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GEOGRAPHIC VARIATION IN SYLLABLES OF HOUSE FINCH SONGS

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ABSTRACT.—Bird songs often can be described as strings of individually distinct units called syllables. Toward furthering our understanding of the processes and consequences of vocal learning, geographic variation in vocalizations may be as important at the syllable level as it is at the song level. To examine geographic patterns of song variation at the syllable level in House Finches (*Carpodacus mexicanus*), we analyzed the syllable repertoires of 91 males at 21 sites in northern Colorado. Analyses were performed and comparisons were made among individual birds within and between sites. Using Jaccard's similarity coefficient, we determined that syllable sharing among birds was significantly greater within sites and among sites less than 5 km apart than at greater distances. Within a site, any two birds usually did not share the majority of their syllable types, but discriminant function analysis showed that approximately 63% of the birds possessed syllable repertoires that matched most closely those of other birds at the same site. Less than 5% of the birds sang syllables that most closely matched those of birds at a site more than 20 km away. Our results suggest that House Finches in northern Colorado exhibit localized syllable sharing and that syllable sharing decreases exponentially with distance, but we found no evidence for discrete syllable dialects. Geographic variation in bird song typically has been evaluated using whole songs. Depending on how birds assess the singing behavior of other individuals and perceive differences in songs, it may be important to examine geographic variation and population differences at the syllable level as well. *Received 8 January 1998, accepted 17 November 1998.*

MICROGEOGRAPHIC VARIATION in vocalizations often is referred to as "dialect" variation, which occurs when a group of conspecific males shares vocal traits that differ discretely from those of other groups (Baker and Cunningham 1985). By an earlier tabulation, about 64 to 75 species of birds have been shown to exhibit vocal dialects (Kroodsma and Baylis 1982, Mundinger 1982), including the House Finch (*Carpodacus mexicanus*; Mundinger 1975). The individual or combined roles of mate choice, aggressive interactions, and juvenile dispersal in perpetuating song dialects remain obscure in most of these species.

Like many other oscines, House Finches acquire their songs through a process of cultural transmission whereby individuals learn songs by hearing those of conspecifics during early development (Bitterbaum and Baptista 1979; also see Kroodsma 1982). One potential consequence of this learning process is geographic variation in songs (see Krebs and Kroodsma 1980). A number of species show patterns of dialect discrimination in song playback experiments with males and in song stimulation of female sexual behavior (Baker et al. 1981, 1987; Tomback and Baker 1984; Baker and Cunningham 1985; Balaban 1988). Evidence also suggests that dialect differences may influence natal dispersal (Baker and Mewaldt 1978, Rost 1990), although there is contrary evidence on this issue as well (McGregor et al. 1988).

Most studies of geographic variation in avian vocalizations have examined geographic patterns in whole songs, which are usually composed of strings of distinct units called syllables (Shiovitz 1975). Some of the same syllables, however, may be found in the songs of a number of different individuals in a population. Thus, it is possible to identify a set of syllable types, a syllable pool, common to a certain population and from which all the songs in the population are composed. It is theoretically possible for every song in a local population to be unique and yet exhibit much sharing of syllables. Factors involved in the cultural transmission and stability of a pool of syllable types may differ from those governing whole songs. Studies of the mechanisms of song learning in some species of birds indicate that songs may be learned, not as whole units, but rather as series of learned syllables or phrases (e.g. Nelson et al. 1995). Cultural evolution in a population of birds may occur rapidly at the song level

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while the pool of syllables remains stable over time. For example, Payne et al. (1981) found that few song themes persisted from 1963 to 1980 in a population of Indigo Buntings (*Passerina cyanea*), whereas syllable types remained stable over the same period of time. If the mechanisms of cultural transmission for songs are not the same as those for syllables, then different patterns of geographic variation could occur at the song and syllable level, and the functional significance of the variation could differ as well.

We examined geographic variation in the songs of House Finches at the syllable level in northern Colorado. In doing so, we addressed several questions concerning syllable repertoires of birds and syllable pools of local populations: (1) What sample sizes are required to describe a bird's syllable repertoire and a population's syllable pool? (2) How does the similarity of syllable repertoires change as distance between birds increases? (3) Do discrete dialects of syllables occur within the study area?

METHODS

Song recording.—We recorded 4,290 songs of male House Finches at 21 sites in northern Colorado during the spring and summer of 1994 and 1995. Ten of the sites were in Ft. Collins (1,490 to 1,660 m elevation), six in Loveland (1,520 to 1,710 m), three in Estes Park (2,290 to 2,440 m), one in Masonville (1,650 m), and one in Timnath (1,480 m; Figs. 1A and B). We recorded an individual's songs until it either stopped singing or flew out of recording range. We considered all birds that were recorded within 0.5 km of each other to be from the same site. Distances between sites ranged from 1.0 km (F to L) to 55 km (T to Y; see Fig. 1).

In 1994, recordings were made with a Uher 4200 Report Stereo IC recorder at 9.5 cm/s and a Uher M517 microphone mounted in a 60-cm parabolic reflector. In 1995, recordings were made with a Marantz PMD201 cassette recorder and a Sennheiser MD402 microphone mounted in a 60-cm parabola. Songs were analyzed and sonograms produced with a Kay Elemetrics DSP Sona-Graph Model 5500, with the following settings: frequency range DC-8000 Hz, 100-point transform (300 Hz), flat shaping, hamming analysis window, and no averaging.

In 1995, we captured, color banded, and released male House Finches at the USDA Crops Research Laboratory near Aggie Village, just south of the Colorado State University campus in Ft. Collins (site A in Fig. 1A). Included in our analysis are the songs of 16 individuals color banded at this site in 1995 and 7 unbanded individuals in 1994.

We recorded banded males at Aggie Village individually from once to several times throughout the 1995 breeding season and included all songs recorded from these birds in the analysis. We used songs from unbanded birds at all sites in the analysis only if we could determine that songs from the same birds recorded during a different song bout were not already included in the analysis. Individual males can usually be distinguished by song (Mundinger 1975, Bitterbaum and Baptista 1979), and we verified that all song bouts included in this analysis were from different birds. If we could not determine with certainty that two song bouts were given by different birds, we excluded one from the analysis. If we acquired multiple bouts from what appeared to be the same unbanded bird, we included in the analysis only the bout containing the most songs.

To estimate the number of songs we needed to sample to acquire the full syllable repertoire of an individual, we plotted the cumulative number of syllable types found in a repertoire versus the *n*th song sampled for 13 unbanded birds from which at least 20 songs were recorded in 1994. In each case, at least half of the apparent total repertoire of syllables had been revealed by the sixth song recorded (see Results). Thus, a minimum sample of six songs was required for a bird's repertoire to be included in our analysis. The repertoires of 75 unbanded birds were used in the analysis (one to seven birds per site). Factors that severely limited the number of birds used at other sites relative to the number at Aggie Village include harassment by the public, inaccessibility of private property, lower numbers of House Finches at these sites, and our inability to acquire bouts of at least six songs from many unbanded birds.

Syllable identification.—Mundinger (1975) defined a House Finch syllable as "the basic structural unit of a song, separated from adjacent syllables by a silent period of 0.02 to 0.2 seconds." Syllables consist of one or more individual notes (i.e. single traces on a sonogram) that either overlap in time or are separated by a silent interval of less than 0.02 s. In a few cases, notes were separated by less than 0.02 s but were classified as separate syllables when those notes were found independent of each other in other songs. As was done in previous studies (Mundinger 1975, Bitterbaum and Baptista 1979), we excluded vocalizations of fewer than four syllables from the analysis. We cut sonograms of the whole songs of each bird into their component syllables and coded the back of each syllable with the bird's identity. We compared syllables from each bird's repertoire with those from every other bird and grouped like syllables from different birds together with consideration of syllable shape and frequency (Fig. 2). A syllable catalog of 666 different syllable types was compiled in this manner. We then included in the catalog 61 unique syllable types acquired solely from birds not included in the analysis because fewer than six of

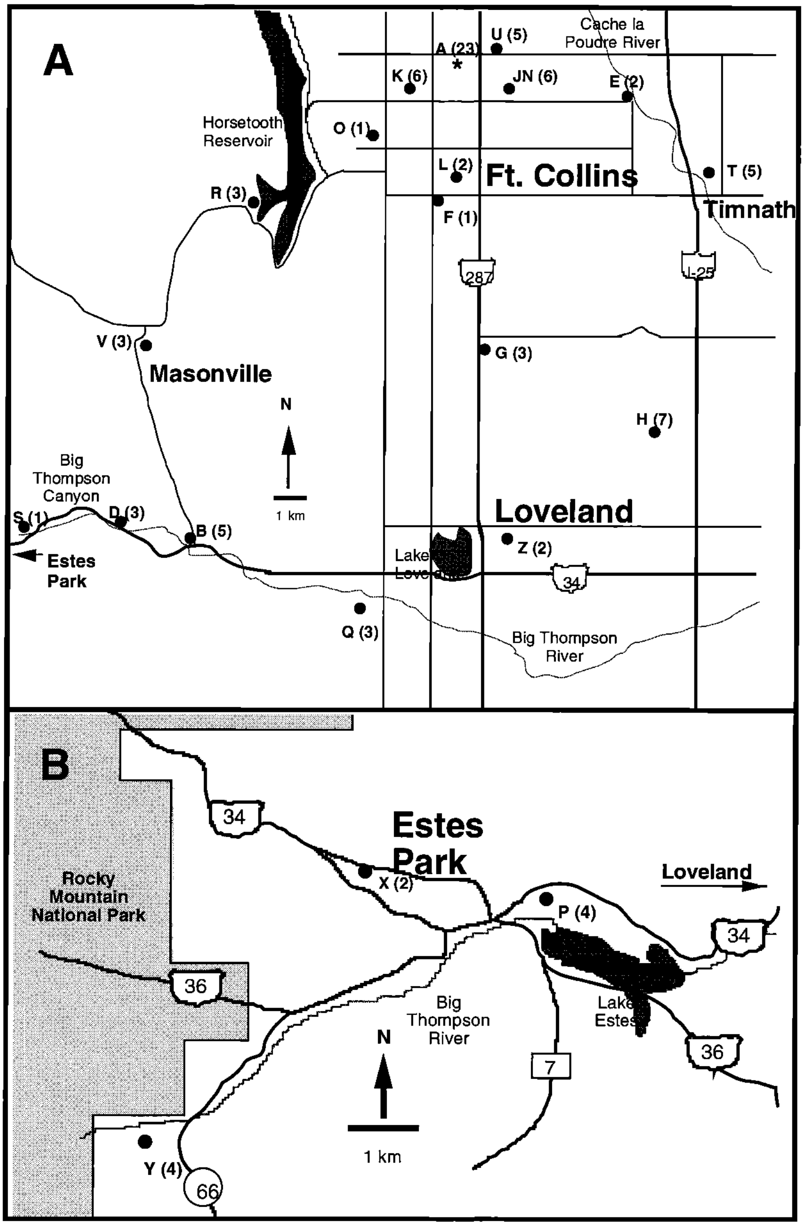

FIG. 1. (A) Locations of recording sites in Ft. Collins, Loveland, Timnath, and Masonville. Banded birds were recorded at site A, denoted with an asterisk. Numbers in parentheses indicate the number of birds included in the analyses from each site. (B) Locations of recording sites in Estes Park.

their songs were sampled. Thus, a total of 727 syllable types was found in the study area. Two independent observers compiled syllable catalogs and agreed on approximately 95% of their syllable classifications. Of the disagreements in syllable grouping, 76% were settled by discussion, and a third independent observer settled the remaining disputes. More objective approaches to syllable classification are available (e.g. Baker and Boylan 1995), but we felt that this visual technique of syllable classification was sufficient, because a more time-consuming digital technique for analyzing Black-capped Chickadee

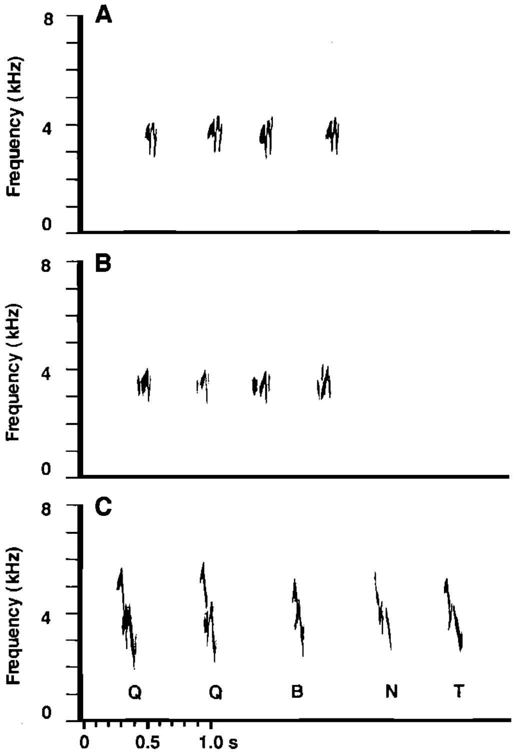

FIG. 2. Syllable types varied from being highly conserved to highly variable between birds. (A) Examples of conserved syllable type 32L recorded at site H. (B) Examples of variable syllable type C recorded at site A. (C) Examples of variable syllable type 12A recorded at four different sites. Site of recording is indicated beneath each syllable. Note that variation within a syllable type occurs both within and between sites.

(*Poecile atricapillus*) vocalizations provided similar results to a visual classification system (Nowicki and Nelson 1990).

Comparison of syllable repertoires.—To determine the number of songs necessary to be recorded from each bird to describe its entire repertoire of syllables, we plotted the cumulative number of syllable types found versus the *n*th song sampled for each bird. To estimate the number of syllable types in the syllable pool of a recording site and the number of birds' repertoires necessary for this estimation, we plotted saturation curves of the cumulative number of syllable types detected at Aggie Village as a function of the *n*th bird sampled. We numbered birds in random order and plotted the number of syllables in the repertoire of the first bird. We then compared the syllable repertoires of all subsequent birds with those of the preceding birds and added the numbers of new syllable types to the cumulative total. We performed five iterations of this randomization procedure.

To determine the amount of syllable sharing among birds, both within and between sites, we used Jaccard's similarity coefficient (S_j), which is commonly used with binary (presence/absence) data to measure similarity between assemblages of species (Krebs 1989, Podos et al. 1992). We calculated Jaccard's coefficient as follows:

$$S_j = a/(a + b + c), \qquad (1)$$

where a = the number of syllables shared in both repertoires, b = the number of syllables in B's repertoire but not A's, and c = the number of syllables in A's repertoire but not B's.

The similarity coefficients for binary data range from 0 (complete dissimilarity) to 1 (complete similarity; Krebs 1989). However, in the case of comparisons in which sizes of syllable repertoires are not equal, the maximum possible S_j for the comparison would be <1. This is because there would be at least as many non-matches ($b + c$) as the difference in repertoire size. We adjusted S_j for differences in sample size because (1) birds varied in the manner in which they displayed their repertoires (see Results), so we could not assume that we had sampled every bird's entire repertoire; (2) the numbers of songs recorded and analyzed varied from bird to bird; and (3) we could not classify some syllables from some birds into syllable types because of poor sonogram quality.

The adjustment to S_j that we used controlled for problems associated with different sample sizes by subtracting the difference in sample size from the number of non-matches. S_j(adj) was calculated as follows:

$$S_j(\text{adj}) = a/(a + b + c) - s, \qquad (2)$$

where s is the difference in detected syllable repertoire size between birds A and B. We calculated S_j(adj) for each bird compared with all other birds within the same site and with all birds at all other sites. We then averaged each bird's S_j(adj) values over all birds at each site and subsequently averaged these means over all birds within each site. Thus, the values progressed from individual versus individual, to individual versus site, to site versus site.

All subsequent statistical procedures were carried out with SAS (1985). We used Pearson correlation analysis to determine whether similarity in syllable repertoires declined as distance between sites increased. We also grouped site comparisons into 5-km intervals and used Tukey's *W* procedure for multiple comparisons (Ott 1993) to determine whether and at what distance from a site repertoire similarity decreased significantly.

Discriminant function analysis.—We performed a discriminant function analysis with cross-validation and pooled covariance matrices to determine whether a bird's syllable repertoire matched most closely the syllable repertoires of other birds at the same site. Every syllable was an independent variable in this analysis, and the data for each bird consisted of presence/absence of all syllable types. In this analysis, a discriminant function was computed for all birds in the data set except the bird being classified. The process was repeated for every bird. We used the repertoires of 80 birds from 14 sites, because we included a bird's repertoire only if three or more birds were recorded from that site.

Concerned that the large disparity in sample size between Aggie Village and the other sites may have misclassified birds as possessing Aggie Village repertoires, we randomly assigned all Aggie Village birds to one of four discriminant function analyses that included all the other birds. Each of these analyses included a subset of five or six Aggie Village birds. We used the subset analyses to derive a consensus classification for each bird.

RESULTS

Analyses of song and syllable repertoires.—Songs typically ranged from 1 to 4 s in length and contained 4 to approximately 30 syllables (Figs. 3A–C). Songs often ended with a diagnostic buzz or series of buzzes (Fig. 3A), which usually were unique to birds within a site. Individual males displayed variation within song themes; sometimes a bird would skip a syllable within a song, and on many occasions songs were not sung to completion (see Mundinger 1975, Bitterbaum and Baptista 1979).

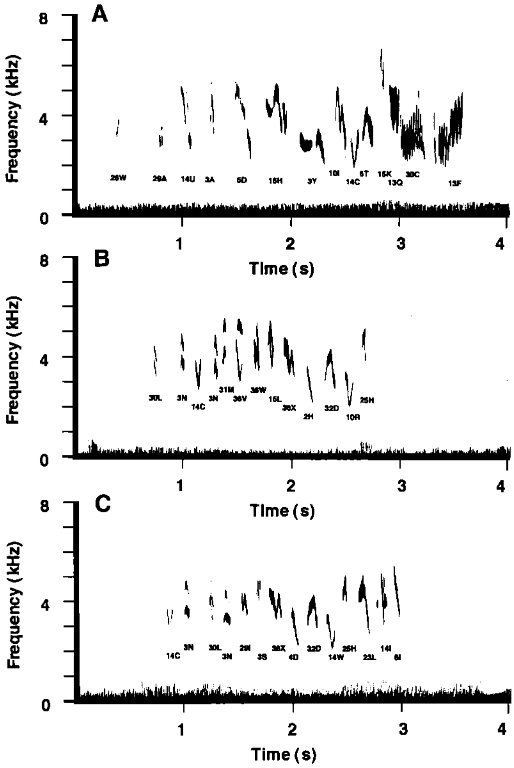

FIG. 3 (A and B) Two song themes given by bird Yi. Note the terminal buzzes in song 3A. This buzz series was unique to birds at site Y. Syllable types are indicated. (C) Song theme given by bird Ya. Several syllable types of bird Ya match those of bird Yi.

Between 6 and 287 songs ($\bar{x}$ = 23) from each bird were included in the analysis. Birds included gave between two and seven different song themes. We obtained 17 songs from a single bird that issued only one song theme. We excluded this bird from the analysis as anomalous, because all other 91 birds from which six or more songs were recorded sang at least two different song themes. Between 8 and 52 syllable types from each bird ($\bar{x}$ = 29.7) were included in the analysis, but most birds had additional syllables in their repertoires that were of degraded quality and not classifiable. For example, syllables recorded during a flight song often were degraded in quality because the

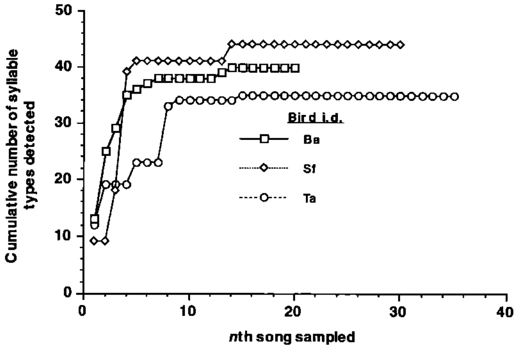

FIG. 4. Cumulative number of syllable types found plotted against the *n*th song sampled for three different birds. For these and other birds, few or no new syllable types were detected after the 15th song sampled, and at least 50% of the apparent syllable repertoire was detected within the first six songs sampled. The first letter of the bird identification indicates recording site.

TABLE 1. Summary of sampling effort and number of syllable types detected for unbanded birds in 1994 from which 20 or more songs were recorded.

Bird ID[a]	Number of songs recorded	Number of syllable types detected[b]	Number of syllable types detected by 6th song[b]
Ul	25	31	30 (96.8)
Ga	22	30	30 (100)
Gj	22	31	17 (54.8)
Qg	21	72	48 (66.7)
Qj	26	64	48 (75.0)
Sf	30	45	42 (93.3)
Da	50	38	32 (84.2)
Df	52	41	32 (78.0)
Vg	20	34	19 (55.9)
Ta	35	35	23 (65.7)
Tt	22	58	29 (50)
Pk	29	43	35 (81.4)
Ba	20	40	37 (92.5)

[a] First letter of indicates recording site.

[b] Includes unclassifiable and redundant syllable types (% of total in parentheses).

bird was flying away from the recorder. Other birds had redundant syllable types in their repertoires, which occurred when two or more slightly different forms of the same syllable type were detected. Males sometimes gave high pitched (ca. 8 kHz) "squeak" syllables, used in courtship, that were interspersed throughout their songs (Thompson 1960, Bitterbaum and Baptista 1979); these squeaks were not included in analyses because most birds were not recorded performing these courtship displays and because song themes interspersed with squeaks were consistent with song themes given by the same birds at other times.

Using the 75% similarity criterion, birds at the same site often shared at least one song theme. Different birds normally did not sing identical themes, although this occurred occasionally. Birds at different sites typically did not share song themes, but birds as far apart as 55 km had a few syllable types in common. Syllable types varied both within and among sites (Fig. 2C).

We plotted the cumulative number of syllable types found in a repertoire versus the *n*th song sampled for unbanded birds from which at least 20 songs were recorded (Fig. 4). After approximately the 15th song sampled, few or no new syllable types occurred in a bird's repertoire. This was the case even for banded birds that were recorded throughout the breeding season. This is consistent with other work that found no seasonal variation in House Finch songs (Mundinger 1975). Individual variation occurred, however, in how quickly the curves leveled off before the 15th song. For example, bird Ta leveled off more slowly than birds Ba and Sf (Fig. 4). For unbanded birds in 1994 from which at least 20 songs were analyzed, 50 to 100% ($\bar{x}$ = 76.5%) of the total detected number of syllable types had been issued by the sixth song sampled (Table 1). We used six songs sampled as the cutoff for inclusion of a bird's repertoire in subsequent analyses because (1) at least half the bird's syllable repertoire had been sampled, and (2) S_j(adj) values for 11 thoroughly sampled birds ($\bar{x}$ = 29.9 songs sampled, range 21 to 52) were not significantly different from those values computed using only syllables from their first six songs recorded (Wilcoxon test, $S = 95.5$, $P = 0.302$).

We generated plots of the cumulative number of syllable types detected at Aggie Village as a function of the *n*th bird sampled in 1995 and 1994 and 1995 combined (Figs. 5A and B). Neither plot reached an asymptote with the acquired sample size; the 1995 curve reached an asymptotic value of 151 syllable types at the 26th bird sampled, and the combined curve reached an asymptotic value of 211 syllable types at the 29th bird sampled. Thus, sample sizes (1 to 7) at sites other than Aggie Village

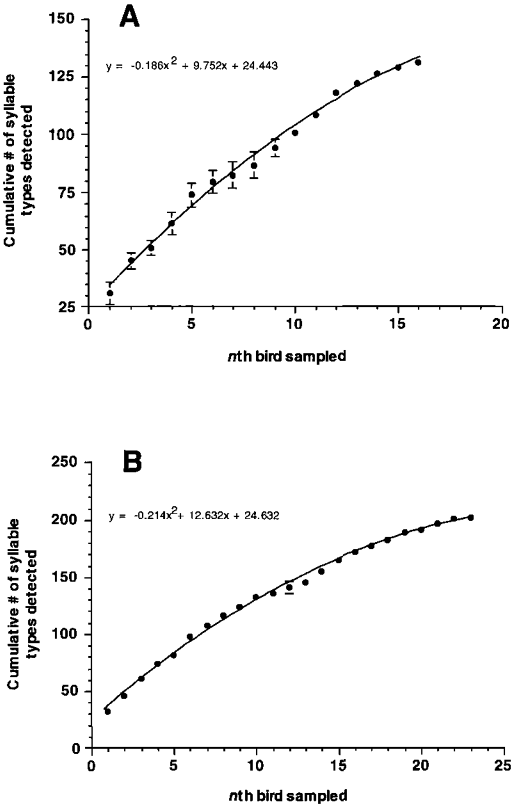

FIG. 5. Cumulative number of syllable types at Aggie Village (site A) in (A) 1995, and (B) 1994 and 1995 combined, plotted against the *n*th bird sampled. Most standard error bars were too small to be shown. Plots level off considerably, indicating that few new syllables were detected after 10 to 15 birds were sampled. Second-order polynomial curves were fit to the data, and curve-fit equations (shown) were used to estimate the size of the site syllable pool. Plot of 1994 data (not shown) did not exhibit much leveling off, because only seven birds were sampled.

were inadequate for comparisons of syllable pools among sites.

Similarity versus distance.—S_j(adj) values for bird versus bird comparisons ranged from 0 to 1. Two birds at site D had $S_j(\text{adj}) = 1$. Birds within sites generally had higher similarity coefficients than birds between sites. Within-site S_j(adj) means ranged from 0.193 (site P) to 0.667 (site D) (mean of 18 sites = 0.353), whereas between-site means ranged from 0 (Z vs. D, and Z vs. F) to 0.272 (L vs. K; mean of 210 comparisons = 0.061). The mean within-site S_j(adj) values were higher at than those of between-site comparisons. We did not calculate within-site S_j(adj) values for the three sites from which only one bird was included in the analysis.

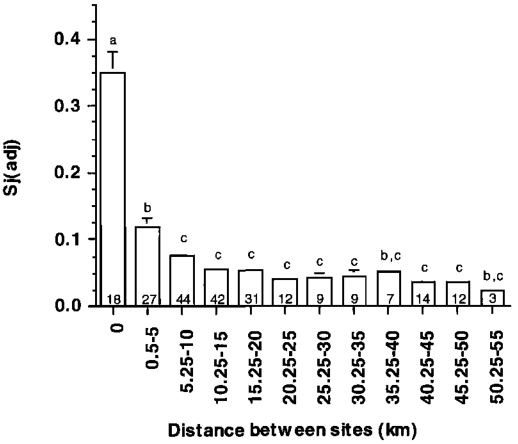

FIG. 6. Results of test comparing means between sites grouped into 5-km distance intervals. Histogram bars with the same letters indicate groups that are not significantly different at $\alpha = 0.05$ for experimentwise error rate (Tukey's *W*). Number of comparisons within distance intervals are indicated. Most standard error bars were too small to be shown.

S_j(adj) values were significantly negatively correlated with distance between sites ($r = -0.468$, $F = 69.43$, df = 227, $P < 0.0001$). A rapid decline in S_j(adj) occurred between 0 (within-site) and approximately 5 to 10 km, above which the decline leveled out. A natural log function fit to the data described more of the variance in S_j(adj) ($r = -0.535$, $F = 98.37$, df = 227, $P < 0.0001$) than did the linear model.

An overall comparison of similarity coefficients grouped into 5-km intervals indicated significant heterogeneity ($F = 15.74$, df = 227, $P < 0.0001$). We performed pairwise comparisons among all groups using Tukey's *W* procedure for multiple comparisons. At $\alpha = 0.05$ for experimentwise error rate, within-site similarity coefficients were significantly greater than all between-site similarity coefficients. Beyond a 5-km distance, all pairwise site groupings were not significantly different from each other (Fig. 6), indicating a rapid decline at short distances followed by a leveling off at greater distances.

Discriminant function analysis.—Of the 57 birds included in all four subset discriminant function analyses, disagreement in classification occurred for only five birds. For all but two

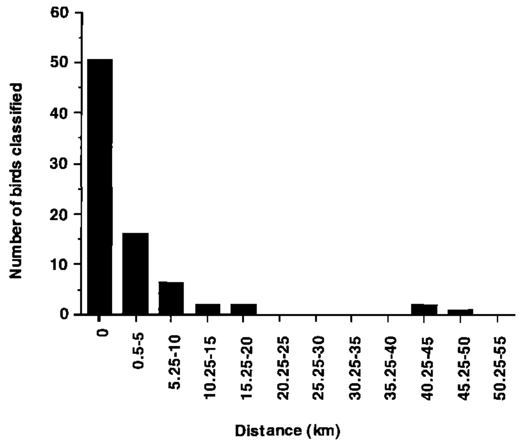

FIG. 7. Results of discriminant function analysis, indicating the number of birds classified into each distance category. Birds were classified into sites by syllable repertoire. Distance represents distance between bird's site of recording and site of classification. Birds at distance 0 indicate those that were correctly classified into their home sites.

birds, either three or all four subset analyses agreed on a classification; these classifications were considered to be the consensus classifications. In one case, a bird was classified twice into site A, once into site K, and once into site JN; therefore, site A was considered the consensus classification. In another case, a bird was classified twice into site JN and twice into site T, and its consensus classification was split between the two sites. By design, each of the 23 Aggie Village birds was classified in only one of the four analyses. The results of our discriminant function analyses indicated that approximately 63% of the birds possess syllable repertoires that were most similar to other birds at their site of recording, approximately 33% were classified into a different site within 20 km, and three birds from Estes Park were classified as having syllable repertoires from sites in Ft. Collins (42 to 50 km distant; Fig. 7).

DISCUSSION

Syllable sharing among male House Finches was highest within a site and dropped off rapidly as distance between sites increases to 5 km, beyond which the decline leveled off. Furthermore, a bird's repertoire typically matched most closely the repertoires of other birds at the same site. However, approximately 37% of the birds exhibited repertoires that most closely matched those of a distant site, even as far away as 50 km. Contrary to findings for House Finches in California (Bitterbaum and Baptista 1979), birds within a site in our study typically did not share the majority of their syllable types with another bird. Also, relatively few syllable types were shared among all birds within a site. Conversely, approximately 12 syllable types were shared among most of the sites in our study. Even birds from the most distant sites in our study had a small number of syllable types in common. These results indicate that less syllable variation exists within a local area than between distant sites, but the syllable types occurring within local populations do not define discrete vocal dialects.

House Finches in the northeastern United States exhibit distinct song dialects that occur over an area a few kilometers on a side and with boundaries separating dialects (Mundinger 1975). Sixteen of the 19 song dialects found were "structurally related;" however, the extent of syllable sharing within a dialect versus across dialect boundaries was not described. If the amount of sharing between related dialects is as high as the amount within a single dialect, then perpetuation of dialect boundaries cannot be attributed to syllable-level song differences. Dialects in the northeastern United States have been attributed to a multiple-founder effect (Mundinger 1975) because the populations have only recently (1940s to 1950s) established themselves from a small number of escapees (Elliott and Arbib 1953).

In California, House Finches in a single area sang many of the same themes, but no distinct dialect boundaries occurred (Bitterbaum and Baptista 1979). Rather, syllable repertoires and songs became gradually less similar with increasing distance, and few syllable types were shared at sites 4 to 5 km apart. These results were similar to ours in that localized syllable sharing was found. However, Bitterbaum and Baptista (1979) did not examine syllable sharing at distances exceeding 5 km, so it is unclear whether sharing dropped to 0 or whether it leveled off at a small number of common syllable types. Also, they compared syllable repertoires of individuals with a pool of syllables for the site at distance 0, not among individuals within the sites. Such an analysis fails to address the extent of syllable sharing between individuals within a site and between sites.

Song learning in birds traditionally has been thought to occur through a process by which a song is heard and a memory template of the song is formed in the song control centers of a juvenile's brain. The song is then rehearsed, crystallized, and produced later in life (see Arnold 1982, Konishi 1985). Evidence suggests that some species of birds are capable of creating improvisational songs by recombining portions of songs to create novel songs (e.g. Northern Cardinal [*Cardinalis cardinalis*], Lemon 1975; Nuttall's White-crowned Sparrow [*Zonotrichia leucophrys nuttalli*], Nelson et al. 1996). Juvenile Swamp Sparrows (*Melospiza georgiana*) accepted only conspecific syllables for imitation, even when heterospecific syllables were presented in a conspecific-like pattern (Marler and Peters 1977). Thus, the juvenile's choice was based on individual song components and not on the overall song pattern.

These studies have led to the inference that an entire song may not be the unit of song learning, at least in some species. Rather, these birds may be memorizing song components (syllables or phrases) that are strung together into complete songs at a later time (Marler and Peters 1977, Nelson et al. 1996). A comparative study of the process of song development in migratory and sedentary subspecies of White-crowned Sparrows has shown that two migratory subspecies (*Z. l. pugetensis* and *Z. l. oriantha*) "overproduce" song and phrase types during song development; that is, they produce song and phrase types that are lost after the individuals settle in a certain area. The repertoire that each bird sings thus becomes a subset of its learned repertoire. Nonmigratory *Z. l. nuttalli* apparently do not exhibit overproduction. A possible explanation is that migratory birds "overlearn" so that they might be more likely to possess the song components to match their neighbors' songs wherever they settle (Nelson et al. 1996). An efficient way of accomplishing this would be for a bird to learn song components (i.e. syllables or phrases) rather than entire songs.

It has been suggested that House Finches in California possess the ability to build new themes with syllables from several songs (Bitterbaum and Baptista 1979). A syllable-level analysis of geographic variation in House Finch songs may contribute to an understanding of the process of song learning in the species by revealing geographic distributions of what may be units of recombination in songs. House Finches in our study sometimes participated in matched countersinging in which nearby birds sang identical or nearly identical songs almost simultaneously. Bitterbaum and Baptista (1979) observed "song dueling" between males, but it usually did not involve the same song theme. If matched countersinging is adaptive (e.g. naming an opponent in a song duel; see Catchpole and Slater 1995), then it would be advantageous for males to be able to adjust (recombine or drop) syllables or phrases to match their neighbors' songs more closely. Until the benefits of matched countersinging are described in this species, the benefits of the ability to recombine syllables and phrases will remain obscure.

Besides Bitterbaum and Baptista's (1979) study, which included an examination of microgeographic variation in the syllables of House Finches songs over a distance of 5 km, few studies have focused on the geographic distribution of syllables. Baker (1996) compared the syllable pools of island and mainland populations of Singing Honeyeaters (*Meliphaga virescens*) and attributed the depauperate set of syllables on the island to a founder effect. Shiovitz and Thompson (1970) examined syllables in three populations of Indigo Buntings at sites several hundred kilometers apart and found that birds at all three sites shared the same syllables. We found that House Finches only a few kilometers apart do not share most of their syllable types.

One issue that must be addressed in the House Finch is whether syllable types remain stable at a site over time. We found some indication that the lexicon of syllable types detected at Aggie Village may have changed somewhat between 1994 and 1995, but the evidence by no means is conclusive. Some species of birds possess stable syllable repertoires within a site, whereas song themes evolve at a rapid pace, probably because of cultural evolution (e.g. Indigo Bunting, Payne et al. 1981; Chaffinch [*Fringilla coelebs*], Baker and Boylan 1995). Long-term persistence of syllable types within a population, concurrent with rapid evolution of whole songs by recombination of syllables, may indicate different mechanisms in the cultural transmission of songs and syllables. Our results indicate that although many House Finches possess repertoires that most closely resemble those of nearby birds, some possess repertoires that are more similar to those of birds at more distant sites. Such a pattern of syllable sharing suggests that some birds learned their syllables several kilometers from where they were recorded.

The timing of song learning and natal dispersal distance are two factors that may greatly influence geographic song patterns in the House Finch. House Finches begin learning songs within the first two months of life (Bitterbaum and Baptista 1979). However, one individual learned new song types at the age of 10 months, so it appears that song-learning can occur after a bird settles in an area. Dispersal distances for House Finches have not been thoroughly studied. Mundinger (1975) examined band returns of House Finches in the northeastern United States and concluded that, even though the birds were partially migratory, they seemed to return to their natal area to breed. House Finches in the western United States are nonmigratory, and evidence seems to indicate that at least some individuals are philopatric. Numerous adults and juveniles banded in 1995 were found at the same sites in the 1996, 1997, and 1998 breeding seasons.

Our analysis of syllable-level geographic variation suggests other avenues of exploration and research into the processes of House Finch song development, an area that remains largely unexplored. The unit of song learning (whole song or syllable) may affect geographic patterns of song similarity, as might the timing of song learning and dispersal. Furthermore, behavioral responses to local and distant songs should be examined to determine whether birds respond to the geographic differences in syllable types that we describe. Stimulus songs could be constructed of the more common syllables in a local area and their potency as territorial signals or female stimulants compared with songs composed of rare syllables. Because it has been shown in some species of birds that certain syllable types convey specific information about the signaler (e.g. Dabelsteen and Pedersen 1992, Vallet et al. 1998), further investigation into geographic variation and functions of syllables should prove useful in understanding the relative roles of song and syllable repertoires in a variety of bird species.

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LITERATURE CITED

ARNOLD, A. P. 1982. Neural control of passerine song. Pages 75–93 *in* Acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

BAKER, M. C. 1996. Depauperate meme pool of vocal signals in an island population of Singing Honeyeaters. Animal Behaviour 51:853–858.

BAKER, M. C., T. K. BJERKE, H. U. LAMPE, AND Y. O. ESPMARK. 1987. Sexual response of female Yellowhammers to differences in regional song dialects and repertoire sizes. Animal Behaviour 35:395–401.

BAKER, M. C., AND J. T. BOYLAN. 1995. A catalog of song syllables of Indigo and Lazuli buntings. Condor 97:1028–1040.

BAKER, M. C., AND M. A. CUNNINGHAM. 1985. The biology of bird-song dialects. Behavior and Brain Science 8:85–133.

BAKER, M. C., AND L. R. MEWALDT. 1978. Song dialects as barriers to dispersal in White-crowned Sparrows, *Zonotrichia leucophrys nuttalli*. Evolution 32:712–722.

BAKER, M. C., D. THOMPSON, G. SHERMAN, AND M. CUNNINGHAM. 1981. The role of male-male interactions in maintaining population dialect structure. Behavioral Ecology and Sociobiology 8:65–69.

BALABAN, E. 1988. Cultural and genetic variation in Swamp Sparrows (*Melospiza georgiana*). II. Behavioural salience of geographic song variants. Behaviour 105:292–322.

BITTERBAUM, E., AND L. BAPTISTA. 1979. Geographical variation in songs of California House Finches (*Carpodacus mexicanus*). Auk 96:462–474.

CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. Bird song: Biological themes and variations. Cambridge University Press, Cambridge, United Kingdom.

DABELSTEEN, T., AND S. B. PEDERSEN. 1992. Song features essential for species discrimination and behaviour assessment by male Blackbirds (*Turdus merula*). Behaviour 121:259–287.

ELLIOTT, J. J., AND J. R. S. ARBIB. 1953. Origin and status of the House Finch in the eastern United States. Auk 70:31–37.

KONISHI, M. 1985. Birdsong: From behavior to neurons. Annual Review of Neuroscience 8:125–170.

KREBS, C. J. 1989. Ecological methodology. Harper-Collins Publishers, New York.

KREBS, J. R., AND D. E. KROODSMA. 1980. Repertoires and geographic variation in bird song. Advances in the Study of Behavior 11:143–177.

KROODSMA, D. E. 1982. Learning and the ontogeny of sound signals. Pages 1–23 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

KROODSMA, D. E., AND J. R. BAYLIS. 1982. Appendix: A world survey of evidence for vocal learning in birds. Pages 311–337 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

LEMON, R. E. 1975. How birds develop song dialects. Condor 77:385–406.

MARLER, P., AND S. PETERS. 1977. Selective vocal learning in a sparrow. Science 198:519–521.

MCGREGOR, P. K., V. R. WALFORD, AND D. G. C. HARPER. 1988. Song inheritance and mating in a songbird with local dialects. Bioacoustics 1:107–129.

MUNDINGER, P. 1975. Song dialects and colonization in the House Finch, *Carpodacus mexicanus*, on the East Coast. Condor 77:407–422.

MUNDINGER, P. C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. Pages 147–208 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

NELSON, D. A., P. MARLER, AND M. L. MORTON. 1996. Overproduction in song development: An evolutionary correlate with migration. Animal Behaviour 51:1127–1140.

NELSON, D. A., P. MARLER, AND A. PALLERONI. 1995. A comparative approach to vocal learning: Intra-specific variation in the learning process. Animal Behaviour 50:83–97.

NOWICKI, S., AND D. A. NELSON. 1990. Defining natural categories in acoustic signals: Comparison of three methods applied to 'chick-a-dee' call notes. Ethology 86:89–101.

OTT, R. L. 1993. An introduction to statistical methods and data analysis. Duxbury Press, Belmont, California.

PAYNE, R. B., W. L. THOMPSON, K. L. FIALA, AND L. L. SWEANY. 1981. Local song traditions in Indigo Buntings: Cultural transmission of behavior patterns across generations. Behaviour 77:199–221.

PODOS, J., S. PETERS, T. RUDNICKY, P. MARLER, AND S. NOWICKI. 1992. The organization of song repertoires in Song Sparrows: Themes and variations. Ethology 90:89–106.

ROST, R. 1990. Song dialects of the Marsh Tit (*Parus palustris*) and their functional significance: A test of models. Pages 111–122 *in* Current topics in avian biology (R. vanden Elzen, K.-L. Schuchmann, and K. Schmidt-Koenig, Eds.). DO-G Verlag, Bonn, Germany.

SAS INSTITUTE. 1985. SAS user's guide: Statistics. Version 5. SAS Institute, Cary, North Carolina.

SHIOVITZ, K. A. 1975. The process of species-specific song recognition by the Indigo Bunting, *Passerina cyanea*, and its relationship to the organization of avian acoustical behavior. Behaviour 55: 128–179.

SHIOVITZ, K. A., AND W. L. THOMPSON. 1970. Geographic variation in song composition of the Indigo Bunting, *Passerina cyanea*. Animal Behaviour 18:151–158.

THOMPSON, W. 1960. Agonistic behavior in the House Finch. Part I: Annual cycle and display patterns. Condor 62:245–271.

TOMBACK, D., D. THOMPSON, AND M. C. BAKER. 1983. Dialect discrimination by White-crowned Sparrows: Reactions to near and distant dialects. Auk 100:452–460.

VALLET, E., I. BEME, AND M. KREUTZER. 1998. Two-note syllables in canary songs elicit high levels of sexual display. Animal Behaviour 55:291–297.

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