

MICROGEOGRAPHIC VARIATION IN THE SONG OF THE SAGE SPARROW

TERRELL RICH

ABSTRACT.—The Sage Sparrow breeds in large expanses of continuous sagebrush in southern Idaho. Analyses of the song syllables and shared syllable sequences of 40 males from five main study sites in Idaho revealed that individuals tended to be most similar to birds from the same population. Each male had one stereotyped song with only minor variations consisting of the omission of a few syllables from the end of the song. Three males apparently had the same song and same or nearly the same territory for three or four years. The most geographically distant population from the other four populations had the most distinct songs. However, neighbors on adjacent territories were not usually most similar to each other. Several syllables were widespread among males while uncommon syllables were often shared among males within a population. Stepwise discriminant analysis of ten variables from the same populations revealed that mean syllable duration and mean interval between syllables contained enough information to successfully assign 62.5% of the songs to the population to which they belonged. Six of an additional 10 songs recorded at five other sites in southern Idaho were classified into the main population geographically closest.

Geographic variation in song and dialects have been described in sedentary avian populations (Lemon 1966, 1975, Kroodsmas 1974, Baptista 1975, Bradley 1977, Payne 1978, Bowman 1979) and in migratory populations (Harris and Lemon 1972, Baker 1975, Orejuela and Morton 1975, Baptista 1977). Our understanding of dialects depends partly on recognizing the difference between true dialects and geographic variation in song. Differences in the songs of populations of sedentary species are readily explained in terms of the evolution of isolated populations (Bradley 1977, Bowman 1979) or in special social organizations (Jenkins 1977, Payne 1978). In migratory species where there is a greater opportunity for individuals to disperse among populations between breeding seasons and, thus, for population differences to be reduced, classical isolating mechanisms may also be important. Chief among the latter are geographical distance (Wright 1943) and variation in habitat (Nottebohm 1969, 1975, King 1972, Baptista 1977). To determine the nature of song variation in the absence of obvious isolating mechanisms it is necessary to examine populations of a migratory species separated by small distances in continuous homogeneous habitat. In this way geographic variation on the smallest scale might be described.

In this report I describe differences in the songs of populations of the Sage Sparrow (*Amphispiza belli*). This species is migra-

tory and occupies large expanses of continuous homogeneous sagebrush (*Artemisia tridentata*) habitat in southern Idaho. I recorded songs in populations separated by relatively less geographical distance than is customarily done in studies of this type. Even under these conditions where song variation seemed least likely to occur there were substantial differences in several song parameters among populations. I conclude that geographic variation in song among populations, most likely as a result of philopatry, occurs on a fine geographic scale in the Sage Sparrow.

MATERIALS AND METHODS

In 1976 and 1977 I recorded the songs and studied the behavior of four unmarked neighboring territorial males from March to July in Bingham Co., Idaho (Fig. 1, site SA). In May and June of 1978 I recorded 36 males at several localities in southern Idaho and in 1979 I recorded an additional 14 males. Forty males were recorded at five main sites (Fig. 1): SA, main study area; VC, a prominent volcanic cone; BB, Bingham-Bonneville county line; BT, Kettle Butte; MLF, Medicine Lodge Flats. The remaining 10 males were recorded at scattered locations: GR, C, E, JF and DF. I spent one morning at each site and traversed an area of about 2 km² while recording songs.

Vocalizations were recorded with a Dan Gibson Electronic Parabolic Microphone and an Audiotronics model 147A cassette recorder. Audiospectrograms were prepared on a Voice Identification, Inc. Series 700 sound spectrograph with linear scale and automatic frequency marker.

I analyzed geographic variation with both a non-parametric and a parametric approach. For the non-parametric analysis, I defined and catalogued 40 different syllables based on frequency, duration and

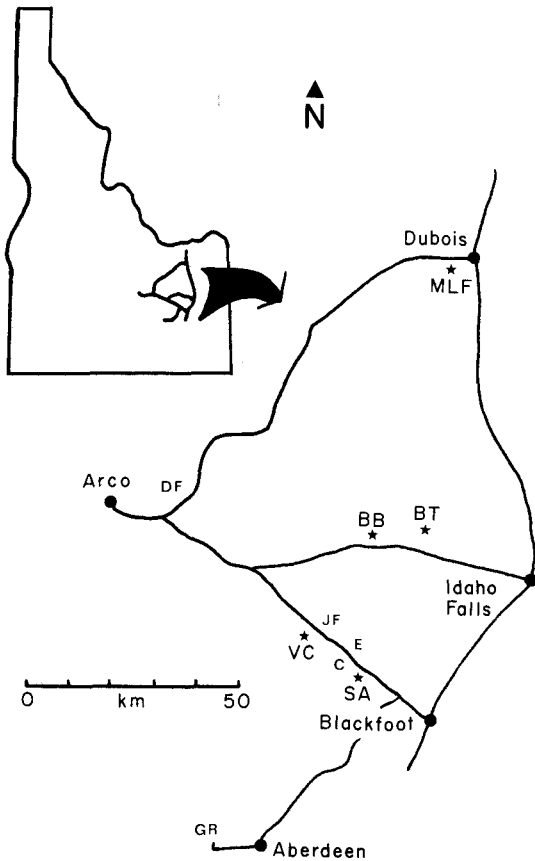


FIGURE 1. Locations of the 10 sites in Idaho where Sage Sparrows were studied and/or recorded. The five main sites are indicated by large letters while the five other sites are indicated by small letters.

sound spectrographic shape from the 50 songs. A syllable consisted of either a continuous trace on the spectrogram or a single trill. Spectrograms were randomized before I defined syllables, some of which are identified in Figure 2. A plot of the cumulative syllables recorded versus the number of birds recorded (Shiovitz and Thompson 1970) showed that I had sampled most of the syllables in the area. Comparison between the songs of each pair of males was then made in two ways. I calculated a similarity value between the songs based on the frequency of occurrence of various syllables in the songs. The value was $2\sum(i_a \min i_b) / (t_a + t_b)$ where $(i_a \min i_b)$ is the minimum of the frequency of occurrence of syllable i in the songs of a given pair of males, a and b . The denominator is the sum of all syllables in both songs. Thus, the similarity value between the songs CCDDE and CCCDFG would be $2(2 + 1 + 0 + 0 + 0) / (5 + 6) = 0.55$. I also counted the number of identical two-syllable sequences (Fig. 2) shared by each pair of males. This analysis incorporates information on the order of syllables in the songs. The songs were then clustered according to the two matrices of values (Figs. 3 and 4). I used a single-link cluster as described by Morgan et al. (1976). For clarity, in both clusters I omitted samples from the five populations with fewer than five males.

For the parametric analysis I defined several variables of duration, frequency and subdivision in the songs: syllables per song, kinds of syllables per song,

mean syllable duration, mean inter-syllable interval, song duration, maximum and minimum frequency, frequency range, syllables/kinds and mean dominant frequency per syllable (that frequency making the darkest trace on the spectrogram). These data were checked for normality and then subjected to a one-way analysis of variance and stepwise discriminant analysis (BMDP7M). The songs of 40 males from the five main sites were used to establish the discriminant functions. All 50 males were then classified by those functions.

RESULTS

Each of the eight male Sage Sparrows studied in detail at site SA had one song type that did not vary significantly throughout most of the breeding season. The song can best be described as a series of short musical buzzes on different frequencies. The mean song duration (\pm SD) of 50 males was 1.77 ± 0.21 s. Males perched in sagebrush and sang in bouts of 1–118 songs delivered at a rate of 8–10 songs/min. They always left a perch just after ending a bout and began a new bout immediately after landing on a new perch. In 1,000–4,000 songs from each of eight males during the breeding season at site SA, the only variation I heard consisted of the occasional omission of a few syllables from the last part of the song (Fig. 2) and, at certain times, more incomplete songs.

At BT, VC, MLF (Fig. 1) and later in other parts of Idaho, I heard males singing songs of variable duration, number of syllables and syllable sequences very early in the season. This variability contrasted with the widespread stereotypy of most males and the lack of variable song heard over most of the breeding season.

Stability from year to year was evident in one male (SA3) recorded in four successive years on the same territory, another (SA6) recorded in three years on the same territory and still another (SA1) recorded in three years on nearly the same territory. Because males were not marked I do not know for certain that they were the same birds, but this is the most reasonable explanation. In addition, two other behavioral measures, songs per bout and songs per hour, were not statistically different for male SA1 in 1976 and 1977 and for male SA3 in those years while there were differences between other pairs of males (unpubl. data).

SONG SIMILARITY

The similarity of the songs among males can be seen by examining a few representative syllables and songs. Songs C and D (Fig. 2) are those of the most similar males, BB6 and BB7, and they differed but slightly. Another similar pair, SA7 and SA10, shared a se-

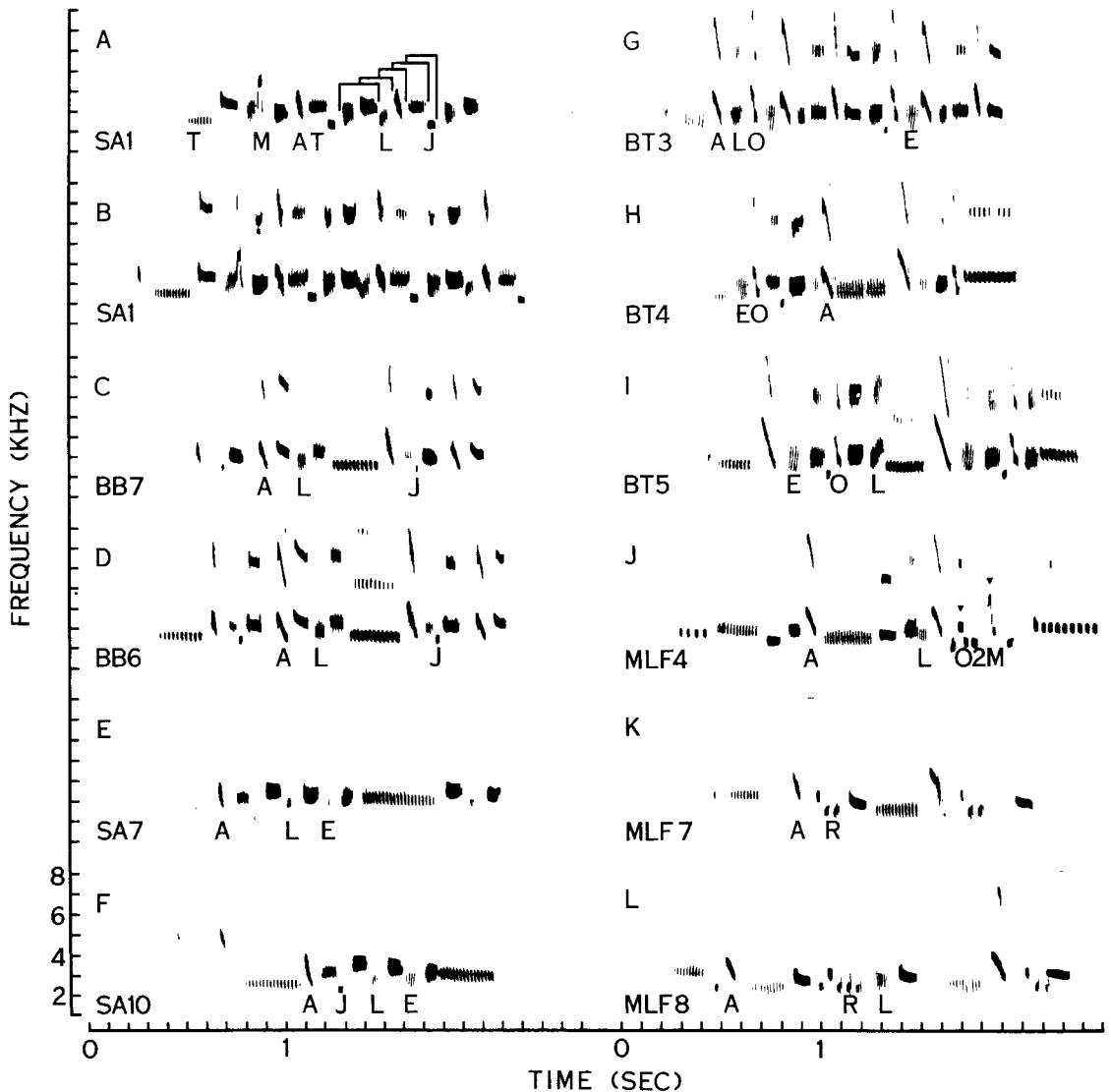


FIGURE 2. A, song of male SA1 in 1976, truncated version. Typical Sage Sparrow trills are labelled T. Two-syllable sequences are outlined by brackets. B, the song of male SA1 in 1977, complete version. C and D, songs of the two most similar males in the study. Songs of other males that had high similarity values were: (E, F), (G, H, I) and (J, K, L). Identical song syllables are identified once in each song in which they occur. Strong harmonics in some songs may be an artifact of recording and analysis. Male's identity is given in the lower left corner of each spectrogram.

quence of nine syllables (Fig. 2: E, F). Some of the syllables that occurred most commonly and the percentage of all males using them at least once in their songs were A (88%), E (83%), L (72%) and J (60%). These syllables are identified once in the songs in which they occur (Fig. 2). Common syllables aided little in discriminating among populations unless they were arranged in unusual sequences. The syllables that often showed obvious similarities between males within populations were those that occurred more rarely. Among these were syllable O in group BT (Fig. 2: G, H,

I) and syllable R in group MLF (Fig. 2: K, L). A few syllables were shared by only two males, e.g., syllable M (Fig. 2: A, J). Two syllables were unique to one male, one of which was O2 (Fig. 2: J).

COMPARISON OF SYLLABLES AND SYLLABLE SEQUENCES

The cluster of songs based on the shared syllables (Fig. 3) reveals a clear tendency for songs from the same population to be most alike. At the first clustering levels, invariably two or three songs from the same population are linked. At reduced levels of

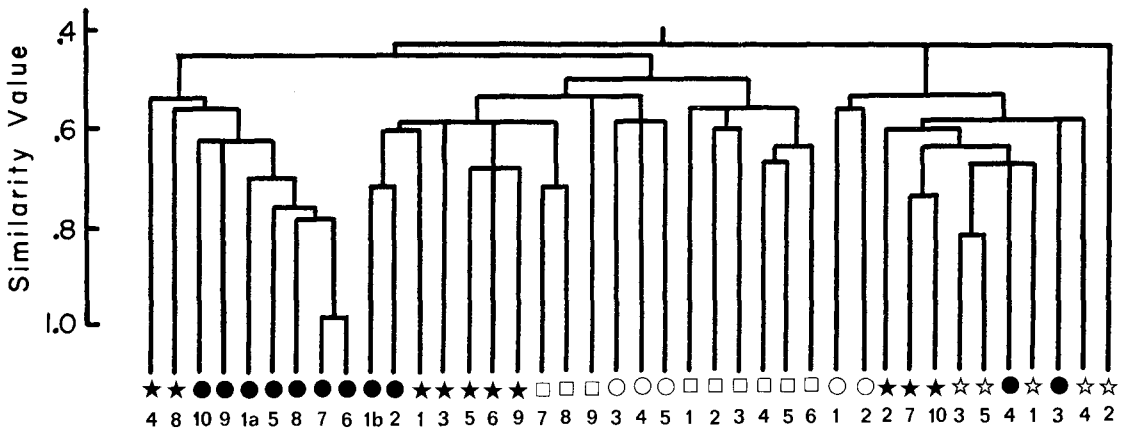


FIGURE 3. Cluster of the songs of 40 male Sage Sparrows based on the number of identical syllables shared (similarity value). Symbols for populations are: closed circle, BB; open circle, BT; closed star, SA; open star, VC; open square, MLF. The number below each symbol is the identification number for each male.

similarity, the clusters become less distinct. Some pairs of songs from the same population, e.g., VC2-VC3, SA4-SA10, BB4-BB6, were as different from each other as any pairs. However, 7 of the 11 songs in BB linked cleanly as did six of the nine songs in MLF. There was also no mixing between VC and MLF.

A clustering of the same songs based on the number of two-syllable sequences shared (Fig. 4) again shows a tendency for songs of the same population to cluster at the highest levels of similarity. Several of the songs in BB and SA form rather concise groups while population MLF is almost perfectly discrete.

Both clusters can be further clarified. First, single-link cluster analysis involves "chaining" wherein details of the similarity structure are sacrificed for simplicity (Morgan et al. 1976). To clarify this structure it is useful to consider which song each was most like. For example, in Figure 3 it is not possible to discern that MLF9 was most similar to MLF8, SA3 was most similar to SA5, or that both SA4 and SA8 were most

similar to songs of BB. Second, in Figure 4 a number of ties resulted, and to break them I examined multiple-sequences to determine most similar pairs.

In order to address these problems I present the number of songs in each population which were most similar to other songs in their population (as opposed to being most similar to songs of other populations) and the number expected by chance (Table 1). This further reveals the similarity within each population and helps explain the situation at Kettle Butte. Figure 4 seems to show no particular unity to this population, but Table 1 reveals that these songs were most similar to each other. Their failure to clump discretely resulted from their high mean number of unique two-syllable sequences (5.8).

NEIGHBORS ON TERRITORIES

The following pairs of males were known neighbors on territories: SA1-SA2, SA1-SA3, SA3-SA4, SA4-SA6. Songs of these males were more similar to songs of males other than their immediate neighbors based

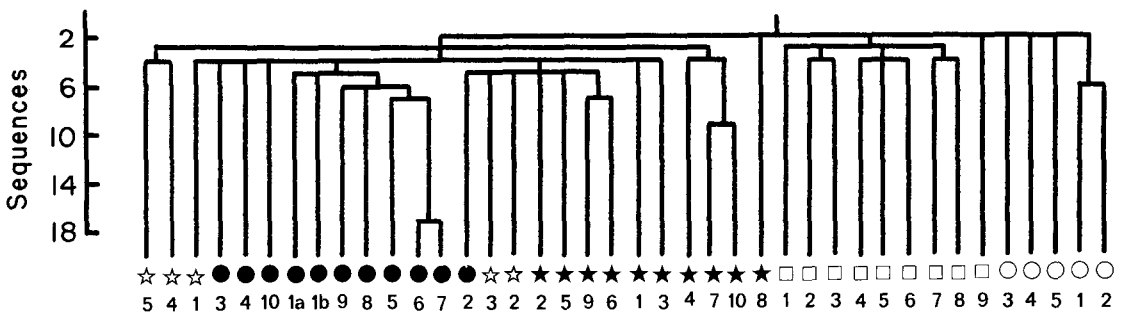


FIGURE 4. Cluster of the songs of 40 male Sage Sparrows based on the number of two-syllable sequences shared. Symbols as in Figure 3.

TABLE 1. Number of songs in each population that were most similar to other songs of their population (see text) based on similarity value (SV), multiple-syllable sequences shared (S) and the number expected by chance (E) where $E = (N_i - 1)^2 / (N_t - N_i)$; N_i is the number of males recorded in each population and N_t is the total number of males ($N_t = 40$). The mean number of unique two-syllable sequences in each population is also given (U).

Population	N_i	SV	S	E	U
SA	10	7	8	3.0	2.2
BB	11	9	8	3.4	2.1
VC	5	4	2	0.5	2.0
BT	5	5	4	0.5	5.8
MLF	9	9	9	2.1	4.4

on either cluster. In group BB, I suspected four pairs of males to be neighbors as they were recorded while singing near each other: BB2-BB3, BB3-BB4, BB2-BB4, BB6-BB7. BB3 and BB4 were most similar to each other by sharing four sequences, but they also were linked to songs of other populations at that level. MLF5 and MLF6 had a similar relationship. Of greatest similarity in the study were BB6 and BB7 who shared 17 sequences and had a similarity value of 0.98. I could not distinguish their songs in the field, and until both were singing, one on each side of me, I was not certain that there were two individuals. In fact, I probably underestimated the similarity within populations because some birds had extremely similar songs. In summary, similarity between pairs was greatest within a population but males on adjacent territories were not usually most similar to each other.

COMPARISON OF PARAMETRIC VARIABLES

Table 2 gives the results of the one-way analysis of variance for 10 variables in the five main populations. Five variables—mean syllable duration, syllables per song, syllables/kinds, minimum frequency, mean inter-syllable interval—had a significant F

TABLE 2. One-way analysis of variance for 10 song variables in five populations of Sage Sparrows.

Variable	F ratio
Mean syllable duration	13.437***
Syllables per song	5.908**
Syllables/kinds	3.870*
Minimum frequency	3.255*
Mean inter-syllable interval	2.700*
Mean dominant frequency	2.170
Song duration	1.762
Frequency range	1.636
Kinds of syllables	0.729
Maximum frequency	0.672

*** $P < 0.001$; ** $P < 0.005$; * $P < 0.05$.

TABLE 3. Discriminant functions used to separate five populations of Sage Sparrows. Characters are mean syllable duration (MSD) and mean inter-syllable interval (MII).

Function	Proportion total dispersion	Character weights		Constant
		MSD	MII	
1	.94	-.808	-.763	10.006
2	.06	-.195	.938	-1.360

ratio. When the data were subjected to the stepwise discriminant analysis only two variables contained enough information to contribute to discrimination among all five populations: mean syllable duration and mean inter-syllable interval. A U-statistic of 0.3944 after mean syllable duration was entered into the analysis revealed its importance in discrimination. The final U-statistic was 0.2503. The discriminant functions are given in Table 3.

The classification functions succeeded in classifying 62.5% of the songs into the population to which they actually belonged (Table 4). While this is not an unusually high value it is good considering the small size of the populations, their proximity and how much information in the data was not used in the classification functions. The functions were especially successful in classifying songs of BT (100% correct), VC (80%) and MLF (77.8%). Populations SA and BB had fewer songs correctly classified, 50% and 36.4%. Nevertheless, SA was not confused with another population as the incorrectly placed songs were scattered among the other populations. Only BB was not clearly discriminated as five of its songs were put in BT, the population geographically closest.

The remaining 10 songs from other sites were also classified. Six of these songs were put into the main population geographically nearest; GR4, GR5, E2 and E3 were placed in SA while DF1 and DF2 were placed in VC. The other four songs were classified as

TABLE 4. Classification matrix from discriminant analysis of five Sage Sparrow populations. Songs classified by the functions but not entering into the latter's formulation are listed in the text.

Group	Percent correct	Number of cases classified into group				
		SA	BB	BT	VC	MLF
SA	50.0	5	1	2	2	0
BB	36.4	2	4	5	0	0
BT	100.0	0	0	5	0	0
VC	80.0	0	0	0	4	1
MLF	77.8	0	0	0	2	7
Total	62.5	7	5	12	8	8

follows: JF in SA, E1 in BT, GR1 in VC and C1 in VC. Even these songs were placed in populations nearby rather than far away. The results of the classification of the 10 songs that did not enter into the formulation of the functions show that the discriminant analysis performed consistently.

DISCUSSION

The Sage Sparrows in this study showed a distinctiveness of song within populations despite continuous habitat and the nearness of populations to each other. The song characteristics that differed among populations were substantial—syllables shared, sequences of syllables shared and time, frequency and meristic variables. Because adult male Sage Sparrows sing a single type of song, may live for three or four years, and return to the same or nearly the same territories to breed in successive years, there exists an important framework for song uniformity within populations. This degree of philopatry is not unusual and contributes to dialects in other species (Kroodsma 1972, 1974, Morton et al. 1972, Lemon 1975).

Payne (1981) discussed three models—historical, racial specialization, and social adaptation—to explain the origin and maintenance of song dialects. The first two seem unlikely to account for my data on Sage Sparrows. The large expanse of continuous sagebrush within my study area has no barriers or large discontinuities that could restrict dispersal. There has been, however, a history of fire, brush removal and grazing, factors that could have produced subtle differences in habitat. Such variations may provide certain preferred areas for Sage Sparrows. The population at BT, for instance, had the highest mean number of unique two-syllable sequences despite its proximity to BB. It was also perfectly grouped by the discriminant functions. This population occupied the side of Kettle Butte, which is partially separated from the sagebrush to the west by cultivated ground. Hence, this small discontinuity may have been enough of a barrier to provide some historical isolation. Other undetected variations in habitat could be important in conjunction with philopatry to restrict dispersal enough to allow differentiation in song among local populations especially if the rate of change in the population dialect is relatively rapid. The differences in songs among populations may arise in several ways (Lemon 1971, Kroodsma 1974, Eberhardt and Baptista 1977). This study implicates reordering of song components (see

also Baptista 1975) as one mechanism. Reordering is probably accomplished readily and could provide the necessary mechanism for rapid change.

Some variation of the social adaptation model (Payne 1981) thus would seem to be most consistent with what is known about Sage Sparrows. The model predicts an asymmetry in song learning whereby young males preferentially learn the song of established males who have some desirable social status. Nothing is known about song acquisition in young Sage Sparrows, although birds singing variable songs early in the year may have been young birds. Given the pattern of song learning in birds in general (Nottebohm 1972) it is likely that young Sage Sparrows learn at least part of their song. If they learn from parents or neighbors before dispersal (Marler and Tamura 1964, Marler 1970) or in the area where the territory will be established (Lemon 1966, Rice and Thompson 1968, Kroodsma 1974, Payne 1978) the distinctiveness of song populations will be enhanced. Most importantly, local similarities in song could be preserved as an artifact of young birds simply learning the refinements in species-specific song, regardless of the status of the model male.

Until more is known about the dispersal and methods of song acquisition by young Sage Sparrows these data cannot be fully assessed. My study nonetheless discloses that small populations of Sage Sparrows without obvious barriers or great distances between them do develop distinct songs.

ACKNOWLEDGMENTS

Charles Trost provided valuable assistance throughout this study. Support was provided by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, a Josselyn Van Tyne Research Award from the American Ornithologists' Union, and a Grant-in-Aid from Sigma Xi. The Department of Biology, Idaho State University provided equipment, supplies and library services. I thank Charles Trost and Jim Perry for stimulating discussion and my wife, Patricia, for patience and support during the field work. The manuscript was improved by the comments of D. E. Kroodsma, L. F. Baptista, R. B. Payne and two anonymous reviewers.

LITERATURE CITED

- BAKER, M. C. 1975. Song dialects and genetic differences in White-crowned Sparrows (*Zonotrichia leucophrys*). *Evolution* 29:226-241.
- 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. 1977. Geographic variation in song and dialects of the Puget Sound White-crowned Sparrow. *Condor* 79:356-370.

- BOWMAN, R. I. 1979. Adaptive morphology of song dialects in Darwin's Finches. *J. Ornithol.* 120:353-389.
- BRADLEY, R. A. 1977. Geographic variation in the song of Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*). *Bull. Fla. State Mus. Biol. Sci.* 22:57-99.
- EBERHARDT, C., AND L. F. BAPTISTA. 1977. Intraspecific and interspecific song mimesis in California Song Sparrows. *Bird-Banding* 48:193-205.
- HARRIS, M. A., AND R. E. LEMON. 1972. Songs of Song Sparrows (*Melospiza melodia*): individual variation and dialects. *Can. J. Zool.* 50:301-309.
- JENKINS, P. F. 1977. Cultural transmission of song patterns and dialect development in a free-living bird population. *Anim. Behav.* 25:50-78.
- KING, J. R. 1972. Variation in the song of the Rufous-collared Sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Z. Tierpsychol.* 30:344-373.
- KROODSMA, D. E. 1972. Variations in songs of Vesper Sparrows in Oregon. *Wilson Bull.* 81:173-178.
- KROODSMA, D. E. 1974. Song learning, dialects, and dispersal in the Bewick's Wren. *Z. Tierpsychol.* 35:352-380.
- LEMON, R. E. 1966. Geographic variation in the song of Cardinals. *Can. J. Zool.* 44:413-428.
- LEMON, R. E. 1971. Differentiation of song dialects in Cardinals. *Ibis* 113:373-377.
- 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 M. TAMURA. 1964. Culturally transmitted patterns of vocal behavior in sparrows. *Science* 146:1483-1486.
- MORGAN, B. J. T., M. J. A. SIMPSON, J. P. HANBY, AND J. HALL-CRAGGS. 1976. Visualizing interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. *Behaviour* 56:1-43.
- MORTON, M. L., J. L. HORSTMAN, AND J. M. OSBORN. 1972. Reproductive cycle and nesting success of the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in the central Sierra Nevada. *Condor* 74:152-163.
- 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.
- NOTTEBOHM, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *Am. Nat.* 109:605-624.
- OREJUELA, J. E., AND M. L. MORTON. 1975. Song dialects in several populations of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. *Condor* 77:145-153.
- PAYNE, R. B. 1978. Microgeographic variation in songs of Splendid Sunbirds *Nectarinia cocciniger*: 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: recent research and new theory*. Chiron Press, New York.
- RICE, J. O., AND W. L. THOMPSON. 1968. Song development in the Indigo Bunting. *Anim. Behav.* 16:462-469.
- SHIOVITZ, K. A., AND W. L. THOMPSON. 1970. Geographic variation in song composition of the Indigo Bunting, *Passerina cyanea*. *Anim. Behav.* 18:151-158.
- WRIGHT, S. 1943. Isolation by distance. *Genetics* 28:114-138.

Department of Biology, Idaho State University, Pocatello, Idaho 83209. Present address: P.O. Box 204, 518 S. Alta, Shoshone, Idaho 83352. Accepted for publication 27 May 1980.