

CHANGES IN SONG DIALECT DISTRIBUTIONS
AND MICROGEOGRAPHIC VARIATION IN
SONG OF WHITE-CROWNED SPARROWS
(*ZONOTRICHIA LEUCOPHRYS NUTTALLI*)

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ABSTRACT.—Multivariate analysis and analysis for spatial autocorrelation of 21 frequency and time characteristics of the songs of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) showed that within a dialect area the songs of neighboring males were no more similar to one another than to the songs of non-neighbors. This result refutes one prediction of the hypothesis that song dialects are maintained because males copy the songs of neighbors to gain an advantage in territorial defense or mate attraction. Historical events were important in producing changes over 10 yr in dialect distributions in an area of secondary contact between two dialects. The dialect distributions changed as the sparrow population invaded a new area where the vegetation had been modified, and the sparrows disappeared from a drought-affected area. The basic structure of the dialects did not change in 18 yr, and the fine structure, measured by 21 variables, did not differ between the 2 yr sampled. In 10 yr the two dialects did not blend to form an intermediate dialect. Received 4 June 1982, accepted 13 January 1983.

MANY songbird species exhibit local variation in song (dialects) in which songs at one location are uniform and different from songs at other locations. Several models have been proposed to explain the maintenance and function of dialects. Recent investigators have realized the importance of social interactions in song development and their influence on geographic variation in song (West and King 1980, Payne 1981b). Here, I have tested one prediction of the social adaptation model of dialect maintenance proposed by Payne (1981a). According to this model, birds benefit by copying the songs of other individuals in an area and thus produce a pattern of local dialects. Young males setting up their first territories may gain an advantage in territorial defense or mate attraction by copying the song of an older established neighbor. Payne considers this song copying a form of social mimicry, which deceives other birds into identifying the young bird as the older neighbor. Indigo Buntings (*Passerina cyanea*) seem to fit this social model. Young males establishing their first territories usually share syllable types and sequences with an established neighbor (Payne 1981b). First-year males that share their song with a neighbor have greater mating, nesting, and fledging success than do first-year males who do not share (Payne 1982).

Petrinovich et al. (1981) have suggested that a social adaptation model might explain dialects in the White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) of coastal California. This nonmigratory subspecies exhibits very local dialects; seven dialects occur within about 180 km² in the San Francisco Bay Area (Baptista 1975). Each male sings usually one stereotyped song, which is shared with the other individuals in a dialect area. Baptista (1975) observed local subdialects where a group of neighboring birds shared nearly identical songs. He also observed that a small number of adult White-crowned Sparrows changed their songs to match a neighbor's after moving to a new territory (L. F. Baptista pers. comm.).

These observations suggest that White-crowned Sparrow dialects might be explained by a social adaptation model under which young males and occasionally adult males benefit by copying the songs of territorial neighbors. A prediction of this model is that neighboring birds within a dialect area should sound alike. Because Baptista (1975) gave no indication of whether subdialects are common or rare, a quantitative test is needed to determine whether or not neighbors sing songs that are more similar to one another than would be expected by chance. To test this prediction I analyzed the microgeographic variation in 21 song

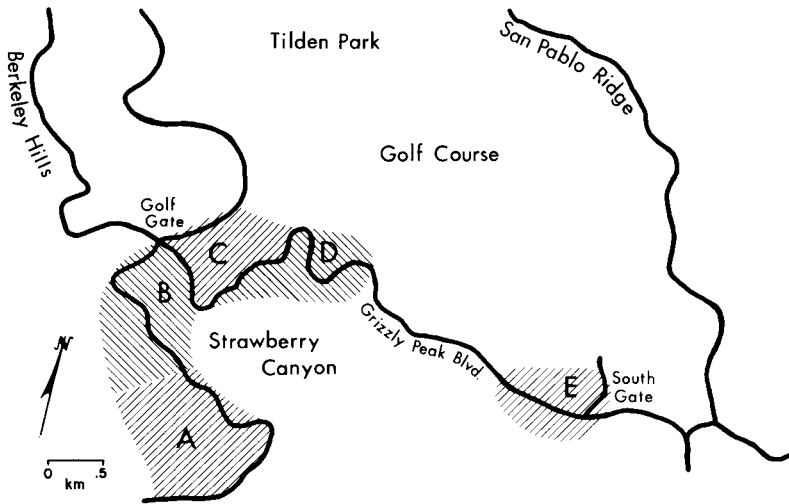


Fig. 1. Map of the study area in the Berkeley Hills, California. White-crowned Sparrow songs were extensively sampled in the shaded areas representing arbitrarily defined localities. A. Lower Strawberry Canyon. B. Upper Strawberry Canyon. C. Archery Range. D. Grizzly Peak Blvd. E. South Gate.

characters of frequency and time using multivariate analysis and analysis for spatial autocorrelation. If neighboring songs were no more similar to one another than expected by chance, then one prediction of the social adaptation model would be rejected. Previous studies of White-crowned Sparrows have been concerned only with between-dialect comparisons and therefore provide no test of the prediction that neighbors should sound alike.

My study site and surrounding area have some history of disturbance and modification. Two White-crowned Sparrow song dialects have been sampled there periodically by previous investigators over a period of 18 yr since the first audiospectrograms of the dialects were made by Marler and Tamura (1962) in 1960. This accumulation of samples offers the opportunity to observe the stability of dialect structure and distribution over time and the effect of habitat disturbance on stability. Two dialects, previously isolated on two hill ridges, came together in a zone of secondary contact, Strawberry Canyon (Fig. 1). Baptista (1975) mapped the distribution of the dialects in Strawberry Canyon in 1969 and 1971. I mapped the dialects again in 1977 and 1978. These four samples, covering a period of 10 yr, form the first documentation of changes in dialect distribution in an area where two dialects mix. I

hoped to discover whether both dialects would persist, one would replace the other, or an intermediate dialect would develop.

STUDY AREA AND METHODS

I recorded the songs of 69 individuals in the field with an Uher 4000 Report IC tape recorder, at tape speed 19 cm/s, and either a Sennheiser model unidirectional microphone or an Uher model microphone mounted on a 61-cm parabolic reflector. I analyzed the tapes with a Kay Elemetrics Corporation Model 6061-B Sonograph using a wide-band setting. I identified the dialect represented by each song by comparing the audiospectrograms to the descriptions of the Berkeley and Tilden dialects given by Baptista (1975). A small number of songs not recorded were categorized by ear in the field. I mapped the position where I recorded each bird. Because the birds were not individually marked, songs recorded from different positions were considered to belong to different individuals. In cases where I recorded birds at the same position on more than one day, the audiospectrograms were identical. The study area, where I attempted to record every male, included Strawberry Canyon, the Archery Range in Tilden Park, and Grizzly Peak Blvd. between Golf Gate and South Gate, Alameda County, California (Fig. 1). I also sampled in the city of Berkeley south of Strawberry Canyon, in the Berkeley Hills west of Golf Gate, in the Tilden Park Golf Course, and along San Pablo Ridge in Tilden Park to see whether or not any change in dialect distribution had occurred in these areas since

TABLE 1. Variation in White-crowned Sparrow song characters recorded in the Berkeley Hills in 1977 and 1978.

Variable ^{a,b}	1977 (n = 38)		1978 (n = 29)	
	Mean	SD	Mean	SD
1. Maximum frequency of type 1 syllables	6.14	0.50	5.86	0.37
2. Minimum frequency of type 1 syllables	3.27	0.21	3.24	0.16
3. Maximum frequency of type 2 syllables	5.06	0.24	5.14	0.25
4. Minimum frequency of type 2 syllables	3.04	0.18	3.04	0.13
5. Maximum frequency of note 1	3.77	0.21	3.73	0.30
6. Minimum frequency of note 1	2.82	0.27	2.86	0.18
7. Mean frequency of note 1 ^c	3.29	0.21	3.29	0.20
8. Frequency envelope of note 1 ^d	0.96	0.26	0.86	0.30
9. Maximum frequency of note 2	5.11	0.55	5.21	0.57
10. Minimum frequency of note 2	3.53	0.38	3.54	0.28
11. Mean frequency of note 2 ^c	4.39	0.69	4.38	0.30
12. Frequency envelope of note 2 ^d	1.58	0.58	1.67	0.67
13. Duration of note 1	604	123	600	190
14. Duration of note 2	366	39.9	346	81.6
15. Interval between syllable types 1 and 2	68.2	18.6	63.0	21.7
16. Interval between note 2 and type 1 syllables	51.2	9.7	54.7	17.8
17. Interval between type 1 syllables	65.9	9.9	59.6	13.5
18. Interval between type 2 syllables	84.7	8.4	78.1	16.9
19. Interval between syllable types 1 and 2	96.9	11.7	90.1	20.1
20. Number of type 1 syllables	3.45	0.72	3.45	0.74
21. Number of nodes in note 1	3.24	0.54	3.24	0.64

^a All frequency variables are in kHz.

^b All time variables are in ms.

^c Minimum + (maximum - minimum)/2.

^d Maximum - minimum.

Baptista's (1975) study. I recorded White-crowned Sparrows from February through June in 1977 and from March through June in 1978.

Multivariate analysis.—To perform the multivariate analysis I used programs available through the Michigan Interactive Data Analysis System. Because the note and syllable types used to distinguish between dialects did not vary within the dialects observed in this study, I measured 21 frequency and time variables from calibrated audiospectrograms to characterize the variation within a dialect (Table 1). Both principal components and cluster analyses were performed for each year separately. I selected for measurement the clearest audiospectrogram from each of 32 individuals in 1977 and 28 individuals in 1978 recorded in the areas shown in Fig. 1. It seemed reasonable to use one audiospectrogram from each bird, because the songs of individual White-crowned Sparrows tend to be stereotyped (Baptista 1977, this study).

To test whether or not the use of one song from each bird was justified for this population, I compared the variance in each of the 21 characters in a sample of 10 songs from a single individual with the variances in a sample of 38 songs from different individuals. *F*-tests showed that the variances in the sample from a single bird were lower than the variances from the sample of different birds; the differ-

ence was significant ($P < 0.05$) for all but one variable.

The principal components were constructed using a matrix of correlation among the 21 variables. For each year the first principal component was plotted against the second and third principal components in two-dimensional scatter diagrams. To facilitate interpretation of these diagrams, I divided the birds into groups representing five arbitrarily defined localities within the study area (Fig. 1). If neighboring birds sang similar songs, then the group of songs indicated by the analysis should contain songs from the same localities.

In the cluster analysis, hierarchical phenograms were constructed using a matrix of phenetic distances (square root of the Euclidean distance) by the single link method. This method joined two clusters at the minimum phenetic distance between two songs, one from each cluster. If neighbors have similar songs then clusters in the phenogram should contain neighboring birds.

Spatial autocorrelation.—For the spatial autocorrelation analysis I used a program written by Neal Oden. The calculation and biological applications of spatial autocorrelation are described in Sokal and Oden (1978a, b). Unlike the multivariate techniques, this analysis considers the information from each variable separately. The procedure tests whether or not

TABLE 2. Distance classes from the analysis for spatial autocorrelation in each of the 21 White-crowned Sparrow song characters. Map distances between all possible pairs of birds in a given year were calculated, and the pairs were grouped into distance classes. The autocorrelation coefficient was calculated at each distance class.

Distance class	Distance range (m)	Number of pairs	
		1977	1978
1	0-197	86	83
2	197-389	125	100
3	389-581	110	42
4	581-773	85	18
5	773-965	65	12
6	965-1,157	28	18
7	1,157-1,349	11	17
8	1,349-1,541	9	24
9	1,541-1,733	18	18
10	1,733-1,925	10	24
11	1,925-2,111	9	20

the value of a variable at one location is dependent on its value at other locations.

Birds may assess song similarity in two ways, each predicting slightly different results of the autocorrelation analysis. Males may assess the overall similarity of songs, so that, if neighbors sing similar songs, several variables should be autocorrelated. If only one or a small number of characters is important to convey similarity in songs, however, then a small number of variables should be autocorrelated in both years.

The statistic calculated was Moran's coefficient, I . To test for significant autocorrelation, I compared the observed value of Moran's I to the set of values it could take for all possible permutations of the observations over the map positions. This model makes no assumptions about the statistical distributions of the variables. I considered a variable autocorrelated if the value of Moran's I was significant with $P < 0.05$.

Autocorrelation was analyzed for each of the 21 variables and the ordination values of the first three principal components. The principal component values were considered composite variables that summarize the structure of each song. Two methods were used to analyze the autocorrelation. First, out of a matrix of all possible pairs of birds in a given year, I designated certain pairs as neighbors. Moran's I was calculated using only these neighbor pairs. Pairs of birds meeting each of the following criteria were designated as neighbors. (1) No more than 200 m separated neighbors. Beyond 200 m songs may be acoustically degraded and unrecognizable by conspecifics. (2) The map positions indicated that the pair probably shared a territorial boundary. (3) The topography did not prevent interaction between neighbors. For example, two birds recorded less than

200 m from each other were not considered to be neighbors if their territories were on different sides of a hill such that they could not hear each other sing. In 1977 and 1978 there were 38 and 31 pairs of neighbors, respectively. If neighbors sang similar songs, I expected some of the variables to be positively autocorrelated. This method tested the model that the structure of a bird's song is most influenced by the songs of neighboring birds within hearing distance. According to this model, if males wander off their territories, the songs they hear from non-neighbors would not have an important effect on the structure of their songs.

Making no assumptions about the effects of social interactions, I designed the second method of analysis to describe the pattern of geographic variation in the variables. Instead of constructing a matrix of neighbors, I calculated the distance between every pair of birds from map coordinates using the computer program. Pairs were grouped into classes of increasing distance, and the autocorrelations were performed at each distance class (Table 2). Thus, the song characters of an individual were used repeatedly to calculate coefficients at several distance classes. The value of Moran's I was plotted at each distance class to produce a correlogram for every variable (Fig. 8). Distance class 1 included all neighbor pairs as well as close pairs that did not meet the criteria as neighbors used in the first analysis. The longest distance class included birds separated by about 2 km. The correlograms show the geographic pattern in each song character over the entire study area. If proximate birds sing more similar songs than distant birds, then variables should be positively autocorrelated at close distance classes and either not autocorrelated or negatively autocorrelated at far distance classes.

RESULTS

Distribution of dialects.—The White-crowned Sparrow songs I recorded fit the description for the Berkeley and Tilden dialects given by Baptista (1975). Baptista described several variations of these dialects not observed in my study. All of the songs I recorded fit the following descriptions. Each song began with two introductory notes followed by a two-parted trill, each part consisting of a series of identical syllables (Fig. 2). In Berkeley themes, note 1 is a pure-tone whistle, sometimes with more than one node of high amplitude. The second note is also a whistle. The first series of syllables have a dominant frequency higher than the second series (Fig. 2A). In Tilden themes, note 1 is a whistle, usually with more than one node and often slurring down in frequency. Note 2 is a wide-banded buzz, and the two types of

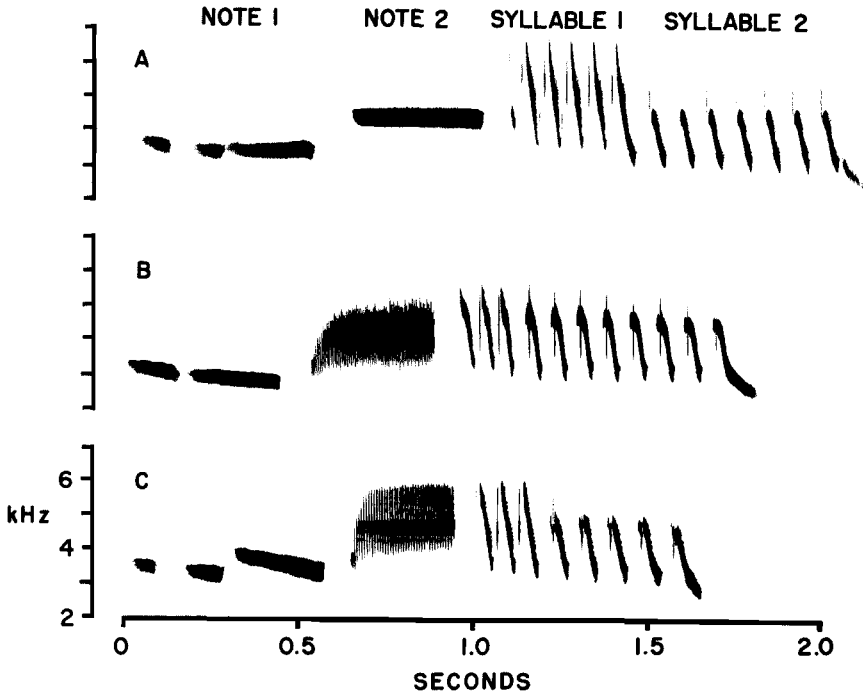


Fig. 2. Audiospectrograms showing the four components of White-crowned Sparrow songs recorded in the Berkeley Hills study area. A. Berkeley theme. B. Tilden theme. C. Cultural hybrid theme.

syllables in the trill have about the same dominant frequency (Fig. 2B). I also observed cultural hybrid song types containing elements of both themes. For example some hybrid song types had a Tilden-type introduction and a Berkeley-type trill (Fig. 2C). The structure of the song themes did not change between 1977 and 1978. Out of 21 characters, only variable 1 differed significantly between the two years (two-tailed t -test, $P < 0.014$) (Table 1).

All of the birds I sampled in the Berkeley Hills west of Golf Gate and in Berkeley south of Strawberry Canyon sang Berkeley themes, and the birds at the Golf Course and San Pablo Ridge sang Tilden themes, indicating no change in song-type composition since Baptista's study. The distribution of song types in Strawberry Canyon, however, changed between 1969 and 1978 (Fig. 3). The numbers of White-crowned Sparrows declined from 24 and 27 during Baptista's study to 11 and 7 during my study. With the exception of two birds singing Berkeley themes, all the birds in the Canyon sang Tilden themes in 1977 and 1978. In contrast, Baptista found in both years a small number of Berkeley and hybrid songs among the Tilden themes.

He also found a bilingual bird singing both the Berkeley and Tilden themes.

During the interval between Baptista's study and mine, White-crowned Sparrows settled new habitat in the Archery Range and along Grizzly Peak Blvd. to the east. In 1971 Baptista found only two White-crowned Sparrows singing Tilden themes in the Tilden Park Archery Range. In 1977 and 1978, however, 18 and 19 males occupied the Archery Range and Grizzly Peak Blvd. Of the birds I observed in 1977, 17 sang Tilden motifs, 1 sang a Berkeley motif, 3 sang hybrid songs, and 1 a Berkeley and a Tilden theme. In 1978, 16 birds sang Tilden themes, 3 sang Berkeley themes, and 3 sang hybrid songs. The structures of the 1978 Berkeley and hybrid songs did not match any of the songs recorded in 1977 and may have been from different individuals. In 1977, three males singing Tilden themes lived along the ridge near South Gate, an area unoccupied by White-crowned Sparrows during Baptista's study. In 1978, the number of males had increased to 10, all singing Tilden themes.

Multivariate analysis.—In 1977 and 1978, respectively, the first two principal components

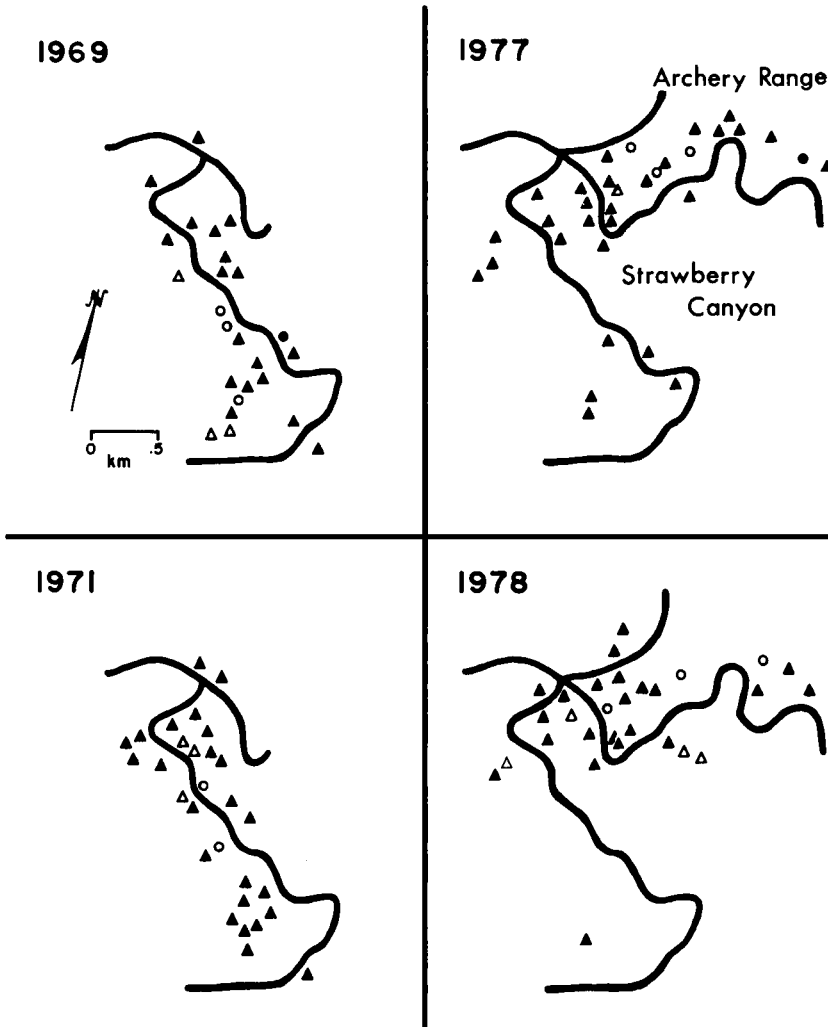


Fig. 3. Changes in distribution of White-crowned Sparrows in Strawberry Canyon, California. Songs were recorded in 1969 and 1971 by Luis Baptista and by myself in 1977 and 1978. Solid triangles represent Tilden themes, open triangles Berkeley themes, open circles cultural hybrid themes, and closed circles bilingual birds (after Baptista 1975).

accounted cumulatively for 39.3% and 44.5% of the total variance in the data matrix, and the first three accounted for 51.8% and 58.0% (Table 3).

A scatter plot revealed that in 1977 the 8 birds singing Berkeley themes could be separated from 27 birds singing Tilden themes on the basis of the values of their first and second principal components (Fig. 4). The three birds with intermediate songs were distributed throughout the scatter plot. Similarly, in 1978, three out of four birds with Berkeley themes

clumped together in the scatter diagram, while hybrids occurred throughout.

To find the variables most likely to be responsible for the separation of the two dialects in 1977, I compared the mean values of each of the 21 variables between dialects. Nine of the variables were significantly different between the two dialects (two-tailed *t*-test, $P < 0.025$) (Table 4). Eight of these nine variables are the same characters used to categorize the dialects by inspection of audiospectrograms. Seven of these eight variables had their greatest load-

TABLE 3. Variable loadings and percentage of cumulative variance from principal components analysis of White-crowned Sparrow songs within a dialect area.

Variable	1977			1978		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
1	0.009	-0.159	0.231	-0.003	0.064	0.142
2	0.260	0.039	-0.148	-0.223	0.028	0.121
3	0.332	0.008	0.028	0.229	0.086	-0.026
4	0.284	0.165	-0.171	0.139	0.084	0.241
5	0.206	0.359	-0.002	0.285	0.145	0.313
6	0.309	-0.057	-0.341	-0.026	0.139	0.374
7	0.304	0.210	-0.194	0.205	0.175	0.413
8	-0.095	0.303	0.311	0.297	0.059	0.082
9	0.316	-0.012	0.338	0.321	0.201	-0.294
10	0.271	-0.158	0.243	0.034	0.050	0.340
11	0.151	-0.106	0.504	0.316	0.212	-0.117
12	0.193	0.094	0.239	0.261	0.151	-0.398
13	-0.010	0.394	0.054	0.314	-0.242	-0.043
14	-0.293	0.176	-0.167	0.032	-0.378	0.225
15	-0.066	-0.222	0.167	-0.038	-0.312	-0.122
16	-0.136	-0.216	-0.001	0.066	-0.306	-0.131
17	-0.250	0.258	0.110	0.245	-0.340	0.096
18	-0.071	0.220	0.255	0.229	-0.340	-0.024
19	-0.304	0.138	0.049	0.085	-0.410	0.132
20	0.000	-0.235	-0.102	-0.328	-0.044	0.000
21	-0.016	0.402	0.101	0.248	-0.042	0.069
Component	4.68	3.57	2.63	4.73	4.61	2.84
Cumulative variance	22.3%	39.3%	51.8%	22.5%	44.5%	58.0%

ings on the first two principal components. Thus, as one might expect, the numerical analysis separated the dialects by the same criteria as the qualitative inspection method.

A scatter diagram of the first versus the second principal component in 1977 revealed a great deal of overlap among localities, indicating that songs within a region were often similar to songs in another region. A finer analysis within each locality revealed that neighboring birds often did not have songs close to each other on the two axes. These trends were also apparent in 1978. The scatter diagram of the first versus the third principal component for 1977 revealed no tendency for neighboring birds to group together (Fig. 5). In 1978, however, songs from the same localities often fell close together on the scatter diagram (Fig. 5). For example, most songs from the Archery Range fell in the lower half of the diagram. When broken up into west, central, and east regions within this locality, songs usually occurred near a song from the same region. A few songs from other localities grouped with the Archery Range songs, however. Individuals 62, 68, and 69 sang Berkeley themes, and individ-

ual 71 sang a hybrid theme, which probably explains why they did not group with others from the same location.

The cluster analysis produced results similar to the scatter diagram of the first versus the third principal components. In 1977, 4 out of 5 songs in the lower part of Strawberry Canyon clustered together at low phenetic distances. With the exception of these songs, I found little tendency for songs from the same localities to cluster together (Fig. 6). Clusters usually contained individuals from more than one location. In 1978, songs from the same localities often clustered together (Fig. 7). In many cases, however, songs were phenetically closest to songs from other locations. Three Berkeley themes and one hybrid theme were dissimilar to all other songs.

Spatial autocorrelation.—In the test for autocorrelation among neighbors' songs in 1977, only variable 16 was positively autocorrelated. Variable 11 showed the only significant negative autocorrelation. In 1978, variables 3 and 17 and the third principal component were positively autocorrelated ($P < 0.025$). Four more variables, 2, 6, 7, and 20, were positively auto-

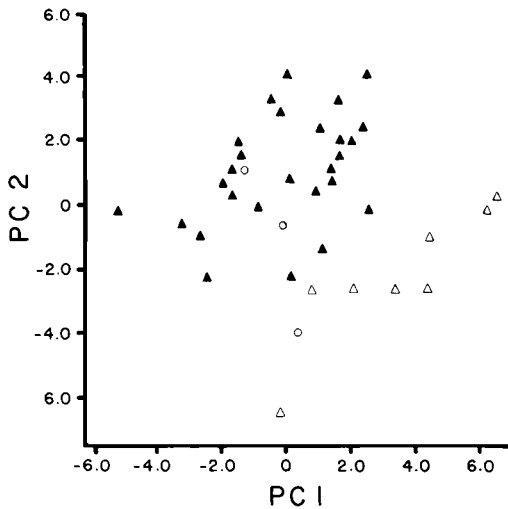


Fig. 4. Principal component ordination values for all White-crowned Sparrows recorded in 1977. The symbols are the same as in Fig. 3.

correlated ($P < 0.05$). Thus, in 1977 neighbors did not have similar songs. In 1978 neighbors tended to have songs more similar to each other than they were in 1977, although the songs were similar in only 6 out of 21 variables. None of the variables was positively autocorrelated in both years, indicating that individuals do not consistently share single song characters.

For each of the variables, the results of the second autocorrelation analysis for both years usually fell into one of four categories (Table 5). Of the 21 song characters in 1977, only variable 18 was positively autocorrelated at distance class 1 (Fig. 8). Three variables were neg-

atively autocorrelated at distance classes 2, 3, or 4. Ten variables had either a negative trend or a negative peak in autocorrelation significant at a distance class greater than 7. Nine variables had no pattern of autocorrelation. In 1978, 6 variables were positively autocorrelated at distance class 1. Seven variables were negatively autocorrelated at distance classes 2, 3, or 4. Six variables had a negative trend or a negative peak beyond distance class 7. Nine variables showed no pattern of autocorrelation. Out of 19 variables having some sort of significant pattern of autocorrelation in either 1977 or 1978, only 4 showed the same pattern in both years; all 4 variables had negative trends in both years (Table 5). In each year, about half the variables showed a significant negative autocorrelation in at least one of the longer distance classes (>7). Thus, for several variables, birds more than 1 km apart within a dialect area tended to have songs that were dissimilar in several characters.

DISCUSSION

The multivariate and autocorrelation analyses revealed no subdialects in my study area. In both years neighbors did not have songs more similar overall than expected by chance, although similarity among neighboring songs was slightly greater in 1978. Males did not seem to mimic neighbors using a small number of song characters, as none of the characters was autocorrelated among neighbors in both years. These results do not support the prediction of the social adaptation model. The analysis of microgeographic variation in song characters

TABLE 4. White-crowned Sparrow song characters significantly different between the Berkeley and Tilden dialects in 1977. The differences between dialects in the variables not listed were not significant ($P > 0.025$).^a

Variable	Berkeley (n = 8)		Tilden (n = 27)		Significance level
	Mean	SD	Mean	SD	
3	4.80	0.28	5.13	0.18	0.0003
6	3.09	0.31	2.78	0.19	0.0017
8	0.69	0.18	1.02	0.23	0.0006
9	4.66	0.27	5.26	0.49	0.0026
10	3.91	0.40	3.42	0.32	0.0012
12	0.75	0.21	1.83	0.35	0.0000
13	483	76.1	646	115	0.0007
15	95.6	13	59.5	11	0.0000
18	76.6	7.2	86.9	7.7	0.0021

^a Two tailed *t*-test. Units are the same as in Table 1.

showed that the values of most variables were randomly distributed with respect to distance between pairs of birds. About half of the characters, however, were dissimilar among birds more than 1 km apart. Mimicry of neighbors' songs apparently has not been important in producing the pattern of microgeographic variation in my study area.

The social adaptation model I tested is a very specific one. It is based on the assumption that social interactions important in song development occur only between neighbors at the territorial boundary. While the results did not support this specific model, social interactions may nevertheless be important during song development yet not produce subdialects. For example, if males, having copied the song of a neighbor, sometimes move to a different territory and fail to mimic a new neighbor, then adjacent birds would not necessarily have similar songs. It is also possible that social interactions with birds that are not neighbors influence song structure. In the summer, juvenile birds gather in flocks and travel throughout the territories of adults (Petrinovich and Patterson 1982). They have opportunities to interact with several adult males before establishing their own territories. Evidence suggests that some floater individuals do not establish territories until their second or third year (Petrinovich and Patterson 1982). These floaters may engage in disputes with territory owners. Thus, interactions occurring before territorial establishment may influence song development.

In view of these possibilities for social interactions to influence song development, other social models of dialect maintenance should be tested for White-crowned Sparrows. Perhaps models more appropriate than the specific one I tested could be developed. To test other social models by examining geographic song variation, one must identify the individuals expected to sound alike (such as neighbors) and compare the observed pattern of geographic variation with that expected under a random model. It may be impossible to specify which individuals influence the song development of others unless detailed histories of individuals are followed, as Payne (1981b) has done with Indigo Buntings.

The analysis for spatial autocorrelation is a powerful tool for testing models where one may specify individuals expected to sound alike. It is also useful for describing variation in song

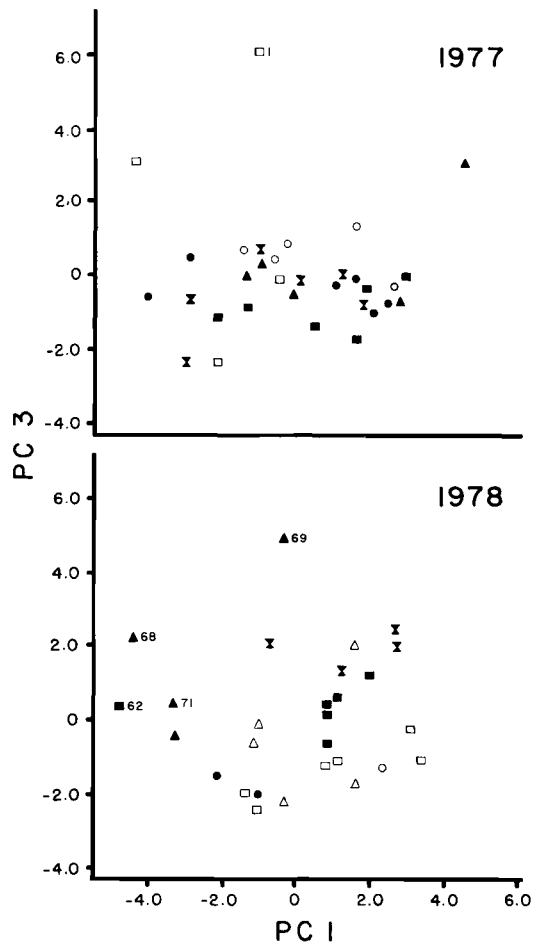


Fig. 5. Principal component ordination values for 1977 and 1978. Open squares represent individuals from West Archery Range, closed squares central Archery Range, hourglass shapes East Archery Range, open circles lower Strawberry Canyon, closed circles upper Strawberry Canyon, open triangles South Gate, and closed triangles Grizzly Peak Blvd. (see Fig. 1). Individual 1 in 1977 sang a hybrid theme. Individuals 62, 68, and 69 in 1978 sang Berkeley themes, and 71 sang a hybrid theme.

characters over distance. Previous investigators have achieved this by plotting a multivariate measure of song dissimilarity between all pairs of birds against geographic distance between the pairs (Payne 1978, Payne and Budde 1979, Bradley 1981). The violation of assumptions prevented testing the significance of the correlations, however, because the comparisons were not independent; each song was compared to every other song. Testing the signifi-

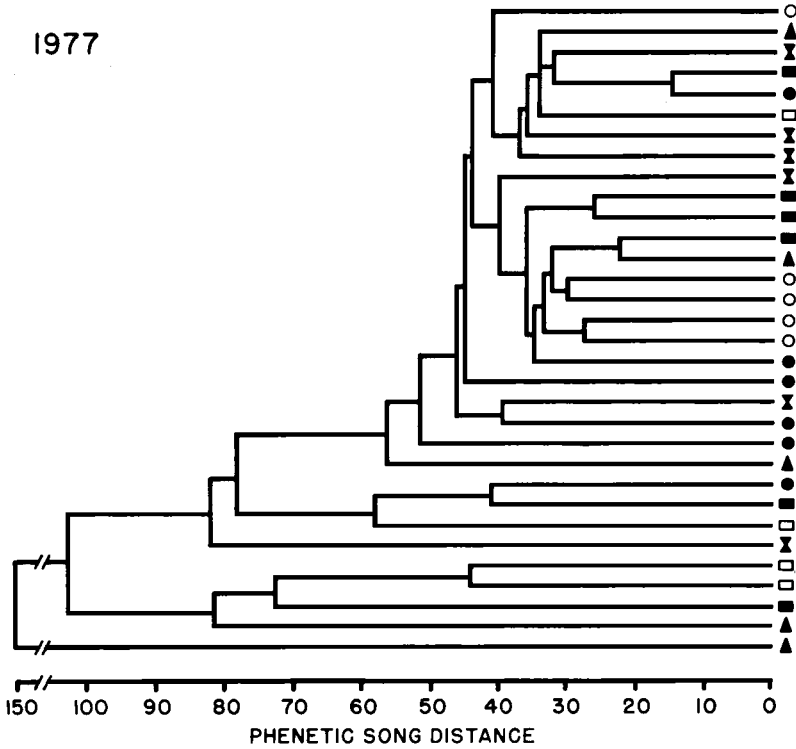


Fig. 6. Distance phenogram of White-crowned Sparrow songs recorded in 1977. Using the square roots of the Euclidean distances, songs were clustered by the single-linkage method. The symbols are the same as in Fig. 5.

cance of the autocorrelations does not assume independence of comparisons. Furthermore, autocorrelation analysis has the power to detect significant patterns over part of the distance range even if the pattern is random over the other distances. I used autocorrelation analysis to describe details in variation in several song characters. Caution must be used when interpreting multiple significance tests, as some of the autocorrelations may be spurious. Nevertheless, examining separate characters may prove helpful in identifying the song characters used by males to assess song similarity. Variables that are positively autocorrelated among proximate birds could be tested in the field using taped playback to determine whether similar or dissimilar values elicit differential responses in males.

The result that neighboring songs are no more similar to each other than each is to non-neighboring songs is consistent with two other widely discussed models of dialect mainte-

nance: the genetic specialization and the historical models. According to the genetic specialization model, assortative mating restricts gene flow between dialect populations genetically adapted to local conditions (Nottebohm 1969). Dialects are maintained, as young males learn their songs early in life and do not disperse far from the natal area. To maintain local adaptations, females mate preferentially with males who sing the dialect of the females' natal areas.

Baker and Mewaldt (1978) observed a lower than expected dispersal of young birds across a dialect boundary in the absence of a geographic barrier. Dispersal across a control line within each dialect was unrestricted. Therefore, they interpreted dialects to be dispersal barriers. Payne (1981a), however, argued that with the observed 4% of the population crossing the boundary per generation, pronounced genetic differentiation of the population by random processes would be prevented. The

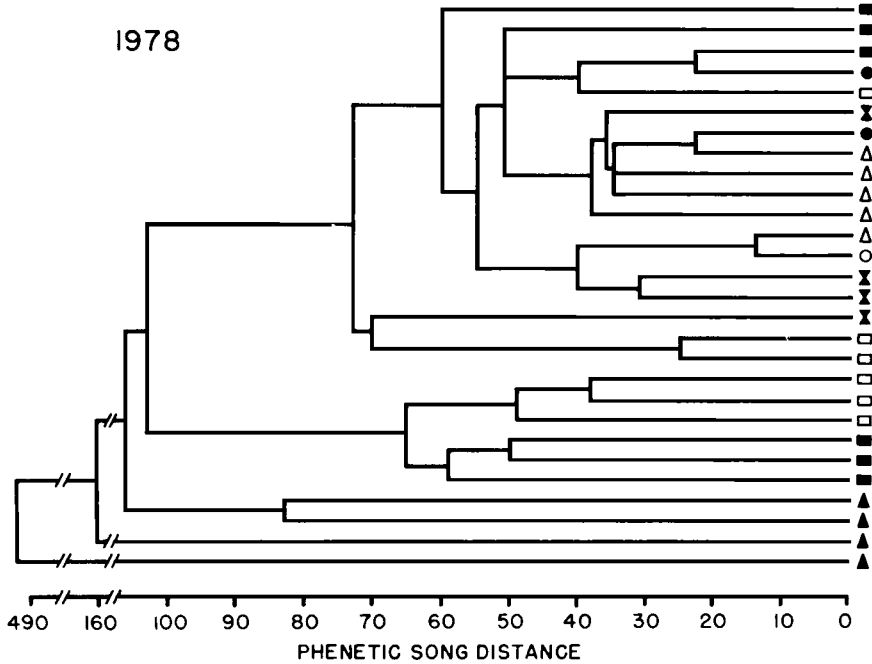


Fig. 7. Distance phenogram of White-crowned Sparrow songs recorded in 1978. Procedures and symbols as in Fig. 6.

similarity of habitats in these two areas (Baker 1975) did not suggest differences in selective forces.

Using electrophoretic techniques, Baker (1975) found that gene frequencies differed significantly between the two dialect areas in 2 out of 6 variable loci. Despite this, Payne (1981a) has pointed out that the same alleles were present in both dialect areas and that the same allele was most common in each area. Therefore females would gain little toward preserving favorable alleles in their offspring by mating only with males who sing the local dialect. Thus, although Baker's (1975) data do not refute the idea of assortative mating, they fail to demonstrate the degree of differentiation necessary for individual females to benefit by choosing males from the same dialect area. In fact there is little evidence that females mate assortatively according to dialect. Observations of *Z. l. oriantha* in the mountains indicated that only 2 out of 10 females injected with testosterone sang the same dialect as their mates (Baptista and Morton 1982). Similarly, *Z. l. nuttalli* females in San Francisco seldom sang the same dialect as their mates (Petrinovich et al. 1981). In sum-

mary, predictions of the genetic specialization model were not supported; dialect populations were not strongly differentiated, and pairs did not mate assortatively by dialect.

According to the historical model of dialect maintenance discussed by Baker (1975) and Payne (1981a), dialects diverge with time in areas isolated by distance or geographic barriers. Alteration of habitat may cause changes in both distribution and structure of dialects through founder effects and isolation over time. Song differences are maintained as a result of the timing of song learning, dispersal patterns, and geographic barriers, but they have no special social or genetic significance.

Historical events have been important in influencing the distribution and structure of White-crowned Sparrow dialects in my study area. The two dialects apparently developed in isolation on two moist ridges separated by a more xeric valley; the Tilden dialect occurred on the San Pablo Ridge, and the Berkeley dialect occurred in the Berkeley Hills (Fig. 1). In 1945 a golf course was built in Tilden Park, providing a corridor of moist habitat along which the White-crowned Sparrows spread

TABLE 5. Pattern of autocorrelation in White-crowned Sparrow song characters with increasing distance class. Variables with one of the first three types of patterns had at least one significant coefficient ($P < 0.05$) within the specified range of distance classes. Variables with no pattern of autocorrelation had no significant coefficients at any distance class.

Variable	Positive at distance class 1		Negative between distance classes 2-4		Negative between distance classes 7-11		No pattern	
	1977	1978	1977	1978	1977	1978	1977	1978
1					X			X
2					X			X
3					X	X		
4			X		X			X
5		X					X	
6		X				X	X	
7		X		X		X	X	
8					X	X		
9		X					X	X
10				X	X			
11				X			X	
12		X		X	X			
13				X			X	
14							X	X
15				X	X	X		
16		X					X	X
17							X	X
18	X		X			X		
19					X			X
20				X	X			
21			X					X
PC 1			X	X	X	X		
PC 2							X	X
PC 3		X		X			X	

from one ridge to the other. The two dialects came into secondary contact at Strawberry Canyon, where Tilden themes appeared and a few hybrid themes developed (Baptista 1975).

A few years after Baptista (1975) sampled songs in Strawberry Canyon, the vegetation on the Berkeley Hills ridge underwent alteration. A prolonged freeze in December 1972 killed most of the blue gum (*Eucalyptus globulus*) trees in Tilden Park (Beatty and Pattillo 1976). The dead trees were removed in 1973 and 1974 (Nicoles 1976), creating an open environment with shrubs and blue gum suckers suitable for colonization by White-crowned Sparrows. This resulted in an increase in the number of sparrows occupying the Archery Range and Grizzly Peak Blvd. from 3 in 1971 to 19 in 1978 (Fig. 3). The sparrows also spread along the ridge as far as South Gate (Fig. 1).

By the time of my study, the Berkeley dialect had almost disappeared from Strawberry Canyon; only two birds sang Berkeley themes. This may be the result of a long-term tendency for

Tilden themes to replace Berkeley themes in Strawberry Canyon. It is also possible, however, that the Berkeley themes were eliminated by chance when the number of White-crowned Sparrows declined by 40% between 1971 and 1978 (Fig. 3). The decline was probably due to the severe drought that occurred in 1976 and 1977. The number of birds at the Archery Range and Grizzly Peak Blvd. was not affected by the drought, probably because these areas along the ridge receive fog drip. It is interesting to note that the area where dialect mixture occurred shifted from Strawberry Canyon during Baptista's study to the Archery Range and Grizzly Peak Blvd., paralleling a shift in the White-crowned Sparrow population.

Despite the changes in distribution of dialects apparent within the 10 yr spanning Baptista's study and mine, the structures of the dialects remained stable. A comparison of audiospectrograms made by Marler and Tamura (1962), Baptista (1975), and myself in the same areas revealed no change in basic struc-

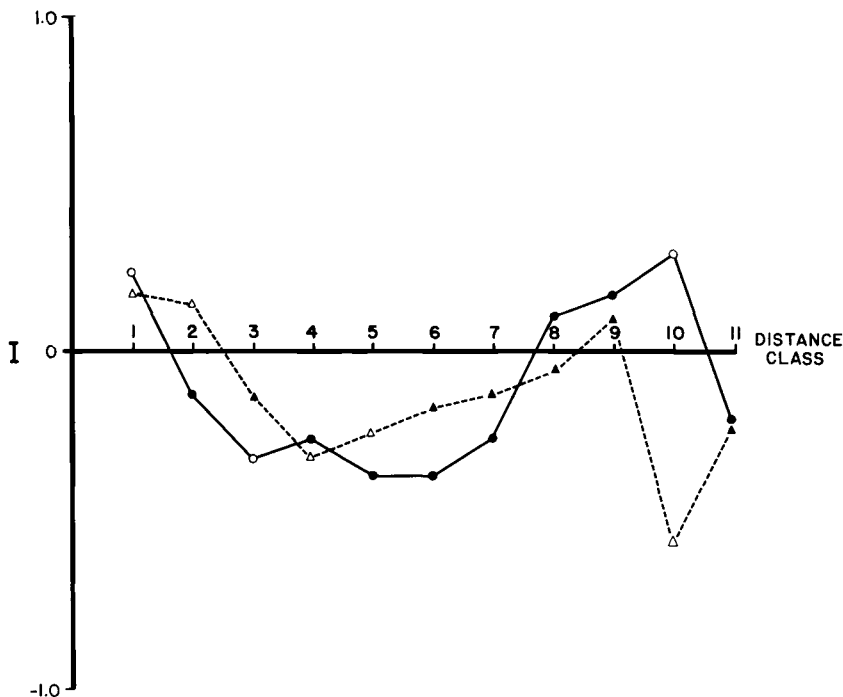


Fig. 8. Correlogram of Moran's coefficient I at each distance class. The solid line shows the autocorrelation of variable 18 in 1977. The broken line represents the third principal component in 1978. Open symbols are significant autocorrelations ($P < 0.05$). The expected value of Moran's I approaches 0 for large sample sizes.

ture of the Tilden and Berkeley dialects in 18 yr. Furthermore, the fine structure of songs measured by 21 variables in my study area remained essentially the same for 2 consecutive years (Table 1). Even in the contact zone the dialects maintained their integrity. The number of hybrid themes recorded did not increase from Baptista's samples to mine, indicating no tendency for the two dialects to blend into an intermediate form.

Baptista (pers. comm.) has observed a slightly greater amount of change in White-crowned Sparrow song structure and distribution at the subdialect level in San Francisco, California. A syllable type and buzzy phrase disappeared, and local song variants shifted locations, but the dialect remained recognizable as the one present 10 yr earlier. These results suggest that White-crowned Sparrows exhibit a striking degree of stability in song structure when compared with other species.

The few species with dialects in which changes in song structure and distribution have been examined exhibited greater change in lo-

cal song composition than did White-crowned Sparrows. For example, male Saddlebacks (*Creadion carunculatus*) shared from 1 to 4 song types with males on nearby territories. The boundaries of most song types changed little year to year, but new song variants sometimes arose and spread in the course of a few years (Jenkins 1978). Indigo Bunting song types at the George Reserve, Michigan, usually went extinct in 1 yr, and most of about 50 song types did not persist over a period of 15 yr (Payne et al. 1981). Similarly, most of the 23 Chaffinch (*Fringilla coelebs*) song types recorded in a Sussex woods were not present 18 yr later (Ince et al. 1980).

Two nonterritorial species also exhibit substantial change over time in local song composition. Individual male Village Indigobirds (*Vidua chalybeata*) had repertoires of about 18 shared song types. Slight changes in the song types accumulated each year until song types recorded at the same localities 5 yr apart could not be matched (Payne 1979). Yellow-rumped Cacique (*Cacicus cela*) song types in Suriname

usually did not persist in the same areas for more than 1 yr (Feekes 1982).

In all these species song learning and modification continue after young birds disperse and in the case of indigobirds and caciques probably continue into adulthood (Thorpe 1958; Jenkins 1978; Payne 1981a, b; Feekes 1982). Payne (1981a) considers it likely that social interactions in these species influence song development and may be important in maintaining song dialects. Historical events may be less important in creating the patterns of geographic variation than are postdispersal song copying and rapid propagation of newly introduced song types. Because of the unusual stability of song structure in White-crowned Sparrows, historical events can have pronounced effects on song-type distributions; they are not overshadowed by rapid turnover of song types. This suggests that if social interactions are important in maintaining White-crowned Sparrow dialects, the mechanism is likely to be different from that in these other species.

While historical events are apparently important in producing the pattern of geographic variation in White-crowned Sparrow song, social interactions may nevertheless play a role in maintaining dialect boundaries. Singing the same dialect as neighbors may provide social advantages other than deceptive mimicry. Perhaps White-crowned Sparrows singing the local dialect, although not mimicking a neighbor, can establish and defend a territory more effectively than males not sharing the local theme. Playback experiments showed that males and females responded differently to their own dialect than to an adjacent dialect (Baker et al. 1981, Petrinovich and Patterson 1981). Whatever the cause of the differences in response, these results suggest that birds singing local or foreign dialects might receive different treatment, perhaps resulting in an advantage to birds that sing the local theme. The observation that birds disperse somewhat less between two dialects than within (Baker and Mewaldt 1978) may be due to a preference to settle near birds singing the same dialect. If neighbors singing the same dialect are at an advantage, then one would expect the more common theme eventually to replace the less common one in areas where dialects mix. In this way social interactions would maintain dialects without necessarily producing subdialects.

To examine the role of social interactions in maintaining song dialects it would be useful (1) to observe directly the process of song development and dispersal of individuals, (2) to investigate the relative effectiveness of local and foreign song types in territorial defense, and (3) to compare the reproductive success of birds singing the same dialects as or different dialects from their neighbors. Describing the geographic variation in song is fundamental to the direct testing of dialect models. Observing dialects over time and comparing observed patterns with a random model provides information useful for understanding how song dialects are maintained.

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