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GEOGRAPHICAL VARIATION IN SONG AND SONG DIALECTS OF MONTANE WHITE-CROWNED SPARROWS

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ABSTRACT.—We sampled the songs of 18 populations of montane White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in order to define their dialect groups, if any, and to explore vocal affinities with other western subspecies of *Z. leucophrys*. We found a clear-cut regional differentiation of song primarily on the basis of syllabic morphology and secondarily on the sequence of elements in the song. The birds of the Sierra Nevada and the San Bernardino Mountains of California constitute a fairly homogeneous dialect group related to another distinct group in the Warner Mountains, California, which are separated from the Sierra Nevada to the north by habitat unsuited to breeding *oriantha*. Those in two nearby but isolated desert ranges share a unique song type resembling that of *Z. l. gambelii*. *Oriantha* in the Wallowa Mountains, Oregon, to the northeast of the Steens Mountains, are allied with the dialect region of the northern Rocky Mountains. Syllabic morphology and the sequence of song elements also suggest certain vocal affinities of *oriantha* with other western subspecies of *Z. leucophrys*. For instance, the songs of *oriantha* in the Sierra Nevada, Warner Mountains, and San Bernardino Mountains have elements in common with those of *nuttalli* in central California and *pugetensis* north of the Columbia River. The songs of *oriantha* at Hart Mountain and in the Steens Mountains are very similar to those of *gambelii* in Alaska and the western Canadian Rockies. The songs of *oriantha* in the San Bernardino Mountains (a population founded after 1907) are identical with those of the central Sierra Nevada, and thus trace the origin of the founding group. We postulate that these and other data are consistent with Rand's interpretation of the subspecific differentiation of these sparrows in Pleistocene refugia.

Local sharing of song themes or parts of themes has been described in many avian taxa (e.g., Thielcke 1969, Marler and Mundinger 1971, Lemon 1975), and produces what are commonly called local "dialects." The degree of sharing may differ between subspecies or populations within a subspecies (Williams and MacRoberts 1977, 1978, Eberhardt and Baptista 1977). Before we can hope to assess why song dialects develop in some populations and not in others and the adaptive significance of dialect formation, we must continue to describe dialect systems across phylogenetic groups and ecological types (Avery and Oring 1977).

The songs of the crowned sparrows (*Zonotrichia* spp.) are the most thoroughly studied of any group (reviews in King 1972, Nottebohm 1975, Baptista 1977). Theme sharing in White-crowned Sparrows (*Z. leucophrys*) appears to be absent in the migratory subspecies *gambelii* (DeWolfe et al. 1974), but shared themes (dialects) range over large areas in the migratory form *pugetensis* (Baptista 1974, 1977) and the montane breeding populations of *oriantha* in Colorado (Baker 1975). Both of these forms appear to occupy more or less continuous habitat. Song dialects are very local in the sedentary subspecies *nuttalli* (Marler and Tamura 1962, Baker 1975, Baptista 1975), and in populations of *oriantha* in the Sierra Nevada of California (Orejuela and Morton 1975). The highly localized dialect system in *nuttalli* may result in part from the relative sedentariness of this subspecies (Blanchard 1941), whereas the local dialects in migratory Sierran *oriantha* may be attributed to patchiness of suitable habitat, each isolated meadow being an ecological island (Baker 1975, Orejuela and Morton 1975).

Between 1970 and 1978, we sampled songs of montane White-crowned Sparrows from 12 populations (Fig. 1, Table 1). Colleagues provided recordings from six additional localities. Two populations (Tioga Pass, Mount Lassen) were sampled earlier by Orejuela and Morton (1975), and allow

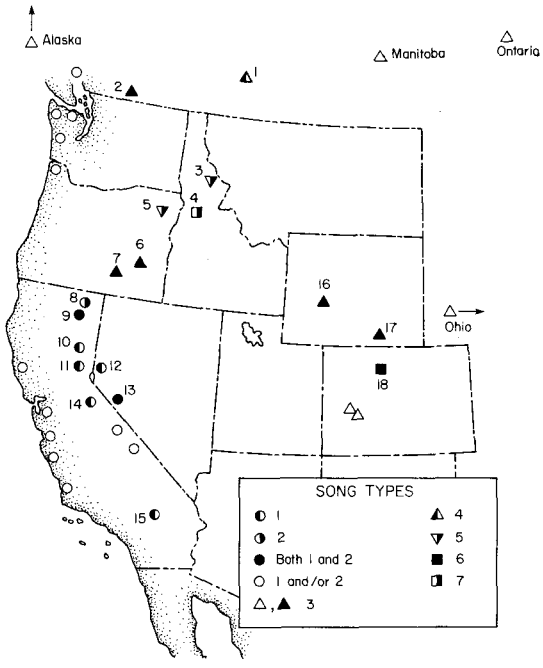

FIGURE 1. Localities (numerals correspond to sample sites in Table 1) where White-crowned Sparrow songs were recorded for this investigation (blackened or half-blackened symbols) or previously by other investigators (clear symbols).

the evaluation of the relative stability of song dialects over several years. The other samples represent northern and southern extensions of the transect made by Orejuela and Morton (1975), or other populations hitherto unsampled (Fig. 1, Table 1).

Except for two birds recorded at Manning, British Columbia, which are referable to the white-lored subspecies, *gambelii*, all birds sampled were from black-lored populations (*oriantha*). Songs from Alberta (Turner Valley) are from an intergrade zone between *gambelii* and *oriantha*.

The goals of our investigation were (1) to define further the geographic variants in the songs of *Z. l. oriantha*, (2) to ascertain the extent to which song variants ("dialects") are correlated with currently recognized subspecies or with populations and regions, and (3) to explore the use of song to trace the affinities of the subspecies and populations of *Z. leucophrys* in the western United States.

MATERIALS AND METHODS

The montane form of the White-crowned Sparrow, *Zonotrichia leucophrys oriantha*, is a migrant, typically breeding in subalpine meadows at elevations up to

TABLE 1. Gazeteer of sampled localities and numbers of birds and songs recorded.

Locality[a]	Number of birds	Number of songs
Northern Rocky Mountains:		
1. Turner Valley, Alberta	9	68
2. Manning Provincial Park, B.C.	2	17
3. Fish Lake, Idaho Co., ID	11	73
4. Smith Mountain, Adams Co., ID	1	9
Isolated Western Ranges:		
5. Wallowa Mountains, Wallowa Co., OR	13	68
6. Steens Mountains, Harney Co., OR	14	68
7. Hart Mountain, Lake Co., OR	34	157
8. Warner Mountains, Modoc Co., CA[b]	13	78
Sierra Nevada and San Bernardino Mountains:		
9. Mt. Lassen National Park, CA	14	71
10. Yuba Pass, Sierra Co., CA	3	3
11. Independence Lake, Nevada Co., CA	14	101
12. Incline Village, Storey Co., NV	1	5
13. Cottonwood Creek, Mineral Co., NV[c]	2	20
14. Tioga Pass, Mono Co., CA	8	53
15. Mt. San Gorgonio, San Bernardino Co., CA	4	37
Central Rocky Mountains:		
16. Pinedale, Sublette Co., WY	1	10
17. Medicine Bow, Albany Co., WY	1	4
18. Niwot Ridge, Boulder Co., CO	23	155
TOTALS	168	997

[a] Numbered localities correspond to numerals in Figure 1.
[b] Two localities: Bear Camp Peak/Patterson Campground and Mahogany Ridge.
[c] Wassuk range, an isolated group about 65 km east of the summit of the Sierra Nevada.

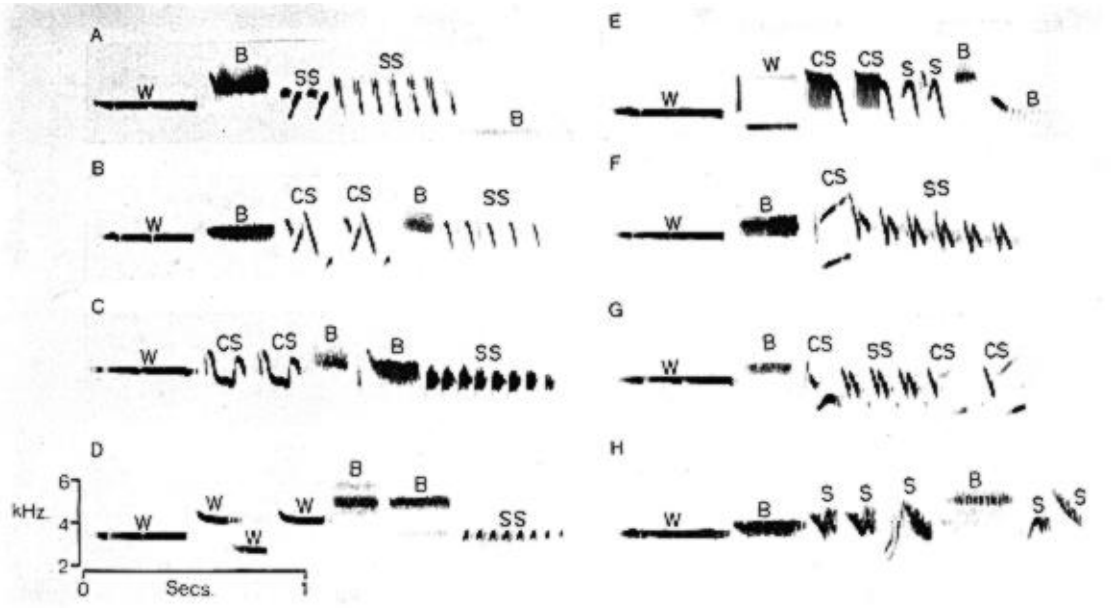

FIGURE 2. Examples of the seven song types: A. Song type 1, Tioga Pass, Mono Co., CA. B. Song type 2, Warner Mtns., Modoc Co., CA. C. Song type 3, Steens Mtns., Harney Co., OR. D. Song type 4, Turner Valley, Alberta. E. Song type 5, Wallowa Mtns., Wallowa Co., OR. F and G. Song type 6, Niwot Ridge, Boulder Co., CO. H. Song type 7, Smith Mtn., Adams Co., ID. W = whistle, B = buzz, CS = complex syllable, SS = trill of simple syllables.

about 3,700 m, and also less commonly in riparian habitat in transition-zone conifer woods and shrubsteppe vegetation as low as 1,800 m and, exceptionally, down to 1,500 m. At various points we compare the songs of *oriantha* to those of the Pacific maritime forms—*nuttalli* (nonmigrant, northern California south to Point Concepcion) and *pugetensis* (migrant, breeding from northern California to southern British Columbia)—and the northern forms—*gambelii* (migrant, breeding in Alaska and adjacent Canada) and *leucophrys* (migrant, breeding in the taiga zone from the Yukon to Newfoundland; distribution map in Cortopassi and Mewaldt 1965). Morphometric variation in these sparrows is remarkably slight in spite of their extensive breeding range. The chromatic extremes in feathering are likewise subtle (darker in the maritime forms, generally lighter in the inland and northern forms), which makes an analysis of the vocal repertoire of unusual interest, as an index of subspecific differentiation. The only clear-cut chromatic feature to which we will refer is the color of the lore: white in the westernmost forms (*nuttalli, pugetensis* and *gambelii*), black in the eastern or montane forms (*leucophrys, oriantha*), and variable in zones of intergradation (Banks 1964).

About a thousand songs were recorded from 168 individuals (Table 1). Field recordings were made on a Uher Report-S tape recorder using a Dan Gibson parabolic microphone at a tape speed of 19 cm/s. Sound spectrograms were prepared on a Kay Elemetric Sonagraph (Model 7029A) with high shape and wide band filters.

Since variation in White-crowned Sparrow song is slight within individuals (Baptista 1977:360), the cleanest spectrogram from each individual was selected for analysis of the following characters: (1) duration of each song in seconds, (2) number of elements (syllables plus phrases), (3) number of syllables in the terminal trill (4) number of kinds of elements, (5) highest frequency in kHz, and (6) lowest frequency in kHz.

TERMINOLOGY

We use the terms and symbols defined by Baptista (1977) to describe the songs of White-crowned Sparrows. Symbols are shown in brackets: *note* [no symbol]; *syllable* [S]; *complex syllable* [CS]; *whistle* [W]; *buzz* or *vibrato* [B]. In addition, we define (1) **phrase:** a whistle or buzz, excluding syllables; (2) **song type:** a fixed sequence of phrases, simple syllables and/or complex syllables characterizing a population or group of populations (Fig. 2); (3) **theme:** a song in a population containing characteristic syllable types, often shared by several, but not necessarily all, members of the population; (4) **dialect:** local or regional predominant theme or group of similar themes.

Each population or group of populations may thus be characterized by a specific song type. Several themes may occur within a song type, based on different complex syllables or variants of the terminal simple syllables (e.g., Hart Mountain, Table 3). Each population or group of populations may also have syllable types in common, placing them within a dialect area.

RESULTS

INDIVIDUAL VARIATION AND REPERTOIRE SIZE

This topic has been treated by various authors (reviewed in Baptista 1977), and will be discussed only briefly here. Individual White-crowned Sparrows usually sing only one theme throughout a season. Variation consists of additions or omissions of terminal trills, or omissions of terminal buzzes when present. Rarely, an individual varies the number of complex syllables.

At Tioga Pass, the Steens Mountains,

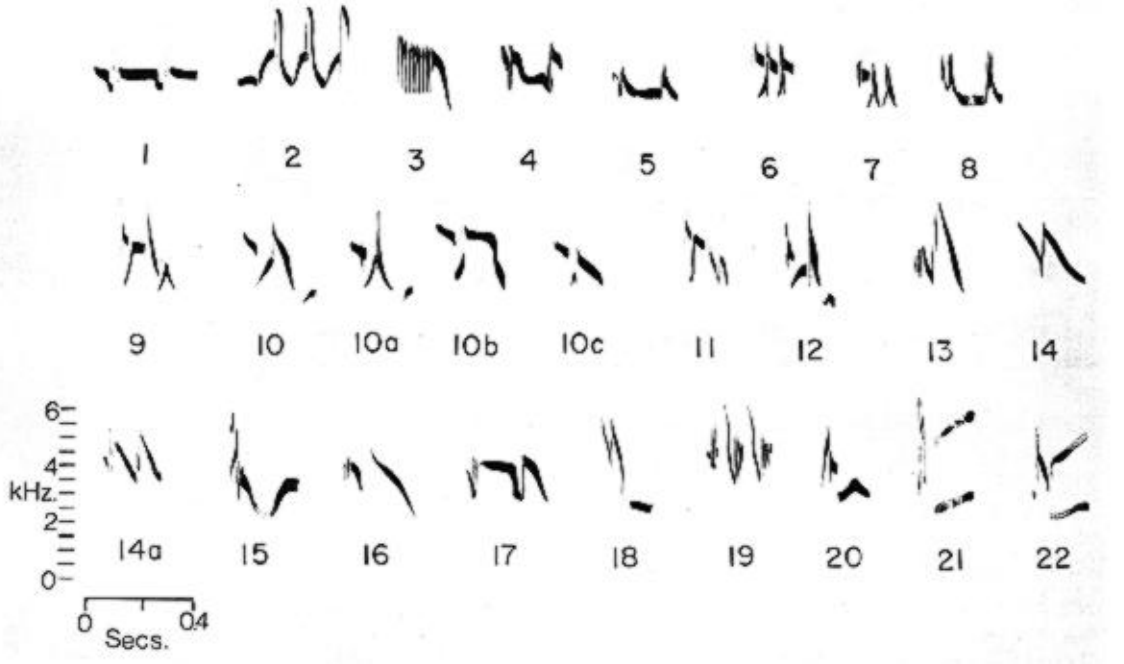

FIGURE 3. Tracings of complex syllables found in *Z. l. oriantha* songs. Except for syllable type 22, these are the first syllable types encountered in all songs. Syllable type 22 is found at the end of the terminal trills of Niwot Ridge, Colorado, songs.

Mount Lassen, Hart Mountain, and Niwot Ridge, where more than one theme was recorded for each population, one individual from each of these localities sang two of the local themes.

STABILITY OF SONG FROM YEAR TO YEAR

Our data from Tioga Pass and Mount Lassen did not contain any themes not encountered previously by Orejuela and Morton (1975). A theme recorded by Mans at Lassen in 1965 was not encountered by Orejuela and Morton, but this could be a result of sampling error. Hart Mountain was sampled in 1975 (34 birds) and again in 1976 and 1977 (11 birds). Only one bird sang a theme not recorded in 1975, but this song was aberrant for the area (see Exceptional Songs). Three color-banded birds at Hart Mountain sang the same theme over three years.

DESCRIPTION OF SONG TYPES

On the basis of the sequence of elements, we distinguish seven song types:

Song type 1. This song type consists of an opening whistle, followed by a buzz, two short trills, and then another buzz, or W-B-SS-SS-B (Fig. 2A). Either or both of the two short trills may be replaced by single complex syllables or single simple syllables (e.g., W-B-CS-SS-B). In songs of some individuals the first buzz may be absent (W-SS-SS-B).

Song type 2. This song type consists of an opening whistle, followed by a buzz, two complex syllables, a buzz, and a trill, or W-B-CS-CS-B-SS (Fig. 2B). This song differs from type 1 in the addition of a terminal trill.

Song type 3. This song type consists of an opening whistle, followed by one to five complex syllables (usually two), two buzzes, and then a long trill, or W-CS-CS-B-B-SS (Fig. 2C). The two buzzes and terminal trill are most often descending in pitch. The terminal trill may be replaced by a buzz, or W-CS-B-B-B. Sometimes the complex syllables may be replaced by a trill or W-SS-B-B-SS.

Song type 4. This song consists of four alternating low and high whistles, followed by two buzzes, and a trill, or W-W-W-W-B-B-SS (Fig. 2D). These songs differ from type 3 only in the replacement of the complex syllable(s) by three whistles.

Song type 5. This song consists of a whistle, then a note-whistle which is followed by two buzzy complex syllables, two simple syllables, and finally two buzzes, or W-W-CS-CS-S-S-B-B (Fig. 2E). The second whistle is always lower pitched than the first and

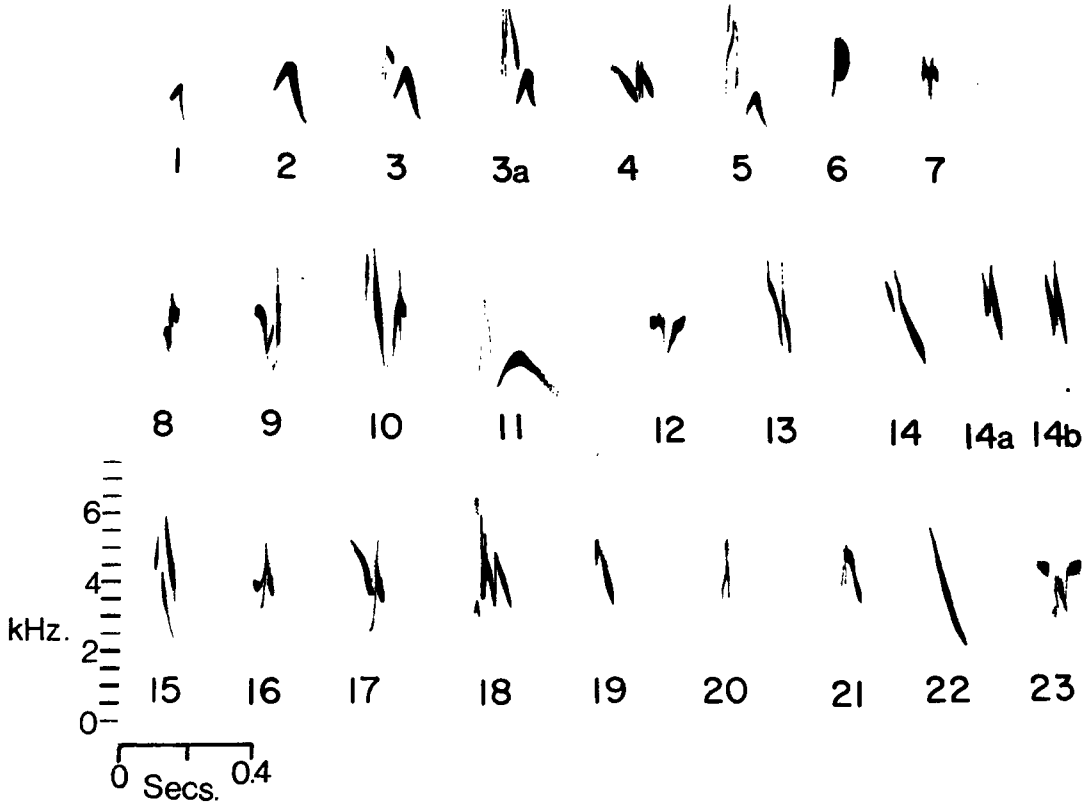

FIGURE 4. Tracings of simple syllables found in *Z. l. oriantha* songs. Except for syllable types 4 and 12, all syllables illustrated are from terminal trills. Syllable types 4 and 12 are the first syllable types in songs from Smith Mountain, Idaho, and Tioga Pass, California, respectively.

is preceded by a note. There is sometimes a faint overtone above the second whistle.

Song type 6. This song type begins with a whistle, which is followed by a buzz, then a whistle with an overtone (which is apparently harmonically unrelated), followed by a trill, or W-B-W-SS (Fig. 2F). The second whistle is preceded by a note. Because the note-whistle in song 2F (Fig. 2) is sometimes replaced by a complex syllable (Fig. 2G), we are treating it as a complex syllable and hence designate it as W-B-CS-SS (see Fig. 3, syllable 21).

Song type 7. This is based on nine indistinct recordings from one bird on Smith Mountain, Idaho. The song consists of a whistle, a buzz, two or three like syllables, one unlike syllable, a buzz, and then two unlike syllables, or W-B-S-S-S-B-S-S (Fig. 2H).

VARIATION WITHIN AND AMONG POPULATIONS

This section is included as a contribution to the archives of *Zonotrichia* vocalization. Readers not concerned with these details may wish to proceed directly to summaries presented in the Discussion section.

Turner Valley. Seven of the nine birds sampled sang song type 4. Two birds sang song type 3. One bird used complex syllable 1, and one used 2 (Fig. 3). Songs of the other seven birds contained no complex syllables. Complex syllables normally following the introductory whistle were replaced by three alternating low and high whistles (Fig. 5, songs G and H). The terminal trills of seven birds were entirely of simple syllable type 1 (Figs. 4, 5).

Manning Provincial Park. Both birds sampled sang song type 3, and both used complex syllable 1. Complete songs terminated with buzzes (Fig. 5F).

Fish Lake. The 11 birds sampled here sang song type 5, very similar to those in the Wallowas (Fig. 6). All trills began with complex syllable 3 (Fig. 3), followed by simple syllables 2 and 3 (Fig. 4).

Smith Mountain. Only one bird is represented from this population (song type 7, Fig. 2H). The recordings are not clear, but the bird appears to be using two type 4 simple syllables in its trill. The penultimate syllable may be of type 5. The rest cannot be ascertained. This song is unique in its sequencing of elements.

Wallowa Mountains. The songs of nine birds were recorded at Aneroid Lake, three at Lily Lake and one on the shores of Wallowa Lake. All birds sang song type 5 (Fig. 6). All birds began their trills with complex syllable 3, but ended differently. Eleven birds terminated their trills with simple syllable 2 followed by

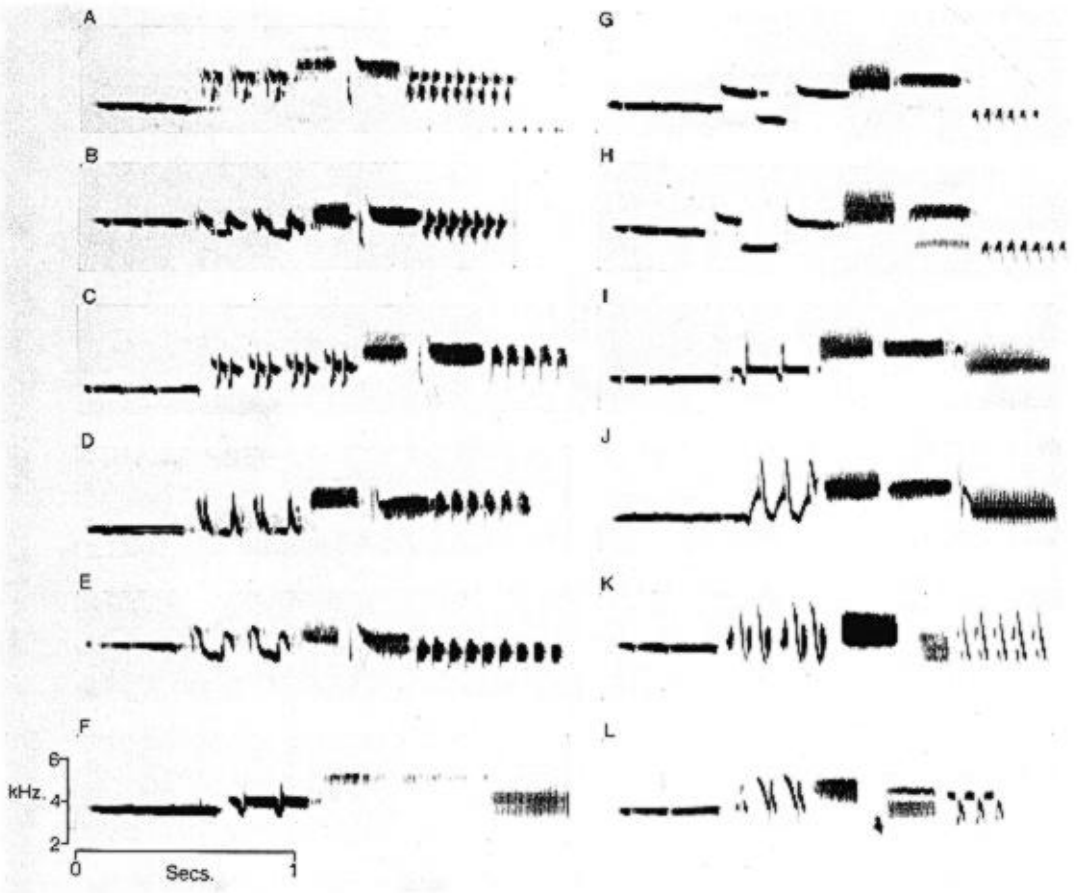

FIGURE 5. Examples of song types 3 and 4: Except for G and H, all spectrograms represent song type 3. G and H are of Song Type 4. A and B, Hart Mountain. C to E, Steens Mountains. F, Manning Provincial Park, B.C. G to J, Turner Valley, Alberta. K, Pinedale, Wyoming. L, Medicine Bow, Wyoming. Songs F, I, and J are typical of *gambelii* in Alaska. Note that in song L, the whistle is followed by a trill instead of a complex syllable. Note that all songs terminate with buzz-buzz-buzz or buzz-buzz-trill. Terminal syllables are similar within populations (e.g., songs C to E or G and H).

syllable 3, and two with syllables 1 and 3a. Syllable 3a is a variant of syllable 3 and is very similar to syllable 5 of Mount Lassen (Fig. 4).

Steens Mountains. All 14 birds sampled sang song type 3. However, based on complex syllables, four themes may be distinguished (Fig. 5). Five birds used complex syllable 5, five birds used type 6, four used type 8, and only one used type 7 (Fig. 3). The bilingual individual mentioned earlier used complex syllables 6 and 8. Terminal trills of 14 birds consisted entirely of simple syllable 6 (Fig. 4).

Hart Mountain. The songs of 34 birds were recorded. Songs of this population differ from those of the Steens Mountains only in the morphology of the terminal syllables (Fig. 5). On the basis of the complex syllables following the introductory phrases, five themes may be recognized. The two predominant themes contained complex syllable 4 (12 birds) and complex syllable 5 (10 birds). Additionally, two birds used type 6, six used type 7, and five used type 8. The bilingual individual used types 4 and 8. It is noteworthy that no birds in the Steens Mountains used type 4, and that type 7 was rare there, but was used by six birds at Hart Mountain.

Although all birds in the Steens Mountains used only one type of terminal syllable, two terminal trills are represented at Hart Mountain. Sixteen birds at Hart Mountain used syllable 7, 12 used 8.

The other spectrograms were not clear enough to identify simple syllable types.

Warner Mountains (1). All songs recorded in the Warner Mountains were of type 2 (Fig. 7). However, from the morphology of terminal syllables, two dialectal subpopulations may be recognized, one using simple syllable 9 and the second using simple syllable 10 (Table 3). The songs of 8 birds were recorded in sagebrush-riparian habitat, on the south slopes of Mahogany Ridge. Two birds used complex syllable 9, and six birds used complex syllable 10. One bird used complex syllable 10a, which is clearly a variant of 10. These same birds ended their songs with simple syllable 9 and are grouped together as singing the same dialect.

Warner Mountains (2). The songs of four birds were recorded on the west slopes of Bear Camp Peak, and one near Patterson Campground. Two birds used complex syllable 10, two used type 11, and one used type 12. One bird ended its trill with simple syllable type 9, and four used type 10. Although sample sizes were small, it is noteworthy that some differences are ap-

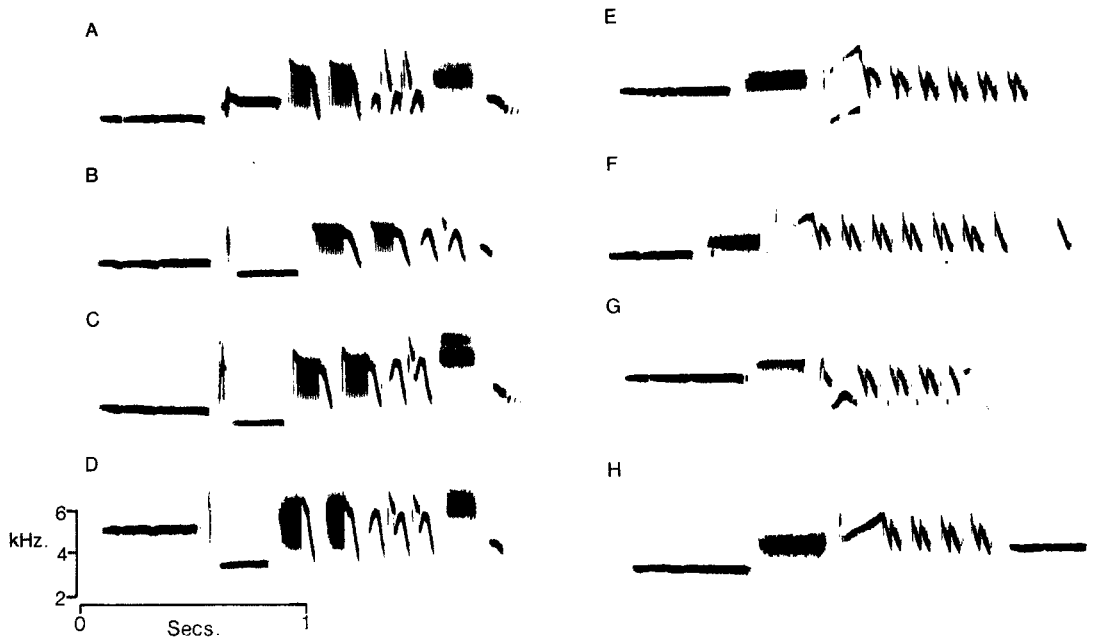

FIGURE 6. Examples of song types 5 and 6: Songs A to D are of song type 5 and E to H are of song type 6. A and B, Aneroid Lake, Wallowa Mtns., OR. C and D, Fish Lake, ID. Note similar songs at the two localities. E to H, Niwot Ridge, CO. Song H is aberrant in that there is a terminal whistle not found in other songs from the area.

parent in the terminal syllables in the two localities in the Warner Mountains. Simple syllable type 10 was not found in the Mahogany Ridge sample.

Mt. Lassen. We recorded songs from two individuals at Hat Lake in 1975. These data were pooled with the eight individuals recorded by Orejuela and Morton in 1970 and four individuals recorded by Marie Mans in 1965, giving a total of 14 birds. Eleven birds sang song type 1, two used song type 2, and one used song type 3. Orejuela and Morton (1975) recorded three birds at the southern entrance to the park, one at King's Meadow, and four at Hat Lake. Mans recorded two birds at King's Meadow, one at Hat Lake and one at Dersch Meadow.

These samples represent the most heterogeneous collection of songs encountered in our studies. Three birds sang songs from localities to the south and one bird sang a song of another subspecies; these will be treated separately later. The other 10 birds used complex syllables 13, 14, and 16, and thus resembled birds from Independence Lake and/or Jackson Meadow, Nevada County. However, three of these birds sang aberrant songs with two consecutive buzzes. One bird's song from Hat Lake began with a whistle, followed by two complex syllables (type 14), two buzzes separated by a note, a trill of three complex syllables (type 13) and one simple syllable (type 5), or W-CS-CS-B-B-CS-CS-CS-S. A song recorded at King's Meadow also had two buzzes but ended with a trill of simple syllables (W-CS-CS-B-B-SS). The latter and a second bird from King's Meadow had terminal trills with simple syllable 22 (Fig. 4) unique to these two individuals. A unique bird used complex syllable 14a (Fig. 3), which appears to be a variant of syllable 14. A bird recorded at Hat Lake in 1965, with two buzzes in its song, did not use a terminal trill (W-CS-CS-B-B). One bird at Hat Lake was bilingual, using complex syllables 13 and 14, respectively, in each of two themes.

Yuba Pass. All three birds sampled sang a similar version of song type 1. All trills began with complex syllable 13 and ended with simple syllable 11.

Independence Lake. The songs of 14 birds were recorded: one bird sang song type 3, and the rest used song type 1 (Fig. 7E). Trills of the main theme began with complex syllable 16, and were sung by 12 birds (Table 2). One bird used complex syllable 17 and one used type 13. Eleven birds used simple syllable type 11 (Table 3) and two used syllable 5. One bird's songs contained no simple syllables.

Incline Village. The single bird recorded sang song type 1, beginning its trill with complex syllable 13 and ending its song with simple syllable 5.

Cottonwood Creek. Two birds were recorded: both sang song type 2 (Fig. 7F) and both used complex syllable 18. Terminal trills were of simple syllable 13. One bird's songs lacked the buzz following the complex syllables, or W-B-CS-CS-SS.

Tioga Pass. The songs of eight birds were recorded: all sang song type 1. Both themes recorded here by Orejuela and Morton (1975) were found in this study. All eight birds ended their trills with simple syllable 14 or the variants thereof (14a, 14b) (Table 3). Five birds began their trill with simple syllable 12 (Table 3), and one bird began its trill with complex syllable 15. Two birds used complex syllables 10b and 10c, respectively. These appear to be variants of complex syllable 10. One bird was bilingual.

Mt. San Gorgonio. The songs of four birds were recorded. All sang song type 1. All birds sang the same theme (Fig. 7). The trill began with a single complex syllable 15 (Table 2) followed by a trill of type 14 simple syllables (Table 3). These songs are identical with one of the themes from Tioga Pass (Fig. 7).

Pinedale. The single bird sampled in this population sang song type 3. The two complex syllables (type 19) are unique, as are the terminal syllables (type 15).

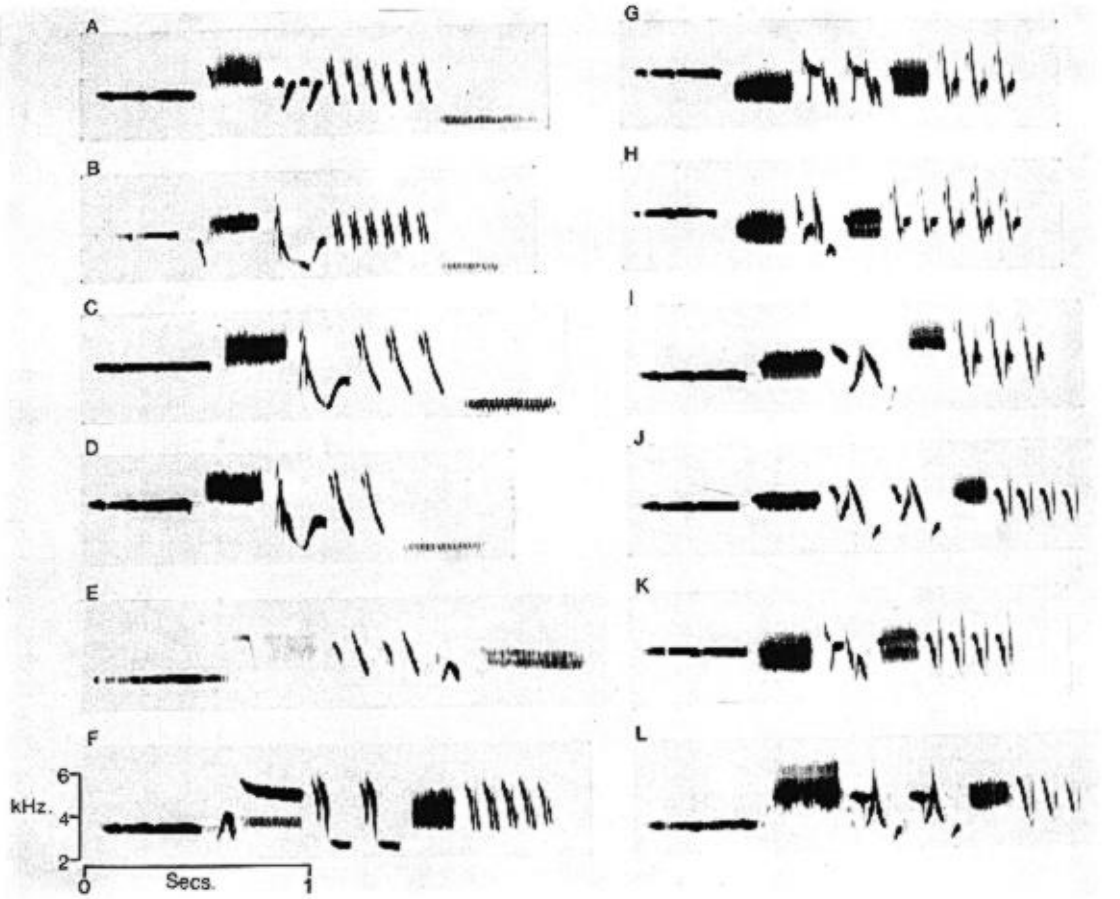

FIGURE 7. Examples of song types 1 and 2: Songs A to E are of song type 1. A and B are from Tioga Pass, CA. C and D, San Bernardino Mtns., CA. Note similarity of songs between the two locations. Song E from Independence Lake, CA. Songs F to L are of Song Type 2. Song F from Cottonwood Creek, NV. Songs G to L are from the Warner Mtns., CA. G to I are from the west slopes of Bear Camp Mountain. J to L are from south slopes of Mohogany Ridge. Note different terminal syllables from the two localities.

Medicine Bow. Only one bird was recorded, singing song type 3 (Fig. 5L). Three simple syllables following the introductory whistle were of types 16 and 17. The three terminal simple syllables were of type 23. All syllables were unique to this individual.

Niwot Ridge. The songs of 23 birds were recorded. Twenty-two birds recorded sang song type 6 (Fig. 6). Two themes are represented in the population: eight birds used complex syllable 20 and 15 used type 21. One bird's song contained no complex syllable (Fig. 8, B1). Twenty-three birds used simple syllable 18. Nine birds ended their trills with complex syllable 22. One bird (Fig. 6H) sang an aberrant song ending with a whistle. Some songs of *nuttalli* from the Point Reyes Peninsula of California regularly end with whistles (Baker 1975, Baptista unpubl.).

Thus, on the basis of morphology of complex syllables (Table 2) in central trills, from one (Mt. San Gorgonio) to five themes (Hart Mountain) may be recognized within each population. Most adequately sampled populations had terminal trills (if present) consisting of one predominant syllable type (e.g., Steens Mountains or Niwot Ridge, Table 3). Songs at Hart Mountain ended with two types of terminal trill (Table 3). Songs from the Warner Mountains also ended with two types of terminal trill that appear to be separated altitudinally, but this has to be confirmed with larger samples. Populations not sharing terminal syllable types could often be grouped according to complex syllable types in the middle portions of their songs (Table 2, e.g., Hart and Steens Mountains).

METRIC CHARACTERISTICS OF Z. *L. ORIANTHA* SONGS

To discern possible correlations between qualitative (morphological) and quantitative features of *oriantha* song, we assemble in Table 4 the mean values of several metric characteristics of the sonograms. Secondarily, this is a contribution to the growing

TABLE 2. Geographic distribution of complex syllables in Z. *l. oriantha*. See Figure 3 for syllable types.

Locality[a]	Song type[b]	Number of birds	Number of birds with complex syllable type																				
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Northern Rocky Mountains:																								
1. Turner Valley	4[c]	9	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2. Manning Provincial Park	3	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3. Fish Lake	5	11	–	–	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4. Smith Mountain	7	1[d]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isolated Western Ranges:																								
5. Wallowa Mountains	5	13	–	–	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6. Steens Mountains	3	14	–	–	–	–	5	5	1	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7. Hart Mountain	3	34	–	–	–	12	10	2	6	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8. Warner Mountains—1	2	8	–	–	–	–	–	–	–	–	2	6	–	–	–	–	–	–	–	–	–	–	–	–
9. Warner Mountains—2	2	5	–	–	–	–	–	–	–	–	–	2	2	1	–	–	–	–	–	–	–	–	–	–
Sierra Nevada:																								
10. Mt. Lassen	1 & 2	14	–	–	–	–	–	–	–	–	–	2	–	–	6	6	1	1	–	–	–	–	–	–
11. Yuba Pass	1	3	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–
12. Independence Lake	1[e]	14	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	12	1	–	–	–	–	–
13. Incline Village	1	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
14. Cottonwood Creek	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
15. Tioga Pass	1	8	–	–	–	–	–	–	–	–	–	2	–	–	–	–	2	–	–	–	–	–	–	–
16. Mt. San Gorgonio	1	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–
Central Rocky Mountains:																								
17. Pinedale	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
18. Medicine Bow	3	1[d]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19. Niwot Ridge	6	23	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	15	9

[a] See Table 1.
[b] See Figure 2.
[c] Two song type 3, seven type 4.
[d] Syllable type not clear.
[e] Thirteen sang type 1, one type 3.

TABLE 3. Geographic distribution of simple syllables in *Z. l. oriantha*. See Figure 4 for syllable types.

Locality[a]	Song type[b]	Number of birds	Number of birds with simple syllable type																						
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Northern Rocky Mountains:																									
1. Turner Valley	4[c]	9	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2. Manning Provincial Park	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3. Fish Lake	5	11	–	11	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4. Smith Mountain	7	1	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isolated Western Ranges:																									
5. Wallowa Mountains	5	13	2	11	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6. Steens Mountains	3	14[d]	–	–	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7. Hart Mountain	3	34[d]	–	–	–	–	–	–	16	12	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
8. Warner Mountains—1	2	8	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
9. Warner Mountains—2	2	5	–	–	–	–	–	–	–	–	1	4	–	–	–	–	–	–	–	–	–	–	–	–	–
Sierra Nevada:																									
10. Mt. Lassen	1 & 2	14[d]	–	–	–	–	5	–	–	–	–	3	1	–	–	1	–	–	–	–	2	2	–	2	–
11. Yuba Pass	1	3	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–
12. Independence Lake	1[e]	14	–	–	–	–	2	–	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–	–	–
13. Incline Village	1	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
14. Cottonwood Creek	2	2	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
15. Tioga Pass	1	8[d]	–	–	–	–	–	–	–	–	–	–	–	5	–	9	–	–	–	–	–	–	–	–	–
16. Mt. San Gorgonio	1	4	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–
Central Rocky Mountains:																									
17. Pinedale	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
18. Medicine Bow	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	1
19. Niwot Ridge	6	23[d]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	24	–	–	–	–	–

[a] See Table 1.
[b] See Figure 2.
[c] Two sang type 3, seven type 4.
[d] One bird sang two themes.
[e] 13 sang type 1, one type 3.

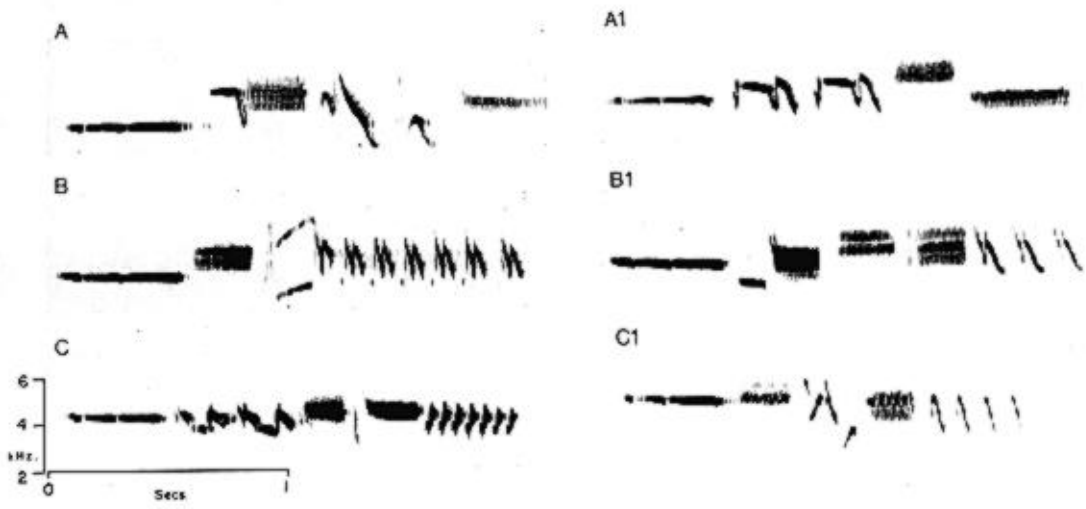

FIGURE 8. Exceptional songs in *Z. l. oriantha*. A typical song from Independence Lake, California. A1, Independence Lake bird with *gambelii* song typical of the Kenai Peninsula, AK. B, Niwot Ridge, CO. B1, Niwot Ridge bird with *Z. l. leucophrys*-like song. C, Hart Mountain, OR. C1, Hart Mountain bird with song containing syllable typical of Warner Mountains, CA (compare with Fig. 7, songs I and J).

body of comparative statistical information on *Zonotrichia* songs (e.g., King 1972, Orejuela and Morton 1975, Baptista 1975, 1977). Trends in the data and statistically significant differences (by two-tailed *t*-test) will be cited in the Discussion section.

EXCEPTIONAL SONGS IN *Z. L. ORIANTHA*

Whereas most birds at a locality sang songs typical of their area, nine individuals sang themes that were entirely or partly similar to songs from other populations (Fig. 8).

Hart Mountain. One of 34 birds recorded in 1976 sang a song containing a syllable identical with that of the Warner Mountains, California (Fig. 8, C1). The terminal syllables were not typical of any population of *oriantha* studied to date.

Mt. Lassen. Most birds here sang songs similar to those at Independence Lake. However, one bird used a theme similar to *Z. l. leucophrys* described by Borror (1961). One bird used a theme similar to that at Tioga Pass, and two sang themes typical of Sonora Pass as described by Orejuela and Morton (1975).

Independence Lake. One of 14 birds sang a song typical of *gambelii* of the Kenai Peninsula, Alaska (Fig. 8, A1). The syllables contained in its song are identical with "warble number 10" in Figure 4 of DeWolfe et al. (1974).

Tioga Pass. Two of eight birds sang songs containing syllables described by Orejuela and Morton (1975) as typical of Sonora Pass (see Fig. 3, syllables 10b, 10c). These appear to be variants of the syllables found in songs of the Warner Mountain populations (Fig. 3, syllable 10).

Niwot Range. One of 23 birds sang a song containing three consecutive buzzes followed by a trill (Fig. 8D). The syllables in the terminal trill are typical of the population. Songs with three buzzes are typical of other races of White-crowned Sparrows (see Discussion).

DISCUSSION

GEOGRAPHIC VARIATION IN THE SONG OF *Z. L. ORIANTHA*

Sources of variation. Differentiation of the songs of *oriantha* is compounded of variants of morphology (song type, or sequence of elements, and spectrographic form of syllables) and of metric features (pitch, number of elements, number of kinds of elements). Morphological features are loosely intercorrelated, as we will show later, but metric features appear to vary almost independently of song morphology. For instance, the populations of *oriantha* in the Sierra Nevada and San Bernardino Mountains (sample 9–15, Table 1) are nearly homogeneous in terms of song type and the sharing of complex syllables (Table 2). However, by dividing this region into southern (14, 15) and northern segments (9–11, Table 4) to create statistically adequate sample sizes we find that songs tend to be more complex in the south in terms of the number of elements ($P < 0.001$) and the number of syllables in the trill ($P < 0.001$). The minimum frequency of the song is higher in the south ($P < 0.001$), and the maximum frequency is also higher, but probably not significantly so ($0.1 < P < 0.2$). The two subregions are alike in the variety (number of kinds) of elements in the songs. This suffices to show that metric and morphological features are not in general covariant. Additional examples are apparent

TABLE 4. Descriptive statistics (mean ± SD, *n*) for songs of *Zonotrichia leucophrys oriantha*.

Population[1]	Duration (seconds)	Number elements	Number syllables	Number kinds of elements	Maximum freq. kHz	Minimum freq. kHz
Northern Rocky Mountains:						
1. Turner Valley, Ata.[2]	1.97 ± 0.07 (9)	10.6 ± 3.4 (9)	5.0 ± 2.6 (9)	5.6 ± 0.4 (9)	6.11 ± 0.18 (9)	2.75 ± 0.25 (9)
2. Manning, B.C.	1.52 (1)	5.0 (1)	1.0 (1)	5.0 (1)	5.50 (1)	3.00 (1)
3. Fish Lake, ID	1.97 ± 0.09 (7)	8.4 ± 0.5 (7)	4.4 ± 0.5 (7)	7.0 (7)	6.86 ± 0.22 (9)	2.66 ± 0.30 (11)
Isolated Western Ranges:						
5. Wallowa Mountains, OR	2.00 ± 0.08 (9)	8.1 ± 0.6 (9)	4.2 ± 0.4 (9)	6.9 ± 0.3 (9)	6.06 ± 0.56 (12)	2.46 ± 0.21 (12)
6. Steens Mountains, OR	1.94 ± 0.14 (14)	11.7 ± 1.5 (14)	8.6 ± 1.7 (14)	5.0 (14)	5.77 ± 0.35 (14)	2.75 ± 0.31 (14)
7. Hart Mountain, OR	1.81 ± 0.11 (25)	12.1 ± 2.9 (30)	9.4 ± 2.8 (28)	5.0 (31)	5.83 ± 0.33 (19)	2.86 ± 0.31 (18)
8. Warner Mountains, OR	1.79 ± 0.11 (13)	8.2 ± 0.9 (13)	5.2 ± 0.9 (13)	5.0 (13)	6.21 ± 0.46 (13)	2.27 ± 0.30 (13)
Sierra Nevada and San Bernardino Mountains:						
9. Mt. Lassen, CA	2.19 (1)	8.0 (1)	5.0 (1)	6.0 (1)	6.25 (1)	2.25 (1)
10. Yuba Pass, CA	2.00 ± 0.03 (3)	6.3 ± 0.6 (3)	3.3 ± 0.6 (3)	5.0 (3)	5.75 ± 0.43 (3)	1.92 ± 0.29 (3)
11. Independence Lake, CA	2.03 ± 0.21 (13)	5.8 ± 0.9 (13)	2.8 ± 0.7 (13)	5.0 (13)	6.48 ± 0.28 (14)	2.04 ± 0.36 (14)
9 + 10 + 11	2.03 ± 0.19 (17)	6.1 ± 1.0 (17)	3.0 ± 0.9 (17)	5.0 ± 0.4 (17)	5.57 ± 0.35 (18)	2.03 ± 0.34 (18)
12. Incline Village, NV	1.71 (1)	6.0 (1)	4.0 (1)	5.0 (1)	6.00 (1)	2.75 (1)
14. Tioga Pass, CA	2.00 ± 0.07 (6)	11.4 ± 1.1 (7)	8.4 ± 1.1 (7)	5.0 (7)	6.21 ± 0.19 (6)	2.13 ± 0.14 (6)
15. Mt. San Gorgonio, CA	1.76 ± 0.19 (4)	7.0 ± 0.8 (4)	4.0 ± 0.8 (4)	5.0 (4)	6.19 ± 0.13 (4)	2.38 ± 0.25 (4)
14 + 15	1.91 ± 0.18 (10)	9.8 ± 2.4 (11)	6.8 ± 2.4 (11)	5.0 (11)	6.20 ± 0.16 (10)	2.23 ± 0.22 (10)
Central Rocky Mountains:						
18. Niwot Ridge, CO	1.84 ± 0.15 (21)	9.2 ± 1.4 (21)	7.0 ± 1.6 (21)	4.4 ± 0.6 (22)	6.23 ± 0.34 (21)	2.24 ± 0.23 (21)

[1] Population numbers correspond to those in Table 1.
[2] Includes two birds singing pure *gambelii* songs.

from a comparison of Tables 2, 3, and 4. Finally, with exceptions to be noted later, we find no regional clusters of metric features that can be consistently associated with populations of *oriantha* or with the morphological features of their song. We therefore turn to the latter to explore geographic variation and regional dialects.

Morphological song variants and dialects. The form of the complex syllables provides the clearest regional differentiation of themes, as we attempt to show in the boxed groups in Tables 2 and 3. Complex syllables 1, 2 and 3, and simple syllables 1–3 are shared by populations of the northern Rocky Mountains and the Wallowa Mountains. *Oriantha* in the Wallowas share song type 5 (and complex syllable 3) with the population at Fish Lake in the Bitterroot Range of the Rocky Mountains, about 200 km eastward, but show no vocal affinities to more southerly populations. This might be expected, since the avifaunas of the Wallowas and other isolated eastern ranges of the Great Basin share features with those of the nearby Rocky Mountains (e.g., Miller 1939, Behle 1963, Johnson 1978).

The Steens Mountains are about 290 km southwest of the Wallowas, and Hart Mountain is about 80 km southwest of the Steens. These ranges are separated from each other and from nearby ranges (Wallowas and Warners) by dry shrubsteppe plains that are not inhabited by White-crowned Sparrows during the breeding season. The songs of *oriantha* in the Steens and at Hart Mountain are alike in sequence (song type 3), which they share also with remote populations in the Rocky Mountains. They are also alike, but distinct from all other populations, in sharing complex syllables 5–8 (Table 2), but differing in simple syllables (Table 3). Furthermore, they are statistically indistinguishable from each other in metric features (Table 4), but differ from the nearby populations in the Wallowas and Warners. The birds of the Steens-Hart dialect group are thus allied with the Rocky Mountain populations through song type 3, but their relative isolation has apparently led to the acquisition of a unique syllabic morphology. This situation resembles that which Lein (1979) reported for a disjunct "island" population of *oriantha* in the Cypress Hills of southeastern Alberta, 250–300 km east of the main populations in the northern Rocky Mountains. The *oriantha* of the Cypress Hills utter a song that is distinct from the songs of *oriantha* in the cordillera with regard to type (sequence of elements), and is likewise richer in the number of kinds of elements.

The next dialect region southward from Hart Mountain (about 65 km) appears to be centered in the Warner Mountains. This range is the northeastern extension of the Sierra Nevada, but is separated from the cordillera by low-lying countryside unsuited to breeding *oriantha*. Our samples from the Warner Mountains include a unique assemblage of complex syllables (9–12, Table 2) that overlap with those of the northern and southern Sierra Nevada at Mount Lassen and Tioga Pass, respectively. Simple syllable 9 is also unique to the Warner populations, and simple syllable 10 is shared with the population at Mount Lassen (Table 3). The birds of the Warner Mountains utter song type 2, which occurs also in the Mt. Lassen population as well as in the Wassuk Range of western Nevada (Cottonwood Creek, Table 2) but not elsewhere among our samples. In most metric features, the songs of the Warner Mountains are intermediate between those of Hart Mountain and the northern Sierra Nevada (Table 4). In short, the available evidence strongly suggests that the birds of the Warner dialect group are related more closely to those of the northern Sierra Nevada than to those of the northern Rocky Mountains or the intervening desert ranges.

From Mt. Lassen southward in the Sierra Nevada to Mt. San Gorgonio we find another cluster of populations that share unique complex syllables (13, 15, and 16, Table 2) and song types 1 or 2. The clustering of simple syllables is not so clear, and we are unable to depict it effectively by boxes in Table 3. Simple syllables 5, 11, and 14, however, are both nearly unique to this region and shared by a substantial range of its population. Simple syllable 5 may also occur at Smith Mountain, in the northwestern Rockies, but the spectrogram is poor and our interpretation is uncertain. In sum, on the basis of the relative homogeneity of the nearly exclusive song type 1 and various syllables, we regard the Sierra Nevada as a dialect region related to that of the Warner Mountains.

The distinct dialect regions that occur in the western axis of the distribution of *oriantha* are not accompanied by morphometric disjunctions or clines (Miller 1941, Banks 1964). On the basis of plumage color ("darker and more grayish"), Oberholser (1974) proposed a new subspecies (*Z. l. aphaea*) as the breeding form of the northern Rockies in Idaho and northwestern Wyoming.

TABLE 5. Distribution of song types in five subspecies of White-crowned Sparrows.

Population	Subspecies	Song types			Source
		1 and/or 2[1]	3 and/or 4[2]	Other	
Coastal British Columbia	*pugetensis*	+			Baptista 1977
Coastal Washington	*pugetensis*	+			Baptista 1977
Coastal Oregon	*pugetensis*	+			Baptista 1977
Bodega Bay, CA	*nuttalli*	+			Baptista, unpubl.
San Francisco Bay, CA	*nuttalli*	+			Baptista 1975
San Mateo, CA	*nuttalli*	+			Baker 1974
Carmel, Monterey Co., CA	*nuttalli*	+			Blanchard 1941; Baptista, unpubl.
Morro Bay, CA	*nuttalli*	+			Baptista, unpubl.
San Bernardino Mtns., CA	*oriantha*	+			This study
Sierra Nevada, CA	*oriantha*	+			Orejuela & Morton 1975
Mt. Lassen, CA	*oriantha*	+			Orejuela & Morton 1975
Incline Village, NV	*oriantha*	+			This study
Warner Mtns., CA	*oriantha*	+			This study
Hart Mtn., OR	*oriantha*		+		This study
Steens Mtns., OR	*oriantha*		+		This study
Wallowa Mtns., OR	*oriantha*			+	This study
Smith Mtn., ID	*oriantha*			+	This study
Fish Lake, ID	*oriantha*			+	This study
Turner Valley, Alberta	*oriantha*		+		This study
Niwot Ridge, CO	*oriantha*			+	This study
Kebler Pass, CO	*oriantha*		+		Baker 1975
Pinedale, WY	*oriantha*		+		This study
Alaska	*gambelii*		+		DeWolfe et al. 1974
Manning, BC	*gambelii*		+		This study
Ohio	*leucophrys*		+		Borror 1961[3]
Ontario	*leucophrys*		+		W. W. Gunn, unpubl.[3]
Manitoba	*leucophrys*		+		W. W. Gunn, unpubl.[3]

[1] Song types 1 and 2 are similar, differing only in the presence of a terminal trill in the latter, i.e., W-B-SS-SS-B versus W-B-SS-SS-B-SS. SS may be replaced by CS in some themes.
[2] Song types 3 and 4 are similar, differing only in the absence of complex syllables in the latter, i.e., W-$(CS)_n$-B-B-SS versus W-$(W)_n$-B-B-SS. The subscript n denotes a variable number. Type 4 was found only in the Canadian Rockies.
[3] Spectrograms in Moore Laboratory of Zoology.

Browning (1974) disagreed, and maintained that the breeding birds of Idaho are of the nominate subspecies (*Z. l. leucophrys*). Our data are not adequate to resolve this issue, although we present later some speculations about subspecific affinities. In any case, the data that we have already presented demonstrate that dialect regions in this species are not concordant with subspecific limits as defined by traditional morphometric or chromatic traits.

We have only scattered samples of *oriantha* songs beyond the limits of the western axis just described, but mention them here as a contribution to what we hope will become a more thorough spectrographic atlas. A fairly large sample from a subalpine meadow near Niwot Ridge in the Front Range of Colorado sings song type 6, a sequence unlike any recorded in the western populations, and likewise utters distinctive syllables (Tables 2, 3; Figs. 3, 4). This repertoire differs from recordings of *oriantha* obtained by Baker (1975) in the central Rocky Mountains about 175 km southwest of Niwot Ridge near Crested Butte. All of Baker's birds sang song type 3.

A single bird from Medicine Bow, Wyoming, sang song type 3, and was the only bird in our samples that uttered three syllables following the introductory whistle. Finally, we have spectrograms from a single sparrow near Pinedale in the Wind River Mountains (a spur of the central Rockies) in Wyoming. This bird sang song type 3, but with a complex syllable unlike those of *oriantha* in Colorado or *gambelii* in southern Canada (Table 2).

COMPARISONS WITH OTHER SUBSPECIES

By combining similar element sequences into song-type groups we can discern various patterns of similarity and difference among the recognized subspecies of White-crowned Sparrow. These are accompanied by similarities and differences in clusters of syllable types.

Songs from populations 9 through 13 (Table 5) from the western cordillera and the Warner Mountains are similar in the sequencing of their elements to songs of *Z. l. pugetensis* north of the Columbia River (Baptista 1977) and to the songs of some populations of *nuttalli*, most obviously

those from Lake Merced near San Francisco. Some of the syllables in these *oriantha* populations also resemble those of *nuttalli* and *pugetensis*. Syllables 1 and 2 (Fig. 4) are similar to terminal syllables of *nuttalli* from the Presidio of San Francisco (Baptista 1975). Syllable 11 (Fig. 4) is similar to the terminal syllables of *nuttalli* from Marin County (Baker 1975). Syllable 22 (Fig. 4) is identical with *pugetensis* syllable 11 (Fig. 4 of Baptista 1977).

Songs of *oriantha* from Hart Mountain and the Steens Mountains are identical in sequencing to songs of *gambelii* in Alaska, although the number of different syllables (=warbles of DeWolfe et al. 1974) in *gambelii* songs (1–2) is fewer than in *oriantha* songs (1–6). The form of the syllables, however, is almost identical in *gambelii* and *oriantha* (compare syllables 4, 5, and 6 [Fig. 3] of Hart Mountain and the Steens Mountains birds with warbles 3, 6, 7, and 8 of Fig. 4 in DeWolfe et al. 1974). The trained ear immediately recognizes these songs as similar, if not identical, to those of *gambelii*, although these populations consist entirely of black-lored individuals (Banks 1964, this study). The nearest known population of undoubted *gambelii* (white-lored) is at Hart's Pass in the Cascade Mountains of northern Washington, about 650 km from the Steens Mountains. (Although Banks [1964] reported one black-lored individual among four collected here, observations of many free-living birds make it clear that this is exceptional. All others observed at Hart's Pass had white lores [Farner 1958, pers. observ.].)

One possible explanation for this enigma is that the ancestor of *Z. l. gambelii* in Alaska was red-backed, sang a song similar to that of extant populations, but was polymorphic for lore-color as suggested by Banks (1964). The ancestral *gambelii* may have ranged further south (to Hart Mountain and the Steens Mountains). Owing to differential selection, the northern populations were selected for white lores whereas the southern populations were selected for black lores, and thus resembled their relatives from a southern refugium (next section). Thus, Steens and Hart Mountain birds may represent remnants of populations that came south from Alaska after the ice sheet receded.

THE AFFINITIES OF *Z. L. ORIANTHA* IN THE SAN BERNARDINO MOUNTAINS

Grinnell (1908) thoroughly surveyed the vertebrate fauna of the San Bernardino Mountains in 1906–1907 and did not find any White-crowned Sparrows. Small (1956) subsequently reported one breeding pair in this range at Mt. San Gorgonio. In 1977 we found four breeding pairs there, two of which were attending nestlings or fledglings on 7 July 1977. The songs of this population are identical with those at Tioga Pass, about 450 km northward (Orejuela and Morton 1975). The populations of *oriantha* nearest to those at Mt. San Gorgonio are in southern Sequoia National Park, about 300 km to the north. It is thus reasonable to speculate on the basis of song morphology and proximity that the founders of the Mt. San Gorgonio population are from the southern Sierra Nevada.

Populations of *oriantha* on the periphery of their breeding range may reflect the tenuous equilibrium with environmental constraints that we might expect at such geographical limits. DeWolfe and DeWolfe (1962), in fact, documented several verifiable or probable extinctions of populations of *oriantha*, particularly at the northwestern limits of their range in the Cascade Mountains of southern and central Oregon. The colonization of Mt. San Gorgonio is the inverse of this, and the data available at present, while too sparse for conclusive generalizations, suggest a contraction of geographical range in the north and an expansion in the south. Balda et al. (1970) have previously documented a southern expansion of *oriantha* from New Mexico to the San Francisco Mountains of Arizona.

SONGS IN A ZONE OF INTERGRADATION BETWEEN TWO SUBSPECIES

Two of the nine White-crowned Sparrows whose songs were recorded at Turner Valley, in the eastern foothills of the Canadian Rockies, were identical in the sequencing of elements and in syllabic morphology with *gambelii*. The syllables used by these two individuals are identical with warbles 1 and 2 of Alaskan *gambelii*, as reported by DeWolfe et al. (1974). The other seven birds uttered songs like those of migrating *leucophrys* recorded in Ohio. The complex syllables in these songs have been replaced by three whistles. Otherwise the songs are similar in sequencing of elements to those of *oriantha* in other parts of the Rockies (Baker 1975, Lein 1979). They represent part of Banks' (1964) northern Rocky Mountain intergrade population between *oriantha* and *gambelii*. At Turner Valley, about 75% of the breeding White-crowned Sparrows have black lores (Lein, pers. comm.), thus ap-

proximating the proportion (78%) of *oriantha*-like songs in our small sample. While it is of interest that birds in a zone of intergradation utter songs of two subspecies, we have already noted in our samples from Hart Mountain and the Steens Mountains that there is no mandatory linkage between lore color there (black) and song type, since these birds mimic the songs of white-lored *gambelii*.

EXCEPTIONAL SONGS

We described in the Results five cases in which individual sparrows consistently uttered themes not typical of the local population. These exceptional themes could result either from (1) dispersal of an individual to a distant breeding site in the year after it had learned the theme of its natal locality, or (2) "misimprinting"—learning the theme of an alien tutor encountered during migration or in winter. In the cases in which an individual sings the theme of a distant population of its own subspecies (e.g., cases at Hart Mountain and Tioga Pass; see Results) the mismatch with the local dialect may result from long-distance dispersal and a lapse from philopatry. This is unlikely, however, when an individual sings the theme or dialect of a different subspecies (e.g., Mt. Lassen, Independence Lake, Niwot Ridge), and we suggest that at least these cases result from the belated learning of song from an alien tutor. The arguments favoring this hypothesis involve both the capacity and the opportunity for learning alien songs.

With regard to capacity, laboratory experiments have shown that both *nuttalli* and *oriantha* can learn songs from other subspecies (Petrinovich *in* Baptista 1974; Baptista, unpubl.). Field studies suggest strongly that *nuttalli* occasionally learn songs from overwintering *pugetensis* or from birds in passage (Baptista 1974, 1977, Baptista and Wells 1975). Sometimes, only portions of songs from winter visitors or from migrants may be incorporated into the songs of *nuttalli* (Baptista 1975). The postnatal period during which crowned sparrows learn and stabilize their song pattern has not been determined. Experiments with hand-reared *nuttalli* exposed to tutor tapes in the laboratory indicated that song learning ceases at about 50 days of age (Marler 1970). We have records, however, of a single color-banded *nuttalli* from the Presidio of San Francisco, California, that changed its song between its first and second breeding seasons (Baptista, unpubl.). This suggests that the period of song learning and stabilization may be more plastic than has been revealed thus far by experimental studies. The social context of song learning in *Zonotrichia* has not been investigated although social effects on the song patterns of other taxa are well known (Thielcke 1970, Kroodsma 1974, Verner 1975, Payne and Payne 1977, Jenkins 1978, Todt et al. 1979). A live male in a natural setting may be a more effective tutor than a tape-recording.

Last, with regard to opportunity for tutoring by alien males, we note that late-hatched *oriantha* encounter early migrants in passage belonging to the races *gambelii* and *oriantha* from more northerly localities (Morton et al. 1973:83; Mewaldt and King, unpubl.). *Oriantha*, *nuttalli*, and *pugetensis* intermix on their wintering grounds in California, and *oriantha*, *leucophrys*, and *gambelii* do so in Arizona (Phillips et al. 1964; King, unpubl.) and probably also in northern Mexico. Wintering *gambelii* and *leucophrys* may overlap in western Texas. Although singing by migrating or wintering individuals is much less frequent than on the breeding grounds, it is nevertheless not uncommon, especially during violations of individual distance (Baptista, pers. observ.).

In sum, young *oriantha* have both the capacity and the opportunity for learning songs from alien tutors even though this is undoubtedly not the norm. We hypothesize that this accounts for the exceptional songs that we have described. For instance, the individual at Independence Lake appears to have learned an entire *gambelii* song. The exceptional individual at Niwot Ridge (Fig. 8, B1) might have learned its song from more northerly *oriantha* or *gambelii*. Orejuela and Morton (1975) pointed out that an exceptional song recorded at Mt. Lassen resembled songs of eastern populations of *leucophrys* described by Borror (1961). Lein (1979) discovered a black-lored bird singing a *gambelii* song in a disjunct population of *oriantha* in the Cypress Hills of Alberta.

SONG AND THE AFFINITIES OF THE SUBSPECIES

Rand (1948a, b) postulated that the ancestors of the currently recognized subspecies of White-crowned Sparrows originated from four different refugia isolated during glacial times. These refugia parallel those postulated for four extant forms of spruce (*Picea*) by Halliday and Brown (1943).

According to Rand's schema, *Z. l. gambelii* originated in an unglaciated Yukon refugium paralleling *Picea glauca albertina*. In post-glacial times, these birds spread

eastward, meeting *Z. l. leucophrys* which had evolved in a northeastern refugium. A southern refugium in the Rocky Mountains gave rise to *oriantha,* paralleling *P. engelmanii. Picea sitchensis,* which survived maximum glaciation south of the ice, moved northward along the Pacific Coast, paralleling *Z. l. nuttalli-pugetensis.*

Banks (1964) disputed this schema, arguing that it implied an improbably close relationship between the montane and coastal populations, which would have arisen from the southern refugium. Banks also maintained that Rand's schema masked the close relationship between the montane birds and those of eastern Canada (both forms with reddish backs), and the relationship between coastal birds and *gambelii* (both with white lores). His alternative theory proposed that the ancestors of *gambelii-oriantha* were once a continuous red-backed population, polymorphic for lore color, ranging from Alaska to the western mountains. At some later date there was differential selection for lore color, with the result that black-lored forms predominated in the lower latitudes (*oriantha*), and white-lored forms to the north (*gambelii*). Banks proposed that a southern spread of *Z. l. gambelii* down the Pacific Coast gave rise to *Z. l. pugetensis-nuttalli,* which evolved in subsequent isolation.

Hubbard (1969) agreed with and expanded on Rand's ideas. If their schema is correct, then the remarkable similarity between songs of western montane populations of White-crowned Sparrows (*oriantha*) and those of the Pacific Northwest (*nuttalli-pugetensis*; Table 5) may not be coincidental. If similarity in song indicates relationship, then *oriantha* and *pugetensis-nuttalli* both arose from a southern refugium. They may have once formed part of a continuous red-backed population, isolated very early from the Rocky Mountain birds. We further theorize that *Zonotrichia l. nuttalli-pugetensis* was subsequently isolated from *oriantha* and invaded the Pacific Northwest. The paleobotanical data (Fig. 7 in Hubbard 1969) appear to support a continuum between coastal and Sierran boreal regions during the Pleistocene. The dark backs of the coastal forms might have been acquired still later in isolation from the montane form in response to the more mesic maritime climate. House Sparrows (*Passer domesticus*) have acquired regional differences in plumage color within 70 years since their introduction to North America (Johnston and Selander 1964). House Finches (*Carpodacus mexicanus*) introduced from California into the eastern United States showed color changes within nine years after introduction (Aldrich and Weske 1978). Our data on song conflict with the importance of back color as evidence of taxonomic relationship, as proposed by Banks (1964), and support the conclusions of Rand and Hubbard.

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LITERATURE CITED

ALDRICH, J. W., AND J. S. WESKE. 1978. Origin and evolution of the eastern House Finch population. Auk 95:528–536.

AVERY, M., AND L. W. ORING. 1977. Song dialects in the Bobolink (*Dolichonyx oryzivorus*). Condor 79:113–118.

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

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

BALDA, R. P., G. WEISENBERGER, AND M. STRAUSS. 1970. White-crowned Sparrow (*Zonotrichia leucophrys*) breeding in Arizona. Auk 87:809.

BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrow *Zonotrichia leucophrys*. Univ. Calif. Publ. Zool. 70:1–123.

BAPTISTA, L. F. 1974. The effects of songs of wintering White-crowned Sparrows on song development in sedentary populations of the species. Z. Tierpsychol. 34:147–171.

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 Sparrows. Condor 79:356–370.

BAPTISTA, L. F., AND H. WELLS. 1975. Additional evidence of song-misimprinting in the White-crowned Sparrow. Bird-Banding 46:269–272.

BEHLE, W. H. 1963. Avifaunistic analysis of the Great Basin region of North America. Proc. XIII Int. Ornithol. Congr. (1962):1168–1181.

BLANCHARD, B. D. 1941. The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publ. Zool. 46:1–178.

BORROR, D. J. 1961. Songs of finches (Fringillidae) of eastern North America. Ohio J. Sci. 61:161–174.

BROWNING, M. R. 1974. Taxonomic remarks on recently described subspecies of birds that occur in the northwestern United States. Murrelet 55:32–38.

CORTOPASSI, A. J., AND L. R. MEWALDT. 1965. The circumannual distribution of White-crowned Sparrows. Bird-Banding 36:141–169.

DEWOLFE, B. B., AND R. H. DEWOLFE. 1962. Mountain White-crowned Sparrows in California. Condor 64:387–389.

DEWOLFE, B. B., D. D. KASKA, AND L. J. PEYTON. 1974. Prominent variations in the songs of Gambel's White-crowned Sparrows. Bird-Banding 45:224–252.

EBERHARDT, C., AND L. F. BAPTISTA. 1977. Intraspecific and interspecific song mimesis in California Song Sparrows. Bird-Banding 48:193–205.

FARNER, D. W. 1958. A breeding population of *Zonotrichia leucophrys gambelii* in the northern Cascade Mountains of Washington. Condor 60:196.

GRINNELL, J. 1908. The biota of the San Bernardino Mountains. Univ. Calif. Publ. Zool. 5:1–170.

HALLIDAY, W. E. D., AND A. W. A. BROWN. 1943. The distribution of some important forest trees in Canada. Ecology 24:353–373.

HUBBARD, J. P. 1969. The relationships and evolution of the *Dendroica coronata* complex. Auk 86:393–432.

JENKINS, P. F. 1978. Cultural transmission of song patterns and dialect development in a free-living bird population. Anim. Behav. 26:50–78.

JOHNSON, N. K. 1978. Patterns of avian geography and speciation in the intermountain region. *In* Intermountain biogeography: a symposium. Great Basin Nat., Memoir No. 2:137–159.

JOHNSTON, R. F., AND R. K. SELANDER. 1964. House Sparrows: rapid evolution of races in North America. Science 144:548–550.

KING, J. R. 1972. Variation in the song of the Rufous-collared Sparrows, *Zonotrichia capensis*, in northwestern Argentina. Z. Tierpsychol. 30:344–374.

KROODSMA, D. E. 1974. Song learning, dialects, and dispersal in the Bewick's Wren. Z. Tierpsychol. 35:352–380.

LEIN, M. R. 1979. Song pattern of the Cypress Hills population of White-crowned Sparrows. Can. Field-Nat. 93:272–275.

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.

MARLER, P., AND P. MUNDINGER. 1971. Vocal learning in birds, p. 389–450. *In* H. Moltz [Ed.], The ontogeny of vertebrate behavior. Academic Press, N.Y.

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

MILLER, A. H. 1939. The breeding *Leucosticte* of the Wallowa Mountains of Oregon. Condor 41:34–35.

MILLER, A. H. 1941. A review of centers of differentiation for birds in the western Great Basin region. Condor 43:257–267.

MORTON, M. L., J. L. HORSTMANN, AND C. CAREY. 1973. Body weights and lipids of summering mountain White-crowned Sparrows in California. Auk 90:83–93.

NOTTEBOHM, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. Am. Nat. 109:605–624.

OBERHOLSER, H. C. 1974. The bird life of Texas. Univ. Texas Press, Austin.

OREJUELA, J., 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., AND K. PAYNE. 1977. Social organization and mating success in local song populations of Village Indigobirds, *Vidua chalybeata*. Z. Tierpsychol. 45:113–173.

PHILLIPS, A., J. T. MARSHALL, AND G. MONSON. 1964. Birds of Arizona. University of Arizona Press, Tucson.

RAND, A. L. 1948a. Glaciation, an isolating factor in speciation. Evolution 2:314–321.

RAND, A. L. 1948b. Birds of southern Alberta. Natl. Mus. Can. Bull. 3.

SMALL, A. 1956. Southern Pacific coast region. Audubon Field Notes 10:409–411.

THIELCKE, G. 1969. Geographic variation in bird vocalizations, p. 311–339. *In* R. A. Hinde [Ed.], Bird vocalizations, Cambridge University Press.

THIELCKE, G. 1970. Lernen von Gesang als möglicher Schrittmacher der Evolution. Z. Zool. Syst. Evolutionsforsch. 8:309–320.

TODT, D., H. HULTSCH, AND D. HEIKE. 1979. Conditions affecting song acquisition in Nightingales (*Luscinia megarhynchus* L.) Z. Tierpsychol. 51:23–35.

VERNER, J. 1975. Complex song repertoire of male Long-billed Marsh Wrens in eastern Washington. Living Bird 14:263–300.

WILLIAMS, L., AND M. H. MACROBERTS. 1977. Individual variation in songs of Dark-eyed Juncos. Condor 79:113–118.

WILLIAMS, L., AND M. H. MACROBERTS. 1978. Song variation in Dark-eyed Juncos in Nova Scotia. Condor 80:237–240.

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