GEOGRAPHIC VARIATION IN SONG AND DIALECTS OF THE PUGET SOUND WHITE-CROWNED SPARROW

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Because of their simplicity of structure and geographic variation, songs of crowned sparrows (*Zonotrichia* spp.) have been popular subjects of bioacoustical studies. DeWolfe et al. (1974) described geographic variation in song of the migratory subspecies *gambelii* of the White-crowned Sparrow (*Zonotrichia leucophrys*) but found no dialects. However, song dialects have been described for the sedentary subspecies *nuttalli* (Marler and Tamura 1962, 1964, Baker 1974, 1975, Baptista 1975) and the migratory, montane breeding subspecies *oriantha* (Baker 1975, Orejuela and Morton 1975). Although a few audiospectrograms of songs of the migratory Puget Sound White-crowned Sparrow (*Z. l. pugetensis*) have been illustrated (Baptista 1974), a detailed study of song in this subspecies of White-crown has not been undertaken previously.

Taxonomists distinguish two racial complexes of White-crowned Sparrows, the darker *nuttalli-pugetensis* group of the Pacific coast and the paler *gambelii-oriantha-leucophrys* complex of the mountains and interior (Banks 1964, Cortopassi and Mewaldt 1965). Song may be a character separating these two subspecies complexes (Baptista 1975). However, until songs of all the forms are studied in detail, the use of vocalizations as a taxonomic tool cannot be evaluated properly.

Song dialects of migratory White-crowned Sparrows may function as a valuable means for students of bird migration to identify the wintering grounds of each breeding population (DeWolfe et al. 1974). Regional dialects of birds may also be used as markers in the study of interactions between populations or subpopulations (Banks 1964:18, Payne 1973, Baptista 1975). Song dialects may be used to trace the origins of invading populations (Baptista 1975, Mundinger 1975). Additionally, King (1972:344) pointed out that, "Geographical variation of avian song is of interest as an index of speciation."

This paper treats geographical variation in song of the migratory subspecies *pugetensis* of the White-crowned Sparrow, describes regional dialects for this taxon, and discusses the consequences of interactions between overwintering *pugetensis* and resident *nuttalli*. Data are compared with those for other emberizines, and the evolutionary and ecological significance of these findings are discussed.

METHODS AND MATERIALS

Songs were sampled from 36 localities in Oregon, Washington and British Columbia (Table 1, Fig. 1), between 7 June and 4 July 1970. Field recordings were made on a Uher 4000 Report-S tape recorder with a Uher microphone mounted on a 24-in. parabolic reflector. Tape speed was 7.5 ips. Songs were spectrographed on a Kay Elemetric Sonograph Machine (Model 7029A) set at high shape and wide band settings. In the laboratory songs were played on Ampex and Uher 4000 Report 1C tape recorders.

Some 1668 songs from 270 individuals belonging to the subspecies *pugetensis* were recorded. Notations were made of the songs of 22 individuals that could not be recorded (Table 1). As in Baptista (1975), quantitative variation in the following characteristics were treated: (1) duration of each song in seconds, (2) number of elements (syllables plus phrases), (3) number of syllables in the terminal trill, (4) number of kinds of elements, (5) repetition index, i.e., number of elements divided by the number of kinds of elements, (6) highest frequency in kHz, and (7) lowest frequency in kHz.

Each recorded song was assigned a number. By reference to a random number table, a single song from each bird was selected for statistical treatment. If the audiospectrogram thus selected proved unclear due to some recording artifact, I used the next cleanest audiospectrogram from which the above quantifiable characteristics were taken. Individuals were grouped according to dialect area, the latter based on visual inspection of the terminal trills in each song. Six dialect areas were thus recognized (Fig. 1).

Based on observation of adults attending fledglings, feeding nestlings, or directing high intensity alarm calls at the investigator, I concluded that all populations sampled were breeding.

TERMINOLOGY

Terms and symbols used to describe *pugetensis* song are those of Baptista (1974) and are illustrated in Figure 2. These are defined below with the symbols appearing in brackets.

1) *Note*: any continuous trace on the audiospectrogram.

2) *Syllable* [S]: the unit of repetition in a trill. In this paper "TRILL" refers specifically to the terminal trills (Fig. 2A, B) symbolized by SS.

3) *Complex syllables* [CS]: groups of four or more notes forming more or less coherent units (Figs. 4, 6). They follow the introductory whistle (song B, Fig. 2) or the introductory buzz (song A, Fig. 2) in *pugetensis* themes.

4) *Whistle* [W]: a continuous trace on the audiospectrogram generally exceeding 0.2 sec and constant in pitch. This introduces every *pugetensis* song.

5) *Buzz* or *Vibrato* [B] (of Marler and Tamura 1962): a frequency-modulated whistle containing 30

or more pulses/sec, following the criterion of Borror (1960).

6) *Buzz-whistle* [BW]: a buzz attached to a whistle, occurring as the second phrase in some songs (e.g., H3 in Fig. 7).

7) *Phrase*: a whistle, buzz, or buzz-whistle. This term does not include syllables.

8) *Song type*: used interchangeably with theme and motif to denote all the elements listed above in various permutations and combinations.

Using symbols, song A (Fig. 2) may be described as W-B-CS-CS-B-SS, and song B as W-CS-B-SS.

HABITAT

Z. l. pugetensis in my study areas occupied three different types of habitat (Table 1):

RESIDENTIAL AREAS

As in sedentary *nuttalli* (Blanchard 1941, Banks 1959, Marler and Tamura 1962, Baptista 1975), *pugetensis* often was found in parks and gardens. Shrubbery was used for nest sites, lawns provided foraging areas, and tall trees and roof tops often served as singing perches.

FOREST CLEARINGS AND EDGES

Lewis (1975) studied *pugetensis* on Camano Island, Washington and pointed out that logging activity probably increased habitat available to White-crowned Sparrows. Recently-logged areas, in early successional stages because of grazing, provide breeding habitat for the species. Banks (1964:42) reported on populations of *pugetensis* near the North Santiam River, Oregon, that had invaded recently-logged areas.

I found these sparrows at the ecotone between coniferous forests and the grassy areas on the Pacific coastal sand dunes (e.g., at Fort Stevens, Table 1). On San Juan and Vancouver islands they often occupied forest clearings such as those described by Lewis and Banks.

SAND DUNES

Large areas of the Oregon and Washington coastal dunes are covered by thick mats of grasses (e.g., *Ammophila arenaria, Festuca rubra, Poa macrantha*) and sedges (*Carex* sp.). These grasslands may be dotted with small conifers (*Pinus contorta, Picea sitchensis*), shrubs such as Scottish broom (*Cytisus* sp.), lupines (*Lupinus littoralis, L. arborius*), and coyote bush (*Baccharis pilularis*). At some localities (e.g., Ocean City, Washington) small trees and bushes are rare, so that White-crowned Sparrows sang from the ground or used pieces of driftwood as singing posts. Nests were probably built on the ground.

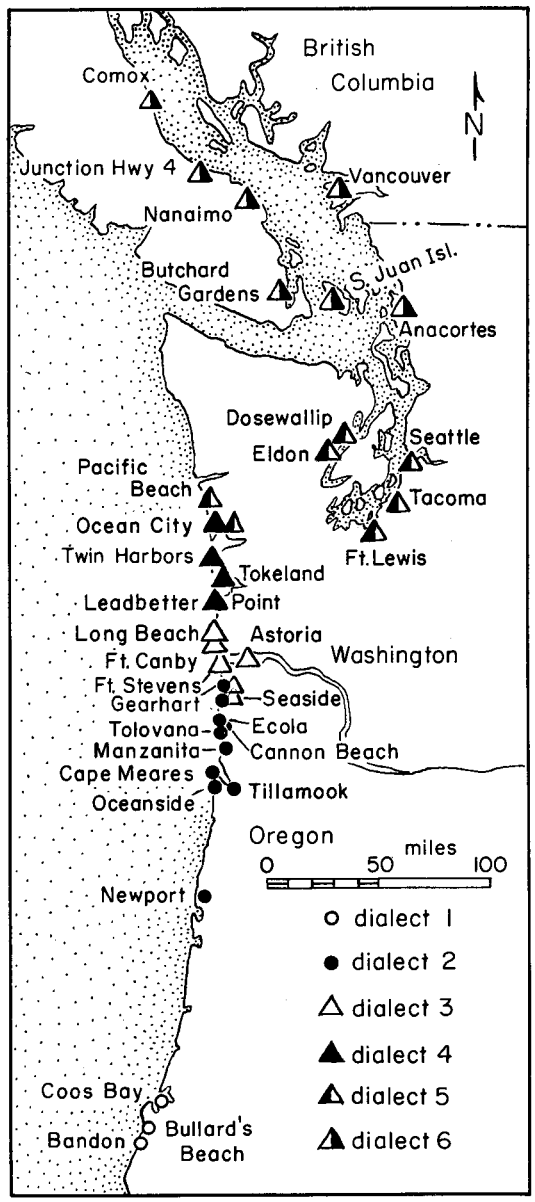

FIGURE 1. Map of localities sampled. Round symbols signify populations singing southern themes. Triangular symbols designate populations singing northern themes. Different patterns represent different dialects.

At Fort Canby and Leadbetter Point, Washington, willows (*Salix* sp.) are a very conspicuous part of the flora. Habitat at these localities is reminiscent of that occupied by montane White-crowned sparrows, *Z. l. oriantha* (DeWolfe and DeWolfe 1962, Morton et al. 1972).

Flora and topography of the Oregon coastal dunes have been treated in detail by Wiedemann et al. (1969). At some localities sand

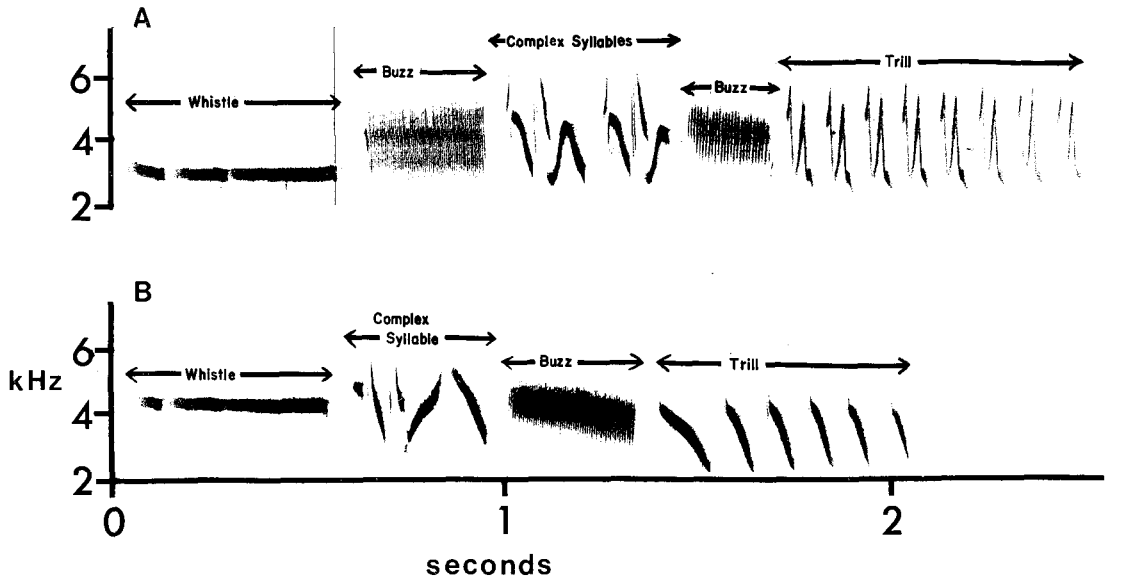

FIGURE 2. A northern theme (A) and southern theme (B) illustrating terminology used.

TABLE 1. Numbers of birds singing northern (N) and/or southern (S) themes.

Localities	N	Both	S	Hybrids	Dialect No.	Brdg. Noted[1]	Habitat[2]
Bandon Beach	—	—	12	2	1	b	d
Bullard Beach	—	—	3	—	1	b	d, f
Coos Bay	—	—	4(3)[3]	—	1	—	r
Newport	—	—	14	—	2	—	r
Tillamook	—	—	5(1)	—	2	b	r
Oceanside	—	—	5(4)	1(1)	2	b	r
Cape Meares	—	—	5	—	2	—	f
Manzanita	—	—	13(2)	—	2	b	d
Tolovana	—	—	1	—	2	—	r
Cannon Beach	—	—	1	—	2	—	r
Ecola	—	—	4(2)	1	2	—	f
Seaside	2	1	11	—	2, 3	—	r
Gearhart	3	2(1)	2	—	2, 3	—	r
Astoria	3(2)	—	—	—	3	b	r
Fort Stevens	15	—	—	—	3	b	d, f
Fort Canby	13	—	—	1	3	—	d
Long Beach	3(2)	—	—	—	3	—	r
Leadbetter Pt.	4	—	—	—	4	—	d
Tokeland	11	—	—	—	4	—	d
Twin Harbors	5	—	—	—	4	b	d
Ocean City	24	—	—	—	4, 5	b	d
Pacific Beach	1	—	—	—	5	b	d
Dosewallips	2	—	—	—	5	—	f, r
Rainbow Lodge	6(2)	—	—	—	5	b	f, r
Eldon	2	—	—	—	5	—	r
Fort Lewis	4(1)	—	—	—	5	—	r
Tacoma	3	—	—	—	5	—	r
Seattle	3	—	—	—	5	b	r
Anacortes	2(1)	—	—	—	6	—	r
San Juan Island	62	—	—	—	6	b	f, r
Butchard Gardens	6	—	—	—	6	—	r
Nanaimo	5	—	—	—	6	—	r
Junc. Highway 4	4	—	—	—	6	—	f
Comox	13	—	—	—	6	—	f
Cleveland Dam	5	—	—	—	6	—	r
Stanley Park	3	—	—	—	6	—	r
Totals	204(8)	3(1)	80(12)	5(1)			

[1] b = attending nestlings or fledglings.
[2] d = dunes; f = forest clearings or forest edge; r = residential areas.
[3] All numbers in parentheses represent subtotal of birds heard but not recorded.

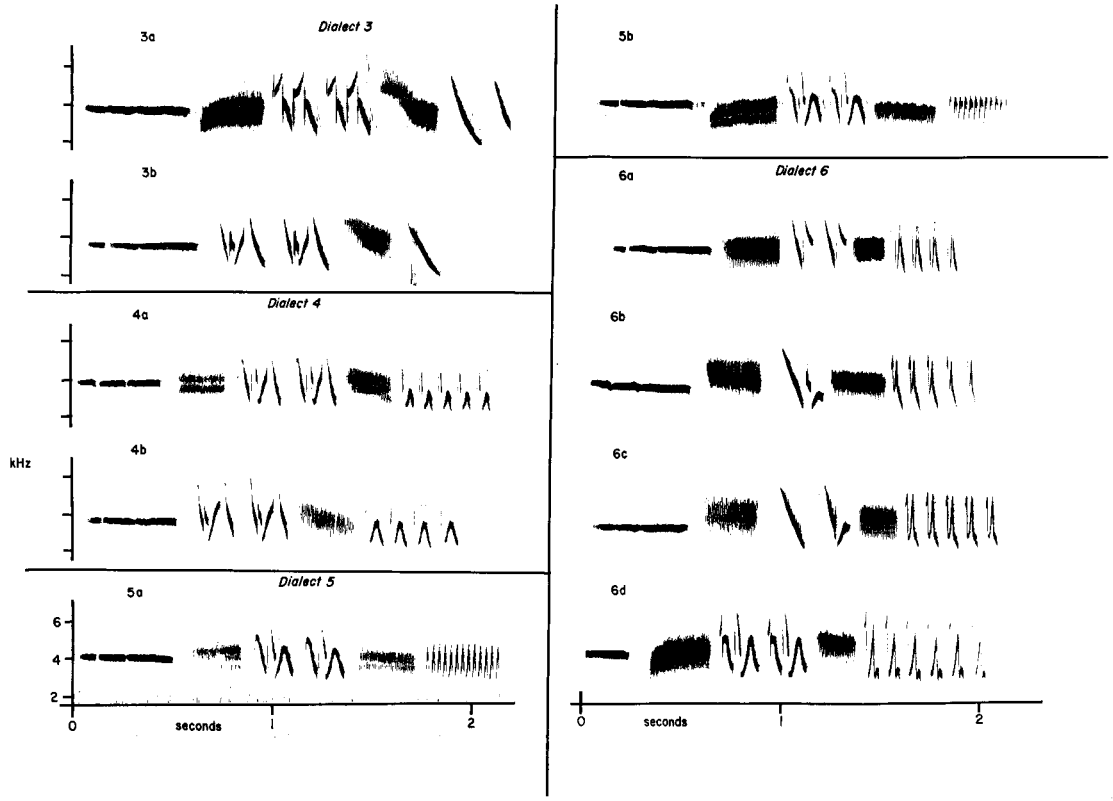

FIGURE 3. Four dialects within northern themes: 3a–3b: two motifs recorded at Fort Canby, Washington; 4a–4b: two songs recorded at Tokeland, Washington; 5a: a song recorded at Ocean City, Washington; 5b: a theme from Seattle, Washington; 6a–6d: four motifs from San Juan Island, Washington. Note the variation in the morphology of the terminal syllables in the four songs.

dunes occur between the Pacific Ocean and the grassy stretches occupied by the sparrows. At other localities (e.g., Fort Canby), grassy areas and the attendant sparrows were found almost to the water's edge.

DeWolfe and DeWolfe (1962) described and compared habitats for three taxa of White-crowned Sparrow, including the subspecies *pugetensis*. All habitats encountered in my study bore the characteristics listed by these authors, namely, grassland, bare ground, and shrubbery. The dunes occupied by *pugetensis* were the most open of all the habitats encountered as bushes and small trees were patchy and virtually absent in some areas.

THEMES OF *PUGETENSIS*

The song of *Z. l. pugetensis* is about two seconds long and between two and eight kHz in frequency. Based on differences in the sequencing of whistles, buzzes, complex and simple syllables, and distinct complex syllable types, I distinguished two geographical groups of songs; these will be referred to as Northern and Southern themes.

THE NORTHERN THEME

Typically, the northern theme begins with a whistle and is followed by a buzz, two complex syllables, another buzz, and a terminal trill (W-B-CS-CS-B-SS; Fig. 2A). Some birds sang songs containing only one complex syllable (W-B-CS-B-SS; Fig. 3, song 6b). Two birds sang songs (not illustrated) with three complex syllables (W-B-CS-CS-CS-B). A few individuals sang songs lacking the first buzz which normally constitutes the second phrase (W-CS-CS-B-SS; Fig. 3, song 3b). The complex syllables and terminal trills vary geographically and will be treated in detail.

THE SOUTHERN THEME

In contrast to the above, the typical southern theme begins with a whistle and is followed by a complex syllable, a buzz, and finally a trill (W-CS-B-SS; Fig. 2B). The complex syllables in southern themes are quite unlike those in northern themes (compare Figs. 4 and 6) and will be discussed later. The terminal trills in southern themes are more or less population specific.

DISTRIBUTION OF NORTHERN AND SOUTHERN THEMES

Figure 1 illustrates the distribution of the two song types. With a few exceptions birds breeding in the 11 sampling localities from Bandon to Ecola, Oregon, sang the southern theme (dialects 1 and 2). Along the Pacific coast, birds breeding at Fort Stevens and Astoria, Oregon, and birds breeding in Washington from Fort Canby to Pacific Beach sang northern themes (dialects 3, 4 and 5). Birds sampled at localities in Puget Sound sang northern themes (dialects 5 and 6). The latter included populations on the mainland of Washington and British Columbia as well as birds on San Juan and Vancouver islands.

The southern theme is thus distributed in almost pure form for at least 200 mi of the Pacific coastline (Fig. 1). The northern theme ranges over 140 mi of this same coast. Birds singing northern themes from mainland localities on Puget Sound range at least 170 mi. On Vancouver Island, the same song theme occurs from Butchard Gardens to Comox, a distance of at least 120 mi.

CONTACT AREAS BETWEEN NORTHERN AND SOUTHERN THEMES

At Gearhart and Seaside, Oregon, birds singing northern or southern themes occurred together (Table 1). Three birds sang both themes. The two song types appear to occur sympatrically along at least 10 mi of coastline.

One "bilingual" bird recorded at Seaside, Oregon on 12 June 1970 was observed matching northern and southern themes sung by four neighbors. I tried to get it to match songs played from my tape recorder but was unsuccessful. In contrast, a bird (*pugetensis*) recorded at Crescent City, California, and several birds (*nuttalli*) recorded in the San Francisco Bay area, California, sang two song types each and would match themes sung by neighbors as well as playback of recorded song (Baptista 1975).

At Ecola, Oregon, I could find only five singing White-crowned Sparrows. Four birds sang typical southern themes, and one bird sang two atypical northern themes (Fig. 7) described later.

REPERTOIRE SIZE AND VARIATION WITHIN THEMES

Five birds out of 292 sang two themes, each theme containing different syllable types. The rest sang one theme each. This is similar to data for other taxa of *Zonotrichia* (King 1972, DeWolfe et al. 1974, Orejuela and Morton 1975) and for another emberizine, the Ortolan Bunting, (*Emberiza hortulana*; Conrads and Conrads 1971:93). Although I did not record any birds who sang three themes, Banks (1964) reported such an individual of *pugetensis*.

A bird recorded at Tokeland, Washington, sang a theme with a whistle and a buzz in the introduction (W-B-CS-CS-B-SS) and a variant of the latter with the introductory buzz absent (W-CS-CS-B-SS). Five individuals each sang a song with two complex syllables (W-B-CS-CS-B-SS) and varied it by sometimes dropping one complex syllable (W-B-CS-B-SS). One bird recorded at Seaside, Oregon, would habitually drop one of its complex syllables when replying to playback of its own song. A *nuttalli* in Berkeley, California, "misimprinted" with a *pugetensis* theme, behaved likewise (Baptista 1974).

Except as noted above, variation within each northern or southern theme consisted mostly of lengthening or shortening the introductory whistle, lengthening or shortening the vibrati, or varying the number of syllables in the terminal trills. This degree of stereotypy has been reported for other races of White-crowned Sparrow, namely, *nuttalli* (Marler and Tamura 1962, Konishi 1965, Baker 1974, Baptista 1975), *gambelii* (DeWolfe et al. 1974) and *oriantha* (Orejuela and Morton 1975).

As an example of individual variation, audiospectrograms of 12 songs recorded from one bird at Anacortes, Washington, yielded the following statistics: duration in seconds: 1.83–1.99 ($\bar{x}$ 1.92 ± 0.47 s.d.); no. of elements: 11–14 ($\bar{x}$ 12.41 ± 0.79); no. of terminal syllables: 6–9 ($\bar{x}$ 7.33 ± 0.89); no. of kinds of elements: 4 in all 12 audiospectrograms; repetition index: 2.75–3.50 ($\bar{x}$ 3.10 ± 0.20); highest frequency (kHz): 6.25–7.00 ($\bar{x}$ 6.58 ± 0.22); lowest frequency: 3.00 kHz in all audiospectrograms.

SONG DIALECTS

NORTHERN THEMES

Geographic variation in terminal trills. Data on the geographic distribution of terminal trills are summarized in Table 2 and illustrated in Figure 3. Terminal trill 3a (song 3a, Fig. 3) occurred in "pure" form from Astoria, Oregon to Long Beach, Washington (Table 2, Fig. 1). At Seaside and Gearhart, Oregon, these songs were found sympatrically with southern themes (Table 1).

Trill 4a (Fig. 3) was recorded in Washington from Leadbetter Point to Twin Harbors.

TABLE 2. Distribution of eight terminal trill types.

Localities	2a[1]	3a[2]	4a	5a	6a	6b	6c	6d
Seaside	11	3						
Gearhart	2	4						
Astoria		1						
Fort Stevens		15						
Fort Canby		13						
Long Beach		1						
Leadbetter Pt.			4					
Tokeland			11					
Twin Harbors			5					
Ocean City			2	22				
Pacific Beach				1				
Dosewallips[3]				2				
Brinnon				4				
Eldon				2				
Fort Lewis				3				
Tacoma				3				
Seattle				3				
Anacortes					1			
San Juan Island[4]					24	11	18	7
Butchard Gardens[4]						6		
Nanaimo[4]							1	1
Junc. Highway 4[4]								4
Comox[4]								12
Cleveland Dam[5]								5
Stanley Park[5]						1		2
Total	13	37	22	40	25	18	19	31

[1] Terminal trills of southern themes as in song 2a, Fig. 5.
[2] 3a to 6d are the terminal trills of the northern themes in Fig. 3.
[3] Dosewallips is the state park on the outskirts of Brinnon.
[4] Vancouver Island.
[5] Vancouver City.

At Ocean City two birds used this terminal trill whereas 22 used trill number 5 (song 5a, Fig. 3). Songs 4a and 4b (Fig. 3) illustrate individual variation in the morphology of the syllables making up the terminal trills in a population; the inverted "V" shaped note is larger in song 4b than in song 4a.

Terminal trill 5a (Fig. 3) was recorded at two localities along the Pacific coast and six localities on Puget Sound (Table 2) from Dosewallips to Seattle.

On San Juan Island in Puget Sound, four variants of the terminal trill were present (Fig. 3, songs 6a to 6d). The two vertical lines in the terminal syllables of song 6a are approximately the same length. In song 6b the second vertical component in the terminal syllable is noticeably longer than the first. In song 6c, the second longer vertical arm appears thickened near the bottom extremity. In song 6d the thickened portion is twisted so that each syllable terminates with a small inverted "U." I found no evidence of clumped distribution ("subdialects") of these terminal syllables on San Juan Island. However, on Vancouver Island, trill 6b was found to the south (Butchard Gardens, Table 2) and trills 6c and 6d in more northerly localities (Nanaimo to Comox). The single bird recorded at Anacortes used trill 6a, and seven of eight birds recorded at Vancouver City (Cleveland Dam and Stanley Park) used trill 6d (Table 2). One bird in Stanley Park, Vancouver City, used trill 6b. Trills 6a to 6d, therefore, seemed to reappear in geographically distant localities on San Juan and Vancouver islands as well as Anacortes and Vancouver City on the mainland near Puget Sound. Thus, whereas trills 3a to 5a are quite uniform in morphology within populations, terminal syllables represented in songs from the northern Puget Sound populations are more variable, four variants having been recorded (trills 6a to 6d).

Geographic variation in complex syllables. Two complex syllables normally follow the two introductory phrases in the typical northern theme (W-B-CS-CS-B-SS). Usually both complex syllables are morphologically similar, but in a few cases they were unlike (Fig. 3, song 6c). Eight complex syllable types were represented in the songs sampled (Fig. 4, 1 to 8). Syllable types 9 to 11 (Fig. 4) are simpler in structure and are merely the first subsyllables of syllables one, three and four, respectively.

Most complex syllables are distributed in mosaic fashion, i.e., the same syllable type may be repeated in geographically distant loca-

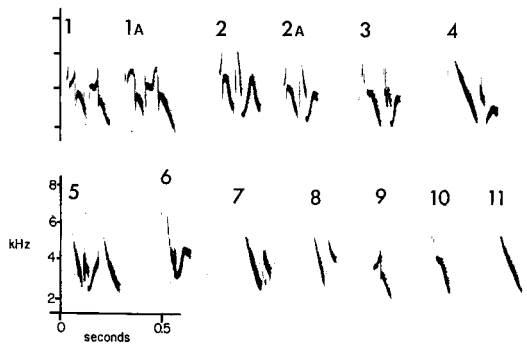

FIGURE 4. 1–8: Complex syllables and their variants from northern themes. Syllable 1A is a variant of syllable 1, differing slightly in the morphology of the second subsyllable. Syllable 2A is a variant of syllable 2, again differing in the morphology of the second subsyllable. The latter is an inverted "V" in syllable 2 and a streak in syllable 2A. 9–11: Subsyllables of complex syllables used by some individuals. They represent fragments of complex syllables 1, 3 and 4, respectively, which appeared in place of complex syllables in some songs (e.g., song 6c in Fig. 3).

tions (Table 3). Nonetheless, a geographical trend is evident. Syllable type 1 (Table 3) is the dominant form in the populations from Seaside, Oregon to Long Beach, Washington. Most birds singing dialect 3 also use syllable type 1 (45 out of 48 birds recorded or 93.7% of sample). Data for dialect 3 are, therefore, similar to those found in *nuttalli* in which variability within populations was also low (Marler and Tamura 1962, 1964, Baker 1975, Baptista 1975). Complex syllable 2 first makes its appearance at Tokeland, Washington (Table 3) and continues to occur until Comox, Vancouver Island. At Ocean City, Washington, syllable 2 occurred in the songs of 16 of 24 birds (66.7% of sample). On San Juan Island, Washington, seven of the eight complex syllables illustrated in Figure 5 occurred (92% of sample). Type 3 was the dominant complex syllable on the island but was found in only 26 birds (40% of the sample). This syllable type was found at no other locality.

Syllable type 8 occurred only once (Fig. 3, 6a), in a song from San Juan Island. However, Baker (1974, Fig. 3) illustrated songs of *nuttalli* from San Mateo Co., California containing syllables similar to type 8 (Fig. 4, this study).

SOUTHERN THEMES

Geographic variation in terminal trills. In song 1a (Fig. 5) all the syllables in the terminal trill are morphologically similar. In songs 1b to 1d, the first syllable in the terminal trill is more gently sloping (i.e., slurred differently) from the rest of the syllables in the

TABLE 3. Frequency of occurrence of syllables in northern themes. Syllable numbers correspond to those in Figure 4.

Localities	1	2	3	4	5	6	7	8	9	10	11	Other	Dialect #
Seaside	2			1									3
Gearhart	4												3
Astoria				1									3
Fort Stevens	15												3
Fort Canby	13				1							1*	3
Long Beach	1												3
Leadbetter Pt.	1					3							4
Tokeland	1	3			7								4
Twin Harbors	2	3											4
Ocean City	6	16			2								4–5
Pacific Beach		1											5
Dosewallips		2											5
Brinnon		4											5
Eldon		2											5
Fort Lewis		3											5
Tacoma	1	1			1								5
Seattle	1	1			1								5
Anacortes		1											6
San Juan Island	4	11	26	12		7	1	1	1	1	1		6
Butchard Gardens				5		1							6
Nanaimo		2		1		2							6
Junc. Highway 4				3		1							6
Comox	7	1		5									6
Cleveland Dam	1					4							6
Stanley Park						3							6
Total	59	51	26	26	12	21	1	1	1	1	1	1	

* Theme H1 in Fig. 7.

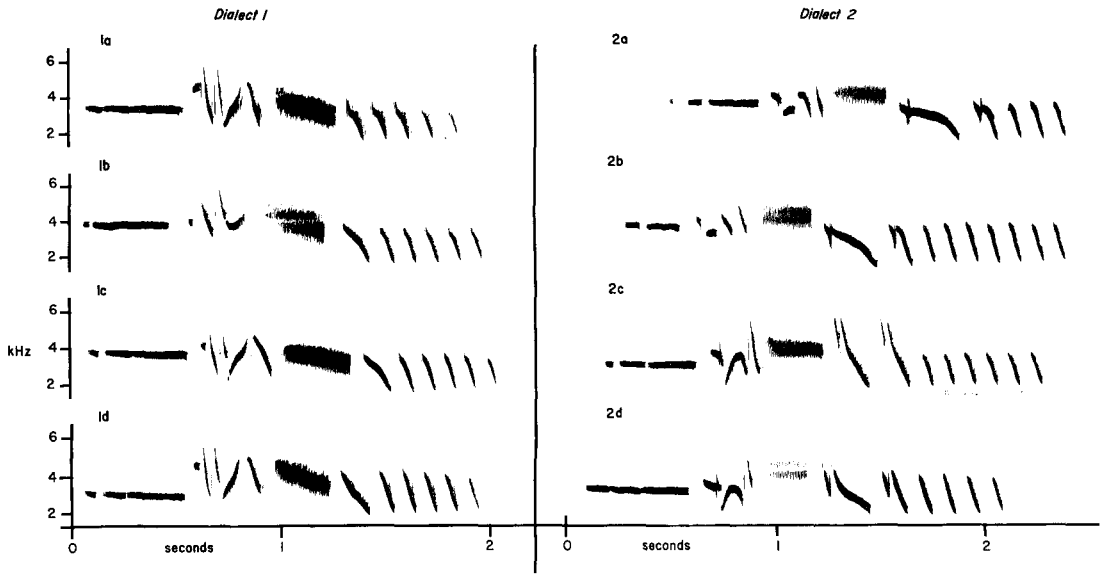

FIGURE 5. 1a to 1d: four versions of dialect 1. Songs 1a to 1c were recorded on Bandon Beach, Oregon. Song 1d was recorded on Bullard Beach, Oregon. 2a to 2d: four variations of dialect 2. Song 2a was recorded at Tillamook, Oregon. Song 2b was recorded at Cape Meares, Oregon. Song 2c is from Manzanita, Oregon. Song 2d is from Newport, Oregon.

trill. All the syllables, however, are similarly shaped. In songs 2a to 2d, (Fig. 5) the first two syllables following the buzz are more elaborately structured than the rest of the syllables in the terminal trills. These first syllables may be notched (songs 2a and 2b, Fig. 5) or may consist of paired notes (songs 2c and 2d, Fig. 5). The rest of the syllables in these trills are simpler in structure, and morphologically similar to each other and to the syllables in the trills of songs 1a to 1d.

Although the terminal simple syllables are similar in all southern themes sampled from Bandon Beach to Gearhart, Oregon (Fig. 1), based on the presence or absence of the two more elaborate paired or notched syllables immediately following the buzz (Fig. 5, songs 2a to 2d), two dialect regions may be distinguished. Dialect 1 ranges from Bandon Beach to Coos Bay, Oregon and dialect 2 from Newport to Gearhart, Oregon (Table 4, Fig. 1). In addition to differences in syllabic structure, the carrier frequencies in the vibrati found in song dialect 2 (Fig. 5, songs 2a to 2d) vary little, whereas the buzzes in dialect 1 are noticeably inflected downward (Fig. 5, songs 1a to 1d).

Song dialects in Z. *capensis* (Nottebohm 1969, 1975, King 1972) and Z. *l. nuttalli* (Marler and Tamura 1962, Baptista 1975) are based mainly on the structure of the syllables in the terminal portions of the trill. Dialects in southern *pugetensis* themes (this study), however, are distinguished on the basis of elements in the middle portions of the song (complex syllables, buzzes, paired syllables). In this respect southern *pugetensis* dialects are reminiscent of some song dialects of the Short-toed Tree-Creeper (*Certhia brachydactyla*; Thielcke 1961).

Geographic variation in complex syllables. I distinguish six complex syllable types in southern themes (Fig. 6). Type 12 differs from type 13 in the shape (frequency span) of each note, e.g., the first note is longer in 12, but the last note is longer in type 13. Although the differences are small, I treat 12 and 13 as separate categories because each occurred 18 or more times and because their relative frequencies varied across populations. Types 13A, 13B, and 13C are clearly variants of type 13. Complex syllable 13B occurred only once, in the song of a bird recorded at Seaside, Oregon; complex syllable 13C also was found only once, in the song of a bird recorded at Cape Meares, Oregon. Numbers of birds using syllable types 13, 13A, 13B, and 13C were pooled in Table 4.

Syllables 14 and 14A are also very similar. Syllable 14A was found in only two birds, recorded at Newport, Oregon. Numbers of birds using 14 and 14A were also pooled in Table 4.

Complex syllable types 12 to 14A (Fig. 6) are distributed geographically in mosaic fashion (Table 4), occurring in different frequen-

TABLE 4. Frequency of occurrence of complex syllable in southern themes. Syllable numbers correspond to those in Fig. 6.

Localities	12	13	14	15	16	17	Other	Dialect #
Bandon				10	2[a]		1[b]	1
Bullard's Beach				3				1
Coos Bay				1				1
Newport	1	7	4			2		2
Tillamook	2		2					2
Oceanside	1							2
Cape Meares	2	1	2					2
Manzanita	8						3[c]	2
Tolovana		1						2
Cannon Beach	1							2
Ecola		1	1				1	2
Seaside	4	6	2					2
Gearhart	1	2						2
Fort Canby	1[d]							3
Total	21	18	11	14	2	2	5	

[a] One hybrid theme (Fig. 7, H2) in this sample.
[b] Hybrid theme (Fig. 7, H3).
[c] Birds represented by unclear spectrograms identifiable only as southern themes.
[d] Hybrid theme (Fig. 7, H1).

cies in widely separated populations. With only one exception (song H1 in Fig. 7), these complex syllables were used only by birds singing dialect 2 (Table 4).

Complex syllables 15 and 16 (Fig. 6) were used solely by birds in dialect area one (Table 4). Although structurally similar to complex syllables 15 and 16, complex syllable 17 was found only in the songs recorded from two birds at Newport, Oregon (Table 4), i.e., in dialect area two. It is conceivable, therefore, that with more samples, especially from localities intermediate between dialect areas one and two (i.e., between Coos Bay and Newport, Fig. 1), all the complex syllables in Figure 6 may be shown to occur with terminal trills of both dialects 1 and 2. It is nonetheless noteworthy that on the basis of present data the two dialect areas have no complex syllables in common (Table 4, Fig. 5).

Geographic variation in the introductory phrases. DeWolfe et al. (1974, Fig. 3) distinguished three types of introductory whistles (Phrase A of Marler and Tamura 1962) in the songs of *Z. l. gambelii.* These were designated Continuous, Segmented, or Broken.

Phrase A in *pugetensis* themes is remarkably uniform geographically (Figs. 2, 3, 5 and 7). These whistles were all "segmented" due to amplitude modulation, appearing in audiospectrograms as three more or less straight dark lines joined by two lighter areas. Frequency modulation was slight in these whistles. Audiospectrograms in Orejuela and Morton (1975) and Baker (1975) indicate that

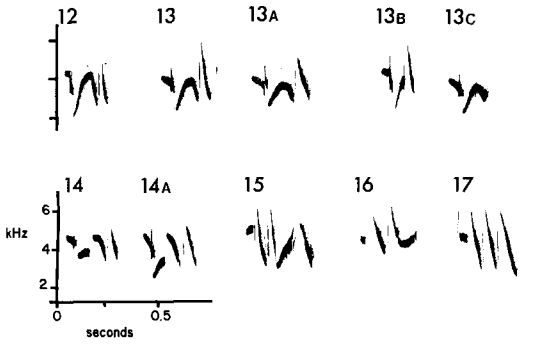

FIGURE 6. Complex syllables and their variants from southern themes.

introductory whistles in songs of *oriantha* are similar to those in *pugetensis.*

In contrast, Phrase A in *nuttalli* in the San Francisco Bay area may show great individual variability in both amplitude modulation and frequency modulation (Baptista 1972, 1975). This was especially evident in the songs from Treasure Island, San Francisco Bay.

The second introductory phrase (Phrase B of Marler and Tamura 1962) is also sometimes quite variable in *nuttalli* themes. These are most commonly a pure whistle or a buzz, and sometimes buzz-whistles, whistle-buzzes, or short trills (staccato phrases of Baptista 1975).

Phrase B is absent in southern themes of *pugetensis* (Fig. 5). However, within the northern themes, with only three exceptions described later, Phrase B when present was a vibrato in *pugetensis* motifs. Whistles and buzz-whistles as second phrases were quite rare in the populations sampled.

EXCEPTIONAL SONGS

Although most individuals in a song population sang one of the local themes terminating with trills characteristic of groups of populations, a few exceptions were encountered. These are described below, according to locality.

VARIANT THEMES

Seaside, Oregon. Eleven birds in this population sang typical southern themes (W-CS-B-SS). One other individual sang a song substituting the buzz with a buzz-whistle (W-CS-BW-SS; song V1, Fig. 7). This buzz-whistle was the only one of its kind encountered.

Newport, Oregon. Eleven of 14 birds recorded at this locality sang the local southern theme (W-CS-B-SS). These songs typically

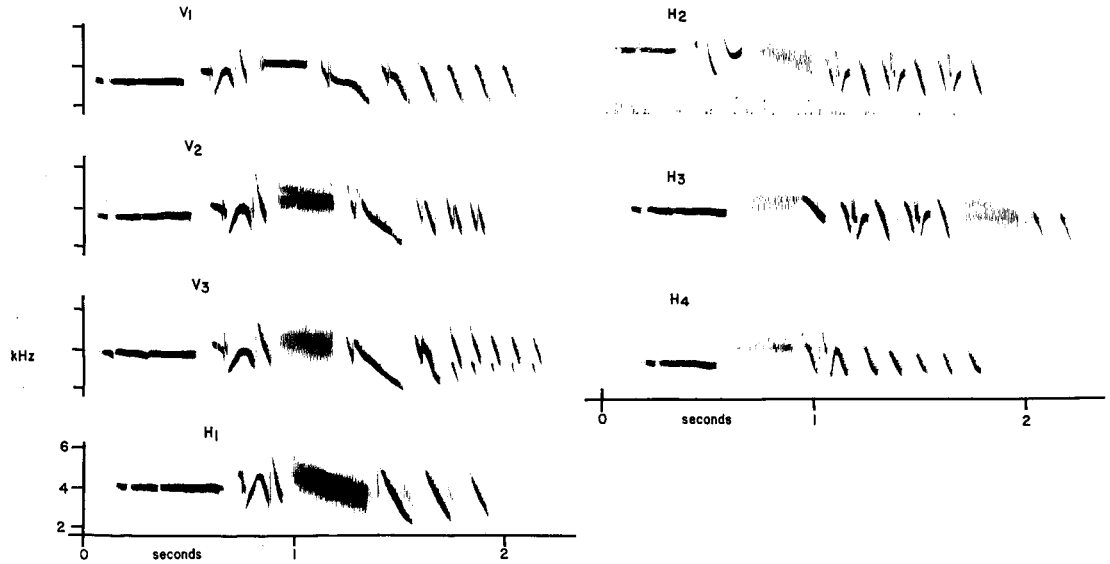

FIGURE 7. V1 to V3 are variant themes. V1 recorded at Seaside, Oregon. V2 and V3 recorded at Newport, Oregon. H1 to H4 represent some hybrid themes. H1 recorded at Fort Canby, Washington. H2 and H3 recorded at Bandon, Oregon. H4 recorded at Ecola, Washington.

ended with a trill of simple syllables, each consisting of one downward inflected note (Fig. 5, 2a to 2d). However, three birds sang songs ending with syllables consisting of paired notes; one bird sang songs with terminal syllables illustrated in V2 (Fig. 7), and two birds sang theme V3. A typical terminal trill is illustrated in V1 (Fig. 7) for comparison.

Astoria, Oregon. One bird sang a song (not illustrated) with two whistles in the introduction (W-W-CS-CS-B-SS). This was the only song of this kind recorded (see also section on geographic variation in phrases). Although this individual sang an unusual theme, it was mated and was observed feeding a fledgling.

HYBRID THEMES

Fort Canby, Washington. Thirteen of 14 birds sampled sang northern themes. One bird (H1 in Fig. 7) sang a theme which appeared to be a typical southern theme with regard to sequencing of elements in the introductory portion (W-CS-B-SS). However, the last three terminal syllables were morphologically similar to those in the local northern themes (compare with song 3a, Fig. 3). The long downward-inflected buzz was probably also borrowed from a northern theme (compare with second buzz in song 3a, Fig. 3).

Bandon, Oregon. Twelve of 14 birds recorded at this locality sang one of the local southern themes (Fig. 5, songs 1a and 1b). Two individuals sang what appeared to be "hybrid themes" consisting of elements from northern and southern themes combined. One of these (H2 in Fig. 7) sang a song which began with a whistle, followed by a type 16 (Fig. 6) complex syllable, a buzz, and then three type 5 (Fig. 4) complex syllables. The last three (type 5) complex syllables probably were borrowed from a northern theme, and the introductory (W-CS-B) portion from a southern theme. The second bird (H3 in Fig. 7) sang a theme which appeared to be a typical northern theme with regard to sequencing of elements, i.e., W-BW-CS-CS-B-SS. The two complex syllables are typical of northern themes (type 5, Fig. 4). However, the last two simple syllables are typical of the local southern themes (see song 1a, Fig. 5). The buzz-whistle comprising the second phrase in H3's song is atypical of *pugetensis*. It was the only one of its kind encountered.

Oceanside, Oregon. One bird that sang infrequently and could not be located for recording, sang a theme similar to H2 (Fig. 7).

Ecola, Oregon. Four birds sang typical southern themes; one bird, however, sang theme H4 (Fig. 7). This begins with a whistle, followed by a buzz, a complex syllable, and then a trill of simple syllables. The complex syllable is typical of northern themes (type 2, Fig. 4). The terminal syllables, however, are typical of the dominant local southern theme (compare with terminal syllables in theme 2C, Fig. 5). This bird sang a single second theme (not illustrated) which ap-

TABLE 5. Descriptive statistics (mean ± sd) of themes in six dialect populations of *pugetensis*. Numbers in parentheses are sample sizes.

Dialect	Duration (sec)	No. elements	No. syllables	No. kinds of elements	Repetition index	Highest freq. (kHz)	Lowest freq. (kHz)
1	(12) 1.78 ± 0.24	(17) 7.82 ± 1.94	(17) 4.64 ± 1.97	(17) 4.53 ± 0.51***[a]	(17) 1.74 ± 0.47**	(11) 6.54 ± 0.37***	(11) 2.61 ± 0.17***
2	(30) 1.88 ± 0.18	(38) 8.34 ± 1.60***	(38) 5.34 ± 1.60***	(38) 5.84 ± 0.37***	(38) 1.44 ± 0.31	(23) 5.91 ± 0.37***	(26) 2.30 ± 0.19
3	(22) 1.92 ± 0.20	(23) 6.65 ± 1.03***	(23) 2.09 ± 1.24***	(23) 4.87 ± 0.34	(23) 1.37 ± 0.25*	(20) 6.55 ± 0.41	(21) 2.36 ± 0.22***
4	(13) 2.00 ± 0.14	(14) 9.57 ± 2.03***	(14) 4.79 ± 2.08***	(14) 4.79 ± 0.43*	(14) 2.02 ± 0.48***	(10) 6.65 ± 0.21*	(11) 2.73 ± 0.08
5	(12) 2.00 ± 0.09	(18) 16.56 ± 2.09***	(18) 11.61 ± 2.03***	(18) 5.00 ± 0.00	(18) 3.31 ± 0.42***	(8) 6.28 ± 0.57**	(7) 2.75 ± 0.14
6	(69) 2.03 ± 0.17	(77) 10.70 ± 2.00	(77) 5.69 ± 2.02	(77) 5.05 ± 0.22	(77) 2.12 ± 0.41	(57) 6.79 ± 0.41	(56) 2.85 ± 0.28

[a] One-sided *P*-value (*t*-test) when tested against neighboring population appearing immediately below on this table. * = $0.005 < P \leq 0.05$; ** = $0.0005 < P \leq 0.005$; *** = $P \leq 0.0005$.

peared to be an incomplete northern theme (W-B-CS-CS). This individual appeared to be mated.

In *pugetensis*, as in *nuttalli* (Baptista 1974, 1975), then, most birds in a breeding population sing a song identifiable as one of the local themes. However, a few birds sing variant themes modifying some of the phrases and syllables. Still others improvise by combining elements from northern and southern themes and constructing "hybrid" themes. Among emberizines, improvisation of this kind is rare in White-crowned Sparrows (Baptista 1975) and Ortolan Buntings (*Emberiza hortulana*; Conrads and Conrads 1971:93). However, syllable borrowing appears to be the rule in song development in some populations of Song Sparrows (*Melospiza melodia*; Harris and Lemon 1972, Eberhardt and Baptista 1977).

In *nuttalli*, hybrid themes were found only in zones of secondary contact where two "parental" themes were found sympatrically (Baptista 1975). However, hybrid *pugetensis* themes described above were found some distance away from secondary contact zones. How then were these themes acquired? First, these birds may have hatched in areas of secondary contact between two dialects where they developed their hybrid themes and then dispersed to the places where they were recorded (Table 1). Second, they could have picked up elements of a second theme from migrants in passage. Third, individuals in the sampled localities could be singing other dialects not encountered by the investigator. These second themes could have influenced song development in some individuals, giving rise to hybrid themes. Fourth, if some learning in *some* individuals takes place beyond a short critical period (typical of *nuttalli*, Marler 1970), these individuals could borrow syllables from flock mates during migration or on their wintering grounds.

QUANTITATIVE ASPECTS OF SONG VARIATION

Milligan and Verner (1971) demonstrated that White-crowned Sparrows may distinguish between song dialects. Baptista (1975) found that individuals can distinguish themes within dialects, individuals with bivalent repertoires matching specific themes during playback experiments. Frequency and/or temporal characteristics of avian song often serve for recognition of species or individuals. (Falls 1963, Emlen 1972, Brooks and Falls 1975). Temporal and frequency parameters of song fur-

nish rhythms and pitch differences which could function along with syllable morphology in recognizing dialects or themes. To quantitatively examine song variation, I summarized data from seven parameters for each of the six dialects (Table 5). If song dialects act as ethological barriers to pair formation between dialect areas (Nottebohm 1969), it would be meaningful to test differences between dialects that are actually geographically juxtaposed in nature. Thus, as in Baptista (1975) I conducted univariate tests between neighboring pairs of dialects for the seven parameters measured (Table 5). Based on *t*-tests, dialect pairs differed in four or five of the seven quantified characteristics.

Although dialects 1 and 2 seemed on average to be briefer than dialects 3 to 6, *t*-tests demonstrated their differences to be insignificant (Table 5). Song length, therefore, is similar in all population pairs of *pugetensis* tested.

Although *t*-tests showed the differences in mean number of elements between dialects 2 and 3 to be significant (Table 5), I do not believe this to be biologically real. Having spent many hours in the field with White-crowned Sparrows, I believe that several birds in populations 1 and 2 were not singing "complete" songs, i.e., when the birds were fully motivated their songs would have contained more terminal syllables, thus more elements, and consequently would have lasted longer.

Significant differences between populations tested were found in the (1) number of elements and kinds of elements, (2) repetition index, (3) highest, and (4) lowest frequencies. These data differ from those in viduine finches (*Vidua* spp.) in which Payne (1973) found no differences in the same parameters tested across dialect populations.

DISCUSSION

COMPARISONS WITH *NUTTALLI*

Song dialects of sedentary *nuttalli* studied by Marler and Tamura (1962, 1964), Baker (1975), and Baptista (1975) are very local in distribution. Song dialects of migratory *pugetensis* are more widespread (Fig. 1). In this respect the latter are reminiscent of *oriantha*, studied by Baker (1975) in Colorado.

Channels of water 0.25 to 3.5 mi wide appear to be effective barriers to the dispersal of *nuttalli* in the San Francisco Bay area of California, so that distinct song dialects occur on islands in the Bay (Baptista 1975). *Pugetensis* recorded on San Juan and Vancouver islands in Puget Sound sang the same themes as birds taped at Anacortes and Vancouver City on the British Columbia mainland (Fig. 1, Table 2), suggesting some dispersal between island and mainland populations.

Contact zones between neighboring *nuttalli* dialects are often narrow (Baker 1975, Baptista 1975). In contrast, the one contact area between northern and southern themes of *pugetensis*, studied in detail herein, is at least 10 mi wide (Table 1, Fig. 1).

Where northern and southern *pugetensis* themes occur sympatrically, a few birds sing both song types. In *nuttalli* a few birds also sang two dialects in zones of secondary contact (Baker 1975, Baptista 1975). Baker (1975) found birds singing two dialects early in the breeding season but not later. He could not determine whether "bilingual" individuals had moved or had remained and failed to use one song type. One possible explanation for Baker's observations is that because of countersinging and song matching, the more common theme in the area is used more and more often by individuals with bivalent repertoires, and the rarer song is soon left unused (Baptista 1975). The number of "bilingual" individuals in both *pugetensis* and *nuttalli* may thus be higher than that reported by field investigators.

PUGETENSIS AS SINGING TUTORS OF *NUTTALLI*

Pugetensis arrive at the San Francisco Bay area about mid-September and do not leave until early or mid-April (Blanchard 1941, 1942). Fall arrival is often announced with song (Blanchard 1941, Davis 1958:334). In late February, about four weeks prior to migration, song begins to be more frequent and louder (Blanchard 1941, DeWolfe 1968). Birds belonging to the sedentary subspecies *nuttalli*, hatched early or late in the breeding season in the San Francisco Bay area would thus hear the songs of wintering *pugetensis* or birds in passage. As a result, eight of nine resident territorial individuals recorded in the San Francisco Bay area singing *pugetensis* themes were identified as *nuttalli* misimprinted with songs sung by migrants (Table 6). One of these (P2) could have been a *pugetensis* that remained in its wintering grounds through the following spring. Seven of the nine individuals sang northern themes and two sang southern themes (Table 6). Because complex syllable types 1, 2, and 6 were the most often encountered in northern themes of *pugetensis* (Table 3), it is not surprising that the complex syllables used by misim-

TABLE 6. Summary of data on song-misimprinted *nuttalli* in California[a].

Individual	County	Complex Syllable Type				Trills[d]	Years recorded
		1[b]	2[b]	6[b]	17[c]		
P1	Marin	+[e]				2a	1969
P2[f]	Contra Costa		+			3a	1969
P3	Alameda		+			3a	1968–70
P4	Alameda	+				none	1971
P5	Contra Costa	+	+	+		none	1971
P6	Alameda				+	2a	1971
P7	Alameda		+			none	1971
P8[g]	Alameda				+	2a	1974
P9[h]	San Francisco		+			5a	1975
Total		3	5	1	2		

[a] Data from Baptista 1974 unless otherwise noted.
[b] See Fig. 4 for illustrations of these syllables.
[c] See Fig. 6 for illustration of this syllable.
[d] Terminal trills as in Figs. 3 and 5.
[e] Variant of type 1.
[f] Subspecies unknown.
[g] Data from Baptista and Wells 1975.
[h] Data from Baptista, unpubl.

printed *nuttalli* singing northern themes were also of these widespread forms (Table 6).

Three birds sang *pugetensis* themes with no terminal trills (Table 6). Perhaps as a result of low androgen levels, visitant *pugetensis* frequently sang partial songs. The three *nuttalli* in question probably had incomplete *pugetensis* songs as models for mimesis (Baptista 1974).

P1 sang a northern *pugetensis* theme ending with portions of a southern *pugetensis* trill. P1 and P4 occasionally tacked on the local *nuttalli* trills to their *pugetensis* motifs. The other six birds sang complete songs typical of breeding populations on the Pacific coasts of Oregon, Washington and Puget Sound. Banding studies have shown that Pacific coastal and Puget Sound populations of *pugetensis* do indeed winter in the San Francisco Bay area (Blanchard 1941, Cortopassi and Mewaldt 1965). Themes sung by winter visitants matched those sung by the misimprinted *nuttalli* (Baptista 1974).

Because occasional *pugetensis* may remain on their wintering grounds the following breeding season (Blanchard 1941), and because song is not necessarily a barrier to pair formation, I suggested that *pugetensis* may occasionally mate with female *nuttalli* encountered on their wintering grounds (Baptista 1973, 1974).

SONG DIALECTS AND THE STUDY OF MIGRATION

Out of 226,516 White-crowned Sparrows banded over 43 years, only 198 were recovered (Cortopassi and Mewaldt 1965). Only six song dialects were distinguishable in the many hundreds of miles of *pugetensis* habitat. Variation within populations was low as in *nuttalli*. It would seem possible, therefore, to identify the origins of populations of *pugetensis* on their wintering grounds by analyzing their songs. Prerequisite to this would be (1) demonstrating the stability of these song dialects from year to year, (2) recording songs from the isolated interior populations, e.g., in the Willamette Valley, (3) obtaining recordings of birds in the gaps in my transect, e.g., between Coos Bay and Newport or between Newport and Tillamook, Oregon.

GENETIC STRUCTURE OF POPULATIONS

Individual variation in the song learning process is well documented and has been interpreted by some authors as imperfect copying (Marler 1960:362, Lemon 1965, Payne 1973, Kroodsma 1974, Baptista 1975), and by others as a positive process termed "drift" (Harris and Lemon 1972, Lemon 1975). There is abundant evidence of individual variation in theme copying in the songs of *pugetensis*, giving rise, for example, to variants of the complex syllable types (Figs. 4, 6), or to occasional individuals singing songs missing a second phrase (Fig. 3, 3b). Given geographic isolation, oral tradition and the passage of time, these minor deviations may accumulate, resulting in larger differences and new distinct dialects. Because the differences between dialects (terminal trills) are smaller than the differences between the northern and southern themes (morphology of complex and simple syllables and sequencing of elements), I postulate that dialect popula-

tions were separated from each other for a shorter time than the populations singing northern versus southern themes. It is tempting to speculate, therefore, that the genetic differences between neighboring dialect populations are smaller than the genotypic differences between populations singing northern versus southern themes. This hypothesis may perhaps be tested in a study of protein polymorphisms such as Nottebohm and Selander (1972) and Baker (1974, 1975) have employed for several taxa of *Zonotrichia.*

SONG DIALECTS IN RELATION TO HABITAT

Nottebohm (1969, 1975) and King (1972) found that each song dialect in *Zonotrichia capensis* corresponded to a different habitat. Baker (1975) and Baptista (1975) found no correlation between habitat and song dialects in sedentary *Z. l. nuttalli.* There appears to be no correspondence between song dialects and habitat in migratory *pugetensis.*

GENETIC RELATIONSHIPS OF THE PUGET SOUND POPULATIONS

Banks (1964:42) discussed these populations and stated that, "The Puget Sound populations probably do not represent recent invasions from more strictly coastal groups. Geographically and morphologically they are obviously closely related to the Vancouver Island birds."

Based on the morphology of syllables constituting the terminal trills, I distinguished two song dialects on Puget Sound. Songs recorded from Vancouver City and Anacortes were similar to themes from San Juan and Vancouver islands. However, motifs recorded from Dosewallips to Seattle on the southern shores of the Sound were similar to songs from Ocean City and Pacific Beach on the Pacific coast. This suggests that the Puget Sound populations may represent at least two distinct gene pools. The northern mainland populations (Anacortes, Vancouver) may be genetically similar to those on Vancouver Island as proposed by Banks (1964). However, the southern mainland populations (Dosewallips to Seattle) may be genetically closer to Pacific coast populations.

SUMMARY

Geographic variation in song, and song dialects were studied in breeding populations of the migratory subspecies *pugetensis* of the White-crowned Sparrow. Using morphology and sequencing of elements, two widely distributed song themes were distinguishable. At zones of secondary contact between these two song types a few birds were "bilingual." Syllables in the medial portions of the songs tended to reoccur in mosaic fashion over hundreds of miles. With few exceptions, syllables in the terminal trills were characteristic of groups of adjacent populations thus permitting the distinction of six "dialect" areas. Variation within populations in five of these dialects was low, reminiscent of the dialects of *nuttalli.* Song dialects of *nuttalli* are more local in distribution than those in *pugetensis.* A few *nuttalli* may occasionally learn partial or complete songs from overwintering *pugetensis.*

Based on song morphology, I suggest that dispersal across water barriers probably has been more frequent in *pugetensis* than in *nuttalli.* In contrast to *Zonotrichia capensis,* I could find no correspondence between song dialect and specific habitat types in *pugetensis.* The possible use of song as a tool in the study of migration in *pugetensis* was treated. Finally, I comment on the possible relevance of song variation to the genetic structure of populations of *pugetensis* along the Pacific coast and in Puget Sound.

ACKNOWLEDGMENTS

I thank Barbara DeWolfe, Ned K. Johnson, Martin L. Morton, Paul Mundinger, and Lewis Petrinovich who read the manuscript and offered valuable comments. Field work was made possible by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History. Audiospectographic work was conducted in the Moore Laboratory of Zoology. Carol Beuchat and Eric Dawson assisted in the preparation of the figures. Gene M. Christman prepared the map. This study was conducted while I was a student at the Museum of Vertebrate Zoology, University of California, Berkeley.

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