SONG DIALECTS IN SEVERAL POPULATIONS OF MOUNTAIN WHITE-CROWNED SPARROWS (*ZONOTRICHIA LEUCOPHRYS ORIANTHA*) IN THE SIERRA NEVADA

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Species identification is one of the basic functions attributed to bird song, although little is known about the actual parameters which make it specific. In order to elucidate such species-specific parameters, several studies have concentrated on the evolution of intraspecific variation in song patterns. Intraspecific variations have been analyzed in terms of subunits of song. These subunits may vary in frequency distribution within a population of birds or between geographically separated populations of birds (Emlen 1972, Helb 1973).

Geographic variation in the song of a species refers to differences in song over distance and between populations which normally do not mix (Nottebohm 1969). Vocal differences occurring in neighboring populations are often called dialects. The songs of the Chaffinch (*Fringilla coelebs*) (Thorpe 1958), Cardinal (*Cardinalis cardinalis*) (Lemon 1966), and Song Sparrow (*Melospiza melodia*) (Borror 1965, Harris and Lemon 1972) show differences between neighboring populations. Additional examples have been noted by Thielcke (1969).

Vocal variation within subspecies in crowned sparrows (*Zonotrichia*) has been described by Chapman (1940), Marler and Tamura (1962), Borror and Gunn (1965), Nottebohm (1969), and Baptista (1973, 1974). Marler and Tamura (1962) showed the existence of a system of dialects for the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). They found great stereotypy among the members of a population and differences between neighboring populations. Nottebohm (1969), Egli (1971), and King (1972) also found differences between neighboring populations of Rufous-collared Sparrows (*Zonotrichia capensis*).

The present study was undertaken with the hope of providing a detailed analysis of intrapopulation and interpopulation variation of song in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada of California.

MATERIALS AND METHODS

About 1000 songs were recorded and analyzed from 142 individuals belonging to 14 breeding locations along the north-south axis of the Sierra Nevada in California. Figure 1 shows the recording locations, and table 1 lists recording locations.

Z. l. oriantha breeds in high altitude mountain meadows in the West, wherein the suitable habitat is scattered and often in limited supply. The habitat suitable for breeding can be defined in terms of five elements: grass, bare ground, dense scrub (often willows or scrub conifers), water, and tall conifers on the periphery (DeWolfe and DeWolfe 1962).

Field tape recordings were made, using a portable Uher 4000 S Report Recorder operating at 7.5 inches per second. Most of the recordings were made with an Electro-Voice A omnidirectional dynamic microphone mounted at the focal point of a fiberglass reflector 61 cm in diameter. The recorded songs were analyzed with a Kay Electric Sound Spectrograph, using the "wide" band-pass filter (300 Hz) and the high-shape circuit. The tapes were played back on an Ampex Tape Recorder (Reproducer Model 60) at 7.5 i.p.s.

The terminology of Marler and Tamura (1962) was used. The distinction made by Borror (1960) regarding the differentiation of trills and buzzes was adopted.

RESULTS

DESCRIPTION OF ADULT SONG

The song of *Z. l. oriantha* consists of a whistled portion followed by a note complex and a trilled portion. Each of these three portions typically is made up of two phrases. In some cases the trilled portion is followed by a buzz. The song is delivered loudly and repeatedly from the same singing post. The duration of song is about 2 sec and the frequency range between 2 and 6 kHz.

The songs shown in figure 2 are labeled as consisting of four to five phrases which are indicated by Roman numerals I-IV or I-V. Phrase I is a plain whistle with mid-frequency at about 3 kHz. It usually has two short breaks. It is present in all songs of *Z. l. oriantha*, although its length and frequency range vary in different locations. Phase II usually consists of a short note immediately followed by a vibrato of frequency range of

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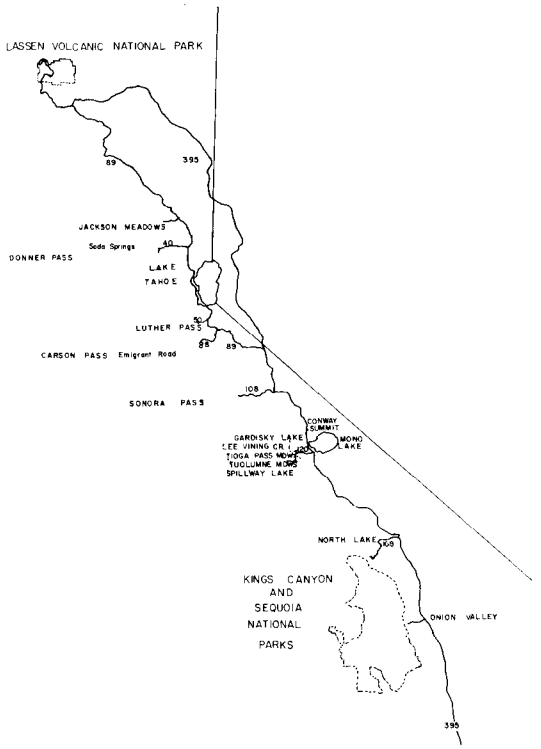

FIGURE 1. Map showing locations where *Zonotrichia leucophrys oriantha* were recorded. Numbers indicate highways.

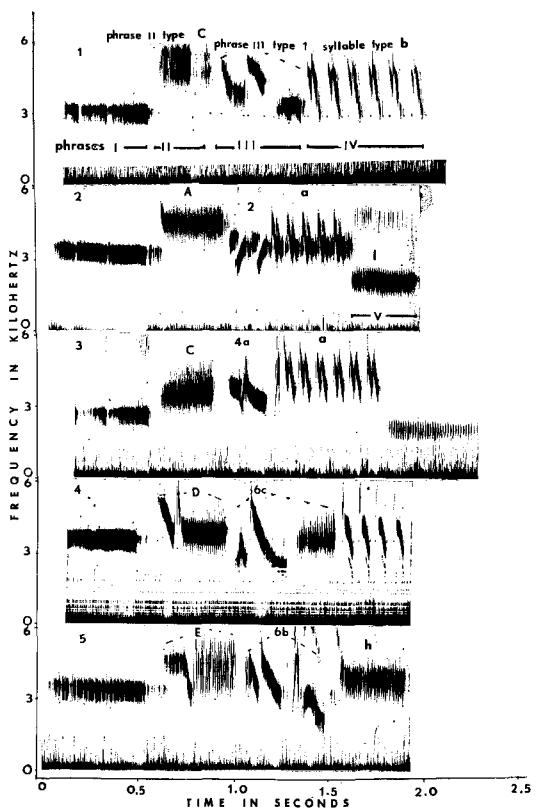

FIGURE 2. Morphological structure of five *Zonotrichia leucophrys oriantha* song patterns and terminology used in describing different parts of song. Songs of five males are shown: Spectrogram 1, individual from Onion Valley; Spectrogram 2, individual from Tioga Pass; Spectrogram 3, individual from Sonora Pass; Spectrogram 4, individual from Carson Pass; Spectrogram 5, individual from Donner Pass. Phrases indicated by roman numerals I–V. Phrase II variation indicated by capital letters A, C, D, E. Phrase III variation indicated by arabic numbers. Minor structural variations in lower case letters 1, 2, 4a, 6b, 6c. Phrase IV syllable variations indicated by lower case letters a and b. Phrase V variation indicated by h (high) and l (low).

about 2 kHz. The small note at the beginning of phrase II is absent from the songs of individuals from Onion Valley and Sonora Pass (fig. 2, spectrograms 1 and 3). Variation in this phrase is shown in the middle row of figure 3. Phrase III includes a heterogeneous aggregate of notes (note complex). The bottom row of figure 3 shows the variation in this phrase; lower case letters indicate variation of a similar theme. The first syllable of

TABLE 1. Summary of *Zonotrichia leucophrys oriantha* studied in the Sierra Nevada.

Locations	County	Latitude	No. birds	No. Songs	No. spectrograms	Distance (km)
Onion Valley	Inyo	36°45′	3	37	9	0
North Lake	Inyo	37°14′	6	35	21	60
Spillway Lake	Tuolumne	37°51′	8	42	25	152
Tuolumne Meadows	Tuolumne	37°53′	17	129	64	153
Tioga Pass Meadow	Mono	37°55′	22	152	71	155
Lee Vining Creek	Mono	37°56′	11	77	33	158
Gardisky Lake	Mono	37°57′	3	16	7	159
Conway Summit	Mono	38°05′	3	19	10	167
Sonora Pass	Mono-Tuolumne	38°18′	20	148	55	213
Carson Pass	Alpine	38°45′	25	177	80	265
Luther Pass	Alpine	—	4	25	12	—
Donner Pass	Nevada	39°17′	7	58	26	349
Jackson Meadows	Nevada	39°30′	5	73	15	364
Lassen National Park	Lassen	40°30′	8	49	28	512
Total 14	6	3°45′	142	1,037	456	512

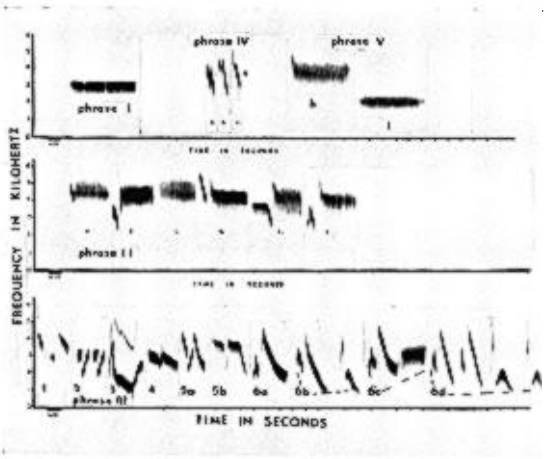

FIGURE 3. Structural features of the songs of *Zonotrichia leucophrys oriantha* in the Sierra Nevada. Top Row: Phrase I, syllables of Phrase IV: a (Tioga Pass, Sonora Pass), b (Onion Valley-North Lake), c (Carson Pass): Phrase V: high buzz (Donner Pass-Jackson Meadows), low buzz (Tioga Pass, Sonora Pass). Middle Row: Variation in Phrase II A–F: A, B (Tioga Pass), C (Onion Valley, North Lake, Sonora Pass), D, E, F (Carson Pass), E (Donner Pass-Jackson Meadows). Bottom Row: Variation of Phrase III 1–6: 1 (Onion Valley-North Lake), 2, 3 (Tioga Pass), 4, 5 (Sonora Pass), 6 (Carson Pass, Donner Pass and Jackson Meadows).

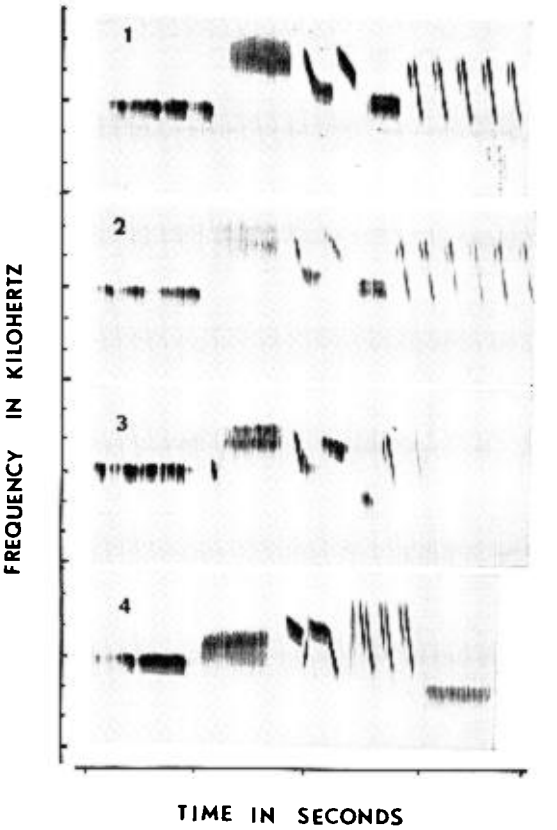

FIGURE 4. Songs of four individual Z. *l. oriantha* from the Onion Valley-North Lake area. Spectrograms 1 and 2, individuals from Onion Valley. Spectrograms 3 and 4, individuals from North Lake.

phrase IV marks the end of the note complex phrase. This trilled phrase shows some variation according to syllable type (top row, fig. 3). Individuals from Donner Pass and Jackson Meadows lack the trill phrase (fig. 2, spectrogram 5). Phrase V is the concluding phrase. It is a buzz of either high frequency (about 4 kHz) as in figure 2, spectrogram 5, or a low frequency (about 2 kHz) as in figure 2, spectrograms 2 and 3.

VARIATION IN THE INDIVIDUAL

Each bird sang essentially the same song pattern through the breeding season, with the exception of one bird. The same situation has been found in other *Zonotrichia* (Banks 1964; Borror and Gunn 1965; King 1972; Baptista 1973, 1974). A series of 10 consecutive songs was analyzed from an individual from Tioga Pass. The most common variation in pattern consisted of the addition or omission of one or more syllables in the trilled phrase (IV) or the absence of phrase V. This type of variation is similar to that reported by Marler and Tamura (1962) for Z. *l. nuttalli* and King (1972) for Z. *capensis*. The following results were obtained from measurements of songs of the Tioga Pass individual. Song duration: 1.80 ± 0.2, CV = 11.4 (mean in seconds ± one standard deviation, coefficient of variation), maximum frequency (kHz): 5.66 ± 0.34, CV = 5.9, minimum frequency: 2.0 ± 0.6, CV = 27. Almost all songs from this bird were identical in pattern. When differences were encountered, they were usually minor and generally occurred at the beginning of bouts. The relatively high coefficient of variation for minimum frequency was due to the absence of phrase V in a few songs. The overall impression from a visual inspection of the spectrograms is one of remarkable constancy and minimal variation. One variation was that with songs of more than seven syllables there was a definite reduction of frequency range from the initial syllable to the concluding syllables in the phrase.

VARIATION AMONG POPULATIONS

Onion Valley-North Lake populations. There was a small area suitable for breeding of Z. *l. oriantha* at Onion Valley. The North Lake habitat approximately 60 km north of Onion Valley was larger. Three of the six individuals recorded at North Lake showed song pattern R which was similar to song

TABLE 2. Song patterns of *Zonotrichia leucophrys oriantha* according to phrase sequence.

Locations[a]	Song[b] pattern	No. birds	% all *Z.l.o.* studied	Phrase sequence I	II	III	IV	V
Onion Valley	Q	3	2.1	I	B	1	b	–
North Lake	R	3	2.1	I	B	1	b	1
	Other[c]	3	2.1					
		9	6.3					
Tioga Pass	S	38	26.8	I	A	2	a	1
	T	21	14.8	I	B	3	a	1
	Other	2	1.4					
		61	43.0					
Sonora Pass	U	17	12.0	I	C	4	a	1
	Other	3	2.1					
		20	14.1					
Carson Pass	V	5	3.5	I	F	6a	c	–
	W	7	4.9	I	D	6c	c	–
	X	7	4.9	I	D	6c,6d	c	–
	Other	6	4.2					
		25	17.5					
Donner Pass-	Y	6	4.2	I	E	6d	–	h
Jackson Meadows	Z	4	2.8	I	E	6c	–	h
	Other	2	1.4					
		12	8.4					

[a] Locations excluded Conway Summit (3 birds), Luther Pass (4 birds), Lassen National Park (8 birds). The songs of the individuals of these populations exhibited characteristics of more than one general dialect area.
[b] Only song patterns shared by 3 or more individuals.
[c] Refers to individuals with other song patterns but not all of the same song pattern.

pattern Q, characteristic of Onion Valley birds (table 2). Song patterns R and Q were characterized by phrase III of type 1 (fig. 3, bottom row), and the syllables making up the trill phrase (IV) were of type b (fig. 3, top row). Songs of four males from Onion Valley-North Lake are shown in figure 4 (1–2 Onion Valley, 3–4 North Lake). The other three individuals had a song pattern similar to those at Sonora Pass (U).

For statistical treatment, the individuals with song patterns Q and R were treated as a group. This lumping may account for the relatively high values of the coefficients of variation in table 3. The relatively short songs were due to the few syllables (mean of 4.1) making up the trill phrase.

Tioga Pass area. Near the entrance to Yosemite National Park at Tioga Pass, there are a number of meadows which support dense

TABLE 3. Summary of song characteristics of *Zonotrichia leucophrys oriantha* in five dialect areas in the Sierra Nevada.

	OV-NL	TP	SP	CP	DP-JM
Song length[a] (sec)	1.86 ± 0.2 10.75	1.97 ± 0.2 10.15	1.99 ± 0.2 10.05	1.76 ± 0.1 11.36	2.09 ± 0.1 4.78
Maximum[a] Frequency (KHz)	5.76 ± 0.2 3.47	5.69 ± 0.3 5.27	5.90 ± 0.2 3.38	5.90 ± 0.2 3.38	5.99 ± 0.3 5.00
Minimum[a] Frequency (KHz)	2.13 ± 0.4 18.77	1.77 ± 0.2 11.29	1.99 ± 0.4 20.10	2.02 ± 0.2 9.90	1.56 ± 0.1 6.41
Song pattern	Q, R	S, T	U	V, W, X	Y, Z
Trill type[b]	b	a	a	c	—
Syllables per trill	4.1	6.0	5.5	4.0	—
Buzz type	low buzz	low buzz	low buzz	—	high buzz

[a] Mean ± standard deviation, with coefficient of variation (S.D. × 100)/$\bar{x}$ below.
[b] Syllable type in trill.

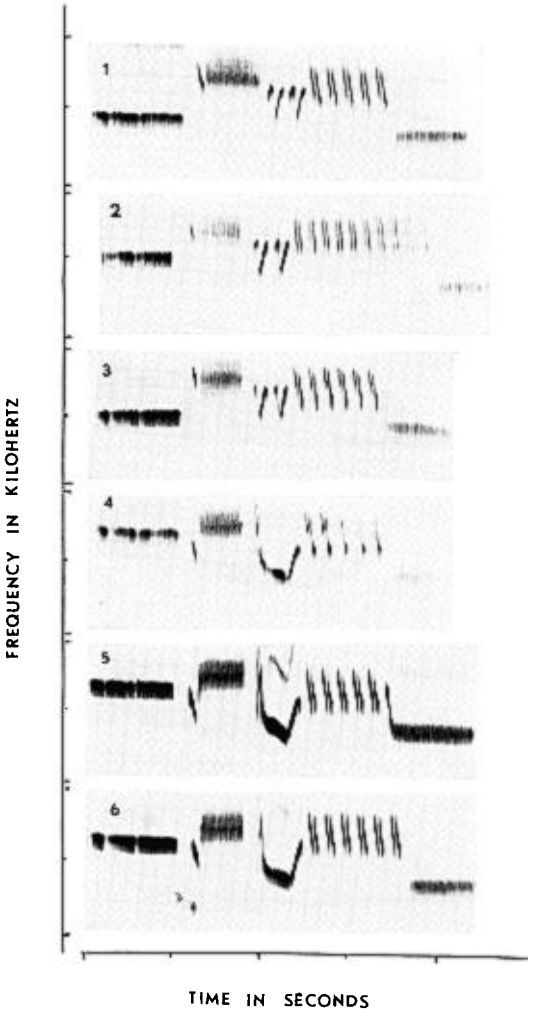

FIGURE 5. Songs of six individual Z. *l. oriantha* from the Tioga Pass area. Spectrograms 1–3, song pattern S; Spectrogram 4–6, song pattern T; Spectrograms 1 and 2, Lee Vining Creek individuals; Spectrograms 3 and 4, Tioga Pass Meadow; Spectrograms 5 and 6, Tuolumne Meadows.

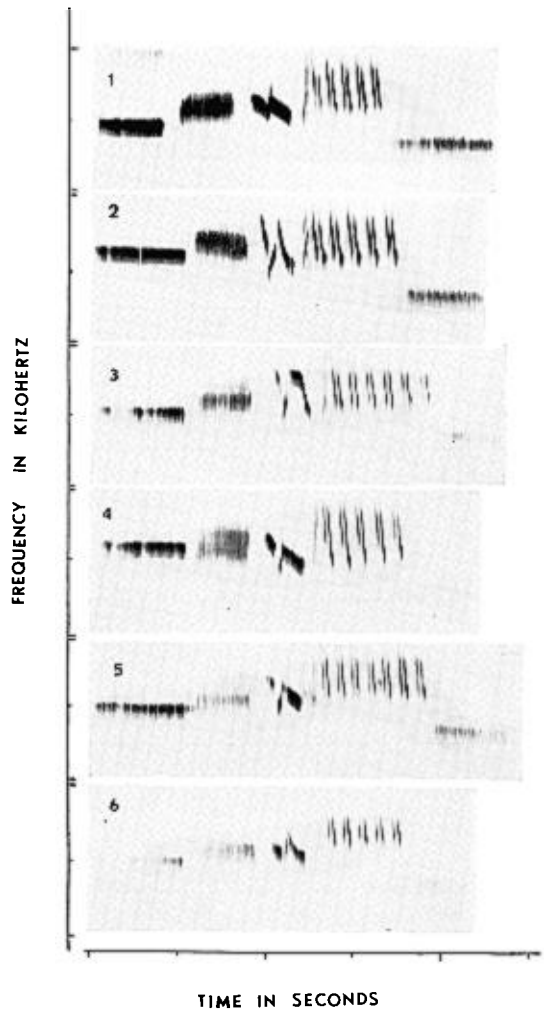

FIGURE 6. Songs of six individual Z. *l. oriantha* from Sonora Pass. There is some variation in phrase III.

populations of Z. *l. oriantha*. Birds were recorded at the following locations: Spillway Lake, Gardisky Lake, Lee Vining Creek, Tuolumne Meadows, and Tioga Pass Meadow.

Two main song patterns were represented: song pattern S (fig. 5, spectrograms 1–3) and song pattern T (fig. 5, spectrograms 4–6). The phrase sequence for the two song patterns shown at Tioga Pass are listed in table 2.

The main distinguishing features of song pattern S were phrase II of type A and phrase II of type 2. Song pattern T shows phrase II of type B and phrase III of type 3. The introductory note of phrase II was at a higher frequency level in song pattern S than in song pattern T (fig. 3, middle row, A and B, and fig. 5). Two individuals from the Tioga Pass area showed song patterns similar to Sonora Pass birds.

Statistics on 59 individuals indicate a homogenous grouping with stereotypy in song and generally low coefficients of variation in song length, frequency parameters, and repetitive units (table 3).

Sonora Pass area. Twenty Z. *l. oriantha* were recorded in a large, grassy, flat meadow. Analysis revealed one common song pattern (U), the characteristic phrase sequence of which is listed in table 2. The main distinguishing features included phrase II of type C, phrase III of type 4, trill made up of syllables type a, and a low buzz (fig. 6, spectrograms 1 and 4–6). Spectrograms 2 and 3 in figure 6 show the song pattern of three birds which varied in phrase III. Data from 17 individuals show relatively little statistical variation (table 3).

Carson Pass area. The habitat consisted of

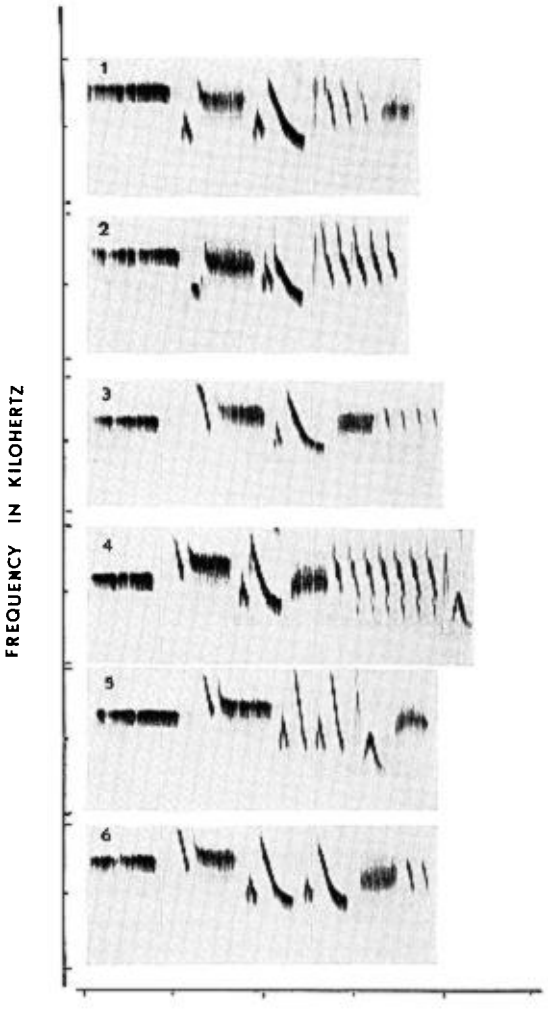

FIGURE 7. Songs of six individual Z. *l. oriantha* from the Carson Pass area. Spectrograms 1 and 2, song pattern V, eastern meadows; Spectrograms 3 and 4, song pattern W, central; Spectrograms 5 and 6, song pattern X, western meadows.

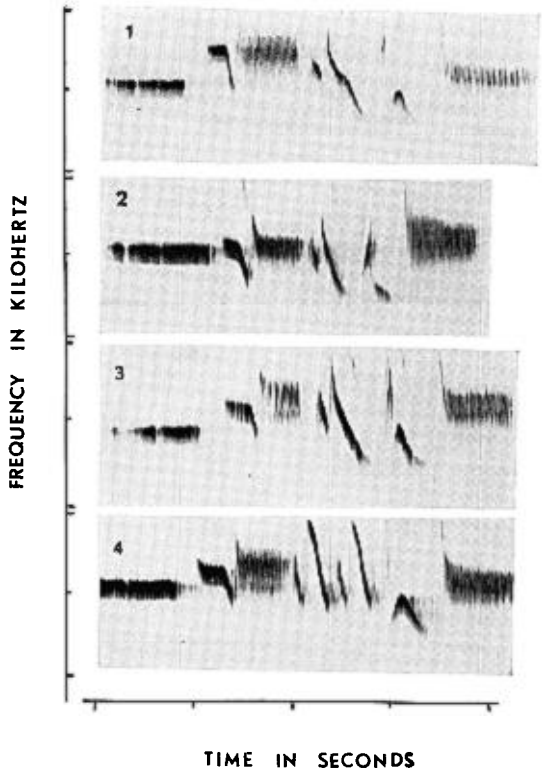

FIGURE 8. Songs of four individual Z. *l. oriantha* from the Donner Pass-Jackson Meadows area. Spectrograms 1–3, Donner Pass. Spectrogram 4, Jackson Meadows.

a series of small meadows, partially isolated from one another by tall conifers and narrowed at the ends of meadows. Five song patterns were distinguished. Of these, only three were shared by more than three individuals.

The main features of song pattern V were a high-frequency whistle (phrase I) followed by phrase II of type F and phrase III of type 6a (fig. 7, spectrograms 1 and 2). Song pattern W was characterized by phrase II of type D, phrase II of type 6c (fig. 7, spectrograms 3 and 4). Song pattern X was characterized by phrase III of type 6c with an additional slurred component and 6d with a short buzz following (fig. 7, spectrograms 5 and 6). In some individuals there was no trilled phrase (IV). All individuals from the Carson Pass area had similar syllables (type c) in the trill phrase and they lacked a terminal buzz phrase. The sequence of phrases is listed in table 2.

There was a distributional continuity of song patterns from west to east. Individuals with song pattern X tended to be concentrated in the partially isolated western meadows, A, B, and C, along the Emigrant Road (Carson Pass). Individuals with song pattern W were concentrated in the central portion of the gradient in meadows D and G, while individuals with song pattern V were concentrated in the eastern meadows, E and F. The remaining six individuals had other song patterns, but their song patterns were not shared by more than two individuals and their distribution along the gradient was random.

The most variable phrase of individuals from Carson Pass was phrase III of type 6. The Carson Pass birds showed the greatest variation in song patterns of all Z. *l. oriantha* studied. However, there was greater similarity of song patterns among individuals from this area than between Carson Pass individuals and other general areas. Statistics for Carson Pass birds are presented in table 3.

Donner Pass-Jackson Meadows populations. These two localities are separated by a distance of about 15 km. Individuals at these localities showed very similar song patterns. All birds recorded exhibited phrase II of type E, lacked a trill phrase, and showed phrase V (high buzz). The only difference between the two locations was in phrase III, which was of type 6b in Donner Pass, and of type 6d in Jackson Meadows. For this reason song patterns Y (Donner Pass) and Z (Jackson Meadows) were considered jointly (fig. 8, 1–3 for Donner Pass; 4 for Jackson Meadows). Phrase sequences are listed in table 2. Two individuals recorded near Soda Springs (Donner Pass) showed a song pattern similar to those of Carson Pass. Statistics of 12 individuals from these areas are given in table 3.

Lassen National Park. A total of eight birds was recorded, three at the southern entrance, one at Kings Meadow, and four at Hat Lake on the northern side of the park. The habitat elements in this last location seemed suboptimal for breeding of *Z. l. oriantha* (excess tall grass and woody willows with little open space).

Analysis of songs revealed a heterogeneous sample. Each individual had a song pattern different from the others (fig. 9). Three exhibited song patterns typical of other northern locations such as Sonora Pass, Carson Pass, and Jackson Meadows. One of the birds in this locality exhibited a song pattern similar to that shown by Borror (1961) for the eastern White-crowned Sparrow (*Z. l. leucophrys*). The song of the individual from Kings Meadow resembled closely the songs from Tioga Pass.

Summary. Inspection of the data presented here shows that in each general area there was a definite preference for certain song patterns with distinct characteristics of subunits of song in terms of length and frequency parameters. These characteristics fit closely Nottebohm's (1969) definition of a system of dialects.

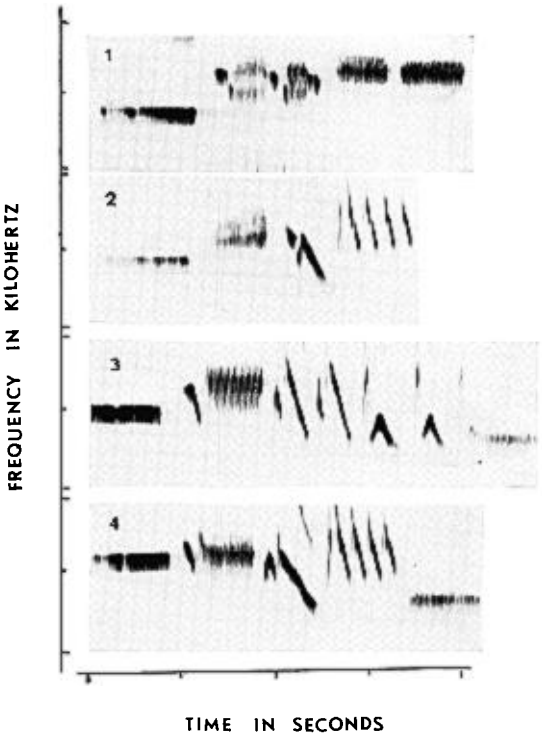

FIGURE 9. Songs of four individual *Z. l. oriantha* from the Hat Lake population (Lassen National Park). Spectrogram 1 resembles eastern WCS; Spectrogram 2 resembles individuals from Sonora Pass; Spectrogram 3 resembles Jackson Meadows individuals; and Spectrogram 4 resembles Carson Pass individuals.

DISCUSSION

SPECIES, INDIVIDUAL, AND POPULATION IDENTIFICATION

Species-specific and individual characteristics seem to occur in different parts in the song of *Z. l. oriantha.*

Parameters of song which are least variable according to coefficients of variation may function in species identification. Such parameters include phrase I, which is always present and delivered at about the same frequency, maximum frequency of song, and number of phrases. Other parameters are more variable, perhaps in response to selection for individual recognition. These include, for example, number of syllables per trill, succession of phrases, and some frequency parameters such as minimum frequency. Other parameters, such as introductory note of phrase II and choice of note-complex (phrase III), may serve as population markers due to their localized variation.

SONG VARIATION AND POPULATION STRUCTURE

Within a particular location, the constancy of song pattern appeared to be related to the size of the habitat available, the density of the breeding unit, and the degree of geographical isolation. Song variation was minimal where the population density was high, where the habitat suitable for breeding was large and continuous, and where the geographical features promoted isolation from other breeding units. This situation occurred at Tioga Pass and at Sonora Pass. At Carson Pass, on the other hand, where there was a group of small breeding units occupying reduced habitats suitable

for breeding, there was greater song variation. In areas where the habitat elements seemed suboptimal for breeding there was also great variation of song patterns, as at Hat Lake. The congregation of birds with different song patterns at Hat Lake may have been the result of a delayed snowmelt in areas more suitable for breeding. This may have caused movement of individuals away from preferred breeding areas to suboptimal habitats. The area at Hat Lake may have been a temporary "meeting place" for these individuals.

IMPORTANCE OF DIALECTS

Temporal constraints are placed upon the reproductive season of Z. *l. oriantha* due to the relatively short summer season at high altitude. In this situation it would seem advantageous to have a mechanism that minimizes the prebreeding interval on the breeding ground. A system that enhances the consistent return of individuals to breeding areas and commits them to breed in their hatching areas would receive selective encouragement. Once the birds reached the breeding areas, faster sex recognition and pairing might facilitate breeding success. A system of dialects such as the one described above might guide returning migrants to their breeding locales, thus promoting adaptation to localized variations in environment.

Several requirements must be met if such a system is to operate effectively: (1) individuals should return from year to year to breed in the same areas where they were hatched; (2) they should develop an auditory commitment to the song of the areas where they were hatched; and (3) there should be a preferential mating response toward individuals with the local song type.

During 1968–70, a banding study at Tioga Pass meadow disclosed a marked tendency for the same individuals to return to breed at the same home meadow year after year (Morton et al. 1972). Of the adults captured in 1970, 51.2% (22 of 43) of the males and 56.8% (21 of 37) of the females had been captured on the meadow during 1968 and 1969. Among returnees in 1970, six males and nine females had been hatched in Tioga Pass meadow in the previous two years. From banding records and an accurate map of the meadow, a high fidelity to the breeding locale was shown by Morton et al. (1972). Several females were found nesting in exactly the same sites as in a previous year. The Song Sparrow is another species with dialects (Harris and Lemon 1972) in which philopatry has also been documented (Johnston 1956).

Assuming that Z. *l. oriantha* responds similarly to its close relative Z. *l. nuttalli*, we have indirect evidence for the rest of the requirements. An auditory commitment to the song of the area where Z. *l. nuttalli* were hatched was demonstrated by Marler and Tamura (1964), Konishi (1965), and Konishi and Nottebohm (1969). A greater response of Z. *l. nuttalli* from one locality to songs of their own dialect was shown by Milligan and Verner (1971). We have also shown that the song patterns of Z. *l. oriantha* remain constant from year to year and that they are not randomly distributed. These different lines of evidence suggest the importance of dialects in the population structure and evolution of Z. *l. oriantha.*

Dialects may also aid in achieving some behavioral isolation of local populations, thereby increasing the ecological flexibility of the species as a whole (Marler 1970). This feature is especially important if breeding occurs in environments, such as those at high altitude, that are subject to relatively rapid, even capricious changes. The propensity of Z. *l. oriantha* to return to hatching areas, their assumed selective mating, and their partial geographical isolation may offer a favorable situation for correlating vocal and genetic differences among populations of songbird species. By means of dialects a compromise between maximum adaptation to local conditions (Nottebohm 1969) and conservation of ecological flexibility may be obtained.

SUMMARY

Song structure and variation were studied in 14 populations of Mountain White-crowned Sparrows in the Sierra Nevada in California in the summer of 1970. The song of Z. *l. oriantha*, about 2 sec long, consisted of four or five phrases making up whistled and trilled portions. Each bird sang the same song from year to year. Different parts of the song may serve to identify the subspecies, dialect, and individual.

Ten songs patterns were exhibited by Z. *l. oriantha* (common to at least three individuals) in the Sierra Nevada. When the song patterns were similar and generally restricted to common areas they were called dialects. On this basis it was possible to establish five dialect areas: (1) Onion Valley-North Lake; (2) Tioga Pass; (3) Sonora Pass; (4) Carson Pass; and (5) Donnor Pass-Jackson Meadows. Birds at Lassen National Park exhibited a

conglomerate of song patterns; therefore, they cannot be classified as representing a dialect area.

Within each dialect area there was considerable stereotypy of song pattern. Song variation was minimal in large meadows where many individuals could be heard singing. Where the habitat consisted of small, partially isolated meadows, songs were more varied. Song variation was great in marginal, suboptimal breeding habitat, as in the Hat Lake location (Lassen National Park).

If both sexes are attracted to breed in areas where they hear the song type learned in their youth, the learned song may lead to some degree of inbreeding and behavioral isolation. In this way dialects may have direct repercussion upon the genetic constitution of the populations to which they belong.

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