MICROGEOGRAPHIC SONG VARIATION IN THE NUTTALL'S WHITE-CROWNED SPARROW[1]

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Abstract. Intradialect variation in the song of 138 male Nuttall's White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) was examined using multivariate cluster analyses on both quantitative (frequency and temporal) and qualitative (structural) variables. Mapping of song groups revealed local song clusters with a high degree of spatial overlap and the occurrence of "satellite" males located well outside the spatial cluster of their song type. This pattern is suggestive of predispersal song learning and is thus more consistent with the genetic adaptation hypothesis than with one version of the deceptive mimicry hypothesis.

Key words: White-crowned Sparrow; microgeographic song variation; avian vocal learning; song dialects; population structure; genetic adaptation; deceptive mimicry.

INTRODUCTION

Vocal development in the songbirds (oscines) is a cultural phenomenon. Young birds acquire their songs through exposure to adult models during a sensitive phase early in life (for reviews, see Marler and Mundinger 1971; Nottebohm 1972; Kroodsma 1978, 1982; Slater 1983; Baker and Cunningham 1985). The relative timing of the sensitive phase for song learning and dispersal, together with the opposing tendencies toward conformity and variation inherent in the learning process result in geographic song dialects (Lemon 1975; Kroodsma 1978, 1982; Baker and Cunningham 1985). Indeed, the existence of song dialects is taken as indirect evidence for vocal learning (Kroodsma 1982).

The White-crowned Sparrow (*Zonotrichia leucophrys*; especially the nonmigratory Nuttall's subspecies, *Z. l. nuttalli*) has held a central position in research and discussion on avian vocal learning and geographic song variation (for reviews, see Kroodsma et al. 1984, Baker and Cunningham 1985). On the coast of central and northern California it exhibits contiguous discrete song dialect populations. There are six dialect populations on the Point Reyes Peninsula which average about 10 × 3 km in size and in-

clude about 300 to 800 territorial pairs (pers. observ., Baker 1981, Baker and Thompson 1985). Baptista (1975) reported seven dialects within about 180 km² in the San Francisco Bay Area. While most attention has focused on this dialect variation among the Nuttall's White-crowned Sparrow populations, there is a hierarchical pattern to geographic song variation in this subspecies. Within dialect populations, there is obvious variation among individuals (Marler and Tamura 1962, Baptista 1975, Cunningham 1985), and small, local "subdialects" have been reported (Baptista 1975, Cunningham 1985). At the other end of the spectrum, some dialects are more similar than others, and two "superdialects" have been described on the Point Reyes Peninsula (Baker and Thompson 1985).

Unfortunately, there is as yet no standard criterion for identifying and comparing among species the potential hierarchical levels of geographic song variation, either in terms of the song components studied, in the geographic size of, or number of individuals in the song populations (Lemon 1975, Baker and Cunningham 1985). Moreover, differences in song population structure reported for different species of songbirds may arise from differences in the song learning/dispersal relationship and probably reflect differences in the proximate function of vocal learning for different species (Slater 1983, Baker and Cunningham 1985). Thompson (1970) recognized that different patterns of microgeographic song variation might result from differences in
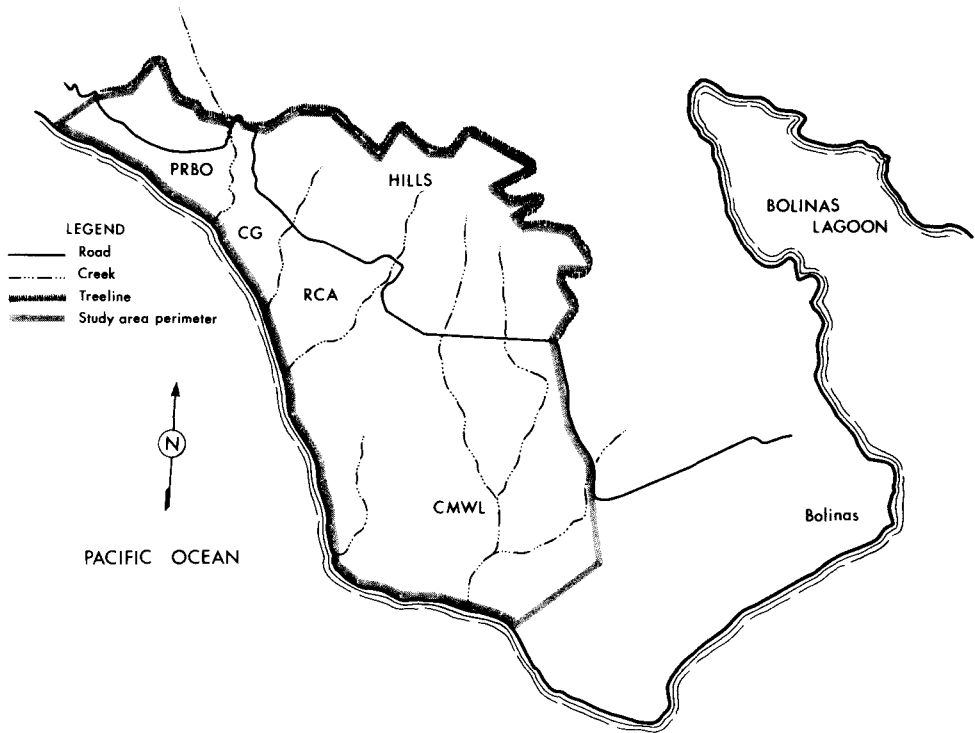
[261]

FIGURE 1. Five study areas within the "Clear" dialect study area: Point Reyes Bird Observatory (PRBO), Coast Guard transmitter site (CG), R.C.A. antenna field (RCA), Commonweal (CMWL) and Hills (HILLS).

the relative timing of song learning and dispersal; and Trainer (1983) has examined microgeographic song variation in the Nuttall's White-crowned Sparrow to test a prediction of one hypothesis proposed to explain the function of song learning and the maintenance of song dialects. Here we examine, using multivariate statistical techniques, local song variation within a dialect population of the Nuttall's White-crowned Sparrow, and relate the microgeographic pattern of song variation to the relationship between vocal learning and dispersal.

MATERIALS AND METHODS

We recorded territorial male White-crowned Sparrows ($n = 138$) between 22 April and 26 June 1980 in the southwestern two-thirds of the "Clear" dialect region (Baker 1975, Baker and Thompson 1985) on the Point Reyes Peninsula, Marin Co., California. The study area extended from the Bolinas mesa, above the town of Bolinas, to the Palomarin trailhead in the Point Reyes National Seashore (Fig. 1). This area was bi-

sected by a road running along the coastal plateau, from the mesa to the Palomarin trailhead. On the coastal side of the road, we worked in four contiguous study areas: the Point Reyes Bird Observatory study grids (PRBO), the U.S. Coast Guard Transmitter Station (CG), the old R.C.A. antenna field (RCA), and a continuation of the R.C.A. antenna field situated on the mesa and under the stewardship of Commonweal (CMWL). We also recorded birds in the contiguous hills (HILLS) above the road.

Prior to recording, we color banded males in RCA and CG to identify individuals and to estimate the proportion of individuals recorded in the area. On the PRBO study grids, volunteers banded all territorial pairs and mapped their territories. Approximately 80% of the males in PRBO, CG, and RCA were recorded. Males in the areas HILLS and CMWL were not banded, but we estimate that approximately 50% of the males there were recorded; in many cases these were males on neighboring territories.

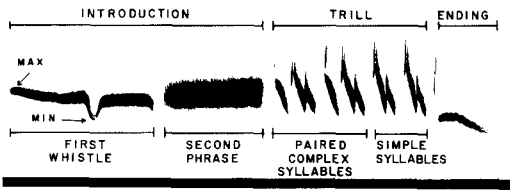Recordings were made on a Uher 4200 Report

FIGURE 2.   Sound spectrogram of the song of a male Nuttall's White-crowned Sparrow indicating major components of the song and several examples of measurements of quantitative (temporal and frequency) variables. Bars indicate duration measurements, arrows point to a measurement of a maximum and minimum frequency. See Table 1.

TABLE 1.   Variables used in quantitative analysis of song of White-crowned Sparrows.

A. Measured variables:
  Dominant frequency of first whistle of the introduction
  Dominant frequency of second phrase of the introduction
  Duration of the total song
  Duration of the total introduction
  Duration of the first whistle of the introduction
  Duration of the second phrase of the introduction
  Duration of the total trill
  Duration of all complex syllables in the trill
  Duration of the first complex syllable in the trill
  Duration of all simple syllables in the trill
  Duration of the ending

B. Derived variables:
  Difference between initial and dominant frequencies of the first whistle of the introduction
  Difference between dominant and minimum frequencies of the first whistle of the introduction
  Difference between maximum and minimum frequencies of the first whistle of the introduction
  Difference between maximum and minimum frequencies of the second phrase of the introduction
  Difference between maximum and minimum frequencies of the ending
  Duration of the buzzy portion of the second phrase divided by the total duration of the second phrase of the introduction
  Duration of the total introduction divided by the duration of the total trill

Stereo IC tape recorder set at 9.5 cm/sec with a Uher 517 microphone mounted in a 60-cm parabolic reflector. Generally, we recorded several songs from each male in the field. We later selected the cleanest of the songs from each male, representing all of the audible variation in the sample, and transferred them to a "summary tape." Samples on the summary tape ranged from 1 to 23 songs (median = 10) per male. After each male was recorded, his location was noted on photocopies of U.S. Geological Survey aerial photographs. Males were assigned individual codes (used below) as follows: RCA (101–130), CG (201–224), PRBO (301–326), HILLS (401–448) and CMWL (501–512).

We used the cleanest recording from each male to make a sound spectrogram on a Kay Elemetrics Co. 7029A Sona-Graph set for wide band (300 Hz) filter and the 80 to 8,000 Hz frequency range. From these spectrograms, we selected quantitative and qualitative characters for use in subsequent statistical analyses. The quantitative variables consisted of measurements of 16 frequency and 12 temporal variables (Fig. 2), and 10 additional variables derived from the 28 measured variables (Cunningham 1985:appendix A). We identified highly correlated variables in the data set using bivariate correlation analysis (SPSS, PEARSON CORR, Nie et al. 1975). In most cases where pairs of variables were correlated at $r \geq 0.5$, one of the variables was eliminated. We retained the one that most completely described the song in combination with other remaining variables. This screening process reduced the number of variables to 22.

In order to determine which variables contributed most to the variation in this data set, we subjected the remaining 22 variables to a principal components analysis (SPSS, FACTOR, PA1, VARIMAX, Nei et al. 1975). This analysis produced eight principal components with an eigenvalue ≥ 1.0 and accounted for 83.5% of the variance in the data set. Eighteen of the 22 variables had factor loading coefficients ≥ 0.75 on at least one of the eight principal components. The factor loadings of the other four variables indicated a weaker contribution (maximum loading coefficients ranging from 0.38 to 0.72), and these variables were not considered further. Subsequently, we performed cluster analyses on the 18 remaining original variables (Table 1), after standardization.

Measurements of frequency and temporal characters often do not capture the fine structure present in the notes and syllables of bird song.
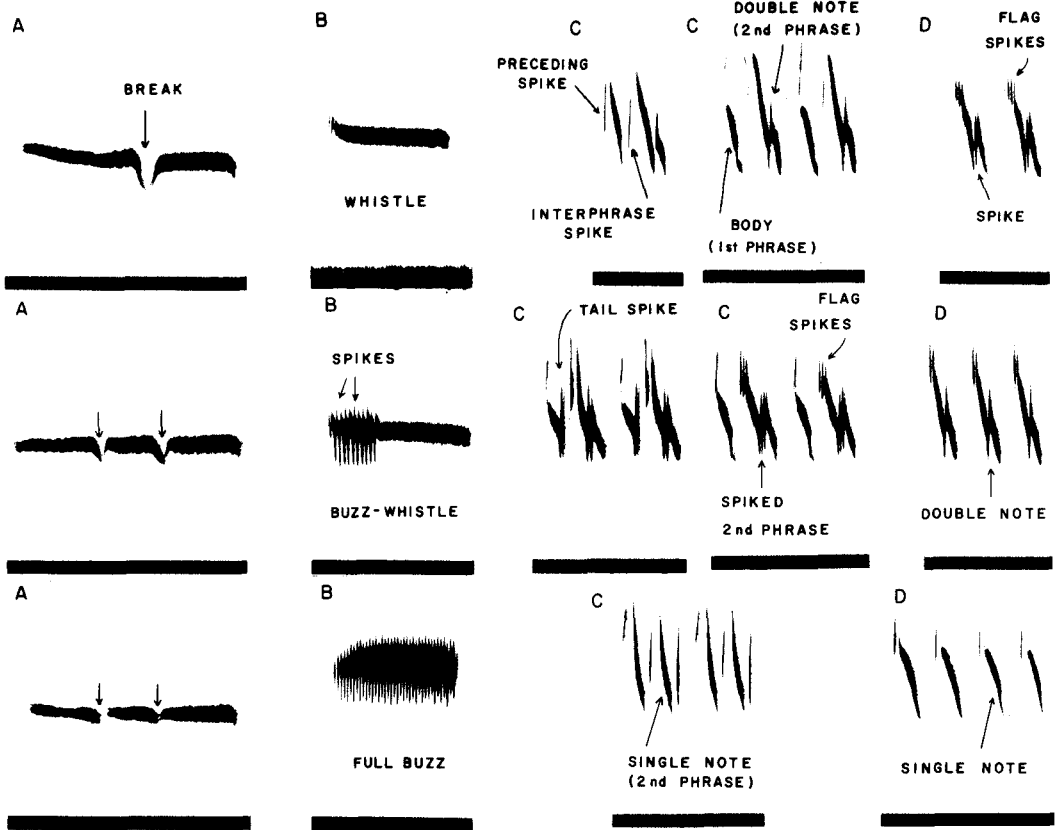
FIGURE 3. Examples of some qualitative variables defined in (A) the first whistle of the introduction, (B) second phrase of introduction, (C) complex (2 phrase) syllables, and (D) simple syllables. See Table 2.

In an effort to describe some of this detail, we defined 24 qualitative characters from the sampled song spectrograms (Cunningham 1985:appendix B). These qualitative variables (Fig. 3, Table 2) were given numerical scores for use in subsequent cluster analyses. Depending upon degree of variation, variables were scored on integer scales ranging from 0 to 9 (Cunningham 1985:appendix B). Because these quantitive scores were discrete and some characters could be scored only for presence or absence, this data set was not standardized prior to subsequent cluster analyses.

Both quantitative (frequency and temporal measurements) and qualitative (structural categories judged subjectively) data sets were examined by hierarchical cluster analyses (BMDP, P2M, CENTROID linkage, Dixon et al. 1981). The quantitative data set was standardized to z-scores by the sum of squares method (SUM-OFSQ). We did not weight variables in either data set (Sneath and Sokal 1973). Visual inspection of the distance phenograms produced by these hierarchical analyses suggested to us that some males had relatively unique songs and should be treated as individuals rather than grouping them with other singers. Thus, to increase within-group homogeneity, we withheld 19 males in the quantitative data set and 22 males in the qualitative data set from the following analyses.

Because we were interested in the spatial relationship of individuals whose intragroup song similarity was greater than that between groups, we also used a clustering technique that produced a specified number of discrete groups ("K-means" clustering, BMDP, PKM, Dixon et al. 1981). For the quantitative data, we initially specified 5, 10, 20, and 40 clusters in separate analyses. Output from the K-means analysis provided histograms
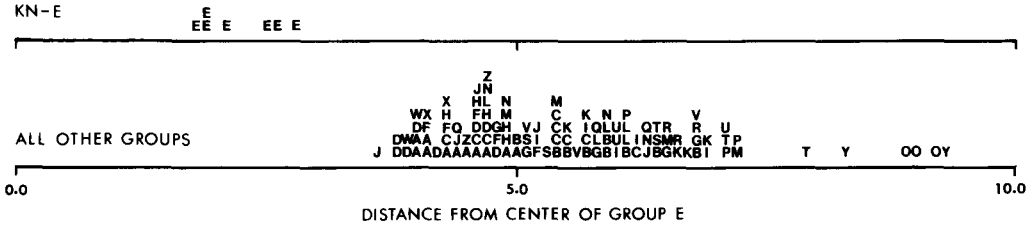
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KN-E              E
               EE E    EE E
                            Z
                           JN
                       X   HL  N      M
                      WX  H  FH  M     C    K  N  P        V
                       DF  FQ  DDGH  VJ CK IQLUL  QTR   R  U
ALL OTHER GROUPS      DWAA CJZCCFHBSI  CC CLBUL INSMR  GK TP
                   J  DDAADAAAAADAAGFSBBVBGBIBCJBGKKBI  PM    T   Y    OO OY
0.0                              5.0                                 10.0
                  DISTANCE FROM CENTER OF GROUP E
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FIGURE 4.   Sample histograms of a single group (KN-E) vs. all other groups formed from the BMDP K-means cluster analysis. This histogram indicates the separation in multivariate space of the individuals of a particular song group from the individuals of all other song groups.

indicating the distance from a given cluster's center for both that cluster's members and all other individuals in the sample (Fig. 4). By comparing overlap among these distributions, we were able to select a set of clusters where most had little or no overlap in distance from the cluster's center with members of different clusters. Inspection of the first four K-means analyses and additional screening suggested 26 clusters (17 with no over-

lap, seven with 50% or less overlap, and two with greater than 50% overlap on the K-means histograms). These 26 K-means clusters will be referred to as KN song groups.

TABLE 2.   Variables used in qualitative analysis of song of White-crowned Sparrows.

A. First whistle of introduction

Depth of breaks (three possible breaks)
Frequency plane change (difference between initial and dominant frequencies)

B. Second phrase of introduction

Structure (whistle, buzz-whistle, full buzz)
Vibrato frequency envelope (maximum–minimum, range in mm)
Vibrato rate (no. spikes/cm)

C. Complex syllables of trill

Number of complex syllables
Preceding spike present
Structure of 1st phrase, body of note (% total)
Number of tail spikes following first note
Number of interphrase spikes
Interphrase spike or 2nd phrase flag spikes forked
Structure of 2nd phrase, shape (single or double note)
Structure of 2nd phrase, body–1st note (% total)
Structure of 2nd phrase, body–2nd note (% total)
Number of spikes within 2nd phrase

D. Simple syllables of trill

Usual number of simple syllables
Number of flag spikes preceding note
Flag spikes forked
Structure of phrase, shape (single or double note)
Structure of phrase, body–1st note (% total)
Structure of phrase, body–2nd note (% total)
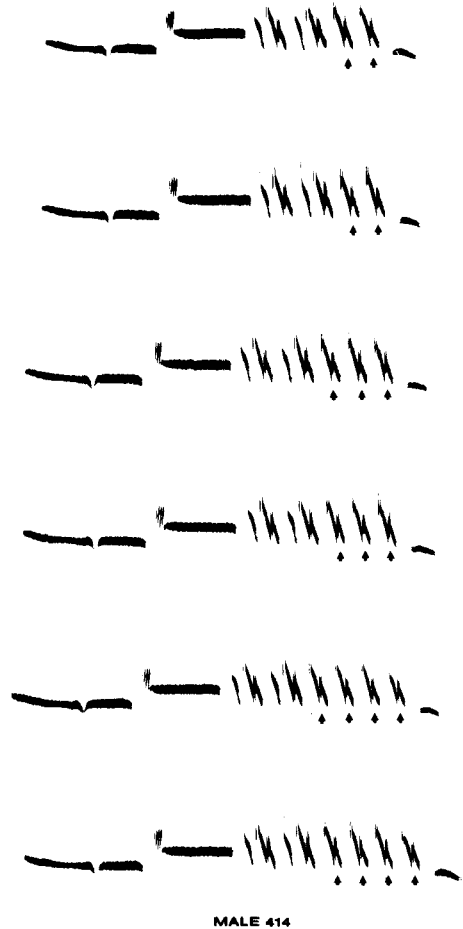Number of spikes within note

MALE 414

FIGURE 5.   Sound spectrograms of six songs produced by male 414. Arrows indicate variation in number of simple syllables.
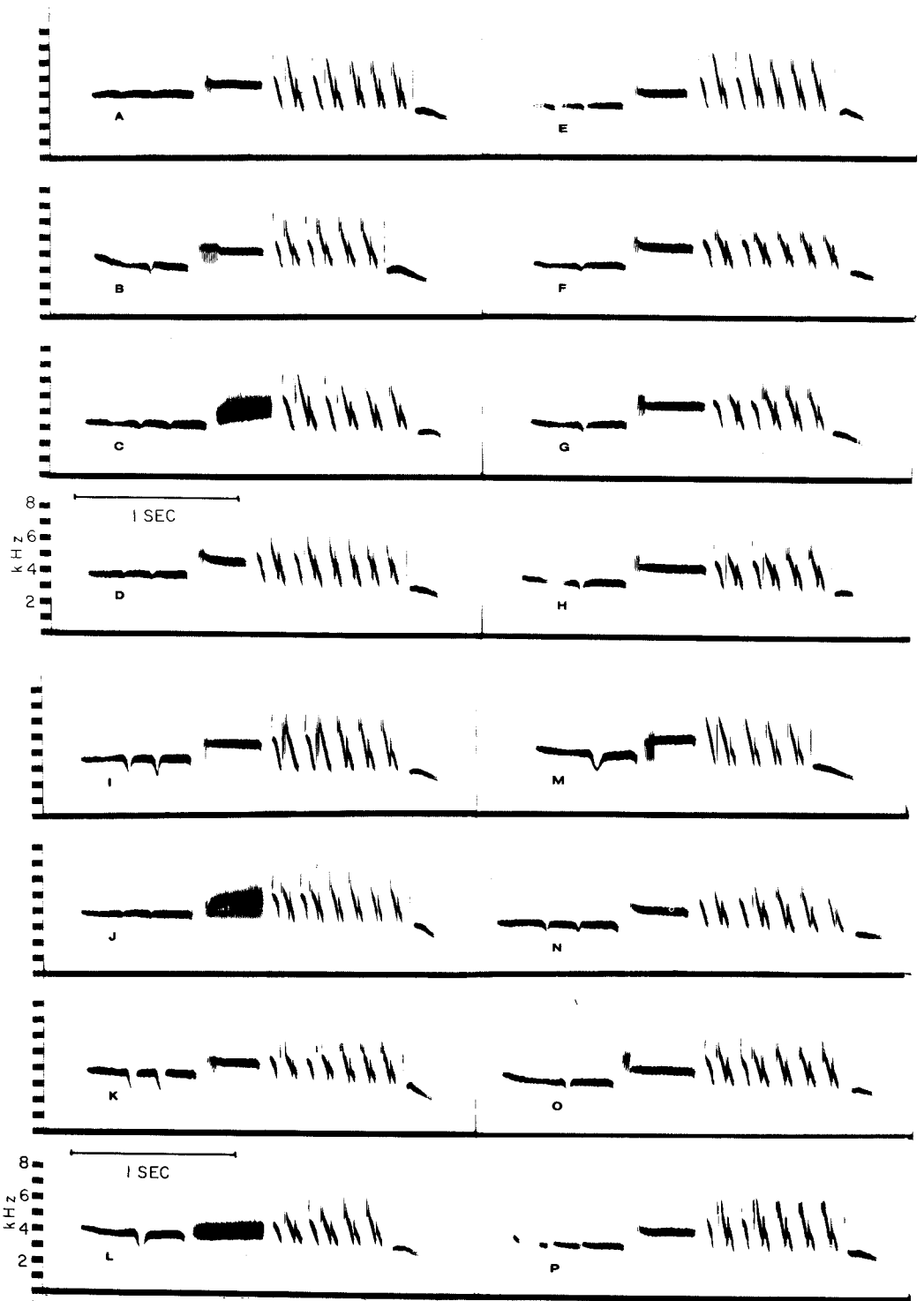
FIGURE 6.   Sound spectrograms from a representative male for each KL song group. This sampling shows the range of song variation within the Clear dialect and differences among the 24 KL song groups.
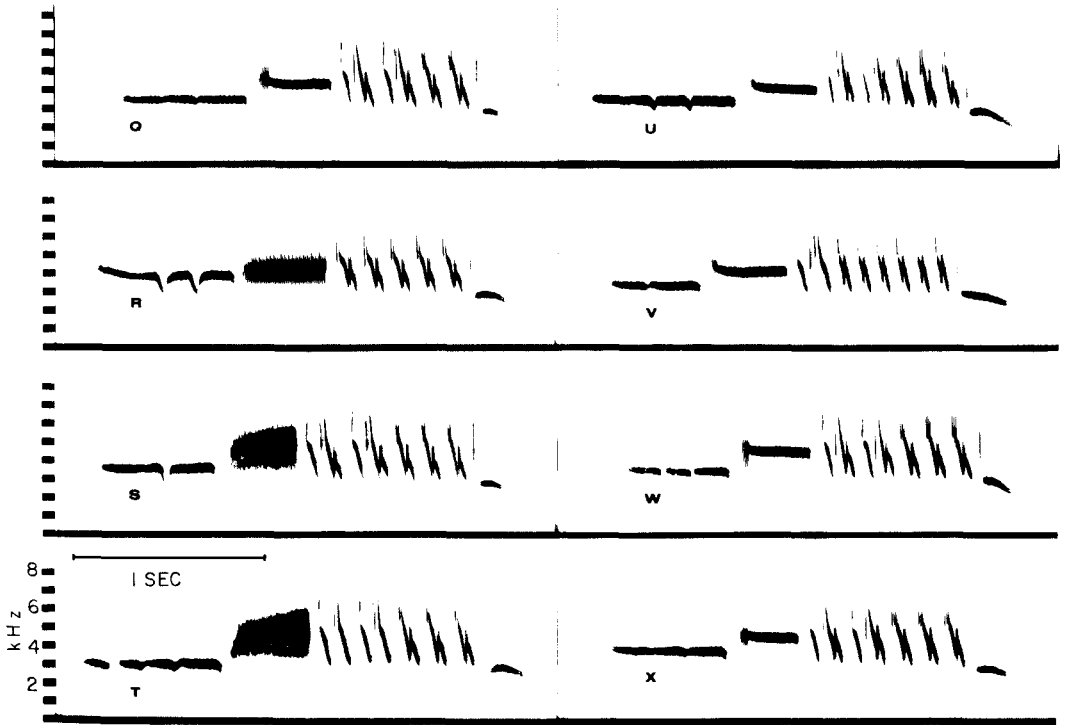
FIGURE 6.   Continued.

The qualitative data set was also subjected to K-means clustering. For comparative purposes, we specified 26 clusters in the first analysis. However, two of the 26 clusters formed from this data set, were composed of single individuals. The hierarchical analysis had indicated that these two males were most similar to each other and joined other clusters prior to the 22 individuals already withheld. Therefore, we reduced the specified number of K-means clusters until these two males joined together; this occurred at 24 clusters (16 with no overlap, seven with 50% or less overlap, and one with greater than 50% overlap on the K-means histograms). These 24 K-means clusters will be referred to as KL song groups.

In order to access the spatial structure of the song groups derived by the K-means algorithm, we compared map distances among males of each K-means song group with map distances among males of 10 randomly selected groups of equal size. We limited this analysis to the 14 KN and 15 KL groups of four or more males, as smaller groups were insufficient for statistical comparison. The random groups were, therefore, selected from the subset of individuals comprising these

14 KN and 15 KL song groups. We determined map distances between all possible pairs of males in each of the KN, KL, and their 10 respective random groups. The map distances for the KN and KL groups were then compared with their corresponding random groups (Wilcoxon's Rank Sum Test, Hollander and Wolfe 1973) to determine if males in the K-groups were more clustered geographically than an equal number of randomly chosen males. For the purpose of comparing the relative degree of spatial clustering of the KN or KL song groups, we compared each song group of the same size to the same set of 10 random groups of that size. Thus, for example, KN groups F to L of five males each were compared with the same 10 randomly drawn groups of five males each. This procedure of comparing song groups to sets of randomly-generated groups follows the spirit of the permutation test procedure used by Mielke (1984, 1985, 1986; Zimmerman et al. 1985). We also considered the 14 KN and 15 KL song groups as single samples and then compared their minimum, median, and maximum map distances with those of their respective sets of random groups ($n =$

TABLE 3. Comparison of map distances between all possible pairs of males for K-means song groups with 10 random groups of equal size.

KN groups:			KL groups:		
Group	Group size/ no. pairs	KN vs. random, no. sig.	Group	Group size/ no. pairs	KL vs. random, no. sig.
A	11/55	2	A	13/78	5
B	9/36	9	B	9/36	7
C	9/36	5	C	8/28	10
D	8/28	8	D	7/21	0
E	7/21	0	E	7/21	10
F	5/10	7	F	7/21	5
G	5/10	7	G	6/15	0
H	5/10	4	H	6/15	2
I	5/10	4	I	5/10	10
J	5/10	7	J	5/10	0
K	5/10	0	K	5/10	2
L	5/10	5	L	4/6	0
M	4/6	0	M	4/6	10
N	4/6	2	N	4/6	0
			O	4/6	3

Pairwise comparisons of K-means vs. random groups by Wilcoxon's Rank Sum Tests. KN and KL groups are K-means groups derived from quantitative variables and qualitative variables respectively. KN and KL groups with the same letter designation are not necessarily the same group of males (usually not). Random groups were drawn from the subsets of cases which formed the KN or KL groups used in these tests. The number of significant comparisons, out of 10, is indicated for one-tailed tests at $P \leq 0.05$.

14 KN vs. 60 random, $n = 15$ KL vs. 70 random, Wilcoxon's Rank Sum Test, Hollander and Wolfe 1973). Finally, to determine the pattern of the potential microgeographic clustering of song groups we mapped the positions of all males and indicated their K-means song group affiliation.

RESULTS

The male Nuttall's White-crowned Sparrow typically sings a single song that usually remains consistent through life (Marler and Tamura 1962, 1964; Marler 1970; Baptista 1975; but see Baptista and Petrinovich 1984). A small proportion of the males in our sample (2.2%, 3 of 138 males) sang two songs (see also Baptista 1975). The most common variation among songs of an individual was the number of simple trill syllables (Fig. 5). Of 138 males, 58 (42.0%) varied the number of simple syllables. This variation in simple syllable count changes the duration of the song, but does not alter its qualitative structure. Because the song of an individual male is highly stereotyped, studies of song variation in White-crowned Sparrows have typically used a single spectrogram to represent an individual (Marler and Tamura 1962, Baker 1974, Baptista 1975, Trainer 1983). Therefore, we used the modal type in the sample from an individual whenever any variation was

obvious (e.g., number of simple syllables or multiple song types). Song variation among individuals is considerably larger, however, than that within individuals (Fig. 5 vs. Fig. 6; Trainer 1983).

The song groups formed by the K-means cluster analyses ranged in size from two to 13 males (11 males for the KN groups), with the median being four males for both the KN and KL groups. Comparison of membership of the KN and KL song groups (Cunningham 1985:appendix C) indicated that only three song groups were identical in both sets: KN-H and KL-K (five males), KN-O and KL-R (three males), and KN-Y and KL-V (two males). There was, however, considerable partial common membership among KN and KL groups. For example, the 13 males of KL-A included four of the five males of KN-I and three of the nine males of KN-C. The nine males of KL-B included two of the five males of KN-F, four of the five males of KN-G and two of the three males of KN-S. The eight males of KL-C included six of the eight males of KN-D and two of the four males of KN-N. The other two males of KN-N were "satellite" males of KL-J (see below). The two males of KN-Z were two of the three males making up the core cluster of KL-J in CMWL. KL-I was composed of KN-W (two males), KN-X (two males) and male 116. Also, the four males of KL-M included two of the three males of KN-T.

Song spectrograms of a representative for each KL group are shown in Figure 6. Using 26 groups for the set of quantitative variables and 24 groups for the set of qualitative variables, the K-means analyses successfully grouped individuals with similar songs. There was, nevertheless, some obvious intragroup song variability in some groups. For example, in group KL-G (Fig. 7A), there were small differences among males in their first whistle. There was some obvious variability in the trill syllables as well, but also some common features, particularly in the number of spikes within the second phrase of the complex syllables and in the number of flag spikes preceding the simple syllables. On the other hand, the males in song groups KL-I (Fig. 7B), KL-M and KL-R (Fig. 7C) showed a very high degree of intragroup song similarity. The degree of intragroup song variability among the KL groups generally ranged between these examples. The KN song groups were sorted on the basis of quantitative measures of frequency and duration of major song characters. Visual inspection of KN song groups suggested higher intragroup song variability than

TABLE 4. Wilcoxon's Rank Sum Tests on minimum, median, and maximum map distances (in meters) for K-means song groups vs. random groups.

| Median values for map distance	Minimum	Median	Maximum	
KN groups (using quantitative variables)				
KN groups	96	795	1,980	$n = 14$
Random groups	162	1,151	2,639	$n = 60$
	$W = -1.836$	-2.470	-2.512	
	$P = 0.033$	0.007	0.006	1-tail test
KL groups (using qualitative variables)				
KL groups	108	1,115	2,236	$n = 15$
Random groups	226	1,337	2,880	$n = 70$
	$W = -1.585$	-2.778	-2.357	
	$P = 0.056$	0.003	0.009	1-tail test

with KL song groups because structural details not accounted for the by quantitative measurements tended to be visually more obvious.

Within the Clear dialect population sampled, the geographic distribution of individual song types was nonrandom. Eleven of the 14 KN groups and 10 of the 15 KL groups tested were clustered more closely geographically ($P < 0.05$, Wilcoxon's Rank Sum Tests) than at least two of the 10 random groups of equal size to which they were compared (Table 3). Some song groups (KN: E, K, and M; KL: D, G, J, L, and N) were not statistically more clustered than the randomly-drawn groups to which they were compared. A second examination of the overall difference between the K-groups and the random groups considered each set as a single sample and compared their minimum, median, and maximum map distances between pairs of males. Both KN and KL groups had shorter map distances for all three measures than their comparative random groups (Table 4). These tests indicate that, generally, males with similar songs were clustered in space.

Inspection of the KN and KL group mappings (Figs. 8A, B) revealed extensive overlap among song groups as well as the presence of "satellite" males, located outside of their main song cluster. For example, in the areas of highest density of recorded males (PRBO, CG, and RCA; coordinates: x = 0–2,500, y = 250–1,000 in Figs. 8A, B), for both KN and KL groups, there were nonrandom clusters that were highly interspersed. The KL groups appeared more spatially distinct (Fig. 8B), but even here there was considerable mixture as well as satellite males for several groups. KL group B was a highly nonrandom

group of nine males in two spatial clusters. Four males form a pure subgroup in the upper center of the map (2,200, 1,900) with one more below and to the right, near males singing other song types. The remaining four males are in the heterogeneous swarm centered about (1,900, 700). KL group C consisted of eight males. Five surrounded a J male at (1,500, 1,500) with one more below among five neighbors with different songs. The remaining two were distant satellites. KL groups D and E had most of their members in the lower left at (500, 700). Here these two subgroups crossed each other and shared the area with males singing four other KL song types (G, H, V, and W) and six males with unique songs. The five members of KL group I were the most highly clustered group of more than four males (RCA area, centered at 1,800, 600). Yet five individuals singing four other song types (B, F, N, and dot) were interspersed within the area occupied by KL group I. KL group K had five males, four clustered about (4,000, 700) and a satellite male at (2,000, 700). KL group J had five males, three around (4,200, 700), a satellite surrounded by the subcluster of five C's at (1,500, 1,500), and another satellite near the four M's at (2,900, 1,700). Finally, there were two small and highly clustered song groups, M at (3,100, 1,800) and R at (2,000, 2,200) that enclosed individuals singing other song types (J, L, and dot). Additional examples of extreme overlap in song groups and satellite males can be found in these KN and KL assemblages.

Both the extensive overlap of song groups and the location of satellite males were more obvious when lines were drawn to enclose the spatial clusters of song groups (Figs. 9A, B). The area of the

A

B

8
kHz 6
4
2

I SEC

C

8
kHz 6
4
2

I SEC

270
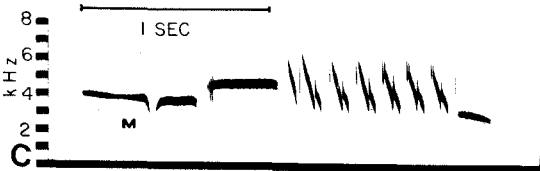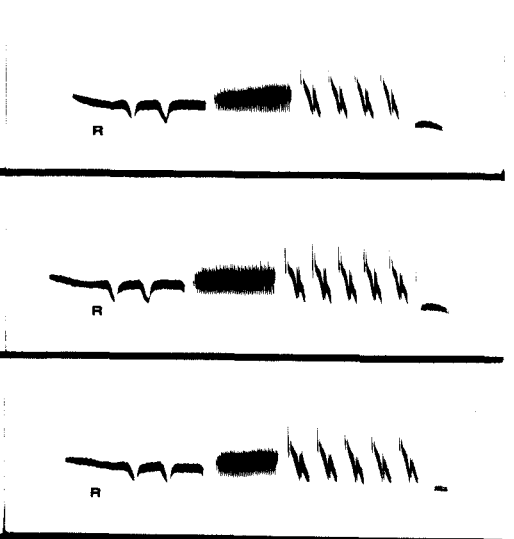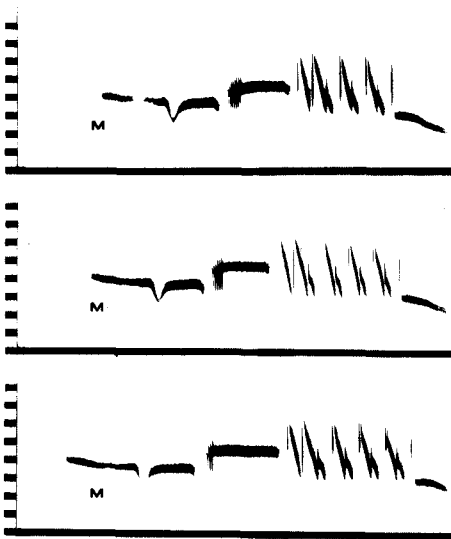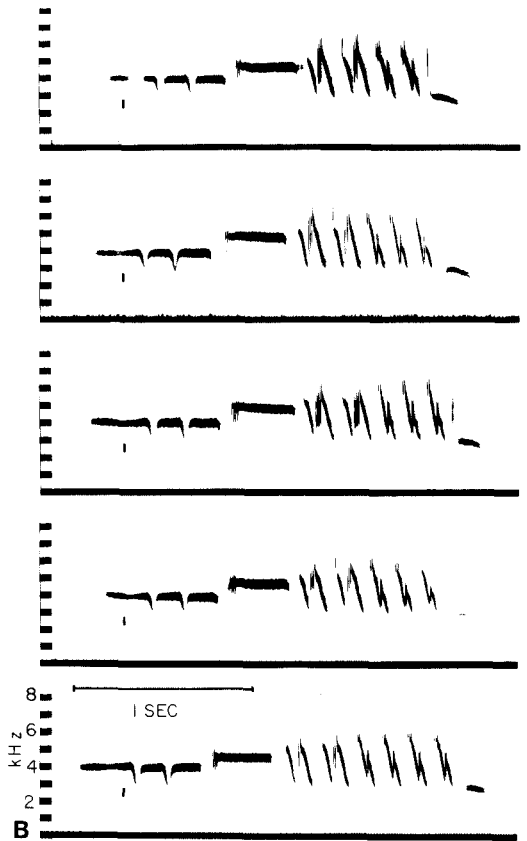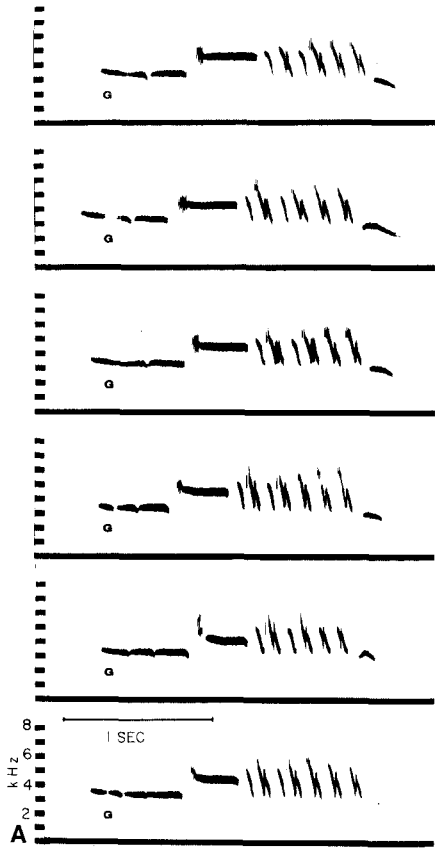
enclosed song groups and whether or not an individual located away from the main cluster of his song group would be shown as a satellite would depend upon the decision of how far the enclosures are expanded. In some cases, this decision is obvious; in other cases, it is more arbitrary. Greater expansion would produce larger areas for each group, increasing overlap among song groups while decreasing the number of satellite males. Somewhat larger enclosures were drawn around the KN groups (Fig. 9A) than around the KL groups (Fig. 9B), but the general patterns of song group overlap and satellite males are the same for both.

DISCUSSION

In the present study, the microgeographic distribution of song variation in the Nuttall's White-crowned Sparrow was nonrandom (Figs. 8A, B; 9A, B). Local song groups were clustered spatially, but there was a high degree of spatial overlap among song groups such that neighboring males often did not have similar songs. Additionally, some satellite males occupied territories well beyond the main spatial cluster of their song group and among males singing other song types.

Thompson (1970) suggested that the spatial distribution of song types could provide insight into the timing of song learning. He pointed out that young birds that learned their song prior to dispersal from their natal area would most likely have learned the pattern of their father's song. He considered it unlikely that returning first-year birds would be able to settle consistently adjacent to the male from whom they had learned their song prior to dispersal. Thus, he expected that similar song types would often be separated by other song types. This would indicate that returning birds were able to settle near their natal territory but not immediately adjacent to it. Alternatively, Thompson argued that a bird learning its song during its first spring, following dispersal, would most likely learn from an immediate neighbor. Therefore, he expected that postdispersal song learning should result in territorial neighbors having similar songs. Elsewhere, we developed a similar line of reasoning (Cunning-

ham 1985), before rediscovering Thompson's earlier statement of the expected patterns.

Two general hypotheses proposed to explain the adaptive function of avian vocal learning and the maintenance of geographic song variation are predicated on the relative timing of learning and dispersal. Nottebohm (1969) first proposed the genetic adaptation hypothesis, suggesting that song dialects might identify local populations and reduce gene flow, thus promoting the evolution of physiological adaptations to local environmental conditions. The correlation of dialect variation and environmental heterogeneity was suggestive of this view (Nottebohm 1969). Subsequently, Shields (1982, 1983) argued that even in relatively homogeneous environments a certain level of inbreeding could be adaptive and he suggested that dialects might promote positive assortative mating and regulate dispersal (see also Bateson 1978, 1979, 1980). Moreover, the establishment of new populations by colonization will likely be accompanied by only a subsample of the gene pool of a parental population and often will occur in novel physical and biotic environments. Under such conditions, protection of the divergent and coadapted genetic system could be accomplished quickly by the behavioral mechanism of early song learning by males and females, promoting assortative mating in the daughter population. The overall result would be a population structure that Wright (1978) suggested would favor rapid evolutionary diversification, a pattern characteristic of oscine birds (Baker 1981). Thus, assumptions of the genetic adaptation hypothesis are that song is learned prior to philopatric dispersal, with dialect boundaries acting as partial barriers to dispersal (Baker and Mewaldt 1978).

The second hypothesis, proposed by Payne (1981, 1982), has been given several names describing the behavior of the song learner: social adaptation, social convergence, and competitive or deceptive mimicry. Accordingly, young males learn their song, following dispersal, by copying the songs of older males in the area where the young males settle. This song mimicry is thought to facilitate entry into the local social group where

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FIGURE 7.   Sound spectrograms of songs from males comprising four song groups: (A) KL-G, (B) KL-I, and (C) KL-M and KL-R. This sampling indicates the range of song variation within the KL song groups.
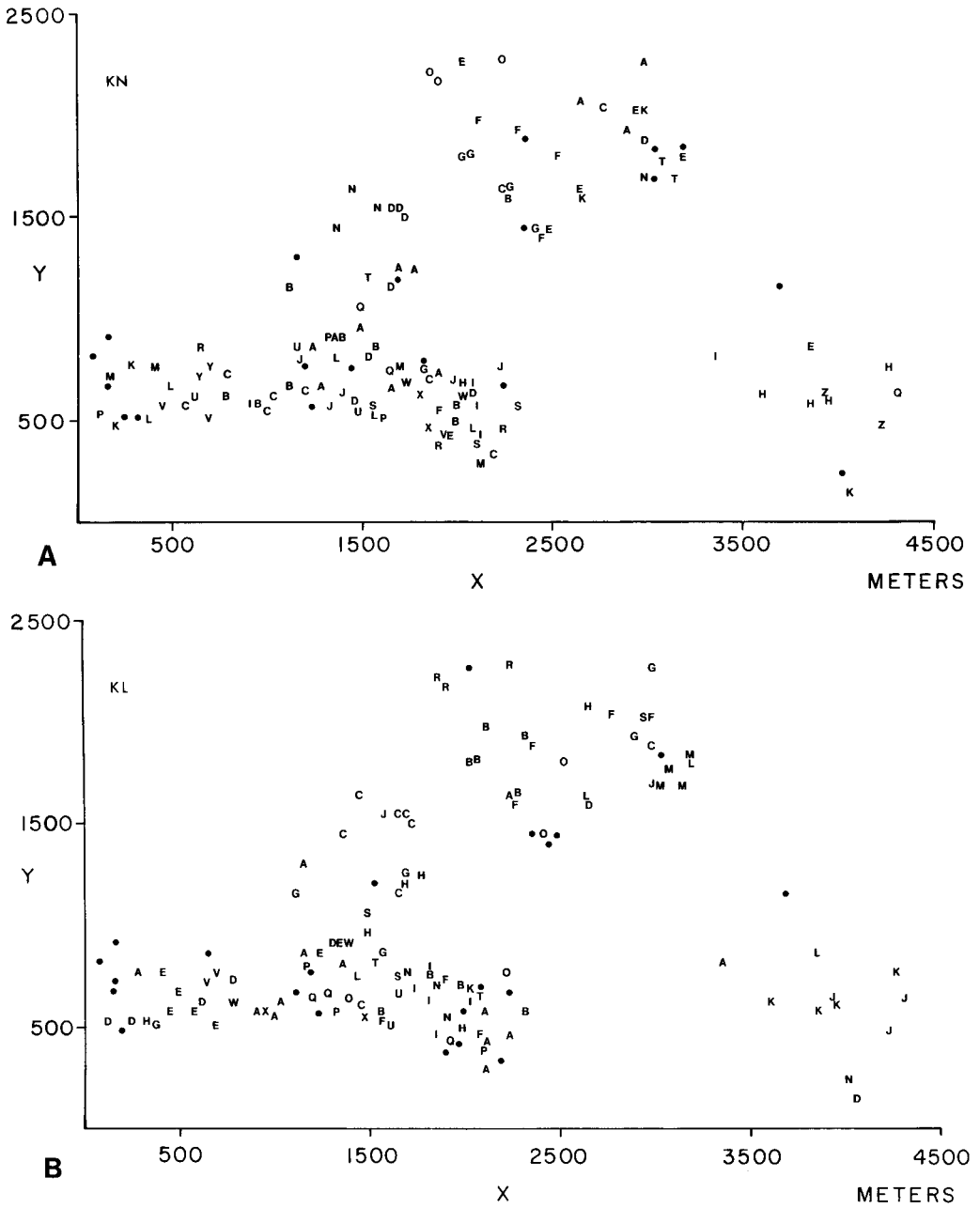
FIGURE 8.   Map of individuals in (A) KN and (B) KL song groups. Letters indicate song group affiliation; dots indicate individuals that were withheld from the K-means clustering processes. The X-axis roughly parallels the Pacific coastline.

the copying male gains an advantage in obtaining and maintaining a territory and/or in attracting a female. There are two versions of the deceptive mimicry hypothesis which differ in the adult song model for the postdispersal song learner (McGregor and Krebs 1984). In one version, the young male copies the songs of the previous owner of the territory that the young male is at-
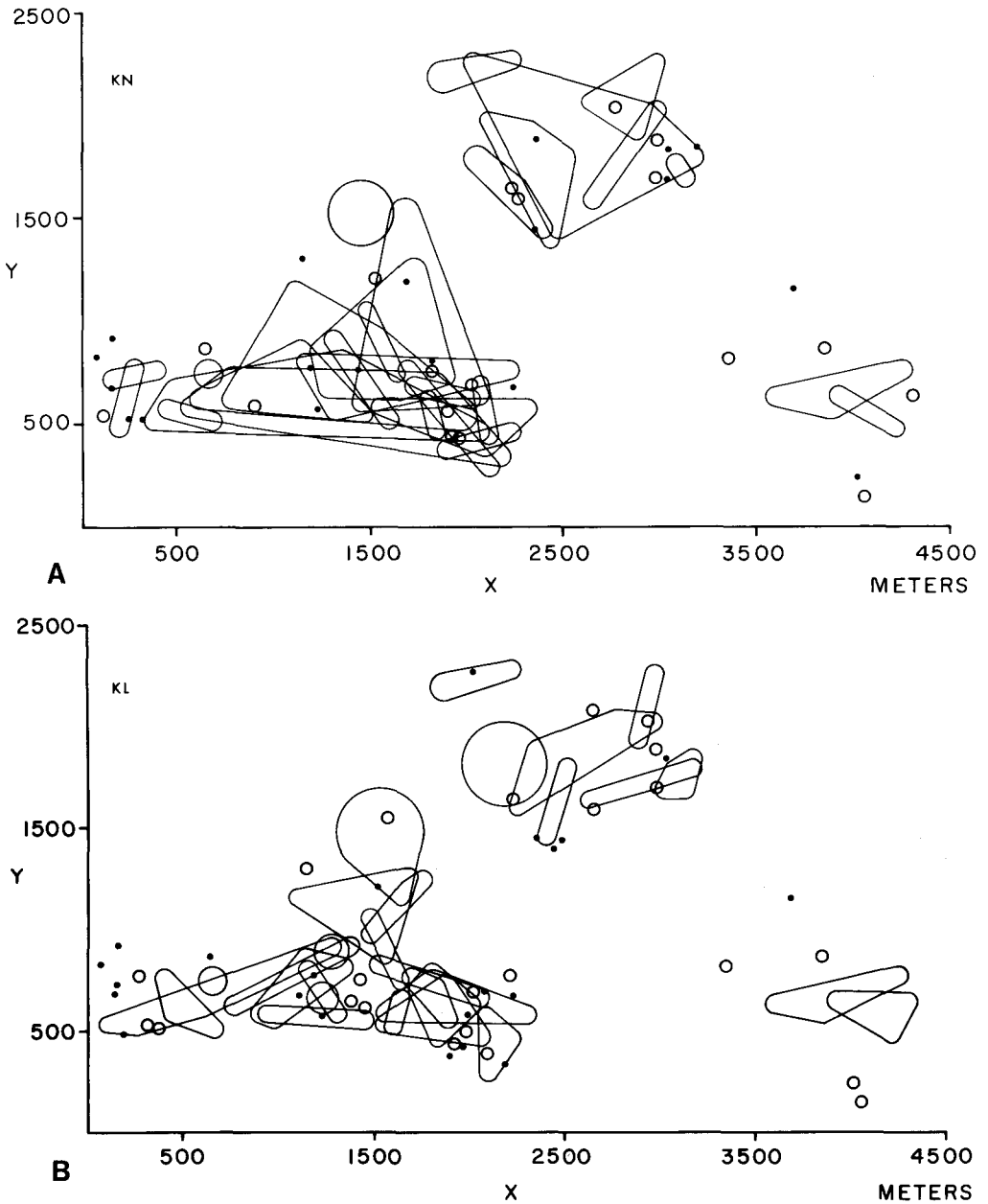
FIGURE 9.   Enclosure of spatial clusters of similar songs for (A) KN and (B) KL song groups. Dots indicate individuals that were withheld from the K-means clustering processes. Small circles indicate individuals that were spatially distant from others belonging to the same song group (see Fig. 8); these would include "satellite" males.

tempting to acquire (Payne 1981). In the second version, the young male copies the songs of older neighbors, thus conforming to the local social dialect (Payne 1981, 1982). In both cases, the young male gains by giving the deceptive impres-

sion of being an established male. Thus, post-dispersal song learning allows a young male to acquire an appropriate song wherever it settles.

Clearly, Thompson's (1970) expectation that territorial neighbors will have similar songs giv-

en postdispersal song learning is a prediction of the second version of the deceptive mimicry hypothesis (Payne 1982, McGregor and Krebs 1984). Using both univariate and multivariate analytical techniques, Trainer (1983) tested this prediction in a population of Nuttall's White-crowned Sparrows. She was unable to demonstrate that neighboring males had similar songs, and thus rejected this version of the deceptive mimicry hypothesis. Our analytical methods differed from Trainer's and we did not focus our analysis on neighboring males, but our findings are similar in that neighboring males in our study population often did not have similar songs (Figs. 8A, B). The pattern of microgeographic song variation we found was closer to that suggested by Thompson (1970) for predispersal song learning. Moreover, this conclusion is consistent with results from our laboratory study of song learning (Cunningham and Baker 1983) and field work on dispersal (Baker et al. 1982). Taken together, these studies suggest that song learning generally precedes dispersal in these populations (see also Marler 1970, Petrinovich 1985).

The microgeographic pattern of song variation reported here is similar to that reported by Payne (1978) for the Splendid Sunbird (*Nectarina coccinigaster*), in which birds near each other tended to have similar songs, but close neighbors sometimes had quite distinct songs; while in some cases males with the most similar songs were not each other's nearest neighbor. Likewise, Rich (1981) reported for the Sage Sparrow (*Amphispiza belli*) that song similarity was greatest between pairs of males within populations but that the songs of territorial neighbors were usually not the most similar. Hultsch and Todt (1981) reported that male European Nightingales (*Luscinia megarhynchos*), which have large vocal repertoires, shared fewer song types with very close and more distant neighbors than with neighbors at intermediate distances.

It is unclear to us what pattern of microgeographic song variation should result from postdispersal song learning where the mimic copies from the previous territory owner. It would seem that if there is a very high degree of conformity among the population for copying the songs of previous territory holders that the distribution of song types would tend to be perpetuated. That song distribution, however, would probably depend upon historical processes (such as colonization) and habitat distribution, and thus may be quite variable among populations and species.

It also appears that in some species postdispersal song learning may have evolved for reasons other than deceptive mimicry (McGregor and Krebs 1984). Thus, while we agree with Thompson (1970) and Trainer (1983) that the microgeographic distribution of song variation might provide some insight to the song learning process, the interpretation of these patterns should be made cautiously.

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LITERATURE CITED

BAKER, M. C. 1974. Genetic structure of two populations of White-crowned Sparrows with different song dialects. Condor 76:351–356.

BAKER, M. C. 1975. Song dialects and genetic differences in White-crowned Sparrows (*Zonotrichia leucophrys*). Evolution 29:226–241.

BAKER, M. C. 1981. Effective population size in a songbird: some possible implications. Heredity 46:209–218.

BAKER, M. C., AND M. A. CUNNINGHAM. 1985. The biology of bird song dialects. Behav. Brain Sci. 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., G. L. SHERMAN, T. C. THEIMER, AND D. C. BRADLEY. 1982. Population biology of White-crowned Sparrows: residence time and local movements of juveniles. Behav. Ecol. Sociobiol. 11:133–137.

BAKER, M. C., AND D. B. THOMPSON. 1985. Song dialects of White-crowned Sparrows: historical processes inferred from patterns of geographical variation. Condor 87:127–141.

BAPTISTA, L. F. 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). Univ. Calif. Publ. Zool. 105:1–52.

BAPTISTA, L. F., AND L. PETRINOVICH. 1984. Social interaction, sensitive phases and the song template hypothesis in the White-crowned Sparrow. Anim. Behav. 32:172–181.

BATESON, P.P.G. 1978. Sexual imprinting and optimal outbreeding. Nature 273:659–660.

BATESON, P.P.G. 1979. How do sensitive periods arise and what are they for? Anim. Behav. 27:470–486.

BATESON, P.P.G. 1980. Optimal outbreeding and the development of sexual preferences in Japanese quail. Z. Tierpsychol. 53:231–244.

CUNNINGHAM, M. A. 1985. Vocal learning in Nuttall's White-crowned Sparrow: deceptive mimicry or genetic identity? Ph.D.diss., Colorado State Univ., Fort Collins.

CUNNINGHAM, M. A., AND M. C. BAKER. 1983. Vocal learning in White-crowned Sparrows: sensitive phase and song dialects. Behav. Ecol. Sociobiol. 13:259–269.

DIXON, W. J., M. B. BROWN, L. ENGLEMAN, J. W. FRANE, M. A. HILL, R. I. JENNRICH, AND J. D. TOPOREK. 1981. BMDP statistical software, 1981 ed. Univ. Calif. Press, Los Angeles.

HOLLANDER, M., AND D. A. WOLFE. 1973. Nonparametric statistical methods. John Wiley & Sons, New York.

HULTSCH, H., AND D. TODT. 1981. Repertoire sharing and song-post distance in Nightingales (Luscinia megarhynchos B.). Behav. Ecol. Sociobiol. 8:183–188.

KROODSMA, D. E. 1978. Aspects of learning in the ontogeny of bird song: where, from whom, when, how many, which, and how accurately?, p. 215–230. In G. Burghardt and M. Beckoff [eds.], Ontogeny of behavior. Garland Publishing, New York.

KROODSMA, D. E. 1982. Learning and the ontogeny of sound signals in birds, p. 1–23. In D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds. Academic Press, New York.

KROODSMA, D. E., M. C. BAKER, L. F. BAPTISTA, AND L. PETRINOVICH. 1984. Vocal "dialects" in Nuttall's White-crowned Sparrow, p. 103–133. In R. F. Johnston [ed.], Current ornithology. Vol. 1. Plenum Publishing Co., New York.

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

MARLER, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. J. Comp. Physiol. Psychol. Monogr. 71:1–25.

MARLER, P., AND P. MUNDINGER. 1971. Vocal learning in birds, p. 389–450. In H. Moltz [ed.], Ontogeny of vertebrate behavior. Academic Press, New York.

MARLER, P., AND M. TAMURA. 1962. Song "dialects" in three populations of White-crowned Sparrows. Condor 64:368–377.

MARLER, P., AND M. TAMURA. 1964. Culturally transmitted patterns of vocal behavior in sparrows. Science 146:1483–1486.

McGREGOR, P. K., AND J. R. KREBS. 1984. Song learning and deceptive mimicry. Anim. Behav. 32:280–287.

MIELKE, P. W., JR. 1984. Meteorological applications of permutation techniques based on distance functions, p. 813–830. In P. R. Krishnaiah and P. K. Sen [eds.], Handbook of statistics. Vol. 4. Elsevier Science Publishers, Amsterdam.

MIELKE, P. W., JR. 1985. Geometric concerns pertaining to applications of statistical tests in the atmospheric sciences. J. Atmospheric Sci. 42:1209–1212.

MIELKE, P. W., JR. 1986. Non-metric statistical analyses: some metric alternatives. J. Statist. Plann. Inference 13:377–387.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the social sciences. 2nd ed. McGraw-Hill, New York.

NOTTEBOHM, F. 1969. The song of the Chingolo, Zonotrichia capensis, in Argentina: description and evaluation of a system of dialects. Condor 71:299–315.

NOTTEBOHM, F. 1972. The origins of vocal learning. Am. Nat. 106:116–140.

PAYNE, R. B. 1978. Microgeographic variation in songs of Splendid Sunbirds Nectarinia coccinigaster: population phenetics, habitats and song dialects. Behaviour 65:282–308.

PAYNE, R. B. 1981. Population structure and social behavior: models for testing the ecological significance of song dialects in birds, p. 108–120. In R. D. Alexander and D. W. Tinkle [eds.], Natural selection and social behavior. Chiron Press, New York.

PAYNE, R. B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in Indigo Buntings. Ecology 63:401–411.

PETRINOVICH, L. 1985. Factors influencing song development in the White-crowned Sparrow (Zonotrichia leucophrys). J. Comp. Psychol. 99:15–29.

RICH, T. 1981. Microgeographic variation in the song of the Sage Sparrow. Condor 83:113–119.

SHIELDS, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. State Univ. New York Press, Albany.

SHIELDS, W. M. 1983. Optimal inbreeding and the evolution of philopatry, p. 132–159. In I. R. Swingland and P. J. Greenwood [eds.], The ecology of animal movement. Oxford Univ. Press, London.

SLATER, P.J.B. 1983. Bird song learning: theme and variations, p. 475–499. In A. H. Brush and G. A. Clark, Jr. [eds.], Perspectives in ornithology. Cambridge Univ. Press, Cambridge.

SNEATH, P.H.A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco.

THOMPSON, W. L. 1970. Song variation in a population of Indigo Buntings. Auk 87:58–71.

TRAINER, J. M. 1983. Changes in song dialect distributions and microgeographic variation in song of White-crowned Sparrows (Zonotrichia leucophrys nuttalli). Auk 100:568–582.

WRIGHT, S. 1978. Evolution and the genetics of populations, Vol. 4: Variability within and among natural populations. Univ. Chicago Press, Chicago.

ZIMMERMAN, G. M., H. GOETZ, AND P. W. MIELKE, JR. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology 66:606–611.