders of the East Coast population had, collectively, a small pool of syllables. Because population density was low in the early stages of colonization, juveniles likely were exposed to a relatively impoverished acoustic environment. Both the limited song pool of the original foun-

ders and the low number of individuals from which to copy songs may have contributed to juveniles copying entire songs essentially unaltered from only one or a few individuals. The outcome was clusters of individuals sharing a few complete song types.

Juveniles on the West Coast, on the other hand, learn within a rich acoustic environment because they are exposed to a large number of songs and syllable types. Western juveniles learn individual syllables as units, which they segregate and recombine independently during song production (Bitterbaum and Baptista 1979). Incorporation of syllables from multiple tutors, and the recombination of syllables into unique song patterns, prevents the formation of discrete dialects. The founder effect hypothesis suggests that the number of different songs heard as a juvenile influences the length of the copied unit or sequence, which in turn is correlated with the amount of variability within song types.

The founder effect model of colonization predicts that isolated colonies at low densities will have decreased song repertoires, increased song stereotypy, and more discrete dialect boundaries than that of the parental population. Whereas this appears to be the pattern in the early East Coast expansion (Mundinger 1975), censuses suggest that the early Wisconsin colonies were not sparsely populated and therefore the predictions of the founder effect model would not be expected. For example, Christmas Bird Counts report sightings of 5 House Finches in Milwaukee in 1987, 10 in 1988, 45 in 1989, and 90 in 1990 (no report for Milwaukee was given in 1991) (American Birds 1987–1991). Christmas Bird counts in Ozaukee County, north and adjacent to Milwaukee, indicate an increase from 4 House Finches seen in 1989 when they were first sighted there, to 10 in 1990, and 181 in 1991 (Riveredge Nature Center Newsletter 1992). Furthermore, census data from Illinois and Indiana indicate that colonization of Wisconsin occurred at the border of a dense population of potential colonizers. For instance, between 1987 and 1989 Christmas Bird Counts of House Finches increased from 0 to 6 to 157 in Decatur, in central Illinois. During these three years, 10, 57, and 108 House Finches were sighted in Calumet City in northern Illinois on the Indiana border. Similar trends were noted in northern Indiana. In Fort Wayne, House Finch sightings increased from 2 to 27 to 129 to 340

between the years 1986 and 1989. In Grant County, Indiana, Christmas Bird Counts report 104 House Finches seen in 1986, and 299, 533, and 1,079 the following three years (American Birds 1986–1991). Although bird counts provide only a rough indication of population densities, it is nevertheless apparent that between 1986 and 1989 there were reported sightings of large and increasing numbers of House Finches in regions to the south and east of Wisconsin. Models of colonization based on theories of island biogeography predict that when the population of potential colonizers is very large, and/or very near to the new settlement sites, then colonies generally are founded by large numbers of individuals and are established over multiple colonization events (MacArthur and Wilson, 1967). This prediction is supported by the substantial and nearly instantaneous increases in House Finch population sizes in Wisconsin during the early years of colonization. Therefore, it is not clear that the small and isolated populations necessary for the founder effect existed for long, if at all, in the early colonies. Thus, factors other than the founder effect must be proposed to explain the changes in song characters in Wisconsin House Finches from those of the parental East Coast population.

Ewert and Kroodsma (1994) have shown that resident populations of Eastern Towhees (*Pipilo erythrophthalmus*) have larger song repertoires and more song sharing than migratory populations. However, the relationship between repertoire size and song sharing seems to be reversed in House Finches. Small song repertoires found in eastern House Finches are correlated with a high degree of song sharing, whereas larger repertoires found in California and Wisconsin populations are associated with a low degree of song sharing (Mundinger 1975, Bitterbaum and Baptista 1979, this study). Furthermore, Mundinger (1975) concluded from banding studies that the eastern population was partially migratory and therefore maintenance of the integrity of dialects is not clearly correlated with sedentary behavior. Although resident and migratory behavior in House Finches demands more study, it is not immediately apparent that these behaviors are correlated with the differences found in singing behaviors.

The withdrawal of learning hypothesis has been proposed to explain geographical variation in song syntax (Thielcke 1969, 1973). This hy-

pothesis suggests that juveniles settle new areas after exposure to songs from the natal region, but before crystallization of the adult song. The result of song development in the absence of adult song models is the improvisation of new syllables and a loose syllable syntax in the founding populations.

Mundinger (1975) described the propagules of new colonies as composed of a significant percentage of the juveniles from the parental population. House Finches begin song learning during the first few months after hatching, but adult songs may not crystallize until males reach their breeding ground the following spring (Mundinger 1975). The age of colonizers and the timing of song learning, therefore, appear to be consistent with the requirements necessary for the withdrawal of learning hypothesis. However, this hypothesis, like the founder effect, requires that juveniles colonize unsettled or sparsely settled regions rather than invade highly populated communities or move to the margins of their range. As noted above, this is likely not the case in the Wisconsin colonies. Instead, it is possible that colony founders, and/or their progeny, developed new singing patterns not in the absence of interactions with adults as proposed by the withdrawal of learning hypothesis, but through interactions with other colonizers from areas with regional song differences. The difference between the stereotyped song patterns on the East Coast and the variable songs in Wisconsin may be due to an increased amount of heterogeneity of song types in the colony population.

The suggestion that heterogeneity of song types is associated with variable syntax in House Finches is supported by the singing behavior of an anomalous eastern population reported by Mundinger (1975). A significantly greater number of song types was recorded in Mamaroneck, New York, than in any other East Coast recording site. Mundinger proposed that Mamaroneck had been settled by individuals with different song traditions. Colonizing flocks of House Finches originating from different natal areas may bring different syllable types to new settlements. Individual House Finches in Mamaroneck also had larger repertoires and showed a high degree of variability and reorganization of songs, combining syllables from several different song types, similar to singing characteristics seen in Wisconsin. The number of different syl-

lable types found within populations may therefore influence the copying patterns of juveniles as proposed by Bitterbaum and Baptista (1979).

Wisconsin House Finches descend from generations of individuals experiencing colonization over the course of approximately 57 years (1940–present). The repeated pattern of syllable repertoire mixing during colony formation may have increased the heterogeneity of syllables found within populations. In addition, a difference in the numbers of founding colonizers and colonization events establishing the East Coast (Elliot and Arbib 1953) and Wisconsin populations (American Birds 1987–1990) also may have contributed to the difference in degree of song type heterogeneity found in the two regions. This hypothesis differs from the withdrawal of learning hypothesis in that increased variability in songs does not result from an impoverished learning environment. Instead, I attribute song changes to an acoustic richness along the edge of the House Finch range which Bitterbaum and Baptista (1979) predicted would lead to increased song variability, increased repertoire size, and decreased song sharing, as is seen in Wisconsin.

Additional research is necessary to determine whether the changes in song characteristics described in this study may result from selection or drift (Kroodsma and Canady 1985), or are indeed primarily a result of the social environment in which song learning occurs. Whereas there is support from other studies for the conclusion that the learning environment influences repertoire size, patterns of song sharing and song syntax (Krebs and Kroodsma 1980, Kroodsma 1982, Mundinger 1982), this study suggests, in addition, that the degree of intraspecific song syntax variability may be more plastic than is often evident from established and stable populations and may similarly be modified by social circumstances.

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