

# SONG PATTERN VARIATION IN THE SAGE SPARROW (*AMPHISPIZA BELLI*): DIALECTS OR EPIPHENOMENA?<sup>1</sup>

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**ABSTRACT.**—I investigated variation in the songs of Sage Sparrows (*Amphispiza belli*) breeding in the northwestern Great Basin over a 3-yr period. Individuals sang a single song type, which did not change during the day, through the breeding season, or between years. Although different individuals and populations differed in song parameters such as duration, delivery rate, and notes and note types per song, these variations exhibited no overall patterns with respect to geography or habitat. Similarity matrices based upon the sequential arrangement of note types in songs were used to draw comparisons within and between populations. Within-population vocal similarity of individuals varied considerably, from populations in which most neighboring individuals sang similar or identical songs to situations in which most individuals sang quite different songs; in one population, song variation was arrayed in "neighborhoods" of 3–5 individuals sharing similar songs, which differed markedly from those of adjacent clusters of individuals.

Song variation between populations was significantly greater than that within populations. Some populations located close to one another shared many song elements and patterns, but other nearby populations were totally different and showed greater similarity with populations located some distance away. The degree of song similarity between populations was neither a simple function of the physical distance between the populations, nor was it related to the distribution of topographic barriers in this region. Populations with greater between-individual dissimilarity in song patterns were also more variable from one year to the next and occurred in habitats of lower vegetation stature and greater patchiness. Generally, however, the patterns of vocal variation within and between populations were unrelated to features of habitat structure, to the densities of Sage Sparrows or of other coexisting species, or to avian community attributes.

I suggest that Sage Sparrows may have a simple, single-song repertoire because the song serves simple functions, and selection favoring a more elaborate song may be absent. The variety of patterns of within- and between-population vocal similarity may be associated with differences in population turnover rates, song ontogeny, dominance relationships, and dispersal, all of which require documentation to establish the foundations of vocal variation in this system (and others). The variety of population patterns, however, argues against a simplistic categorization of this species as dialectal or nondialectal. Much of the variation that is expressed may be a consequence of chance events and represents "epiphenomena" that are random with respect to natural selection. Received 22 July 1981, accepted 10 November 1981.

THE songs of many bird species vary geographically. This variation may involve changes in the occurrence, structure, or sequencing of elements in songs, in the types of songs used by individuals, or in the size of the song repertoire of individuals and may be expressed within local populations, between populations, or over large geographical areas (Thielcke 1969, Baptista and King 1980, Krebs and

Kroodsma 1980). Confronted with such diversity, we attempt to discern some consistent pattern in the geographical variation of a species' vocalizations. In several species, song variation is expressed in local dialects—suites of neighboring individuals sing quite similar songs, which differ more or less abruptly from those of more distant individuals. Song variation within a given local population is thus low, and variation between different local populations may be substantial.

Unfortunately, "dialect" is defined some-

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times in terms of boundaries separating groups of individuals singing different songs, sometimes simply in terms of song-sharing among neighbors. Further, the spatial scale on which song variation is considered to represent a dialect pattern may vary over several orders of magnitude. Despite such imprecision, several alternative explanations of the origin or function of dialects have been proposed. Dialects may thus represent (1) epiphenomena of no adaptive or functional significance, resulting from historical events unique to different localities (e.g. founder effects); (2) adaptive features that enhance local genetic specialization of individuals in relation to habitat or other environmental features; (3) social adaptations, which act in male-male competition or in mate selection and promote assortative mating; (4) shared responses of individuals to acoustic limitations of the physical environment that may influence sound transmission and communication; or (5) artifacts of sampling procedures (Nottebohm 1972, Baker 1975, Payne 1981a).

Payne (1981a) proposes that one must frame such explanations as hypotheses yielding testable predictions in order to begin to sort out the various alternatives. Before one can pursue such hypothesis-testing, however, it is necessary to determine exactly how vocalizations vary in a given species. A bounded local dialect pattern is one possibility, but songs might also vary more or less continuously, both within and between populations—differences in vocalizations might be a roughly linear function of distance separating individuals (e.g. Bitterbaum and Baptista 1979). Alternatively, song variation might follow no discernible geographical pattern at all. Careful measurement and comparison of song variation within and between local populations of individuals are necessary to distinguish such alternative patterns and thus to determine whether tests of dialect hypotheses, or perhaps of some other hypotheses of geographical variation in song structuring, are appropriate for a given species. Here I describe and analyze the geographical patterns of song variation in a migratory temperate fringillid, the Sage Sparrow (*Amphispiza belli*), a species well-suited to a study of such variation (see King 1972).

Sage Sparrows are widely distributed as a breeding species throughout shrub deserts of the Great Basin, central and southern Califor-

nia, and northern Baja California. At least in the northern portion of this range, breeding densities vary directly with the ground coverage of big sagebrush (*Artemisia tridentata*), and habitats dominated by spinescent shrubs such as cottonthorn (*Tetradymia spinosa*) and greasewood (*Sarcobatus vermiculatus*) are generally avoided (Wiens and Rotenberry 1981). In areas of Oregon where we have studied their breeding biology intensively, populations do not completely saturate the available habitat with territories, the birds mate monogamously, and we have no evidence that any unmated birds or "floaters" are present in the area after breeding has begun. Birds in Oregon often rear but a single clutch, although some early-breeding individuals may complete two clutches if weather conditions are benign. Foraging by both sexes is concentrated within the area defined by the singing territory, but excursions well beyond the territory boundaries into areas occupied by other individuals are not infrequent (J. A. Wiens and J. T. Rotenberry, pers. obs.). Adult birds that have previously bred successfully in an area often return to the same general location the following season [as Rich (1980) also observed in Idaho]. Our intensive banding of nestlings, however, has produced no returns in subsequent years, despite careful searches of natal areas and their surroundings.

Males sing from the tops of shrubs within their territories from their arrival in early spring until after young are fledged. Singing tends to be interspersed with bouts of foraging (Rich 1980) and ceases during midday on hot days. During singing bouts, songs are repetitively uttered at 10–20-s intervals.

#### METHODS

During the breeding seasons of 1977–1979, I recorded the vocalizations of 252 individual Sage Sparrows at 15 locations in the shrubsteppe of southeastern Oregon and northern Nevada (Table 1, Fig. 1). In 1977 I recorded a minimum of 10 songs for each individual; analysis of these records indicated little within-individual variation in song features (see below). In 1978 and 1979 individuals were monitored until at least two good-quality recordings were obtained. I recorded the individuals that I encountered while walking along a measured line transect. This allowed me to map the locations of individuals, ensuring that the same individual was not recorded more than once during a given year. All recording was done during a single morning at each site, and all sites were visited during the peak of the breeding

season, in the latter half of June and early July. Color-marked individuals were available for study at the Cabin Lake locations. Analysis of the songs of these birds permitted a determination of the daily, seasonal, and annual stability of song structure of individuals.

Songs were recorded on tape cassettes using a Sony TC-56 recorder, a Sony dynamic microphone, and a 37-cm diameter parabolic reflector. Most birds were recorded from a distance of 5–25 m under calm conditions.

*Analysis of song patterns.*—Sonograms of the song of each individual recorded were produced using a Kay Elemetrics 6061 B Sona-Graph with the wide-band filter setting. These sonograms were then examined in detail to determine several quantitative parameters of individual songs, the note types or elements present in the populations, and the patterns of within- and between-population similarity in vocal structure. Here I define "note type" or "element" as a continuous, discrete tracing on the sonogram; tight series of traces such as buzzes are considered single note types (see Fig. 2). A "song pattern" or "song type" is the particular sequence of note types that comprises the song of an individual (Bradley 1977).

Gauging the patterns of similarities and differences in songs among populations, however, requires something other than a subjective, qualitative comparison of how songs sound. Recent applications of multivariate statistical techniques to song analysis (e.g. Payne 1978, Sparling and Williams 1978, Payne and Budde 1979, Martindale 1980) provide a means of generating objective, quantitative measures of song-pattern relationships. I followed a procedure developed by Bradley and Bradley (in press). First, a lexicon of the 41 discrete and readily identifiable note types present in the songs of the Sage Sparrows that I recorded was developed [Rich (1981) detected 40 different note types in songs of the 50 individuals he recorded in southeastern Idaho]. These note types were defined subjectively on the basis of their form and time-frequency durations after a careful study of the sonograms of all individuals, and their discreteness was confirmed by measurements of time-frequency characteristics on a subsample of the most similar-appearing notes. Each of the types was assigned a two-unit alphabetic code, the first letter indicating the general category of the note type (e.g. downslur, low-frequency buzz, trill), the second letter a specific variant within the general category that was usually distinguished by time and/or frequency characteristics. The note types were copied from sonograms onto plastic overlays, which could then be used to assign each note of an individual's song to the appropriate coded category. In this manner, the song of each of the 252 individuals was translated into a code sequence reflecting the sequence of note types within the song (see Fig. 2).

Next, the sonogram traces of each note type were examined visually, and the notes grouped according to their structural similarity. In this manner, a dendrogram defining the hierarchical patterns of similarity among the note types was derived and used to build a matrix of inter-note similarities. This step is important to the analysis of song similarities, in that it allows songs that differ by virtue of having similar note types substituted for one another to be assigned a higher degree of similarity than songs with an equal number of note differences but involving quite different note types.

Given this matrix of inter-note similarities (or distances) and the coded sequences of notes for the song patterns of the 252 individuals, a sequence-comparison algorithm was then used to generate a matrix of the overall similarities of the songs (the inter-song distances). This procedure optimizes the comparison of two sequences of note types by placing greatest emphasis upon notes that occur in the same relative position in the song and by also recognizing the contribution to intersong distance of identical sets of note sequences that may occur in different positions in the compared songs. This analysis thus is more detailed than that of Rich (1981), who assessed the similarity of Sage Sparrow vocalizations by determining the proportion of shared note types or note-type couplets. Additional details are provided by Bradley and Bradley (in press); details of the FORTRAN programs that perform these analyses are available from David Bradley, Data Processing Department, California State University, Long Beach, California 90840.

The  $251 \times 251/2$  matrix of intersong distances thus obtained may be analyzed in a variety of ways. I considered subsets of this matrix that contained the individuals recorded at a location in a given year and over all years combined. These submatrices were then analyzed using cluster analysis (based on average linkage between merged groups; see Anderberg 1973) to discern the relationships between local populations, between years, or between individuals occupying a location.

A possible bias in the analyses employing data combined over the 3 yr of this study should be noted. Because few of the birds I recorded were banded, individuals could not be identified from one year to the next. Thus, if site fidelity and survival of birds in a given location were high, some individuals might inadvertently have been recorded in successive years. Inclusion of such individuals in the samples would increase the degree of overall vocal similarity. Unfortunately, there is no way to assess the importance of this bias, or to control for it, without intensive banding. This is a problem that plagues most multi-year studies of vocalizations.

*Other variables.*—Because the recordings were made in conjunction with ecological studies, several measures of the bird communities and habitat fea-

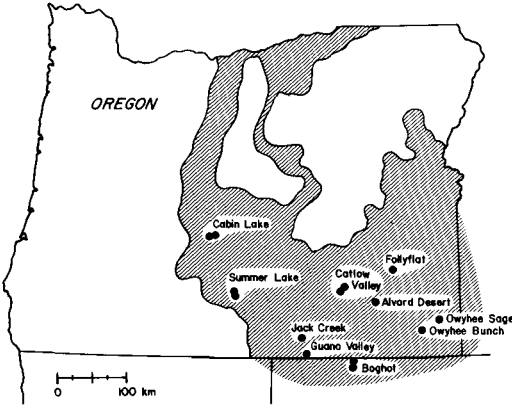


Fig. 1. Locations of the sites at which Sage Sparrow vocalizations were recorded (see Table 1). The shaded region represents the extent of shrub desert and shrubsteppe in Oregon. Sage Sparrows are found throughout this region.

tures associated with the local populations of Sage Sparrows were available for analysis. These provide some indication of the ecological context in which the patterns of within- and between-population intersong distances are expressed. Bird populations were censused along 610-m linear transects at each location following the procedures outlined by Emlen (1971, 1977). These surveys yielded estimates of the population density of each of the bird species encountered, from which avian community measures could be derived. Here I considered the densities of Sage Sparrows and of their congeners, Black-throated Sparrows (*Aphispiza bilineata*), the total density of all species combined, the number of bird species encountered, and bird species diversity (measured as  $N = 1/\sum p_i^2$ , where  $p_i$  is the proportion of total density contributed by the  $i^{\text{th}}$  species in the sample). In addition, the coefficients of variation (CV) of Sage

Sparrow densities and of total bird densities for the different yearly samples taken at a location were used as a coarse approximation of the stability or turnover of the populations or communities.

Features of habitat (primarily vegetation) configuration were sampled following procedures described in Wiens and Rotenberry (1981). For the present analysis, I used the following measures:

(1) Sagebrush coverage—the proportion of 100 point samples taken at a location at which sagebrush was encountered.

(2) Shrub species diversity—the diversity of shrub species present at a location, measured using the above equation, with  $p_i$  indexing the proportion of total shrub coverage contributed by the  $i^{\text{th}}$  shrub species.

(3) Physiognomic coverage diversity (PCD)—the diversity of coverage of plant structural types, with  $p_i$  now given as the proportional coverage of the  $i^{\text{th}}$  structural type (e.g. shrub, grass, forb).

(4) MAXHGT—the average highest 10-cm interval in which vegetation contacted a thin rod (the point sampler) passed vertically through the vegetation, taken over 100 samples.

(5) TOTHITS—the mean total number of contacts of vegetation with the point sampler, over 100 samples; this and MAXHGT index variation in the vertical structuring or heterogeneity of shrubsteppe vegetation (Wiens and Rotenberry 1981).

(6) CVMAXHGT—the coefficient of variation of the MAXHGT measure among the 100 sample points.

(7) CVTOTHITS—the coefficient of variation of TOTHITS; as the sampling points were arrayed over horizontal space within a transect area, these two CV measures index horizontal heterogeneity or patchiness of habitat structure.

(8) PD-30—a diversity measure using the proportions of the total vegetation contacts on the vertical point sample occurring in the 0–10-cm, 10–30-cm, and >30-cm height intervals as the  $p_i$  values; this provided an index of vertical heterogeneity or patchiness.

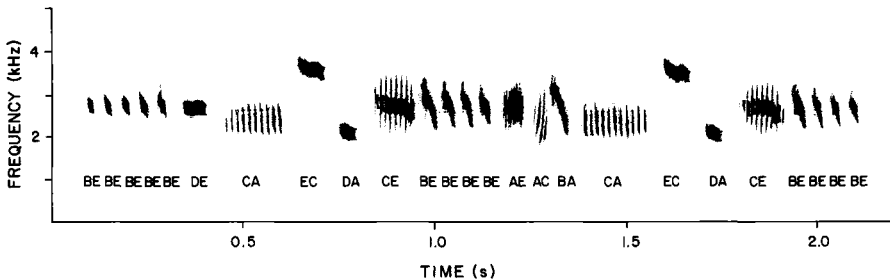


Fig. 2. Sonogram of a Sage Sparrow recorded at the Cabin Lake Sage plot, indicating the way in which note types were differentiated and coded for the analyses of this study.

TABLE 1. Attributes of the songs of Sage Sparrows at several locations (see Fig. 1). Yearly samples are combined.

Site	n (individ.)	Years sam- pled	Duration (s)		Notes/song		Song rate <sup>a</sup>	Note types/ individual		Redun- dancy <sup>b</sup>
			$\bar{x}$	SD	$\bar{x}$	SD		$\bar{x}$	SD	
Cabin Lake Sage	15	3	1.49	0.11	17.5	1.64	11.7	9.4	0.63	1.86
Cabin Lake M1	18	3	1.69	0.16	21.1	2.63	12.5	10.9	0.96	1.94
Summer Lake Sage	10	3	1.62	0.23	15.2	3.33	9.4	7.9	0.57	1.92
Summer Lake Grease	3	1	1.50	0.00	14.0	0.00	9.3	11.0	0.00	1.27
Jack Creek	5	1	1.72	0.25	18.2	2.28	10.6	8.6	0.55	2.12
Guano Valley	42	3	1.72	0.22	17.6	2.38	10.2	10.6	1.35	1.66
Boghot Sage	23	3	1.73	0.23	16.6	2.71	9.6	9.7	1.40	1.71
Boghot Grease	7	3	1.77	0.21	18.0	3.27	10.2	7.4	1.90	2.43
Catlow Valley North	16	3	1.82	0.15	17.2	2.23	9.4	8.7	0.77	1.98
Catlow Valley South	10	2	1.63	0.21	18.3	3.92	11.2	9.0	1.25	2.03
Alvord Desert	27	3	1.68	0.22	15.5	2.49	9.2	8.6	1.22	1.80
Follyflat	28	3	1.62	0.20	13.5	2.06	8.3	9.2	0.83	1.47
Owyhee Bunch	9	2	1.57	0.07	17.1	0.33	10.9	9.7	1.00	1.76
Owyhee Sage	39	3	1.68	0.18	15.8	1.44	9.4	9.7	1.28	1.63

<sup>a</sup>  $\bar{x}$  notes per second, calculated as the  $\bar{x}$  notes/song  $\div$   $\bar{x}$  song duration.

<sup>b</sup>  $\bar{x}$  notes per song  $\div$   $\bar{x}$  note types/individual.

## RESULTS

### INDIVIDUAL SONG STABILITY

Any attempt to determine the patterns of song similarity within or between populations is facilitated if the song patterns of individual birds do not change through time. To examine the stability of individual Sage Sparrow song patterns, I recorded several color-banded individuals at the Cabin Lake sites at different times of day, on different days through the breeding cycle, and in successive years. Comparisons of the sonograms of these individuals revealed no detectable changes through time. These were birds that returned to roughly the same location to breed in successive years, and there is no way to determine whether the song pattern of an individual might change if it established residence in a population of birds singing quite different song patterns, as may occur in saddlebacks (*Philesturnus carunculatus*, Jenkins 1978) or Village Indigobirds (*Vidua chalybeata*, Payne 1973). Rich (1980, 1981), however, also observed annual stability in the song patterns of three unmarked Sage Sparrows in an Idaho population. Apparently, then, the song pattern of an individual Sage Sparrow, once formed, is stable through time.

Some birds did vary their song pattern by occasionally adding 1–4 notes at the end (see also Rich 1980, 1981), or, less often, 1–2 notes

at the beginning. These variations were infrequent, however, and did not affect the structure of the "core" of the song pattern. The songs used in the following analyses lacked such "extra" notes.

To conduct population analyses of vocal patterns, it is also necessary to establish whether or not individuals sing more than a single pattern. Sage Sparrows apparently do not. None of the individuals that I recorded sang more than one song type, and during a decade of research on Sage Sparrows in central Oregon I have heard only one individual sing more than a single song pattern. Likewise, the birds that Rich (1981) studied sang a single song type per male.

### SONG PARAMETERS

Before we examine variation in Sage Sparrow song patterns, variations in several basic parameters of the songs should be described (Table 1). The mean duration of songs varied from about 1.5 to 1.8 s. Rich (1981) reported an overall mean song duration of 1.77 s for 50 birds from 10 locations in southeastern Idaho. There were no significant differences among the means of the populations I studied, nor was any systematic pattern of geographic variation apparent when the values were mapped by site location. The mean number of notes per song varied from 13.5 to 21.1. Statistical dif-

TABLE 2. Mean intersong distance measures among the individual Sage Sparrows sampled at each site in 1977, 1978, 1979, and for the years combined. Values of 0.000 indicate identity in song patterns; values of 1.000 indicate maximum dissimilarity of song patterns. Sample sizes are given in parentheses.

Site	Year			
	1977	1978	1979	Combined
Cabin Lake Sage	0.173 (8)	0.547 (3)	0.354 (4)	0.316 (15)
Cabin Lake M1	0.274 (7)	0.207 (4)	0.148 (6)	0.224 (17)
Summer Lake Sage	0.000 (1)	0.000 (2)	0.326 (7)	0.303 (10)
Summer Lake Grease	—	0.000 (3)	—	0.000 (3)
Jack Creek	0.337 (5)	—	—	0.337 (5)
Guano Valley	0.365 (11)	0.409 (13)	0.357 (18)	0.394 (42)
Boghot Sage	0.414 (3)	0.383 (6)	0.376 (14)	0.397 (23)
Boghot Grease	0.572 (3)	0.637 (2)	0.501 (2)	0.515 (7)
Catlow Valley North	0.361 (7)	0.326 (7)	0.512 (2)	0.356 (16)
Catlow Valley South	—	0.331 (4)	0.224 (6)	0.386 (10)
Alvord Desert	0.247 (7)	0.397 (9)	0.347 (11)	0.380 (27)
Follyflat	0.154 (9)	0.335 (10)	0.168 (9)	0.251 (28)
Owyhee Bunch	—	0.004 (3)	0.197 (6)	0.199 (9)
Owyhee Sage	0.310 (9)	0.235 (13)	0.265 (17)	0.273 (39)

ferences in this parameter were apparent only between the Cabin Lake M1 plot and the Grease plot at Summer Lake and between Cabin Lake M1 and Follyflat ( $P < 0.05$ ,  $t$ -test). Given the large number of comparisons in Table 1, it is possible that such statistical correlations are spurious (Type 1 error). At most plots, there was a moderate amount of variation between individuals in these song parameters. No geographic pattern in the variations in notes/song could be discerned. The mean number of notes uttered per second (notes/song  $\div$  song duration) also varied considerably among the populations (8.3–12.5 notes/s), but none of the values differed significantly from any other, and there was no discernible geographic pattern to the variation.

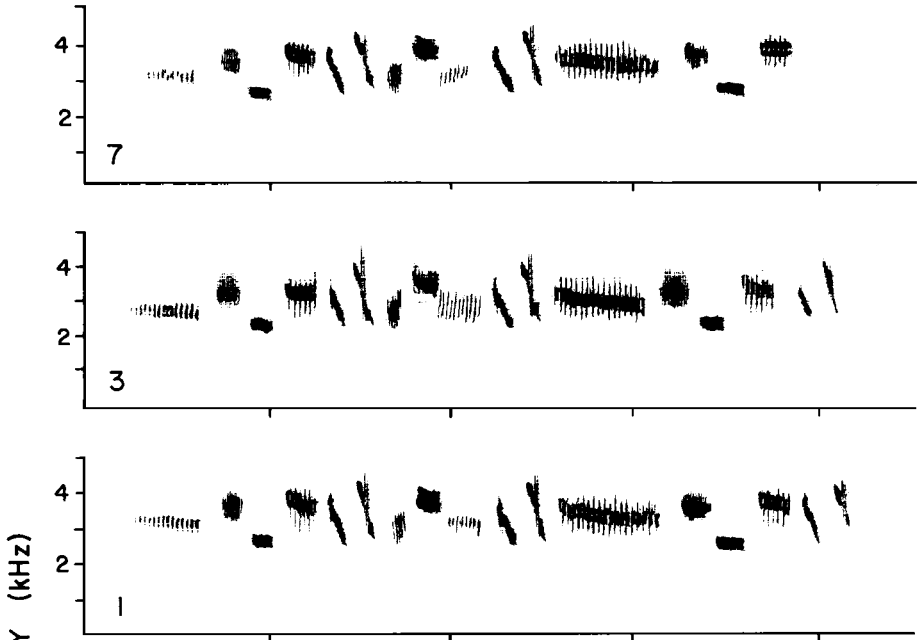
Variations in the number of different note types in the songs of individuals at the different plots are important insofar as they may influence the inter-song similarity patterns. The mean "note-repertoire" values ranged from 7.4 at the Boghot Grease site to 11.0 at the Summer Lake Grease plot; the only significant difference between values, however, was for those at Summer Lake Sage (7.9) and Cabin Lake M1 (10.9) ( $P < 0.05$ ). The size of the note repertoire of birds at a location bears no detectable relationship to the total number of notes contained in individual songs. Thus, variations in vocal richness among these locations are not simply a consequence of increasing the number of notes in the song. This relationship can

be expressed in a redundancy measure (see Table 1), which indexes the degree of repetition of note types within individual songs. Mean values of this parameter ranged from 1.27 to 2.43.

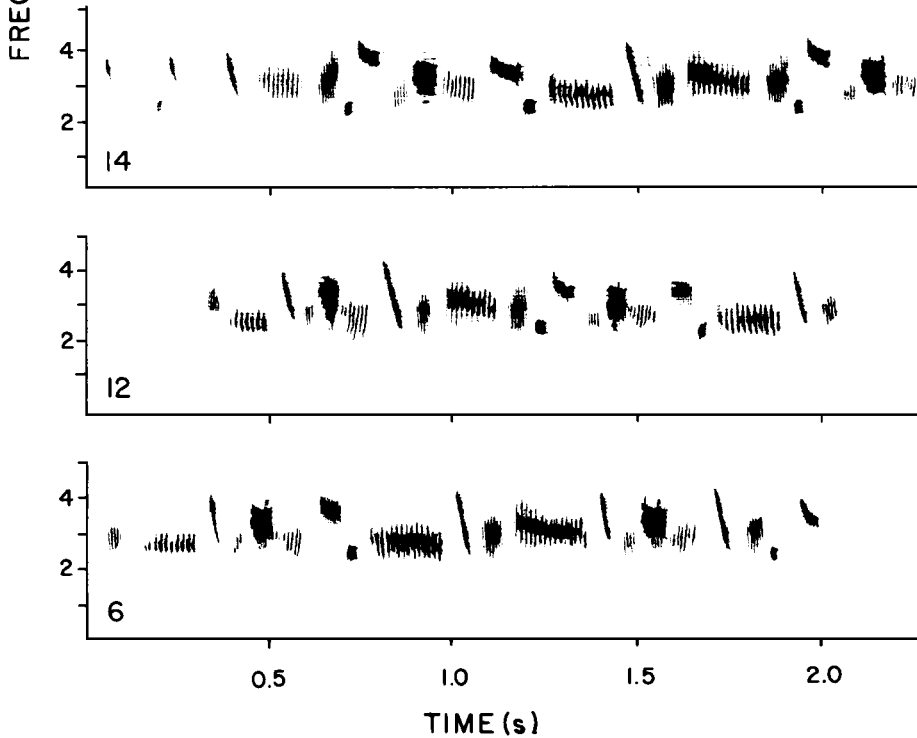
#### WITHIN-POPULATION VARIATION

One of the features that differentiates the hypotheses stated in the introduction is the amount and pattern of between-individual variation in songs within local populations. True dialects should be evidenced by a high degree of similarity among locally co-occurring birds. Considerable and continuous variation among individuals, on the other hand, indicates that such a dialect pattern is absent or quite weak. To determine the patterns of song variation present in each population, intersong distances were calculated among all individuals in the population, both separately for each year and for all years combined. The average intersong distance calculated from the distance matrix for all individuals in the population is thus a single measure of the within-population song-structure variation. These values (Table 2) varied considerably, from total identity in the song patterns of the individuals sampled (distance = 0.000) to substantial individual variation (0.637, Boghot Grease 1978). Some sample sizes are regrettably small, however, and a better impression of the extent of within-population variation can be obtained from the distance measures for the years combined.

A. FOLLYFLAT 1979



B. BOGHOT SAGE 1979



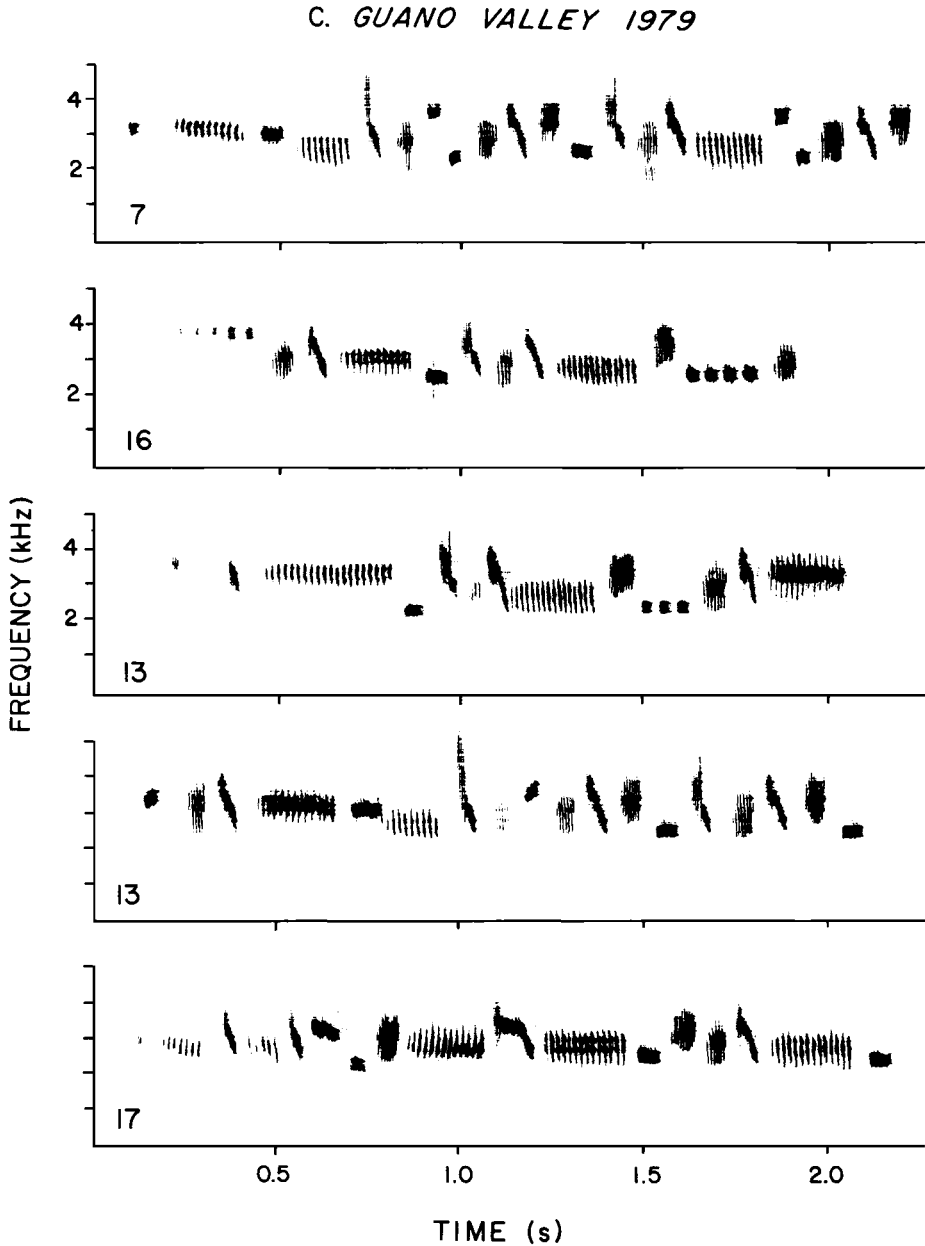


Fig. 3. Representative sonograms of the vocalizations of individuals at the Follyflat site (A), the Boghot Sage location (B), and Guano Valley (C). Numbers are keyed to the individuals represented in Fig. 4.

These ranged from 0.199 (Owyhee Bunch; the Summer Lake Grease site = 0.000, but there  $n =$  only 3) to 0.515 (Boghot Grease). It is obvious that the degree of song-pattern similarity among the individuals within a local population differs considerably among populations.

The patterns of within-population song distances may be explored in greater detail by examining three specific populations, each of which exhibits a different pattern from the others.

*Follyflat 1979.*—Sonograms for three of the



nine individuals recorded at Follyflat in 1979 are shown in Fig. 3A. Similarities in the details of note structure and note-type sequences are obvious. For this population, the mean intersong distance among all individuals was 0.168. The cluster analysis dendrogram based on individual intersong distances for this population (Fig. 4A) indicates that the songs of 6 of the 9 individuals were identical, with the remaining 3 differing moderately from these, and from each other. Because singing individuals were sampled along a measured transect, the approximate positions of each individual recorded in the population could be mapped. This permits a comparison of the song distance separating individuals (as graphed in the cluster diagram) and the physical distance separating their activity areas. Two features of these maps should be noted: (1) The mapped areas do *not* depict breeding territories, which were not determined, but rather approximate areas of activity for the individuals during the short period of my observations. Intensive studies elsewhere, however, indicate that singing Sage Sparrows tend to remain within a limited area that corresponds closely with their territory. (2) The spaces between activity areas on the maps are real, and indicate areas unoccupied by singing males during the period of my observations. Our intensive studies indicate that such a pattern of territory dispersion is typical, as Sage Sparrows often appear not to saturate available breeding habitat fully (Wiens 1981).

Examination of the mapped positions of the Follyflat individuals (Fig. 4A) indicates that two of the three individuals with nonidentical songs (individuals 8 and 9) were separated from the main "cluster" of birds, but another (bird 2) was a close neighbor of an individual that shared its song pattern with the remaining birds. Birds at Follyflat, especially those located close together, sang identical or similar songs; this pattern also emerged from an analysis of the 1977 and 1978 records from Follyflat.

*Boghot Sage 1979.*—Even a cursory examination of the sonograms of individuals recorded at the Boghot Sage plot (Fig. 3B) reveals substantial differences in the occurrence and positioning of note types within the songs. Overall, the mean intersong distance among individuals in this population was 0.376, substantially greater than that at Follyflat. The dendrogram derived from the cluster analysis

of these intersong distances (Fig. 4B) exhibits a more or less steadily increasing dissimilarity among individuals from the top to the bottom of the dendrogram, with few major discontinuities between clusters. In other words, here the songs of individuals generally differed from one another substantially, and the within-population variation in song structure was roughly continuous. A close comparison of areas of these individuals (Fig. 4B) with their positions on the dendrogram indicates that, in general, song dissimilarity increased with increasing distance between individuals. The birds with the most similar songs (birds 8 and 10) occurred together at one end of the transect, while birds at the opposite end of the transect (birds 2, 3, and 4 and birds 1 and 14) were the last to enter the stepwise clustering algorithm.

*Guano Valley 1979.*—Another pattern of within-population variation in song structuring was exhibited at the Guano Valley site. The dendrogram based upon intersong distances among individuals (Fig. 4C) reveals distinct clusters of individuals, in contrast to the more or less gradual clustering exhibited by the Boghot Sage birds. Groups of 2–7 individuals with similar song patterns are evident, but the groups themselves differ substantially. By arbitrarily adopting an intersong dissimilarity level of greater than 0.3 (Fig. 4C), five distinctive clusters of song-pattern types are defined. Sonograms of representatives of these five song patterns are shown in Fig. 3C. Each song-pattern type is associated with a group of individuals that cluster together on the dendrogram, and the mapping of activity locations (Fig. 4C) indicates that these individuals generally were neighbors in physical space as well. The only exceptions were birds 8, 9, and 16, which cluster together but which did not occupy contiguous activity spaces. The mean intersong distance for the Guano Valley population was 0.357, so the overall variation in this population was about the same as that as Boghot Sage. The mean intersong distance *within* the five groups, however, was 0.122, that between the groups 0.428. Here, then, distinctive song types are arrayed in "neighborhoods," with groups of contiguous individuals singing closely similar songs that are distinctly different from the songs of individuals within other groups, even though the groups themselves are usually contiguous.

Linear regressions of song dissimilarity

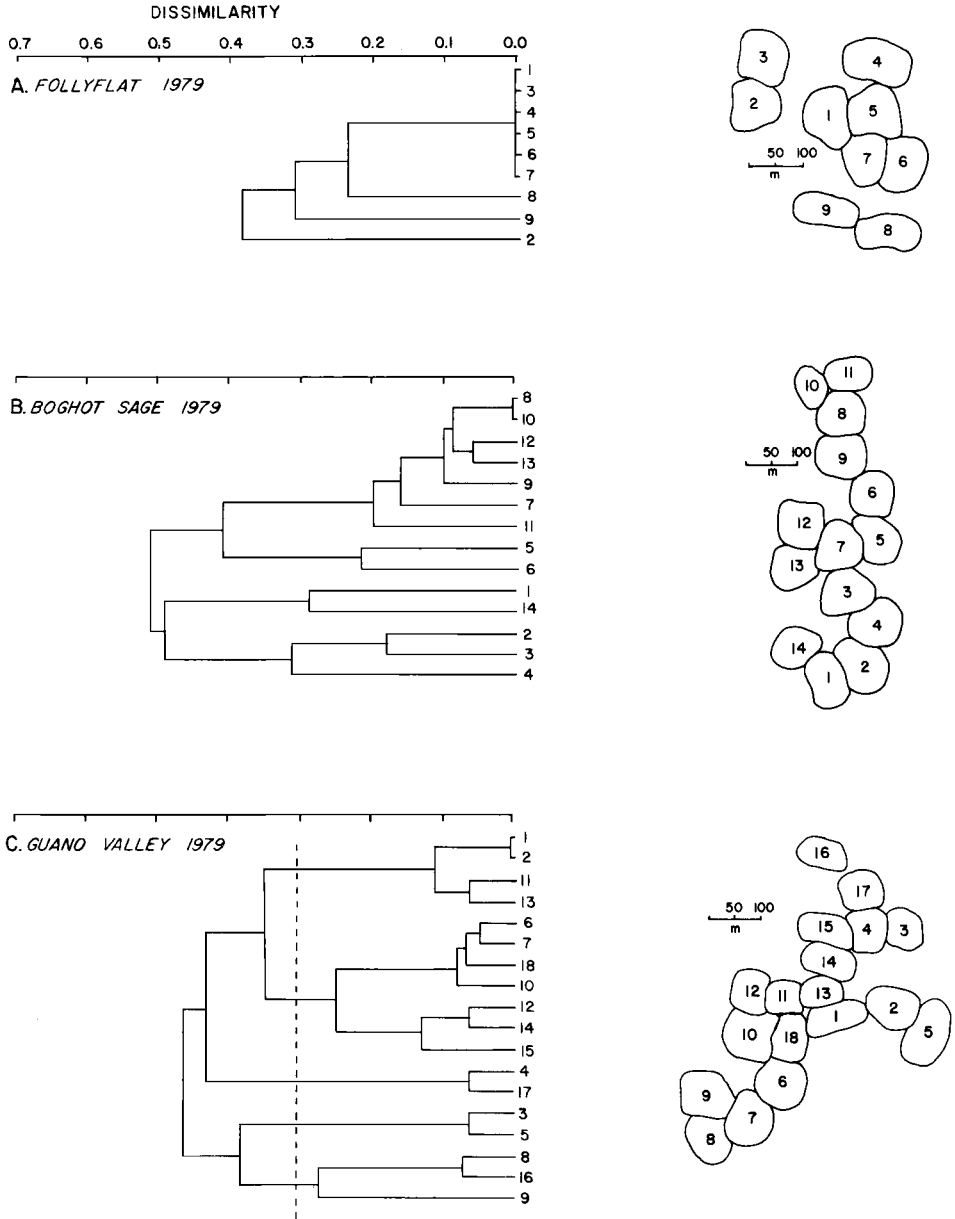


Fig. 4. Left: dendrograms of individual Sage Sparrows based upon a cluster analysis of their vocal dissimilarity (or intersong distance), for Follyflat (A), Boghot Sage (B), and Guano Valley (C). Right: mappings of the locations of the individuals recorded at each site and included in the dendrogram. Note that (a) these do not represent "defended-area" territories, but the general areas of activity of recorded birds during one morning; and (b) the gaps within the matrix of occupied areas represent places in which no birds were present, while areas beyond the set of mapped areas were occupied by other birds that were not recorded.

against the distance between individual territories at these locations suggest a tendency for more widely separated birds to differ more in their song patterns than do close neighbors

(Follyflat:  $n = 35$ ,  $r^2 = 0.117$ ,  $F = 4.51$ ,  $P < 0.05$ ; Boghot Sage:  $n = 90$ ,  $r^2 = 0.143$ ,  $F = 14.91$ ,  $P < 0.001$ ; Guano Valley:  $n = 152$ ,  $r^2 = 0.142$ ,  $F = 25.13$ ,  $P < 0.001$ ). This statistical

TABLE 3. Mean intersong distance measures between years, for successive years and between 1977 and 1979.

Site	1977– 78	1978– 79	1977– 79
Cabin Lake Sage	0.278	0.383	0.432
Cabin Lake M1	0.241	0.210	0.228
Summer Lake Sage	0.143	0.319	0.307
Guano Valley	0.406	0.398	0.412
Boghot Sage	0.386	0.431	0.383
Boghot Grease	0.478	0.480	0.533
Catlow Valley North	0.352	0.399	0.356
Alvord Desert	0.381	0.372	0.444
Follyflat	0.277	0.306	0.203
Owyhee Sage	0.300	0.251	0.301

analysis is not entirely appropriate, however, as each territory is involved in several comparisons, and thus the data points are not independent. Further, the slopes of these regressions (0.0016, 0.0012, 0.0010, respectively) are so shallow that the relationships, albeit significant (perhaps), are quite weak. In any event, it is apparent from Fig. 4 that the relationship between spatial location of individuals and song distance is patterned in important ways that are not revealed by simple linear relationships. The three populations reveal different internal patterns of vocal similarity among individuals, incorporating in different populations of a single species Lemon's (1975) "low conformity" and "high conformity" categories (which were developed as *species* categorizations), as well as intermediate states. Sage Sparrows thus defy a simple categorization of the form of their within-population vocal structuring.

#### BETWEEN-YEAR VARIATION

Given that a substantial variety in vocal patterns is expressed by different individuals within populations in a single year, one might expect additional between-year variation, due to the annual flux or turnover of individuals in local populations. In particular, we might predict that populations exhibiting substantial within-population variation in vocal patterns might also vary substantially from one year to the next and that the variety of songs represented in a population should increase with time, as more turnover occurs.

To examine such between-year patterns, in-

tersong distances were derived between the songs of individuals recorded at the same location in successive years. Overall, the average between-year song distance ( $\bar{x} = 0.348$ ,  $SD = 0.092$ ,  $n = 23$ ) was somewhat greater than the average within-year song distance ( $\bar{x} = 0.293$ ,  $SD = 0.171$ ,  $n = 25$ ), although not significantly so. Within-population intersong distances were highly correlated with between-year song distances ( $r = 0.89$ ,  $P < 0.001$ ); populations with greater between-individual variation in songs do indeed exhibit greater turnover or difference in songs between years. Given the stability of an individual's song, the foregoing suggests that such populations may be characterized by lower survival and/or site fidelity. Only two populations (Alvord Desert and Cabin Lake Sage), however, exhibited any tendency for the songs recorded in 1977 and 1979 to be more dissimilar from those recorded in successive years (1977–1978 and 1978–1979; Table 3). Neither of these populations was characterized by unusually large within-population vocal variety (Table 2). There is thus no evidence of any tendency for song types represented in a population to become more diverse with time. The basic configurations of within-population song variation, such as those at Follyflat, Boghot Sage, and Guano Valley discussed above, remained unchanged between years.

Another indication of the relative magnitude of between-year differences in song patterns within populations is provided by a cluster analysis in which each sample was the set of individuals recorded at a given location in a given year (Fig. 5). With one exception (Catlow Valley South), the initial clustering of samples is of different years at the same location. Thus, the individuals present at a given location from year to year generally sang songs more similar to one another than to those in populations at different locations in any year.

#### BETWEEN-LOCATION VARIATION

Because songs were analyzed from populations that were located in the same region, patterns of regional geographic variation in vocalization structure can also be examined. Overall, the mean between-population song distance (0.508) was significantly greater than the mean within-population song distance (0.305;  $P < 0.01$ ). Thus, although song patterns varied among individuals at a given lo-

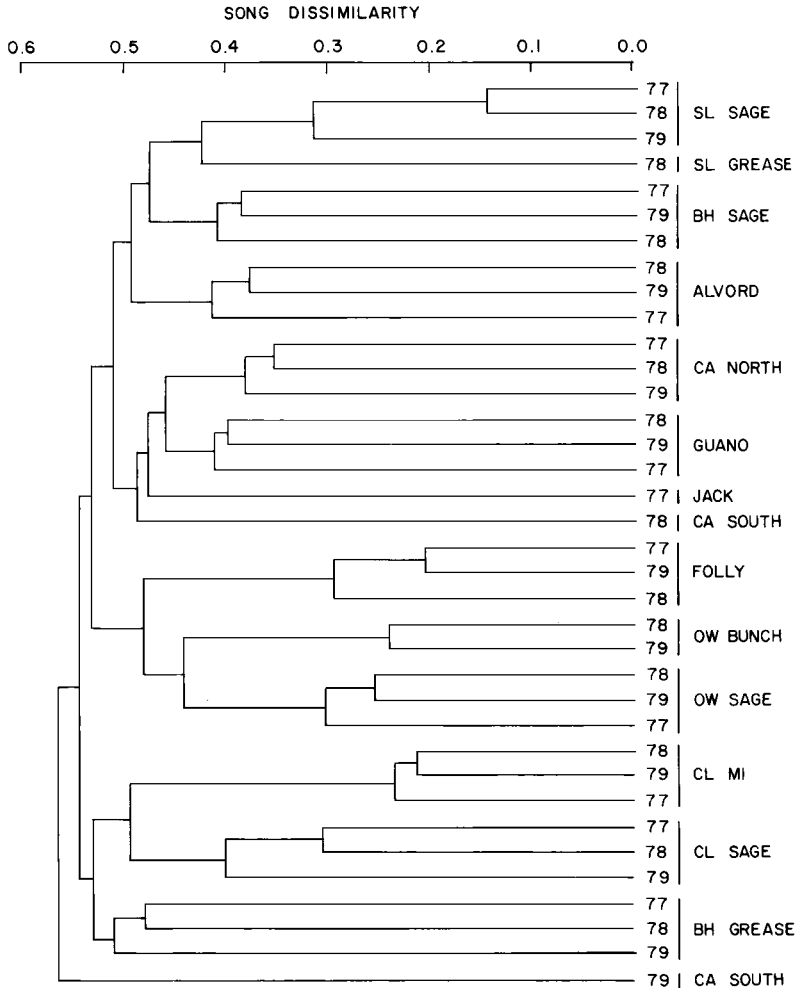


Fig. 5. A dendrogram based upon a cluster analysis of population intersong distances. For this analysis, the assemblage of individuals recorded at a location in a given year was considered a population, and between-population song distances or dissimilarity values were derived by comparing the individuals within each population with those in the other population.

cation, the songs of individuals at other locations were, on average, more distinct. This is also apparent from Fig. 5; different locations cluster together only after a song dissimilarity value of 0.4 has been exceeded.

If vocalization patterns vary more or less continuously over a large area (as might be expected if local populations were continually exchanging individuals via dispersal, in a "stepping-stone" fashion), we would predict that the average song dissimilarity between populations would increase with increasing physical distance between them. The relation-

ship between these variables (Fig. 6) displays considerable scatter, although a general trend that accords with our expectations is statistically significant ( $n = 90, r^2 = 0.111, F = 11.06, P < 0.01$ ).

The sites are not spatially arranged in a linear fashion, however, and it is instructive to examine their relationships in song-space in more detail. Rather than attempting to describe the maze of between-site relationships contained in the cluster dendrogram of Fig. 5, I have mapped the groupings of locations that are apparent at successively greater song dis-

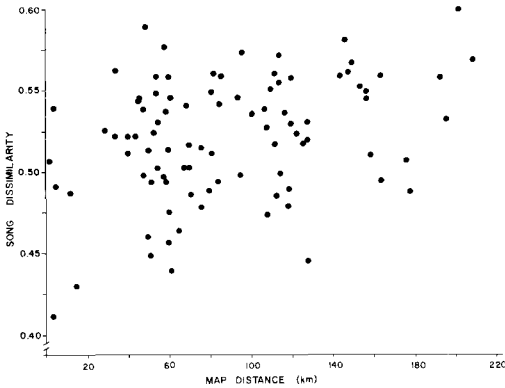


Fig. 6. The relationship between the linear map distance separating populations and the average dissimilarity of songs between those populations.

similarity values (Fig. 7). At a dissimilarity level of 0.475, three groupings of locations emerge: the Summer Lake plots group with Boghot Sage, Catlow North groups with Jack Creek and Guano Valley, and the two Owyhee sites group together. Increasing the dissimilarity index to 0.500 adds Alvord Desert to the first group, Catlow South to the second group, and Follyflat to the third; in addition, the two Cabin Lake plots now cluster together to form a fourth group. Finally, at a dissimilarity value of 0.525, all of the locations in the Summer Lake group and the Catlow North group cluster together to form one large group, the Owyhee-Follyflat cluster remains distinct, and the Boghot Grease location has entered the Cabin Lake cluster.

So, while there is a tendency for the songs of populations in distant locations to differ more than those in nearby locations (Fig. 6), the actual relationships of the locations (Fig. 7) show how misleading this correlation really is. Some nearby locations do in fact share many song elements and patterns (e.g. the Summer Lake sites; the Owyhee plots), but other nearby sites are totally different in the vocal patterns they contain and instead show greater similarity with populations located some distance away (e.g. Summer Lake with Guano Valley, Alvord Desert with Boghot Sage and Summer Lake rather than the nearby Follyflat or Catlow Valley, or Boghot Grease with Cabin Lake rather than Boghot Sage).

Perhaps the pattern of grouping of locations portrayed in Figs. 6 and 7 reflects the influ-

ences of topographic barriers. The simple expectation that song distance might be related to straight-line map distance may be naive in this region, where a series of fault-block mountain ranges separates relatively flat valleys that are blanketed with sagebrush, forming continuously suitable habitat for Sage Sparrows. Even a casual inspection of the relation of these "barriers" to the patterns of site clustering (Fig. 7) indicates that topographic separation has little effect on the degree of similarity or dissimilarity in vocal patterns of populations. Some locations with relatively low song dissimilarity are separated by several mountain ranges and many habitat discontinuities (e.g., Summer Lake and Boghot Sage or Alvord Desert), while others do seem related to topographic features (e.g. the clustering of Catlow Valley with Jack Creek and Guano Valley, which are in different portions of the same valley system). Most instructive, however, are the locations that are quite dissimilar in vocalization patterns but that are located near to one another with no discernible topographic or habitat breaks separating them. The two Boghot plots, for example, are located 4 km apart on the floor of the same valley. Despite their close proximity, birds in the two locations sing quite different song patterns ( $\bar{x}$  song distance = 0.539); Boghot Sage shows greatest affinities to the Summer Lake plots, roughly 110 km away, while Boghot Grease is fairly distinctive but eventually clusters with the Cabin Lake plots, roughly 155 km away. Neither topography nor distance seems to have much to do with the degree of vocal dissimilarity between Sage Sparrow populations in this region.

#### RELATIONSHIPS TO ENVIRONMENTAL FEATURES

Both the structure and variety of avian vocalizations may be affected by features of the physical and biotic environment. Several studies have measured the relationship between habitat structure and the attenuation of various note types with increasing distance from the source and have argued that habitat imposes strong selective forces on physical parameters of bird song (Morton 1975, Linskens et al. 1976, Marten and Marler 1977, Wiley and Richards 1978). Habitat variables may also be associated with changes in song dialects in some species (e.g. King 1972, Handford and Nottebohm

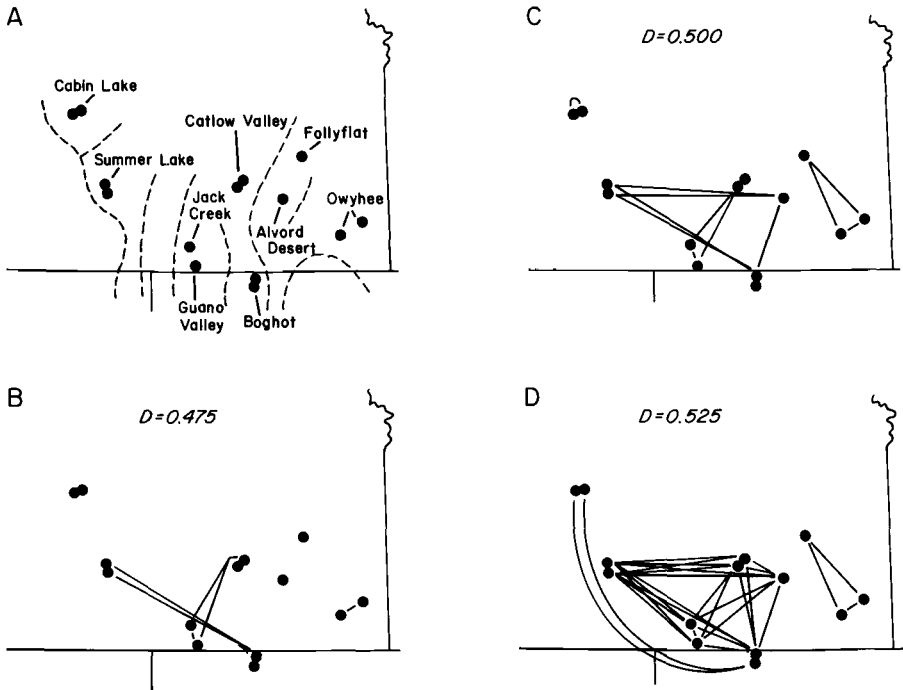


Fig. 7. A. Southeastern Oregon, showing the locations of the sites at which vocalizations were recorded and the position of major mountain ranges that separate the sagebrush-dominated valleys in which Sage Sparrows occur. B-D. Linkages of sites that cluster together in the dendrogram of Fig. 5 at dissimilarity levels of 0.475, 0.500, and 0.525.

1976, Handford 1981), but not others (Payne 1973, 1978, 1981a). Thielcke (1965) found Short-toed Treecreeper (*Certhia brachydactyla*) songs to be more variable at the periphery of the species' range, where habitat was patchily distributed, than in areas more centrally located in the range. Variations in avian population or community composition may also influence vocalizations; Kroodsma (1977), for example, showed that wren species singing more varied song patterns characteristically occupied habitats low in bird-species diversity. In general, such correlations have been drawn by making comparisons across several species, although Hunter and Krebs (1979) found that major variations in Great Tit (*Parus major*) songs between populations were associated more strongly with habitat differences than with geographical separation, and Kroodsma (1974) documented larger repertoire sizes in high-density populations of Bewick's Wrens (*Thryomanes bewickii*) than in low-density populations.

I used correlation analysis to search for statistical associations between habitat and bird-

community variables and features of song structure. Of the 138 correlation tests (Table 4), 21 were significant. Although this is somewhat greater than the proportion of such tests that would be expected to be significant by chance alone, it is probable that some of the significant correlations are spurious (Type I error), and caution should thus be exercised in their interpretation. In the following descriptions, however, all will be considered possibly meaningful biologically.

*Song parameters.*—Sage Sparrows occupy open habitat and sing from exposed positions, so if variations in habitat structure do influence features of song structure in populations, we might expect these effects to be rather subtle. In the shrubsteppe, habitat structure variables are strongly intercorrelated: areas of high values of vertical-structure variables (MAXHGT and TOTHITS) also have low values of measures of horizontal heterogeneity or patchiness (CVMAXHGT and CVTOTHITS) (Wiens and Rotenberry 1981). Few correlations between song parameters and features of habitat struc-

TABLE 4. Statistically significant correlations between parameters of Sage Sparrow songs and song variation and features of habitat structure, bird community attributes, and other song parameters. Blank spaces indicate nonsignificant correlations ( $P > 0.10$ ); + or - indicates correlations for which  $0.10 > P > 0.05$ . \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

Site	Song duration	Notes/song	Song rate	Note types/individual	Redundancy	Within-pop. dist.	Between-pop. dist.	Song turnover
Habitat features								
Sagebrush coverage								
Shrub species diversity								
Physiognomic cover diversity (PCD)	-							-
MAXHGT	-0.62*	-0.77**			-0.68*	-0.80***		-0.90***
TOTHITS	-0.64*					-0.59*		-0.87***
CVMAXHGT	+					0.56*		0.81**
CVTOTHITS	+					0.57*		0.77**
PD-30			-0.59*					
Bird community features								
Sage Sparrow density								
CV Sage Sparrow density								
Black-throated Sparrow density								
Total density								
CV total density								
Number of species								-0.69*
Bird species diversity				-0.56*				
Song features								
Within-population distance	0.62*			-0.68**	0.72**		+	0.89***
Between-population distance		+		+	0.65*	+		
Song turnover					0.60*	0.89***		

ture emerged, however. Songs of individuals occupying areas of greater vertical structure were generally shorter, less complex, and lower in redundancy than songs of individuals in habitats of lower stature. Song rate was inversely related to PD-30 (a measure of vertical heterogeneity or patchiness of the vegetation); the meaning of this correlation is obscure.

There was no apparent tendency for songs to be shorter, longer, or to contain more notes in high-density populations of Sage Sparrows or in more diverse communities. The number of note types per individual, while unrelated to Sage Sparrow density, was negatively related to species diversity. Note variety was also relatively low in populations with relatively high between-individual variation in song patterns. Birds in such populations also sang longer songs, and, as a consequence, the redundancy of elements in songs was greater than in populations with lower within-population song distances. Greater within-population song variety is thus characteristic of populations con-

taining individuals singing relatively long but simple and redundant song patterns.

*Population song variation (intersong distance).*—The populations with greater individual variation in song patterns (within-population song distance) were also more variable between years. These populations occupied habitats with significantly lower vertical structure (low values of MAXHGT and TOTHITS) and greater horizontal heterogeneity (high values of CVMAXHGT and CVTOTHITS) than did populations with greater vocal homogeneity. Thus, as habitat became generally sparser (shorter and patchier), individual variation in song patterns increased. Neither measure of vocal variety in populations, however, approached statistical significance in relation to Sage Sparrow density or its variations, total community density or its fluctuations, or community diversity (although annual song turnover was negatively correlated with the number of bird species present). The intersong distance patterns between the locations were statistically unrelated

to variations in any of the habitat or avian community features. Thus, the spatial patterns of song similarities among localities shown in Fig. 7 cannot be explained by concordant variations in the habitat, population, or community characteristics that I measured.

#### DISCUSSION

The characteristics of Sage Sparrow vocalization systems, as indicated by this study, can be summarized as follows. Individual Sage Sparrows sing a single, simple song that, once formed, apparently does not change during the life of an individual. Different individuals within a local population may sing song patterns quite similar to one another, all different from one another, or shared with groups of neighboring individuals. Different local populations may share song elements or patterns or may be quite different, but these between-population similarities are not closely related to the physical distance separating the populations or to the degree of topographic contiguity of the sites. Generally, the patterns of variation in songs within and between populations are unrelated to features of habitat structure or to the densities of Sage Sparrows or of other co-occurring species.

Sage Sparrow vocalization systems thus exhibit a wide array of different patterns within a rather limited portion of the species' range. This variety invites speculation but, at the same time, renders the development of a general explanation rather difficult. Two aspects of Sage Sparrow vocalization systems merit attention, the limited repertoire size of individual males and the apparently nondialectal population structure.

#### WHY A SIMPLE SONG REPERTOIRE?

The patterns of within- and between-population vocal variety in Sage Sparrows are built upon individual song patterns that are invariant. Most songbirds, however, have a song repertoire that includes several distinct song types (Hartshorne 1973, Dobson and Lemon 1975), and much effort has been devoted to explanations of the adaptiveness of large repertoire size (Krebs 1977). Left largely unexplored, however, is the question of why individual males of so few species sing a single, unvarying song (Kroodsma 1978). Further, repertoire size appears to be an evolutionarily labile trait,

as different members of the same genus (e.g. *Melospiza* sparrows) may differ markedly in song complexity. The genus *Amphispiza*, to which the Sage Sparrow belongs, contains only one other species, the Black-throated Sparrow. Black-throats sing complex, variable songs, which may incorporate as many as nine distinct song types (Heckenlively 1970), and thus contrast sharply with the individual simplicity and stereotypy of Sage Sparrows, despite the close phylogenetic relationship of the species (Hubbard 1974).

Several advantages of large repertoire sizes have been suggested (see Krebs and Kroodsma 1980), and some insight into the vocal simplicity of Sage Sparrows may be derived by examining how Sage Sparrow systems relate to those hypothesized for large-repertoire species. Thus:

1. Males with large repertoires might be favored by females. This may be especially evident in some polygynous species (e.g. wrens; Kroodsma 1977) but may also occur in monogamously mating species if males with larger repertoires pair earlier. These factors seem unlikely to be important in Sage Sparrows, which mate monogamously, do not exhibit a marked asynchrony in the initiation of breeding after establishing territories in the spring, and usually arrive on the breeding grounds already paired (Rich 1980, Wiens and Rotenberry pers. obs.). Further, we have found no evidence of unmated females or "floaters" at our intensively studied plots at Cabin Lake. The possibility that variations in male song complexity might affect female choice in Sage Sparrows seems slim; as the birds may sing during migration, however, this possibility remains open.

2. Males singing larger repertoires may be more effective in obtaining and defending high-quality territories (Krebs and Kroodsma 1980, Krebs et al. 1978, but see Payne 1979). In Sage Sparrows the song is employed in territorial advertisement, but it is difficult to discern the selective forces that might promote sufficient male-male competition to favor enhancement of repertoire size. Usually the habitats occupied by Sage Sparrows are not completely saturated with territories. Birds often forage outside the territory boundaries determined by singing positions or flush-censusing, and between-territory variations in "quality" (e.g. abundance of food resources, nesting



sites, or sheltered microclimates) have escaped our detection even in our intensive studies. It thus seems that intense male-male competition over territories is unlikely.

3. A large repertoire may enable an individual to communicate specific information about its position in its territory, its motivational state, or its dominance status by employing different song types in different contexts or by song matching between birds (Lein 1978, Kroodsma 1979, Payne 1979). Although neighboring Sage Sparrows occasionally counter-sing, the differences in the extent of within-population variation in the single song type of individual males would seem to argue against a role in communicating specific contextual information.

4. Hartshorne (1973) has proposed that large repertoires serve to prevent monotony in the vocalization, and thus habituation. To the human ear, the song of an individual Sage Sparrow is monotonous, but the relationship of this monotony to habituation is unclear (Krebs and Kroodsma 1980). If it does lead to habituation, this might facilitate recognition of any individual entering the territory singing a different song, as its vocalization would contrast with the habituated stimulus. In at least some Sage Sparrow populations, however, neighboring individuals sing similar or identical songs, so the adaptiveness of such habituation would vary between different populations. Why this should be enhanced by selection is unclear.

How, then, might the postulated advantages of small repertoire size relate to the Sage Sparrow system? It has been suggested, for example, that a small repertoire may facilitate individual recognition by reducing the complexity of an individual's song, thus rendering its identity less ambiguous (Krebs and Kroodsma 1980). Small repertoires might also foster the development of sharp dialect boundaries among local populations, as it should be much easier to establish a dialect pattern among individuals sharing a single song type than among individuals that each sing a large number of song types (Kroodsma 1978). The clearest demonstrations of individual recognition have indeed been in species with only a single song type per male, and the most apparent examples of dialects are also among one-song species (but see Payne and Payne 1977, Payne 1979, for a counter-example). For individual recognition to occur, it is necessary that the song be rela-

tively invariant within individuals but highly variable between individuals, while dialects are generally founded upon between-individual identity in at least some portions of the song. In Sage Sparrows, the requirements for the song to serve in individual recognition are met in some populations (e.g. many of the birds at Boghot Sage), while others (e.g. Follyflat) exhibit the sort of song homogeneity among individuals required for dialect recognition. It hardly seems a parsimonious explanation to propose that in some populations selection favors a simple repertoire to enhance individual recognition, while in other populations a short distance away the selective forces are totally different.

It is possible that Sage Sparrows, like saddlebacks (Jenkins 1978), actually have a flexible repertoire that may include several song types, birds changing to use the song pattern characteristic of their neighbors at a given time. My statement that Sage Sparrow males sing only a single song type is based upon banded birds that have returned to roughly the same location in successive years, and thus it is possible that they might learn other song types that, were they to move elsewhere, could be used. The marked birds, however, had different neighbors in different years, and there was no evidence that their song was altered to match that of their neighbors, or vice versa. Further, the heterogeneity of vocal structuring among different populations argues against the suggestion that individuals change their song to match that of neighboring individuals; it is difficult to imagine why that would occur in some populations but not others.

Perhaps the song of Sage Sparrows is simple and relatively stereotyped because its functions are simple. If the song serves primarily to advertise species identity and the location of an individual within its territory and to maintain the pairbond, a single song perhaps will do, and a more varied song might well increase the ambiguity of these basic messages. Given a variable, relatively simple habitat that is customarily not fully packed with breeding individuals and a migratory species that mates monogamously (perhaps before arriving on the breeding grounds), selection favoring increased elaboration of the vocal system may well be absent. Despite the individual and population variation that I recorded in this study, the song is instantly recognizable as that

of a Sage Sparrow. A single song that adheres to the general pattern of a Sage Sparrow song, repeated frequently from exposed locations, may be quite sufficient to serve the necessary functions. The results of preliminary experiments conducted during 1981 on six birds at Cabin Lake indicate that males usually respond strongly and actively to playbacks of Sage Sparrow songs within their territories. They apparently do not respond differentially to similar versus dissimilar songs: the Cabin Lake birds responded no differently to playbacks of a Cabin Lake bird than to playbacks from Owyhee Sage or from Alvord Desert.

#### THE QUESTION OF DIALECTS

Why, then, do the songs of individuals vary, and why is this variation inconsistent within and between populations? The population structure of Sage Sparrow vocalizations seemingly does not match the sharp differentiation of dialect areas found in White-crowned Sparrows (*Zonotrichia leucophrys*) (Baptista 1975, 1977; Baker 1975; Baptista and King 1980; Heinemann 1981), Rufous-collared Sparrows (*Z. capensis*) (King 1972, Nottebohm 1975, Handford and Nottebohm 1976, Handford 1981), or isolated populations of sedentary Belding's Savannah Sparrows (*Passerculus sandwichensis beldingi*) (Bradley 1977), for example, although there are some similarities to the more loosely defined patterns of song variation that Payne (1978) documented in Splendid Sunbirds (*Nectarinia coccinigaster*). Whether Sage Sparrows may be considered to exhibit local song dialects depends upon how broadly "dialect" is defined (Krebs and Kroodsma 1980); certainly a definition would need to be rather broad (perhaps to the point of losing its utility) to include populations as different as those at Follyflat, Boghot Sage, or Guano Valley.

Little is gained, in any case, by simply categorizing a species as dialectal or nondialectal. It may be more fruitful to examine how the Sage Sparrow system relates to the major features that may influence individual and population variability in vocalizations: the ontogeny of song acquisition, the imitative or improvisational abilities of individuals, site tenacity and dispersal, and population stability or turnover (Lemon 1975, Krebs and Kroodsma 1980, Payne 1981a).

Most songbirds learn at least some elements

of their song. In some species, development of the final adult song is not completed until after the young have dispersed from the natal area (Lemon 1975, Kroodsma 1974, Payne 1981a, b). Young or first-year birds may then be exposed to the songs of adjacent territory holders and, if their imitative abilities are well-developed, match those song patterns. This delayed maturation and imitation will lead to sharing of song patterns among neighboring individuals. Alternatively, if neighbors do not share song types, this may reflect earlier, pre-dispersal learning of the song (perhaps by imitation) or a greater role of improvisation in the development of song patterns; this latter tendency might be more apparent in vagile than in sedentary or site-tenacious species (Krebs and Kroodsma 1980). In addition, the timing of the final maturation of adult song may be influenced by environmental features such as photoperiod or the exposure of individuals to adult song during different stages of their ontogeny, with the result that the sensitive period for song learning may vary between different individuals in the same population (Kroodsma and Pickert 1980).

Nothing is known of the ontogeny of vocalizations in Sage Sparrows. The fact that at least some neighboring Sage Sparrows sing identical songs, however, suggests that they do have imitative abilities. In some populations, however, most neighbors sing different song patterns, indicating that this imitative process is not ubiquitous and that improvisation may also play some role in the formation of songs.

Alternatively, such within-population variation in song types may imply that individuals differ in the timing or the circumstances of song development. In the Oregon populations we have studied, adults usually raise only a single brood, and nesting is confined to a period of 2 months or so. After the young fledge, they are accompanied by the adults for 2-3 weeks. Most breeding adults have departed by late July, but we continue to see groups of birds in juvenal plumage well into September. A consequence of this curtailed breeding period of adults is that young have rather limited opportunities to hear a variety of songs during the period between fledging and their own migration from the area. This breeding phenology might favor delayed maturation of the final song types of young birds until the following breeding season. It also means that

late-hatching young may hear rather little adult song, while early-hatching birds may have the opportunity to hear most of the birds in their local population. The song formation process within a local population might thus be heterogeneous, early-hatchers learning a complete song during their natal summer, late-hatchers delaying song development until winter or the following spring. If predation intensity were to differ between local populations, thereby affecting the proportions of early- versus late-hatchers (via renestings), populations might differ in the magnitude of this heterogeneity.

How such features of song ontogeny are translated into patterns of within- and between-population variation is dictated by the demographic structure of local populations, especially the turnover of individuals between years (Baker 1975, Avery and Oring 1977, Baker and Mewaldt 1978). Although adult Sage Sparrows that have previously bred successfully may return to the same general location in successive years, mortality (or adult dispersal) does occur, and there is thus a turnover in the individual membership of a local population from year to year. Further, our banding studies show that young birds do not return close to their natal area to breed. These attributes suggest that Sage Sparrow populations might undergo annual changes in membership that could vary between different local populations. Depending upon the magnitude of annual turnover in populations, one would predict varying degrees of within-population variation in song patterning. Further, if the causes of low or high population turnover are independent of the locations of the local populations, a substantial amount of between-population variation and a general absence of clear geographic patterns to this variation could easily result.

Local dominance relationships may also interact with population turnover to influence the patterns of within-population song similarity (D. and M. Balph pers. comm.). Thus, for example, young might initially learn their father's song, but retain some flexibility (as in Bewick's Wrens; Kroodsma 1974). Arriving at the breeding grounds the following year, a first-year individual might then sing its father's song if it settled in an area some distance from other males. If, instead, it arrived and settled with other birds, or arrived after most territories were established, it might alter its

song pattern to match that of the dominant individual among its neighbors. If returning adults tend to arrive earlier than first-year breeders or are more likely to be dominant to them, their songs would establish the foundation types for such suites of individuals. Returning adults likely would not alter their song to match that of neighboring individuals. Given this scenario, in populations with high yearly replacement of individuals, the identity of the dominants and the timing and settling locations of first-year birds would change from year to year, producing considerable song heterogeneity. In low-turnover populations, on the other hand, many returning individuals would be adults sharing a common song type, and the few new birds to establish residence might then match their song type, leading to homogeneity of song patterns. "Neighborhoods" such as those at Guano Valley could result if returning adults in an intermediate-turnover population settled some distance apart, the intervening spaces then being occupied by first-year birds that would match the song of the nearby dominant.

Finally, it is possible that the patterns of vocal variety within Sage Sparrow populations are not as diverse as I have portrayed. The characteristics noted for the Follyflat, Boghot Sage, and Guano Valley sites, for example, might represent the same pattern expressed on quite different spatial scales. For example, all populations might really express a "neighborhood" structure with broader sampling. At Guano Valley this structure was apparent, but perhaps at Boghot Sage the "neighborhoods" were larger in size, included more individuals, and were not so discretely bounded. This might give the impression of gradual change, and in fact one can define several groups of birds with generally similar songs in the dendrogram of Fig. 4B. At a site like Follyflat, the "neighborhoods" containing individuals singing quite similar songs might have been so large that most of my sampling was conducted within one such group. Had I sampled over a broader area, a different pattern might have emerged. I attempted to record songs over areas of roughly the same size at all localities, however, and to consider this proposal seriously one must accept that different populations might differ substantially in the scale of within-population vocal differentiation. Why this might occur is unclear, especially in the

absence of habitat discontinuities or of strong correlations of within-population vocal variation with habitat features. Variations in the extent of population turnover or of site fidelity might contribute to such variations in the scale of population patterns. In the absence of broader sampling of song variations at each location, however, these suggestions remain unsubstantiated.

#### CONCLUDING COMMENTS

Such arguments are of necessity quite speculative, but they point to the sort of information that is necessary to develop a more rigorous explanation of the array of within- and between-population variations exhibited by Sage Sparrows. Additional field studies may resolve the patterns of variation in greater detail, but, without better knowledge of how and when Sage Sparrows form their song, how extensively they disperse from natal areas, how much turnover in individual membership characterizes different populations, and how or whether dominance is expressed among neighbors, it is unlikely that explanations of the processes underlying the patterns can progress from speculative inferences to empirical documentations.

Even without such information, the large array of patterns of within- and between-population variation in song structure in Sage Sparrows complicates attempts at generalization. Much of the theory relating to the possible adaptiveness of different patterns of vocal similarity or variation among individuals is based upon between-species comparisons, with each species characterized by studies of only one or perhaps a few populations. This ignores the rich texture of variation that may exist within a species. Consider, for example, how one would characterize the population structure of Sage Sparrow vocalizations if studies had been conducted only at Follyflat, or only at Boghot Sage.

Attempts to generalize are also usually based upon the presumption that all of the variation observed must be adaptive, and explanations based upon adaptation are thus necessary. But it is appropriate to ask how much variation between individuals one should expect without seeking an explanation in terms of natural selection (Slater 1980). In a variable environment in which populations and communities

are not in equilibrium (Wiens in press) and the available breeding habitat is not saturated with individuals, it may indeed be adaptive for individuals to sing a song pattern that is clearly recognizable as that of a Sage Sparrow, as the preliminary playback experiments suggest. The variations on that theme, however, may well be epiphenomena resulting from historical or chance effects of song learning, population turnover, dispersal, and the like, for which no adaptive explanation is warranted. The different populations may thus vary in song patterning more or less independently of habitat features or of location relative to one another, largely as a result of chance effects. Much of the variation in Sage Sparrow songs may thus represent epiphenomena that may well be random with respect to selection.

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