

SONG DIALECTS OF WHITE-CROWNED SPARROWS: HISTORICAL PROCESSES INFERRED FROM PATTERNS OF GEOGRAPHIC VARIATION

MYRON CHARLES BAKER

AND

DANIEL B. THOMPSON

ABSTRACT.— We described geographic variation in the syllabic structure of the song of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) resident in coastal California. We identified six large and relatively homogeneous populations that differed discretely at one locus in the song, the complex syllable, and have called these “dialect” populations. Two “superdialects” were also identified on the basis of two other loci in the song, the introduction and the ending. Using another part of the song, the simple syllable locus, we also identified large-scale geographic clusters of similarity that were moderately concordant with dialect variation. From the patterns of geographic variation shown by the four song loci, we hypothesize that our study area was colonized by two ancestral populations. The existing song populations are therefore interpreted to be in secondary contact. Relatively narrow zones of “overlap” at dialect borders are identified and their widths estimated. Application of cline theory to the data suggests that 100–200 years have elapsed since secondary contact.

One can approach the study of local geographic variation in cultural patterns, such as avian song dialects, in the same way that an evolutionary biologist approaches the study of geographic variation in morphological characters or gene frequencies (Cavalli-Sforza and Feldman 1981). An important difference is that, in many bird species, variation in song results from learning, not from genetic transmission. Recent surveys indicate that cultural inheritance of song is the rule for most oscine birds—nearly half of the world’s avian species (Kroodsma and Baylis 1982). In this report, we apply a conceptual framework from evolutionary biology to interpret the spatial distributions of song variants in a population of birds. This application is appropriate because we hypothesize that in songbirds, as in humans, culturally transmitted traits affect the course of genetic evolution (Wyles et al. 1983).

For long-term research on the biological significance of song variation, it is important to obtain a comprehensive description of the microgeographic variation in song among a series of contiguous populations. Such information provides a basis for understanding existing patterns of genetic differentiation of the populations, behavioral responses of both sexes to field and laboratory experimental manipulations (such as playback of male song of different dialects), and patterns of dispersal within and between dialects (Baker 1975; Baker and Mewaldt 1978; Payne et al. 1981; Petrinovich and Patterson 1981, 1982; Baker et al. 1982;

Baker 1983; Tomback et al. 1983). Moreover, one may be able to suggest explanations of how song populations are related to one another in an historical sense (Baptista 1975).

We assume that populations with similar vocal patterns are more closely related than those with different vocal patterns, and that vocalizations can therefore be used to reconstruct patterns of colonization (Baptista 1975, Mundinger 1975, Baptista 1977, Baptista and King 1980). Observations of zones of intergradation and hybridization, geographic variation, and clines have provided important information for interpreting evolutionary processes (Mayr 1963, Endler 1977), and our approach to interpreting song variation derives from this tradition. By analyzing song variation within and among the dialects of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) occupying the Point Reyes National Seashore, we have developed a hypothetical model of how the dialects were derived. Because these populations occupy natural habitat in relatively undisturbed conditions within the protected boundaries of a National Seashore, our description of the geography of song may be of value in understanding the dynamics of song variation, both in the immediate and distant future. Evaluation of changes in the trait should provide an informative window for observing the process of cultural evolution in avian communication (Jenkins 1978; Slater and Ince 1979; Ince et al. 1980; Mundinger 1980, 1982; Payne et al. 1981).

MATERIALS AND METHODS

We recorded the songs of 380 territorial male White-crowned Sparrows with a Uher 4200 IC recorder and Uher microphone mounted in a 60-cm parabolic reflector. Songs were converted to audiospectrograms on a Kay Elemetrics 7029A sonograph with 80–8,000 Hz frequency range and wide-band (300 Hz) filter settings.

We sampled the population within the Point Reyes National Seashore, Marin County, California, as well as within an area extending from the southern end of the Seashore to Bolinas (Fig. 1). Variations in weather conditions, reproductive status of individuals, and habitat patchiness, all contributed to spatially non-uniform sampling. We obtained songs, however, from birds in virtually all suitable habitat. From visual and auditory counts made while recording, we estimated the total breeding population of the study area as approximately 3,000–4,000 pairs. Thus, our recordings comprised about 10% of the male population.

Males become persistently territorial by March–April in this region, with first nesting in late April or early May. Two or three complete nesting episodes commonly are undertaken through the summer season by each monogamous pair. Clutch size is usually 3–5 eggs. Territory size is about 1 ha or less. The general breeding biology, reproductive physiology, and demography of these populations have been detailed elsewhere (Mewaldt and King 1977, Baker et al. 1981b).

Each male sings a single stereotyped song about 2 s in duration at a rate of approximately one song every 15 s during sustained bouts of singing. A small proportion of males (2–4%) has two songs (Baptista 1975; this study), but such bilingual birds were not included in this analysis. As in most passerines, the song functions in territorial defense and mate attraction (Blanchard 1941, Falls 1978, Yasukawa et al. 1980, Yasukawa 1981). Repeated songs of the same male within a season as well as across seasons typically remain unchanged (Baptista 1975, Cunningham and Baker 1983).

We adopted standard terminology for describing White-crowned Sparrow songs (Marler and Tamura 1962, Baptista 1975). A “note” is a continuous trace on a sonogram; a “syllable” is a repeated figure, usually a note or group of notes; a “phrase” is a note or group of notes not repeated in the song. We divided the typical song into four sections (Fig. 2): (1) introduction, consisting usually of one or two notes or phrases, (2) complex syllables, groups of notes with two or more components, (3)

simple syllables, usually repeated single notes or phrases, and (4) end, usually a single note. Together, complex and simple syllables constitute the trill section of the song.

A typical Nuttall’s White-crowned Sparrow song from our study area (Fig. 2) may have two types of introductory phrases. The first is a whistle type of note, essentially a sine wave at a single frequency, but this can vary among individuals from a single constant note to one that is pulsed or gradually descending in frequency. The second phrase of the introduction may also be a pure tone, or, as in the example, predominantly a rapidly frequency-modulated note called a “buzz” or “vibrato.” In the example, the second phrase also includes a brief note just preceding the buzz. In the typical case, the second phrase of the introduction is at a higher mean frequency than the first. Some dialects in our area have a single phrase introduction, usually a single whistle type of note, whereas others typically have two phrases. The complex syllables of the trill section are usually paired identical units consisting of a variety of notes or phrases in each complex syllable. In the example (Fig. 2), each of the complex syllables consists of three basic parts, two high-to-low frequency sweeps bracketing a buzz of rapid frequency modulation. The complex syllables are distinct, to our hearing, in the six dialect regions and constitute the principal basis for our population dialect distinctions. The second part of the trill consists of single syllables repeated 2–11 times (mode = 5). Most commonly, they are high-to-low frequency sweeps. The song ends with either a single whistle note (Fig. 2) or a buzz. In both cases, the ending occurs at a relatively low sound frequency.

There is no universally accepted definition of “dialect” in bird song research, but this lack should not affect our descriptions here. We call a population of males sharing a common complex syllable a “dialect population.” This terminology emphasizes geographic variation in the terminal portion of the song, as has been traditional in descriptions of White-crowned Sparrow song (Marler and Tamura 1962, Baptista 1975, Baptista and Morton 1982), and should not detract from our primary emphasis upon describing the patterns of geographic variation in all the components of the song.

Our analyses follow established methods used in recent studies of variation in vocal signals of songbirds by employing an evaluation of the geographic locations of types of syllables and notes contained in the song (Baptista and King 1980, Payne et al. 1981, Adret-Hausberger 1982, Kroodsma 1982, Marler and Peters 1982, Mundinger 1982). We classified

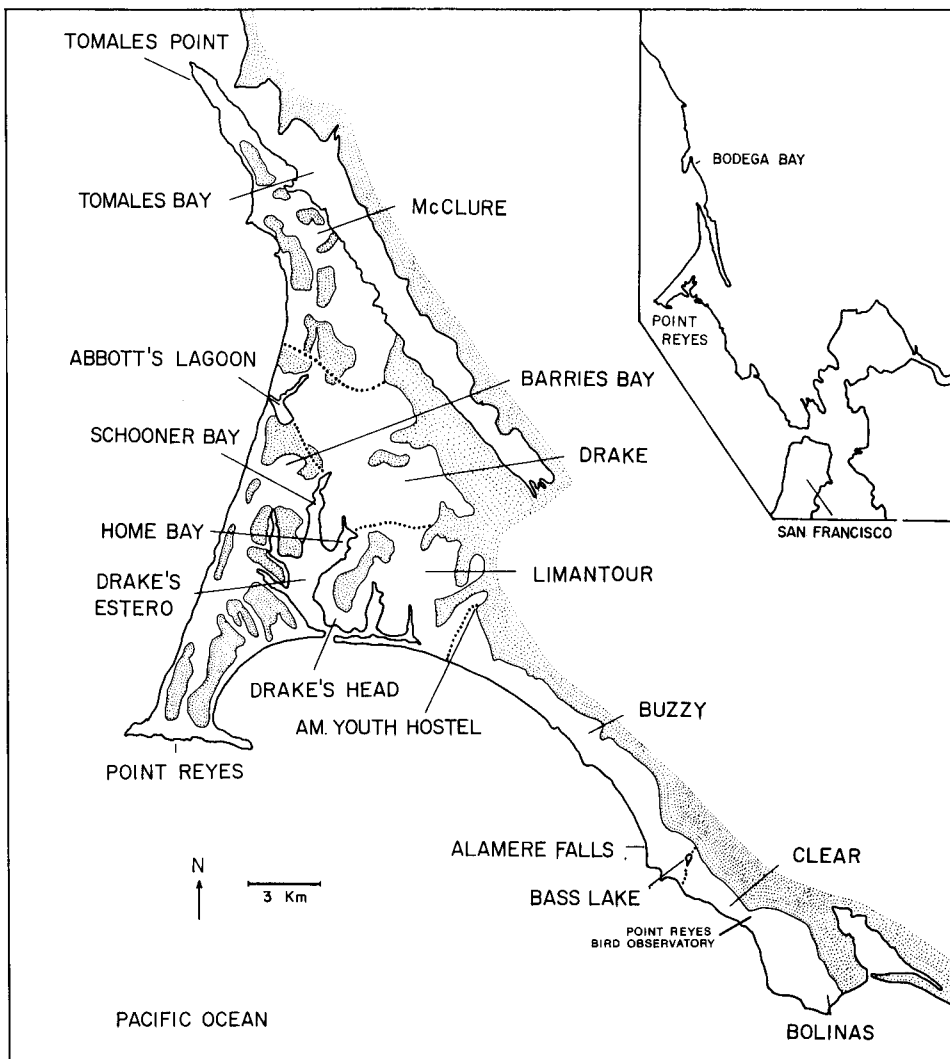


FIGURE 1. System of six dialects in the Point Reyes National Seashore. Dialect regions are named along the right side of the Point Reyes peninsula (McClure, Barries Bay, Drake, Limantour, Buzzy, Clear) and several reference landmarks are indicated along the left. Stippled areas represent habitat unsuitable for breeding White-crowned Sparrows (forest, heavy shrub growth, sand, pastures). Heavy dotted lines are borders between dialects (populations sharing similar complex syllables).

syllables into categories before identifying the geographic locations of the singers.

RESULTS

GENERAL

In normal song delivery, geographic differences in introductions, complex syllables, and endings are distinct to the human ear, whereas the simple syllables of the trill often are not. On the basis of the complex syllables, we identified six dialect populations (Fig. 1). Three of these were discovered several years ago (Baker 1975) with sonographic descriptions provided for two of the dialects. These early descriptions of the three dialects were based upon the structure of the complex syllables. We have now obtained more complete coverage of the entire

Point Reyes system of dialects which reveals interesting patterns of variation in the other components of the song.

The gross distinctions among song populations are readily seen by examining a set of

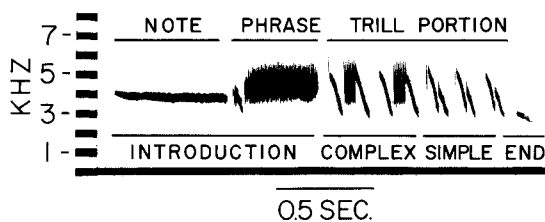


FIGURE 2. Spectrogram of a White-crowned Sparrow song from the study area indicating the four components (loci) of the song and the terminology used in this report.

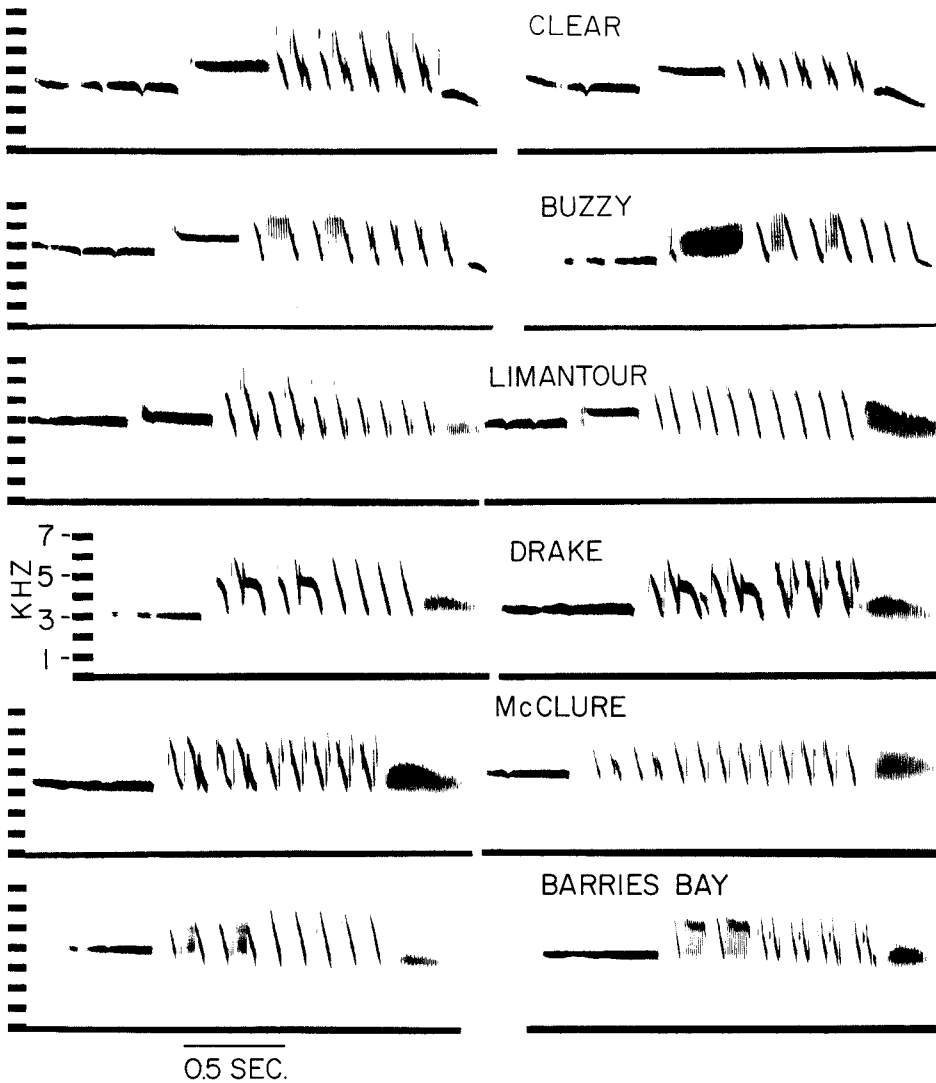


FIGURE 3. Spectrograms of songs of two typical males from each of six dialects of White-crowned Sparrows.

recordings of typical songs from the study area (Fig. 3). The Clear dialect has a two-phrase introduction, paired complex syllables lacking a buzzy component, simple syllables usually like the second element of the complex syllable, and a whistle ending (Fig. 3). Songs of the Buzzy dialect have a two-phrase introduction, paired complex syllables containing a buzzy (vibrato) element inserted between two frequency sweeps, simple syllables that can be like a single element of the complex syllable or like the simple syllables of the Clear dialect, and a whistle ending that is either a free-standing note or attached as a tail to the last simple syllable (Fig. 3). The Limantour dialect also has a two-phrase introduction, paired complex syllables that are usually simple frequency sweeps originating in a thin, high frequency element and descending rapidly, simple syl-

lables that are usually like one of the elements of the complex syllable, and a broad-band buzzy ending (Fig. 3). Songs of the Drake dialect have a single note introduction, paired complex syllables composed of one frequency sweep followed by a note that begins at high frequency and falls, then rises, then falls again in frequency (producing a characteristic "h" shape on a sound spectrogram; Fig. 3), simple syllables that are not clearly derived from complex syllables, one type being a rapid decrease then increase in frequency (producing a chevron shape on the spectrogram) and one, a simple frequency sweep, and ending with a buzz (Fig. 3). McClure songs have a single note introduction, complex syllables each usually composed of a frequency sweep followed by an element which includes a brief vibrato in the middle portion, simple syllables that rap-

idly decrease then increase in frequency (chevrons), and a buzzy ending (Fig. 3). The dialect at Barries Bay is composed of a single note introduction, paired complex syllables that contain a buzzy portion, usually bracketed by two frequency sweeps as in the Buzzy dialect, simple syllables of several possible types ranging from a simple frequency sweep to a multiparted syllable containing short vibrato segments, and a buzzy ending (Fig. 3).

This brief overview indicates that the three dialects occupying the northern parts of the Point Reyes area, Drake, McClure, and Barries Bay, formed a group sharing the characteristic of an introduction consisting of a single phrase (usually a simple pure tone), whereas the other three dialects, Limantour, Buzzy, and Clear, had a two-phrase introduction (whistle-whistle or whistle-buzz). Examination of the ending of the songs of all dialects permits the creation of another, somewhat different, dichotomy. The four northern dialects, Drake, McClure, Barries Bay, and Limantour, had buzzy endings, whereas the two southern dialects, Buzzy and Clear, had endings of a single descending whistle.

CLEAR DIALECT

The Clear dialect extended from the village of Bolinas to the vicinity of the drainage outlet of Bass Lake, where the Buzzy dialect was encountered (Fig. 1). The complex syllable typical of the Clear dialect was C1 (Figs. 4 and 6, Table 1) which was present throughout the dialect area. In our sample, we found one individual that sang a complex syllable typical of the Limantour dialect (C3), two that sang complex syllables found in only one other bird, located in the Drake dialect (C11), one bird with C2 complex syllables, more frequent in the Buzzy and Barries Bay dialects, and one bird with a C9 complex syllable, more often found in Drake and McClure dialects although infrequent there as well. Thus, 42 of 47 birds (89%) sang songs containing the same type of complex syllable (Table 1).

The simple syllables of the trill in the Clear dialect were predominately of the S1 type (44 of 47, 94%; Figs. 5 and 6). Two birds sang S4, the simple syllable common in the Limantour dialect, and one bird had the S2 type common in four of the other five dialects (Table 1).

BUZZY DIALECT

The Buzzy dialect extended, in a narrow belt of habitat along the coast, from its contact with the Clear dialect in the south to contact with the Limantour dialect in the north, in the vicinity of a wide ravine running seaward from the American Youth Hostel (Fig. 1). The com-

TABLE 1. Distribution of complex and simple syllables among six dialect regions of White-crowned Sparrows in the Point Reyes National Seashore.

Complex syllable	Dialects					
	CLEAR	BUZZY	LIMANTOUR	DRAKE	McCLURE	BARRIES BAY
Common types						
C1	42	1	0	0	0	0
C2	1	34	0	2	1	20
C3	1	4	50	4	1	0
C4	0	0	1	33	1	0
C5	0	0	1	33	3	4
C6	0	0	0	7	41	0
C7	0	0	1	0	0	34
C8	0	0	0	0	0	10
C9	1	0	0	5	0	7
Rare types						
C10	0	0	0	0	1	1
C11	2	0	0	1	0	0
C12	0	0	0	2	2	0
C13	0	0	0	2	0	0
C14	0	0	0	2	4	1
C15	0	0	0	0	2	0
C16	0	0	0	2	0	1
C17	0	0	0	2	0	0
C18	0	0	0	0	5	0
C19	0	0	0	0	0	1
C20	0	0	0	0	0	1
C21	0	1	0	0	0	0
C22	0	0	0	3	1	0
Simple syllables						
S1	44	15	0	0	0	0
S2	1	19	13	62	4	17
S3	0	0	1	0	0	19
S4	2	6	39	11	2	4
S5	0	0	0	0	0	36
S6	0	0	0	25	56	0
S7	0	0	0	0	0	4

plex syllable typical of the Buzzy dialect was C2 (34 of 40 birds, 85%; Table 1, Figs. 4 and 7). One male in the area of the Clear-Buzzy border sang complex syllables typical of the Clear dialect (C1). Four males in the area of the Buzzy-Limantour border sang C3 complex syllables typical of the Limantour dialect. One individual sang a unique complex syllable (C21) similar to C1 but lacking one element.

The simple syllables encountered in the Buzzy dialect were of two types (Figs. 5 and 7). Predominating in the area near the Buzzy-Clear transition was S1, the simple syllable common in the Clear dialect songs. In this area, 15 males sang songs containing S1 simple syllables, 13 had the C2 complex syllable marking the Buzzy dialect, one had S1 in combination with the C1 complex syllable typical of the Clear dialect, and one had the unusual C21 complex syllable mentioned above (Table 1).

From the location of this cluster of 15 males, near Alamere Falls, simple syllable S2 predominated throughout the rest of the Buzzy

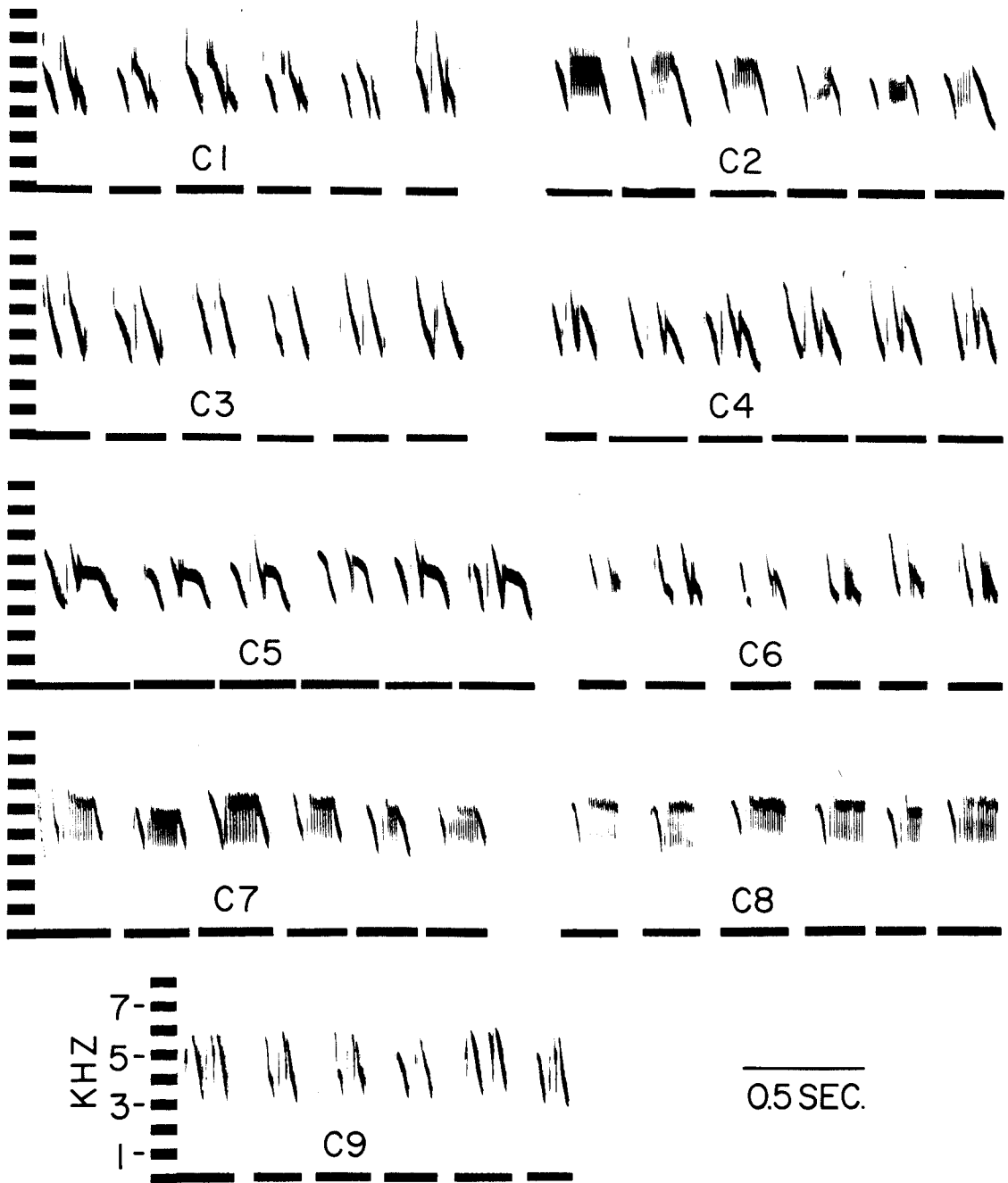


FIGURE 4. Nine common types of complex syllables found in the study area. Six examples of each type are illustrated to show the range of variation within each category.

dialect to the border with the Limantour dialect. In the neighborhood of this border, however, six birds sang S4 simple syllables, a type predominating in the Limantour dialect.

LIMANTOUR DIALECT

This dialect extended from the border with the Buzzy dialect and occupied a broad region bordered by Drake's Estero and Home Bay on the west and by the transition with the Drake di-

lect, which extended in a roughly easterly direction from the upper reaches of Home Bay (Fig. 1). The complex syllable dominating the Limantour dialect was C3 (50 of 53 birds, 94%; Table 1, Figs. 4 and 8). Of the three birds that sang songs containing alien complex syllables, one sang C7, the syllable typical of the Barries Bay dialect, one sang C4 and one C5, both typical of the Drake dialect. One of these latter two males was on the Drake-Limantour border

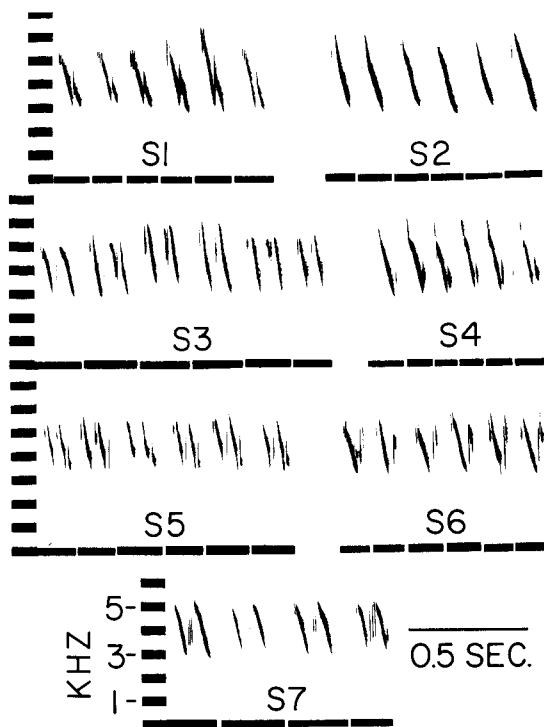
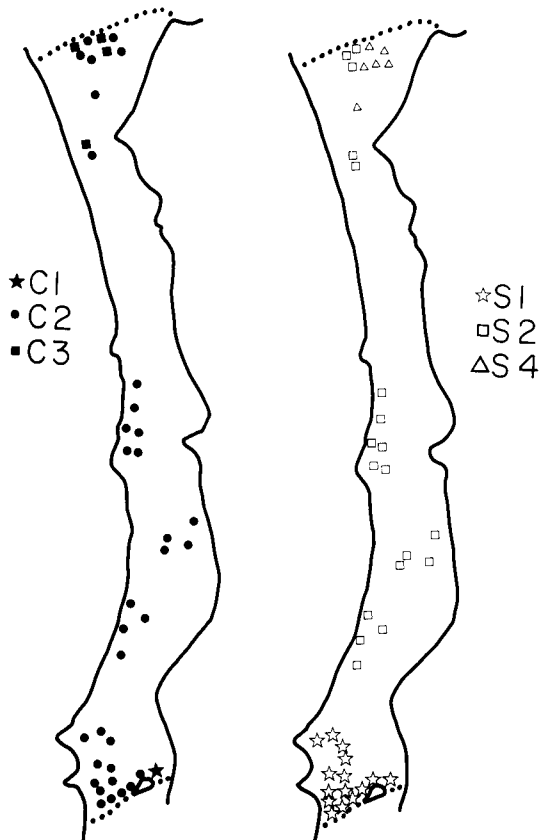


FIGURE 5. Seven types of simple syllables found in the study area. Several examples of each type are illustrated to show the range of variation within each category.

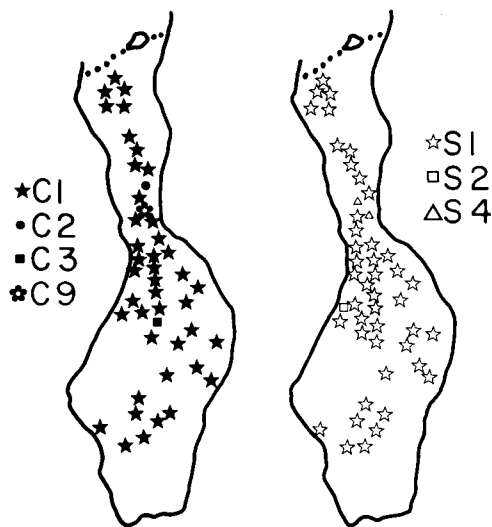
BUZZY DIALECT



COMPLEX SIMPLE

FIGURE 7. Buzzy dialect geographic distribution of complex and simple syllable types (rare types not illustrated).

CLEAR DIALECT



COMPLEX SIMPLE

FIGURE 6. Clear dialect geographic distribution of complex and simple syllable types. Rare types of syllables (<5 individuals in the total recorded sample) not included on the map (but see Table 1 for summary of rare types).

and therefore not truly embedded within the Limantour dialect.

We found two major types of simple syllables in the Limantour dialect, S2 and S4 (Figs. 5 and 8). Simple syllable S4 (39 birds) predominated throughout the eastern part of the dialect region adjacent to Buzzy. Simple syllable S2 (13 birds) was characteristic of the western part of the Limantour dialect on a broad peninsula called Drake's Head.

DRAKE DIALECT

This dialect extended from the border with the Limantour dialect in a northwesterly direction, bordered to the west by Schooner Bay and the Barries Bay-Drake dialect transition, which extended approximately from Schooner Bay to Abbott's Lagoon, and on the north by the McClure-Drake dialect transition (Fig. 1). The Drake dialect was dominated by two closely related complex syllables C4 and C5

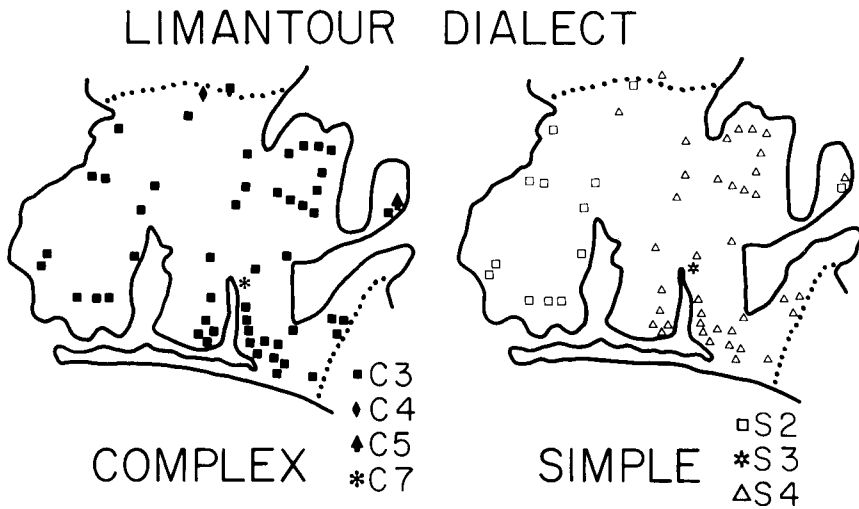


FIGURE 8. Limantour dialect geographic distribution of complex and simple syllable types (rare types not illustrated).

(together 66 of 98 birds, 67%; Table 1, Figs. 4 and 9). Syllable C12 is a related variant of C5, however, and if we include the two birds with this type then 68 of the 98 birds (69%) in the sample shared similar complex syllables.

Complex syllables C4 and C5 differed primarily in the final frequency sweep of the syllable. The C4 syllable, which predominated in the southern region of Drake toward the Limantour dialect, had a final frequency sweep that decreased sharply in time. The C5 syllable,

which predominated in the rest of the Drake dialect, had a final frequency sweep that decreased in frequency with time more slowly in the early part of the note followed by a rapid decrease; on a sound spectrogram, this produced an “h” shape (Fig. 4). It was usually easy to assign complex syllables to either C4 or C5 groups, but there were a few intermediates. We are reasonably confident in the groupings, however, and because we made the classifications without knowing the map lo-

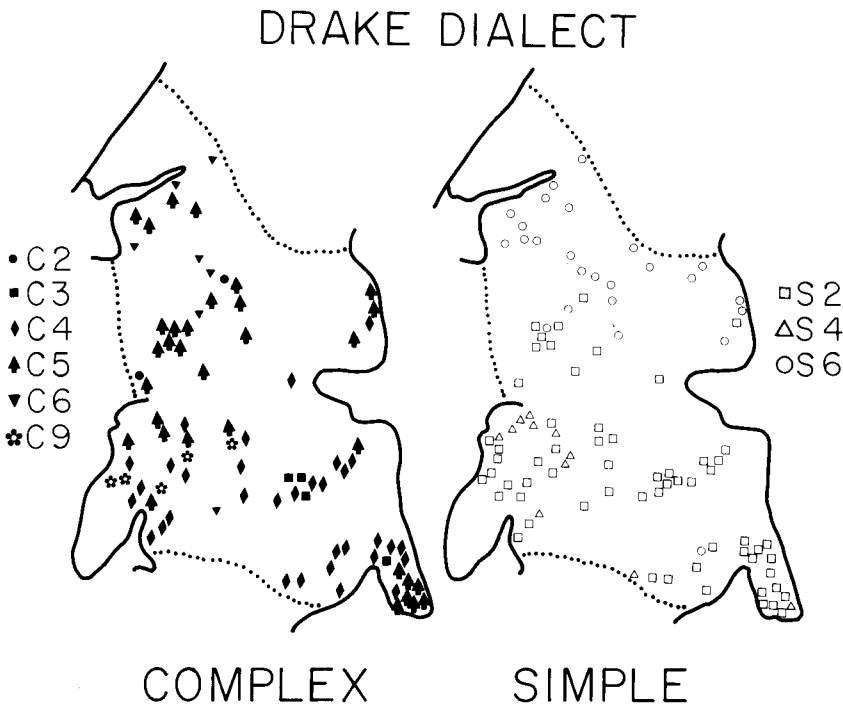


FIGURE 9. Drake dialect geographic distribution of complex and simple syllable types (rare types not illustrated).

cations, the pattern of concordance between syllable type and general geographic location is reliable.

The remaining 30 birds in the Drake dialect region had complex syllables distributed into 10 categories. One bird sang complex syllable C11 and two sang C14 which were closely related to the common complex syllable found in the Barries Bay dialect. Two birds sang C13 and two sang C16, both of which types were related to C4 and C5 of Drake and possibly to C6, the common type in the McClure dialect. Two birds sang C2, common in Buzzy; five birds sang C9, also found in low numbers in Barries Bay; seven birds sang C6, the major complex syllable in the McClure dialect; four birds sang C3, the type predominating in the Limantour dialect; three birds sang C22, probably a derivative of C3; and two birds sang a unique complex syllable, C17.

Simple syllables in the Drake dialect were distributed into three categories (Table 1, Figs. 5 and 9). The predominant simple syllable was S2, found in 62 of 98 birds (63%); the next most frequent was S6, found in 25 birds (26%); and the remaining 11 birds sang S4 (11%).

McCLURE DIALECT

The McClure dialect extended from its southern border with the Drake dialect northward to the end of Tomales Point, a narrow peninsula bordered on the east by Tomales Bay and on the west by the Pacific Ocean (Fig. 1). One complex syllable, C6, dominated this region (41 of 62 birds, 66%; Table 1, Figs. 4 and 10). The C6 complex syllables seemed more variable than those found in the dominant categories of other dialects. This variation was not clustered around several typical complex syllable morphologies, as in other dialects, but instead was characterized by more continuous variation in many elements of the syllable. Twenty-one additional birds in the McClure dialect sang complex syllables that were distributed into 10 categories. One bird sang C2, common in Buzzy and Barries Bay; one sang C4 and three sang C5, both common in Drake; one sang C3, common in Limantour; one sang C10, four C14, and two C15, all three of which types were related to C7, C8, and C2 of Barries Bay; two sang C12, a variant of C5 which was common in Drake; five sang C18, a complex syllable that had affinities with C6 of the McClure dialect; and one bird sang C22, a syllable related to C3 of the Limantour dialect.

In the simple syllables of the trill, 56 of 62 birds (90%) sang S6, the second most common simple syllable in the Drake dialect neighboring to the south (Table 1, Figs. 5 and 10). Four

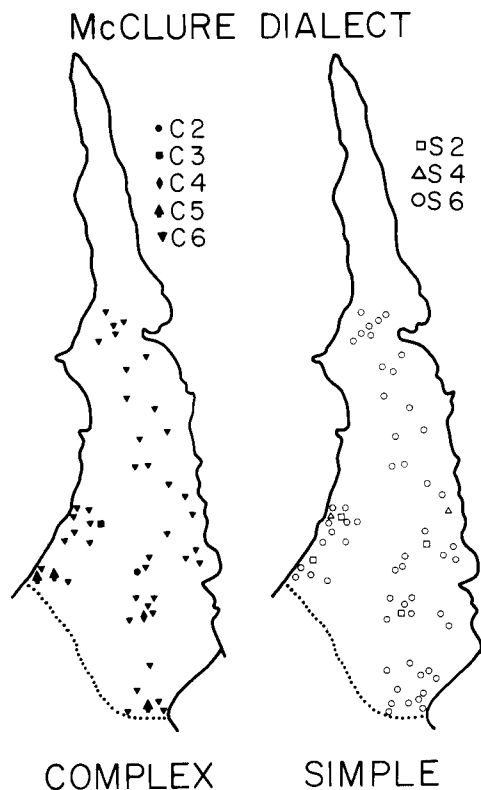


FIGURE 10. McClure dialect geographic distribution of complex and simple syllable types (rare types not illustrated).

other individuals sang S2 and two sang S4 simple syllables, also frequent in the Drake dialect.

BARRIES BAY DIALECT

This dialect had contact with the Drake dialect in the north along a border running from approximately Abbott's Lagoon to Schooner Bay, was separated from the Drake and Limantour dialects on the east by Schooner Bay and Drake's Estero, and then extended southward out to the lighthouse at Point Reyes (Fig. 1).

A closely related group of complex syllables, C7 (34), C8 (10), and C2 (20) dominated the Barries Bay dialect (64 of 80 birds, 80%; Table 1, Figs. 4 and 11). By ear, we could not distinguish between these three complex syllables, but when we transformed them into spectrograms, we could easily separate them by the presence or absence of the last simple frequency sweep and the frequency of the most intense vibrato in the "buzzy" element. Moreover, when mapped (Fig. 11) following assignment to categories, the three types occurred in a sequence along the linear dimension of the dialect region and were not randomly intermixed. The remaining 16 birds sang complex syllables distributed into seven categories. Seven birds sang C9, a type represented by five

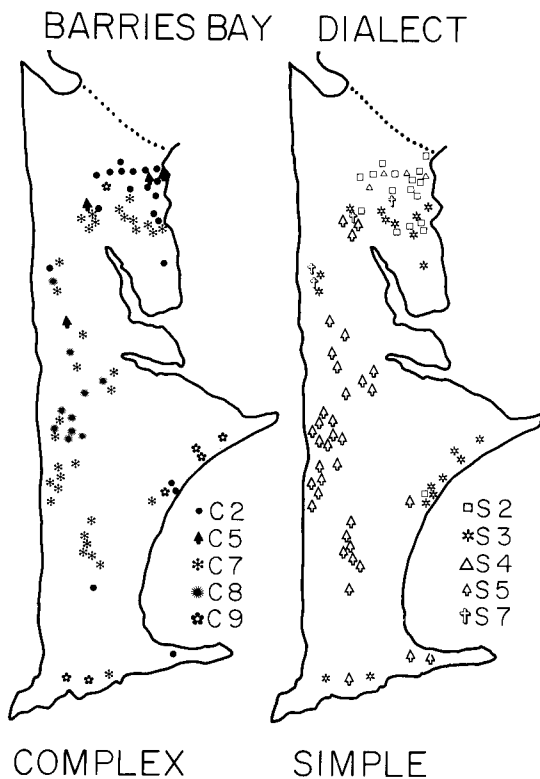


FIGURE 11. Barries Bay dialect geographic distribution of complex and simple syllable types (rare types not illustrated).

birds in the neighboring Drake dialect. Four birds sang C5, a common syllable in Drake. The five complex syllables C10, C14, C16, C19, and C20 were sung by five individuals in the Barries Bay dialect area (Table 1).

Five different types of simple syllables occurred in the Barries Bay dialect. Seventeen birds (21%) sang S2, the most common type in the Drake dialect, and most of these individuals were located in a zone adjacent to the Drake dialect. Thirty-six birds (45%) sang the S5 simple syllable, unique to this dialect. Nineteen birds (24%) sang S3, a type found in only one other bird that lived in the Limantour dialect area. In addition to these three major categories, four other birds sang S4, the common simple syllable of Limantour, and four sang S7, also unique to the Barries Bay dialect.

DISCUSSION

Analysis of note and syllable variation in the song of the White-crowned Sparrow reveals a pattern of population subdivision into geographically distinct groups. The four parts of the song (introduction, complex syllables, simple syllables, and ending) divide the entire Point Reyes population at several levels. The introduction and ending separate the total population into northern and southern parts, and

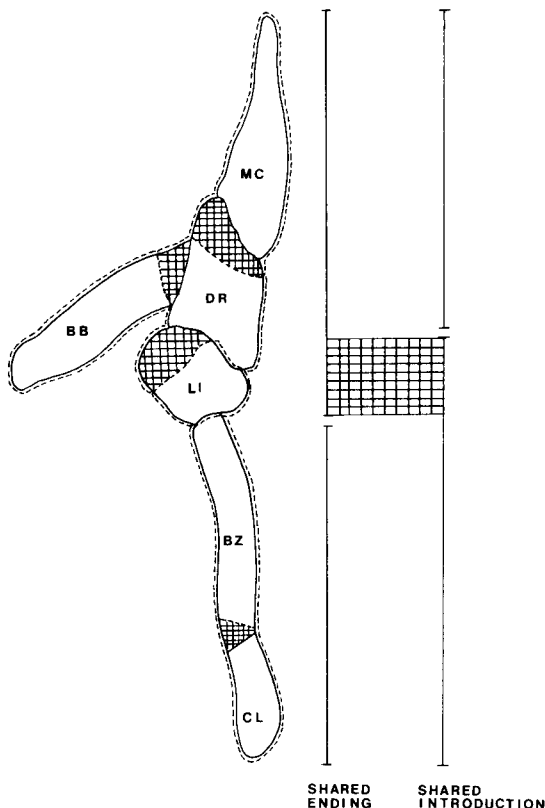


FIGURE 12. Patterns of geographic variation in four parts of White-crowned Sparrow song in the Point Reyes National Seashore. Solid lines enclose populations sharing complex syllables (MC = McClure, DR = Drake, BB = Barries Bay, LI = Limantour, BZ = Buzzy, CL = Clear), dashed lines those sharing simple syllables. Cross-hatched areas encompass males with the complex syllable of one population and the simple syllable of the adjacent population ("hybrid songs"); these are zones of song intergradation. Brackets on the right indicate that song groups MC, DR, BB, LI, share a common syllable at the end of their songs different from the ending shared by BZ and CL. Song groups MC, DR, and BB share a similar introductory syllable that differs from the introduction shared by LI, BZ, and CL. Intergradation between these two major "superdialects" is noted by the cross-hatching on the right.

the complex and simple syllables further subdivide the population into smaller segments (Fig. 12). We have described the dialects on the basis of characteristic complex syllable groups, because these were easily distinguishable by human ear, have been used in other descriptions of dialect variation in this species, and the boundaries of the complex syllable distribution of Limantour coincide with the boundaries of the introduction and ending portions. The distribution of simple syllables is somewhat offset from that of the dialects, with the result that two adjacent dialects usually share a simple syllable in the region of the dialect border (Fig. 12).

The different song components have differ-

ent patterns of variation around the dialect borders. The border between the northern group of birds with one introductory phrase and the southern group of birds with two introductory phrases coincides exactly with the Drake-Limantour complex syllable border. Without exception, birds with the Drake complex syllables (C4, C5, and their variants) have one introductory phrase and birds with the Limantour complex syllable (C3) have two. The border between the buzzy type of ending in northern birds and the whistle type of ending in southern birds coincides with the Buzzy-Limantour dialect border, but a few birds in the southern corner of the Limantour dialect, near the border, have a whistle-like ending or no ending at all. In general, the boundaries of regions with common simple syllables do not coincide with boundaries defined by the introduction, complex syllable, or ending (Fig. 12). In the region of the Buzzy-Limantour dialect border, however, the intergradation of simple syllables between dialects is minor, with only six birds in the Buzzy dialect singing the simple syllables characteristic of the Limantour dialect.

The song components (introduction and complex syllables) that delineate dialect regions with no intergradation in the composite song are also heard first in normal singing. Birds often sing a partial song, including only the introduction and complex syllables, possibly because of lower motivation (Falls 1969, pers. observ.). Thus, simple syllables and endings occur less predictably in the singing behavior of individuals, which may indicate that these portions of the song are not as reliable for population discrimination. Perhaps they are less important in this aspect of communication than are the introduction and complex syllables.

The Drake dialect borders on three dialects and intergrades simple syllables with all three. Furthermore, the Drake and McClure dialects resemble each other; this pair also has the longest common border. Perhaps the degree of similarity and intergradation of song syllables between dialects is indirectly influenced by the length of the border and the number of bordering dialects. Early learning experiences in the border areas, such as copying some song components of a neighboring area, or occasional dispersal between areas with different songs combined with learning the local song types following dispersal, may be increased under these conditions.

Our extensive experience in the recording areas gave us the impression of a positive correlation between song syllable diversity and habitat patchiness, perhaps suggestive of how

dialect variation could originate (Thielcke 1965, Baptista and Johnson 1982). For example, the McClure and Barries Bay dialects vary substantially in complex syllables. These two dialects are also characterized by patchy habitat; suitable habitat for breeding by White-crowned Sparrows is interspersed among sand dunes along the coast and large pastures elsewhere. Assuming that colonization is coupled with errors and improvisations in song learning (Lemon 1975), the net result could be to increase song differentiation in the McClure and Barries Bay dialects. This line of reasoning, developed here on a small geographic scale, is similar to that of Miller (1951), who postulated that the high degree of subspecies differentiation on the geographic scale of the west coast of the U.S. was caused by environmental heterogeneity. We did not illustrate rare types of complex syllables (5 or fewer individuals; Table 1), but note that their geographic distribution is essentially uniform over each dialect, rather than restricted to marginal or isolated areas. This indicates a potential for copy error and improvisation, and the origination of song variation throughout a dialect.

We now consider a reconstruction of the origins of this particular system of six dialects, together with the possible relationships among dialects. We first reconsider the morphology of the entire song and its pattern of geographic variation. Considering a single portion of the song at a time (introduction, complex syllables, simple syllables, or ending), we identified discrete groups of birds with each group usually occupying contiguous geographic space. Considering all four portions of the song as separate characters of the whole song phenotype, however, there are few precisely concordant geographic patterns. The result is somewhat analogous to the geographical patterns of discordant variation and clines in morphological and allozyme characters of various other organisms (Wilson and Brown 1953, Johnson 1975, Schennum and Willey 1979), and presents similar problems in interpretation.

In the case of song variation in the populations at Point Reyes, we can use the discordant variation of the four parts of the song to formulate an interpretation of dialect relationships. Traditional ways of interpreting patterns of intergradation (e.g., Mayr 1963, but see Endler 1977 for alternative view) see an abrupt step-change in character state as evidence that two contiguous populations diverged in allopatry and are therefore in secondary contact. A more gradual change in character state is taken as evidence of primary intergradation with differentiation having occurred in sympatry.

Our six dialects can be grouped into two larger superdialects. One superdialect is characterized by a single introduction phrase and a buzzy ending, and is represented by three northern dialects: McClure, Barries Bay, and Drake. The other superdialect is characterized by a two-phrase introduction and a whistle ending, and is represented by two southern dialects: Clear and Buzzy. Reference to populations outside the Point Reyes area may be made in an attempt to identify primitive retentions in the song which would suggest an historical pattern of colonization for our system of song populations. Populations south of our study areas, including the San Francisco Bay area, rarely contain birds who sing songs with a buzzy ending (an exception is the Lake Merced area; Baptista 1975), and the whistle type of ending is predominant. Populations north of Point Reyes, as a rule, have songs with buzzy endings. Single-phrase introductions are also fairly rare south of Point Reyes (an exception is Brooks Island; Baptista 1975), with the two-phrase introduction predominating. North of Point Reyes, single-phrase introductions are common, for example, at Westport and Albion, California (Baker et al. 1984), but the populations nearest the northern limits of our study area, for example, Bodega Bay, have two-phrase introductions. Therefore, although outgroup comparison does not produce a clear picture, on the basis of the ending components of songs, the two southern dialects in our study area, Buzzy and Clear, are most likely derived from populations farther to the south, whereas the three northern dialects of McClure, Barries Bay, and Drake, may be derived from populations farther north. Evidence from the introductory components of the songs is less helpful in suggesting colonization patterns but weakly supports the concept of northern and southern ancestral populations.

Consequently, by one interpretation, the whole Limantour dialect can be regarded as an intergrade between the two superdialects, with a two-note (southern) introduction and a buzzy (northern) ending. An alternative view would be to consider the Limantour dialect a result of multiple founding events from more than one source population. In either case, we hypothesize that the Point Reyes area was founded by two ancestral groups, one in the northern area and one in the southern, that met in secondary contact somewhere in the area occupied by what we refer to as the Limantour dialect.

We can also address the issue of contact zones between populations on the basis of complex and simple syllables. Using complex syllables, we identified two southern dialects, Clear and

Buzzy. Simple syllables usually do not vary in space in precise concordance with the complex syllables. In the region just north of the Buzzy-Clear border, birds sing complex syllables of the Buzzy dialect and simple syllables of the Clear dialect (Fig. 12). The simple syllable characteristic of the McClure dialect is distributed southward into the Drake dialect (Fig. 12). In this "overlap" area, birds sing Drake complex syllables and McClure simple syllables. In the upper reaches of Schooner Bay, the dialects of Barries Bay, Drake, and Limantour are nearby, although Limantour birds are not in direct contact with Barries Bay birds. In this region, the simple syllable characteristic of the southern three-fourths of the Drake dialect extends across the dialect border into the Barries Bay dialect (Fig. 12). In this overlap area, birds sing Barries Bay complex syllables and Drake simple syllables. Similarly, the same Drake simple syllable is distributed southward onto Drake's Head in the western portion of the Limantour dialect. In this area, birds sing Limantour complex syllables and Drake simple syllables (Fig. 12). We postulate that these several "overlap" zones formed by the spatial association of complex and simple syllables represent secondary contacts between populations that were formerly separate.

A contrast to these common kinds of overlap areas can be seen in the vicinity of the Buzzy-Limantour border. Just south of the border were six birds with complex syllables of one dialect and simple syllables of another dialect. Most were located near the dialect border, making a much narrower overlap than at other dialect borders. Four birds sang Limantour simple syllables with Buzzy complex syllables, and two sang Buzzy simple syllables with Limantour complex syllables. Three other birds that were recorded here sang both Limantour simple and Limantour complex syllables. Our auditory surveys in this area revealed that only a few birds sang Limantour complex syllables; the great majority sang the Buzzy dialect. Although our sample of recorded songs in this region is small, it suggests that the overlap is smaller and perhaps more complicated than in other dialect pairs.

The patterns of intergradation of song populations raise several questions about the song transmission process and the origin of the intergrade zones. The intergrades, or song "hybrid" zones, have several properties: (1) only rarely do they contain parental song types, (2) usually only one type of hybrid song occurs in each zone, although at least two are possible in the case of simple and complex syllables, and, (3) the broad song intergrades tend to occur between populations that differ only in

complex and simple syllables. Three parts of the song differ between Drake and Limantour, and between Limantour and Buzzy, but intergradation is relatively limited in the former and virtually absent in the latter.

Studies of song learning in White-crowned Sparrows (Marler 1970) indicate that usually the entire tutor song is copied. Therefore, the hybrid songs probably arise during the song learning process. This could occur in at least two general ways. First, a bird developing a hybrid song from hearing two different songs during the sensitive phase could colonize the area between two dialects, and the hybrid song could spread by immature copying in subsequent years. In this model, the hybrid zone resembles a "mini-dialect" and arises from a single learning event and the normal song transmission process—a view supported by the occurrence of only one hybrid type in each zone. Second, the hybrid song population could arise from multiple learning (copying) events. Several birds may learn components from two song types in the region of a dialect border; this could be followed by the gradual spread of one syllable type into an adjacent dialect region. This model of spread is analogous to the spread of an allele, at some selective advantage, gradually replacing an alternative allele at a particular gene locus. In the case of learned song, we would need to postulate some "selective" advantage of the new combination. It might be easier to learn, it might propagate better than the old combination in the local area, or it might be more stimulating to females. If the hybrid zones arise by this second explanation, their formation requires a transmission process as yet undiscovered in White-crowned Sparrows. At least it is clear that the hybrid song in the intergrade zone is not a random association of syllables from the adjacent dialects, and birds with "parental" songs do not appear to be carrying them into the hybrid zones. Even if some birds can change songs after dispersing to a new area, this does not explain the origin of existing stable geographic patterns.

If the song populations in our study arose from two ancestral song groups, then similarities between two song populations could represent either convergence or similarities already shared by the two ancestral song groups. The pattern of song variation within and between dialects suggests that note and syllable variation is constrained within some bounds around a common song phenotype. Some types of learning and development errors or improvisations may be more common than others. If dialects are initiated by founder populations with deviant songs occurring from either

copying errors or improvisations, we might expect to find similar syllables recurring in dialects of different ancestry. This could explain the buzzy sounding complex syllables found in the northern (Barries Bay) and southern (Buzzy) superdialects, and the simple syllables shared by the Drake, Limantour, and Buzzy dialects. Instead of common ancestry, perhaps these similar syllables represent convergence between dialects from recurrent learning errors or improvisations.

To summarize our theory of the historical patterns of dialect formation in this system, we postulate that two ancestral populations of White-crowned Sparrows colonized the Point Reyes coastal habitat. Perhaps all six dialect areas were colonized about the same time, with founders from a southern ancestral population colonizing habitat in what is now the Clear and Buzzy populations, and founders from a northern ancestral population colonizing what are now the McClure, Barries Bay, and Drake song regions. The existing overlap between the northern and southern superdialects in the current Limantour dialect area could have been caused either by simultaneous colonization by founders from both superdialects, or by some type of spreading process from northern and southern areas into the Limantour region. It is also possible to postulate a series of founding events with daughter populations founded progressively northward from southern ancestral populations and southward from northern ancestral populations. This model implies that the Buzzy population was derived from Clear, and that the McClure population generated Drake and Barries Bay song groups.

A major result of our study is the documentation of abrupt borders between most dialects (populations of complex syllables), with relatively limited but consistent intergradation in simple syllables and endings of songs, but no intergradation of introduction and complex syllables. We interpret the patterns as indicating that intergradation was brought about by song-copying deviations or improvisations following founding events and secondary contact. We further hypothesize that the entire system of dialects originated by multiple founder episodes from two ancestral populations on the Point Reyes peninsula.

We can extend our analyses to consider a theoretical aspect of cultural evolutionary processes. Specifically, we apply aspects of population genetics theory to song as a culturally transmitted trait (Cavalli-Sforza et al. 1982) by considering the song of White-crowned Sparrows as analogous to a chromosome on which there are four loci to which we have referred as introduction, complex syllables,

simple syllables, and ending. The accuracy of the analogy is not critical but only is asserted heuristically because of similarities in the behavior of cultural and genetic traits in theoretical analysis of the evolutionary process (Cavalli-Sforza and Feldman 1981).

We interpret our data as indicating secondary intergradation between populations whose songs differentiated in allopatry. Our view best approximates the allo-parapatric model described by Endler (1977). Endler pointed out problems that can arise in distinguishing primary and secondary intergrades, and factors that influence patterns of clinal and non-clinal character variation. In spite of the problems, Endler developed theoretical models that predict the elapsed time since the occurrence of secondary contact. We use the theoretical model which assumes that natural selection plays a significant role in producing an equilibrium zone of intergradation, by opposing the influence of gene flow. We assume selection is important because results in other studies on these same White-crowned Sparrow populations suggest that behavioral mechanisms of male and female discrimination and of biased juvenile dispersal may reduce exchange of birds between dialects (Baker and Mewaldt 1978, Baker et al. 1981a, Baker 1983, Tomback and Baker 1984). Pertinent to our analysis of the current data is Endler's equation for the time since secondary contact:

$$T = 0.64(w/l)^2,$$

in which T = time in generations, w = equilibrium width of the cline (intergrade zone), and l = root mean square distance of gene flow. The value of 0.64 is derived from simulation of a model which assumes that the habitats of the two populations are selectively different (for derivation, assumptions, and details, see Endler 1977).

We estimated the width of the intergrade zones between the dialects of our study populations as the width of the zone in which birds sing the complex syllable of one dialect and the simple syllable characteristic of the adjacent dialect. These approximate values are Clear-Buzzy = 1.5 km, McClure-Drake = 1.75 km, Drake-Barries Bay = 2 km, Drake-Limantour = 2 km (the latter distance measured as the approximate width of Drake's Head). The intergrade between Buzzy and Limantour was not used because of small sample size. To apply the model to traits of cultural transmission instead of genetic transmission, we estimated the probability of leaving a deme from:

$$l = X(g)^{1/2},$$

(Endler 1977), in which l is the potential flow of song traits, given that X = mean dispersal

distance (614 m for males; Baker and Mewaldt 1978) and g = expected rate of entering an adjacent dialect (13/198 males, 0.066; Baker and Mewaldt 1978). Using these values, we calculated that $l = 157$ m. Putting the values for l and w into the equation for T gives the following results for the 2 km intergrades of Drake-Barries Bay and Drake-Limantour:

$$T = (0.64)(2,000/157)^2 = 104 \text{ generations.}$$

For the Clear-Buzzy dialect pair, $T = 58$ generations, and for McClure-Drake, $T = 80$ generations. These values can be translated into years by multiplying them by 1.8, which is the generation time for Nuttall's White-crowned Sparrow (Baker et al. 1981b). Thus, assuming that the intergrade zones are at equilibrium width, the time since secondary contact among dialects ranges from about 100–200 years.

Interpretations of historical processes are speculative, but we have some evidence of a different kind that supports the general form of our explanatory model. In our studies of the genetic properties of some of these dialects (Clear, Buzzy, Limantour, and Drake), we found that the farther apart the dialects were in distance, the farther apart they were genetically (Baker et al. 1982), and for some allozyme loci, the allelic frequencies appeared to be clinal. These are patterns that one would expect to find in a series of populations in secondary contact after a sequence of founding events distributed along a coastal environment.

ACKNOWLEDGMENTS

We thank A. E. M. Baker, M. A. Cunningham, G. L. Sherman, W. M. Shields, and D. F. Tomback for discussions and assistance, M. A. Cunningham for providing most of the recordings from the Clear dialect, and J. Freiberger for help with data analysis. We also are grateful to L. F. Baptista, P. K. McGregor, L. R. Mewaldt, and R. B. Payne for criticisms, M. Mitchell for drawing Figure 12, and the Point Reyes Bird Observatory and Point Reyes National Seashore for their cooperation. This project was supported by National Science Foundation grants DEB-78-22657 and BNS-82-14008.

LITERATURE CITED

- ADRET-HAUSBERGER, M. 1982. Social influences on the whistled songs of starlings. *Behav. Ecol. Sociobiol.* 11:241–246.
- BAKER, M. C. 1975. Song dialects and genetic differences in White-crowned Sparrows *Zonotrichia leucophrys*. *Evolution* 29:226–241.
- BAKER, M. C. 1983. The behavioral response of female Nuttall's White-crowned Sparrows to song of the natal and alien dialects. *Behav. Ecol. Sociobiol.* 12:309–315.
- BAKER, M. C., M. A. CUNNINGHAM, AND A. D. THOMPSON, JR. 1984. Cultural differentiation of two subspecies of White-Crowned Sparrow. *Condor* 86:359–367.
- BAKER, M. C., AND L. R. MEWALDT. 1978. Song dialects as barriers to dispersal in White-crowned Sparrows, *Zonotrichia leucophrys nuttalli*. *Evolution* 32:712–722.

- BAKER, M. C., D. B. THOMPSON, G. L. SHERMAN, AND M. A. CUNNINGHAM. 1981a. The role of male-versus-male interactions in maintaining population dialect structure. *Behav. Ecol. Sociobiol.* 8:65-69.
- BAKER, M. C., L. R. MEWALDT, AND R. M. STEWART. 1981b. Demography of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*). *Ecology* 62:636-644.
- BAKER, M. C., D. B. THOMPSON, G. L. SHERMAN, M. A. CUNNINGHAM, AND D. F. TOMBACK. 1982. Allozyme frequencies in a linear sequence of song dialect populations. *Evolution* 36:1020-1029.
- 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 song dialects of the Puget Sound White-crowned Sparrow. *Condor* 79:356-370.
- BAPTISTA, L. F., AND J. R. KING. 1980. Geographical variation in song and song dialects of montane White-crowned Sparrows. *Condor* 82:267-284.
- BAPTISTA, L. F., AND R. B. JOHNSON. 1982. Song variation in California Brown Creepers. *J. Ornithol.* 123:131-144.
- BAPTISTA, L. F., AND M. L. MORTON. 1982. Song dialects and mate selection in montane White-crowned Sparrows. *Auk* 99:537-547.
- BLANCHARD, B. D. 1941. The White-crowned Sparrow (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. Calif. Publ. Zool.* 56:1-135.
- CAVALLI-SFORZA, L. L., AND M. W. FELDMAN. 1981. Cultural transmission and evolution: a quantitative approach. Princeton Univ. Press, Princeton, NJ.
- CAVALLI-SFORZA, L. L., M. W. FELDMAN, K. H. CHEN, AND S. M. DORNBUSCH. 1982. Theory and observation in cultural transmission. *Science (Wash. DC)* 218:19-27.
- CUNNINGHAM, M. A., AND M. C. BAKER. 1983. Vocal learning in White-crowned Sparrows: sensitive phase and song dialects. *Behav. Ecol. Sociobiol.* 13:259-269.
- ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, NJ.
- FALLS, J. B. 1969. Functions of territorial song in the White-throated Sparrow, p. 207-232. *In* R. A. Hinde [ed.], *Bird vocalizations*. Cambridge Univ. Press, Cambridge.
- FALLS, J. B. 1978. Bird song and territorial behavior, p. 61-89. *In* L. Krames, P. Pliner, and T. Alloway [eds.], *Aggression, dominance and individual spacing in the study of communication and affect*. Vol. 4. Plenum Press, New York.
- INCE, S. A., P. J. B. SLATER, AND C. WEISMANN. 1980. Changes with time in the songs of a population of Chaffinches. *Condor* 82:285-290.
- JENKINS, P. F. 1978. Cultural transmission of song patterns and dialect development in a free-living bird population. *Anim. Behav.* 25:50-78.
- JOHNSON, M. S. 1975. Comparative geographic variation in *Menidia*. *Evolution* 28:607-618.
- KROODSMA, D. E. 1982. Song repertoires: problems in their definition and use, p. 125-146. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*. Vol. 2. Academic Press, New York.
- KROODSMA, D. E., AND J. R. BAYLIS. 1982. A world survey of evidence for vocal learning in birds, p. 311-337. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*. Vol. 2. Academic Press, New York.
- LEMON, R. E. 1975. How birds develop song dialects. *Condor* 64:385-406.
- MARLER, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. *J. Comp. Physiol. Psychol.* 71:1-25.
- MARLER, P., AND S. PETERS. 1982. Subsong and plastic song: their role in the vocal learning process, p. 25-50. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*. Vol. 2. Academic Press, New York.
- MARLER, P., AND M. TAMURA. 1962. Song "dialects" in three populations of White-crowned Sparrows. *Condor* 64:368-377.
- MAYR, E. 1963. *Animal species and evolution*. Harvard Univ. Press, Cambridge, MA.
- MEWALDT, L. R., AND J. R. KING. 1977. The annual cycle of White-crowned Sparrows, *Zonotrichia leucophrys nuttalli*, in coastal California. *Condor* 79:445-455.
- MILLER, A. H. 1951. An analysis of the distribution of the birds of California. *Univ. Calif. Publ. Zool.* 6:531-644.
- MUNDINGER, P. C. 1975. Song dialects and colonization in the House Finch, *Carpodacus mexicanus*, on the East Coast. *Condor* 77:407-422.
- MUNDINGER, P. C. 1980. Animal cultures and a general theory of cultural evolution. *Ethol. and Sociobiol.* 1:183-223.
- MUNDINGER, P. C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds, p. 147-208. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*. Vol. 2. Academic Press, New York.
- PAYNE, R. B., W. L. THOMPSON, K. L. FIALA, AND L. L. SWEANY. 1981. Local song traditions in Indigo Buntings: cultural transmission of behavior patterns across generations. *Behaviour* 77:199-221.
- PETRINOVICH, L., AND T. L. PATTERSON. 1981. The responses of White-crowned Sparrows to songs of different dialects and subspecies. *Z. Tierpsychol.* 57:1-14.
- PETRINOVICH, L., AND T. L. PATTERSON. 1982. The White-crowned Sparrow: stability, recruitment, and population structure in the Nuttall subspecies (1975-1980). *Auk* 99:1-14.
- SCHENNUM, W. E., AND R. B. WILLEY. 1979. A geographical analysis of quantitative morphological variation in the grasshopper *Arphia conspersa*. *Evolution* 33:64-84.
- SLATER, P. J. B., AND S. A. INCE. 1979. Cultural evolution in Chaffinch song. *Behaviour* 71:146-166.
- THIELCKE, G. 1965. Gesangsgeographische Variation des Gartenbaumlaufer (*Certhia brachydactyla*) im Hinblick auf das Artbildungsproblem. *Z. Tierpsychol.* 22:542-566.
- TOMBACK, D. F., D. B. THOMPSON, AND M. C. BAKER. 1983. Dialect discrimination by White-crowned Sparrows: reactions to near and distant dialects. *Auk* 100:452-460.
- TOMBACK, D. F., AND M. C. BAKER. 1984. Assortative mating by White-crowned Sparrows at song dialect boundaries. *Anim. Behav.* 32:465-469.
- WILSON, E. O., AND W. L. BROWN, JR. 1953. The subspecies concept and its taxonomic application. *Syst. Zool.* 2:97-111.
- WYLES, J. S., J. G. KUNKEL, AND A. C. WILSON. 1983. Birds, behavior, and anatomical evolution. *Proc. Natl. Acad. Sci. U.S.A.* 8:4394-4397.
- YASUKAWA, K. 1981. Song and territory defense in the Red-winged Blackbird. *Auk* 98:185-187.
- YASUKAWA, K., J. L. BLANK, AND C. L. PATTERSON. 1980. Song repertoires and sexual selection in the Red-winged Blackbird. *Behav. Ecol. Sociobiol.* 7:233-238.

Zoology Department, Colorado State University, Fort Collins, Colorado 80523. Present address of second author: Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721. Received 3 April 1984. Final acceptance 30 October 1984.