

SONG DIALECTS AND COLONIZATION IN THE HOUSE FINCH, *CARPODACUS MEXICANUS*, ON THE EAST COAST

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Since the description of local song dialects in Chaffinches (*Fringilla coelebs*) (Poulsen 1951, Marler 1952), this form of song variation has been described in a number of passerines (Nottebohm 1969, Payne 1973, reviewed in Thielke 1969). Recent workers have focused on the function and biological significance of song dialects (Nottebohm 1969, Nottebohm and Selander 1972, Baker 1975), but have also warned that the usefulness of the emerging dialect concept may be impaired if the term is applied uncritically. The term, "dialect," should meet specific criteria. Marler and Tamura's (1962) analysis of song dialects in the White-crowned Sparrow (*Zonotrichia leucophrys*) remains the classic study. They found consistent differences in song patterns among populations, but within a population they found extreme stereotypy in some aspects of song patterning which was repeated from one year to the next. Working with the closely related Chingolo (*Zonotrichia capensis*), Nottebohm (1969) found that where contiguous populations meet, the integrity of the respective dialects is maintained with a boundary between them. These attributes provide a reasonable definition of song dialect.

As part of a study of song ontogeny in the House Finch, *Carpodacus mexicanus* (Mundinger, in prep.), I recorded examples of natural song. Preliminary spectrographic analysis of the songs of wild House Finches nesting in the vicinity of New York City suggested that this finch may have song dialects. The occurrence of song dialects in this species would be significant since the House Finch was introduced to the east coast only recently (Elliott and Arbib 1953), and the recency of this event would provide known time limits for the emergence of new dialect patterns. The analysis of geographic variation in House Finch song was expanded to determine if populations on the east coast had song dialects, and to relate the pattern of song variation to the history of House Finch colonization.

METHODS AND DEFINITIONS

I recorded 9 males in 1971 and 146 males in 1973, all in southeastern New York and Connecticut, a

region that likely includes direct descendents of the original founders (Fig. 1). To survey song variation in this region I applied three related sampling techniques. At the most local level, I color banded and recorded nine breeding males, and several of their banded females, in the 1971 and 1973 nesting seasons. All birds in this local, banded sample were recorded within a 3 ha area (100 × 300 m) surrounding the banding station. A more extensive sample was made in 1973 in a quadrangular area, 12.2 km on a side, surrounding the banded population. This is called the block sample and consisted of the recorded songs of 98 unbanded males, plus songs of the banded population and of a coastal sample included within the block. Finally, a coastal sample was made up of 43 unbanded males recorded at eight stations spaced at 10–20 km intervals along the Long Island Sound coastline, from Manhattan to Milford, Conn., plus one station in the Hudson River Valley at Poughkeepsie, N.Y. Three males were recorded at one coastal station (station #1), five males were recorded at each of the other eight stations; station #3 was sampled in 1971, all of the other coastal stations were sampled in 1973.

Since most of the recorded birds were unbanded I could have recorded unknowingly the same bird more than once. To prevent or reduce such duplication each bird was recorded only when it was visible to me; when it flew out of sight the recording session ended and no other recordings were made within 160 meters (0.1 mile on an auto odometer) of that site. The only exceptions involved situations when two or three males were seen together. If I was able to keep them in view as I recorded them in sequence, they were treated as different individuals sampled at the same site.

A Nagra III (3¾ ips) and Sennheiser 804 microphone were used to record songs. All the recorded songs were spectrographically analyzed on a Federal Scientific Ubiquitous spectral analyzer (Hopkins *et al.* 1974). After viewing these spectrographic analyses, representative songs from each male were also spectrographed on a Kay Electric Sonograph (model 660; using high shape, wide band). Pattern analysis, the principal analytic technique used in this study, was applied to all of the Ubiquitous audiospectrograms. Kay audiospectrograms were used for illustrations and some temporal measurements.

The pattern analysis consisted of labelling the constituent syllables of a song to form a song formula. Definitions of terms used in this pattern analysis follow: *syllable*—The basic structural unit of a song, separated from adjacent syllables by a silent period of .02–.20 sec. Some syllables consist of a single trace (mark) on the spectrogram (syll. "v" and "x," fig. 2), other syllable types are composed of separate traces that may either overlap in time, or, if they do not overlap, are separated by a brief (0.–.02 sec) silent gap (e.g. syllable "s," fig. 2). The different syllable types were labelled with either letters or numbers. *song formula*—A series of letters and/or numbers representing the sequential order of the different syllable types composing a given song. The middle and end portions of songs were found to be the most

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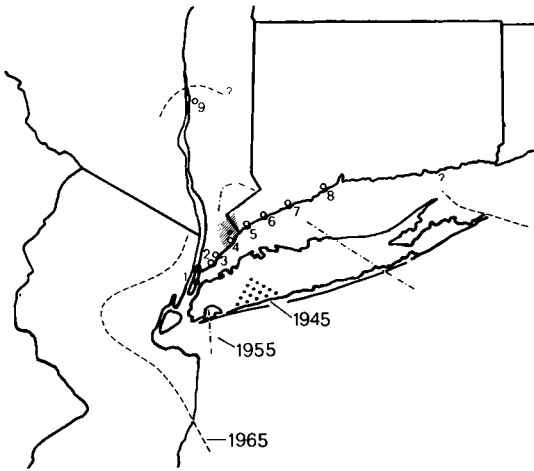


FIGURE 1. Study area, and the extent of the eastern breeding range of the House Finch at three different dates. 1-9, coastal sample sites; cross-hatching, block sample; single dot, locus of banded population; extent of breeding range by 1945 (triangle of dots), by 1955 (dot and dash), and by 1965 (dashes).

stable, and syllables there, called terminal syllables, were usually designated with letters. The introductions to songs were more variable, both within and among individuals, and the introductory syllables were designated with numbers and with reverse ordering. Fig. 2 illustrates some songs and their formulae. *theme*—Individual birds sang 1-6, $\bar{x} = 2.23$, different song types or themes. Two songs are considered different themes if they differ in at least 25% of their constituent syllable types. *theme variant*—Often a

given male sang two or more versions of a given theme, the versions differing by fewer than 20% of their syllable types. In most instances theme variants differed by only one or two syllable types (fig. 2, E and F). *song repertoire*—The number of themes (not theme variants) sung by a given individual bird or by the birds sampled in a local population.

These are working definitions and apply only to the material collected in this study; they may not precisely apply to all House Finch songs.

RESULTS

BANDED POPULATION

How uniform are songs at a single location? An answer is provided by describing variation, both within the local population and within individual birds.

Population variation. Songs within a population were stereotyped in both syllable structure and in song pattern. Syllable variation was determined by visual inspection of spectrograms. If a comparison between songs was restricted to a local population then syllable structure was considered remarkably stable. For example, syllable "s" in fig. 2 reveals as much intra-population variation as I found for any one syllable type. I found almost as much variation in the form of "s" within a song of an individual (fig. 2A) as in the songs of this individual recorded in different years (fig. 2A and 2B), or in the songs of different individuals (fig. 2A, 2C, 2D). Other syllable types varied to about this degree, or even less, as may be seen by selecting a syllable type at

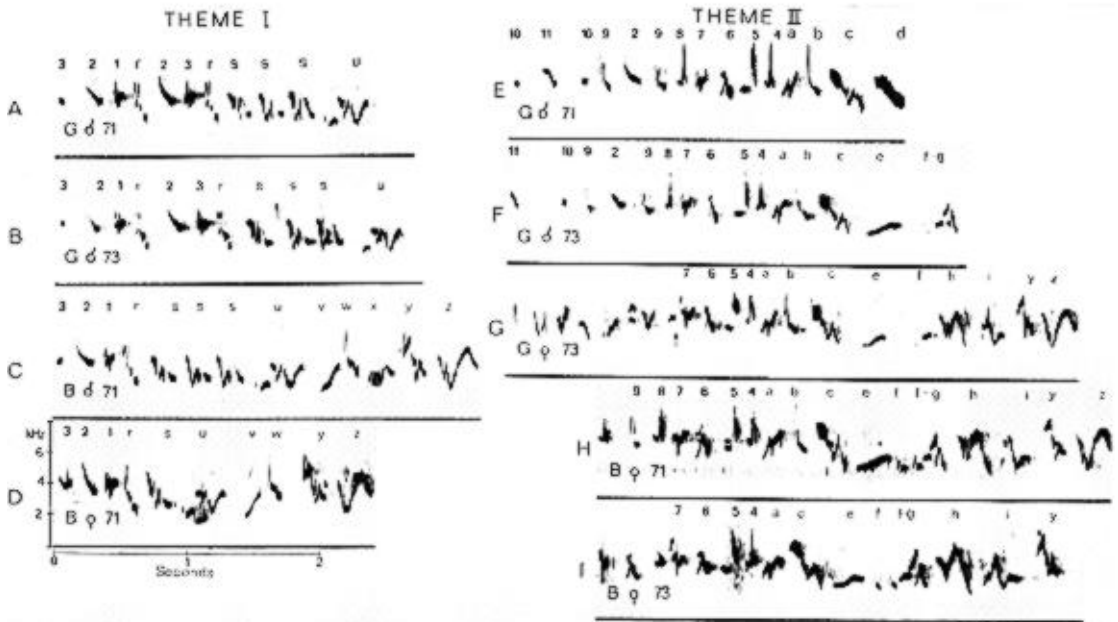


FIGURE 2. Songs from the banded population. Theme I: A-B, Green male in different years; C-D, male Blk 71 and his mate Blk female; Theme II: E-F, two theme variants of Green male recorded in different years; G, song of his mate Green female (arrow indicates ending of appended syllables); H-I, Blk female songs from different years.

TABLE 1. Song formulae of known, breeding males.

	N	THEME I ^a		N	THEME II ^a	
		Intro.	Termination		Intro.	Termination
1971 Population						
Black 71	179	123	rsssvvwxvxyz	7	10,11,9,11,987654abc	(de) fgh
Fuchsia	76	123(r)23	rsssvvwxvxyz	9	11,10,987654abc	(de) fghi
Green	16	123(23)	rsssvvwx	7	10,9,2,987654abc	d
1973 Population						
Green	33	123(23)	rsssvvwxvxyz	9	11,10,9,2,987654abc	(de) fg
Black 73	171	123	rsssvvwxvxyz	24	10,987654abc	(de) fghi
Red	96	123	rsssvvwxvxyz	51	10,987654abc	(de) fghi
Blue	11	123	rsssvvwxvxyz	0		
White-green	14	123	rsssvvwxvxyz	2	11,10,987654abc	(de) fghixy
Red-green ^b	3	??3	rsssvv	1	? ?87654abc	
Pink ^b	0			2	? ?87654abc	e fghi
Representative formulae:		123	rsssvvwxvxyz		10,987654abc	(de) fghi

^a Formulae were from the most complete songs available; (), indicates syllables that were variably expressed; ??, refer to unknown syllables either obscured on the spectrogram or appended syllables associated with the context of flight.
^b Only flight song recorded (upon release of the newly banded bird).

random and comparing its form in several songs illustrated in fig. 2 or fig. 6, which illustrate songs in two different local populations. When songs of different populations were compared, variation in syllable form was much greater (compare "s" in fig. 4A-C).

Song patterns within a population were also stereotyped, as shown by the formulae in table 1. Seven of the nine color-banded males recorded sang Themes I and II, illustrated in fig. 2. Two males (Blue and Pink) were recorded infrequently, and only one of the two themes was recorded from each. For those males with reasonable sample sizes, Theme I was predominant; on average 85% of the songs sung by breeding males were Theme I. The Theme I formula, 321r³sssvvwxvxyz, reveals this song is typically a series of 13 syllables, 11 syllables unique and one (syllable "s") repeated three times. Theme II (formula: 10,987654abc(d)(e) fghi) occurs as two theme variants. One variation contains "e" but not "d", the other contains "d" and not "e". The banded population's Theme II song is therefore a sequence of about 15 entirely different syllables. Songs combining syllables of both themes occur occasionally; these usually involve one or two introductory syllables of one theme occurring early in the introduction of the other theme (e.g. 10,9321r³ss . . .).

Similar song patterns were recorded in 1971 and 1973. This was not due to recording the same birds in the two years. Except for Green male, different individuals were sampled in 1971 and 1973 (table 1). Since the average life expectancy of small north temperate passerines is less than two years (Lack 1954) different generations of finches are probably

represented in the 1971 and 1973 samples. Since House Finches learn their song (Munding, in prep.), the temporal stability of song structure within this population implies that accurate copies are passed on from one generation to the next.

I found many incomplete songs. As House Finch song is a sequence of different syllable types, I could determine whether incomplete songs ended at characteristic syllable types or whether the birds stopped at any point along the series. Repertoires of five, well-recorded, nesting males were combined, and the frequency for each syllable type ending a song was plotted (fig. 3). The same general pattern emerged for the five males analyzed individually. Figure 3 reveals that only 17% of Theme I and 22% of Theme II were sung through to completion. Few songs were complete. A shortened song could end after any syllable type, but there were preferences. For Theme I, which provides the larger sample, table 3 reveals these songs were generally ended: 1) after two or three introductory syllables were sung (e.g. after syllable "3"); 2) after syllable "u" (a preferred stopping point); or 3) they were sung to completion.

Since song fragments are common, song duration is strikingly variable. Black 71 male had the largest sample of recorded songs. The average duration for his Theme I songs was \bar{x} = 1.47 sec (S.D. = .95 sec, n = 175 songs), and the coefficient of variation is large, CV = 66. But if songs of comparable completeness are measured, variability is small. Considering only song fragments ending with syllable "u", or only complete songs ending with syllable "z", the average song durations were \bar{x} =

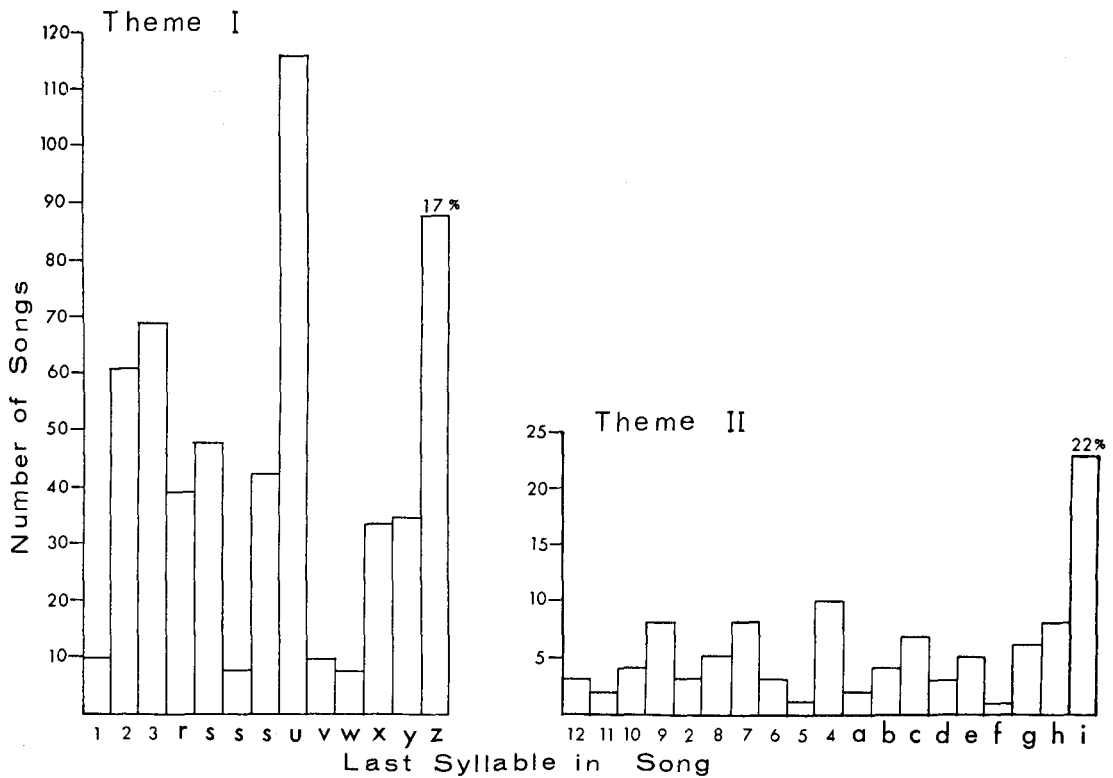


FIGURE 3. Frequency distribution of the final syllable in the songs of five banded males. A, Theme I; B, Theme II.

1.64 sec (S.D. = 0.03, $n = 17$ songs), and $\bar{x} = 2.78$ sec (S.D. = 0.07, $n = 19$ songs) respectively. By measuring only songs of comparable completeness the coefficient of variation is small, as expected for a stereotyped song pattern: CV = 1.8 for songs ending with "u"; CV = 2.5 for complete songs.

The stereotypy of House Finch song is also revealed in the consistency of syllable ordering. Occasionally a short sequence of introductory syllables is repeated (e.g. Theme I may begin 12323rs . . . etc.) or an introductory syllable of the alternate theme may appear in the introduction (fig. 2E and F), but other than this I never observed any inversion of syllable order in songs of the 9 banded males.

Individual variation. Analysis of the songs of known individuals reveals occasional variations in song structure. Examples already referred to are the two variants of Theme II, which differ by one syllable type, and the occasional variations in syllable order in the introduction. Other minor variations occur when some syllables are occasionally left out (e.g. the male Blk71 occasionally dropped "vwX" from his Theme I) and when individuals sing in different contexts. One context for male song is the courtship display (Thompson 1960a).

When a male sings in display the proportion of his Theme II may increase; the proportion of complete songs increases; and the intersong interval is reduced, in many instances to nearly zero so that adjacent songs are linked. Also an unusual, high-pitched (about 8 kHz), syllable is often appended to the very beginning of his song. Yet the basic syllable order is rigidly maintained in courtship song, and in other contexts such as singing in flight.

Female House Finches sing too, usually when soliciting for copulation or courtship feeding. Female songs often have short clusters of soliciting calls (which also occur unattached to song) appended to the front of their songs (fig. 2G). Appended syllables also occur irregularly in the songs of males. Not all of the contexts in which such "appended" syllables appear have been identified and therefore I have ignored the "appended" syllables in this study. This procedure simplifies presentation of results, and does not affect analysis of basic song structure at the population level. "Appended" syllables may be important in assessing the motivational state of a bird.

Other than the minor variations described above, my analysis of songs sung by known individuals in different years reveals no sig-

TABLE 2. Song formulae of male House Finches in block sample.

Population (males)	N	THEME I		THEME II	
		Introduction	Termination	Introduction	Termination
Armonk	7	18 17 16 15	r s s u v w x y z	9 8 7 6 5 4	a b c d- f g h-(x y z)
Byram	3	25 24 23 22 r 21	r s s u v w x y z	9 8 7 6 5 4	a b c(d e) f g h- x y z
Port					
Chester	13	25 24 23 22 r 15	r s r s s u v w x y z	9 8 7 6 5 4 a' b'	a b c(d e) f g h i
Rye	8	28 27 26	r s r s s (u)- w x y z	9 8 7 6 5 4	a b c(d e) f g h i
White Plains	6	132313023(3231302r)	r s s u v w x y z	9 8 7 6 5 4 a b a b c(d e) f g h i	
Indian Vil.	16	3 2 1	r s s s u v w x y z	9 8 7 6 5 4	a b c(d e) f g h i
Harrison	9	35 34 33(r) 2 1	r s s u v w x y z	9 8 7 6 5 4	a b c(d e) f g h i
Scarsdale	3	3 2 r' 2	r' s' s s u	9 8 7 6 5 4	a b c(d e) f g h i (x y z)
Peningo	14	42 41 40 39 38 37 36	r s t' u v(w)-y z(ghid')	59 → 46	a b' c' d' e-(x y z) g h i d'
Larchmont	11	66 65(64 63) 62 61 60	r' s' t' u' v' w x y z	79 → 70	a b c(d e) f g h -(x y z)
"X"	2	version of Theme I		version of Theme II	
Mamaroneck	20	87 86 85 84 83 82 81 81	131415161718192021	1234(5)6789(1011)12131415161718192021	Theme A

() indicates syllables that are variably expressed or not expressed.
 - indicates syllables present in most songs in the block but absent in this particular population.
 Prime ' indicates modification of syllable structure.
 "x" indicates two neighboring males with unrepresentative songs; possibly both have hybrid songs (see Fig. 5).

nificant change in an individual's basic song pattern. Three birds from the banded population, one male and two females, were recorded in 1971 and again in 1973. As illustrated in figure 2, syllable structure and order remained constant over the two year period. At the level of the neighborhood, I conclude that breeding males and females sing the same set of song themes. Except for minor variations in the introduction, the songs characterizing an individual are stable for a period of years. Since neighboring males sing the same songs, which are basically unaltered over at least 3 breeding seasons, it follows that the song patterns characterizing a localized population remain unchanged for several years.

BLOCK SAMPLE: CONTIGUOUS POPULATIONS

To determine the geographic distribution of song variation a larger area was sampled. With the banded population as a center, I expanded the size of the sample area in all directions until, judging by ear, I had recorded several different sets of song themes. Spectrographic analysis of the recordings later showed that several contiguous song populations were sampled, and that approximate dimensions of some song populations could be established.

The 112 males constituting the entire block sample include 9 color banded males from the banded population, 5 unbanded males from coastal site #4 (which was included in this

sample area), and 98 unbanded males distributed throughout the 12.2 x 12.2 km block. The number of songs recorded from each male ranged from 1 to 195. The banded males, whose breeding behavior was followed, provided the larger individual samples; the unbanded males provided smaller samples, averaging 12.4 (range 1-39) songs per bird.

Identifying Populations. Most of the males sang two themes which often had terminal syllables like those in the banded population's songs. Thus most song formulae can be treated as modifications of Theme I and II. A few songs were totally different, having no syllables in common with the banded population's songs. In these instances new formulae were coined in which numbers represent both introductory and terminal parts of the songs.

Males living close to one another often had nearly identical songs, or songs whose formulae differed by only the elimination or addition of an introductory syllable or two. Table 1 illustrates how representative formulae were established for the banded population. In table 2 representative formulae, similarly derived, describe the themes of the different groups of males recorded in the block. Males with the same set of representative song formulae are considered members of the same song population, and each population was named for a nearby village or geographical feature. For example, seven males recorded in the vicinity of Armonk (a village in SE New York) share most of the introductory

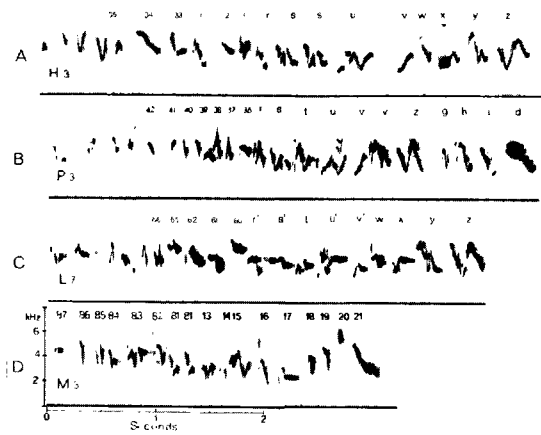


FIGURE 4. Representative songs from four contiguous dialect areas. A, Harrison, Theme I; B, Peningo, Theme I; C, Larchmont, Theme I; D, Mamaroneck, Theme F.

syllables in their two song themes and the terminal portions of their two themes were alike (table 2).

The different populations are primarily separated by consistent differences in their Theme I song formulae, best seen in the introductions. Secondly, the Theme II formulae usually revealed parallel differences between populations, although fewer differences occur in the Theme II introductions. A third criterion used to differentiate populations was the existence of changes in syllable structure, as expressed on a spectrogram. When syllable structure was obviously modified, a prime (') was suffixed to that syllable in the population's representative formula. Syllable modification of a lesser degree cannot be expressed in the formulae. In sum, differences in Theme I, especially in the introduction, generally identify populations. Differences in Theme II and in the structure of analogous syllable types provided supplementary evidence for differentiating populations.

In Table 2 eleven different song populations are identified, each characterized by its own unique set of song themes. In any one population the males sing the same songs. The songs of ten of these populations are modifications of Theme I and II, first identified in the banded population (part of the Indian Village song population). Most of these ten populations even had the Theme II variants involving the "d" and "e" syllables.

Some of these ten populations have very similar songs. Compare, for example, the Byram vs. Port Chester and the Indian Village vs. Harrison song formulae. Although the

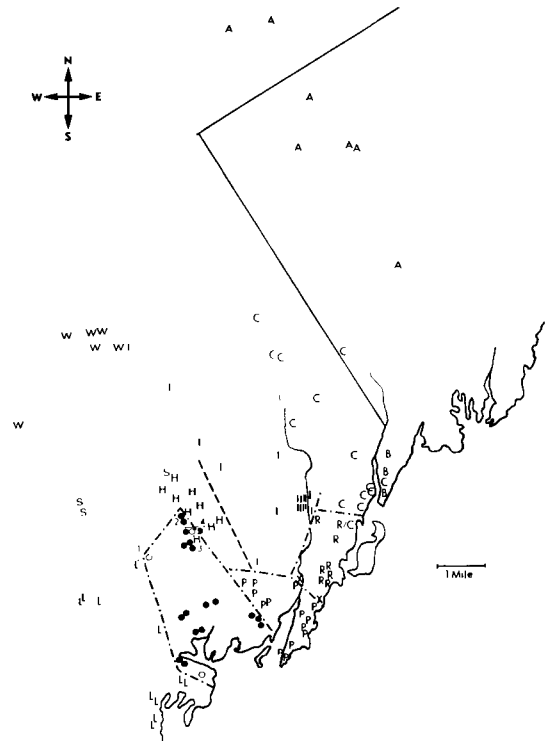


FIGURE 5. Geographic distribution of song dialects in southeastern New York and Connecticut. Solid dots, Mamaroneck males; letters indicate the positions of males from the first ten populations in Table 2; 1-4 (in the Mamaroneck area) indicate the loci of four boundary estimates (see text); open circles indicate males with mixed repertoires.

differences were often subtle, for example note the slightly modified introduction and the extra "s" syllable in Theme I of Indian Village males in comparison to Harrison males, they were consistent.

In table 2 the populations are organized vertically along an approximate north-south axis. In the southern part of the block, differences in song structure were more marked. Rye, Harrison, Peningo and Larchmont have the basic Theme I and II songs but their Theme I and II introductions differ, and the terminal portions of their song also show clear differences in pattern and syllable form. For example, the Rye Theme I lacks a "v" and often "u", while Peningo lacks "x" and often "w". Changes in syllable structure can be seen by comparing representative spectrograms, e.g. syllables "s", "u", and "v" in figure 4 which illustrates a representative theme for each of the more distinctive southern dialects.

One southern population, Mamaroneck, had highly distinctive songs. Mamaroneck males generally sang 3-4 themes and none of these themes were at all like the two basic and widespread Themes I and II (see table 2;

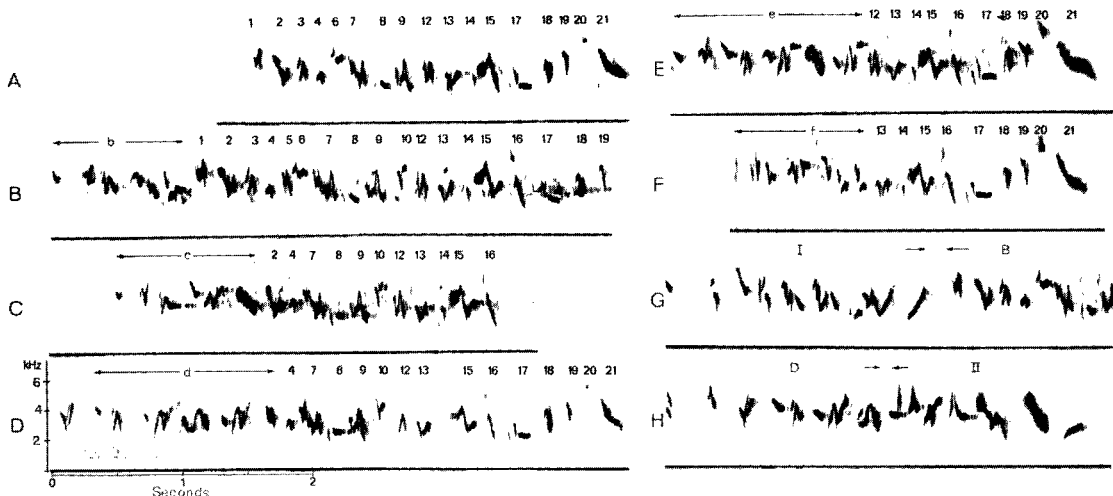


FIGURE 6. Six themes of the Mamaroneck dialect, and hybrid songs. A–F, Themes A–F of Mamaroneck males (b–f, represent introductions to Themes B–F); G–H, hybrid songs of a boundary male (I, II, B, D indicate portions of Themes I, II, B and D respectively; arrows indicate juncture of the different themes).

fig. 4). The structural uniqueness of Mamaroneck songs suggests this population is part of a song tradition different from the song tradition of the other ten populations. The Mamaroneck population was therefore studied in more detail (see below).

Geographic extent of population. The map in figure 5 plots the position of each male and his population's designation. No boundaries were drawn between populations in the northern part of the block, where songs were similar and sampling sparser. The approximate position of boundaries was drawn between populations in the south where song differences were distinctive and sampling was denser.

The map reveals that the song populations are true song dialects. The pattern of geographic variation in song is not clinal but resembles a mosaic distribution. The populations are contiguous and are not separated by ecological or geographic barriers. All the males within a dialect area sing alike and there is no geographic overlap of different populations.

The geographic extent of a given song dialect is rather small. The Mamaroneck dialect is largest, approximately 4.8×2.5 kilometers and the Rye dialect occupies the smallest area, about 2.5×1.6 km. Yet these small areas support a good-sized breeding population whose members, dispersed throughout the dialect area, are by no means all within hearing of each other. Population size appears to be substantial. The estimated density of pairs nesting on a 35 ha island (coastal station #3, which provides a suburban-like mix of ivy-covered buildings, open fields, ornamental

plantings) was about 1.1 pairs/ha, estimated from a nestling banding program begun in 1973. Extrapolating from this figure, several hundred to a few thousand pairs may occur in each of the dialect areas bordering Long Island Sound. Some of the northern and inland dialect areas may be geographically larger than those along the coast, but the pairs there seem more widely dispersed.

The Mamaroneck dialect. The Mamaroneck population is discussed in more detail since its unique songs aid in locating boundaries with neighboring populations. Also banding data are available, shedding light on the dispersal patterns of this population.

The 333 songs recorded from the 20 males of the Mamaroneck population ($\bar{x} = 16.6$ songs/male) were difficult to organize according to pattern for they were so unlike Theme I and II. The Mamaroneck song patterns were obviously less stereotyped than Theme I and II. Each male sang a wide variety of patterns, and individual variation in a given pattern was high. However syllable structure and certain syllable sequences were stereotyped throughout the population. This, and the fact that all Mamaroneck songs have many terminal syllables in common, aided the eventual identification of themes. I identified six basic themes (fig. 6) and generally three variants of each theme. No one male sang all six themes, but individual repertoires of three or four themes were common ($\bar{x} = 3.55$ themes per male).

The distribution of themes was determined by geographically dividing the Mamaroneck dialect area into sectors (NW, N, SE, S, SW,

Central), which mirrored the positions of the recorded males. The occurrence of themes in each of the six sectors was then compared. Some themes were widespread: Theme F occurred in five sectors, and Theme A occurred in all six sectors. But other themes were found in only one or a few sectors. For example, none of the seven males in the North sector sang Theme C, but there Theme D was widespread and sung frequently. In contrast Theme C was common in the Central sector where Theme F, otherwise widespread, was absent. The overall picture is not one in which all themes occur throughout the dialect area. Instead there are sub-units, each of which has its own characteristic set of (generally) four themes. This heterogeneity suggests a tendency toward the partitioning of this dialect area. Continuation of the trend could result in the formation of new, related, song dialects.

Several differences in singing behavior exist between the Mamaroneck population and the other ten populations in the block sample. Two stereotyped themes (occasionally three themes in the Peningo population) characterize the ten populations. As many as six somewhat variable themes characterize Mamaroneck. The Mamaroneck population has greater syllable diversity; 46 syllable types identified in Mamaroneck themes versus 28 syllable types in the Indian Village dialect (banded population). There is significant sharing of syllables among the different Mamaroneck themes, while the absence of syllable sharing characterizes the two themes of the other ten dialects. Mamaroneck males have larger individual song repertoires: $\bar{x} = 3.55$ themes per Mamaroneck male (range 2–6, $N = 20$ males); $\bar{x} = 1.91$ (range 1–3, $N = 87$ males) themes per male in the other populations. These differences suggest that the Mamaroneck birds have had a very different song tradition and history. This implies that the mainland of New York and Connecticut was originally colonized by at least two different parental stocks, one the precursor of the present-day Mamaroneck population, the second the possible precursor of the other sampled populations.

Boundaries. Dialect boundaries are of special interest. If song serves as a population isolating mechanism, the boundary between two different dialects should be narrow and gene flow across the boundary should be reduced. No estimate of gene flow was made, but recordings at several boundary sites revealed that birds with mixed repertoire may occur along boundaries (fig. 5). The Mamaroneck population provided a good oppor-

tunity to examine mixed repertoires, and estimate the width of the boundary at some places.

Three males, recorded at three different sites along the Mamaroneck boundary, had mixed repertoires. All three sang themes typical of both the Mamaroneck and the neighboring dialect area. All three males also sang hybrid songs, i.e. songs containing syllables from the two adjacent dialects (fig. 6G and H). One of these males had a (mixed) repertoire of six themes, making it the largest individual song repertoire recorded in this study. The precise mechanism of song learning in the wild is unknown but it obviously permits an occasional bird at the boundary to learn themes from two dialect areas.

The width of the Mamaroneck boundary was estimated from four measurements taken at places where by chance I recorded birds singing different dialects in the course of the same sampling session. Three cases involved 2 or 3 males singing at the same time from the crowns of neighboring trees: 1) a male with a hybrid repertoire, but primarily Mamaroneck songs, was singing within 20 m of a male singing songs similar to the Larchmont dialect (fig. 5-1); 2) two Mamaroneck males sang from the crowns of neighboring trees while a Harrison male sang from the crown of a tree about 40 m away, all trees bordering the same roadway (fig. 5-2); 3) three Mamaroneck males and one Harrison male were singing about 70 m apart. Repeated visits to the third site revealed at least two Mamaroneck males with females on nests. On these visits Harrison songs were uncommon and irregularly heard, suggesting that Harrison males were transient there. The fourth boundary location was a transect across the Mamaroneck border at a point between sites 2 and 3 (fig. 5-4). Beginning on the Mamaroneck side, the transect produced the following sequence of males and approximate distances between them: Mamaroneck male, 200 m, Mamaroneck-Harrison "hybrid" male, 200 m, Mamaroneck male, 900 m, Harrison male, and then a continuation of Harrison males. Sampling was done by driving slowly along a roadway. I began to listen for new birds only after I had driven 160 m (0.1 mi) from the previous recording site. This procedure would have me pass males in the 900 m interval if they were silent or temporarily absent at the time I drove by.

The four instances where the Mamaroneck population met adjacent dialects suggests that the Mamaroneck boundary is narrow—a width of <100 to 200 m is a rough estimate.

Dialect areas and dispersal. The small

circumscribed dialect areas with narrow, discrete, boundaries suggest either sedentary populations or populations with an ability for precise returns following a post-breeding dispersal. The region sampled provides an unexpected dividend, for in the 1950's and 1960's, early in the history of these eastern populations, two banding stations were active in the area. One, active from 1958-1962, was situated on the coast within the current Mamaroneck dialect area near its Peningo border. It is possible that the birds banded there were precursors of the 1973 Mamaroneck population. At about the same time, 1951-1964, a second banding station was active in Greenwich, Conn., 12 km northeast of Mamaroneck along the coast. The Greenwich station is surrounded by several populations sampled in 1973, all of which are characterized by some version of Theme I and II (e.g. Armonk, Byram and Greenwich Point populations). These birds banded in Greenwich may well have sung versions of Themes I and II.

Banding returns from the two stations reveal that House Finches disperse, migrating as far south as Philadelphia in winter (Cant and Geis 1961). But the published data were not organized to determine if birds, hatched or breeding in a given area, disperse and later return to that same area. Through the courtesy of Gilbert Cant, I have organized his banding returns, supplemented by data from Greenwich and a station near Philadelphia, to answer these questions (table 3). Only birds banded or recovered in the breeding season are considered. I assumed that adults banded or recovered in the breeding season were nesting near where banded, and that juveniles banded in the breeding season hatched from nests near the banding station.

Table 3 shows that both the early Mamaroneck and the early Greenwich breeding populations included birds that had previously nested in the respective home areas, plus birds known to have hatched there in previous years. Some juveniles and adults apparently remained in the home area overwinter; the minority of these, 11 of 44 (25%), were juveniles. Table 3 also reveals that in winter many juvenile and adult birds migrated. Of the 74 birds captured in both a breeding season and a non-breeding season, 40 per cent (30 of 74) were found at alien banding stations in winter. The percentage of migrant birds may be even higher than the figures in table 3 suggest, for recovery at a foreign banding station is less likely than a recovery at the home station. Most of these migrant birds were trapped about 175 km southwest of the home station, near Phila-

TABLE 3. Summary of banding records involving two metropolitan banding stations, 1951-1964.

Condition	Inference	Home station			
		Mamaroneck		Greenwich	
		Adult	Juv.	Adult	Juv.
1	Breed in home area	7	15	6	7
2	Possible emigrants	1	2	0	0
3	Winter in home area	6	2	27	9
4	Migrate in winter	7	14	6	3

Conditions:

1. Home banded 15 Mar.-30 Sep./home recovered a subsequent 15 Mar.-30 Sep.
2. Home banded 15 Mar.-30 Sep./alien recovered a subsequent 15 Mar.-30 Sep.
3. Home banded (recovered) 15 Mar.-30 Sep./home recovered (banded) 1 Nov.-15 Mar.
4. Home banded (recovered) 15 Mar.-30 Sep./alien recovered (banded) 1 Nov.-15 Mar.

delphia, Penn.: 25 captures (83%) were from Philadelphia, two (7%) from New Jersey, and three (10%) from metropolitan New York locations other than the home banding stations. A large number of juveniles, 17 of 30 (57%), were migrants.

The migrants presumably returned north to Mamaroneck and Greenwich. Most of the evidence for this is indirect. For example, ten of the 30 migrant birds were originally banded in Philadelphia and later were recovered in either Mamaroneck (2 birds) or Greenwich (8 birds). Direct evidence of return to the home area requires birds with records of multiple recoveries. Twelve of the birds in table 3 were recovered at least twice after initial banding, but ten of these were recovered twice at either the home station or the alien station. However, one Mamaroneck juvenile was banded in Mamaroneck in August, recovered in its first March in northern New Jersey (about 32 km WSW of Mamaroneck along the migratory path of metropolitan populations), and recovered again in Mamaroneck in its first breeding season (April 20). This is proof of return to the natal area following a period of winter dispersal.

The other multiple recovery involved a juvenile that may have emigrated. Banded in Mamaroneck in July, it was twice recovered in Philadelphia in its first winter (in December and early March), then finally recovered again in Greenwich late in its first March, a time when some late migrants have not yet completed their passage. Since Greenwich is only 12 km northeast of Mamaroneck it is possible that this individual overshot its northern destination and had yet to complete that journey which could end at Mamaroneck. But it is also possible that this bird emigrated and settled near Greenwich, and that is the interpretation taken. Table 3 reveals a small num-

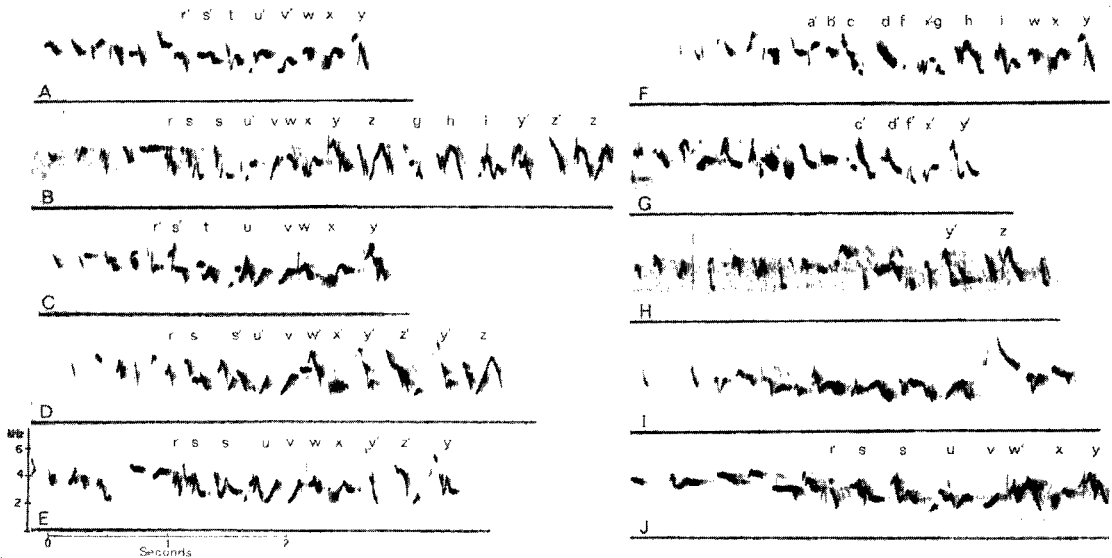


FIGURE 7. Representative songs in the coastal sample. A-E, and J, Theme I from: A. Davids Is., B. Greenwich Pt., C. Noroton, D. Southport, E. Milford, J. Poughkeepsie; F. Theme II, Davids Is.; G. modified Theme II, Manhattan; H. second theme, Manhattan; I. a theme from Throgs Neck. Theme I from the Peningo coastal station is illustrated in Fig. 4.

ber of potential emigrants, including one other juvenile and an adult. The adult was found dead only a few kilometers south of Mamaroneck and may not have been an emigrant. But the second juvenile record provides the best evidence for emigration. This bird was banded in its natal summer (August) in Mamaroneck and was subsequently recovered in two successive summers (June, both years) in Greenwich, Conn.

From this portion of my study I conclude that House Finches in SE New York and Connecticut are distributed in a mosaic pattern of song dialects. These dialect areas are small, on the order of a few square kilometers. Neighboring dialects are contiguous. They meet along a narrow, discrete boundary where males with hybrid song repertoires can be found. Maintenance of the integrity of the different dialects is not due to a sedentary population. Both juveniles and adults can migrate after the breeding season, but may

return to their home dialect areas to breed in succeeding years. However, it is possible that some birds may leave their natal area and be found within the boundaries of another dialect area in later breeding seasons. The relationships between songs of the sampled dialect areas suggest that ten dialects are derived from one initial early colonization; one dialect probably had a separate derivation.

COASTAL SAMPLE: REGIONAL ANALYSIS

The nine sites in this sample include eight scattered along the Long Island Sound coastline at intervals ranging from 10–20 km. If dialect areas are generally as small as those identified in the block then each coastal station would sample a different dialect. Table 4 summarizes the results of sampling along the New York-Connecticut coast and up the Hudson Valley. Figure 7 illustrates some representative audiospectrograms.

TABLE 4. Partial song formulae of two themes from nine coastal sites.

Sample station	First theme	Second theme
1. Manhattan (R.U.)	100—————→110 y'z	111 112 c d'—f'g'y'
2. Throgs Neck (Bronx)	120—————→129	130—————→136
3. Davids Is., N.Y.	r's't u'v'w x x y	a'b'c(d e)f'g'h i w x y
4. Peningo Point, N.Y.	r s t' u v(w) —y z(g h i d')	a b c'd'e—g h i d'(x y z)
5. Greenwich Pt., Conn.	r s s u'v w x y z(g h i y'z'z)	a'b'a b c(d e)f g h i
6. Noroton, Conn.	r's—u v w x y	a b c d—(f g h)
7. Southport, Conn.	r s s' u'v w'x'y'z'(y'z)	a'b'c'd d'd'f'g h
8. Milford, Conn.	r.s s u v w x y'z'(y'z'y z)	150 151 y'z'y z
9. Poughkeepsie, N.Y. (Vassar)	r s s u v w'h i(y'y'z'y x y)	a b a'b'c'(d e)f g h(i z'y z)

Many of the coastal stations were characterized by songs that can be interpreted as modifications of Theme I and II, which is similar to previous results. But differences between the song patterns of the more scattered coastal populations were usually greater than differences among the song patterns of the ten contiguous populations in the block sample. In table 4 only the terminal parts of the song formulae are represented. Introductory syllables were omitted since they were different at each of the nine stations.

In general the five males sampled at each coastal station had the same songs (judged by introduction as well as terminal portion), but there were exceptions. One male at Greenwich Point sang themes that bore little resemblance to songs recorded anywhere else. The other exception involved the five males sampled at Noroton, Conn. The Noroton sample could be subdivided into two groups, each with their own set of similar themes. The Noroton station may have included members of two adjacent and similar dialects.

Seven of the nine populations, including the Poughkeepsie population on the Hudson, sang variations of the same two themes (I and II) that were so widespread in the block sample. But two coastal populations were exceptional. The Throgs Neck population had songs completely different from all other populations sampled. The unique patterning of these songs adds support to the thesis that the eastern House Finches sampled in this study have derived from more than one founder population. The Manhattan population had one almost unique song pattern, but the second Manhattan theme was interpreted as a modified Theme II (fig. 7). The relationship of the Manhattan population to those in Connecticut is not clear.

Finally, female singing was widespread. The females were sexed by plumage and by the intense soliciting behavior associated with their singing. No male in red plumage was ever seen to solicit. I heard females sing in 7 of the 9 stations and recorded females at 3 stations. Analysis of these recordings revealed that the females sang songs that were like those of the males in their dialect areas.

I conclude from this regional analysis that nine scattered sites in SE New York and Connecticut sampled at least nine different dialects. Indirectly this provides additional evidence that the geographic extent of a song dialect along the coastline is limited, probably only a few kilometers in any direction. Seven populations sang songs derived from the basic Themes I and II; one of the nine coastal popu-

lations had a totally different set of songs; and one population showed many differences and some similarities to the basic Theme I and II structure.

DISCUSSION

My investigation shows that eastern populations of the House Finch do have song dialects. Contiguous populations inhabiting relatively small areas, up to a few kilometers on a side, have specific sets of two to six song themes. Although some populations have unique song patterns, more often the songs of neighboring populations are structurally similar, differing primarily in the introductory portion of their songs. The song patterns of individual birds are stable over a period of several years, and the songs identifying a given population are essentially uniform even when different individuals are sampled in different years. This, and the fact that the songs are learned (Munding, in prep.) indicates a stable, learned song tradition.

These eastern song dialects have evolved in little more than two decades, for the New York and Connecticut mainland was initially colonized in the early 1950's (Bull 1964). From this small foothold, and from earlier colonies established on Long Island in the mid-1940's, nesting House Finches have spread north to Maine, south to Virginia and North Carolina, and west to the shores of Lake Erie (Audubon Field Notes 1955-1970, American Birds 1971-1973). The introduced House Finch thus provides a rare opportunity to assess the evolution and function of song dialects in the light of active colonization.

It is unlikely that the founders possessed all the song diversity that can now be found on the east coast. New song patterns must have evolved and the results of this survey provide evidence for two, related, origins of new dialects. The incipient partitioning of the Mamaroneck population suggests that new dialects may arise when part of a population develops a local idiosyncrasy in its song pattern which is perpetuated and enhanced from generation to generation giving rise to new themes. Apparently this has not yet occurred with the Mamaroneck population, perhaps because it is encircled by populations with radically different song types which may hamper geographic expansion. However other modern dialects (Harrison and Indian Village, Byram and Port Chester populations) are both contiguous and are characterized by very similar sets of themes. They may have originated by partition.

The related colonization hypothesis (Baker

1975) proposes that dialects arise when peripheral habitats are colonized. Originally proposed to explain dialect formation in California White-crowned Sparrow populations, the hypothesis suggests that, as a result of colonization, peripheral populations become geographically isolated from the mother population. Then the propagule's song patterns, with the accumulation of copy errors, may gradually diverge from the song of the mother population. Juveniles are examples of potential propagules likely to have an error-prone song ontogeny. If song divergence is sufficiently great, the mother and colony populations would retain their separate integrities should they meet at some later time. The history of the House Finch colonization of metropolitan New York and the system of song dialects described here provide empirical evidence supporting this hypothesis.

Both on Long Island and on the mainland the first known breeding colonies were few and were separated by distances of 5–37 km (Elliott and Arbib 1953, Bull 1964). Later, as numbers increased, intervening areas were colonized leading to eventual contact of once-separated populations. The history of the mainland colonization is discussed here as it relates more directly to the song dialects described in this paper.

The first known colony settled in Greenwich, Conn., about 1952, and two years later the second known colony was reported in Pound Ridge, N.Y., 22 km north of Greenwich (Cant and Geis 1961). In early 1958 Cant (pers. comm.) first noted the arrival of House Finches in Mamaroneck, N.Y., 12 km southwest of Greenwich, and he banded his first juveniles that summer. This third reported breeding colony was the likely precursor of either the Peningo or the Mamaroneck dialect. (In the first case the birds could have come from the original Greenwich colony, but in the second case I believe the totally different Mamaroneck and Greenwich song patterns imply that the Mamaroneck birds came from elsewhere, perhaps one of several colonies then known to be active on Long Island.) Thereafter the birds spread rapidly into communities within the Greenwich-Pound Ridge-Mamaroneck triangle. This spread was more noticeable along the coastline, although later it also included more inland locations (Cant 1962). The mobility of some juveniles at this time (see table 3) suggests that juveniles were included in the invasion of these new suburban habitats. The results of the 1973 block sample revealed extensive secondary contact between local populations, this contact

occurring within two decades after the initial Greenwich founding.

These data are consistent with the interpretation that soon after colonizing Greenwich, Conn., unoccupied habitats some kilometers distant were colonized by members (juveniles?) of this colony. Song divergence, especially in the introduction to Theme I, followed. With population growth, and aided by man's transformation of woodland (poor habitat) to suburban developments (optimum habitat), these local populations expanded geographically, and many eventually met. Where song divergence was sufficiently extensive, for example along the coastline, discrete boundaries occurred between adjacent dialects. The available evidence also indicates that under conditions of active colonization the evolution of new dialects probably occurred in about 10 years (e.g. 1952–1962) and certainly within 20 years. This is surprisingly rapid even for a culturally transmitted behavior pattern.

My sampling identified 19 song dialects. Sixteen of these are structurally related and form a widespread system of dialects based on Theme I and Theme II. I consider this evidence that these 16 dialects originated from a single source, probably the original Greenwich founder population. The current diversity within this system of dialects may then be the result of continued colonization, and also the result of partitioning among established populations. Of the three other dialects, the songs of one, the Manhattan population, reveal some similarities to the dialect system. Manhattan was colonized late (Bull 1964) and whether these similarities, identified in just one small Manhattan population, reflect an emigration south from northern suburbs or west from Long Island is not known.

The two remaining populations, from Throgs Neck (Bronx) and Mamaroneck, have no syllables in common with any other sampled dialects. These two populations may have derived from other founder populations. Ultimately all the mainland populations probably derived from birds that colonized Long Island in the 1940's, although there may have been a series of smaller introductions before 1940 (Cant 1962). These Long Island founders were birds captured in large numbers from various California localities; they were sold by the thousands in the pet trade, and, in 1940, were released in large numbers on Long Island by bird dealers faced with federal prosecution for selling a protected species. By 1943–1945, breeding colonies were found in four scattered Long Island communities (El-

liott and Arbib 1953). This founder stock probably represented many California populations, and a rich variety of song patterns. This would explain the apparent polyphyletic origin of populations encountered in this study.

Marler and Tamura (1962) suggested that dialects function to maintain the integrity of populations. In the absence of measures of gene flow among populations, this function is best assessed by focusing attention on the nature and maintenance of dialect boundaries. A broad zone of intergrading song types suggests relatively open exchange between adjacent populations. In contrast, a narrow and discrete boundary, such as that observed between the Mamaroneck population and its adjacent neighbors, indicates limited exchange of adults. Classical isolating mechanisms such as geographic separation or ecological differences do not maintain House Finch dialect boundaries since the populations are contiguous and occur in the same habitats. Neither can sedentary behavior be responsible, for these finches do migrate and return to their home dialect area to nest. However, other forms of behavior, such as semi-colonial nesting habits and song, may function in maintaining boundaries and thereby the integrity of the populations.

Thompson (1960b) found House Finches to be gregarious and often to nest semi-colonially; territorial behavior is infrequent and the territory is limited to a few meters around the nest. Agonistic behavior usually occurs in the context of social hierarchies rather than territorial defense. The highly integrated society of this passerine may serve as a barrier to the intermixing of different dialects. Should an isolated pair from an alien dialect nest near a loose, but socially integrated, colony, the alien male would provide but one model for his song tradition while the several males of the colony would provide multiple models. Young birds reared by the pair may then learn from the colony. Such a hypothetical situation may reduce the exchange of song traditions between adjacent populations but would not necessarily reduce gene flow.

Gene flow, as well as song tradition, could be reduced if song itself served as an isolating mechanism. Here, female choice may play an important role. Milligan and Verner (1971) demonstrated a greater attractive valency of the home dialect song, as compared to alien dialect songs, for female White-crowned Sparrows. Also Nottebohm (1969) suggested that a female's hormonal state may be stimulated by hearing her mate's song, the effect possibly

being enhanced in a dialect system where the neighboring males sing the same song pattern. The natural history of the House Finch provides added support for the hypothesis that, mediated by female choice, song may function to limit gene flow between adjacent populations.

The song patterns of female House Finches are like those of neighboring males. The House Finch song itself has a strong sexual valency as evidenced by both sexes directing their songs at their mates during critical stages in reproduction. After pairing, most male singing occurs during the nest building phase. Then, while the female builds, the male faces the nest and the female and, from a perch a short distance away, sings consistently. Later, in the copulatory phase, the male's courtship singing is directed at the female from less than a meter away (pers. obs. of banded pairs). For her part, the female sings primarily during the period of copulation and courtship feeding and again at the end of incubation and brooding. At these times the female orients toward her mate and sings, often soliciting simultaneously. Female singing is especially intense as the male approaches (pers. obs. of 4 banded pairs).

These observations suggest that song functions to stimulate both sexes sexually. Since the males and females in a dialect area sing the same song, we know the central nervous system of both sexes is organized to produce the same song pattern. The nervous system may also be organized to respond preferentially to that same pattern. A similar output-input paradigm resulting in stimulation of the reproductive system operates in at least one other avian species. Brockway (1967) showed that testis growth in Budgerigars (*Melopsittacus undulatus*) is stimulated by the male performing and hearing his own "song"; the "songs" of other males are not as effective. In a similar fashion, specific song patterns may stimulate male and female finches, restricting pairing and effective reproduction to those individuals sharing the same kind of song learning experience. Since song learning in the House Finch can occur in the second month of life (Mundinger, in prep.) this experience is often hearing the natal dialect. This pattern, once learned, would limit an individual's future reproductive activity to the natal area, effectively maintaining the genetic integrity as well as the song tradition of the population.

If this is a function of song, then House Finch song dialects correspond to demes. The map of the contiguous dialect areas (Fig. 5) does resemble a mosaic of demes. The dimen-

sions of each dialect area are too large to explain the song homogeneity within each one as due to the inhabitants being within hearing of each other during their period of song learning. Yet the area is small enough so that every finch in a dialect area has ready geographic access to all parts of it when choosing a mate or nest site. This function of organizing the species into coherent, semiclosed, breeding units leads to consideration of other important functions of song dialect.

Nottebohm (1969) hypothesized that dialects function to promote local adaptation. In the Chingolo, noticeable changes in song patterns occur at points of abrupt habitat shifts (Nottebohm 1969). Presumably the extreme differences in song between populations inhabiting adjacent but very different habitats severely limit gene flow, enhancing adaptation of each population to its own local conditions. This intriguing hypothesis cannot be tested with the data collected from eastern populations of the House Finch, first because different life zones did not occur in the study area (the limited diversity encountered, e.g. coastal versus inland suburbia, was included within individual dialect areas), and second because any large differences in song patterns can be attributed to the progenitors originally being taken from diverse California localities.

But Nottebohm extended aspects of the hypothesis to colonizing species by suggesting that mechanisms enhancing local adaptation, e.g. song dialects, are encouraged when invading species exploit new environments. This statement essentially proposes that colonization promotes dialects. One can also state the reverse, that dialects can promote colonization. Although seemingly circular the two statements apply to different events.

From arguments already presented, as a consequence of continued colonization a system of House Finch dialects *evolved* in southern New York and Connecticut. In at least this sense colonization promotes dialects. But this does not imply that song dialects evolved *de novo* on the east coast. Western populations may have dialects, and the possession of song dialects, prior to introduction, may have enhanced the survival of the east coast founder population. A different hypothesis, that song dialects promoted the successful *establishment* of new House Finch colonies, can be examined in the light of the survivorship theory of colonization. This theory states that successful survival of a newly established colony is directly proportional to the number of effective colonizers and to a large ratio of r/λ (MacArthur and Wilson, 1967, chap. 4). I contend

that both the number of effective colonizers (successfully breeding pairs) and r/λ (r is the intrinsic rate of population increase; λ is birth rate) are optimal for founders with a dialect organization coming from the same dialect area.

First, the number of actual or potential breeding pairs is increased. Flocks from the same dialect area can contain established pairs, an assertion bolstered by the observation that breeding pairs of House Finches continue to associate, as pairs, in winter (pers. obs. of four color-banded pairs). The number of potential pairs is also increased since all possible pair combinations in a group of birds from the same dialect area will have the same song patterns. Second, a maximum ratio of r/λ is attained by increasing r through the optimal use of breeding season time to rear young. The intrusion of courtship and pairing behavior into the breeding season can reduce the time available for procreation and parental care. Pairing in cardueline finches costs time. It involves courtship feeding and call imitation, social behavior that may require months to accomplish, but that may also occur outside the breeding season in winter flocks (Mundinger 1970). Since vocal imitation is involved, birds with a common dialect heritage could hold some of this social behavior in common before, or soon after, flocking, and achieve the necessary bonding sooner, on average, than associations of birds from diverse localities and vocal traditions. Moreover, both sexes of a flock from the same dialect area will share the same song patterns which would promote prompt and effective onset for the reproductive function of singing. The temporal advantages gained would permit pairs from uniform dialect founder flocks to initiate zygote production at the earliest time following their arrival in unoccupied habitat, with the consequent increase of r/λ . These same advantages would also apply to their progeny, accelerating the time when population growth makes the colony's continued existence more secure.

But do House Finch flocks consist of birds from the same local population? The limited data available suggest that this occurs. I analyzed east coast banding recoveries (from 1948–1973) for flock composition, arbitrarily defining a flock as three or more recovered birds originally banded in the non-breeding season, at the same station, on the same day, and with nearly sequential sets of numbered bands. Seven such flocks contained at least two individuals recovered in a subsequent breeding season. One of these flocks contained

three breeding birds recovered at three different stations, implying that it was a heterogeneous flock. Six flocks contained breeding birds recovered at only one or, for two flocks, two stations. Of these six flocks three were apparently non-migratory, for all nine birds were banded and later recovered (8 birds in the breeding season) at the same New York station. The three remaining flocks were migratory. In these migratory flocks, 9 birds were recovered in the breeding season and seven of these (78%) were recovered at the flock's presumed home station (the station where all, or most of the "breeding" individuals in the flock were recaptured). From this I infer that House Finches from the same dialect area associate in winter flocks, and that some uniform, or nearly uniform, dialect flocks migrate long distances. These flocks would provide the best propagule for further House Finch colonization.

Finally, using songs dialects and published records as a guide, we can speculate on the pattern of early House Finch colonization of the New York metropolitan area. A dialect behavioral organization applied to a vocally heterogeneous group of birds (e.g. the probable founder stock from California) might be constraining, resulting in a relatively ineffective propagule. However, if the heterogeneous group were numerically large and the several constituent dialects were represented by many individuals of each sex, then optimum conditions for effective colonization are potentially present—for this is the equivalent of several uniform dialect flocks released at the same time and place. These conditions may have pertained in the original 1940 introduction. It is possible that many birds from each of several California dialects were captured, shipped, and eventually released together.

Once the earliest Long Island colonies were established they could have served as reservoirs for further colonization. Although each early colony might have represented a different song dialect, it seems logical to assume that each might have provided vocally homogeneous propagules. Colonization proceeded rapidly with the finches spreading eastward to the tip of Long Island and westward to the mainland (fig. 1). The basic similarity of the songs of the descendants of one postulated mainland propagule, the Greenwich colony, is consistent with the concept of vocal homogeneity within that early mainland founder.

If these speculations are close to actual events, song dialects may be a useful tool to trace pathways of range expansion in the House Finch, which continues to spread at a

rapid pace in the east, as well as for other colonizing species.

SUMMARY

The songs of 155 banded and unbanded male House Finches were sampled in a study of song variation along the southwestern coastline of Long Island Sound. Song variation occurs as a series of local song dialects, the birds in each dialect inhabiting an exclusive area a few kilometers on a side. Boundaries between adjacent dialects appear to be discrete, and a few hundred meters wide. Males with hybrid song repertoires may occur in the boundary regions. There was no significant yearly variation in the songs characterizing known individuals or their local population. The geographic distribution of dialects, the patterns of dispersal inferred from the banding records of two dialect areas, and the history of the early founder populations are discussed with respect to House Finch colonization and the evolution of new dialects.

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LITERATURE CITED

- AMERICAN BIRDS. 1971-1973. Regional reports (eastern sight records). National Audubon Society, N.Y., Vol. 25-27.
- AUDUBON FIELD NOTES. 1955-1970. Regional reports (eastern sight records). National Audubon Society, N.Y., Vol. 8-24.
- BAKER, M. 1975. Song dialects and genetic differences in White-crowned Sparrows (*Zonotrichia leucophrys*). *Evolution* 29:226-241.
- BROCKWAY, B. F. 1967. The influence of vocal behavior on the performer's testicular activity in Budgerigars (*Melopsittacus undulatus*). *Wilson Bull.* 79:328-334.
- BULL, J. 1964. Birds of the New York area. Harper and Row, N. Y.
- CANT, G. 1962. The House Finch in New York State. *Kingbird* 12:68-72.
- CANT, G., AND H. GEIS. 1961. The House Finch: a new east coast migrant. *EBBA News* 24:102-107.
- ELLIOTT, J. J., AND R. S. ARBIB. 1953. Origin and status of the House Finch in the eastern United States. *Auk* 70:31-37.

- HOPKINS, C., M. ROSETTO, AND A. LUTJEN. 1974. Continuous sound spectrum analyzer for animal sounds. *Z. Tierpsychol.* 34:313-320.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J.
- MARLER, P. 1952. Variation in the song of the Chaffinch, *Fringilla coelebs*. *Ibis* 94:458-472.
- MARLER, P., AND M. TAMURA. 1962. Song "dialects" in three populations of White-crowned Sparrows. *Condor* 64:368-377.
- MILLIGAN, M., AND J. VERNER. 1971. Inter-population song dialect discrimination in the White-crowned Sparrow. *Condor* 73:208-213.
- MUNDINGER, P. 1970. Vocal imitation and individual recognition of finch calls. *Science* 168:480-482.
- MUNDINGER, P. (in prep.) Song learning in the House Finch, *Carpodacus mexicanus*.
- NOTTEBOHM, F. 1969. The song of the Chingolo, *Zonotrichia capensis*, in Argentina: description and evaluation of a system of dialects. *Condor* 71:299-315.
- NOTTEBOHM, F., AND R. K. SELANDER. 1972. Vocal dialects and gene frequencies in the Chingolo sparrow (*Zonotrichia capensis*). *Condor* 74:137-143.
- PAYNE, R. B. 1973. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. *Ornithol. Monogr.* 11.
- POULSEN, H. 1951. Inheritance and learning in the song of the Chaffinch (*Fringilla coelebs*). *Behaviour* 3:216-228.
- THIELCKE, G. 1969. Geographic variation in bird vocalizations, pp. 311-339. In R. A. Hinde [ed.], *Bird vocalizations*, Cambridge Univ. Press.
- THOMPSON, W. L. 1960a. Agonistic behavior in the House Finch part I: annual cycle and display patterns. *Condor* 62:245-271.
- THOMPSON, W. L. 1960b. Agonistic behavior in the House Finch part II: factors in aggressiveness and sociality. *Condor* 62:378-401.

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