

GEOGRAPHICAL VARIATION IN SONGS OF CALIFORNIA HOUSE FINCHES (*CARPODACUS MEXICANUS*)

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ABSTRACT.—The songs of 102 male House Finches (*Carpodacus mexicanus*) were sampled in southern California. Additionally, songs were induced with testosterone in 10 captive females. Females sang only 1 or 2 themes, whereas males averaged 4 themes; males in each recording location shared a repertoire of similar phrases and songs. Song types sung by neighboring males were more similar to each other than to songs of more distant birds. Some females sang themes identical to male songs; others sang simpler songs with fewer syllable types. In a 5-km transect from Occidental to Montecito, four populations (identifiable by population-specific phrases in their songs) were described in a continuum, one replacing the other over a distance of 5 km. Clumped distribution of theme types suggests song development by male-male interaction, as has been reported for other passerines. California House Finches exhibited greater syllable diversity, more themes per locality, and more themes per individual than eastern birds. California House Finches did not exhibit distinct song dialects as did eastern populations; possible reasons for this difference are that eastern House Finches have fewer themes to mimic and thus learn whole songs. California House Finches are older populations with large repertoire sizes and tend to improvise by building new themes with syllables from several songs. It is also possible that California House Finches vary geographically in their tendency to share songs. Song learning in House Finches may promote individual recognition due to improvisation and theme matching by mated pairs. *Received 3 July 1978, accepted 27 February 1979.*

AVIAN calls and songs have been popular subjects of study in recent years (Hinde 1969, Thielcke 1970). Some workers have focused on song as a tool in tracing the origins of invading bird populations (Thielcke 1969, Baptista 1975, Mundinger 1975). Others have investigated the species-specific parameters of bird song (Emlen 1972, Shiovitz 1975). Ascertaining species-specific parameters in song of any species necessitates a detailed look at song variation within the individual, the population, and between populations.

Song dialects are said to occur when songs of conspecifics in an area are alike but differ from those in other areas (reviews in Thielcke 1969, Lemon 1975). Although geographical variation in avian song and song dialects has been investigated widely over the past two decades, the adaptive significance of dialects still remains unknown (Avery and Oring 1977). Actually, song dialects are known in relatively few birds. Moreover, theme or syllable sharing may vary geographically even within species (Eberhardt and Baptista 1977, Williams and McRoberts 1977). It is, therefore, important to continue to document this phenomenon when and if it occurs. Perhaps in knowing more about the distribution of dialects among avian taxa, we may finally come to understand their function(s).

Earlier observations on singing behavior and song variation in the House Finch were published by Miller (1921, 1929, 1952), Thompson (1960), Baptista (1972), and most recently by Mundinger (1975) and served as background information for this study. Mundinger (1975) studied song dialects and colonization in House Finches (*Carpodacus mexicanus*) in New York that were introduced from California in the 1940's (Aldrich and Weske 1978). He found that House Finch dialects replace one

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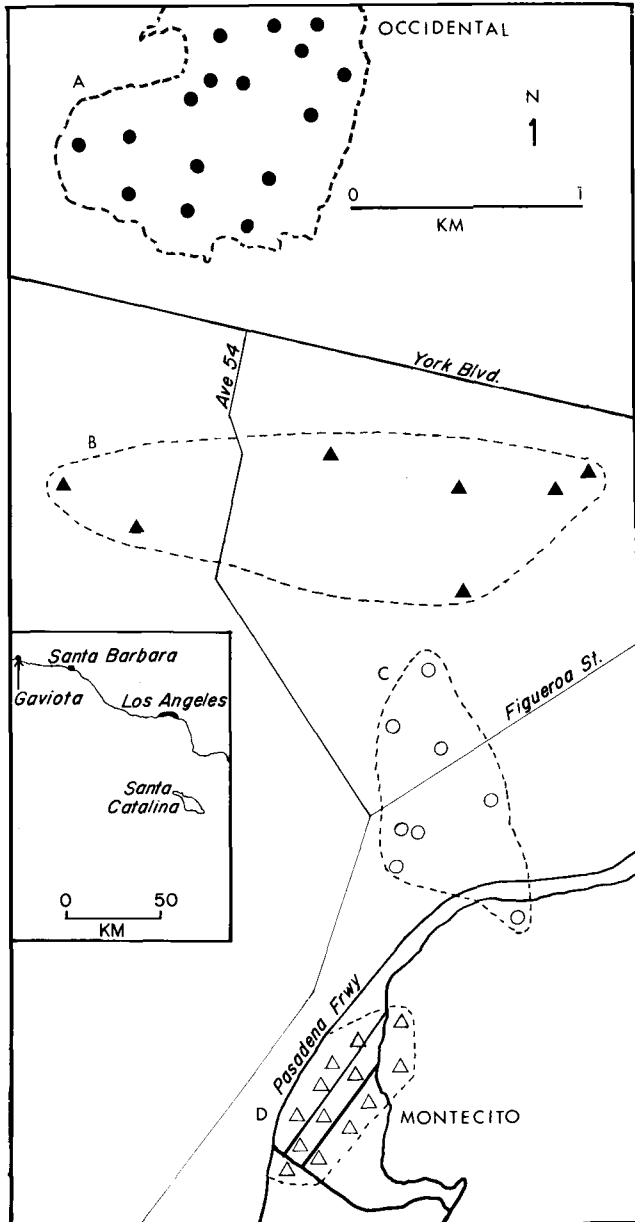


Fig. 1. Map showing locations where House Finches were recorded. Letters A-D are the recording localities in Los Angeles: (A) Occidental College, (B) City 1, (C) City 2, (D) Montecito Heights. Dotted lines enclose study areas where birds share similar songs.

another geographically; where their ranges adjoined, discrete dialect boundaries were found. This paper is an account of song variation in House Finches (*Carpodacus mexicanus frontalis*) from the mainland of southern California and from Santa Catalina Island (*C. m. clementis*).

The goals of our study were: (1) to ascertain intra-individual, intra-population, and inter-population variability in House Finch song; (2) to determine if, as in

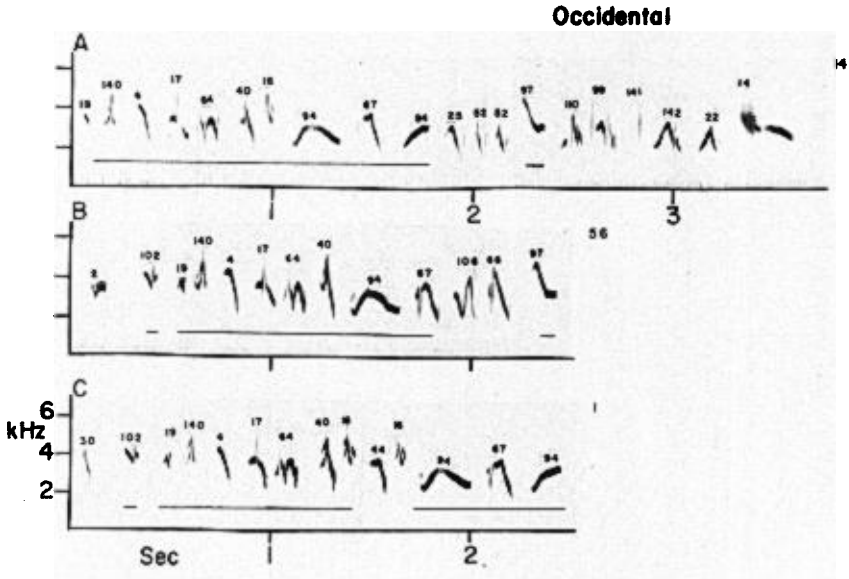


Fig. 2. Population specific phrases common to more than one bird in a population. The larger numbers on the right of each song represent individual birds from Occidental. The underlined syllable sequences are shared between birds in a population. The numbered syllables allow for comparison between birds, as in Mundinger (1975).

eastern House Finches, distinct dialects exist in western House Finch populations, and if so, the size of each dialect area; (3) to ascertain differences and/or similarities that might exist between the songs of insular Santa Catalina populations versus those from the mainland, as songs of island populations are often much simpler or more complex than those from mainland populations (Marler and Hamilton 1966, but see also Thielcke 1969, Mirsky 1976).

MATERIALS AND METHODS

Four different populations of House Finches were studied in 1975, and one population was resampled in 1976 (Fig. 1, Table 1). Birds were recorded on: (1) the campus of Occidental College; (2) Montecito Heights Park, Los Angeles; (3) a transect covering 5 km running between Occidental and Montecito Heights in 1976 (two sampling localities intermediate between the end-points are hereafter referred to as the City 1 and City 2 populations); (4) Gaviota State Beach Park, 38 km west of Santa Barbara; and (5) Santa Catalina Island, 28 km from the nearest point on the California mainland.

From 102 individuals, 857 songs were recorded and analyzed. Field recordings were made using either a portable Uher 4000 Report 1c tape recorder or a Sony TC-800B tape recorder, and an Altec 684A microphone mounted on a 24-in fiberglass parabolic reflector. Tape speed was 9.52 cm/s. Songs were analyzed with a Kay Electric Sonagraph Model 7029A using wide band and high shape filters. Birds were usually recorded at a distance of 15–20 m from the microphone. Care was taken not to record the same individual twice. When sonagrams suggested that the same individuals were being resampled, the duplicated material was not used in the analysis. We are mindful of the possibility that two birds may have identical theme repertoires. However, we usually found small differences in syllable structure that distinguished identical themes from different individuals. Recordings were concentrated between 0700 and 1200. Usually a minimum of eight songs was recorded from each bird to evaluate individual variation. If more than one bout was recorded, then a silent interval of 60 s or more was regarded as an interval between bouts in the analysis. Notes and syllables were individually labelled and catalogued for each population as in Mundinger (1975).

TABLE 1. Summary of descriptive statistics in House Finch song.

	Location and dates of recording				
	Occidental, March 1975– April 1976	City, February 1976	Montecito, March 1975– June 1975	Santa Catalina, June 1975	Gaviota, April 1975
Number of birds	45	15	13	14	5
Number of songs	546	125	75	42	69
Number of themes/population	71	36	21	13	15
Themes sung/individual ^a	4.0 ± 0.6	4.0 ± 0.4	4.4 ± 0.5	5.1 ± 1.1	5.2 ± 0.8
Song length (s) ^a	2.1 ± 0.6	2.0 ± 0.4	1.6 ± 0.2	2.1 ± 0.3	1.8 ± 0.3
Syllables/song ^a	13.0 ± 2.8	13.6 ± 2.7	11.3 ± 1.9	14.8 ± 1.2	12.6 ± 1.3
Maximum frequency (kHz) ^a	8.4 ± 1.4	8.4 ± 1.3	7.9 ± 1.5	8.0 ± 1.3	8.0 ± 0.8
Minimum frequency (kHz) ^a	1.8 ± 0.8	1.9 ± 0.2	2.0 ± 0.6	2.0 ± 0.6	2.0 ± 0.3
Frequency range (kHz) ^a	6.6 ± 0.9	6.4 ± 0.8	5.8 ± 0.8	6.0 ± 0.6	6.0 ± 0.8

^a Mean ± standard deviation.

It is difficult to sample female House Finch song in the field, as they sing less frequently than males (Thompson 1960). Songs were, therefore, induced with testosterone (G. B. Searle, Sc-16148, 50 mg/cc) in 10 females from Occidental to compare repertoire size and syllable and theme sharing between the sexes. Female songs were recorded indoors at 9.52 cm/s with a Sony TC-800B portable recorder and a Sony F-26S microphone. Singing usually occurred within a week after injection. Four birds required additional doses of 0.15 cc of testosterone 10 days after the initial injection, and singing commenced within 4 days. Birds were sexed by laparotomy prior to injection, as first-year males of *Carpodacus* species may on rare occasions retain female-like plumages (Ridgway 1901, Moore 1939).

The following parameters of House Finch song were quantified: (1) duration of individual songs in seconds, (2) number of syllables per song, (3) maximum and minimum frequencies in kHz on the spectrogram, (4) frequency range in kHz (the maximum minus the minimum frequency), (5) mean frequency (the sum of maximum and minimum frequency divided by two), and (6) singing period (the interval between the beginning of one song and the beginning of the next).

Here we follow the terminology of Borror (1961), Mulligan (1966), Baptista (1975), and Munding (1975), which includes the following: Note, Syllable, Buzz-whistle, Trill, Phrase, and Bout. Additionally, we use the word theme to denote a unique combination of syllables in a stereotyped sequence. "Song variant" is songs that differ in only a few syllables (usually in the introductory portion), rather than being distinct song types. As in Munding (1975), two songs are considered the same theme if 80% of the syllables are shared.

GENERAL DESCRIPTION OF THE HOUSE FINCH SONG

The song of the male House Finch is rapid, complex, and highly variable within and between individuals (Thompson 1960, Munding 1975). The male possesses a repertoire of songs peculiar to himself and each sampling locality. A typical song of the species consists of an introduction made up of a series of syllables, sometimes followed by an additional trill and a terminal buzz (Fig. 2A). Three birds began their songs with contact calls, but this is not normal. Duration of each song was approximately 2 s (Table 1). Mean number of syllables per song was 13 ($N = 857$ songs, range 4–26). The minimum and maximum frequencies were 1.4 and 8.2 kHz, respectively.

Performance time, or the percent of actual time singing, was computed by dividing the sum of all song lengths by the total duration of the recording, then multiplying by 100 (after Kroodsmas 1975). Total singing time for 20 birds chosen at random was 28%.

Spectrograms of songs from Occidental College from two different seasons indicated no major changes. This is similar to Munding's (1975) data on banded eastern House Finches, which yielded no evidence of any change in repertoire,

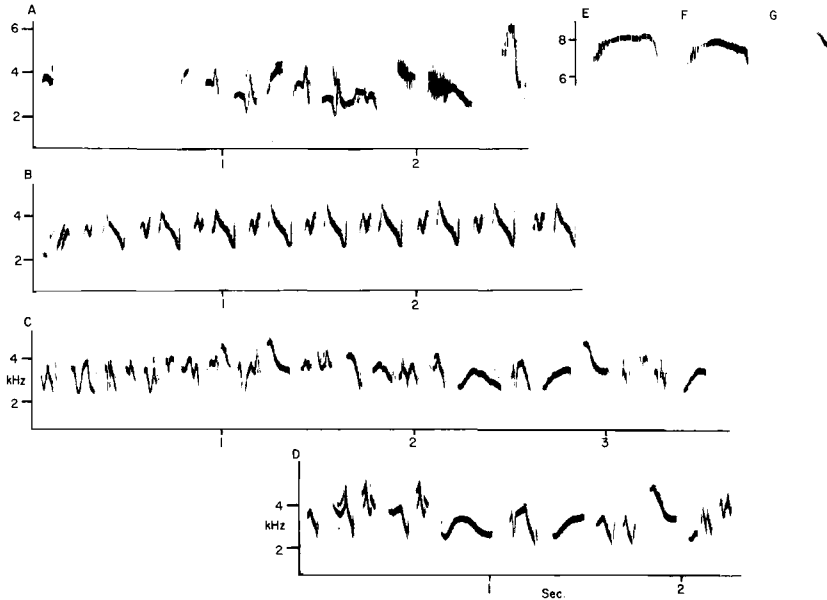


Fig. 3. Comparison between female and male songs and squeak syllables. (A–C) Female testosterone-induced songs from Occidental College. (D) Male song from Occidental shares a similar sequence of syllables with female Song C. Female Song A ends with a squeak syllable as found in male songs. Male Squeaks E and F from Occidental are similar to female Squeak G.

themes, or syllable types through the season or from one year to the next. Each adult male has a repertoire of song themes that, with minor variations, is repeated throughout the season and perhaps throughout his life.

Directed and undirected song.—Songs given when a female House Finch was within 6 m of a male were considered directed song. When directed at a female, songs were sung at the rate of about 15 per min ($N = 80$ songs). The male usually held his body upright and faced the female. When songs were not directed ($N = 80$ songs) at a female, the rate was significantly slower—5–10 songs per min ($t = 2.34$, $P < 0.05$).

Directed song might consist of a series of 2–4 of the same or different themes strung together to form a run-on song (terminology after Thompson 1972). These are probably sexual in motivation (Mundinger 1975). Three females from Occidental College treated with testosterone also sang run-on songs. Run-on songs have been described for the Indigo Bunting (*Passerina cyanea*) by Thompson (1972) and Emlen (1972). In the latter species, however, the motivation underlying these songs is aggressive and not sexual.

During courtship, the male House Finch often inserts a series of squeaks of about 8 kHz into its song (Fig. 3). Mundinger (1975: 410) found squeaks only in the introductory portion of eastern House Finch song. Squeaks may occur, however, in any part of the California House Finch song. These appear to be high intensity songs often preceding copulation. Squeak songs are sometimes undirected and might function, then, in attracting a mate early in the spring and communicating the physiological state of the singer.

Flight songs.—Ten flight songs were recorded from three populations. Except for

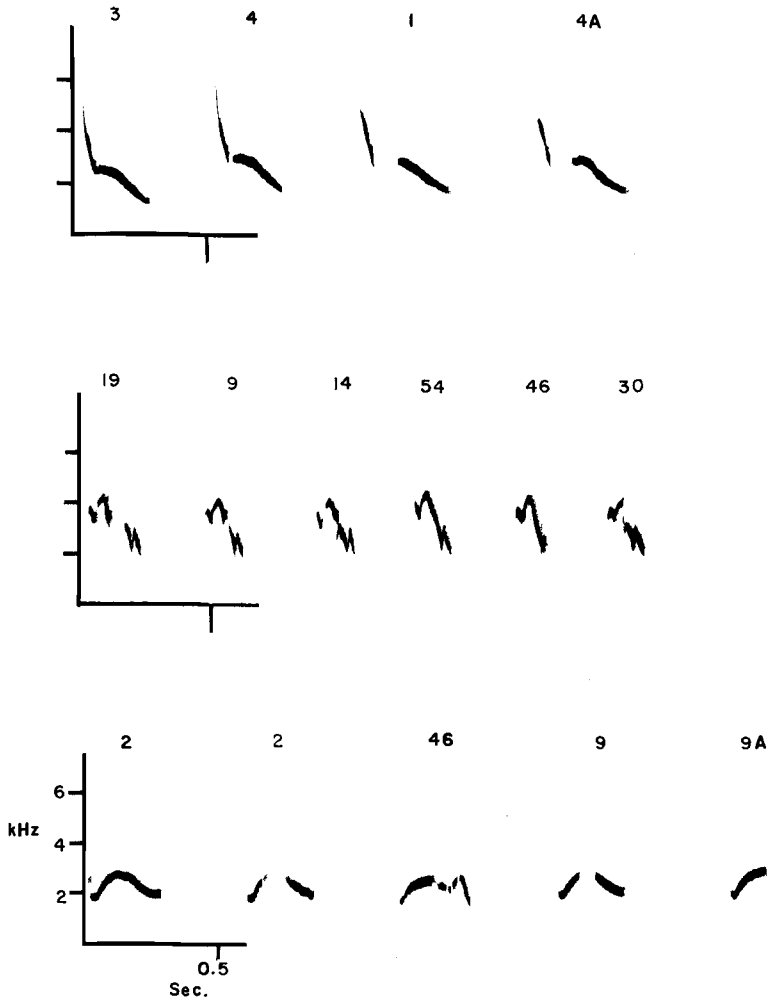


Fig. 4. Variation in syllable types. The numbers above the syllables are the birds to which the syllable belongs. Top row: there is a gradient in morphology from Bird 3 to Bird 4A in Syllable Type 309 from Santa Catalina Island. Middle row: variation in Syllable Type 48 from Occidental College. Bottom row: variation in Syllable Type 94 from Occidental College.

TABLE 2. Sequences of syllable types in songs of representative neighboring House Finches in three sampling localities. Shared phrases are underlined.

Montecito	
Bird 4:	<u>2-260-261-2-260-34-2-259-253-254-95-256-256</u>
Bird 1:	<u>262-261-2-260-34-2-259-253-254-255-256-257</u>
Bird 13:	<u>351-287-281-95-256-256-258-95-274-275-276</u>
City 1	
Bird 5:	<u>37-267-405-406-295-121-256-256-258-408-303-409-276-149</u>
Bird 4:	<u>37-267-405-406-295-302-121-256-256-258-408-303-409</u>
City 2	
Bird 8:	<u>403-23-404-23-21-269-70-111-402-126-275-276-149-23-404-23-21-269</u>
Bird 10:	<u>403-23-404-23-21-269-256-400-401-111-402-111-402-276-149-407-68-54</u>

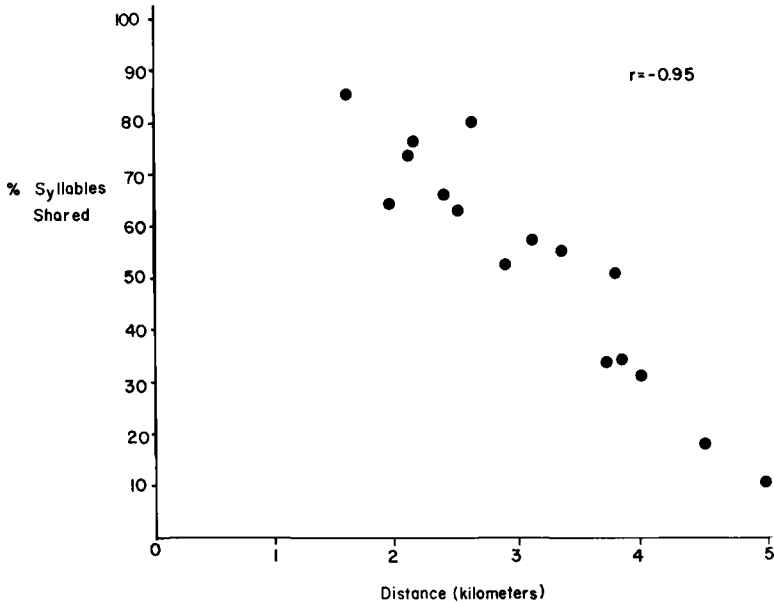


Fig. 5. Syllable sharing along a transect from Occidental College to Montecito Heights. $N = 125$ songs from 16 birds. Each point represents data from a single bird compared against the syllable catalogue from Occidental College (100%).

the absence of terminal buzzes, no noticeable differences were detectable between flight and other songs. Samson (1978) found that flight and other songs were similar in the congeneric Cassin's Finch (*Carpodacus cassinii*).

The individual repertoire.—Each individual in southern California sang from two to 10 themes. When successive renditions of a particular theme in California House Finches are assessed, not only do no two birds sing exactly alike, but even a single bird seldom repeats himself precisely. Song variants involve the omission or addition of syllables in the introductory and/or terminal portions of the song and usually differ in less than 20% of their syllable types. Some variants are sung very infrequently.

FEMALE SONG

Ten females at Occidental treated with testosterone sang only one or two themes each; repertoire size was significantly smaller than that in males ($\bar{x} = 4.01$ from 70 male repertoires, $t = 3.61$, $P < 0.01$). Four female songs contained fewer syllable types than normal male songs and consisted of paired syllables repeated serially (Fig. 3B). Six female songs were similar to male songs in morphology and sequencing of syllables (Fig. 3, songs C and D). Two females inserted squeaks into their songs (Fig. 3, A, G), a characteristic of male courtship songs. The remaining female songs consisted of Occidental syllables arranged in sequences that were not duplicated in male songs.

Double-songs in White-crowned Sparrows (*Zonotrichia leucophrys*) were extremely rare in nature but common in testosterone-injected females (Baptista 1974). Run-on songs in these injected House Finch females in this study may be abnormal, as they were not encountered in the field.

TABLE 3. Theme and phrase-sharing by six House Finches at Occidental College.^a

Bird number	Songs							
	A	B	C	D	E	F	G	H
2	*	+	*		+			
30	+	+		+	*		+	*
29	+				+	*		*
46	+	+			*		+	
14		*	+			+		
56	*		+	*				

^a + = whole themes shared; * = themes containing shared phrases. Themes were never identical as reported by Mundinger (1975) for eastern House Finches, but usually differed in one or two syllables (see text).

VARIATION WITHIN AND BETWEEN POPULATIONS

Variation in each syllable type.—Small differences in syllable morphology from bird to bird may be attributable to individual variation in the learning process, as proposed for other species (Payne 1973, Kroodsma 1974, Baptista 1975, Jenkins 1978). For example, there is a gradient from Bird 3's rendition of syllable 309 (top row Fig. 4), in which two notes are attached, to Bird 1's version, wherein the same two notes are separated by a short interval. Still another variant of syllable 309 is Bird 4A's rendition, in which there is a slight hump in the second note. Similar variations are found for syllable types 48 and 94 (Fig. 4) and others. In constructing our catalogue we group syllables into types as in Fig. 4.

Phrase sharing.—Population-specific phrases common to more than one bird appear to be found mainly in the middle portions of the song. For example, Occidental Songs A, B, and C (Fig. 2) share the sequence of Syllables 19-140-4-17-64-40 in their songs. In Song A, the above syllable sequence is followed by Syllable 16, and then the sequence 94-67-94. Syllable 16 is lacking in Song B; however, the latter shares the sequence of Syllables 94-67 with Song A. In Song C the additional sequence 16-44-16 precedes the sequence 94-67-94, which is shared with Song A. All other localities sampled also contain population-specific phrases (Table 2).

Theme-sharing.—Each male sings a characteristic complement of themes. The repertoires of many birds may contain themes shared with others in the population (Table 3). Themes shared were almost identical, each theme differing in one or two syllable types in the introduction or terminal portions of the song. House Finches at a given locality tend to have more themes in common with each other than with more distant birds. Neighboring House Finches tend to sing shared themes more frequently than they do unshared songs, as noted earlier by Mundinger (1975) for eastern House Finches. Among individual birds living close together, the number of song types shared ranges from 1 to 3 and rarely 4 (Table 3).

Transect from Occidental College to Montecito Heights.—With only one exception (Bird C1), songs from House Finches more than 2,000 m apart (Fig. 1) contained no shared phrases. Some identical syllables, however, were found across the four localities. Using Occidental College as a reference population, the percentage of syllable types shared were plotted against distance (one spot on the Occidental campus was used as a point of reference). These data yielded a negative linear correlation of -0.95 , indicating that fewer syllables were shared with increasing distance from Occidental College (Fig. 5).

Quantitative aspects of House Finch song.—Comparison of House Finch songs

from the different recording localities yielded no differences in the following song parameters: (1) song length, (2) number of syllables per song, (3) maximum frequency, (4) minimum frequency, and (5) frequency range (ANOVA, $P > 0.05$, Table 1). This is similar to Payne's (1973) data for songs of indigobirds (*Vidua* spp.).

DISCUSSION

Comparisons with eastern House Finches.—Differences between Munding's (1975) data and ours were as follows. (1) The mean number of themes per individual was 2.23 for eastern populations and 4.01 for the western birds. (2) The number of themes per population differed in the two studies: there were usually two in each eastern House Finch population. One population (Mamaroneck) had as many as six themes. Seventy-one different themes were recorded at Occidental College, California, the best sampled population. The number of themes for the other California populations ranged from 13 to 36 (Table 1). These differences are real, as the same criterion that Munding used to define a theme was used in this investigation. (3) California populations exhibited greater syllable diversity: 141 syllable types were catalogued for Occidental versus 69 syllable types for Gaviota Park. On the east coast 46 syllable types were identified at Mamaroneck and 28 syllable types at Indian Village. (4) Munding found the terminal portions of songs in New York to be stereotyped, while in California they are quite variable. (5) The California populations sampled exhibited no distinct dialects, i.e. only portions of songs were shared and not by all birds in a population. Following Lemon's (1975) terminology, eastern populations thus far sampled behave as high conformity species, whereas western samples are in the medium conformity category. Theme sharing is microgeographic in western House Finches. In eastern House Finches theme sharing is macrogeographic, as in White-crowned Sparrows (Marler and Tamura 1962, Baptista 1975, 1977), Ortolan Buntings (*Emberiza hortulana*) (Conrads and Conrads 1971), and indigobirds (Payne 1973). (6) On the east coast, birds at several dialect boundaries sang hybrid songs. In California no birds with mixed repertoires were found. This, however, may be due to sample error, as no birds were found singing at critical areas between sampling localities (Fig. 1).

Why the differences between Munding's and our data? Munding (1975) has demonstrated that dialects may develop rapidly in House Finches. Perhaps founders on the east coast arrived with a small pool of syllables and themes. Numbers of individuals per unit area were probably small during the early stages of colonization, so that birds could have few conspecifics to interact with socially. Due to either or both reasons, their descendants were, therefore, born into a relatively poor acoustical environment. The smaller repertoire sizes and distinct dialects on the east coast are, perhaps, partially a result of the small numbers of syllable and theme models for imitation. In California, where juvenile House Finches are exposed to more varied repertoires, improvisation or borrowing of syllables from several themes to make new themes appears to play an important role in song development. Munding (1975) has documented that eastern birds at dialect boundaries behave similarly. In this respect California birds are reminiscent of Song Sparrows (*Melospiza melodia*) from Quebec, Canada, and southern California (Harris and Lemon 1972, Eberhardt and Baptista 1977). On the east coast they appear to behave like sedentary White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*), each individual usually mimicking whole themes from neighbors (Marler and Tamura 1962, Baptista 1975).

Mundinger (1975) found one exceptional population in New York, the Mamaronek, exhibiting a slightly larger repertoire size than the others. It is thus possible that some western populations may exist with very small repertoires similar to eastern birds. Alternatively, with the passage of time and the exchange of individuals across populations bringing with them new themes, repertoire sizes per individual may increase, and the amount of theme sharing may decrease.

Other species have also been shown to have song dialects in one area and not in others. Borror (1961), Harris and Lemon (1972), and Eberhardt and Baptista (1977) found dialects in eastern and southern California Song Sparrows, whereas Mulligan (1966, pers. comm.) reported none in northern California populations. Song dialects exist for the subspecies *pugetensis*, *nuttalli*, and *oriantha* of the White-crowned sparrow (Marler and Tamura 1962; Baptista 1974, 1975, 1977; Orejuela and Morton 1975), but Alaskan White-crowned Sparrows (*gambellii*) show no dialect variation (DeWolfe et al. 1974). Borror (1959) and Kroodsma (1971) found similar results for the Rufous-sided Towhee (*Pipilo erythrophthalmus*): dialects are absent in eastern towhees, but birds in Oregon share similar song patterns. Williams and McRoberts (1977) recently reported geographical variation in theme sharing in Dark-eyed Juncos (*Junco hyemalis oregonus*) in Carmel, California. Juncos in Berkeley, California do not share themes.

Why the clumped distribution of themes?—We have shown that in the transect from Occidental College to Montecito Heights, neighboring House Finches shared more themes than more distant birds. Indeed, no themes were shared by birds across sampling localities. Additionally, syllables segregated independently, and the degree of syllable sharing decreased clinally with distance. One possible interpretation of these data is that young birds copy themes from adults and subsequently disperse only short distances (Marler and Tamura 1962, Baptista 1975, Mundinger 1975). More recent studies, however, have shown that in some species young birds copy themes of adults at the site settled as a result of male-male interaction (Kroodsma 1974, Verner 1975, Avery and Oring 1977, Payne and Payne 1977, Jenkins 1978), resulting in theme sharing by neighbors. In the White-crowned Sparrow, the “classical” dialect species, neighbors tend to share similar themes (subdialects) within a dialect area (see Fig. 5 in Baptista 1975). Neighboring Song Sparrows also tend to share more themes and/or syllables than more distant members of the population (Harris and Lemon 1972, Eberhardt and Baptista 1977). Mundinger (1975) noted that males of eastern House Finches living close together often had nearly identical songs. This phenomenon is probably widespread among songbirds that learn themes.

House Finches begin learning songs around the first or second month of life, and one male still acquired new themes in his repertoire in his first spring when he was about 10 months of age (Mundinger in litt.). This would suggest that a dispersing juvenile could still interact with neighbors and learn new themes. The high degree of syllable sharing (Fig. 5) between neighbors suggests male-male interaction as part of the song learning process in House Finches. The fact that neighbors tend to sing shared themes more often than unshared themes (Mundinger 1975, this study) also suggests that social interaction is involved in the song-learning process. This would also explain the clumped distribution of like themes.

The adaptive significance of song dialects in House Finches.—The proposal that song dialects have no significance (Andrew 1962) does not explain why, during the course of evolution, a learning strategy has evolved from a genetically controlled song strategy (Jenkins 1978). More recently Nottebohm (1975) has presented evi-

dence suggesting that pitch differences in local dialects may have evolved as local adaptations to the acoustic properties of the *umwelt* in the Rufous-collared Sparrow (*Zonotrichia capensis*). House Finches on Santa Catalina Island occupy very open, barren habitat with scrub oak (*Quercus* sp.), cactus (*Opuntia* sp.) and grasses. In contrast, birds from Occidental College and Montecito Heights Park inhabit "urban islands" of various ornamental shrubs and trees. In between these two points, House Finches were located in residential areas with closely situated homes, some trees, and gardens. We found no pitch differences between island and mainland songs (Table 1).

Nottebohm and Selander (1972) described differences in habitat associated with differences in dialect of Rufous-collared Sparrows. They suggested, therefore, that dialects may promote positive assortative mating, fixing adaptive genes within specific habitat types. Geographical variation in California House Finch song is clinal, at least in our 5-km transect traversing residential areas and parkland. Theme sharing was microgeographic in scale, i.e. usually between immediate neighbors at each locality. The ideas of Nottebohm and Selander (1972), therefore, do not apply to California House Finches.

Jenkins (1978) has proposed that Saddleback (*Philesturnus carunculatus*) males prefer to settle and learn themes in areas other than their birthplaces as a mechanism to prevent mating with blood relatives in their natal area. This would necessitate differential dispersal distances between the sexes. However, Jenkins presented dispersal data only for males. This intriguing idea could be tested both with Saddlebacks and House Finches by detailed banding studies.

Payne (1978) presented evidence indicating that in Splendid Sunbirds (*Nectarinia coccinigaster*) young males match very precisely the pitch and rhythmic characteristics of songs of established males, giving rise to microgeographic clustering of neighboring birds with like songs. Payne (1978: 306) suggested further that, in matching an established male's song, the younger male might exploit the former's neighbors' "acquired avoidance of the area where they hear this song." House Finch song appears to be only mildly aggressive in motivation. Munding (1975) (also this study) noted that males often countersang with similar themes. Thompson (1960) noted that singing males tended to perch farther apart than nonsinging males. He also noted, however, that song rarely led to hostile encounters. Song duels at territorial boundaries were never observed. Males sometimes sang perched close to each other. We were unable to get House Finches to respond to playback of recorded song, in contrast to birds that truly use song in territoriality (review in Baptista 1978). Thus Payne's (1978) ideas probably do not apply to House Finches.

Individual recognition through song may be achieved through: (1) variation in syllable types due to improvisation or copy errors (see e.g. Fig. 4), (2) unique syllable sequences in portions of or throughout themes, and (3) combinations of portions of various themes (phrases) to make new themes (see Table 2, Montecito Bird 1). There is abundant evidence of all these processes in both Munding's (1975) and this study. Munding (1975) presented evidence suggesting that both sexes stimulate each other sexually with song. Males sang during courtship, nest building, and as a prelude to copulation. Females sang to solicit courtship feeding and copulation. Alvarez (1971) showed that gonads in male House Finches were less developed in deafened pairs than in intact pairs, again suggesting that vocalizations are sexually stimulatory in function.

Munding (1970, 1975) pointed out that pairing in carduelines takes months to

accomplish, the process involving courtship feeding and call imitation between the sexes. Individual recognition, e.g. by call imitation between pairs, is important in carduelines (Mundinger 1970). Because female song in House Finches is used in a similar context as imitated calls, namely to solicit courtship feeding, song may likewise serve to identify individuals. Thus song-learning in House Finches may be adaptive if: (1) it results in individual, specific themes through improvisation, or (2) females attempt to match characteristics of their mate's song during pair formation, enabling pairs to recognize each other, as has been demonstrated for learned pair specific call-notes (Mundinger 1970, Marler and Mundinger 1975, Samson 1978). This could enhance the effectiveness of song in stimulating each other sexually and in synchronizing their sexual cycles. The fact that neighboring males tend to stimulate each other to sing similar (but never identical) themes (Mundinger 1975, this study) may multiply the stimulatory effects of the male's song, as proposed by Nottebohm (1969). This model does not require that House Finches sing only the songs acquired at their natal area nor breed near their place of birth.

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