

SONG DIALECTS AND MATE SELECTION IN MONTANE WHITE-CROWNED SPARROWS

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ABSTRACT.—Two song dialects are described for montane White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada of California, one at Tioga Pass and one at Gardisky Lake, 3 km to the north. The dialects differ from each other in syllabic morphology and in rhythmic (temporal) and pitch characteristics. Two males sang foreign dialects, one typical of the Canadian Rockies and the other typical of *Z. l. gambelii* of Alaska and Canada. Both "song misimprinted" birds were paired and at least one bred successfully. A third male, singing syllables from Mount Lassen, was also paired. Most females induced to sing with testosterone injections did not match the dialects of their consorts, suggesting that song dialects did not influence mate choice. One female sang a song similar to those from Mount Lassen to the north but was paired to a male singing a Gardisky song.

Four possible explanations for mis-matching of dialects are discussed. The most probable explanation at this time is that mating is random according to dialect and that differential dispersal distances between the sexes account for sex differences in song types. Received 18 September 1981, accepted 25 January 1982.

SONG dialects are well documented in avian species (Krebs and Kroodsma 1980), but the selective advantage of learning a dialect is poorly understood. Song dialects in North American White-crowned Sparrows (*Zonotrichia leucophrys*) were discussed in the early literature (Dawson 1923, Blanchard 1941, Peterson 1941), but it was not until the study of Marler and Tamura (1962) that these dialects were analyzed spectrographically and subjected to statistical analysis. Konishi (1965) first demonstrated that some female White-crowned Sparrows treated with testosterone sang their native dialects, although females are seldom observed singing in the wild (Blanchard 1941, Kern and King 1972, Baptista 1975). Marler and Tamura (1962), Marler (1970), and Konishi (1965) suggested that dialects might function to: (1) induce birds to breed near their natal areas, because they are attracted to their familiar natal dialect; and (2) influence females to select as mates males that sing dialects of the female's natal area, thus promoting assortative mating. Nottebohm (1969, 1972, 1975) expanded on the above ideas with data based on studies of the congeneric *Z. capensis*.

In this study we test the assortative mating theory of song-dialect function by recording and comparing songs of mated pairs of White-crowned Sparrows (*Z. l. oriantha*).

MATERIALS AND METHODS

Montane White-crowned Sparrows are migratory and typically breed in subalpine meadows or riparian woodland at altitudes of about 2,000–3,000 m (DeWolfe and DeWolfe 1962, Morton 1976). The breeding biology (review in Morton 1978) and song dialects of the western populations have been studied in great detail (Orejuela and Morton 1975, Baptista and King 1980).

Our study area is near Tioga Pass, Mono County, California at latitude 37°55' and an elevation of about 3,000 m. In 1978 we discovered a song dialect at Gardisky Lake (Fig. 1) at the northern edge of our study area that was markedly distinct from the Tioga Pass dialect described earlier by Orejuela and Morton (1975).

Birds at all study localities bred in willows and small pines. Gardisky Lake (3,196 m) is separated from Lee Vining Creek by a slope with habitat unsuitable to breeding White-crowned Sparrows. The slope is rocky and barren for the most part, with scattered pine trees. Birds at Lee Vining Creek occupy riparian habitat. The population at Tioga Pass inhabits a meadow and surrounding mountain slopes. Most of our banding activities were concentrated at these three localities (gridded areas in Fig. 1), which supported good numbers of birds. A few birds were also banded in smaller isolated tracts of meadow between Tioga Pass and Lee Vining Creek:

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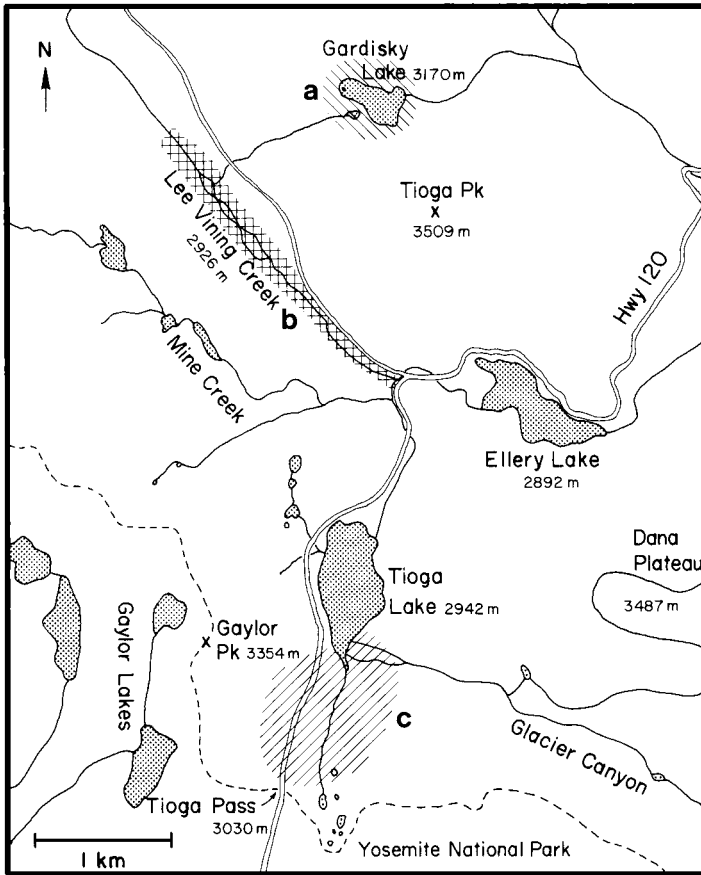


Fig. 1. Map of study area. Hatched areas (Tioga Pass and Gardisky Lake) and cross-hatched area (Lee Vining Creek) are localities of most intense banding activities. At Lee Vining Creek the two dialects occur sympatrically.

with only one exception (a bird at Mine Creek, Fig. 1, that sang the Gardisky Lake dialect), all birds in the isolated meadows sang Tioga Pass themes.

We color banded birds to study breeding success, dispersal between the two dialectal populations, population turnover, and the possibility of assorta-

tive mating according to dialect. Songs of males were recorded in the field on Nagra 4.2 and Nagra E tape recorders using a Dan Gibson parabolic microphone. Songs were analyzed on a Kay electric sound spectrograph (Model 7029A) using high shape and wide band filters. Because individual variation in White-

TABLE 1. Number of birds singing song types at the three recording localities.

Recording localities	Song type					Total
	Tioga	Tioga variant	Bilinguals	Gardisky	Other	
Tioga Pass	14	4	2	1	1 ^a	22
Lee Vining Creek	7	1	2	4	—	14
Gardisky Lake	1	—	—	9	2 ^b	12
Total	22	5	4	14	3	48

^a Song typical of *Z. l. oriantha* in the Canadian Rockies (see Fig. 3).

^b One song typical of *Z. l. gambelii* and one of *Z. l. oriantha* at Mount Lassen (see Fig. 3).

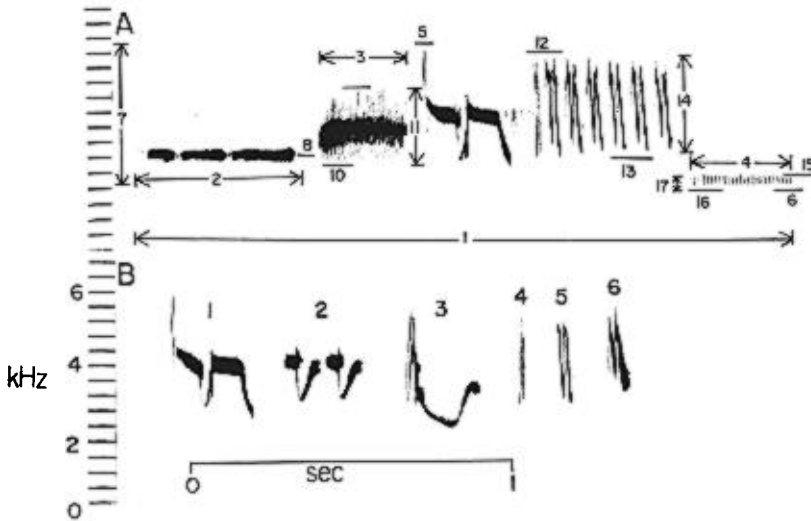


Fig. 2. A. Song typical of Gardisky Lake. Numbers correspond to characters measured and treated statistically in Table 2. B. Syllables occurring in songs recorded at Tioga Pass and Gardisky Lake. 1. Complex syllable typical of Gardisky Lake songs. 2. Two complex syllables typical of Tioga Pass songs. These syllables typically occur in pairs. 3. Complex syllable from variant song recorded at Tioga Pass. 4. Simple syllable preceding terminal trill in Gardisky Lake songs. 5. Simple syllable from terminal trill in Gardisky Lake songs. 6. Simple syllable from terminal trill in Tioga Pass songs.

crown song is slight (review in Baptista 1977), we selected the cleanest spectrogram from each bird to measure 18 parameters (Table 2, Fig. 2).

At the end of the 1979 breeding season, we captured females at Gardisky Lake and Lee Vining Creek mated to males from which songs had been recorded during the breeding season and induced them to sing in the laboratory with 0.2 ml intramuscular injections of testosterone (Searle SC-16148, 50 mg/cc).

RESULTS AND DISCUSSION

INDIVIDUAL VARIATION IN SONG

Four of 48 males in this study sang two song types (Table 1). Two of these bilingual birds were recorded at Tioga Pass and two on Lee Vining Creek (Fig. 1). The rest of the birds sang one theme each, with minor variation typical of White-crowned Sparrow song (Orejuela and Morton 1975, Baptista 1977).

THE SONG DIALECTS

The main theme recorded at Gardisky Lake began with a whistle and was followed by a buzz, a complex syllable, a trill, and a low-pitched terminal buzz (Fig. 2A). Nine of the 12 birds recorded at the lake shore or on the sur-

rounding hillsides sang the Gardisky dialect. One bird sang the dialect of Tioga Pass, one bird sang the song of another population to the north, and one bird sang the song of another subspecies (see beyond). The complex syllable typical of Gardisky was of type 1 (Fig. 2B), and the trills were always preceded by syllable type 4, which is absent in Tioga songs. The trills themselves consisted of syllable type 5.

Songs from Tioga Pass were identical to those of Gardisky Lake in the sequencing of elements but differed in the morphology of the syllables (Fig. 2B). Complex syllables were of types 2 and 3, and simple syllables were type 6. Songs containing complex syllable 3 (=Tioga variant of Table 1) were less common than songs containing complex syllable 2 and were uttered by 6 of 22 birds recorded. Two of these six birds were bilingual, using themes with both syllable types. Themes with syllable type 3 have also been recorded at Mount San Geronio, San Bernardino Mountains, 450 km to the south (Baptista and King 1980). The introductory buzz in Tioga songs was also preceded by a note (Fig. 3E), absent in Gardisky themes.

At Lee Vining Creek 4 of 14 birds (28%) sampled sang the Gardisky Lake dialect and 10

TABLE 2. Characters of Gardisky and Tioga dialects of *Z. l. oriantha*, $\bar{x} \pm SD (n)$.

	Gardisky ^a	Tioga ^{b,c}
Duration (s)		
1. Entire song	1.87 ± 0.12 (13)	1.81 ± 0.16 (21)
2. Introductory whistle	0.45 ± 0.02 (13)	0.49 ± 0.02 (24)*
3. Introductory buzz	0.25 ± 0.02 (13)	0.23 ± 0.02 (24)*
4. Terminal buzz	0.26 ± 0.05 (13)	0.31 ± 0.06 (21)*
Frequency (kHz)		
5. Maximum of song	7.00 ± 0.54 (12)	6.13 ± 0.21 (22)*
6. Minimum of song	2.10 ± 0.19 (13)	2.17 ± 0.34 (22)
7. Frequency envelope of song	4.81 ± 0.48 (12)	3.95 ± 0.35 (22)*
8. Mean of introductory whistle	3.25 ± 0.10 (13)	3.69 ± 0.32 (24)*
9. Maximum of introductory buzz	4.85 ± 0.22 (13)	6.00 ± 0.28 (22)*
10. Minimum of introductory buzz	3.15 ± 0.19 (13)	3.92 ± 0.40 (22)*
11. Frequency envelope of introductory buzz	1.67 ± 0.34 (13)	2.65 ± 0.57 (22)*
12. Maximum of trill	6.33 ± 0.43 (13)	6.03 ± 0.40 (22)*
13. Minimum of trill	3.12 ± 0.26 (13)	3.30 ± 0.21 (22)*
14. Frequency envelope of trill	3.21 ± 0.58 (13)	2.74 ± 0.52 (22)*
15. Maximum of terminal buzz	2.52 ± 0.19 (13)	2.55 ± 0.10 (21)
16. Minimum of terminal buzz	2.10 ± 0.16 (13)	2.17 ± 0.34 (22)
17. Frequency envelope of terminal buzz	0.42 ± 0.12 (13)	0.47 ± 0.15 (18)
Elements		
18. Number of	10.85 ± 1.14 (13)	10.00 ± 1.48 (22)

^a Gardisky songs from Gardisky Lake, Lee Vining Creek, and Glacier Canyon are pooled.

^b Tioga songs from Tioga Pass and Lee Vining Creek are pooled.

^c * = $P < 0.005$ (two-tailed t -tests) when Gardisky and Tioga are compared.

birds (72%) sang Tioga songs. We regard this as an area of secondary contact between the two dialectal populations.

In addition to differences in syllabic morphology, the Tioga and Gardisky dialects also differ from each other in a number of frequency and temporal characteristics. Both song types contain the same number of elements (character 18, Table 2). Song duration also does not differ between the two populations (character 1). The Tioga songs, however, appear to have slightly longer introductory whistles and terminal buzzes (characters 2 and 4). Introductory buzzes are slightly shorter in Tioga songs, and, moreover, each buzz is preceded by a note absent in Gardisky songs (e.g. a note precedes the buzz in song E, but not in songs A to D, Fig. 4).

The pitch of the introductory whistle and introductory buzz are higher in Tioga songs (characters 8, 9, and 10). The frequency envelope (width) of the buzz is also greater in Tioga songs (character 11). Trills in Gardisky songs are slightly higher pitched and have a greater frequency envelope than those in Tioga songs (characters 12, 13, and 14). Although slight,

these differences are real, as we could hear them even before examining the sound spectrograms. Trill syllables also differ in tonal quality (compare syllable types 5 and 6, Fig. 2B). There is more energy distributed in the lower frequencies in Tioga syllables (type 6). The pitch of the song is higher in the Gardisky population (character 5).

In summary, Tioga and Gardisky songs differ in 12 of the 18 characters quantified. Three characters are temporal, and nine pertain to pitch.

Marie Mans sent us songs of eight White-crowned Sparrows recorded at Virginia Lakes, Mono County (elevation 2,926 m), 16 km north of Tioga Pass. Spectrograms of these recordings were immediately recognizable by us as the dialect recorded at Gardisky Lake. Marie (pers. comm.) noted that other birds in the area also sang the same dialect. These data indicate that the songs at Gardisky Lake (this study) represent a southern extension of the more northerly Virginia Lakes dialect.

Playback studies and assortative mating.—Data on female responses to playback are confusing. In a laboratory study, Baker et al. (1981a) found

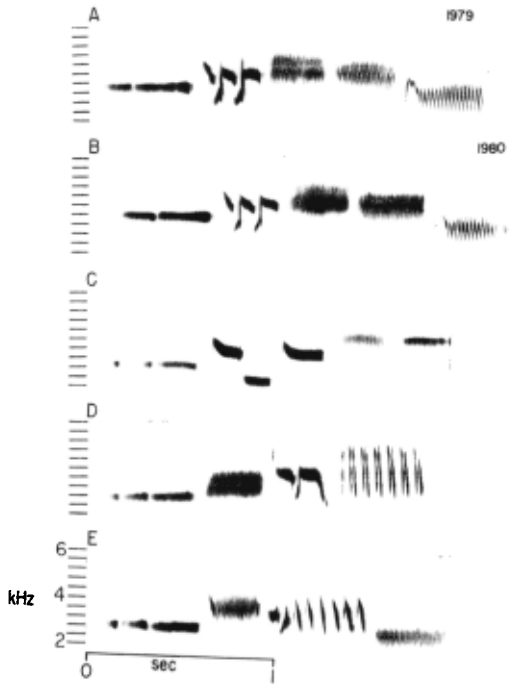


Fig. 3. A, B. Song of *Z. l. oriantha* male at Gardisky Lake, which is similar to *Z. l. gambelii* that migrate through the area, recorded in 1979 and 1980, respectively. C. Song typical of Canadian Rockies sung by bird breeding at Gardisky Lake. D. Typical Gardisky Lake song for comparison. E. Tioga Pass song recorded at Gardisky Lake. The syllable type in the terminal trill is unique to this individual.

that females responded more to the playback of the home dialect than to an alien dialect. In a field study, Petrinovich and Patterson (1981) found that females responded more strongly to the playback of an alien dialect.

Do the songs described herein represent dialects in the functional sense? Are White-crowned Sparrows capable of discriminating between Gardisky and Tioga songs based on the differences described? We have not yet conducted playback experiments utilizing the two dialects; the following observations, however, suggest that birds may distinguish between them.

In the 1981 breeding season we recorded a bird at Tioga Pass singing two themes, one containing complex syllable 2 (Fig. 2) and the

other with complex syllable 3. This individual would increase the proportion of one or the other theme in its reply bouts to match whichever theme we played to it. These data indicate that birds may distinguish between songs containing syllable types 2 and 3. It is thus likely that they can also distinguish between the Gardisky versus Tioga dialects, which differ in the morphology of their syllables as well as in pitch and tempo. This should not be surprising, because coastal White-crowned Sparrows are capable of distinguishing between songs of neighbors versus strangers singing the same dialect (Baker et al. 1981b). Moreover, the differences between responses to songs of neighbors versus strangers (t -test, $P = 0.03$) appear as great as those to songs of home versus alien dialects (t -test, $P = 0.032$) (Baker et al. 1981c).

Petrinovich and Patterson (1981) showed that female responses to the playback of an alien (adjacent) dialect were stronger than to that of the home dialect in all parameters measured. Males, however, sang significantly more to the playback of the home dialect but trilled and fluttered more often in response to the playback of an alien dialect.

If the female responses are regarded as sexual, then the above data support a disassortative mating hypothesis. We agree with Petrinovich and Patterson (1981), however, that the responses are very likely aggressive and that no meaningful conclusion with regard to mate choice based on dialect may be drawn from playback studies.

Exceptional songs.—A male recorded at Gardisky Lake in 1979 sang a song typical of *Z. l. gambelii*, a subspecies that breeds in Canada and Alaska (Fig. 3A). The complex syllable following the introductory whistle in this bird's song was identical with warble type 6 of DeWolfe et al. (1974). We captured and marked this individual and noted its reddish brown bill and black lores, which distinguish *Z. l. oriantha* from *Z. l. gambelii* (the latter having yellowish-pink bill and white lores). This same bird was present at Gardisky Lake in 1980 (Fig. 3B). It was mated, but we were unable to locate its nest and thus cannot comment on its breeding success. Morton et al. (1973, this study) have documented flocks of *Z. l. gambelii* coming through Tioga Pass in September and mingling with the local birds. These migrants often sing in passage, especially during violations of

individual distance (pers. obs.). We have observed fledgling *Z. l. oriantha* being fed by their parents as late as September. Such fledglings could possibly learn alien dialects from birds passing through. Alien songs could also be learned in their wintering grounds, where several subspecies come in contact (Baptista and King 1980).

A second bird recorded at Gardisky Lake in 1979 sang a song that contained most of the characteristics of Tioga songs (Fig. 3E), including the note preceding the introductory buzz and complex syllable 2. The terminal trill and buzz, however, were unlike that of any local bird but matched those of birds recorded at Mount Lassen by Orejuela and Morton (1975). This bird was also mated, but again the mate was not captured and the nest not located.

In 1980 we recorded a Tioga Pass bird singing a song similar to those recorded for *Z. l. oriantha* in the Rocky Mountains of Alberta (Lein 1979, Fig. 3C this study; this bird was banded at Tioga Pass as an adult in August 1979). The four whistles, alternating in low and high frequency followed by two buzzy elements in descending pitch, are typical of songs recorded by Lein. Despite its aberrant song (for Tioga Pass), this bird mated and fledged three offspring. The male paired with a different female in 1981 and fledged three more offspring. Despite singing a foreign dialect, it was paired very early in the breeding season.

What is the relative fitness of this alien singer compared to normal songsters in the population? Fledging success at Tioga Pass between 1968 and 1970 ranged from 1.4 to 2.0 fledglings per pair (Morton et al. 1972). If fledging success may be regarded as an index of fitness, it is noteworthy that this individual's unusual song did not render it less productive than others in the population.

Songs of mated pairs.—Songs of 10 females were analyzed, 3 from Lee Vining Creek and 7 from Gardisky Lake. The quality of female song varied individually and also as a function of the amount of testosterone injected. Some females sang frequently about 3 days after one injection. Others required two or three injections, each 3 or 4 days apart, before large enough numbers of "quality" songs were sung to permit adequate sampling. Some females seldom sang songs of a quality comparable to those of males; e.g. female song F1 (Fig. 4) is

quavering and not crisp as in typical male song (songs A–G). Nonetheless, with only one exception (song B1, Fig. 4), all female songs were unequivocally assignable to the Tioga or Gardisky dialectal populations. Female songs E1–G1 (Fig. 4) clearly contain syllable type 1 (Fig. 2) of the Gardisky population. Songs A1, C1, and D1 contain syllable type 2 of Tioga Pass. Two males from Gardisky Lake that sang the local dialect were mated to females singing the same dialect (songs F and F1, G and G1 in Fig. 4). One male from Gardisky Lake that sang the Tioga dialect (song E in Fig. 4) was mated to a female that sang the Gardisky dialect (song E1). One male singing the Gardisky dialect (song B, Fig. 4) was mated to a female (B1) that sang a song foreign to both dialectal areas in this study. The syllables of her trill are similar to simple syllable 22 of Baptista and King (1980), thus far known only from Mt. Lassen among *Z. l. oriantha* populations (Orejuela and Morton 1975). The other males from Gardisky Lake that sang the local dialect (songs A, C, and D) were mated to females singing the Tioga dialect (songs A1, C1, and D1). The three females from Lee Vining Creek sang the Tioga dialect, whereas their mates sang the Gardisky dialect (Fig. 5). It is noteworthy that the only male singing a Tioga dialect (Fig. 4E) was mated to a female singing a Gardisky dialect, despite the fact that the Tioga dialect was the more predominant among the females sampled.

If data from Gardisky Lake and Lee Vining Creek are pooled, then only 2 of the 10 females sang the same dialect as their mates, indicating that mating may be disassortative (two-tailed binomial probability, $P = 0.11$). If Gardisky Lake data are treated separately, then two pairs match dialects and five pairs do not (two-tailed binomial probability, $P = 0.45$); mating may thus be random with respect to dialects. Both disassortative and random mating hypotheses are treated at greater length below.

Assortative mating.—Prerequisites of the assortative mating theory are that (1) males learn and sing the song of their natal area, and (2) females also learn that song and are selectively attracted to it during pair formation (Nottebohm 1969: 312). Our recordings from testosterone-injected *Z. l. oriantha* do not support the second precondition: only 2 of 10 females sang songs matching those of their mates.

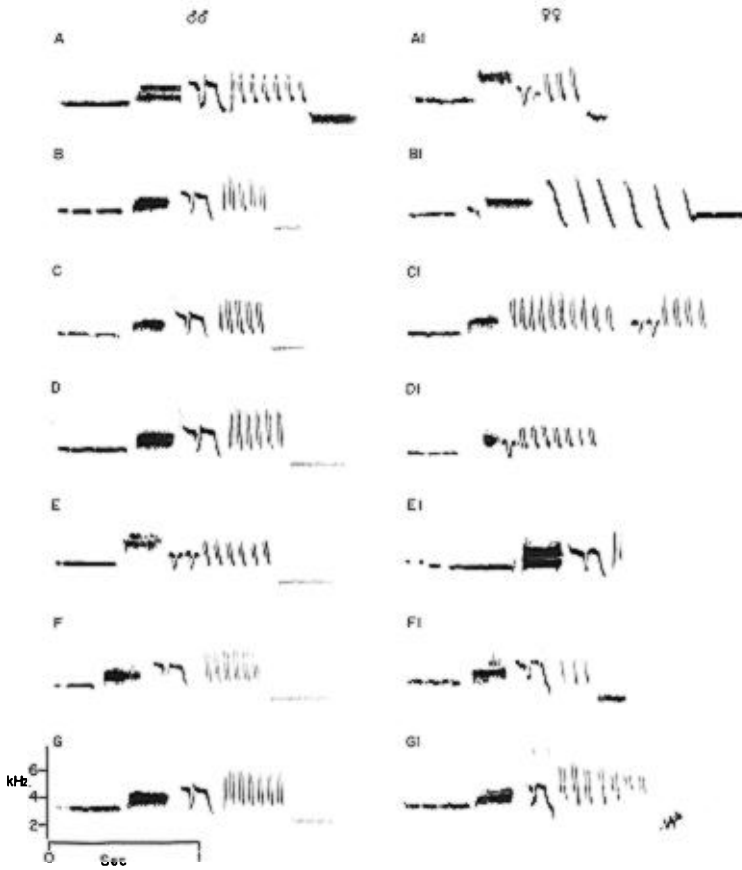


Fig. 4. A to G. Songs of males recorded at Gardisky Lake. Except for song E, which is a Tioga Pass song, all males illustrated sang typical Gardisky Lake songs. A1 to G1. Songs of females from Gardisky Lake. A is mated to A1, B to B1, etc. Note that males F and G are mated to females singing similar (Gardisky Lake) songs. The male singing a Tioga Pass song (song E) is mated to a female singing a Gardisky Lake song (E1). One male singing a Gardisky Lake song (B) is mated to a female singing syllables typical of Mount Lassen songs. The other males singing Gardisky Lake songs (A, C, and D) are mated to females singing Tioga Pass songs (A1, C1, and D1).

Moreover, 3 males and 1 female singing alien dialects were mated, and at least 1 bred successfully. A parallel study with *Z. l. nuttalli* yielded similar results (Baptista 1974; Petrino-vich et al. 1981, in prep.). Female White-crowned Sparrows must be using cues other than natal dialects in selecting consorts.

How might one explain the mismatching of dialects in mated pairs of White-crowned Sparrows? Four possibilities come to mind.

1. Dialects promote disassortative mating and thus ensure outcrossing between demes, i.e. females select males singing songs dissimilar to that of their natal area. Disassortative

mating is known in birds and has been described in the congeneric White-throated Sparrow (*Z. albicollis*; Lowther 1961, Lowther and Falls 1968). The term "disassortative," however, implies a deliberate choice by a female of a mate singing a dialect dissimilar to that of her natal area. While this may be the case, we feel that, until the pair formation process and mate choice are studied in detail, the term "disassortative" is best not used for the White-crowned Sparrow. Simpler alternate explanations are feasible, as developed below.

2. The fact that three males and one female singing foreign dialects were paired suggests

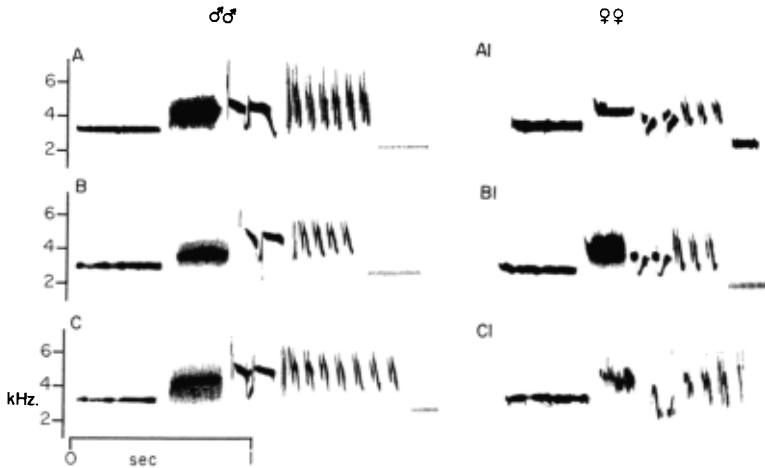


Fig. 5. Songs of three mated pairs of White-crowned Sparrows from Lee Vining Creek. Male songs are illustrated down the left column and those of their mates down the right column. Note that female C1 (paired to male C) uses syllable type 3 of the Tioga dialect, the only female to do so.

that females may not pay attention to song type during pair formation, so that mating may be random with respect to dialect. If so, the mismatching of dialects between mated pairs may be explained by differential dispersal distances between the sexes. That is, males settle in their first breeding season at a short distance from their birthplace, whereas females disperse farther, possibly into another dialectal area.

We recovered a breeding female at Gardisky Lake that was hatched at Tioga Pass 3 km away. The female sang the Tioga dialect of her natal population but was mated to a male singing the foreign (Gardisky) dialect of her breeding area. Differential dispersal distances between the sexes are well known in birds. Females usually disperse farther than males (Greenwood 1980, Van Hecke 1981). Indeed, Baker and Mewaldt (1978) have presented data suggesting that this is so in *Z. l. nuttalli*.

Results of our banding studies on *Z. l. oriantha* also suggest this relationship. Since 1978, we have banded all adults on our study area and as many of their nestlings as we could find, a total of 325. A second group of immature birds was also banded. These were independent juveniles moving onto or through the study area in late summer, a total of 409. Members of this group, although from off the study area, are thought to be local in origin. For example, nestlings that we banded on Mine Creek and in Glacier Canyon (see Fig. 1)

formed part of this sample. From the cohort of 325 nestlings, 15 males and 4 females subsequently returned as breeders (Table 3). From the cohort of 409 dispersing juveniles, 36 males and 17 females returned. All of the remaining recruits, 28 males and 72 females, were observed for the first time on the study area as adults. These data are clearly consistent with a dispersal pattern wherein females emigrate farther than males.

3. Mismatching of dialects could be due to unequal sex ratios of breeding recruits as a result of differential mortality between the sexes. Assuming philopatry and greater annual mortality of females than males, recruitment of breeding females must be from outside, again resulting in mismatched dialects between members of a breeding pair. Thus far, there have been 172 recruits to our breeding population, 79 males and 93 females. These numbers

TABLE 3. Sources and numbers of birds recruited as breeders into the study population.

Sources (n)	Recruits	
	Males	Females
Nestlings (325)	15	4
Dispersing juveniles (409)	36	17
Adults (100)	28	72
Total	79	93

do not deviate significantly from parity ($\chi^2 = 1.13$, $P > 0.05$). Each year, however, there seem to be a few more female than male recruits, and we should not yet rule out the possibility that differential mortality is occurring.

4. Mismatching of dialects could be due to sexual differences in dispositions to learn songs of neighbors at sites settled. We have presented data indicating that most females (72 of 93 or 77.4%) were recruited from outside the study population and were never seen as juveniles. They might have brought with them the dialect of their birthplace and thus do not sing the local dialect. Of 79 of the males recruited, however, 28 (35.4%) were also seen only as adults. Why do most of these sing the local dialect?

Males of some species learn dialects after dispersal, acquiring the songs of territorial males at sites settled (Kroodsma 1974, Verner 1975, Payne 1978). Payne (1981) has termed this "social adaptation," assuming that males better their social status by learning new songs. Males learn songs from their natal area, disperse, and learn new songs from local territorial males in the area settled during male-male interaction. Dispersed propagules soon countersing with local males using the local dialect; the song learned earlier in their place of birth falls into disuse and goes undetected by the field observer. Females also disperse after having learned the dialect of their birthplace. Because females are usually subordinate to males, countersinging between sexes seldom occurs, so that most dispersed females retain the songs brought with them. It is also possible that females have shorter sensitive periods than males, so that females cease learning songs at an earlier age than do males.

If dialects in White-crowned Sparrows do not promote assortative mating, why do birds learn them? Bird song is thought to function in territorial advertisement and in attracting a mate. Brown (1975: 674) has suggested that females of monogamous species choose mates more on the basis of territory quality than on the quality of individual males, in which case the role of song in territory defense would be more important than its role in attracting mates. Vocal copying would then be selected if the more complex culturally transmitted songs were the most effective in repelling males.

A number of authors have suggested, how-

ever, that song may function as a behavioral character externalizing individual fitness. Correlations between breeding success or territory quality and song characteristics have been reported in several species (Kok 1972, Howard 1974, Payne and Payne 1977). Kroodsma (1979) documented leader-follower roles during countersinging in the Long-billed Marsh Wren (*Cistothorus palustris*). He demonstrated that leader-follower roles are ritualized expressions of dominance/subordination and that vocal duelling, together with loudness of delivery, is a reflection of age and size and may be used by females as cues to assess vigor and potential fitness. It has been postulated that young birds (1) learn selectively the songs of fit males (Payne and Payne 1977, Jacobs 1979) or (2) match the songs of territorial males at sites settled, because learning their song bestows some advantage in gaining and holding a territory (Payne 1978). Payne (in press) has recently demonstrated that mating and nesting success of yearling Indigo Buntings (*Passerina cyanea*) was higher in individuals that shared songs with older neighbors than in those that did not share songs. He suggested that their success may be due to some deceptive mimicry directed at other males competing for breeding territories. Baptista (1975) has noted that songs of nearest neighbors are more similar to each other than to those of more distant individuals in *Z. l. nuttalli*, forming "subdialect" groups. This could be due either to birds learning songs in their natal area and dispersing short distances or to birds dispersing from without and learning songs of territorial males at sites settled.

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