

LONG-TERM PERSISTENCE OF SONG DIALECTS IN THE MOUNTAIN WHITE-CROWNED SPARROW¹

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Abstract. This study examined the persistence of local song dialects of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) at several locations in the Sierra Nevada Mountains of California. At two of these locations, where sparrows were numerous and occupied large contiguous habitat patches, song structure remained highly consistent over a 26-year period (1970–1996). Small but significant alterations in some aspects of the component syllables appeared to result from accumulation of slight copying errors. The frequency and duration of the introductory whistle changed little while the trill and complex syllables changed significantly. Dialects at these two locations were unaffected by extinction of syllables or invasion by foreign syllables. In contrast, songs recorded from two other areas (fragmented habitat and small populations) exhibited dramatic qualitative changes in overall structure and component syllables. These changes resulted both from loss of syllables and appearance of new syllables evidently introduced from nearby areas. These findings suggest that evolution of this culturally transmitted trait (song) proceeds more rapidly in smaller populations occupying structurally fragmented habitats than in larger populations occupying large contiguous habitat patches.

Key words: bird song, cultural evolution, population size, song dialects, White-crowned Sparrow, *Zonotrichia leucophrys*.

INTRODUCTION

Many species of song birds exhibit geographic variation in their songs. Local dialects arise when shared songs differ between neighboring groups, i.e., the variation in song between local populations is greater than within populations (Marler and Tamura 1962, Lemon 1975). Local dialects of varying sizes have been described in many bird species (Mundinger 1982). Despite numerous observations and studies regarding local song dialects, their functional significance and the mechanisms sustaining them remain widely debated (Baker and Cunningham 1985, Catchpole and Slater 1995).

Cultural evolution of song can be examined by studying the temporal persistence of regional dialects. Some species exhibit high rates of song modification over time (Village Indigo Birds, *Vidua chalybeata*, and Yellow-rumped Caciques, *Cacicus cela*, Chilton and Lein 1996, Payne

1996). Other species exhibit greater persistence of song types over time, e.g., Short-toed Tree Creeper, *Certhia brachyactyla* (Thielcke 1987), and Savannah Sparrow, *Passerculus sandwichensis* (Bradley 1994).

The microgeographic dialects in populations of White-crowned Sparrows (*Zonotrichia leucophrys*) are among the best studied in birds (Orejuela and Morton 1975, Baptista and King 1980, Chilton and Lein 1996). Understanding of the mechanisms leading to the cultural evolution and persistence of local song dialects in White-crowned Sparrows requires information on how dialect boundaries change, and how and when songs of a given dialect change acoustically. Long-term studies on dialect persistence in this species have concentrated on changes in the geographic distribution of dialect areas rather than the temporal changes in song structure within and among dialects. Trainer (1983) found the geographic distribution of dialect types in Nuttall's White-crowned sparrow, *Z. l. nuttalli*, on the coast of California had changed in 10

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years, but visual observations of sound spectrograms revealed little change in the basic structure of each dialect over an 18-year period. Chilton and Lein (1996) compared recordings of the Puget Sound White-crowned Sparrow, *Z. l. pugentensis*, made by Baptista (1977) with their own and found the geographic distribution of some song dialects (as described by the terminal trill) to have changed over a 23-year period. Petrinovich (1988) concentrated on the cultural transmission of song between father and son in *Z. l. nuttalli*, but also noted only slight changes in the qualitative aspects of the song over an 8-year period. Thus, although the persistence of local song types and dialect boundary shifts have been documented, detailed studies of changes in acoustic structure of dialects over long time periods are warranted.

This study presents a comparison of both quantitative and qualitative structural aspects of Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) song dialects recorded in 1970 and 1995/1996 at several geographic locations in the central Sierra Nevada. Songs at two localities also were recorded in the 1960s. We relate the degree of song change in different dialects to differences in the size and isolation of breeding habitat.

METHODS

FIELD SITES

Songs of male Mountain White-crowned Sparrows were recorded in the Sierra Nevada Mountains of California (Fig. 1 and Table 1). This study primarily compares songs recorded in 1970 and 1990–1996 at five main locations: Tioga, Sonora, Carson, and Donner Passes, and North Lake (Fig. 1). Each location is accessible by state highway, and most birds were recorded within 5 km of the road. Additional recording sites are noted in Figure 1.

Z. l. oriantha breed in high elevation meadows containing combinations of grass, bare ground, dense shrubs, running water, and peripheral conifers (DeWolfe and DeWolfe 1962). These necessary conditions were met in all study areas, but the amount and spatial distribution of suitable habitat varied between locations, as described below in Results.

SONG RECORDINGS AND ANALYSIS

During July of 1970, Orejuela and Morton (1975) recorded 142 male *Z. l. oriantha* from 14

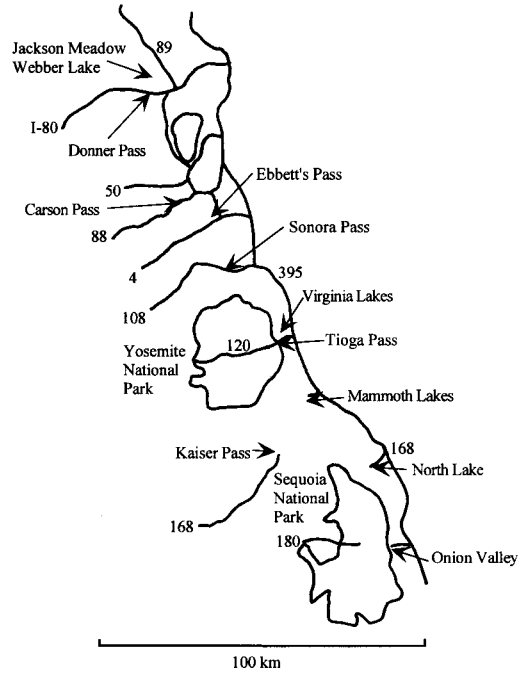


FIGURE 1. Map of recording localities of Mountain White-crowned Sparrow song in the Sierra Nevada Mountains. Road numbers providing access are indicated.

locations along the Sierra Nevada. We obtained songs of about 70 individuals; the songs had been archived in the Florida State Museum, Gainesville, Florida. Sound spectrograms were verified with the published examples (Orejuela and Morton 1975). We also obtained copies of 5 songs recorded in the early 1960s from the Library of Natural Sounds (LNS) at Cornell University, Ithaca, New York.

We recorded 171 individuals from 1990–1996. Harbison and Hahn recorded songs with a Sennheiser ME-66 directional microphone and Sony TCM-5000EV cassette recorder. Nelson used a Sennheiser MKH70 microphone and Sony TC-D10 digital recorder or a Sennheiser MKH815 and Nagra III recorder. On Tioga Pass Meadow, where the population has been studied for 30 years (M. L. Morton, pers. comm.), recorded birds were color banded, and in other locations, to avoid repeated sampling of the same individual, we recorded counter-singing individuals and did not record on the same territory twice. Most birds were induced to sing using playback of conspecific song which was not

TABLE 1. Characteristic phrases distinguishing common song types of *Z. l. oriantha* found in 1970 and 1996. Orejuela and Morton's (1975) song types recorded in 1970 are described using our catalog of phrase types (Fig. 3). Their classification differs from ours. Rare types at each locality are not listed and therefore percentages do not always sum to 100.

Location	Song type	Year	Phrase II	Phrase III	Phrase IV	Phrase V	No. birds (%)
Tioga Pass	S	1970	a	2	a, c, d	l	38 (62)
	T1	1996	c	2	a, c, d	l	63 (71)
	T	1970	b	3	a, c, d, e	l	21 (34)
	T2	1996	b	3	a, c, d	l	19 (21)
Sonora Pass	U	1970	c	4, 5 + 10	a, c, d	l	17 (85)
	S	1996	c	9a,b + 10	a	l	21 (95)
Carson Pass	V	1970	f	6a + 10	g, b	—	5 (20)
	C1	1996	e	6a,b + 8	g	l	10 (29)
	W	1970	d	6a	b	(III) 8	7 (28)
	C2	1996	e	6c + 8 + 10	g	l	11 (32)
	X	1970	d	6a + 6b + 8	—	h	7 (28)
	C3	1996	d	7 + 10	h	l	4 (12)
	E'	1996	c	4c + 10	g	l	6 (18)
Donner Pass	Y/Z	1970	e, c	6b/6c	(III) 8	h	11 (92)
	D	1995	e	6c	(III) 8	h	14 (100)
North Lake	R/U	1970	b/c	1/5a	a/a	l/l	3 (50)/3 (50)
	T2	1995	b	3	i	l	4 (100)
Kaiser Pass	T2	1990	b	3	f	l	2 (100)
Mammoth Lakes	T2	1996	b	3	f	l	4 (100)
Ebbett's Pass	E	1993	c	4c + 10	h	l	3 (100)

necessarily from the local dialect. This did not affect the song type used by the birds, as they responded with consistent vocalizations that often differed from the playback type. From 5 to 30 songs were recorded from each individual. Most of our recordings have been deposited in the collection of the Borror Laboratory of Bioacoustics at Ohio State University, Columbus, Ohio.

Songs were digitized and analyzed using AviSoft-Sonograph Pro software (Raimund Specht, Berlin, Germany; sampling rate 22,050 Hz, sample size 16 bits, FFT = 256 points). Spectrograms in the Figures were produced on a Kay DSP Sona-Graph 5500 with 300 Hz filter bandwidth. Qualitative analysis involved a descriptive comparison and cataloging of song and phrase types based on the printed spectrograms. When possible, the terminology and phrase catalog of Orejuela and Morton (1975) were used (Fig. 2). Quantitative analysis included measurements of the frequency (kHz) and duration (sec) of phrases in the songs. Measurements were made on four to five different songs of the same individual, and statistical tests were performed using the means of these measurements. Coefficients of variation for measurements (including duration, frequency, and frequency range) from

different songs of the same bird were usually less than 5%.

In this paper, we use nomenclature of Baptista and King (1980) and Orejuela and Morton (1975) with one exception (Fig. 2). Following Mulligan (1966), we distinguished between note complexes and syllables. A note was a continuous tracing on a sonagram, separated from other tracings by at least 3 msec. A note complex was a series of one or more notes that was not repeated, in contrast to a syllable, in which the note(s) were repeated identically to form a trill (Fig. 2). Note complexes and complex syllables differ acoustically, so we prefer to maintain this distinction (Nelson, unpubl. data). Complex syllables preceded simple syllables within songs.

The song was broken down into phrases I–V (Fig. 2). Most songs had five phrases; some at Carson and Donner Passes had more. Phrase I was the highly stereotyped introductory whistle found in all *Z. l. oriantha*. The whistle was a pure tone in three pulses at 3–6 kHz, lasting about 0.4 sec. Phrase II contained the vibrato buzz, called a “whistle-buzz” when preceded by a small frequency sweep. The highly variable complex syllable or note complex of phrase III was often used to distinguish between song types (Orejuela and Morton 1975, Baptista and

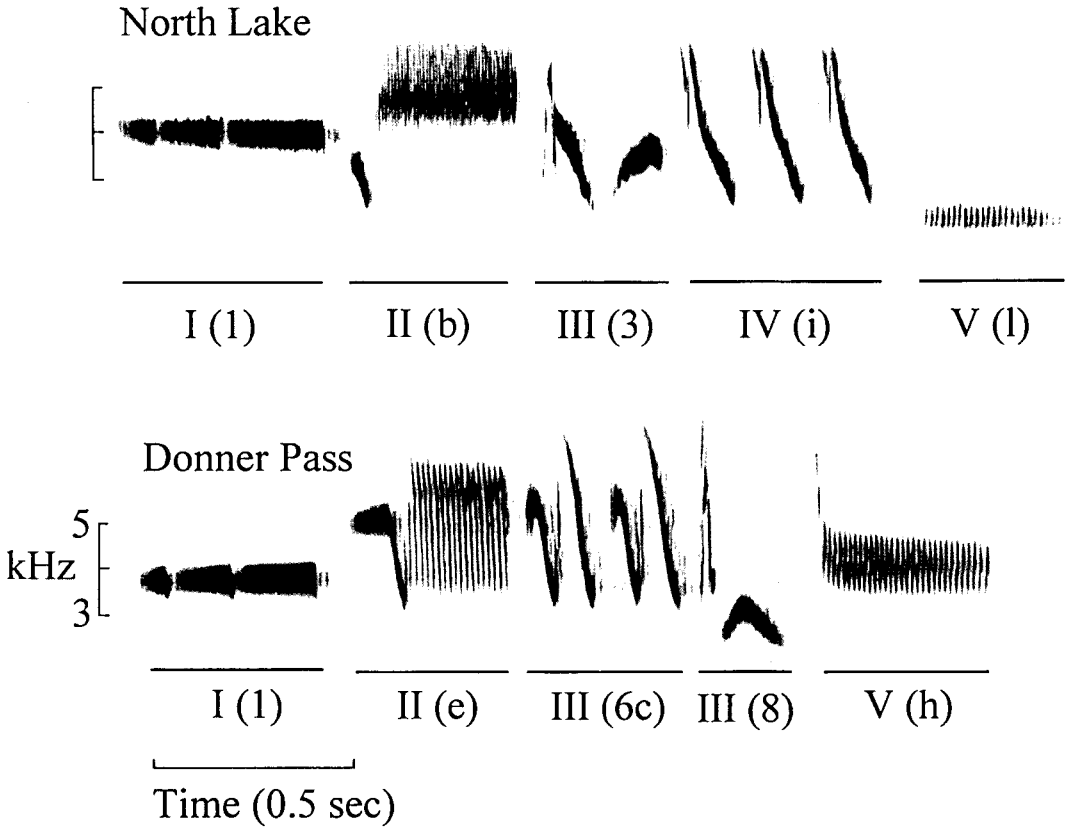


FIGURE 2. Audiospectrograms of *Z. l. oriantha* songs showing the division into phrases I–V. Terms used to describe song structure are defined in the text. The element type from the catalog in Figure 3 is indicated in parentheses after each phrase number. For example, phrase III in the North Lake song is a single type 3 note complex. Phrase III in the Donner Pass song is a pair of type 6c complex syllables, followed by a single type 8 note complex occupying the phrase IV position.

King 1980). Phrase IV contained the highly variable simple syllables, elements which together comprise the trill. Some songs (Donner Pass, Fig. 2) lacked simple syllables, and had two phrase III elements in succession. Phrase V was called the terminal buzz. We continued the original classification of phrase types by Orejuela and Morton (1975) when syllables appeared conserved and added additional types as needed (Fig. 3). A song type was a particular sequence of phrase types. Song types were classified based on the characteristic phrases determined by Orejuela and Morton (1975), but new letters were given to each song type. Thus, the 1970 Tioga Pass song types S and T have been renamed as T1 and T2 (Table 1). Song types that were structurally similar at one location, and dif-

fered from types at other locations, were grouped into a dialect.

STATISTICAL ANALYSES

Coefficients of variation within individuals for measured characters were calculated as the standard deviation divided by the mean times 100%. We compared quantitative features of song structure (e.g., whistle frequency and duration) between years within dialects using nonparametric tests (e.g., Mann-Whitney *U*-test) because in many cases assumptions of parametric tests (e.g., variance homogeneity) were violated. We compared the number of simple syllables in trills using *t*-tests after confirming variance homogeneity with Levene’s test. Change in the frequency of occurrence of song or phrase types

over time was tested with chi-square tests. When expected frequencies were sparse in 2×2 tables, Yates' corrected chi-square was used. Inclusion of rare types or elements as separate categories often violated assumptions of the chi-square test. In these cases, rare song types or syllables were either eliminated from the analysis or lumped with another category if doing so appeared logical (e.g., two distinct song types at Carson Pass in 1995–1996 were both absent in 1970, and therefore were lumped as “new” in the analysis). Because some individuals sang two song types, the total number of songs exceeded the number of birds recorded. Similarly, depending upon the quality of the recordings, sample sizes may be fewer than the number of birds recorded. All statistics were calculated in Systat (Wilkinson 1992).

RESULTS

TIOGA PASS

The Tioga Pass area consists of large meadows with smaller, peripheral habitat patches supporting high breeding densities of *Z. l. oriantha*. This area has undergone only minor changes over the 26 years of this study. Pines have encroached into the meadow slightly and the meadow has become drier, but the continuity of the meadows has remained intact (M. L. Morton, pers. comm.). *Z. l. oriantha* songs here have persisted with only minor alterations. In 1996, 89 birds were recorded from the Tioga Pass area, and these were compared with 31 of the 61 birds reported by Orejuela and Morton (1975) (see Methods section for information on extant 1970 recordings).

Song types. The Tioga Pass dialect contained two distinct, conserved song types (T1 and T2, called S and T by Orejuela and Morton [1975]). The two song types differed in phrases II and III, but not in the simple syllables (Table 1 and Fig. 4). Over a 26-year period, both song types changed only slightly (Fig. 4) and coexisted throughout the Tioga Pass region with T1 sung by about 70% of the birds (Table 1). This proportion did not change significantly between 1970 and 1996 ($\chi^2_1 = 2.61$, $P > 0.1$; 1970: $n = 59$; 1996: $n = 82$).

Phrases. The tri-partite, pure-toned, introductory whistle (phrase I) was highly stereotyped and was sung by all *Z. l. oriantha* recorded (Fig. 3). For the following phrase measurements, the

Tuolumne Meadows birds were used as a representative subset of the Tioga area.

Whistles measured in different songs from the same individual showed little variation in frequency or duration ($CV < 0.02$). Between years, neither mean frequency nor mean duration of the whistle changed significantly (Table 2).

Two types of broad band buzz (phrase II) occurred at Tioga Pass (a and b), distinguished by a small frequency sweep preceding the buzz (Fig. 3). In 1996, the initial whistle of type-a buzzes was smaller and fused with the succeeding buzz. In 1970, both types of whistle-buzz occurred in both T1 and T2 songs. By 1996, only T2 songs contained type-b whistle-buzzes, whereas type-a whistle-buzzes occurred in both song types. This led to a significant change in the prevalence of these two whistle-buzz types between 1970 and 1996 ($\chi^2_1 = 7.43$, $P < 0.01$; 1970: $n = 29$; 1996: $n = 84$).

To assess the differences in phrase IV between years, we measured the frequency range of the simple syllable, and the duration of four consecutive syllables as an index of trill speed. Syllable repetition rate was slower in 1996 than in 1970, and each syllable covered a larger frequency range (Table 2). There also was a trend toward fewer syllables per trill. Using only the 26 birds from Tuolumne Meadows on which the above quantitative analyses were performed, this trend was not significant. However, using the larger sample of all 125 birds from the Tioga area, the trend toward fewer syllables per trill was significant (1970: 5.8 ± 0.23 syllables per trill; 1996: 4.7 ± 0.10 syllables per trill; $t_{125} = -5.15$, $P < 0.001$).

The simple syllables were the most variable portion of the Tioga song. Orejuela and Morton (1975) lumped all the Tioga trill syllables as type a. We further subdivided them into three common types: a, c, and d (Fig. 3, phrase IV). Type a and c syllables were more prevalent in 1996 than in 1970, whereas type d syllables predominated in 1970. Prevalence of the three most common syllable types changed significantly between years ($\chi^2_2 = 51.3$, $P < 0.001$; 1970: $n = 27$; 1996: $n = 83$). Thus, the general trend in simple syllables of phrase IV from 1970 to 1996 appeared to be toward fewer total syllables in the trill, and syllables of longer duration and broader frequency range with asymmetrical first and second frequency sweeps.

The low terminal buzz (phrase V, type I) was

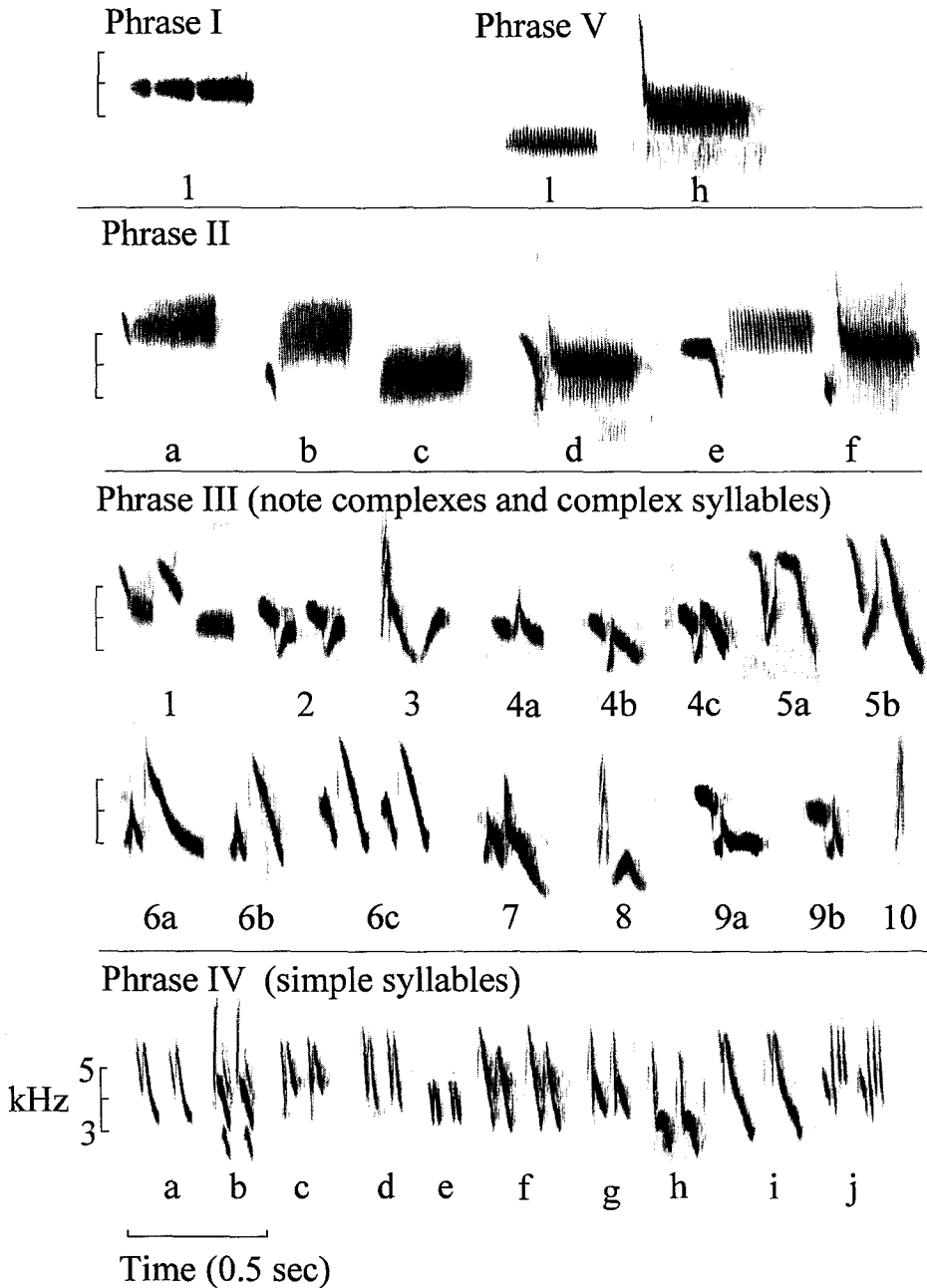


FIGURE 3. Catalog of elements found in *Z. l. oriantha* songs in 1970 and 1996 adapted from Figure 3 in Orejuela and Morton (1975). Phrase I was common to all locations in both years. The low buzz (l) of phrase V was found in all 1996 songs and on Tioga Pass and Sonora Pass in 1970. The high buzz (h) of phrase V was found on Donner Pass and Jackson Meadow in both years. Phrase II buzz: a (Tioga, 1970), b (Tioga, 1970 and 1996), c (Tioga and Sonora, 1996 and Sonora, 1970), d and e (Carson Pass, 1970 and 1996), f (Carson, 1970). Phrase III consists of note complexes and complex syllables. We have added 8 types or subtypes and parsed Orejuela and Morton's (1975) types 6b–6d into smaller units as follows. Their 6b = 6b + 8 here; their 6c = 6a + type c buzz here; their 6d = 6c + two type 8s here. The other types, locations, and years are as follows: 1 (North Lake, 1970), 2 (Tioga, 1970 and 1996), 3 (Tioga, 1970 and 1996), 4a, b, c (Sonora, 1970), 5 (Sonora, 1970 and Tioga, 1970 and 1996), 6a and 6b (Carson, 1970 and 1996), 6c (Donner, 1970 and 1995), 7 (Carson,

a highly conserved feature of both Tioga Pass song types, present in virtually all of the songs recorded in all years.

SONORA PASS

On Sonora Pass, birds were recorded in two large meadows with about 25 pairs of *Z. l. oriantha*. Comparisons of recordings from 1970 ($n = 20$ individuals, but only 10 recordings still available for detailed analysis, see below) and 1996 ($n = 22$ individuals) revealed only small changes over a 26-year period (Fig. 5).

Song types. The main song type on Sonora Pass (type S, called type U by Orejuela and Morton [1975]) was sung by about 90% of the males in both years (Table 1; Yates corrected $\chi^2_1 = 0.39$, $P > 0.5$; 1970: $n = 20$; 1996: $n = 22$).

Phrases. The introductory whistle appeared identical to that at Tioga Pass. Frequency and duration of the introductory whistle did not change significantly at Sonora Pass between 1970 and 1996 (Table 3). The type c buzz (phrase III) was found in all 1970 and 1996 birds and did not change over time.

The note complex consisted of two mainly downward-sweeping notes. In the 1970 Sonora Pass songs, Orejuela and Morton (1975) lumped a few slight variations of the note complex into type 4 (Fig. 3). Two discrete variants occurred in 1996, type 9a and its shortened version, type 9b. The frequency range spanned by the note complex was significantly greater in 1996 than in 1970 (Table 3).

The trill simple syllables (phrase IV) were two short-frequency sweeps similar to those on Tioga Pass. As on Tioga Pass, the individual syllables spanned a greater frequency range and were repeated more slowly with fewer syllables in 1996 than in 1970 (Table 3). In the 1970 sample, three distinct types of simple syllables were evident (types a, c, and d, with d the most common), whereas in 1996 only trill type a was sung at Sonora Pass. The prevalence of the two more common syllables (a and d) in our sample of songs changed significantly between years

(Yates corrected $\chi^2_1 = 16.2$, $P < 0.001$; 1970: $n = 8$; 1996: $n = 22$). This conclusion is not altered if syllable c is included by lumping with d as a "non-a" syllable (Yates corrected $\chi^2_1 = 19.4$, $P < 0.001$; 1970: $n = 10$; 1996: $n = 22$).

The low terminal buzz (phrase V, type l) was sung by virtually all birds in both years at Sonora Pass.

CARSON PASS

The habitat on Carson Pass consisted of small, scattered breeding areas. The total number of *Z. l. oriantha* on Carson Pass was small, and each patch held only a few pairs. Songs were recorded in 1970, 1993, 1995, and 1996. Seventeen of the 25 songs recorded on Carson Pass by Orejuela and Morton (1975) were archived.

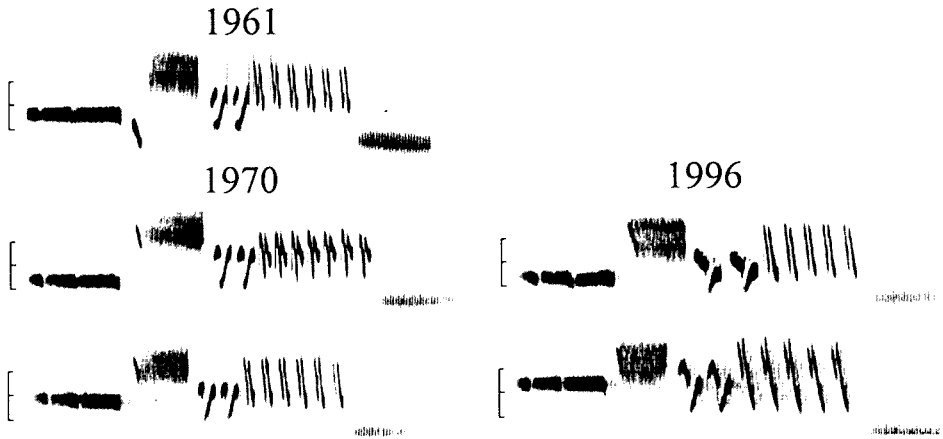
Song types. The basic Carson Pass dialect remained recognizable over the 26-year period, and many of the individual syllables did not obviously change form. However, the appearance and disappearance of syllables and song types, as well as alterations in song syntax, made Carson Pass song unique among the five dialects we studied in detail.

Discrete song types were difficult to categorize on Carson Pass due to a wide variety of syllable arrangements and combinations (Fig. 6). The general sequence was an introductory whistle, buzz, complex syllable(s) or note complex, then trills and/or buzzes in different combinations. Orejuela and Morton (1975) distinguished five song types but only reported the three (V, W, and X) that were shared by at least three birds. Six of their 22 birds did not fit into these song types and were categorized as "other." We arranged the 1995/1996 recordings into modified versions of these types based on phrase III (song types C1, C2, and C3). Song type V was not found in the 1995 or 1996 recordings. Song types W and X were similar to C1 and C2, respectively, whereas song type C3 was new to the 1995/1996 recordings (Table 1 and Fig. 6). Song type E', sung by 20% of birds in 1995/1996, was

←

1996), 8 (Carson and Donner, 1970 and 1996), 9a, b (Sonora, 1996), 10 (Sonora, Ebbett's Pass, Carson, Donner, 1970 and 1995). Phrase IV simple syllables (pairs): a (Tioga and Sonora, 1970 and 1996), b (Carson, 1970), c (Tioga, 1970 and 1996 and Sonora, 1970), d (Tioga, 1970 and 1996 and Sonora, 1970), e (Tioga, 1970), f (Mammoth Lakes, 1996), g (Carson, 1996), h (Carson and Ebbett's Pass, 1996), i (North Lake, 1995), j (Tioga Pass, 1996).

Tioga Pass Song Type T1



Tioga Pass Song Type T2

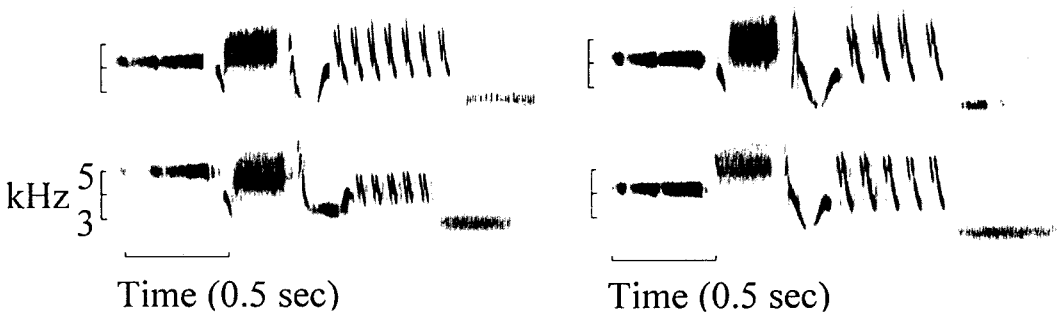


FIGURE 4. Spectrograms representing the two song types from the Tioga Pass region. See Results and Table 2 for detailed analysis of syllable changes. At top is a song recorded on Tioga Pass Meadow in 1961 (LNS 16620). Note the similarity to the other songs with the exception of phrase II, which resembles that in song type T2. Orejuola and Morton (1975) termed T1 songs “S,” and T2 songs “T.”

most like the Ebbett’s Pass dialect (see Fig. 8 and below), and was not present in 1970.

Based on these five song-categories, and lumping types C3 and E’ as new song types in 1995/1996, the proportions of song types found on Carson Pass changed significantly ($\chi^2_3 = 9.20, P = 0.03$; 1970: $n = 19$; 1995/1996: $n =$

31). Note that for this analysis both 1995 and 1996 recordings were used. Redundant inclusion of individuals was avoided by making recordings largely in different locations in each year, and by using extremely similar recordings only once in the analysis.

Phrases. The introductory whistle of Carson

TABLE 2. Summary of quantitative analyses of songs from Tuolumne Meadows (Tioga Pass area). Frequencies are in kHz, and durations are in seconds. Values are \bar{x} (SE).

	Whistle frequency	Whistle duration	Trill duration	Trill frequency range	Trill rate (syllables sec ⁻¹)	<i>n</i>
1970	4.12 (0.18)	0.46 (0.01)	0.32 (0.004)	1.77 (0.08)	5.7 (0.19)	11
1996	3.91 (0.11)	0.47 (0.07)	0.39 (0.008)	2.37 (0.07)	5.0 (0.33)	15
Statistics ^a	104	69	4**	4**	1.60	

^a Mann-Whitney *U*-tests, except for trill rate, which is a *t*-test. ** $P < 0.001$.

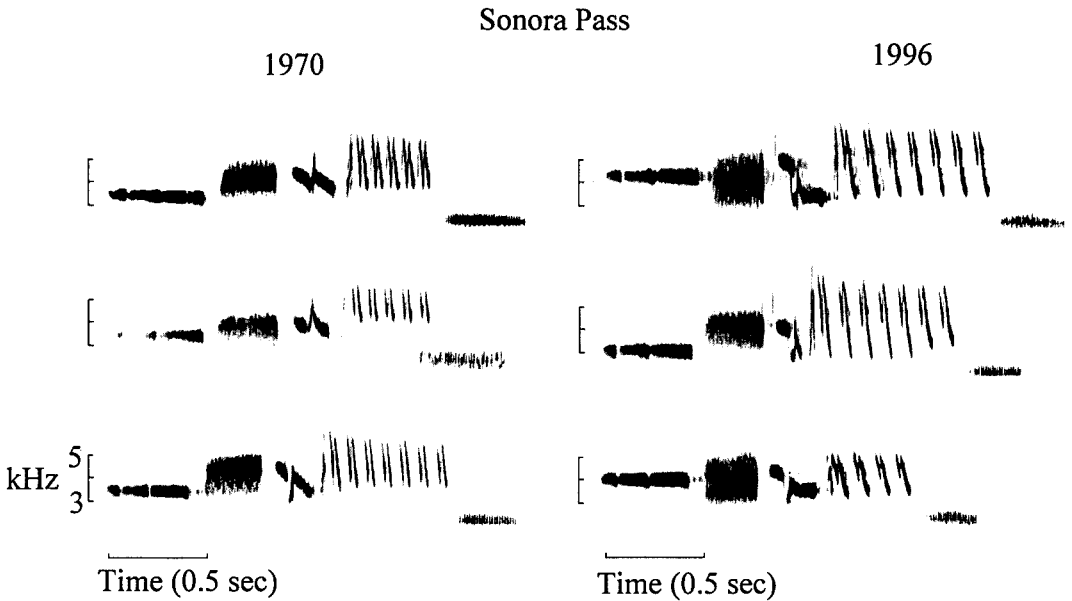


FIGURE 5. Spectrograms of *Z. l. oriantha* on Sonora Pass. Note the differences in the note complex and the trill. The 1970 songs are Orejuela and Morton's (1975) type U.

Pass birds did not change duration from 1970 to 1996, but did decrease in frequency (Table 4).

The different Carson Pass buzzes were distinguished based on the preceding frequency sweep. Buzz types b, d, and e were found in the 1995/1996 recordings (type c occurred in the four birds singing Ebbett's Pass dialect, song type E'). The 1970 buzzes (types d–f) looked similar but displayed larger, more pronounced frequency sweeps (Fig. 3).

Most of the complex syllables and note complexes represented combinations of types 6a–c and 8, all syllables that have remained structurally stable over time. Note complex type 7 appeared only in the 1995/1996 sample, and the second buzz found in the middle of all the 1970 Carson Pass songs disappeared in the intervening 26 years.

The simple syllable of Carson Pass trills con-

tained a single frequency sweep with a short tail. The 1970 simple syllable (type b) consisted of two notes. The trill was preceded in 3 of 16 cases by a type 10 note complex. The type b simple syllable was replaced in 1995/1996 by syllable types g (29–32 out of 36 birds, respectively) or h (4–7 birds), based on the placement of the tail and general shape. Both were always preceded by a type 10 note complex. Note that simple syllable type g also was present in 1970 in the Virginia Lakes/Conway Summit area (Fig. 8). None of the 1995/1996 birds used two separate trill sequences in a single song.

None of the 1970 birds recorded at Carson Pass sang a terminal buzz. By 1995/1996, a terminal buzz like that present on Tioga and Sonora Passes had been acquired by virtually all of the birds on Carson Pass (Fig. 6). In summary, over a 26-year period, Carson Pass songs

TABLE 3. Summary of quantitative analyses of songs from Sonora Pass. Frequencies are in kHz, and durations are in seconds. Values are \bar{x} (SE).

	Whistle frequency	Whistle duration	Note complex frequency range	Trill duration	Trill frequency range	Trill rate (syllables sec ⁻¹)	n
1970	3.43 (0.094)	0.48 (0.008)	1.03 (0.077)	0.35 (0.01)	2.28 (0.145)	6.50 ± 0.37	10
1996	3.65 (0.099)	0.47 (0.004)	1.53 (0.049)	0.46 (0.01)	2.89 (0.080)	5.59 ± 0.19	22
Statistics ^a	78	155.5	8.5**	0**	29**	2.39*	

^a Mann-Whitney U-tests, except for trill rate, which is a t-test. * P < 0.05, ** P < 0.001.

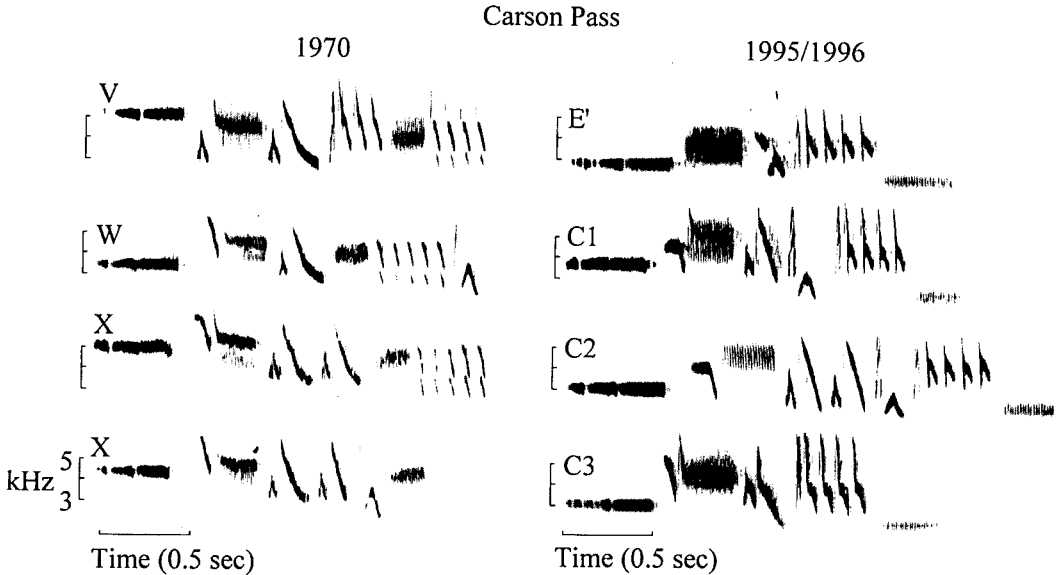


FIGURE 6. Spectrograms of *Z. l. oriantha* recorded on Carson Pass in 1970 and 1995/1996. Note the variation within years and the changes between 1970 and 1996, the disappearance of the second buzz, the appearance of song types E' and C3, appearance of the terminal buzz, and reduced complexity of the song. Orejuela and Morton's (1975) song type designations are shown for the 1970 songs.

lost a buzz in the middle of the song and replaced it with a terminal buzz. Whistle frequency decreased, and new song and simple syllable types appeared.

DONNER PASS

The meadows we visited in the Donner Pass area were small with fewer than six males recorded in each in 1995: Ice Lakes (2 birds), Donner Pass Road (1), Boreal Ski Ranch (2), Jackson Meadows (4), Webber Lake (5). The first three areas were within 5 km of one another, and the latter two were about 20 km to the north. Orejuela and Morton (1975) recorded birds at Ice Lakes (2), Donner Pass (5), and Jackson Meadows (5).

In contrast to Carson Pass, the local song types were highly conserved in the Donner Pass/

Jackson Meadows area between 1960 and 1995 (Fig. 7). Four recordings made between 1960 and 1964 at the Ice Lakes, 4.8 km west of Donner Pass, were very similar to the more recent songs. From 1960 to 1970, the Ice Lakes songs lost the type h Phrase V, and then regained it by 1995. Song I2 (one male) in 1970 appeared to be a hybrid of Sonora type U (phrases I–III) and Carson Pass song type V with a note complex type 8 added (Fig. 7).

Orejuela and Morton (1975) recognized two song types in the Donner Pass area that differed only in phrase III (Fig. 7). The common Donner Pass area song (type D) appeared somewhat similar to the Carson Pass song type C2 but lacked a simple syllable trill and contained a high terminal buzz type h. Donner Pass songs were the only songs to lack a simple syllable trill, having instead a single type 8 note complex. In contrast to most other songs (except type T1 at Tioga and X at Carson), they had a pair of complex syllables. The complex syllable at Donner changed slightly from the type 6a, 6b, or 7 in 1970 (also present on Carson Pass) to the 6c in 1995. A visual comparison between the 1970 and 1995 recordings revealed little change in the syntax or component syllables. Thirteen

TABLE 4. Summary of quantitative analyses of songs from Carson Pass. Values are \bar{x} (SE).

	Whistle frequency (kHz)	Whistle duration (sec)	n
1970	4.27 (0.122)	0.45 (0.008)	17
1996	3.28 (0.066)	0.46 (0.009)	13
Statistics ^a	213**	93	

^a Mann-Whitney U-tests. ** P < 0.001.

Donner Pass Area

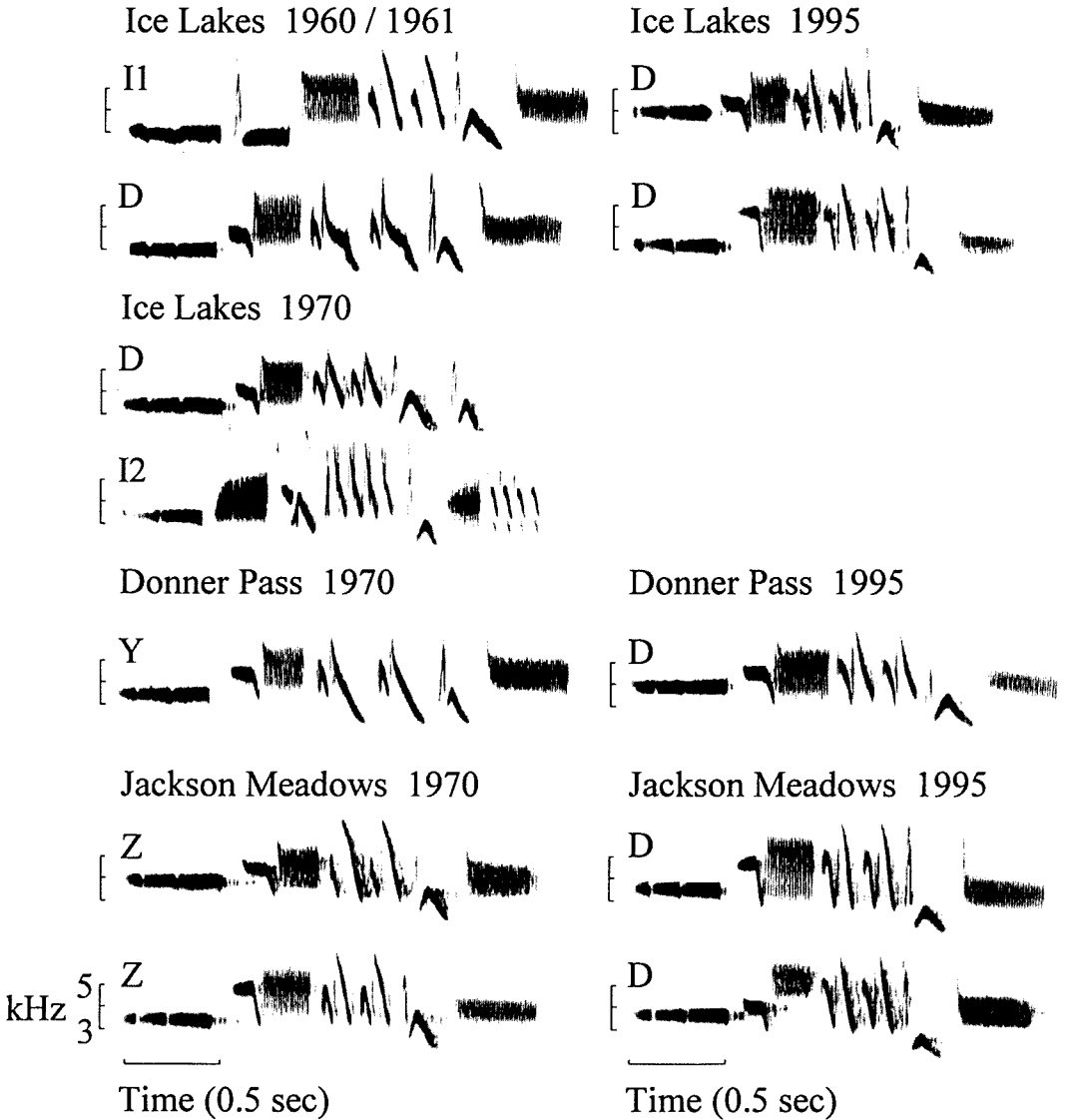


FIGURE 7. Spectrograms of *Z. l. oriantha* recorded in the Donner Pass area. The two top-left songs were recorded in 1960 and 1961 (LNS22967, 22970). Orejuela and Morton's (1975) song type designations are shown for the 1970 songs.

of 14 males recorded by Baptista and King (1980) at Independence Lake (in between the northern and southern sites we sampled around Donner Pass) sang song type D.

NORTH LAKE AND OTHER LOCATIONS

North Lake held a small population of six birds in 1970. Three sang a type R similar to that at

Onion Valley 60 km to the south, and three sang a type U (Fig. 8) that occurred at Sonora Pass and Virginia Lakes. Both types were extinct at North Lake in 1995 as all four birds recorded sang type T2, but with type i simple syllables. Three pairs were nesting in a small meadow at Kaiser Pass in July 1990. The two males that sang gave type T2 songs, but with a distinctive

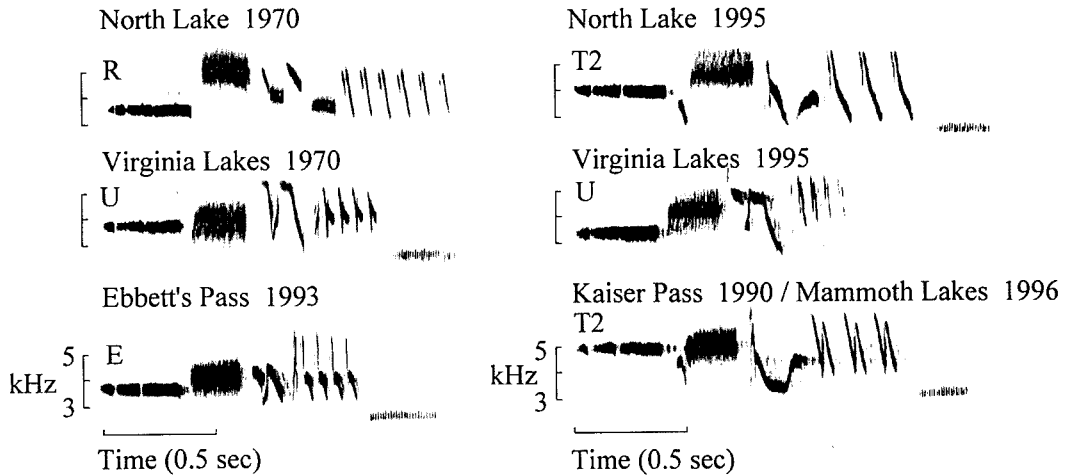


FIGURE 8. Songs of *Z. l. oriantha* recorded in small populations. Three males sang song type U at North Lake in 1970 but with type a simple syllables as in the type R song sung by three other males. The type R song was actually recorded at Onion Valley (Orejuela and Morton's [1975] North Lake recordings were not archived). Song type U still existed at Virginia Lakes/Conway Summit in 1995 but with different simple syllables. Compare the Ebbett's Pass song type E to song type E' at Carson Pass (Fig. 6). Orejuela and Morton's (1975) song type designations are shown for the 1970 songs.

trill syllable, type f (Fig. 3 and 8). Four birds recorded at Mammoth Lakes in 1996 also sang this song type. Baptista and King (1980) found song type T2, with type i simple syllables, in the San Bernadino Mountains, 450 km south of Tioga Pass.

Baptista and Morton (1982) recorded 12 birds at Gardisky Lake (5 km north of Tioga Pass) in 1978. Nine males sang dialect U, similar to eight birds recorded 11 km to the north at Virginia Lakes by Marie Mans (Fig. 8). Of the seven males we recorded at Gardisky Lake in 1996, two sang T1, four sang T2, and one sang both. Song type U was sung by three of five birds recorded at Virginia Lakes/Conway Summit in 1995 (Fig. 8). T1 and T2 were sung by the other two males in 1995. The single song archived from Conway Summit in 1970 was type U. Thus, the Tioga dialect has moved north of Gardisky Lake since 1982, and type U has retreated.

We found three males in 1993 in two small meadows at Ebbett's Pass, roughly equidistant between Carson Pass and Sonora Pass (Fig. 1). All sang song type E (Fig. 8). Song type E appeared to be a temporal and spatial "hybrid" of the Sonora and Carson Pass songs. The whistle-buzz-note complex resembled most closely the 1970 song at Sonora Pass (cf. type 4c note complex to the 1970 version of the Sonora note complex: 4a, 4b, Fig. 3). The simple syllables (type

h) resembled those on Carson Pass in 1996 (Fig. 6). Song type E' recorded from six birds on Carson Pass in 1995/1996 resembled the Ebbett's Pass song.

DISCUSSION

Mountain White-crowned Sparrow populations in the Sierra Nevadas exhibited highly persistent local song dialects over the interval from 1970 to 1996. This study spans a long time interval, 26 years, and concentrates on detailed changes in the song structure and comparison of song persistence at different locations. The main findings are: (1) song types have remained basically consistent over time both in the song structure and in the proportion of different song types in each area, especially in the larger populations, (2) some components of the song have changed more than others, and (3) the song types and component syllables changed more in small populations. These findings have implications for dialect persistence in differing habitats and population sizes, the process of song learning, and the coding of information in song.

DIALECT PERSISTENCE

The results of this study indicate a relationship between dialect persistence and either population size, habitat continuity, or both. There seems to be powerful inertia in the larger and

denser populations found on Tioga and Sonora Pass, resulting in highly consistent songs that are maintained over 25 years despite the annual presence of a few individuals singing foreign dialects. The influence of these foreign songs evidently does not persist beyond their owners' tenure in the population. Carson Pass, in comparison, exhibited greater variation within years (Orejuela and Morton 1975) as well as more distinct changes over time (this study). Studies on other species have found that small isolated populations exhibit greater song variation than large populations (Thielcke 1965, Becker 1977). The habitat patches we visited at Donner Pass also were small, but in contrast to Carson Pass, the songs at Donner remained very stable over the 25-year sampling interval. A possible reason for the difference may be the relatively large population at nearby Independence Lake that Baptista and King (1980) described. This population may act as the large populations on Tioga Pass and Tuolumne Meadows do by providing emigrants to the smaller populations nearby. The extinction of two song types and their replacement by type T2 in the small population at North Lake also indicates the vulnerability of small song populations (MacArthur and Wilson 1967). It must be stressed that we do not know the extent of dispersal between populations or whether the dialects meet and share borders.

If smaller or more fragmented populations exhibit larger variation and less continuity of song over time, the influences of human activity or environmental variation on habitat could greatly affect the persistence of local dialects. Holland et al. (1996) reported that changes in land use and suitability of habitat were responsible for the massive alteration over an 18-year period in both the location and structure of Corn Bunting, *Miliaria calandra*, dialects in England. Similarly, Trainer (1983) attributed the movement of dialect boundaries in *Z. l. nuttalli* to alterations in the available habitat. In contrast, the relatively stable habitat at Tioga Pass has permitted the contact zone between the more southerly distributed T2 type and the more local T1 type to persist unchanged over 26 years.

Environmental factors such as the yearly variation in snowpack could play a key role in the differential transmission of song in populations. In years where the snowpack persists late into the breeding season, some populations may not breed successfully and thus interrupt the trans-

mission of song. King and Mewaldt (1987) reported an insular population of White-crowned Sparrows that exhibited population cycles with years of very low reproductive success. In 1995, the snowpack in August covered some of the meadows that Orejuela and Morton (1975) visited in 1970 and no sparrows were present (pers. observ.). D. A. Nelson visited Luther Pass and Monitor Pass repeatedly between 1990 and 1993, years of relative drought, where Orejuela and Morton (1975) recorded six birds, and never found White-crowned Sparrows (unpubl. data). Smaller populations thus driven to extinction could be populated in subsequent years by immigrants that learned their songs in other locations, causing shifts in dialect boundaries (Baker and Thompson 1985, Chilton and Lein 1996). Repopulation might take several years because production of independent juveniles varies dramatically as an inverse function of spring snow depth (Morton 1992).

SONG LEARNING IN THE FIELD

The mechanisms that allow a local song type to persist over 26 years, as has occurred here, rely heavily on when and from whom the song is learned, as well as the population size. The timing and selectivity of song learning influence the creation and persistence of local dialects (Lemon 1975, Mundinger 1982). The fact that most of the dialects in our study remained constant over time demonstrates that most males learned their song near where they settle to breed (Kroodsma 1982). This could either occur before the first fall migration in males that return as yearlings to the site where the song was memorized, or upon return to the breeding grounds in spring in yearling males that disperse into a new dialect area at that time. Evidence from laboratory studies of song learning in this species is consistent with an early sensitive phase (Nelson 1998).

The existence of hybrid songs and overproduction of song types indicates that some males learn two or more dialects. Use of two or more complete songs in the crystallized repertoire has been documented in the field in *Z. l. oriantha* (4/48 males, Baptista and Morton 1982; 6/172 males in 1990–1996 in this study). Cultural hybrid songs were common in this study. The birds on Carson Pass that sang the Ebbett's Pass dialect combined it with a trill typical of Carson Pass (Fig. 6). Also, two birds recorded in the Tioga Pass area added on an extra type 3 syl-

lable at the end of a complete T1 song. Song type T2 had a type 3 note complex coupled with five different simple syllable types in different populations (Table 1). Cultural hybrid songs also have been described in *Z. l. pugetensis* (Baptista 1977) and *Z. l. nuttalli* (DeWolfe and Baptista 1995). In a laboratory experiment where juveniles were exposed to 32 different tutor songs, 25% of 12 *Z. l. oriantha* crystallized songs that combined phrases from two or more tutors (Nelson et al. 1996).

If males visit and learn several dialects in their hatching summer, then they could settle in any of them to breed the next year and already be familiar with the local song. Through a process of overproduction of song and selective attrition of non-matching song types, males could conform to whichever of these dialects they settle in, even though the sensitive phase for acquisition of songs is over (Nelson and Marler 1994, Nelson et al. 1996). This has been described in one yearling male *Z. l. oriantha* (Baptista and Morton 1988), and four male *Z. l. nuttalli* (DeWolfe et al. 1989). This "action based learning" (Marler 1990) could result in the conservation of local dialects, but further study is needed before we can conclude whether this is a common process in wild White-crowned Sparrows.

The presence of large populations would promote the conservation of local dialects over time if males preferentially learn the commonest song type, a frequency-dependent tutor-selection process (Williams and Slater 1991). In a study on Tioga Pass, only 3 out of 12 males sang the same song type as the father, and the progeny of nonlocal-dialect singers always crystallized the local song, implying oblique transmission of song (Baptista and Morton 1988). Thielcke (1987) and Whitney (1992) also suggested that a frequency dependent process whereby males copied the most commonly heard song was responsible for the stability of song types in Short-toed Treecreepers, *Certhia brachydactyla*, and Wood Thrushes, *Hylocichla mustelina*, respectively. Beecher et al. (1994) found that young male Song Sparrows, *Melospiza melodia*, preferentially crystallized songs that were shared by several adult tutors. If more song variation occurs in smaller habitat patches (e.g., Carson Pass), juveniles and/or settling yearlings in such areas may have more difficulty matching their

song with a "majority" song or choosing a neighbor with whom to match.

CODING OF INFORMATION

Male song birds are able to recognize species (Becker 1982), individuals (Falls 1982), and local dialects (Lemon 1967) on the basis of song. Marler (1960) proposed a segregation of recognition functions within song, with certain features functioning for species, dialect, and individual recognition based on the amount of variation. The observation that some aspects of *Z. l. oriantha* songs remained highly conserved over time while others varied suggests different functions for different phrases in the song. The invariant features hypothesis predicts that the most important aspect of the song for species recognition will vary the least within the species (Nelson 1989).

It follows from this line of reasoning that important species recognition cues also will change the least over time. In this study, the introductory whistle appeared to be the least variable phrase over time in all populations studied. Quantitative measurements of the frequency and duration of the introductory whistle did not change significantly on both Tioga and Sonora Pass over the 26-year period. In line with this, song learning experimental studies on young hand-reared *Z. l. oriantha* indicate that the whistle is an important species recognition cue (Soha 1995). Other aspects of the song that generally remained conserved (except in the Carson Pass songs) included the total duration of the song, the general order of the syllables, and the terminal buzz.

The features of song that vary most among different localities, such as the order and identity of note complexes and syllables, are used to define dialect identity. These features, such as the frequency range and duration of the trill syllables, also changed significantly over time. Thompson and Baker (1993) used playback experiments to demonstrate that male *Z. l. nuttalli* responded most strongly to their own local dialect, and that dialect identity was encoded in the introductory portion of the song. This conclusion may be specific to the particular dialects tested, however, and we do not know if general attentional preferences for certain features exist. Analyzing how the individual phrases of the song have changed through time, combined with further playback studies, could provide infor-

mation about the selective forces that shape the function of song in communication at multiple levels.

CONCLUSION

In this study of Mountain White-crowned Sparrows, multiple factors appear to influence the persistence of dialects. Accumulation of small copying errors may alter some aspects of the songs more than others and may be the main impetus for quantitative changes in large populations. Immigration and mixing of song features from different locations may be more influential in small populations, producing much more dramatic qualitative changes in song. Future consideration of theories relating to song learning, song dialects, and cultural evolution of song should consider the roles of population size and habitat continuity.

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